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Summer Indiana Bat Ecology in the Southern Appalachians: An Investigation of Thermoregulation Strategies And Landscape Scale Roost Selection

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SUMMER INDIANA BAT ECOLOGY IN THE SOUTHERN APPALACHIANS: AN INVESTIGATION OF THERMOREGULATION STRATEGIES AND LANDSCAPE SCALE ROOST SELECTION

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ABSTRACT

In the southern Appalachians there are few data on the roost ecology of the federally endangered Indiana bat (*Myotis sodalis*). During 2008-2012, we investigated roosting ecology of the Indiana bat in ~280,000 ha in the Great Smoky Mountains National Park, Cherokee National Forest, and Nantahala National Forest in the southern Appalachians Mountains of Tennessee and North Carolina. We investigated 2 aspects of the Indiana bat's roosting ecology: thermoregulation and the extrinsic factors that influence body temperature, and landscape-scale roost selection. To investigate thermoregulation of bats at roost, we used data gathered in 2012 from 6 female Indiana bats (5 adults and 1 juvenile) to examine how reproductive condition, group size, roost characteristics, air temperature, and barometric pressure related to body temperature of roosting bats. We found that air temperature was the primary factor correlated with bats' body temperatures while at roost ($P < 0.01$), with few differences detected among reproductive classes in terms of thermoregulatory strategies. To understand how Indiana bats select roosts on a landscape-scale, we created a presence-only model through the program MaxENT using 76 known roost locations to identify areas important to summer roosting habitat within our study area and to identify important landscape-scale factors in habitat selection. The final model showed that Indiana bats selected roosts on the upper portion of ridges on south facing slopes in mixed pine-hardwood forests at elevations of 260-700 meters. Unfortunately, due to small sample size and the large effort required to fully investigate thermoregulation of

Indiana bats in the southern Appalachians, we only were able run correlations with temperature data, and further investigation is needed to make concrete conclusions. However, the new advancements in resolution of landscape cover data and new programs in spatial modeling have enabled us to produce a large scale spatial model for identifying Indiana bat summer roosting habitat within our study area. Our findings have added to our understanding of Indiana bat roosting ecology, particularly in the southern Appalachian Mountains, and will aid land managers in effective management for this federally endangered species.

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CHAPTER 1

INFLUENCE OF EXTRISIC ENVIRONMENTAL VARIABLES ON BODY TEMPERATURE OF FEMALE INDIANA BATS IN SUMMER ROOSTS

Bats are the only true flying mammal and, like birds, have limited energy reserves in order to reduce body weight for flight (Lausen and Barclay 2006). This limitation in energy reserves is problematic in that flight is the most expensive form of locomotion, making energy conservation critical (Butler and Bishop 2000). Bats conserve energy through extreme heterothermia by using torpor, which lowers metabolic rate and suppresses other functions such as gestation and milk production via lowered body temperature (T_b; Lausen and Barclay 2006). In addition to using prolonged torpor (hibernation) in winter, it is assumed that bats enter daily torpor to lower energy costs when inactive during summer (Pretzlaff et al. 2010). In summer, the use of torpor decreases the rate of neonate development and milk production, prolonging gestation and lactation periods (Racey 1973, Wilde and Racey 1999). In laboratory tests, pregnant and lactating female bats use torpor less frequently than non-reproductive individuals (Solick and Barclay 2006). Using torpor may be more costly than beneficial during reproduction because energy demands are higher during pregnancy and lactation (Gittleman and Thompson 1988). By maintaining a warmer body temperature, a mother bat helps ensure the quick development of her young, thereby allowing her pup to become independent sooner and providing more time for both mother and pup to build up reserves for the upcoming winter (Pretzlaff et al. 2010).

Solick and Barclay (2006) found that, while roosting, pregnant and lactating females maintain higher skin temperature (T_{sk}) than non-reproductive individuals. This result suggests that reproductive females are using more energy to maintain higher temperatures while in the roost during the summer than non-reproductive individuals. The use of more energy by reproductive females reinforces the idea that, in the roost, using torpor may be more costly than beneficial to reproductive females. This is because using torpor slows pup growth and increases the amount of time pups are dependent on mothers, thus resulting in an overall greater energy expense for bringing a neonate to maturity. Torpor is highly efficient for non-reproductive individuals because it allows them to slow their metabolic rates and use less energy (Lausen and Barclay 2006). However, torpor's short term energy savings seem to still be outweighed by the long-term costs for reproductive females, making torpor use impractical for reproductive female bats (Solick and Barclay 2006).

Despite the costs, reproductive females use torpor on some occasions (Kerth et al. 2001, Lausen and Barclay 2003, Willis 2006). However, there are discrepancies as to whether pregnant or lactating female bats use torpor less. The general observation is that lactating females use torpor less and then only in short, shallow bouts (Lausen and Barclay 2003), which would suggest that the costs of torpor are even higher during lactation than pregnancy (Willis 2006). In support of this idea, Kerth et al. (2001) and Willis et al. (2006) found that pregnant bats use deep bouts of torpor early in pregnancy to reduce energy costs and even delay parturition until conditions are more favorable (i.e., when temperatures are less severe and insects are more available). Pregnant bats may also use torpor to better synchronize parturition with other females to gain the benefits of cooperative care and clustering when mothers are present in a maternity colony (Willis et al. 2006). Synchronization of births becomes even more important after pups are born, as pups can cluster together to maintain higher temperatures while mothers are foraging away from the roost (Sano 2000, Willis et al. 2006). On the other hand, there is evidence that pregnant and lactating bats merely use torpor in different ways, but for similar amounts of time. In Alberta Canada, pregnant and lactating female big brown bats (*Eptesicus fuscus*) use torpor to a similar extent (same overall time), but pregnant females have fewer torpor bouts and remain in torpor for longer periods of time in each bout (Lausen and Barclay 2003).

Discrepancies in the observed use of torpor between pregnant and lactating bats may relate to differences among species that have been studied. It is also likely that extrinsic factors determine when torpor is the most costly or beneficial, and these factors will vary among geographic locations (Turbill and Geiser 2006). Geographic location and variation in topography (e.g., elevation and climate) may impact the availability of resources and influence the length of the growing season for pup rearing. For example, bats in more northern locations may face more severe weather in early spring as cold weather lingers upon exiting the hibernacula, limiting insect availability and raising the cost of maintaining a homothermic body temperature (Solick and Barclay 2007, Turbill and Geiser 2006). In more southern latitudes, bats may not face as long lasting cold weather in the spring but instead may face strong summer storms that require them to seek shelter and even forgo foraging for periods of time. Geographic location can have a strong impact on a wide variety of extrinsic factors a bat may face and the timing of such stressors, causing variation in the period of the most stress on a reproductive female bat (Solick and Barclay 2007). This variation may result in differing strategies for torpor use even within a particular species across different geographic locations. Thus, we need a better understanding of how extrinsic environmental factors impact torpor use at varying geographic locations (Solick and Barclay 2007, Turbill and Geiser 2006).

Pregnant and lactating female bats often roost in the presence of other reproductive females to gain the benefits of clustering and additive heat (Sano 2000). Clustering and large group sizes have been shown to increase the temperature within the roost and influence individual metabolic rates, costing individuals less to maintain higher body temperatures (Pretzlaff et al. 2010). Reproductive females in a maternity colony typically use "primary" roosts, which are large diameter, tall trees with high solar exposure (Barclay and Kurta 2007). In comparison, non-reproductive individuals often use smaller, shaded trees ("secondary" roosts), which have lower temperatures and, thus, should help to induce torpor (Garroway and Broders 2008). Primary roosts are significant in that they maintain higher and more stable temperatures within the roost throughout the day compared to random roosts (Campbell et al. 2010, Sedgeley 2001). These higher temperatures should enable bats to maintain higher body temperatures, reducing the need for torpor use during the day; large primary roosts also maintain higher temperatures at night, which should help protect young from dropping into hypothermia while mother bats are out foraging (Campbell et al. 2010). For example, Harbusch and Racey (2006) found mortality of non-volant young was higher for roosts with lower roost temperatures (i.e., as would be expected with secondary roosts) compared to more successful roosts.

Beyond reproductive class, it is unclear what other factors influence body temperature fluctuations and strategies in free-ranging roosting bats. We have a fair understanding of roost habitat preferences (Kalcounis-Rueppell et al. 2005, Barclay and Kurta 2007), but there are few data that address the effects of environmental factors on the use of torpor. No published studies have investigated how reproductive stage, ambient temperature, barometric pressure, group size, and roost characteristics all interact to influence body temperature and the use of torpor. For example, barometric pressure may help explain unusual roosting behavior and may influence body temperature, as it is known that bats will move to "secondary" roosts that are more protected when weather fronts start to move in (Callahan et al. 1997). Barometric pressure drops prior to, and during, storms; some animals can detect that change and respond (Heupel et al. 2003, Kreithen and Keeton 1974). Mammals are known to shift their thermoregulation patterns in captivity compared to in the wild, which makes it important to study thermoregulatory strategies in the wild (Geiser et al. 2000, Pretzlaff et al. 2010).

In this study, we investigated how reproductive stage, ambient temperature, barometric pressure, group size, and roost characteristics affect body temperature, and we define normothermia and torpor in Indiana bats, *Myotis sodalis,* in the southern Appalachian Mountains. The Indiana bat, which is native to the eastern part of the United States, was listed as endangered in 1967 due to loss of summer and wintering habitat; since then, the U.S. Fish and Wildlife Service has attempted to recover the species through management of forested habitats and hibernacula (Krusac and Mighton 2002, U.S. Fish and Wildlife Service 2007). Since 2006, this species has also been hard hit by white nose-syndrome (WNS), a disease caused by the fungus *Geomyces destructans,* which impacts bats during winter hibernation (Foley et al. 2011, Lorch et al. 2011). WNS interrupts normal energy conservation during a time of low resources and has resulted in high mortalities for several bat species, including the Indiana bat (Lorch et al. 2011). With the current threats to Indiana bats, it is important to further our knowledge of their ecology and how different thermoregulatory strategies might affect survival of adults and young in the summer. Beyond threatening hibernating bat populations, we can expect WNS-affected bats to exit hibernacula with lower body mass and wing damage (Cryan et al. 2010). Bats with physiological damage may alter their roosting behavior (i.e., thermoregulation behaviors) to compensate for their altered physiological state (Cryan et al. 2013).

Recovery efforts for Indiana bats have led to intensive research and survey work in the Midwest and the Northeast United States (e.g., Britzke et al. 2006, Callahan et al. 1997, Carter et al. 2005). In the southeastern portion of the species' range, however, habitat use is not well studied (Britzke at al. 2003). Considering the growing threat of WNS and habitat loss to Indiana bats, it is important to learn as much as possible about their ecology in all regions of their range, particularly in the vicinity of important Indiana bat hibernacula. There are several known hibernacula in and around the Great Smoky Mountains National Park (Harvey 2002), which may be the winter origin for much of the summer population of Indiana bats in the southern Appalachian Mountains. Summer colonies of Indiana bats have been observed in the region since 1999 when a reproductive female was first captured and a maternity colony located (Harvey 2002, Britzke et al. 2003). The majority of maternity roosts used by Indiana bats within this region are in yellow pine (*Pinu*s subgenus *Diploxylon*) or white pine (*P. strobus*) snags along mid and upper slopes in mixed pine-hardwood forests (Britzke et al. 2003 and O'Keefe et al. unpublished data). Consistent with patterns observed for other tree-roosting bats, primary roosts are in large snags with high solar exposure and secondary roosts are in smaller, more shaded snags (O'Keefe et al. unpublished).

The overall goal of this project was to investigate which environmental factors influence body temperature in different reproductive classes. Our first objective was to determine how reproductive class, group roosting size, roost characteristics, ambient temperature, and barometric pressure influenced body temperature in free-ranging Indiana bats in summer. The second objective was to define normothermia and the active body temperature threshold between torpor and normothermia in free-ranging summer roosting Indiana bats. We hypothesized that there would be distinct patterns in body temperature between reproductive classes. We expected roost characteristics and group size to be significant in influencing body temperature among all reproductive classes through positive relationships (i.e., body temperature would increase with increasing roost size and group size). Further, we predicted that air temperature would be significant in determining the use of torpor in pregnant and lactating females.

STUDY AREA

The study was conducted in the southern Appalachian Mountains in southeastern Tennessee and southwestern North Carolina (N 35° 25', W 83° 55') in the Cherokee National Forest (CNF), the Nantahala National Forest (NNF), and the Great Smoky Mountains National Park (GSMNP). The study area is 281,788 hectares of federal land in Monroe and Blount counties in Tennessee and Swain, Graham, and Cherokee counties in North Carolina.

GSMNP and the two National Forests are classified as mixed pine-hardwood forests in the Appalachian oak section in Dyer’s (2006) updated vegetation mapping based on the works of Braun (1950). The majority of the study area is made up mid-successional growth (41-80 years old), but also includes some mixed early successional and old growth forests depending on disturbance history (Franzreb 2005). The study area ranges in elevation from about 250 meters to 2025 meters above sea level. The mean temperature reported by NOAA for the month of June 2012 was 24.4°C with 30.0 cm of rain, and in July the mean temperature was 27.2°C with 33.4 cm of rain.

METHODS

To locate day roosts for Indiana bats, mist netting was conducted from mid-May through mid-August in 2012. We set mist nets (Avinet, Dryden, NY) over trails, roads, and streams, opened them at dusk, and monitored nets every 8 minutes for 3-4 hours. We recorded species, sex, age (adult or young of the year; Anthony 1988), mass, forearm length, and wing damage score (Reichard and Kunz 2009) for all captured bats. We banded Indiana bats with a unique 2.9 mm aluminum forearm band (Porzana Ltd., East Sussex, UK) for individual identification. If an Indiana bat of suitable mass (>7 g for adult) and health was captured, particularly an adult female, then the bat was fitted with a 0.32-0.42 g temperature-sensitive radio transmitter (Holohil Systems Ltd, Ontario, Canada). Up to 3 bats were outfitted with transmitters on a given night. We primarily targeted female Indiana bats and volant juveniles because they use “primary” roosts, which are the roosts considered the most critical for reproduction and population habitation (Humphrey 1977). During all surveys, we used recommended white-nose syndrome decontamination protocols (USFWS 2011) for minimizing transmission of *G. destructans*. While handling bats, we followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011; ISU IACUC protocol 226895-1) and released bats at the capture site.

Prior to entering the field, all temperature-sensitive transmitters were individually calibrated by Holohil Systems to every 5˚C, from 0 - 50˚C. Temperature-sensitive transmitters vary pulse at different temperatures, so pulse rate is used to measure skin temperature; this is a non-invasive way to estimate body temperature (Campbell et al. 2010, Carter and Feldhamer 2005, Dausmann 2004, Turbill and Geiser 2006). We used polynomial equations in a graphical software package (VinnyGraphics, version v2.05) to convert pulse rates from transmitters on roosting bats to skin temperatures (T_{sk}). We tracked bats using a TR5 receiver (Telonics, Mesa, Arizona, USA) and a 3- or 5-element Yagi antenna (Wildlife Materials, Murphysboro, Illinois, USA) the morning following capture and each day thereafter for the life of the transmitter (8 - 14 days), or until the bat was lost and unable to be relocated. When we located a roost, we recorded the location with a global positioning system (Garmin 60 CSx, Olathe, Kansas, USA) and returned in the fall to measure roost characteristics when chances of disturbing the bats were lower. We measured roost tree height, diameter at breast height, roosting height, and canopy closure, characterized the surrounding stand of trees, and spatially recorded the roost location with a GEO-XT Trimble (Trimble, Sunnyvale, California, USA) with sub-meter accuracy.

