Low winter-temperatures drive hibernation and migration in bats in temperate regions, which in turn can influence mortality via white-nose syndrome (WNS) and wind turbine interactions. However, the low-temperature during winter at which bats are able to be active remains unknown. I describe the species-specific winter low-temperature thresholds (T_{LT}) for bat presence across the state of North Carolina (NC), USA. I defined the T_{LT} as the sunset temperature (T_a) at which there was a certain probability of presence for that night and tested 10% ($T_{LT\,10}$) and 25% ($T_{LT\,25}$) levels. I studied two migratory species, *Lasionycteris noctivagans* and *Lasiurus cinereus*, and two cave hibernating species, *Perimyotis subflavus* and *Eptesicus fuscus*. I predicted that different species of bats would have different T_{LT}, and that larger species would have lower T_{LT}. I also predicted that migratory bats would have lower T_{LT} than cave hibernating bats. I acoustically monitored bat activity from sunset to sunrise in the winter (December to February) of 2017 and 2018, across a large T_a gradient (mean winter temperatures -0.1°C to 11.6 °C). I found all species to be present in the winter: *L. noctivagans* on 611 detector nights, *E. fuscus* on 242 detector nights, *P. subflavus* on 155 detector nights, and *L. cinereus* on 111 detector nights. In contrast to my prediction for migratory bats, the smaller bodied *L. noctivagans* had a lower T_{LT} ($T_{LT\,10}$ 1.01 °C T_a, $T_{LT\,25}$ 7.27°C T_a) than the larger bodied *L. cinereus* ($T_{LT\,10}$ 13.76°C T_a, $T_{LT\,25}$ 18.79°C T_a). In support of my prediction I found that at low T_a, body mass is important in predicting probability of presence in cave hibernating species at $T_{LT\,10}$ (*E. fuscus* 9.65°C T_a, *P. subflavus* 12.53 °C T_a), but as the T_a warms that effect weakens at $T_{LT\,25}$ (*E. fuscus* 16.92°C T_a, *P. subflavus* 17.76 °C T_a). I found lower $T_{LT\,10}$ in species less affected by WNS, suggesting that behavioral adaptations to low winter T_a affect WNS susceptibility. My results can be used to model the progression of WNS in the southern USA, as well as improve our understanding of winter *L. cinereus* wind turbine collisions in NC.

SPECIES-SPECIFIC LOW-TEMPERATURE THRESHOLDS FOR WINTER ACTIVE BATS

IN NORTH CAROLINA

by

Kevin A. Parker Jr.

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CHAPTER I

INTRODUCTION

Bats are facing unprecedented threats across their range (Voigt and Kingston 2016). White-nose syndrome (WNS) has killed more than 6 million bats in eastern North America and continues to spread westward (Frick et al. 2016).Wind energy is responsible for an estimated 650,000 to 1.3 million bat deaths annually (Adams and Pedersen 2013). Habitat fragmentation can decrease the abundance of some bat species, and can decrease species richness (Cosson et al. 1999; Yates and Muzika 2006; Meyer et al. 2008). Climate change can affect the reproductive success of some species of bats (Adams and Hayes 2008; Adams 2010) and change the distribution of many species of bats (Rebelo et al. 2010; Sherwin et al. 2013).

In North America, the most severe threats to bats are related to their inability to stay active on the winter landscape (O'Shea et al. 2016). Low winter-temperatures drive migration and hibernation in temperate bats (Kunz and Fenton 2003), which in turn can influence mortality via wind turbine interactions (Thompson et al. 2017) or WNS (Frick et al. 2016). However, the specific temperatures that limit bat activity on the landscape, and whether limiting temperatures vary by species, are not well understood.

One can consider the low-temperature threshold (T_{LT}) as minimum temperature at which there would be a certain chance of bats being active on the landscape and one can use T_{LT} to represent the tolerance to low ambient temperature for bats in temperate climates. Understanding T_{LT} will help us to better predict the spread of WNS, inform the timing of migratory events, predict potential overwintering grounds of difficult to track migratory bats, predict distribution shifts of species that might respond to anthropogenic change,

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and help us to better understand how bats use their environment in their highest season of mortality, the winter.

Winter is a season of high mortality for temperate bats because the majority of temperate bats are insectivorous. At low temperatures, insects either migrate or go into diapause (Mellanby 1939; Williams 1940; Taylor 1963; Alma 1970; Gaydecki 1984). Thus, in winter bats lose their food source and it becomes energetically inefficient for bats to remain active (Altringham 2011). In order to mitigate this energetic imbalance, bats have adapted two general approaches, hibernation and migration (Kunz and Fenton 2003). In temperate regions, both migratory and hibernating bat species are heterothermic, employing torpor bouts of differing lengths depending on the ambient temperature (Audet and Fenton 1988; Kunz and Fenton 2003; Adams and Pedersen 2013).

The ability to offset energetic costs is particularly important in small bodied mammals, like bats, because thermal conductance is negatively related to body size (Bradley and Deavers 1980). For most bats, basal metabolic rate (BMR), the lower critical limit of the thermal neutral zone, and thermal conductance are all strongly correlated with body mass (Bradley and Deavers 1980; Kunz and Fenton 2003). There are examples from the literature of larger bats being active at cooler temperatures than smaller species. Klüg-Baerwald et al. (2016) found *Myotis* species were less likely to be active at lower temperatures than the larger bodied big brown bat (*Eptesicus fuscus*). In a review of winter bat activity in North America, Boyles et al. (2006) found the lowest recorded temperatures for active bats were from big brown bats, which are large bodied compared to other bat species, supporting the relationship between body size and ability to be active at low temperatures.

In addition to body size, there may be life history adaptations that influence low temperature thresholds during winter. Hibernating and migratory bats could have different low

temperature thresholds in winter. Migratory tree roosting bats are exposed to a wider range of temperatures in the winter than bats that hibernate in caves. Migratory tree roosting bats can also take advantage of warmer nights to passively rewarm (Currie et al. 2014). Warm winter night temperatures will affect migratory bats more quickly in their exposed tree roosts than the more insulated hibernacula of cave hibernating species (Kunz and Fenton 2003). The pelt of some species of migratory bats also have higher insulative capacities than bats that hibernate in caves (Shump and Shump 1980), potentially reducing the energetic cost of activity at cooler temperatures. All of these factors could allow migratory bats to be active at lower low temperatures than cave hibernating species.

North Carolina (NC), USA, is an ideal location to examine low temperature thresholds for bat presence, during winter. North Carolina has a diverse climate, due in part to its large elevational range (~7,000 ft), and to the influence of a warming ocean current on the coastal region (Boyles and Raman 2003). North Carolina is located at ~35° N, which is midway between the equator and the arctic circle representing a temperate climate in the Northern Hemisphere. North Carolina has three distinct physiographic regions, each with a distinct climate: the Mountains, Piedmont and Coastal Plain. Mean annual temperatures at the highest elevations in the Mountains of NC are lower than mean temperatures at a latitude of 42.9 (650 miles north of central NC) and mean annual temperatures in the southern Coastal plain of NC are as warm as mean temperatures at a latitude of 30.2 (520 miles south of central NC). With 17 species, North Carolina has one of the most diverse bat communities in the eastern USA (Reid 2006). The state of North Carolina is home to both hibernating and non-hibernating bat species allowing for investigations of low temperature thresholds for both groups of bats (Li and Kalcounis-Rueppell 2018).