We placed a SRX-DL2 datalogger (Lotek Wireless, Inc., Newmarket, Ontario, Canada) within 10 m of each roost tree and set the datalogger to gather transmitter pulse rate and signal strength, scanning for all enabled tags (normally 1-4 tags enabled at once) every 8 seconds at a gain of 50. We used signal strength to determine the presence of a bat and whether it was roosting or flying near the roost tree based on how steady the signal remained; erratic values were indications of flying. In association with the SRX-DL datalogger, we deployed a H21-002 weather station (Onset Computer Corporation, Bourne, Massachusetts, USA) to gather air temperature and barometric pressure (BP) every 10 minutes in the immediate vicinity of each roost tree. We assessed roosting group size through roost emergence counts on 1 – 4 nights per roost when weather and manpower permitted.

Data analysis

After field collection, all datalogger data were downloaded using Lotek software, (v1.1.467.28) and organized by bat frequency and date. Pulse data were transformed into T_{sk} (˚C). Using signal strength and breaks in data, we extracted T_{sk} data for periods of time when the bat was roosting. We then averaged the 8-second T_{sk} data into 1-minute intervals to identify active temperature thresholds (T_{act}) by using the minimum T_{sk} value <30 minutes prior to emergence for all bat days on which an individual bat was observed. We used methods similar to those of Barclay et al. (2001) to define the active temperature threshold. Barclay et al. (2001) defined T_{act} as the minimum T_{sk} <10 minutes prior to emergence for all days recorded for an individual bat as the threshold between normothermia and torpor. This method assumes that at 10 minutes prior to emergence bats are out of torpor and in their "active" temperature range. We defined T_{act} as the minimum T_{sk} <30 minutes prior to emergence, as we often heard Indiana bats vocalizing in the roost up to 30 minutes prior to emergence (personal observation). We used T_{act} for each individual bat to define the threshold between torpor and normothermia, which is similar to prior work that assumed that drops in T_{sk} below known active temperatures are representative of torpor use in roosting bats (Barclay et al. 2001, Chruszcz and Barclay 2002, Lausen and Barclay 2003, Solick and Barclay 2006, Willis and Brigham 2003). Here, we use the term "torpor" to refer to prolonged body temperatures below normal known active roosting body temperatures.

After identifying the active temperature threshold for each individual bat, we averaged the skin temperature data into 10-minute intervals so that it would be comparable to air temperature and barometric pressure data. For our analysis, we identified "whole bat days" as those days where there was an entire day of roosting data recorded for a bat from the time it entered the roost around dawn to the time it exited the roost at dusk. Using the statistical software program R (v2.15.1, Vienna, Austria), for whole bat day data only, we used Pearson's correlations to test for relationships between air temperature, barometric pressure, and skin temperature. For whole bat day data, we also tested for relationships between air temperature and barometric pressure with skin temperature for the entire bat day, for periods of torpor, and for periods of normothermia. We assessed patterns within the correlations and significance tests (evaluated at $\alpha = 0.05$) to determine the influence of air temperature and barometric pressure on skin temperature. We report means and standard errors generated in Microsoft Excel 2010, for roost characteristics and skin temperature data, but we conducted no further analyses due to low sample sizes for "whole bat days".

RESULTS

During the summer of 2012, we captured 20 Indiana bats, and transmittered and tracked 14 individuals (Table 1). Of those 14 bats, we were able to successfully track 12 individuals to 18 unique roost trees. We tracked for 93 days throughout the summer and were successful in locating a transmittered bat on 57 days. We deployed the SRX-DL2 datalogger at 15 roosts for a total of 75 days and we were successful in detecting a transmittered bat at roost on 51 bat days (where a bat day = 1 bat in 1 roost for 1 day). Of those 51 bat days, we gathered dawn to dusk roosting data on 22 "whole bat days" for 6 individual bats (Table 1 and Figure 1).

In 2012, a typical roost was a large tall pine snag on a south facing mid slope (Table 2). There was 1 crevice roost; all others (n = 17) were exfoliating bark roosts. At 5 of the 18 roosts found in 2012, we were successful in recording at least 1 whole bat day data (i.e., skin temperature data for a bat at roost, and air temperature and barometric pressure for the surrounding area). Hereafter, we only reference the 5 focal roosts at which T_{sk} data was gathered for a whole bat day (Table 3). Each of these focal roosts was a different tree species; 1 was a crevice roost, while the other 4 were bark roosts (Table 3). The focal roosts were larger in diameter and height, and the height at which bats roosted was taller (Table 3) when compared to other roosts found in 2012; therefore, all focal roosts were considered primary roost trees (Table 2). Canopy closure and slope position (Table 3) were similar for focal roosts and other 2012 roosts (Table 2). Air temperature surrounding focal roosts fluctuated throughout the summer (10.9 - 39.3 ˚C) with the roosts experiencing cooler air temperatures in June (3 roosts, 9 bat days, mean = 18.8 ± 6.3 ˚C) and warmer temperatures in July (2 roosts, 13 bat days, mean = 24.7 ± 6.9 ˚C). We classified the 3 focal roosts used in June as cool roosts and the 2 focal roosts used in July as warm roosts, based on air temperatures, solar exposure, and location (Table 4). Because we classified all focal trees as primary roosts, we did not attempt to relate variations in T_{sk} to roost classification (primary or secondary).

In our analysis, we were able to compare whole bat day data for 3 reproductive female groups: lactating, post-lactating, and a non-reproductive juvenile (Table 5, Figure 1). Two lactating adults (bats A and B) used 2 cool roosts in early June and 2 post-lactating adult females (bats C and D) used the same cool roost at high elevation (1265 m) in late June. In July, a post-lactating adult (bat E) used a warm roost in the first portion of the month, and a juvenile (bat F) used a warm roost during the latter part of the month. Group sizes were large in June (≥ 25, lactating) when temperatures were lower, while in early July group sizes were lower (4-6, post-lactating), and higher in late July (16-32, juvenile) when temperatures were warmer (Table 5).

Due to variability in group sizes and a small sample of roosts, no clear influence of group size on skin temperature could be determined.

We found no clear relationship between T_a and BP (Table 6). All correlations between T_a and BP were significant ($P < 0.02$), but the correlation varied from negative to positive (Table 6). Thus, we tested both variables against T_{sk} (Table 6). T_a was always positively correlated with T_{sk} and was significant ($P <0.02$) on 21 of 22 bat days (Table 6, Figure 1). BP and T_{sk} did not appear to be related or were only weakly related. The 2 were negatively correlated a majority of the time (18 out of 22 bat days and significantly correlated on 20 of 22 bat days ($P < 0.05$, but the correlations varied from negative to positive over a large range (Table 6, Figure 1).

We found no relationship between T_a and $T_{sk,}$ or BP and T_{sk}, during the time a bat was in torpor (Table 7). T_a was both positively and negatively correlated with T_{sk}; we noted only 1 strong correlation out of 15 bat days, with significant correlations on 7 out of 15 bat days ($P < 0.05$). BP was both positively and negatively correlated with T_{sk}; we noted only 1 strongly correlated bat day, with only 7 out of 15 days significantly correlated ($P < 0.05$). Similar to the correlations during the entire time a bat was at roost, we found weak relationships between T_a and T_{sk} and between BP and T_{sk} during the time a bat was in normothermia (Table 7). T_a was weakly positively related to T_{sk}, with the majority of the days being positively correlated and significant correlations on 17 out of 22 bat days ($P < 0.05$). BP was generally negatively correlated to T_{sk} (20 out of 22 days), but correlations were significant on only 9 out of 22 days ($P < 0.05$; Table 7).

Lactating bats had higher T_{act} thresholds than the post-lactating and juvenile bat (Table 5), and thus we report separate normothermic ranges for each group. The daily mean T_{sk} for all bats ranged from 26.1 – 38.4 ˚C (Table 5, Figure 1), with no group having distinguishably different mean T_{sk}. Mean T_{sk} for 2 lactating bats was 34.0 ± 19.6 ˚C (Bat A, 3 bat days) and 29.8 ˚C (Bat B, 1 bat day). Mean T_{sk} for 2 post-lactating bats in late June was 30.4 ± 15.2 ˚C (Bat C, 4 bat days) and 29.7 ˚C (Bat D, 1 bat day). The post-lactating female (Bat E) in July had a mean T_{sk} 29.8 ± 13.3 ˚C (5 bat days) and the juvenile female (Bat F) a mean T_{sk} of 32.0 ± 11.3 ˚C (8 bat days). Lactating (n = 2) and post-lactating bats (n = 3) dropped into torpor for 1- 3 bouts per day (Figure 1) and spent a similar proportion of time in torpor (27.9 ± 7.5%; Table 5). Lactating females dropped into torpor 1.3 ± 0.6 times a day (Figure 1, Bats A & B), for 31.1 ± 15.7 % of the time these bats were at roost (Table 5). Post-lactating females dropped into torpor 1.2 ± 0.3 times a day (Figure 1, Bats C, D, & E), spending 26.5 ± 7.7% of the time at roost in torpor (Table 5). The juvenile female used torpor only 0.5 bouts per day (Figure 1, Bat F) and for a shorter portion of time while in the roost (10.9 ± 3.8%; Table 5) compared to the other female groups. However, when in torpor, all bats exhibited similar torpor depths, with the mean skin temperatures of 23.9˚C for lactating bats, 20.9˚C for post-lactating bats, and 22.5˚C for the juvenile (Table 5, Figure 1). Lactating bats, post-lactating bats, and the juvenile had similar mean maximum body temperatures per day, at 39.1 ˚C, 38.2 ˚C, and 38.0 ˚C, respectively (Table 5). The mean daily maximum skin temperatures and the average activity body temperature thresholds for each reproductive group indicate that normothermic ranges are 30.5 - 39.1 ˚C for lactating females, 27.6 - 38.2 ˚C for post-lactating females, and 25.5 - 38.0 ˚C for the juvenile female.

DISCUSSION

We found that air temperature had the most statistically and biological significant correlations with skin temperatures for reproductive female and juvenile Indiana bats in the southern Appalachians. Not only did we see daily trends in skin temperature in relation to air temperature, but also trends throughout the summer that mean bat body temperatures became higher as air temperatures became higher. We have little evidence that reproductive condition affects skin temperature and torpor use. However, we did find evidence that lactating females might exert more control over their body temperature compared to post-lactating and juvenile individuals. The differences we saw in bat skin temperatures among individual roosts seemed to be linked more to air temperature than to roost characteristics, as all focal roosts were large diameter, tall snags that classify as primary roost trees. Barometric pressure was usually negatively correlated with skin temperature, but there was not a strong overall correlation. Future analyses using lag time plotting may reveal a more distinct pattern. Barometric pressure was also negatively correlated with air temperature, which suggested that the two may be linked. However, air temperature was a more reliable predictor of body temperature than barometric pressure, supporting the idea that air temperature was the most influential factor influencing skin temperature. Further statistical analysis using lag time is needed to further examine the relationship of air temperature and barometric pressure with skin temperature. Overall, in this study all bats exhibited similar patterns of torpor (Figure 1), using torpor in the morning and defending (remain at) normothermia in the PM hours, a result that is different from what has been observed in other bat species in cooler climates (Dzal and Brigham 2013, Lausen and Barclay 2003, Solick and Barclay 2006). Our observations of daily correlations between air temperature and body temperature differed from other studies in more northern locations; we believe these patterns warrant further investigation with larger sample sizes and inclusion of pregnant individuals.

Air temperature had an overall positive relationship to skin temperature on a daily basis, but also seemed to have an influence on skin temperature by influencing roosting conditions over long periods throughout the summer. Air temperature influences skin temperature in other bat species, such as for *Myotis evotis* in summer roosts in Canada (Solick and Barclay 2006). In our study, air temperature was strongly correlated with skin temperature when all roosting data were included and during periods of normothermia, but was not strongly correlated with skin temperature during periods of torpor. However, further analysis with lag time plotting and the removal of time dropping into torpor may present more details on the influence of air temperature on periods of torpor. The positive relationship between air temperature and skin temperature was more statistically significant based in the latter portion of the summer when bats were post-lactating or for the juvenile, suggesting that lactating bats, although influenced by air temperature, exert more control over their body temperature. Lactating females in this study seem to be maintaining a higher body temperature more often than other reproductive groups; this observation was supported by lactating females having the highest active body temperature threshold and, therefore, the smallest range for normothermia compared to post-lactating and juvenile individuals. Our findings that lactating females were exerting more control over their body temperature compared to other reproductive groups are consistent with previous work. In other studies, lactating females use torpor less often and expend energy to maintain normothermia, possibly to avoid a decrease in milk production during torpor and to keep young warm (Daniel, et al. 2009, Racey 1973, Solick and Barclay 2006, Turbill & Geiser 2006).

Beyond influencing skin temperature on a daily level, air temperature was lower in June compared to July, probably causing variation in the roosting conditions for the various reproductive groups throughout the summer even though roost characteristics were similar throughout. All focal roosts were tall, large diameter trees that were able to host large groups of bats, which is consistent with other Indiana bat studies on roosting selection that have found maternity colonies primarily in large diameter, tall snags (Carter and Feldhamer 2005, Kalcounis-Rueppell et al. 2005). However, even though all roosts were primary roost trees, there was a distinct difference in the air temperature at the June roost trees compared to the July roost trees. This study would have benefited from microclimate data collected within the immediate vicinity of the bat at roost (i.e., within the crevice or under bark) so that we might understand to what degree fluctuations in outside air temperatures caused fluctuations in temperatures within the roosts. Microclimate within the roost can affect body temperature and the use of torpor in roosting bats (Kerth et al. 2001, Sedgeley 2001). However, due to concerns of impacts to a federally endangered species and the safety issues of placing a probe ≥10 m high in a decaying snag, we were unable to gather microclimate data within the roost. Even without microclimate data, our finding that air temperature influences skin temperature is still consistent with other in situ studies. Solick and Barclay (2006) compared how microclimate and air temperature influenced skin temperature among different reproductive groups in *Myotis evotis* and found that air temperature explained more variation in torpor use among reproductive groups than microclimate, because all groups sought similar roosting microclimates.

Our findings showing that lactating and post-lactating females use torpor in a similar manner contradicts the majority of previous work comparing torpor use between conspecific bats in different reproductive classes (Campbell et al. 2010, Dzal & Brigham 2013, Lausen and Barclay 2003, Solick and Barclay 2006). However, previous work has mainly occurred in more northern locations, primarily Canada (Lausen and Barclay 2003, Solick and Barclay 2006, Willis et al. 2006), New York (Dzal and Brigham 2013), or in controlled laboratory environments

(Wilde et al. 1999). Our study location is in the southern Appalachians and is more southerly than any reported thermoregulation study in North America, which may explain why we found bats using torpor for a lower proportion of their time at roost and no evidence of major differences among bats in different reproductive conditions. Other studies have reported that they observed bats using torpor more than 80% of the time at roost (Lausen and Barclay 2003, Solick and Barclay 2006), while bats in this study used torpor for less than half of the time they were at roost. A general pattern observed in this study was that bats used torpor in the morning when air temperatures were lowest, shifted to normothermia around noon, and remained normothermic until emergence (~ 21:00, Figure 1). On the other hand, bats in more northern areas are reported to use torpor in both the morning and afternoon (Lausen and Barclay 2003, Solick and Barclay 2006). This suggests that by the afternoon, when air temperature rises in the southern Appalachians, defending normothermia is less costly than dropping into or staying in torpor (Willis 2006).

Although they used torpor in a manner that was similar to other individuals, lactating females seemed to exert more control over their body temperature. Lactating females maintained higher active body temperature thresholds than the post-lactating and juvenile bats, which is consistent with previous studies that found reproductive females defend higher body temperatures even with fluctuations in air temperature (Audet and Fenton 1988, Willis 2006). However, lactating, post-lactating, and juvenile bats maintained similar ranges of skin temperature for normothermia within our study, although lactating females had a smaller range. Our calculation of a higher active body temperature threshold for lactating females may relate to the fact that we had fewer data for lactating females compared to the post-lactating and juvenile individuals and, therefore, fewer opportunities to detect lactating bats at lower active body temperatures. However, a potential biological explanation is the possibility that lactating individuals remain at higher temperatures closer to emergence due to clustering with pups to warm them and prepare them for the absence of the mothers for the evening (Solick and Barclay 2006). Little is known about pup survival before pups become volant. However, we speculate that the period prior to volancy is an important period in juvenile survival and that thermoregulation is critical for young pups. Further investigation is needed into the topic of juvenile survival and thermoregulation and the influence of weather. Lactating bats, although influenced by air temperature, may regulate body temperature within a narrower band of body temperature due to reproduction constraints (Daniel, et al. 2009, Solick and Barclay 2006, Turbill & Geiser 2006). Lactating bats may be more likely to defend normothermia and a higher body temperature due to the reduction in milk production at lower body temperatures and the resulting prolonged juvenile care required (Audet and Fenton 1988, Willis 2006). What is not well understood is how much of the defense of normothermia in lactating bats is accomplished through social behavior by clustering compared to the actual exertion of energy (Willis and Brigham 2007). With our small sample size, we did not detect a significant variation in group size throughout our study; however, group sizes were highest during lactation, even though counts excluded young within the roost. Even if we could have recorded more data for lactating females, active body temperatures for lactating bats would likely remain higher due to clustering (Willis 2006) and the tendency for bats in this study to be normothermic in late afternoon. Overall, all reproductive groups' active body temperature thresholds and, therefore normothermic ranges, were similar to other studies that reported such values (Solick and Barclay 2006), although, active body temperature thresholds were slightly higher in this study.

We were limited in the conclusions we were able to make due to a small sample sizes. Currently, we have only used significant correlations to measure the effects of air temperature and barometric pressure on skin temperature. However, we plan to measure correlations with lag time plots to see if this strengthens the relationship between air temperature and skin temperature, and if it reveals anything about barometric pressure. Considering lag times is important because there is a delay in the time it takes for changes in the environment to be felt through the bark and to be experienced by the roosting bats. Time-series analysis is another important tool for investigating relationships between physiological measurements and outside factors. We did not use time-series analysis due to our small sample size for roosts and individuals, but think this approach merits consideration for larger data sets. Also, we would like to revisit the correlations of air temperature and barometric pressure on periods of torpor by first removing the periods of time a bat is dropping into and out of torpor and looking at when the bat is stable in torpor. In this study, the correlations between environmental factors and use of torpor were not that strong, despite the fact that previous work on animals in torpor shows torpor to be greatly influenced by environmental conditions (Racey and Speakman 1987).

This study would have also have benefited from multiple years of data collection to increase the sample size and strengthen the findings. Collecting data on pregnant females might enable us to detect significant differences in torpor use between reproductive and non-reproductive bats because of the more varied air temperature and barometric pressure levels during the time of pregnancy within our study area (May-early June; personal observations). Pregnant and lactating bats may vary in their use of torpor depending on energy use caused by extrinsic factors such as major weather patterns impacting insect availability and temperature within the roost (Daniel et al. 2009, Solick and Barclay 2006, Turbill & Geiser 2006). Within our study area, it is likely that pregnant females would experience more strain due to variable weather in late spring/early summer (unpublished data, 2012). The study would also benefit from the inclusion of microclimate data to determine if bats in differing reproductive states are seeking out similar conditions and if microclimate would relate to skin temperature in a manner that is consistent with previous work (Kerth et al. 2001, Willis et al 2006). While Solick and Barclay (2006) concluded that air temperature probably explained more variation in torpor use between reproductive classes than microclimate in *Myotis evotis,* microclimate is influential in roost selection based on reproductive condition for *M. bechsteinii* in Europe (Kerth et al. 2001). Further, the inclusion of skin temperature from bats roosting in alternate roosts would allow for further investigation into the influence of roost characteristics and potential microclimate on body temperature. This is important given that Indiana bats in our region use alternate roosts at a similar frequency to primary roosts (personal observation), while alternate roosts, which are often smaller, are reported to be used on a less frequent basis in other regions of the Indiana bat range, particularly in the Midwest (Callahan et al.1997, Carter and Feldhamer 2005).

A common practice in bat ecology research is to gather data on as many individuals as possible within a season, even if this means reducing the amount of time focused on a particular individual (Miller et al. 2003). In this study, following a particular individual was the best strategy to maximize good data collection due to the large amount of effort and time required to gather a small portion of usable whole bat day temperature data. Over the field season we had a large number of successful tracking days and datalogger detections. However, due to the difficulty of tracking in our area, the high mobility of bats, and frequent roost switching, we mainly gathered partial days of skin temperature that were not useful for our analyses. Bats in general are known for being highly mobile, especially Indiana bats which switch roosts regularly, often every 1-2 days (Carter and Feldhamer 2005, Foster and Kurta 1999, Kurta et al. 2002). The longer we tracked an individual, the more likely we were to witness a bat remaining in a roost for multiple days and, thus, were able to successfully gather data for a whole bat day. Thus, we recommend that other researchers wishing to investigate thermoregulation in bats in situ focus on following individuals as long as possible, or set dataloggers at roosts to which bats are faithful. With this strategy, whole bat days can be gathered, but likely for fewer individual animals. This strategy will likely require multiyear studies in order to gather a sufficient sample size for strong statistical analysis. The most appropriate strategy for gathering thermoregulation data will vary by study area and with the roosting ecology of the study species.

Better understanding of thermal strategies in situ for not only Indiana bats but all bats has the potential to impact our understanding of roosting habitat selection, juvenile requirements, and potential tools for mitigating the effects of WNS and climate change. As bat populations are impacted by WNS and habitat loss, efforts have been made to protect remaining potential habitat and to supplement natural roosts with artificial roosts. In order to protect habitat and create suitable artificial roosts, we need to understand the thermal properties within and surrounding a roost and how those factors will impact a bat's body temperature and energy consumption. Further, climate change has the potential to alter areas of suitable habitat for bats. A recent study forecasted that the Indiana bat will eventually primarily reside in the southern Appalachians and the northeast due to changes in climate (Loeb and Winters 2012). To understand the potential effects of climate change, we need a better understanding of thermal strategies and the impact of extrinsic climatic factors on those strategies. Beyond climate change, WNS is predicted to cause local extinctions and reduce the Indiana bat population 69% throughout its range (Thogmartin et al. 2012, Thogmartin et al. 2013). WNS is predicted to greatly reduce summer colony sizes which will likely affect bats’ ability to cluster and, hence, could impact colony success and pup survival. Any advances in the study of thermoregulation in bats are likely to help managers deal with the impacts of WNS, climate change, and habitat loss on bats, and to identify areas that in the future may host suitable habitat for bat maternity colonies.

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TABLES

Table 1: Data for 14 Indiana bats followed in a radio telemetry study in the southern Appalachian Mountains, May - August 2012. The table shows bat ID, bat code if used in T_{sk} analysis, sex, age, reproductive condition (RC) with NR representing non-reproductive individuals, and summary of days tracked, roosts used, days that the datalogger (DL) was deployed, detected the bat, and full bat day data.

Bat ID	DL Bat Code	Sex	Age	RC	Total Days Tracked	Successful Days Tracked	Roosts Used	# Days w/ DL	# Usable DL Days
067	--	F	Adult	Preg	7	5	1	3	0
489	--	F	Adult	Preg	5	0	0	0	0
149	A	F	Adult	Lact	6	6	2	4	3
107	B	F	Adult	Lact	9	8	2	3	1
774	--	F	Adult	Lact	6	1	1	0	0
211	C	F	Adult	Post	11	6	1*	7	4
268	D	F	Adult	Post	9	7	2*	9	1
373	--	F	Adult	Post	4	1	1	1	0
570	--	F	Adult	Post	2	0	0	0	0
573	E	F	Adult	Post	7	7	2	7	5
452	--	F	Adult	NR	5	1	1	1	0
593	--	F	Adult	NR	5	3	3	5	0
695	F	F	Juv.	NR	11	10	1	11	8
730	--	M	Adult	NR	6	2	2	0	0
				Total	93	57	18	51	22

* Bats that used the same roost at various periods during the summer

Table 2: Characteristics of 18 roosts used by Indiana bats in the southern Appalachian Mountains, May-August 2012.

Characteristic	**Mean ± SE**	**Min**	**Max**
Diameter at breast hgt (cm)	47.3 ± 7.4	14.7	137.5
Tree Height (m)	20.4 ± 2.0	9	37.3
Roosting Height (m)	11.7 ± 1.1	5.4	20.64
Canopy Closure (%)	9.7 ± 6.1	0	100
Aspect (º)	152˚ ± 20.0	0˚	270˚
Slope Position	39% Lower, 61 % Mid	--	--
Roost Type	6 % Crevice, 94 % Bark	--	--
% White Pine	33%	--	--
% Yellow Pine	50%	--	--
% Hardwood	6%	--	--
% Hemlock	11%	--	--

Table 3: Characteristics of 5 focal roosts used by Indiana bats during 22 “whole bat days” in the southern Appalachian Mountains, June-July 2012. Date herein represent days on which a deployed datalogger successfully gathered bat roosting skin temperature from dusk till dawn.

Roost	**Spp.**	**Dbh (cm)**	**Tree Hgt. (m)**	**Roosting Hgt. (m)**	**% Canopy Closure**	**Plot Aspect º**	**Slope Position**	**Roost Type**
1	PIVI	31.2	23.8	15.2	0	E	Lower	Crevice
2	PIST	62.5	33.5	9.6	0	S	Lower	Bark
3	TSCA	137.5	37.3	15.9	0	S	Mid	Bark
4	PIEC	41.0	19.2	18.9	0	S	Mid	Bark
5	ACRU	21.7	22.9	9.8	50	SE	Mid	Bark
Mean ± SE		58.8 ± 26.3	27.3 ± 12.2	13.9 ± 6.2	10 ± 4.5%	--	--	--

Table 4: Data for bat days at focal roosts used by Indiana bats in the southern Appalachian Mountains, June-July 2012. Reported here are bat day code, the average, minimum, and maximum air temperatures experienced each bat day, and roost temperature classification based on solar exposure and air temperature experienced at roost.

Roost	**Date**	**Bat Day Code***	**Air Temp Min**	**Air Temp Max**	**Air Temp Mean**	**Roost Temp Classification**
1	4-Jun	A11	17.3	24.5	20.4	Cool
	5-Jun	A24	15.4	22.4	18.6	
	6-Jun	A31	11.0	26.2	17.7	
2	5-Jun	B12	15.4	22.4	18.8	Cool
3	19-Jun	C13	14.7	21.1	18.3	Cool
	20-Jun	C23	15.8	22.2	19.4	
	21-Jun	C33	16.5	21.3	18.7	
	22-Jun	C43	15.0	20.8	18.0	
	23-Jun	D13	16.4	21.6	18.8	
4	2-Jul	E14	16.0	27.8	21.1	Warm
	3-Jul	E24	19.6	30.8	24.7	
	4-Jul	E34	19.0	31.2	25.8	
	5-Jul	E44	19.5	32.8	26.4	
	6-Jul	E54	18.1	32.3	26.4	
5	16-Jul	F15	20.8	39.3	25.0	Warm
	18-Jul	F25	19.6	29.2	24.1	
	19-Jul	F35	19.0	30.0	25.7	
	20-Jul	F45	19.1	27.3	23.3	
	21-Jul	F55	18.9	26.6	23.0	
	22-Jul	F65	20.1	28.7	24.3	
	23-Jul	F75	18.3	29.7	24.9	
	24-Jul	F85	19.8	30.4	26.4	

* The bat day code is a representation of an individual bat, date, and roost used on that bat day.

Table 5: Thermoregulatory behaviors for 6 Indiana bats at focal roosts in the southern Appalachian Mountains, June-July 2012. Data reported by bat by date includes roosting temperature classifications, group size, active temperature threshold, skin temperature, and torpor expression by number of torpor bouts, proportion of time in torpor and mean torpor depth.

Bat Day Code	**Date**	**RC**	**Roost Temp Class'n**	**Group Size**	**T_{act}**	**T_{sk} Mean**	**T_{sk} Max**	**# of Torpor Bouts**	**Prop'n of Roosting Time in Torpor (%)**	**Mean Depth**
A11	4-Jun	Lact	Cool	--	31.1	38.4	38.6	0	0.0	--
A21	5-Jun	Lact	Cool	--	31.1	33.7	39.4	3	18.6	28.5
A31	6-Jun	Lact	Cool	39	31.1	29.9	39.5	1	53.4	21.6
B12	5-Jun	Lact	Cool	--	29.8	29.8	38.9	1	53.4	21.7
C13	19-Jun	Post	Cool	37	26.2	33.6	39.0	0	0.0	--
C23	20-Jun	Post	Cool	25	26.2	32.5	38.3	1	20.0	21.9
C33	21-Jun	Post	Cool	--	26.2	29.5	38.5	1	30.0	19.4
C43	22-Jun	Post	Cool	29	26.2	26.1	37.1	2	40.9	15.9
D13	23-Jun	Post	Cool	--	32.4	29.7	38.9	3	57.8	28.0
E14	2-Jul	Post	Warm	4	24.2	26.1	34.6	2	38.2	20.1
E24	3-Jul	Post	Warm	6	24.2	27.1	37.7	1	28.3	20.6
E34	4-Jul	Post	Warm	--	24.2	30.5	37.4	1	28.6	--
E44	5-Jul	Post	Warm	--	24.2	32.6	37.8	0	0.0	20.3
E54	6-Jul	Post	Warm	--	24.2	32.5	42.3	1	21.7	20.3
F15	16-Jul	NR	Warm	16	25.5	32.7	39.5	1	20.9	23.5
F25	18-Jul	NR	Warm	--	25.5	29.9	37.9	1	20.7	22.5
F35	19-Jul	NR	Warm	--	25.5	32.5	37.4	1	17.4	22.4
F45	20-Jul	NR	Warm	32	25.5	30.4	35.8	1	27.9	21.5
F55	21-Jul	NR	Warm	--	25.5	31.0	35.9	0	0.0	--
F65	22-Jul	NR	Warm	--	25.5	32.7	38.6	0	0.0	--
F75	23-Jul	NR	Warm	28	25.5	32.9	36.4	0	0.0	--
F85	24-Jul	NR	Warm	--	25.5	34.0	42.3	0	0.0	--

*T_{act} has only one value per bat, since it is based on the minimum Tb <30 minutes prior to emergence for all days a bat was monitored.