Some bat species in NC are active during the winter in parts of their species distribution range but inactive in other parts of their range (Whitaker 1967; Weller et al. 2016). Two species of conservation concern in North America, the tricolored bat (*Perimyotis subflavus*) and the Northern long-eared Myotis (*Myotis septentrionlis*) hibernate in the cooler Mountain region during the winter (Bosworth 2007), but are active during the winter in the warmer Coastal Plain region (Avery 1985; Morris et al. 2009; Grider et al. 2016). Grider et al. (2016) also found big brown (*Eptesicus fuscus*) and evening (*Nycticeius humeralis*) bats active throughout the year in the Coastal Plain of NC, but inactive during the winter in the cooler Piedmont region of NC. If bat species are active in some climates, but not others, one can investigate the lower temperature thresholds for winter activity.

The aim of this study was to describe species-specific T_{LT} for bat presence on the landscape in North Carolina, during the winter. I hypothesized that T_{LT} would vary by species based on body size and overwintering strategies. I predicted that T_{LT} will be lower for *Eptesicus fuscus* than *Perimyotis subflavus* (both cave hibernators), and lower for *Lasiurus cinereus* than *Lasionycteris noctivagans* (both migrants), due to the body size of each species within each overwintering strategy group. I further predicted that migratory bats would be present at lower temperatures than cave hibernating bats.

CHAPTER II

METHODS

Field data were collected in North Carolina (NC), USA (Figure 1). Sites were chosen that had all four species present during the summer across NC. Sites were also chosen to ensure approximately even spatial distribution across regions in NC. In total, 15 sites were sampled across NC: 6 sites in the Mountains, 5 in the Piedmont, and 4 in the Coastal Plain (Figure 1; Table 1). Not all sites were sampled in each year, with 11 of 15 sampled in 2017 and 14 of 15 in 2018 (Figure 1, Table 1). More sites were sampled in the Mountains due to the larger temperature variation represented in that region, in part due to high variation in elevation (Table 1). To reduce confounding effects of local site characteristics, sites were selected that had similar structural characteristics and had a body of water nearby.

I focused on four species because these species have ranges that cover the entire state, are representative of the body mass ranges of other insectivorous bats in North America, are common, and are relatively easy to identify via acoustics (Li and Kalcounis-Rueppell 2018; Parker et al. 2018). I examined two migratory species, the silver-haired (*Lasionycteris noctivagans*) and the hoary (*Lasiurus cinereus*) bat, and two cave hibernating species, the big brown (*Eptesicus fuscus*) and the tricolored (*Perimyotis subflavus*) bat. From the lowest to the highest body mass, each bat species mass range from Reid (2006) is: tricolored (3-6g), silver-haired (8-12g), big brown (13-20g) , and hoary (20-35g). Herein, I will present these species in order of body mass, from smallest to largest. Acoustic surveys represent a non-invasive, scalable method to investigate seasonal distribution of bat presence on the landscape (Kunz and Fenton 2003).

Acoustic surveys allow for simultaneous and continuous monitoring over many locations, and can function like a museum specimen, allowing for future verification and analysis (Adams and Pedersen 2013). I used passive ultrasonic recording devices to acoustically monitor nightly bat presence at my sites (Grider et al. 2016; Li and Kalcounis-Rueppell 2018; Parker et al. 2018). I used AnaBat SD2 bat detectors (Titley Scientifics, Ballina, New South Wales, Australia) to record bat presence each night from sunset to sunrise. In both 2017 and 2018, detectors were set up in late October/early November and taken down in April of the following year. Only recordings collected in December, January, and February were included for analysis because these months represent the winter season and are the coldest months in NC. At each site, the bat detector was secured in a weather-proof case with a weather-proof microphone and was mounted at least 1.7m above the ground, directed towards the water body. In winter of 2016-2017 detectors were powered with either 2 12v 7.5 Ah batteries or 2 12v 12 Ah batteries connected in parallel giving 15 Ah and 24 Ah respectively. Data were downloaded, and batteries changed, every 21 days in winter 2016-2017. In winter 2017-2018 detectors were powered with either or 2 12v 12 Ah batteries connected in parallel giving 15 Ah or a single 12v 12 Ah battery connected to a 20w solar panel. Data were downloaded, and batteries changed every 25-30 days, in winter 2017-2018.

I used Kaleidoscope 4.3 (Wildlife Acoustics Inc., Maynard, MA), to filter out all noise files that were recorded. I then displayed all bat passes recorded (recorded files that were not identified as noise) as spectrograms using Analook (Titley Scientific, Ballina, New South Wales, Australia). I examined the spectrogram of each recorded bat pass and selected only recordings with at least 5 clear bat calls, for identification. I used an acoustic key (http://www.sonobat.com/download/EasternUS_Acoustic_Table_Mar2011.pdf) to identify all recordings to species. Among hoary, silver-haired, and big brown bats, there is overlap in some

call characteristics. I only recorded a species as "present", for any given night, if I could find one of the diagnostic call types listed in the acoustic key. For each night, I looked for one call that I could definitively identify to species and mark as "present", and then I moved on to the next species. I recorded the species as "no detection" if I could not find a diagnostic call that I could identify to that species for that night.

I extracted nightly temperature (T_a, °C), and wind speed (km/h) at 9 pm from nearby aviation weather stations that record data hourly. Weather stations were on average 19 km from the sites in the Coastal Plain, 24 km from the sites in the Piedmont, and 7 km from the sites in the Mountains (Table 1). In the Mountain region there were no nearby aviation weather stations at similar elevations as the study sites, therefore, I selected personal weather stations from the weather underground network (www.wunderground.com). I used R version 3.4.1 (R Development Core Team 2018) package rwunderground (https://github.com/ALShum/rwunderground) as an interface to access weather data for both aviation weather stations and personal weather stations from the weather underground network. To characterize the local winter climate of each site I used BIOCLIM data from the WORLDCLIM version 2 database, mean coldest quarter (BIO11) (Fick and Hijmans 2017).

Statistical analyses-To test for significant differences in weather covariates between years, I used ANOVA for T_a and a Wilcoxon rank sum test for the wind speed. To test for differences in proportion of nights with bats present, I used a Kruskal–Wallis test and tested species, year, and region separately. If I found significant differences among regions in the Kruskal-Wallis test, I used a Dunn's test to determine which regions were different from one another and I adjusted the p-values for multiple comparisons using the Holm method (Holm 1979).