Table 6: Correlation tests for each whole bat day for measurements taken at Indiana bat roosts in the southern Appalachian Mountains, June-July 2012. Correlations were tested between skin temperature (T_{sk}) as a representative of body temperature, air temperature (T_a), and barometric pressure (BP) for the entire time in roost.

					All Time at Roost			
Bat Day Code	**Date**	**Repro**	**Cor(T_a_BP)**	**P**	**Cor(T_{sk}_T_a)**	**P**	**Cor(T_{sk}_BP)**	**P**
A11	4-Jun	Lact	-0.58	<0.01	0.70	<0.01	-0.16	0.11
A21	5-Jun	Lact	-0.34	<0.01	0.54	<0.01	-0.50	0.00
A31	6-Jun	Lact	0.58	<0.01	0.57	<0.01	0.58	<0.01
B12	5-Jun	Lact	-0.44	<0.01	0.86	<0.01	-0.71	<0.01
C13	19-Jun	Post	0.35	<0.01	0.15	0.15	-0.34	<0.01
C23	20-Jun	Post	-0.29	0.01	0.46	<0.01	-0.51	<0.01
C33	21-Jun	Post	-0.62	<0.01	0.42	<0.01	-0.45	<0.01
C43	22-Jun	Post	-0.48	<0.01	0.34	<0.01	0.43	<0.01
D13	23-Jun	Post	0.85	<0.01	0.86	<0.01	0.76	<0.01
E14	2-Jul	Post	0.79	<0.01	0.67	<0.01	0.72	<0.01
E24	3-Jul	Post	-0.43	<0.01	0.62	<0.01	-0.63	<0.01
E34	4-Jul	Post	-0.68	<0.01	0.79	<0.01	-0.82	<0.01
E44	5-Jul	Post	-0.83	<0.01	0.82	<0.01	-0.79	<0.01
E54	6-Jul	Post	-0.84	<0.01	0.89	<0.01	-0.87	<0.01
F15	16-Jul	NR	-0.74	<0.01	0.66	<0.01	-0.53	<0.01
F25	18-Jul	NR	-0.64	<0.01	0.65	<0.01	-0.36	<0.01
F35	19-Jul	NR	-0.68	<0.01	0.78	<0.01	-0.49	<0.01
F45	20-Jul	NR	-0.81	<0.01	0.76	<0.01	-0.62	<0.01
F55	21-Jul	NR	0.26	0.02	0.31	<0.01	-0.18	0.11
F65	22-Jul	NR	-0.38	<0.01	0.60	<0.01	-0.49	<0.01
F75	23-Jul	NR	-0.70	<0.01	0.77	<0.01	-0.64	<0.01
F85	24-Jul	NR	-0.66	<0.01	0.41	<0.01	-0.32	<0.01

Table 7: Correlation tests for periods of torpor or normothermia for each whole bat day for measurements taken at Indiana bat roosts in the southern Appalachian Mountains, June-July 2012. Correlations were tested between skin temperature (T_{sk}) as a representative of body temperature, air temperature (T_a), and barometric pressure (BP).

			Time Spent in Torpor				**Time Spent Out of Torpor**			
Bat Day Code	**Date**	**Repro**	**Cor(T_{sk}_T_a)**	**P**	**Cor(T_{sk}_BP)**	**P**	**Cor(T_{sk}_T_a)**	**P**	**Cor(T_{sk}_BP)**	**P**
A11	4-Jun	Lact	--	--	--	--	0.70	<0.01	-0.16	0.11
A21	5-Jun	Lact	0.01	0.96	-0.14	0.54	0.43	<0.01	-0.26	0.26
A31	6-Jun	Lact	0.21	0.16	-0.15	0.31	0.58	<0.01	0.59	<0.01
B12	5-Jun	Lact	0.60	<0.01	0.01	0.95	0.70	<0.01	-0.21	0.20
C13	19-Jun	Post	--	--	--	--	0.15	0.15	-0.34	<0.01
C23	20-Jun	Post	0.61	0.81	-0.59	0.01	0.14	0.23	-0.09	0.45
C33	21-Jun	Post	-0.13	0.48	-0.12	0.53	-0.11	0.41	0.54	<0.01
C43	22-Jun	Post	-0.53	<0.01	-0.06	0.70	-0.09	0.53	-0.11	0.44
D13	23-Jun	Post	0.79	<0.01	0.60	<0.01	0.30	0.04	0.22	0.13
E14	2-Jul	Post	0.67	<0.01	0.35	0.04	0.11	0.44	-0.18	0.18
E24	3-Jul	Post	0.05	0.79	-0.48	0.01	0.43	<0.01	-0.17	0.17
E34	4-Jul	Post	0.39	0.04	-0.85	<0.01	0.46	<0.01	-0.57	<0.01
E44	5-Jul	Post	--	--	--	--	0.82	<0.01	-0.79	<0.01
E54	6-Jul	Post	0.49	0.04	-0.42	<0.01	0.77	<0.01	-0.82	<0.01
F15	16-Jul	NR	0.48	0.04	-0.59	0.01	0.42	<0.01	-0.04	0.76
F25	18-Jul	NR	0.02	0.95	-0.57	0.01	0.69	<0.01	-0.12	0.44
F35	19-Jul	NR	-0.03	0.92	-0.43	0.10	0.72	<0.01	-0.19	0.11
F45	20-Jul	NR	0.32	0.13	0.33	0.10	0.52	<0.01	-0.22	0.09
F55	21-Jul	NR	--	--	--	--	0.31	<0.01	-0.18	0.11
F65	22-Jul	NR	--	--	--	--	0.60	<0.01	-0.49	<0.01
F75	23-Jul	NR	--	--	--	--	0.77	<0.01	-0.64	<0.01
F85	24-Jul	NR	--	--	--	--	0.41	<0.01	-0.32	<0.01

FIGURES

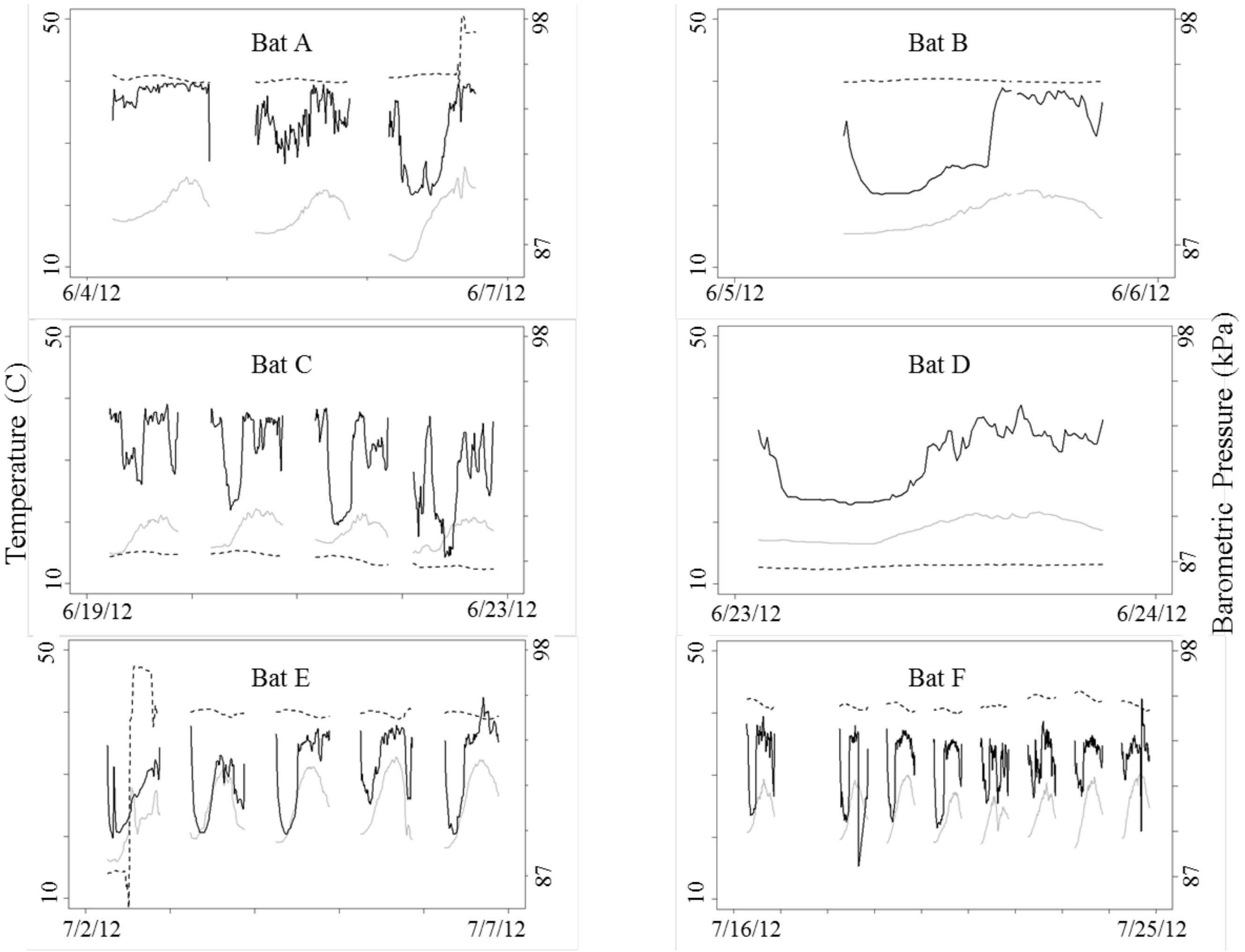

Figure 1: Whole bat day data for 6 Indiana bats tracked to roosts in the southern Appalachian Mountains from June-July 2012. Skin temperature (dark solid line) was measured via a temperature-sensitive radio transmitter attached to the bat’s skin, while air temperature (light gray solid line) and barometric pressure (dark dashed line) were measured with a weather station in the near vicinity of the bat’s roost. Bats A & B were lactating females, bats C, D, and E were post-lactating females, and bat F was a juvenile female.

CHAPTER 2

PRESENCE ONLY MODELING OF INDIANA BAT SUMMER ROOSTING HABITAT IN THE SOUTHERN APPALACHIAN MOUNTAINS

Forests are important to many bat species in North America as both roosting and foraging habitat (Miller et al 2003). However, the high mobility of bats creates a problem for land managers seeking to identify critical habitat within the forest for bats to roost and reproduce (Miller et al. 2003, Weller 2007). This is because the majority of encounters between managers and bats are at night when bats are captured while out on the landscape foraging, sometimes many miles from their roosting areas. The question of where bats are roosting is problematic when planning forest timber harvests and prescribed fires while considering habitat needs for endangered bat species, such as the Indiana bat (*Myotis sodalis*) (Krusac and Mighton 2002). Although many species of bats have been tracked to individual roost sites and those roost trees have been described at tree and small plot scales (Miller et al. 2003, Kalcounis-Rueppell et al. 2005), these data have only shed minor light on the characteristics of suitable roosting sites at the landscape scale (e.g., Carter 2006). Our limited ability to accurately predict the distribution of potential Indiana bat roosting sites across large areas has led to an array of contrasting management decisions (Krusac and Mighton 2002). Currently, some managers work to prevent all potential disturbances in areas of suitable Indiana bat habitat, while other managers lack protocols for maintaining suitable habitat conditions in the form of sufficient forest, snag (dead tree) patches, and large trees for future snags for roosting and foraging (Krusac and Mighton 2002). Indiana bats roost primarily in standing snags, but protecting all snags that might be potential roosts for Indiana bats is not a practical management strategy (Humphrey et al. 1977, Krusac and Mighton 2002, Kurta et al. 2002). Rather, it is critical to identify other important variables that can be used to predict the location of potential roost habitat for Indiana bats; for example, forest composition, forest patchiness, topography, and distance-to resources might be important predictors. Our objective was to develop a model identifying important environmental variables that managers could easily measure to predict the location of potential Indiana bat summer roosting habitat in the southern Appalachians.

The Indiana bat was listed as federally endangered in 1967, and since that time, state and federal agencies have tried to conserve and manage for habitat thought to be critical to the species (Krusac and Mighton 2002). Before 1995, most National Forest plans focused on protecting hibernacula and preserving riparian areas, the latter having been found to be critical Indiana bat summer habitat in the Midwest portion of the Indiana bat's range (Humphrey et al. 1977). However, in 1994, a reproductive female Indiana bat was caught and tracked to upland habitat in Kentucky (Krusac and Mighton 2002), leading to more intensive surveys in the southeastern U.S. (e.g., Gumbert 2001). We have since learned that Indiana bats are not restricted to riparian zones for roosting and also that females are reproducing farther south than previously known (Harvey 2002, Krusac and Mighton 2002). Since the late 1990s, Britzke et al. (2003) and O'Keefe and Loeb (unpublished) have investigated summer roost habitat selection by female Indiana bats in the southern Appalachian Mountains of North Carolina and Tennessee. In this region, the majority of roosts used by Indiana bats are in yellow pine (*Pinu*s subgenus

Diploxylon) or white pine (*P. strobus*) snags along mid and upper slopes in mixed pine-hardwood forests (O'Keefe et al. unpublished).

To create a landscape-scale predictive model of Indiana bat summer roosting habitat in the southern Appalachians, certain landscape variables need to be considered such as forest patch size, heterogeneity of patches of dense forest, canopy closure in patches and surrounding forest, snag density, ridge aspect, and distance-to-water (Barclay and Kurta 2007). In a meta-analysis of roost site selection by forest bats in North America (Kalcounis-Rueppell et al. 2005), no "primary" variable was identified as determining bat presence, but several variables were deemed significant as indicators of bat roost site selection. Kalcounis-Rueppell et al. (2005) concluded that an open canopy near or in the forest, proximity to water, and proximity to other snags were important factors in roost site selection. However, snag availability and canopy closure are difficult to measure on a landscape scale. This led us to use data on forest composition and topographic features, including some unique variables to describe our study area, so that we might be able to identify suitable roost habitat within a forested landscape.

To provide a model to land managers, a suitable modeling system must first be selected that is appropriate for this objective. Bats are often a challenging species for habitat modeling, as absence data are hard to truly identify because bats move across large expanses and are a challenge to track and locate, especially in remote locations (Weller 2007). We used Maximum Entropy modeling (MaxENT) (http://www.cs.princeton.edu/~schapire/maxent/), a presence-only modeling approach that estimates distribution based on known data locations (Phillips 2004, Phillips et al. 2006). An advantage of MaxENT is that the program is less sensitive to modeling with low sample sizes (i.e., <100) than other programs, although larger sample sizes are desirable (Phillips 2004, Phillips et al. 2006). MaxENT outputs can be transferred to geographic information systems (GIS), allowing for interpretation of the logistical output of predicted occurrence based on environmental variables in simple visual format (Baldwin 2009). Further, the program is free online and, hence, available to all land managers who might wish to use these methods in other portions of the Indiana bats' range.