I used nightly presence/no detection (p/n) as a response variable to assess probability of bat presence with logistic regression models. I first modeled each species individually with T_a as an explanatory variable. I included nightly wind speed as a covariate as well as an interaction term between T_a and wind speed (as in Klüg-Baerwald et al. (2016). I also included year as a covariate. Thus, I compared 6 a priori models for each species: p/n ~ T_a, p/n ~ T_a + wind, p/n ~ T_a + year, p/n ~ T_a + wind + year, p/n ~ T_a + wind + $T_a \cdot$ wind, p/n ~ T_a + wind + $T_a \cdot$ wind + year. I ranked models using the Akaike information criterion (AIC) value (Burnham and Anderson 2003). I report the top three models for each species.

For each species, the top model based on AIC was used to calculate the T_{LT}. Specifically, I defined low-temperature thresholds (T_{LT}) as the temperature at which the line of best fit reaches the 25% probability of presence. I chose 25% as the threshold value as it is high enough to allow for the assumption that the observed activity is related to temperature and not from factors such as disturbance (Kunz and Fenton 2003). To assess the uncertainty in T_{LT} estimates, I bootstrapped the best fitting model for each species using 10,000 iterations to predict T_{LT}. I reported the mean of the 10,000 predictions as well as the 95% confidence interval of the mean. I used the confidence intervals to compare T_{LT} between the two species in each group (migratory and cave hibernators). If the 95% confidence interval overlapped, I considered those species to have a similar T_{LT}. I also reported bootstrapped estimates of T_{LT} at the 10% probability of presence level to ensure the observed differences in T_{LT} are not unique to the 25% level, and to if relationships changed with lower temperatures. I use T_{LT} to represent the 25% level, and $T_{LT\,10}$ to represent the 10% level.

To determine if species respond to temperature differently, I modeled all species together with a categorical "species" term as an explanatory variable. Based on the best individual species models (as above), the model for species comparison was p/n ~ T_a + species + species $\cdot$ T_a +

species ·wind. I dropped the year variable as relative species relationships were consistent between years (e.g. both years silver-haired bats were higher than big brown bats) in order to simplify reporting. I used a Tukey honest significant difference test to compare mean nightly bat presence between species. With the multi-species model, I predicted and plotted the entire range of observed probabilities of activity in relation to temperature to evaluate differences in species relationships across the temperatures observed in this study.

All statistical tests were run in program R version 3.4.1 (R Development Core Team 2018). I used the R package MuMIn (Bartoń 2014) to compare models and package ggplot2 (Wickham 2016) for data visualization.

CHAPTER III

RESULTS

I recorded on 2,250 detector nights total over the winters of 2017 and 2018. On 287 nights, data were not collected due to an equipment malfunction, operator error, or battery failure. Thus, I successfully recorded on 1,963 detector nights total over the winters of 2017 (816 nights) and 2018 (1147 nights). There was a large range of T_a across all the sites with mean T_a ranging from -0.1 °C at site 2 to 11.6 °C at site 15 (Table 1). At my study sites, winter 2017 was significantly cooler than winter 2018 ($F_{[1,1900]}= 24.53$, p<0.001) with a mean winter temperature of 7.27 ± 5.89 °C and 8.88± 7.69 °C, respectively (Figure 2A). At my study sites, winter 2018 had lower wind speed than winter 2017 ($W = 5623200$, p<0.001), with a mean winter wind speed of 11.2 ± 9.0 km/h and 12.1 ± 9.0 km/h, respectively (Figure 2B).

The species with the greatest number of winter present nights was the silver-haired bat with 611 present nights. This was followed by the big brown bat with 242 present nights, the tricolored bat with 155 present nights, and the hoary bat with 111 present nights. The lowest nightly temperature where a bat was present differed across all 4 species and was not consistent across region (Table 2).

There was considerable variation among species and sites in the proportion of nights with bat presence. The average proportion of nights with at least one bat present by species was: tricolored bat (mean±SD) 8.04% ± 9.06%, big brown bat 12.25% ± 12.44%, silver-haired bat 31.28% ± 17.01%, and hoary bat 5.73% ± 6.84%. Sites that had the highest proportion of bat presence were not always the warmest. The highest proportion of nights with tricolored bat

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presence was at site 13 in 2017 and site 14 in 2018 (Figure 3). The highest proportion of nights

with big brown bat presence was at site 13 in both 2017 and 2018 (Figure 3). The highes

proportion of nights with silver-haired bat presence was at site 4 in both 2017 and 2018 (Figure

3). In both 2017 and 2018, site 13 had the highest proportion of nights with hoary bat presence

(Figure 3). Many of the colder sites had no nights of hoary bat presence (Figure 3). In 2017, there

was no difference in the proportion of nights with tricolored bat presence among regions (χ^2

=3.75, df=2, p=0.153; Figure 4). In 2018 there was a significant difference in proportion of nights

with tricolored bat presence (χ^2=7.39, df=2, p=0.025) with more tricolored bats present in the

Coastal Plain than the Mountain region (p=0.037; Table 3). There was no significant difference in

probability of big brown bat or silver-haired bat presence among regions in either 2017 (big

brown bat χ^2=0.98, df=2, p=0.612; silver-haired bat χ^2=0.58, df=2, p=0.750) or 2018 (big brown

bat χ^2=1.28, df=2, p=0.526; silver-haired bat χ^2=0.75, , df=2 p=0.687; Figure 4). There was no

difference in the proportion of night with hoary bat presence among regions 2017 (χ^2=2.35, df=2,

p=0.309; Figure 4). In 2018, regions differed significantly in proportion of nights with hoary bat

presence (χ^2=9.09, df=2, p=0.011; Figure 4) with more hoary bats present in the Coastal Plain

than the Mountain region (p=0.017), and less in the Mountain than the Piedmont region

(p=0.035;Table 3).

　　　Tricolored bats, silver-haired bats, and hoary bats had year in the top model to explain

nightly probability of presence (Table 4). Silver-haired bats and big brown bats had wind speed in

the top model to explain nightly probability of presence (Table 4). For all species, T_a was

positively related to nightly probability of presence (all p<0.001, Table 5). Nightly probability of

presence in silver-haired bats and big brown bats was negatively related to wind speed (Table 5).

Tricolored bats, silver-haired bats, and hoary bats had a lower probability of presence in 2018

when compared to 2017 (Table 5).

Comparing all species' mean nightly probability of presence using Tukey honest significant difference test, every possible comparison between bats was significantly different (p<0.001; Table 6, Figure 5). Migratory species differed in their mean nightly probability of presence (p<0.001; Table 6). The mean probability of silver-haired bats being present was 0.25 higher than hoary bats (Table 6). Cave hibernating species also had significantly different mean nightly probability of presence (p<0.001; Table 6). The mean probability of big brown bats being present was 0.04 higher than tricolored bats (Table 6).