MaxENT has been used for a wide variety of species distribution predictions, including for hardwood forests (Weber 2011), gecko species (*Uroplatus spp.*), black bear (*Ursus americanus*) denning habitat, and sage grouse (*Centrocercus urophasianus*) distribution and mapping of nesting habitat (Baldwin 2009). This tool has also been used to assess the influence of climate change on distribution of species such as the Cuban tree frog (*Osteophilus sepentrionalis*; Rödder and Weinsheimer 2009) and even the Indiana bat (Loeb and Winters 2012). MaxENT has also been used successfully to predict the distribution of several bat species; for example, Rebelo and Jones (2010) used MaxENT to model *Barbastella barbastellus* distribution in Portugal, and Mortalli et al. (2011) used MaxENT to model current and potential distribution of *Myotis simus* in Ecuador.

There are a few weaknesses of MaxENT that had to be considered for this study. First, the final product is not easily transferred to non-sampled areas, meaning that the model we created will only be applicable to our study area (Baldwin 2009, Phillips et al. 2006). However, the final model will identify important environmental variables for summer roosting habitat prediction in the southern Appalachians and can later be used as a training model for managers of surrounding areas if they wish to use the same approach. Another potential weakness of MaxENT is that it can be difficult to find an appropriate method to evaluate the models. One popular approach to measure relative goodness of fit of a statistical model and make model comparisons is the information theoretic approach, in which Akaike's information criterion is calculated for candidate models (AIC; Burnham and Anderson 2002). Fortunately, the recent addition of the program ENMTools (http://enmtools.blogspot.com/) makes it possible to use an AIC approach for comparing MaxENT models. This is in improvement over the previous method of using the standard area under the curve (AUC) scores output from MaxENT to evaluate individual model performance and for model comparison, as AUC values do not account for number of parameters and overfitting of data (Warren et al. 2010, Warren and Seifert 2011).

Our overall objective was to create a model to predict suitable and optimal Indiana bat summer roosting habitat in the Great Smoky Mountains National Park, the Cherokee National Forest, and the Nantahala National Forest. We sought to generate a GIS layer that could be used by land managers to understand the probability of presence of Indiana bat roosting habitat across a five county area in the southern Appalachian Mountains. We also sought to identify the important environmental variables in the final model equation that could then be applied outside our study area in other landscapes in the southern Appalachians. We predicted that areas of importance for summer roosting habitat would mainly be concentrated on south facing ridge tops in forests with a pine component and water sources nearby.

STUDY AREA

The study was conducted in the southern Appalachian Mountains in southeastern Tennessee and southwestern North Carolina in the Cherokee National Forest (CNF), the Nantahala National Forest (NNF), and the Great Smoky Mountains National Park (GSMNP). The study area was 281,788 hectares of federal land in Monroe and Blount counties in Tennessee, and Swain, Graham, and Cherokee counties in North Carolina (Figure 1). There were several known hibernacula in and around the Great Smoky Mountains National Park (Harvey 2002). Summer colonies of Indiana bats have been observed in the region since 1999, when a reproductive female was first captured and a maternity colony located (Harvey 2002, Britzke et al. 2003).

GSMNP and the two National Forests were classified as mixed pine-hardwood forests in the Appalachian oak section in Dyer's (2006) updated vegetation mapping based on the works of Braun (1950). The dominant tree species were black gum (*Nyssa sylvatica*), chestnut oak (*Q. montana*), scarlet oak (*Q. coccinea*), northern red oak (*Q. rubra*), red maple (*Acer rubrum*), sourwood (*Oxydendrum arboreum*), Virginia pine (*P. virginiana*), white pine, and white oak (*Quercus alba*). Other tree species encountered in mixed pine-hardwood forests included blackjack oak (*Q. marilandica*), pitch pine (*P. rigida*), shortleaf pine (*P. echinata*), and Table Mountain pine (*P. pungens*). The undergrowth was a mix of flaming azalea (*R. calendulaceum*), great rhododendron (*Rhododendron maximum*), and mountain laurel (*Kalmia latifolia*) (Franzreb 2005). The majority of the study area was mid-successional forest (41-80 years old), but also included young and old-growth forests (Franzreb 2005). The study area ranged in elevation from 250-2025 meters above sea level.

METHODS

To locate day roosts for female and juvenile Indiana bats, mist netting was conducted from mid-May through mid-August 2008 to 2012. We set mist nets (Avinet, Dryden, NY) over trails, roads, and streams, opened them at dusk and monitored nets every 8 minutes for 3-4 hours. We recorded species, sex, age, mass, forearm length, and wing damage score (Reichard and Kunz

2009) for all captured bats. We banded Indiana bats with a unique 2.9 mm aluminum forearm band (Porzana Ltd., East Sussex, UK) for individual identification. If an Indiana bat of suitable mass (>7 g for adult) and health was captured, and was either a female adult or juvenile, then the bat was fitted with a 0.32-0.42 g radio transmitter (Holohil Systems Ltd, Ontario, Canada). We primarily targeted adult females or juvenile Indiana bats due to their tendency to roost in colonies. Up to 3 bats were outfitted with transmitters on a given night, with the goal of tracking up to 20 individuals per summer. During all surveys, we used recommended white-nose syndrome protocols (USFWS 2011) for minimizing transmission of *Geomyces destructans*. While handling bats, we followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011; Clemson IACUC protocol 2009-16, ISU IACUC protocol 226895-1) and released bats at the capture site.

We tracked each transmittered Indiana bat using a TR5 receiver (Telonics, Mesa, AZ) and a 3-element or 5- element Yagi antenna (Wildlife Materials, Murphysboro, Illinois) the morning following capture and each day thereafter for the life of the transmitter (8 - 14 days), or until the bat was lost and unable to be relocated. When we located a roost, we recorded its location with a handheld GPS (Garmin 60 CSx, Olathe, Kansas, USA). We revisited all roost trees after mid-August to more extensively characterize and measure roost trees including species or genus, tree height, roost height, diameter at breast height (dbh), and canopy closure directly above the roost to the nearest 25 % interval. We also recorded the roost location with a GEO-XT Trimble (Trimble, Sunnyvale, California, USA) with sub-meter accuracy.

Occurrence and Environmental layers

MaxENT requires 2 types of file inputs: occurrence data and environmental data in the form of GIS layers. We corrected roost locations using base station data in Pathfinder (Version 5.0, Sunnydale, California, USA), and imported points as occurrence data in MaxENT (v3.3.3K). The environmental layers used as predictors of summer roosting habitat were elevation, aspect, slope, distance-to-ridge, ridge curvature, distance-to-water, distance-to-major roads, distance-to-trails and closed roads, and forest type. Variables were chosen based on the traditional topographic variables used in landscape modeling (elevation, aspect, and slope) and distance-to features that we thought may be important to bats as resources (i.e., distance-to-water) or to potential disturbances (i.e., distance-to-roads and trails). Distance-to-ridge and ridge curvature are two variables that we created to better represent the topography of our study area. All environmental layers were first gathered at a 10 m grid size in ArcGIS 10 to maintain a high resolution base layer and were later resampled to 30 m grid size once clipped to forest type, which was the limiting layer in terms of area covered and resolution of data.

Forest type, which was the only categorical variable, was created from information provided by the CNF, NNF, and GSMNP; due to differences in coding by agency, these data had to be recoded before the three area layers could be merged. The two national forest layers were first merged due to similar coding for forest type. We generated unique codes for vegetation across the entire study area using primary and secondary vegetation species descriptions in the Park Service and Forest Service layers and then merged those two layers based on the new vegetation code field.

Digital elevation models (DEMs) for Tennessee and North Carolina were downloaded from the National Elevation Dataset from the USGS (http://ned.usgs.gov) as 1/3 arc-sec (10 m) resolution. From the DEMs, aspect, slope, distance-to-ridge, and ridge curvature were generated for our study area. Elevation was measured in meters and ranged from 250 - 2025 m. Aspect, due to its circular nature, was separated into East/West and North/South by calculating the cosine and sine values, so that 1 represented one direction and -1 the opposite. To measure slope, distance-to-ridge, and ridge curvature, we first had to remove artifacts from the DEMs through 10 smoothing filters run in Spatial Analyst. Once artifacts were removed, we generated slope and ridge-curvature from their respective tools in Spatial Analyst. Distance-to-ridge required further processing of the elevation base layer. The base layer was first filled to remove sinks, and then the high and low values were reversed using Raster Calculator by multiplying -1.0 by the field value. The Flow Direction tool was run, followed by the Flow Accumulation tool, and a Stream Order raster was generated to identify ridgelines. We applied the Euclidean Distance tool to generate the final distance-to-ridge raster from the ridgeline raster.

Detailed water body and stream water data were acquired from the Tennessee and North Carolina geodatabases of the USGS National Hydrography Dataset (http://nhd.usgs.gov). We merged the flowline shapefiles (streams and rivers) and then we buffered by 1 m to transform the shapefiles into a polygon feature type to merge with the waterbody shapefile. The resulting vector file was then transformed into a 10 m raster file and processed through the Euclidean Distance in the tool Spatial Analyst to generate a distance-to-water layer.

Distance-to-major roads and distance-to-trails/minor roads layers were generated from spatial data provided by the Park Service and Forest Service. The trails/minor roads layer was created from merging all trails files with all roads that were gated or closed. Gated and closed roads were included with trails as these roads have minimal traffic and, therefore, minimal disturbance. We created the major roads layer using roads not included in the trails/minor roads layer. We used the Euclidean Distance tool in Spatial Analyst to generate the distance-to-trails/minor roads and the distance-to-major-roads layers. After clipping each environmental layer to the extent of the federal lands within our study area, we transformed the data into ascii files, which was the final data format required by MaxENT.

MaxENT and ENM tools

Twenty-six candidate models, including a global model, were created based on different hypotheses about roost habitat selection. All variables were used 8 times in various models for a balanced model set (Table 1; Burnham and Anderson 2002). We used the linear and quadratic features option in MaxENT so that all models were comparable and to ensure that results were comparable with data from other studies of roost habitat selection. Eighty percent of the roost data ($n = 61$ roosts) were used to train each model, while 20% ($n = 15$) were set aside to test each model for model performance. To limit bias, test roosts were kept as a separate file so that the same roosts were used to create and test all models. The lambda file (a notepad file of the parameter estimates for the model created) and ascii file from each model output and a text file of their pathways were input into the program ENMTools (v1.3) model selection option to generate an output of corrected AIC scores (AIC_c; Warren et al. 2010). Delta AIC_c scores were generated for each model and the models with values < 2 were selected as the top models (Burnham and Anderson 2002). We also generated AIC_c weights and used them to calculate parameter importance values. Parameter importance values were calculated by summing the AIC_c model weights for each model in which a particular parameter appeared. To calculate average parameter estimates, we rescaled weights for the top models, multiplied parameter estimates for each model by rescaled weights, and averaged these rescaled parameter estimates across top models (Burnham and Anderson 2002).

The final average model was created using the weighted parameter estimates. These values were entered into the raw and logistic equations upon which MaxENT is based:

$$raw = \frac{e^{\Sigma\left(\lambda i * \frac{fi(x) - min_i}{max - min_i}\right) - LinearPredictorNormalizer)}}{DensityNormalizer} \tag{1}$$

$$logistic = (raw * e^{entropy})/(1 + raw * e^{entropy}) \tag{2}$$

The final raw equation (Equation 1) was created as the average model from the AIC_c analysis and was used to create the final logistic equation (Equation 2). The linear predictor normalizer is a constant chosen output by MaxENT so that the exponent is always non-positive (for numerical stability). The density normalizer is a constant output by MaxENT that ensures that all possibilities of the distribution sum to 1 (Phillips et al. 2006). Entropy is the level of "choice" in a distribution; a higher entropy value means fewer constraints on distribution possibilities (Phillips et al. 2006) and is an output value for each model run by MaxENT. The final logistic equation (Equation 2) was input into the Raster Calculator (ArcGIS 10.0) to create the final raster output predicting the probability of presence for Indiana bat summer roosting habitat across the entire study area. Logistic output was used for the final model due to its "intuitive nature" in identifying important areas, which should make it easier to interpret for a broad range of users. Areas where probability of presence was ≥ 0.5 were considered suitable habitat and areas where probability of presence was ≥ 0.75 were considered optimal habitat based on the definitions given by the program MaxENT (Phillips 2010).

RESULTS

Bat and Roost Summary

From 2008 to 2012 we captured and tracked 48 female and juvenile Indiana bats to 76 roosts that were on federal land within our study area. We found 36 roosts in Tennessee (12 in Monroe County and 24 in Blount County), and 40 roosts in North Carolina (13 in Swain County, 4 in Graham County, and 23 in Cherokee County) (Figure 1).

Bats typically roosted under the sloughing bark of dead trees. Most roost trees were ephemeral and only suitable for 1-2 years before losing all bark or falling to the ground. During the study, only 1 roost was used in 2 consecutive years; we noted fewer bats using this roost during exit counts in the second year. Roosts were primarily yellow pine or white pine snags large in diameter, of moderate height, and with low canopy closure (Table 2). We observed that roosts were generally on south facing ridges, often on the upper third of the ridge but generally not at the very top.

MaxENT and ENM tool Results

We used the lambda outputs from MaxENT for each candidate model to perform model comparison using corrected AIC in ENM tools; this resulted in 2 top models (Table 3). Pine 2 ranked as the top model and Pine 1 ranked second (Δ AIC$_c$ = 0.44). These were the only models with ΔAIC$_c$ < 2 of the AICc weight of the top model. Both models accounted for >0.99 of the AICc weights among the models and, therefore, there was a > 99% chance that one of these models was the best approximating model for the data and candidate models we tested. Pine 2 and Pine 1 also performed well (>0.75 AUC value) individually based on area under the curve values (AUC) produced from MaxENT training and test data. Pine 2 performed better than Pine 1, with a training AUC of 0.89 and test AUC of 0.9. Pine 1 had a training AUC value of 0.88 and a test AUC value of 0.86.

The top five variables based on parameter importance values (Table 4) were elevation (importance > 0.99), forest type (> 0.99), aspect north/south (0.55), aspect east/west (0.55), and distance-to-ridge (0.55) (Figure 2). For other variables, parameter importance values were < 0.000002. We examined the response curves for the top 5 variables to describe relationships between the variables and the probability of presence of roosting habitat. Hemlock-Hardwood, White Pine-Upland Hardwoods, Yellow Pine-Hardwoods, Upland Hardwoods-White Pine, Oak - Yellow Pine, and Yellow Poplar were the top (parameter estimate value ≥ 1.5) six forest types in predicting the presence of summer roosting habitat for both Pine 2 and Pine 1 models (Figure 3). The greatest probability of presence (logistic probability of presence ≥ 0.5 in the final model) of roosting habitat was predicted for elevations ranging from 260 to 700 m (Figure 4). Only 6 of the 76 known roost locations occurred at > 750 m in elevation; these included 2 high elevation hemlocks (1265 m), 1 shortleaf pine (815 m), 1 yellow pine unidentifiable to species (795 m), and 1 Table Mountain pine (765 m). All other roosts occurred at elevations between 260 m and 750 m. The aspect north/south response curve showed the probability of presence as being greatest on south facing slopes, with a decrease in probability of presence as aspect became more north facing (Figure 5). The response curve for aspect east/west did not show any directionality for higher probability of presence. Lastly, the response curve for distance-to-ridge showed the greatest probability presence of roosting habitat <150 m from the top of the ridge, with decreasing probability of presence as distance-to-ridge increased (Figure 6).

We created a final averaged model based on the weighted parameter estimates for variables appearing in the 2 best models (Table 4 and 5). The top contributing variables based on averaged parameter estimates in the overall equation were Hemlock-Hardwood (3.010), Yellow Poplar (2.669), White-Pine-Upland Hardwoods (2.605), Yellow Pine-Hardwoods (1.932), Upland Hardwoods-White Pine (1.572), Oaks (1.367), Oak-Hickory (1.377), elevation (-8.268), and aspect north/south (-0.772). Of the 15 forest type categories included in the overall model, 8 of those categories included pine components. Distance-to-ridge contributed to the averaged equation as a squared value (-1.135). Aspect east/west contributed to the power of one value (0.001) and a squared value (0.086).

The final raster generated in ArcGIS 10 (Figure 7) shows predicted areas of suitable and optimal habitat based on habitat conditions from 2008- 2012 as being the western portion of the Great Smoky Mountains National Park, the western portion of the Cherokee National Forest in Monroe County, the western portion of the Nantahala National Forest in Cherokee County, and along Fontana Lake at the intersection of Swain and Graham Counties on the southern portion of the GSMNP and the northern portion of the NNF. Areas classified as suitable habitat accounted for 9 % of the study area, while areas of optimal habitat accounted for 1.5 % of the study area. Areas of suitable and optimal habitat were located in areas with known roosts, but also in areas where no roosts were located, including the west central portion of the CNF, the southern portion of the NNF, and south central portion of the GSMNP (Figure 7). Overall, 66 of 76 known roosts were ≤ 150 m from suitable or optimal habitat; 28 known roosts were located within suitable habitat and 15 known roosts were within optimal habitat.

DISCUSSION

Utility of spatial prediction

The spatial model for Indiana bat summer roosting habitat was successful in predicting critical habitat. The final average model identified areas of pine component forests at elevations 260-700 m on the upper portions of south facing slopes to be important areas for Indiana bat summer roosting habitat. The final output map was a good predictor of areas that were important to Indiana bats during the time of our study, and this map also showed how the model performed in projecting beyond surveyed areas. However, it must be stressed that it is important to focus on the conditions for which the model selected and not the final map, since conditions change over time and shift in location. These results matched well with field observations while tracking, when we found we had the greatest success in capturing and tracking individuals when we focused our efforts near mixed pine-hardwood forests on south facing ridge tops. However, this is contradictory to findings in other portions of the species' range where Indiana bats primarily use bottomland hardwood forests or riparian zones (e.g., Carter et al. 2002, Carter 2006, Miller et al. 2002). The differences between this study and others with respect to landscape-level roost selection suggest that Indiana bats may be flexible in roost habitat selection across different ecoregions with varying topography and land use patterns (Miller et al. 2002, Miller et al. 2003).

Numerous studies have found that bats show high fidelity to areas of suitable habitat compared to individual roosts and will switch roosts within that area, suggesting that landscape variables may be important in determining the suitability of an area (e.g., Cryan et al. 2001, Gumbert et al. 2002, Hein et al. 2008, Miller et al. 2003). However, fewer studies have investigated summer roosting habitat for bats on a landscape level compared to micro-scale roost habitat selection (Miller et al. 2003). Of those that have examined roost habitat selection for bats on a landscape scale, the majority of the studies have focused on land cover data, separating these data into general categories (e.g., bottomland vs. coniferous forest, Carter et al. 2002; pine vs. hardwood and edge vs. open, Hein et al 2008; and forest vs. wooded pasture, Miller et al. 2002). In this study, we found that topographical features and detailed data on forest composition were important predictors of the probability of presence of suitable roost habitat when considered over a large area (>200,000 ha).

The final model predicted summer roosting habitat to be primarily in forest types with a pine component, which supports previous work done in the area on plot- and stand-scale roost selection in this same region (Britzke et al. 2003, O'Keefe et al. unpublished). Unpublished data from the same area indicates that Indiana bats are selectively roosting primarily in yellow pine snags, particularly shortleaf pine, followed by Table Mountain and pitch pine. Indiana bats also used white pine and Virginia pine snags. All the pine species selected by bats in our study area exhibited similar patterns of decay that lead to popped exfoliating bark that will remain attached to the bole of the tree for several months, an important characteristic for Indiana bat roosts (Miller et al. 2002). Further, the yellow pine species in this region tend to be concentrated on south facing ridges (Lafon et al. 2007), thereby providing good solar exposure, which is an important habitat feature for tree-roosting bats (Kalcounis-Rueppell et al. 2005, Menzel et al. 2002).

Elevation has been shown to influence bat species distributions (Jaberg and Guisan 2001), and, in particular, roosting locations for big browns bats (*Eptesicus fuscus)* (Neubaum et al 2006). Further, Cryan et al. (2000) found that there are sex-specific differences in selection for elevation gradients for multiple bat species. Cryan et al. (2000) suggested this may be an effect of temperature and insect availability at different elevation gradients, and the impacts of these factors on torpor and energy restrictions. Elevation may be more critical to the overall model in predicting roosting habitat because elevation influences the temperature regimes that a bat will experience while roosting and, therefore, influences the amount of energy a bat may expend for torpor use. However, within our study area, the final averaged model showed the strongest probability for the presence of summer roosting habitat within the range of 260 m - 700 m in elevation. The model's elevation range is similar to elevation gradient ranges for many of the pine species within the southern Appalachians. In our study area, pines do occur above 700 m, but only Table Mountain pine and pitch pine are known to regularly occur above 760 m based on Forest Service species distribution data (http://www.na.fs.fed.us/spfo/pubs/silvics_manual/Volume_1). Although we found 6 roosts above 750 m, 3 were in high elevation tree species, hemlock and Table Mountain pine, and 1 was unidentifiable beyond the genus *Pinus*. Elevation influences the availability of different forest types across the landscape because climate affects where particular species can grow. Overall, elevation seems to have an influence on the distributions of forests with a pine-component, an important forest component for predicting Indiana bat summer roost habitat within our study area.

The fact that aspect and distance-to-ridge were included in the final model probably relates to that fact that solar exposure is an important factor in bat roosting ecology, especially for maternity colonies (Kalcounis-Rueppell et al. 2005, Menzel et al 2002, Neubaum et al. 2006). The topography within our study area can change drastically over short distances, with sunny ridges adjacent to deep drainages that are visibly cooler and shadier; thus, topography affects temperature regimes for roost habitat. Furthermore, south facing aspects and the upper portion of ridges provide favorable growth conditions for several types of pines (Lafon 2007). While elevation and forest type were important for determining the general locations of potential suitable roosting habitat, including aspect and distance-to-ridge in the model seems to have further narrowed the range of areas predicted to provide optimal conditions for pine growth and greater solar exposure/optimal microclimates for reproductive females and their pups.

Mist netting and radio tracking are not always economically and logistically feasible due to the large effort required to thoroughly survey even a small area for roost sites (O'Farrell and Gannon 1999). This model provides a supplemental, if not alternative, way for land managers to identify important Indiana bat summer roosting habitat areas and consider them in land use plans. However, we note that there will always be exceptions such as the high elevation hemlocks we found in 2012 and that flexibility of the species will always need to be considered. With future validations of the model within our study area and testing in other portions of the southern Appalachians, this model should be an asset to land managers throughout the region. The model will also be beneficial to managers tasked with improving habitat conditions for the recovery of this endangered species, an objective that has been suggested as a priority for federal lands (Krusac and Mighton 2002). Landscape-scale GIS models predicting probability of habitat use may also be useful for other forest bat species (Miller et al. 2003).

Caveats/Considerations

There are some caveats that will need to be addressed in future efforts to refine the overall model. We had hoped to use LiDAR (Light Detection and Ranging) as a way to map canopy closure and snag availability on the landscape. To assess the distribution of potential habitat for 4 snag-dependent avian species, Martinuzzi et al. (2009) successfully used LiDAR to map snag distribution in northern Idaho with 72-80% accuracy. They also used LiDAR data to group the snags into diameter classes with 88% accuracy. However, for our study area, the available LiDAR data (North Carolina only) were no better than random in predicting gaps within the forest as a representation of snag distribution. This may be related to the low resolution of available data and the restriction of modeling at a 30 m cell grid sizes based on forest type, which decreased our ability to detect small canopy gaps (<10 m in diameter) where snags occur. As technology improves and survey methods are advanced, the inclusion of snag distribution data in a future model may help to refine the model for monitoring current conditions. However, snag availability is constantly changing and could only be used for short periods of time before requiring updated data. Even without snag availability data, the current model accurately predicted the location of known Indiana bat roost locations where snags currently exist and where snags would be likely to occur again in the future if management efforts target the regrowth of mixed pine-hardwood forests.

Another factor that may have affected the accuracy of the model is the use of environmental data from multiple agencies, as these data were developed under different collection and classification schemes. GSMNP classified much of their forest type data to a higher resolution, often to a single species or top 2 species, while the Forest Service typically classified by species groups (e.g., Yellow Pine or Oak-Hickory). We tried to address these differences by recoding the data based on primary and secondary species to better represent both sets of data, however, some forest types that had been classified to a single species in the Park (e.g., Shortleaf Pine forests) may have appeared as unimportant when generalized to a more broad forest type. Further, the large number of potential forest types included in the model compared to the sample size of known roosts may have limited our ability to detect the significance of some forest types to an individual tree species. In the future, if available at a high resolution, the use of a more uniform forest type classification may improve the model.

Even though the Forest Service's forest type data were updated in 2012 and the Park's forest type data in 2007, this does not necessarily mean that all areas have been surveyed recently. This may have an impact on model accuracy, especially in areas of pine presence. Known snag roosts used by bats during this study are thought to have died as a result of a southern pine beetle outbreak in the early 2000s (Nowak et al. 2008). As the snags from that outbreak decay to the point at which they have lost their roost potential, we wonder what type of tree will become the next favored roost type. With the absence of fire in the region, mature yellow pine forests are becoming increasingly rare on the landscape (Lafon et al. 2007). There is some speculation that hemlocks may be the next available snag type to serve as potential roost trees for Indiana bats due to the widespread hemlock die-offs from the invasive insect, hemlock wooly adelgid (*Adelges tsugae*; Nucholls et al. 2009). We speculate that, as pine snags decrease on the landscape, bats may shift to using hemlock roosts more often. However, hemlock snags have been available throughout our study and, to date, we have observed low use. Two dead hemlocks used in 2012 were >500 m higher in elevation than the upper end of the optimal range of elevation predicted by our overall model, which suggests that these roosts are not presently in an optimal location for Indiana bats in this region. In the absence of preferred roost types, Indiana bats will use other tree species as roosts (Britzke et al. 2003, Kurta et al. 2002, O'Keefe et al. unpublished). However, this model suggests that pines are favored and that management for future mature pine stands could be important for the recovery of the Indiana bat in the southern Appalachians. As the model will become outdated over time, we suggest that managers focus on identifying the conditions and habitats for which the model selected for, rather than focusing on the particular geographic areas that currently show a high probability of presence on the final model output map (Figure 7).

Climate change and its potential impact on the distribution of tree species was not considered in the models we tested. This may be particularly important, as many trees species are predicted to shift to higher or lower elevations or to become more or less abundant; some tree species, such as *Fagus grandifolia*, may even become restricted to the Appalachians (Iverson and Prasad 2002). This will be important in the future, as the distribution of 3 of the 5 pine species in our study area are presently limited to the same elevation range as defined by the final model (260-700 m). Changes in tree species' distributions will need to be accounted for in future modifications and updates to the model. A recent study found that Indiana bats may shift the core of their range to the southern Appalachians as a result of climate change (Loeb and Winters 2012); thus, it is particularly critical that we try to better understand the species' habitat requirements within this region. Due to the possible shifts in tree species' distributions at certain elevations, we recommend that managers consider potential Indiana bat habitat to occur up to at least 800 m in the southern Appalachians. This takes into account current distributions of pine species, but managers should also consider what potential roosts may be available at higher elevations such as large hemlock snags with exfoliating bark. Further, we caution that changes to the local climate may require a re-evaluation of the model in the future.

Management Implications

The spatial model is a new tool for managers in our study area for managing for Indiana bats, especially when considering the effects of large scale timber harvests and prescribed burns on Indiana bat habitat. Management practices that promote forests with a pine component on upper south facing slopes at elevations from 260 – 800 m and create or preserve large trees should create suitable roosting habitat for Indiana bats. We stress to managers to consider where these selected conditions are located on the landscape and how those conditions shift in location throughout time and to alter their management practices appropriately. Fire, which had been absent from the landscape for almost a century, has been returned to the landscape in the form of prescribed fire, with the goal of returning yellow pines and oaks to the south-facing slopes (Waldron et al. 2007). Prescribed fire is a potential management tool for Indiana bat habitat, but it will be important for managers to consider potential regrowth of pines in burned areas and how to promote large trees with good roosting conditions in the future.

The technique of model creation and comparison based on known occurrence data is one we recommend to managers throughout the Indiana bat's range as an effective method of understanding landscape use by Indiana bats. Although the variables may change outside the southern Appalachians, the methods for identifying important environmental variables and conditions may be valuable for managers throughout the range of the Indiana bat. Regional thinking will improve management for future recovery of the Indiana bat on a larger scale by no longer just protecting current roost trees but also managing for future habitat.

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TABLES

Table 1: Candidate models (n=26) developed to predict probability of presence of roost habitat used by Indiana bats in the southern Appalachian Mountains. Models were built based on presence data collected from May to August, 2008-2012; variables measured and used in models included the following environmental layers: forest type (FT), aspect north/south (NS), aspect east/west (EW), slope (S), Elevation (E), Distance-to-water (W), distance-to-trails/minor roads (TR), distance-to-major roads (MR), distance-to-ridge (R), and ridge curvature (C).

Candidate models
Corridor 1 = TR
Corridor 2 = MR + C
Corridor 3 = W
Elevation = E
Foraging 1 = W + TR + MR
Foraging 2 = S +W + TR
Forest Type = FT
Global = FT + NS + EW + S + E + W + TR + MR + R + C
Humans = TR + MR
Major Roads = MR
Needs 1 = E + W
Needs 2 = FT + W
Needs 3 = FT + W + TR + MR
Pine 1 = FT + E
Pine 2 = FT + NS + EW + E + R
Research Bias 1 = FT + TR + MR
Research Bias 2 = TR + MR + R
Ridge 1 = NS + EW + S + R
Ridge 2 = S + E + C
Ridge 3 = FT + R + C
Sun 1 = NS + EW + R + C
Sun 2 = NS + EW + S + C
Sunny Ridge top = NS + EW +R
Topography 1 = NS + EW + S + E + R + C
Topography 2 = NS + EW + S + E
Water flow = S + W + C

Table 2: Summary statistics for characteristics of 76 Indiana bat roosts located from 2008-2012 in a study area in the southern Appalachian Mountains; these roosts were used as occurrence data for landscape-scale spatial models.