Migratory bats were not active at lower T_{LT} than cave hibernating bats. Silver-haired bats had the lowest T_{LT} of the species examined at 7.27 °C $T_{a,}$ (lower CI=6.20, upper CI =8.20; Figure 6). This was followed by big brown bats at 16.92°C T_a (lower CI=15.85, upper CI =17.85), tricolored bats 17.76°C T_a (lower CI=15.85, upper CI =19.85), and hoary bats 18.79°C T_a (lower CI=16.85, upper CI =20.85) (Figure 6). Between the migratory species there was no overlap in the 95% confidence intervals for T_{LT}, suggesting a significant difference in the T_{LT} between these species. There was overlap in the 95% confidence intervals of cave hibernating species at the 25% level. However, at lower temperatures, and nightly probabilities of presence, there was a significant difference in these two species. At the 10% probability of nightly presence, big brown bats $T_{LT\,10}$ was 9.65 °C T_a (lower CI=8.85, upper CI =10.85) and tricolored bats $T_{LT\,10}$ was 12.53 °C T_a (lower CI=10.85, upper CI = 13.85) (Figure 6).

CHAPTER IV

DISCUSSION

I predicted that larger bodied bat species in each winter strategy group (migrants and cave hibernators) would have lower T_{LT} than smaller bodied bat species, and that migratory species would have a lower T_{LT} than cave hibernating species. I found support for the influence of body mass for cave hibernating species but not for migratory species. I found evidence that at low temperatures body mass is important in predicting probability of presence in cave hibernating species, and as the temperature warms that effect weakens. Rather than the expected relationship of smaller bodied bats active at warmer temperatures compared with larger bodied bats active, I found the largest bodied bat, the hoary bat, to have the highest T_{LT}. I also found evidence that the 25% level of T_{LT} may be too high to detect differences in cold weather adaptations in cave hibernators. Below the 25% level there were differences in all species, above that level there was overlap in the cave hibernators. I recommend future studies use the $T_{LT\,10}$ level to investigate other bat migratory and hibernating species.

I predicted that migratory bats would be active at lower temperatures than cave hibernating bats and that prediction was supported in silver-haired but not hoary bats. Migratory silver-haired bats were present at cooler temperatures than all the other species examined. However, migratory hoary bats required the warmest temperatures to reach their T_{LT}. In the winter, silver-haired bats were recorded on more nights and at colder temperatures than hoary bats. Hoary bats were absent from the coolest sites in the winter, whereas activity from silver-haired bats was relatively common across sites, suggesting silver-haired bats are adapted to

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overwintering at cooler temperatures than hoary bats. This result suggests that factors other than

body mass influence migratory species' ability to be active at lower temperatures.

There are several reasons that silver-haired bats may have been active at lower

temperatures than hoary bats. Pelt insulative capacity or other physiological adaptations, beyond

body size, could allow silver-haired bats to remain active at cooler temperatures than hoary bats

(Kunz and Fenton 2003). Tree roosting bats could reduce the metabolic cost of raising body

temperatures by emerging from torpor on warmer nights, where the ambient temperatures

passively rewarm their cores (Halsall et al. 2012; Currie et al. 2014). Silver-haired bats are a tree

roosting bat that can move into caves or down into crevices in cooler temperatures (Perry et al.

2010). By employing this plastic roosting strategy, silver-haired bats might be able to overwinter

in a larger temperature range than hoary bats. Future work in silver-haired bats should investigate

i.) pelt effectiveness ii.) behavioral adaptations (e.g. roosting locations), and iii.) fat stores.

There are other examples of silver-haired bats being active at lower temperatures than

hoary bats. Dunbar (2007) found that 5 °C was energetically optimal for silver-haired bats

hibernating in Missouri, and Hickey and Fenton (1996) found that when minimum ambient

temperatures went below 13°C female hoary bats went into torpor. These values are both below

the 7.27°C T_{LT} and 18.79 °C T_{LT} I recorded for silver-haired bats and hoary bats, respectively.

Interestingly, Hickey and Fenton (1996) found that when minimum temperatures reached 21.3 °C

all of their hoary bats were active, which is close to our 18.79 °C T_{LT} . However, I measured

temperature at 9 pm, which for our area, was around 4 °C above the minimum temperature for

that night. Thus, the Hickey and Fenton (1996) minimum temperature of 16 °C, where the

majority of their hoary bats were active, is likely close to what I report here. Cryan (2003) found

a similar pattern using museum records, where during the winter months the higher densities of

hoary bats were south of North Carolina, and higher densities of silver-haired bats were in North

Carolina and further north. There are records of silver-haired bats overwintering as far north as ~45°N in latitude (Kurta et al. 2018). Fraser et al. (2017) similarly found silver-haired bats active in the winter at high latitudes. The specific mechanisms that allow silver-haired bats to be active at cooler temperatures remains unknown, however our data suggests that mean body size is not the main factor limiting activity of these two migratory species.

In contrast to my results for migratory species, I found support for the influence of body size on $T_{LT\,10}$ for cave hibernating species. In the winter, big brown bats were more likely to be out at colder temperatures than tricolored bats. Reynolds et al. (2017) also found that smaller bodied eastern-small footed (*Myotis leibii*) bat activity was very low below 10 °C, were the larger bodied big brown bats activity was low below 3 °C. Klüg-Baerwald et al. (2016) also found that big brown bats were more likely to be active at cooler temperatures than smaller bodied *Myotis* species.

In addition to body mass there are several factors that could influence big brown bats' ability to be present on the landscape at lower temperatures than tricolored bats. One potential contributing factor is big brown bats have higher winter pelt insulative capacities (0.293±0.002 °C/kcal/hr/m2) than winter pelts of *Myotis lucifugus* (0.280±0.002 °C/kcal/hr/m2), or *Myotis septentrionalis* (0.281±0.004 °C/kcal/hr/m2)(Shump and Shump 1980). If there is a relationship with hibernacula location and pelt insulative capacity, we should see similar low temperature thresholds between bats that occupy similar hibernacula. Eastern small-footed bats use similar hibernacula to big brown bats (Twente Jr 1955; Hitchcock et al. 1984; Kurta and Baker 1990; Best and Jennings 1997) and larger bodied big brown bats were still active at lower temperatures than eastern small-footed bats (Reynolds et al. 2017), suggesting that body size is a contributing factor in big brown bats' lower $T_{LT\,10}$ than tricolored bats. Another potential factor that could contribute to big brown bats lower $T_{LT\,10}$ is that they hibernate nearer to cave mouths than

tricolored bats, and may take advantage of warm nights to passively rewarm (Fujita and Kunz 1984; Kurta and Baker 1990; Halsall et al. 2012). It is likely that some combination of pelt insulation, surface area to volume ratios, and hibernacula preference, that allows big brown bats to be out at lower temperatures than tricolored bats.

I used bat presence instead of bat activity as my response variable. I did this because presence/no detection measurements are logistically feasible, allows for more confidence in identifications as it relies on only the highest quality calls for any given night, and does not require any assumptions about sampling the same bat more than once (as in activity measures). It would also be interesting to analyze the T_{LT} with respect to winter activity as opposed to presence/no detection but that is beyond the scope of this current study. Importantly, although I use the use the term "presence" to mean that bats are active on the landscape, for any given night that I did not record a bat, they may still be present at the sampling site on any given sampling night, but hibernating or in torpor. If this was the case, I would have recorded the species as "no detection".

There are implication of my results for federal bat survey guidelines. Many federal survey guidelines have a summer minimum temperature for establishing absences of 10°C (U.S. Fish and Wildlife Service 2018). Our results suggest these recommendations may be too low for some species in winter. Only silver-haired bats had reached a 25% probability of presence by 10°C. At 10°C tricolored bats, hoary bats and big brown bats all had near a 10 % probability of nightly presence, indicating there could be bats present in a winter survey area, but not active, and could therefore be falsely recorded as an absence.

Winter has the highest mortality of any season for bats in North America (O'Shea et al. 2016). Most studies conducted in winter have noted temperatures below which there is little bat activity (Venables 1943; Cross 1965; Jones et al. 1965; Funakoshi and Uchida 1978; Izor 1979;

O'Donnell 2000; Pierson et al. 2001; Lausen and Barclay 2006; Johnson et al. 2011, 2017; Wolbert et al. 2014; Bernard and McCracken 2017; Reynolds et al. 2017; Kurta et al. 2018). However, none have tested explicitly temperature thresholds for activity over a wide study area (but see Reynolds et al. (2017)). I found both migratory and cave hibernating bats had different low temperature thresholds and reported those temperature thresholds from a large range of climates. I found that within cave hibernators there was support for body size being important for winter $T_{LT\,10}$. However, there was no support for body mass being important in predicting T_{LT} within migratory bat species. Understanding the temperatures that allow bats to be active on the winter landscape will help us to i) better understand overwintering preferences in migratory species, ii) predict the temperatures that drive migratory bats to other areas, iii) predict the temperatures that force hibernating bats into hibernacula and improve our understanding of WNS, and iv) improve mechanistic models of the effects of climate change on bat communities and distributions. Future work should investigate if silver-haired bats are outliers or if there is a more complex driver for low temperature thresholds for winter activity in bats. There is evidence that bats adapt their metabolic rates to their local climate (Dunbar and Brigham 2010) and future studies could test how regional climate affects low temperature thresholds across a range of species.

My results have conservation implications. The two migratory species in my study have different low temperature thresholds for probability of nightly presence in the winter. Across North America, hoary bats experience twice the mortality of silver-haired bats at wind facilities (Thompson et al. 2017). Hoary bats apparent preference for warmer overwintering grounds implies that they are exposed to more wind energy collision risk than silver-haired bats in North Carolina. In North Carolina the wind energy development is in the warmer Coastal Plain region, where more nights had hoary bat presence relative to the rest of the state. Big brown bats cold

hardiness relative to tricolored bats could be one reason they have been less effected by WNS (Frick et al. 2016). Along with increased torpor length when infected (Moore et al. 2018), and cooler hibernacula than is ideal for the *Pseudogymnoascus destructans* (Pd) fungus (Verant et al. 2012), activity at lower temperatures may allow big brown bats to better combat WNS infection as they could potentially forage and replenish critical fat stores. The mean low-temperature threshold for lepidopteran flight is 7.4 °C (Taylor 1963; Alma 1970), 11.5 °C for Diptera (Mellanby 1939; Taylor 1963), and 17.3 °C for Hemiptera (Mellanby 1939). Wolbert et al. (2014) found insect activity began increasing at 8 °C in Pennsylvania, USA. While I did not monitor insects, the T_{LT} temperatures for bats that I describe are all near reported insect flight temperature thresholds. If insects are active there is the possibility to offset energetic costs in winter by occasional feeding at the temperatures I observed. There are several examples of winter foraging at similar latitudes; coastal North Carolina (~36 °N) (Avery 1985; Grider et al. 2016), eastern Tennessee (~36 °N) (Bernard and McCracken 2017); and at higher latitudes in Missouri (~41°N)(Dunbar et al. 2007). Therefore, for all 4 species studied herein, the potential for winter feeding in North Carolina is high and should be considered as part of conservation management plans.

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APPENDIX A

FIGURES/TABLES

Table 1. Site Details and Characteristics for the Study. 30 yr mean temperature indicates the (1970-2000) mean winter temperature extracted from BIOCLIM BIO11 variable (mean coldest quarter). Observed mean represents the mean nightly T_a for the entire sampled period for that site. Station indicates the station identification code from the weather underground network. Distance column represents the straight-line distance from the sampled area to the weather station.

Name	Region	Site	Elevation (ft)	30 Yr Mean (°C)	Year	Observed mean T_a°C	Weather Station	Distance (km)
Banner Elk	Mountain	1	3668	0.31	2018	0.09	Leese-McRae KNCBANNE9	2.70
Hare	Mountain	2	2590	1.34	2018	-0.10	High Country KNCENNIC2	5.43
Highlands	Mountain	3	3856	1.97	2018	2.89	VZ top KNCHIGHL20	3.67
Pisgah Game Land	Mountain	4	1319	3.10	2017 & 2018	5.93	Patterson KNCLENOI12	6.65
Hanging Rock State Park	Piedmont	5	1659	3.12	2017 & 2018	5.04	Copie Farm KNCKING10	11.15
Swannanoa River	Mountain	6	2046	3.32	2017 & 2018	7.45	Asheville KTDF	20.25
Cherokee	Mountain	7	2082	3.34	2017	5.27	Smokemont MTOSN7	5.26
Hyco Game Land	Piedmont	8	453	4.28	2017 & 2018	7.63	Person Co. KTDF	26.00
Knightdale	Piedmont	9	242	5.30	2018	9.11	Triangle North KLHZ	32.49
Chowan Swamp Game Land	Coast	10	1	5.52	2017 & 2018	8.32	Tri-County KASJ	29.50
Cowan's Ford	Piedmont	11	663	5.55	2017 & 2018	8.57	Concord KJQF	29.61
Uwharrie Game Land	Piedmont	12	644	5.80	2017 & 2018	10.39	Stanley Co. KVUJ	23.87
Lumber River State Park	Coast	13	75	7.48	2017 & 2018	10.62	Lumberton KLBT	30.15
Croatan Game Land	Coast	14	9	7.77	2017 & 2018	10.37	New Bern KEWN	7.99
Wilmington	Coast	15	10	8.77	2017 & 2018	11.58	Wilmington KILN	11.67

Table 2. Lowest Nightly Temperature (°C) When Bat Presence was Recorded Across Regions. Species abbreviations are as follows: *Perimyotis subflavus* (PESU), *Lasionycteris noctivagans* (LANO), *Eptesicus fuscus* (EPFU), *Lasiurus cinereus*, (LACI). Lowest nightly temperature across regions is in bold.

Region	EPFU	LACI	LANO	PESU
Mountain	-0.95	2.11	**-7.09**	-0.09
Piedmont	**-5.00**	6.55	-2.03	-2.03
Coast	-2.20	**-0.60**	-3.66	**-3.90**

Table 3. Kruskal-Wallis Test Comparing Proportion of Nights with Bat Presence by Region and Post-Hoc Dunn's Test. If Kruskal-Wallis test for differences was non-significant, then only that is reported. If Kruskal-wallis test indicated significant differences in proportion of nights with presence, then the Dunn's test is reported. Z scores and adjusted p values (P.Adj) are reported for the Dunn's test (indicated in the comparison column with regions). χ^2 and p-values are reported for the Kruskal-Wallis test, also indicated in the comparison column. All tests had 2 degrees of freedom. Adjusted p-values were adjusted using the Holm method. Significant values are in bold. Species abbreviations are as follows: *Perimyotis subflavus* (PESU), *Lasionycteris noctivagans* (LANO), *Eptesicus fuscus* (EPFU), *Lasiurus cinereus*, (LACI).