Characteristic	Mean ± SE	Minimum	Maximum
Tree Height (m)	19.9 ± 0.9	5.2	38.5
Dbh (cm)	39.8 ± 2.3	13.9	137.5
Canopy Closure %	25.5 ± 3.9	0	100
Elevation (m)	554.2 ± 21.1	266	1266
Aspect (degree˚)	188˚ ± 9.1˚	8˚	344˚
Slope Position	20 % Lower, 45 % Mid, 35 % Upper	--	--
% Yellow Pine	67 %	--	--
% White Pine	29 %	--	--
% Hardwood	1.3 %	--	--
% Hemlock	2.6 %	--	--

Table 3: Eleven top-ranked models and the 2 lowest-ranked models for predicting the presence of Indiana bat summer roosting habitat based on known roost locations from 2008-2012 in the southern Appalachian Mountains. Models were ranked based on the delta AICc value. Pine 2 and Pine 1 were the top two models, with > 99 % chance that one of these two models was the best model considering the data and the other candidate models.

Rank	Model	Number of Parameters	AIC_c Score	ΔAIC_c	w_i
1	Pine 2	5	1732.3	0	0.55
2	Pine 1	2	1732.8	0.44	0.45
3	Topography 2	4	1758.9	26.56	< 0.01
4	Topography 1	6	1759.6	27.31	< 0.01
5	Elevation	1	1762.5	30.15	< 0.01
6	Research bias 1	3	1764.6	32.28	< 0.01
7	Needs 1	2	1764.6	32.29	< 0.01
8	Ridge 2	3	1764.7	32.34	< 0.01
9	Global	10	1765.6	33.33	< 0.01
10	Needs 3	4	1770.8	38.51	< 0.01
11	Forest Type	1	1779.5	47.15	< 0.01
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25	Sun 1	6	1824.0	91.69	< 0.01
26	Corridor 3	2	1824.7	92.35	< 0.01

Table 4: Parameter importance values for variables used in 26 candidate models predicting the presence of Indiana bat summer roosting habitat in the southern Appalachian Mountains based on known occurrence data collected from 2008-2012. Parameter importance values for each variable were calculated based on the AICc weights for each model in which a variable was included. Elevation and forest type were the two most important variables, followed by aspect east/west, aspect north/south, and distance to ridge.

Environmental Variables	Parameter importance
Elevation	0.99
Forest Type	0.99
Aspect East/West	0.55
Aspect North/South	0.55
Distance to Ridge	0.55
Slope	1.68E-06
Curvature	7.36E-07
Distance-to-Major Rds	8.88E-08
Distance-to-Trails/Minor Rds	8.88E-08
Distance-to-Water	8.87E-08

Table 5: Model-averaged parameter estimates for each environmental variable in the top 2 models for predicting the probability of presence of Indiana bat roosting habitat in the southern Appalachian Mountains. These average parameter estimates, along with the normalizers and entropy values, were used to create the final average raw and logistic equations. The linear predictor normalizer is a constant chosen so that the exponent is always non-positive (for numerical stability). The density normalizer is a constant that ensures that all possibilities of distribution sum to 1. Entropy is the level of "choice" in a distribution.

Environmental Variables	Pine 2 Parameter Estimate 1	Pine 1 Parameter Estimate 2	Model Averaged Parameter Estimates (Parameter Estimate 1*0.555) + (Parameter Estimate 2 *0.445)
White Pine	0.564	0.621	0.589
Hemlock-Hardwood	3.141	2.847	3.010
White Pine-Upland Hardwood	2.646	2.554	2.605
Yellow Pine-Hardwoods	1.840	2.046	1.932
Shortleaf Pine	0.574	0.762	0.657
Pitch Pine	0.440	0.491	0.463
Hardwoods-White Pine-Hemlock	0.379	0.178	0.290
Upland Hardwoods-White Pine	1.656	1.467	1.572
Oak-Yellow Pine	2.082	2.149	2.112
White, black, & Yellow Oak	1.376	1.356	1.367
Yellow Poplar	2.840	2.456	2.669
Chestnut Oak	0.528	0.434	0.486
Oak-Hickory	1.455	1.280	1.377
Yellow Poplar-Oak	- 0.063	- 0.323	- 0.179
Early successional Hardwoods	0.846	0.747	0.802
Aspect East/West	0.002	----	0.001
Aspect North/South	- 1.392	----	- 0.772
Distance to Ridge	0.000	----	0.000
Elevation	-8.591	-7.865	-8.268
Aspect East/West^2	0.154	----	0.086
Distance to Ridge^2	- 2.046	----	- 1.135
Linear Predictor Normalizer	2.080	2.512	2.272
Density Normalizer	268.353	373.174	315.040
Entropy	8.127	8.248	8.181

FIGURES

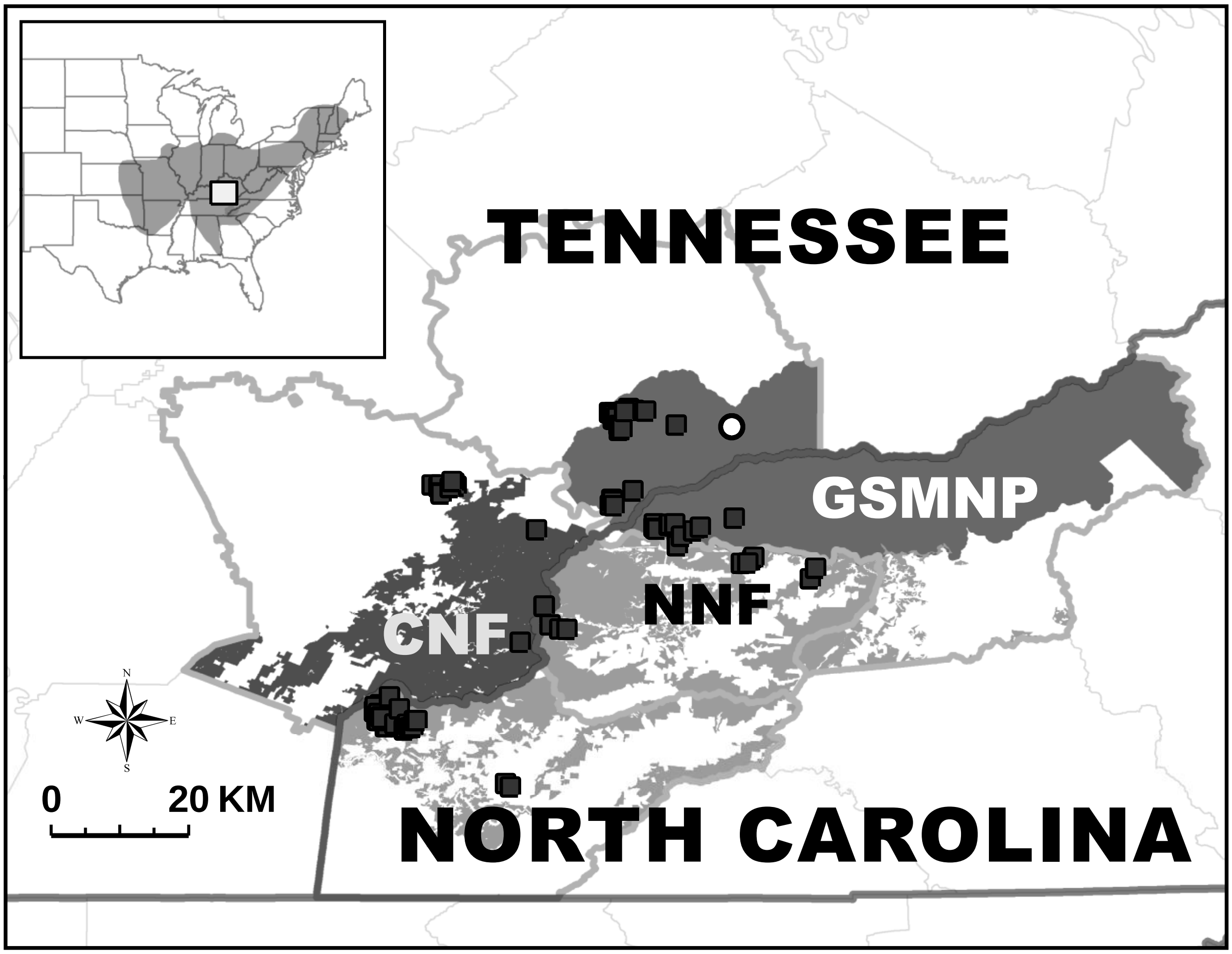


Figure 1: Locations of 76 roosts (squares) used by adult female and juvenile Indiana bats (2008-2012) in the southern Appalachian Mountains. Roosts are within 75 km of a series of caves (circle) thought to be used as hibernation sites by Indiana bats that form summer colonies in this region. The study area (~281,800 hectares) included portions of the Great Smoky Mountains National Park (GSMNP), Nantahala National Forest (NNF), and Cherokee National Forest (NNF); the area was clipped to 5 counties in Tennessee and North Carolina.

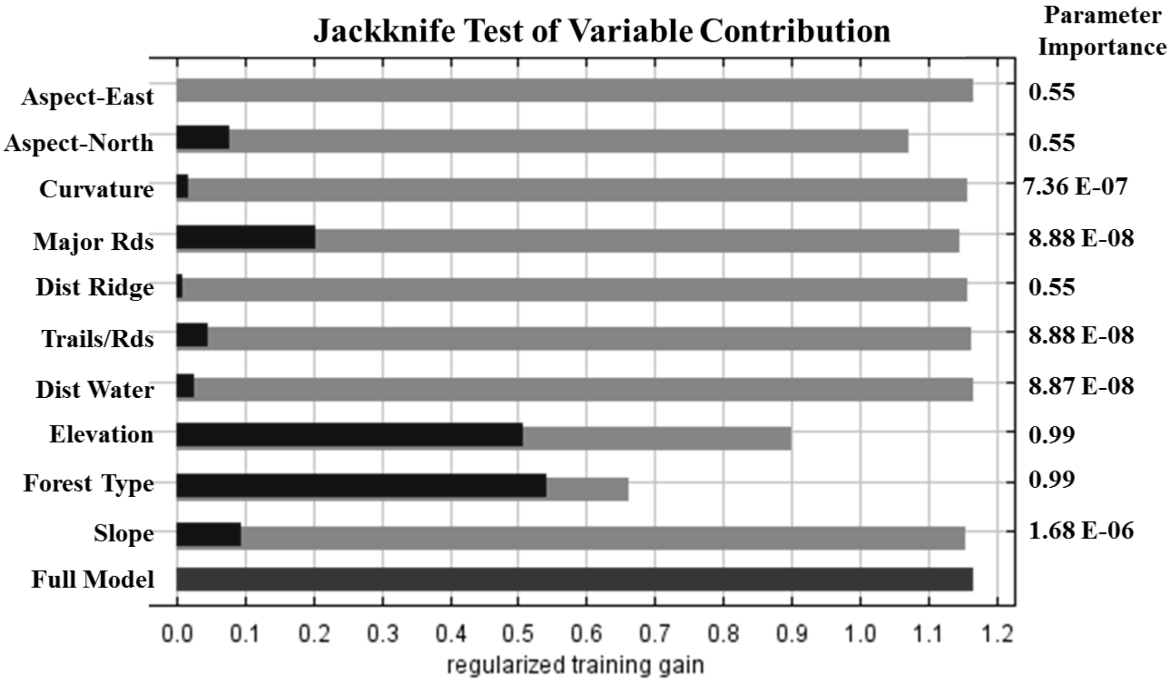


Figure 2: Importance of individual variables in spatial models predicting Indiana bat summer roosting habitat in the southern Appalachians; known roosts from 2008-2012 were used as occurrence data. Variable contributions were derived from a jackknife test of global model, while parameter importance values were calculated based on the AICc weights for each model in which a variable was included (see also Table 4). In the jackknife test, the black lines indicate model performance when only that variable is used, while the gray line shows model performance when a variable is excluded from the global model. Elevation, forest type, and aspect north/south were shown to be important in the jackknife test, and also had the largest parameter importance values for all models. Aspect east/west and distance to ridge were also important relative to other variables tested in spatial models.