Species	Year	Comparison	z/χ^2	*P.Adj/p*
PESU	2017	Kruskil-Wallis	3.75	0.153
	2018	Coast - Mountain	2.45	**0.037**
	2018	Coast - Piedmont	0.45	0.617
	2018	Mountain - Piedmont	-2.12	0.068
LANO	2017	Kruskil-Wallis	0.58	0.750
	2018	Kruskil-Wallis	0.75	0.687
EPFU	2017	Kruskil-Wallis	0.98	0.612
	2018	Kruskil-Wallis	1.28	0.526
LACI	2017	Kruskil-Wallis	2.35	0.309
	2018	Coast - Mountain	2.76	**0.017**
	2018	Coast - Piedmont	0.52	0.601
	2018	Mountain - Piedmont	-2.37	**0.035**

Table 4. Top Three Models Used to Predict the Nightly Probability of Presence in Relation to Ambient Temperature (T_a), Wind Speed (wind) and a Year Term. Models are ranked according to AIC scores, with the lowest score indicating the top ranked model. ΔAIC is the difference in AIC scores between the model in that row and the top-ranked model. AIC model weight (W_i) is the probability of being the best model of the 6 a priori models examined. Species abbreviations are as follows: *Perimyotis subflavus* (PESU), *Lasionycteris noctivagans* (LANO), *Eptesicus fuscus* (EPFU), *Lasiurus cinereus*, (LACI).

Species	Top models	AIC	ΔAIC	W_i
PESU	T_a + *Year*	858.6	0.00	0.39
	T_a	859.7	1.06	0.23
	T_a + *Wind* + *Year*	860.5	1.91	0.15
LANO	T_a + *Wind* + *Year*	1976.3	0.00	0.69
	T_a + *Wind* + T_a × *Wind* + *Year*	1978.1	1.84	0.27
	T_a + *Wind*	1982.7	6.36	0.03
EPFU	T_a + *Wind*	1249.5	0.00	0.42
	T_a + *Wind* + T_a × *Wind* + *Year*	1250.6	1.06	0.25
	T_a + *Wind* + *Year*	1251.4	1.86	0.17
LACI	T_a + *Year*	678.5	0.00	0.55
	T_a + *Wind* + *Year*	680.0	1.50	0.26
	T_a + *Wind* + T_a × *Wind* + *Year*	681.4	2.94	0.13

Table 5. Direction of Relationships and Significance of the Model Variables in the Species-Specific Top-Ranked Logistic Regression Models Based on AIC. Ambient temperature (T_a), wind speed (wind) and year were the terms examined. Species abbreviations are as follows: *Perimyotis subflavus* (PESU), *Lasionycteris noctivagans* (LANO), *Eptesicus fuscus* (EPFU), *Lasiurus cinereus*, (LACI).

Species	Model Term	Coefficient	SE	Z	P
PESU	T_a	0.21	0.02	12.15	<0.001
	Year (2018)	-0.35	0.20	-1.76	0.079
	T_a	0.17	0.01	7.28	<0.001
LANO	Wind	-0.04	0.01	-4.80	<0.001
	Year (2018)	-0.33	0.11	-2.89	0.004
	T_a	0.15	0.17	11.57	<0.001
EPFU	Wind	-0.03	0.01	-2.51	0.012
	T_a	0.22	0.02	10.75	<0.001
LACI	Year (2018)	-0.64	0.24	-2.73	0.006

Table 6. Tukey Honest Significant Difference Test for Difference in Mean Nightly Probability of Presence. Lower and upper limit represent the 95% confidence interval of the difference coefficient. Species abbreviations are as follows: *Perimyotis subflavus* (PESU), *Lasionycteris noctivagans* (LANO), *Eptesicus fuscus* (EPFU), *Lasiurus cinereus*, (LACI).

Comparison	Difference	Lower limit	Upper limit	p
LANO-PESU	0.23	0.21	0.26	<0.001
EPFU-PESU	0.04	0.02	0.07	<0.001
LACI-PESU	-0.02	-0.04	0.01	0.103
EPFU-LANO	-0.19	-0.22	-0.16	<0.001
LACI-LANO	-0.25	-0.28	-0.23	<0.001
LACI-EPFU	-0.06	-0.09	-0.04	<0.001
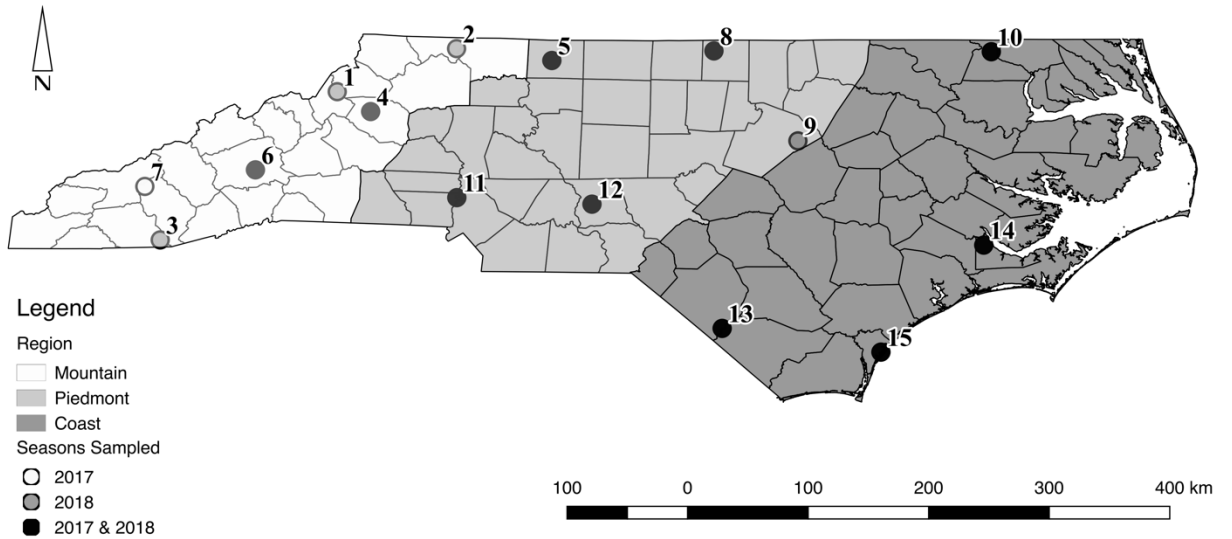
Figure 1. Map of Study Location, Sites, and Regions in North Carolina, USA. Hollow circles sampled in 2016-2017 (2017), grey circles sampled in winter 2017-2018 (2018), black circles sampled both years (2017 & 2018). Mountain region (hollow), Piedmont region (light grey) and Coastal Plain (dark grey). Sites are numbered from the coldest 30 yr (1970-2000) mean winter temperature to the warmest winter temperature from BIOCLIM, BIO11 variable (mean coldest quarter).
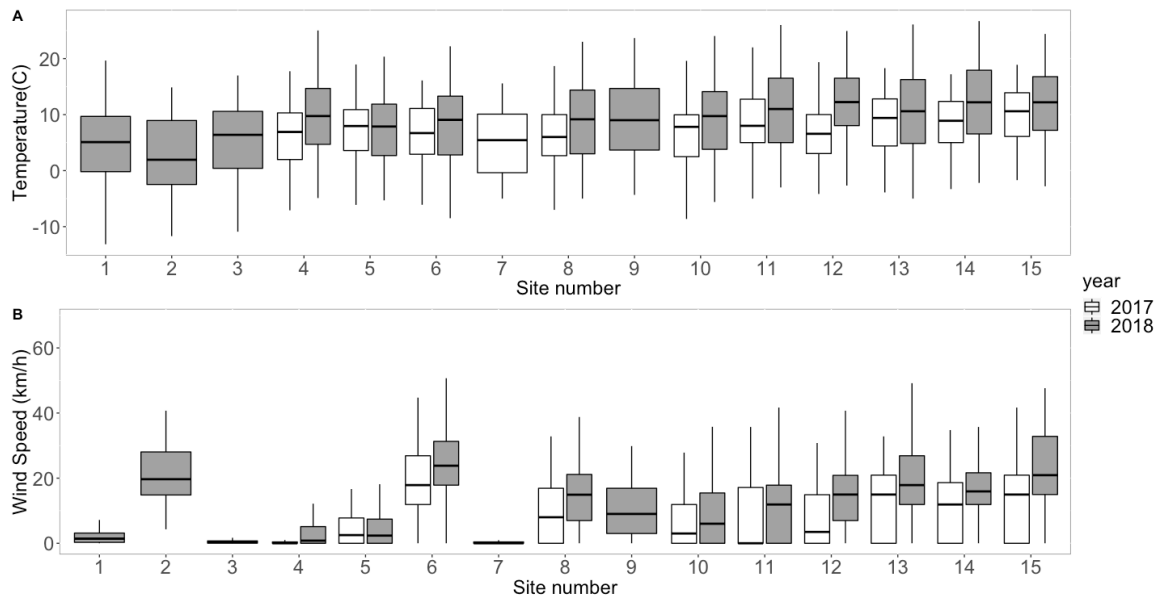
Figure 2. A. Mean Nightly Ambient Temperature of the 15 Study Locations for Winter 2017 and 2018 at Each Site. B. Mean Nightly Wind Speed of the 15 Study Locations. Sites are numbered from the lowest 30 yr (1970-2000) mean winter temperature to the highest from BIOCLIM, BIO11 variable (mean coldest quarter).
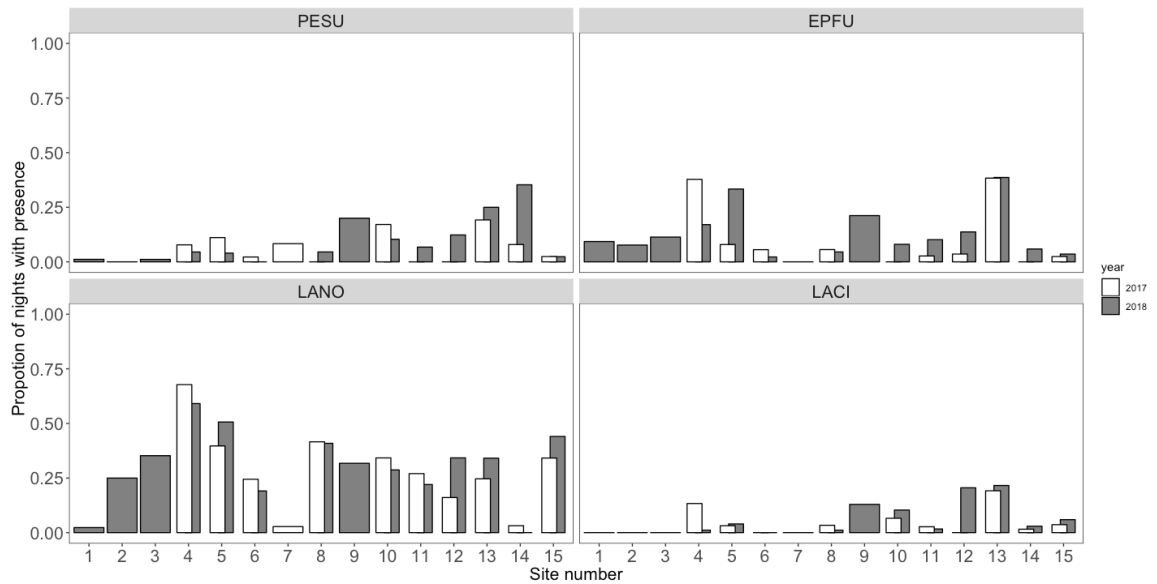
Figure 3. Proportions of Total Nights with Presence/Year at Each Site. Site numbers are ordered from coolest to warmest 30 year (1970-2010) mean winter temperature of each site BIOCLIM, BIO11 variable (mean coldest quarter). See table 1 for temperatures. Hollow bars represent winter 2016-2017 (2017), dark bars represent winter 2017-2018 (2018; grey).
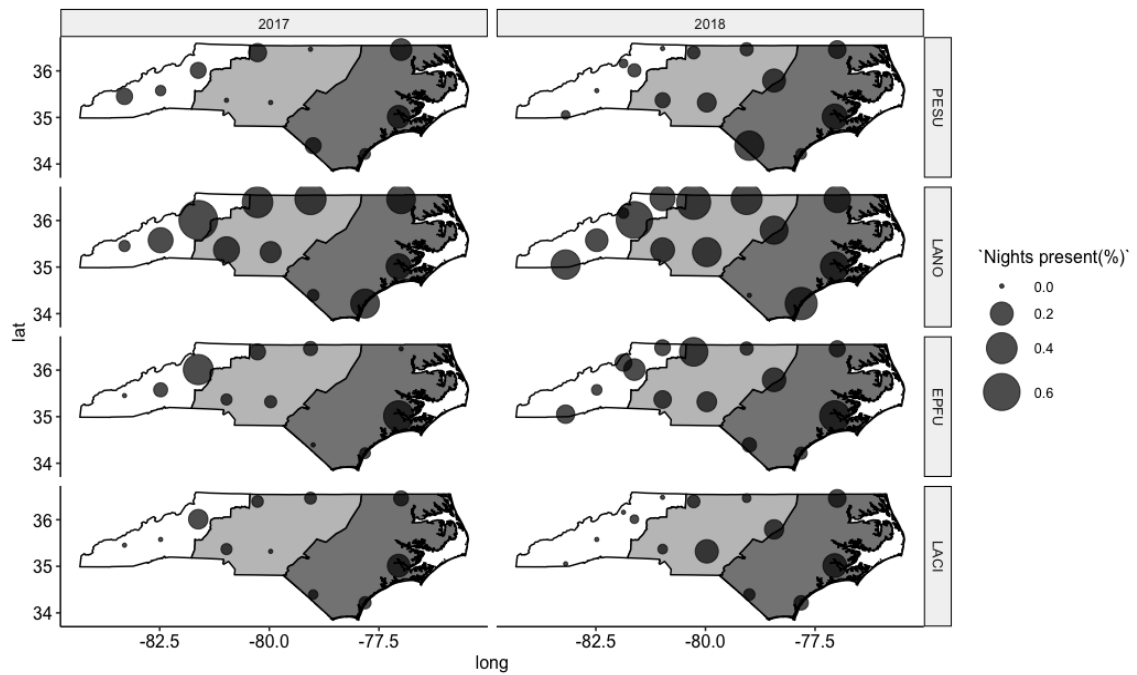