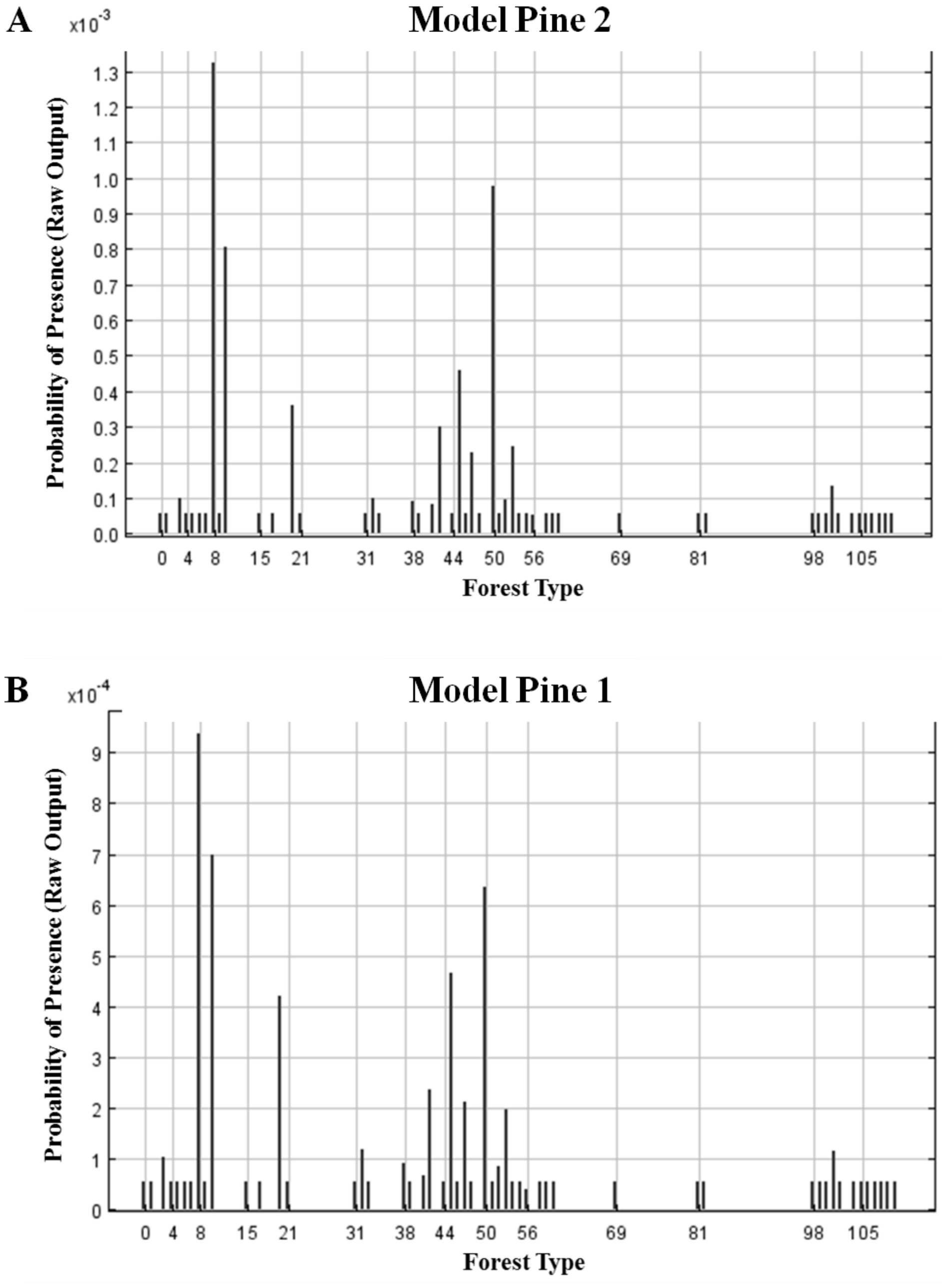
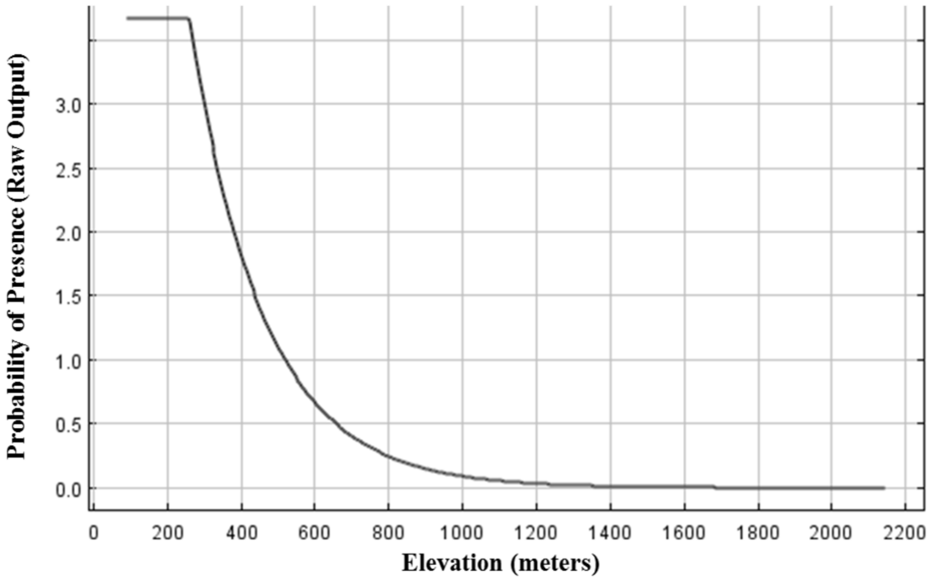


Figure 3: Comparison of response curves for the effectiveness of forest type as a predictor of presence of Indiana bat summer roosting habitat for top-performing models Pine 2 (A) and Pine 1(B). Models were developed using 76 known roost locations for female and juvenile Indiana bat roosts from 2008-2012 in the southern Appalachian Mountains of North Carolina and Tennessee. For both models, the top six forest types in predicting probability of presence for roosting habitat from left to right are forest type 8 (Hemlock-Hardwood), forest type 10 (White Pine-Upland hardwoods), forest type 20 (Yellow Pine-Hardwoods), forest type 42 (Upland Hardwoods-White Pine), forest type 45 (Oak–Yellow Pine), and forest type 50 (Yellow Poplar).

A **Model Pine 2**



B **Model Pine 1**

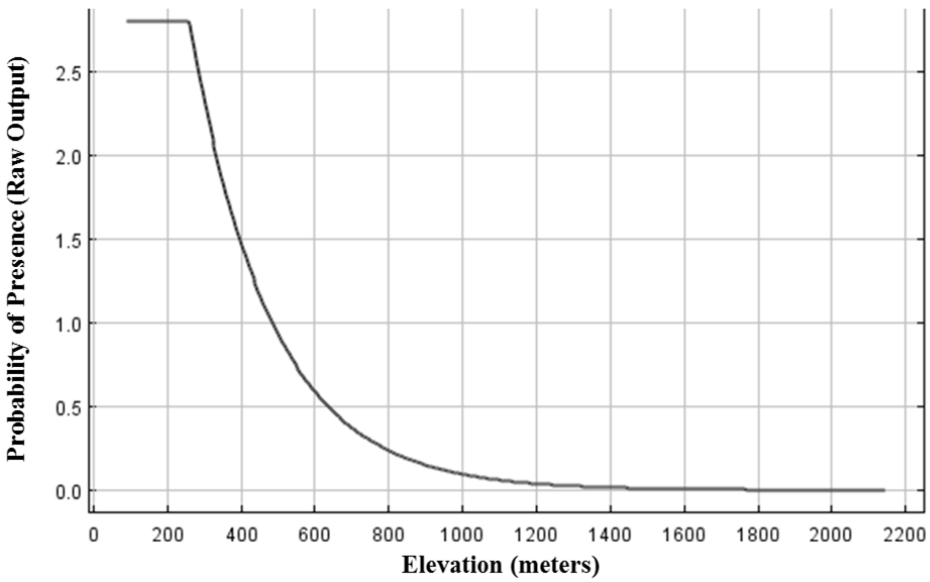


Figure 4: Comparison of response curves for the effectiveness of elevation as a predictor of presence of Indiana bat summer roosting habitat for top-performing models Pine 2 (A) and Pine 1(B). Models were developed using 76 known roost locations for female and juvenile Indiana bat roosts from 2008-2012 in the southern Appalachian Mountains of North Carolina and Tennessee. For both models, the greatest probability of presence for Indiana bat summer roosting habitat from 260 m - 700 m in elevation.

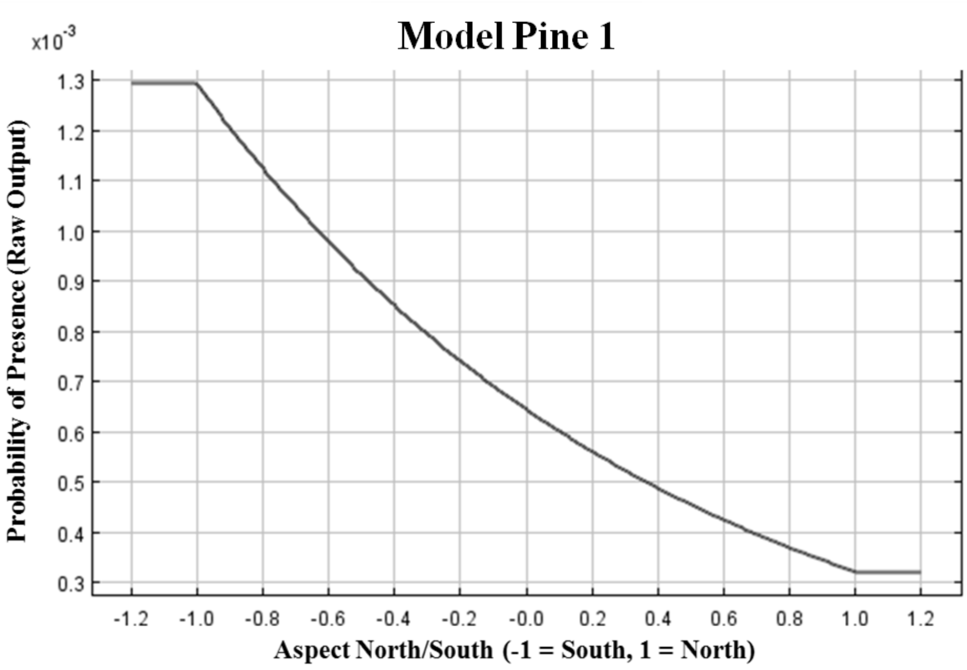


Figure 5: Response curve for the effectiveness of aspect North/South as a predictor of presence of Indiana bat summer roosting habitat for Pine 1, which was 1 of the top-performing models. Models were developed using 76 known roost locations for female and juvenile Indiana bat roosts from 2008-2012 in the southern Appalachian Mountains of North Carolina and Tennessee. The model shows the greatest probability of presence of summer roosting habitat on south facing slopes, with a decreasing probability as a slope becomes north facing.

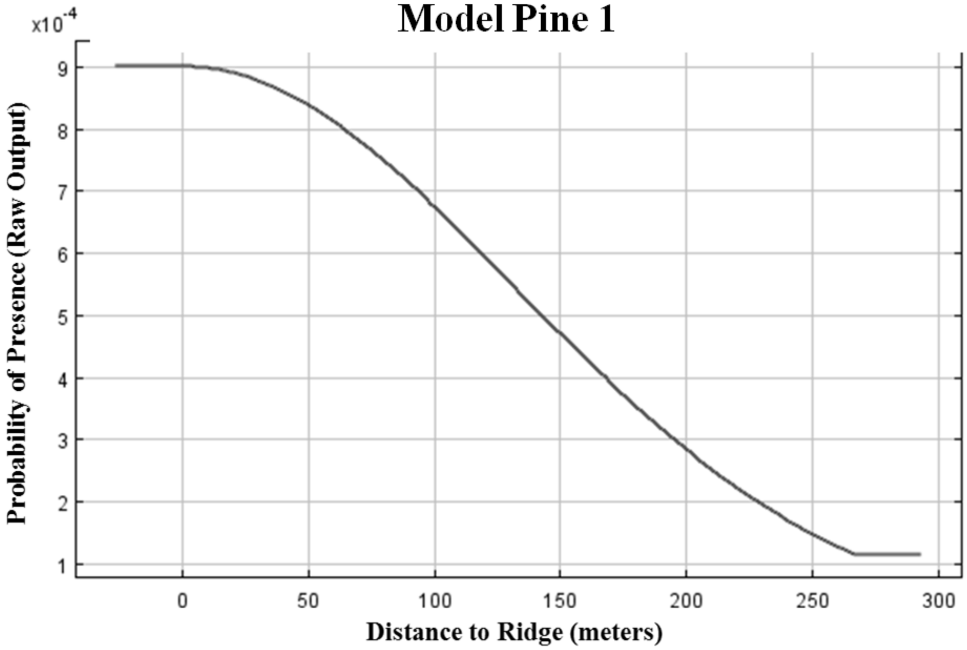


Figure 6: Response curve for the effectiveness of distance to ridge as a predictor of presence of Indiana bat summer roosting habitat for Pine 1, which was 1 of the top-performing models. Models were developed using 76 known roost locations for female and juvenile Indiana bat roosts from 2008-2012 in the southern Appalachian Mountains of North Carolina and Tennessee. The model shows a higher probability of roosting habitat closer to the top of a ridge (< 150 m).

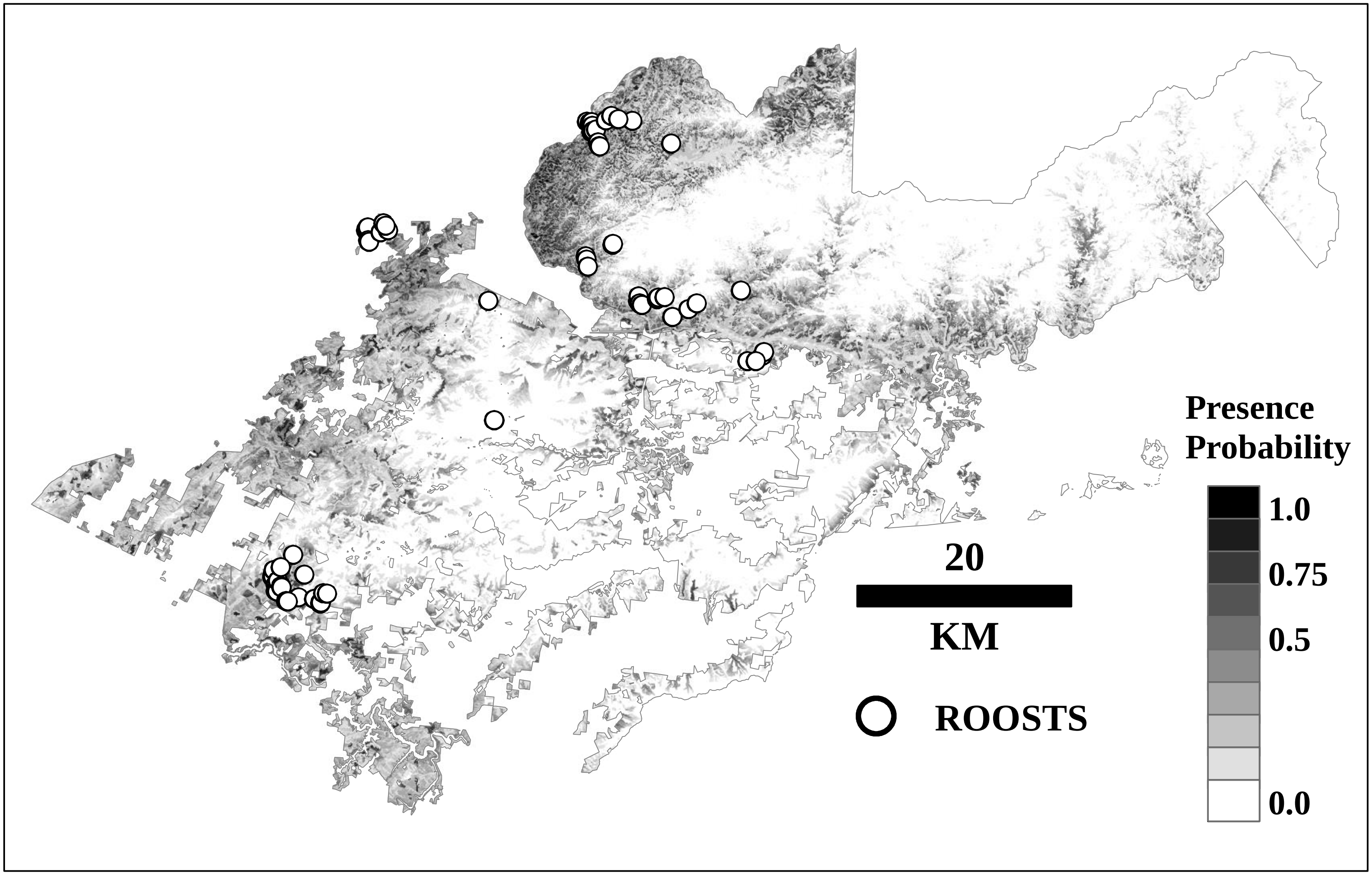


Figure 7: Predicted probability of the presence of summer roosting habitat for Indiana bats based on the average logistic model and 76 known roosts (indicated by the open circles) used by female and juvenile Indiana bats from 2008-2012 in the southern Appalachian Mountains of North Carolina and Tennessee. The predictive map shows areas of importance (gray to black areas) that are either suitable (≥ 0.5) or optimal (≥ 0.75) summer roosting habitat for Indiana bats.