Figure 4. Map of Proportion of Total Nights with Presence at Each Site in Winters of 2017 and 2018. Larger diameter circles represent more nights of presence at that site. Background color represents region with Mountain (hollow), Piedmont (light grey) and Coast (dark grey). See figure 1 for site numbers. Species abbreviations are as follows: *Perimyotis subflavus* (PESU), *Lasionycteris noctivagans* (LANO), *Eptesicus fuscus* (EPFU), *Lasiurus cinereus*, (LACI).
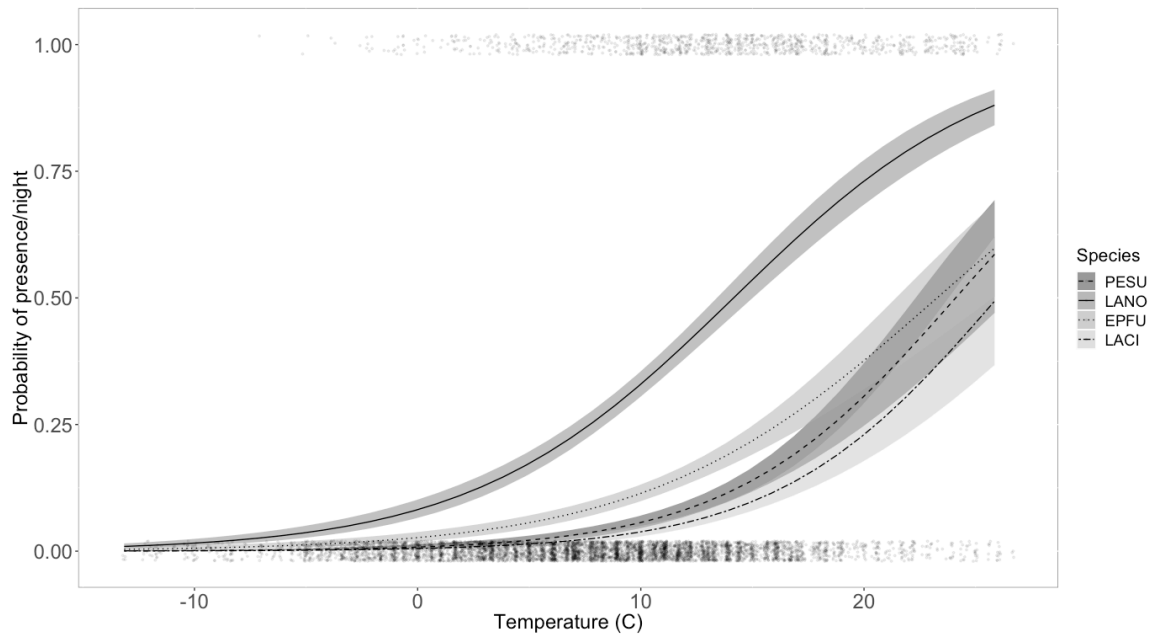
Figure 5. Plot of Nightly Probability of Presence in Relation to Ambient Temperature by Each Species Examined. Shaded areas represent the 95% confidence interval for each species. Each dot on the x-axis represents a bat presence (1)/non-detection (0) and the T_a. Legend is oriented from the lowest mean mass bat at top to the highest mean mass bat at bottom. Species abbreviations are as follows: *Perimyotis subflavus* (PESU), *Lasionycteris noctivagans* (LANO), *Eptesicus fuscus* (EPFU), *Lasiurus cinereus*, (LACI).
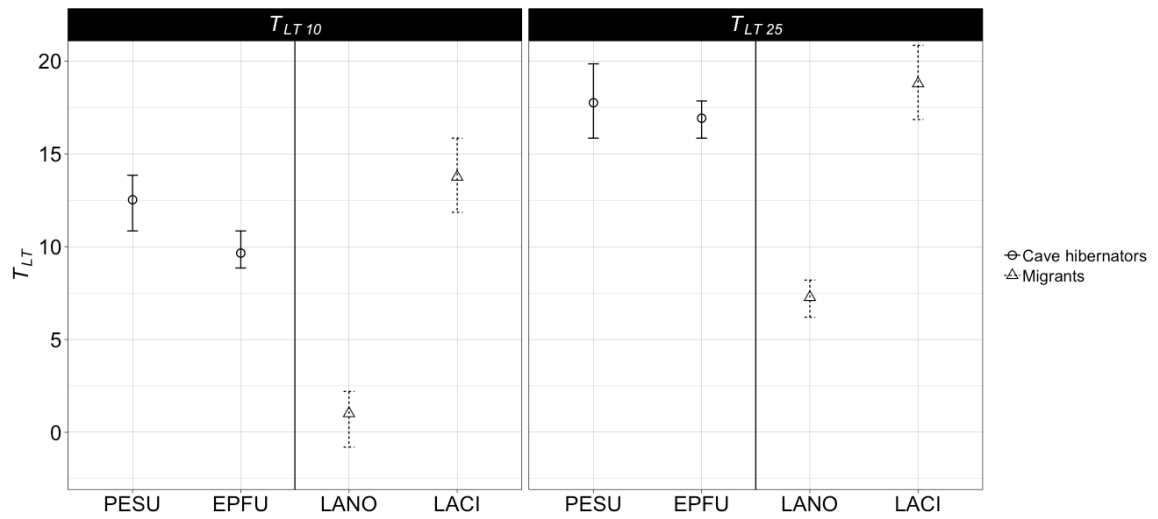
Figure 6. Low Temperature Thresholds (T_{LT}) at the 10% ($T_{LT\,10}$) and 25% ($T_{LT\,25}$) Probability of Nightly Presence Levels by Species and Cold Weather Strategy. Species are organized from lowest mass to highest mass within cave hibernators and migrants, left to right. Vertical bars represent the 95% confidence interval from the 10,000 bootstrapped predictions. Species abbreviations are as follows: *Perimyotis subflavus* (PESU), *Lasionycteris noctivagans* (LANO), *Eptesicus fuscus* (EPFU), *Lasiurus cinereus*, (LACI).