

SUMMER ROOST SITE SELECTION OF A DECLINING BAT SPECIES

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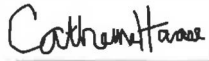
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Sarah Catherine Zirkle

04/18/2022

I dedicate this research to my grandparents: Ron, Trudy, and Omi.

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ABSTRACT

The tri-colored bat (*Perimyotis subflavus*) is a hibernating North American bat species that uses forested landscapes during summer months; however, information on the summer habitat requirements is limited. Summer habitats are critical to population persistence as they support multiple life history stages, including maternity colonies, nursery sites, and foraging locations. As tri-colored bats are highly susceptible to white-nose syndrome, a devastating disease that increases energy expenditure over hibernation, determining the resources that are important for building pre-hibernation fat stores is crucial to their population persistence. My objective was to quantify the characteristics of roost sites selected by tri-colored bats during the summer. I captured, tagged, and tracked 15 bats using radio-telemetry to 55 roost locations. At each roost, I recorded roost habitat characteristics and other forest descriptions within a 0.1 ha circular plot surrounding the roost tree. I repeated these measurements for three random trees per roost tree to serve as available habitat for selection. I used a suite of mixed conditional logistic regression models to test five competing hypotheses describing factors known to influence roost-site selection for various bat species. The top model demonstrated that roost selection was influenced by roost tree height, which may be linked to microclimatic factors. There is a critical information gap for the ongoing recovery of tri-colored bats; better understanding of summer habitat and proper forest management implications, as well as information on scale-specific habitat selection, is needed to better understand tri-colored bat management needs.

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CHAPTER ONE: LITERATURE REVIEW

1 Introduction

Habitat selection is an interactive relationship between species and landscape characteristics that allows for reproduction and survival (Rosenzweig 1981, 1991). Morris (1989) documents that the usage and selection of habitat is dependent upon morphological, physiological, and behavioral adaptations of a species. Predation risk (Viejou et al. 2018), mate availability and breeding areas (Cayuela et al. 2017), geographic and climatic constraints (Copeland et al. 2010), and site fidelity based on reproductive success (Farrell et al. 2012) are likely secondary factors influencing habitat selection. Thus, the term ‘habitat’ has taken on different definitions throughout the years, the most universal definition referring to a collection of environmental features and resources necessary for survival (Fletcher and Fortin 2018).

2 Theory of Habitat Selection

One of the original theories of habitat selection arose from Grinnell (1917) with his discussion of survivorship probability of dispersal based on ecological factors. Thorpe (1945) later went on to further expand the concept and define habitat imprinting, a behavior of selecting and sustaining a ‘home.’ Over time, there have been discrepancies among ecological pioneers on how to define habitat selection. The theory of habitat selection was further explored through the 1970-1980’s by Fretwell and Lucas (1969), Rosenzweig (1974), and Johnson (1980). Rosenzweig (1974) defined habitat selection as a choice made by an individual. This early theory of habitat selection allowed for developments of models that incorporated habitat characteristics and species abundance in a localized area (Rosenzweig 1991).

Early habitat models were created under the assumption that habitat selection is not free of costs but can be driven by density-dependence (Pimm and Rosenzweig 1981). Other models

developed under Fretwell and Lucas (1969) described habitat selection under the ideal free distribution (IFD), which assumes the fitness of an individual is a direct response to the variation in habitat quality and the population density within (Fletcher and Fortin 2018). This model suggests that high quality habitats will be readily selected for and chosen more often (Fletcher and Fortin 2018). The IFD further suggests that when the highest quality habitat is not available, the next ideal habitat will be selected. Through IFD, it is assumed that individuals gain information about resources based on habitat density and abundance, but these factors have recently been emphasized as poor indicators of habitat quality (Fletcher and Fortin 2018). Poor knowledge inferred from habitat use can mislead individuals into ecological traps. Further theoretical models as described by Morris et al. (2004) investigate how misinformation influences fitness through habitat selection.

3 Selection and Scale

Though commonly used in conservation and management, single-scale habitat selection models over-simplify the selective process and forgo critical details linked with different orders of selection needed in recovery plans (Razgour et al. 2011). Habitat selection is recognized as a hierarchical scale-sensitive process that is dependent upon environmental conditions (Mayor et al. 2009). Johnson (1980) described habitat selection through four scales of selection: geographic area (first order), home range (second order), land usage of habitat components (third order), and selection of resources (fourth order). Each scale is selected by choice of allotted resources and are based on habitat attributes that may contribute to an organism's fitness such as temperature, available forage, reproductive potential, prey abundance, and shelter. Multi-scale habitat models are the best representative of an organism's true interaction with their environment, as cross-scale analyses comprise the broad and specific limiting factors (Mayor et al. 2009).

4 Bat Habitat Selection

Chiroptera is the second most diverse mammalian order and occurs on every continent except for Antarctica. Bats have evolved adaptations allowing them to specialize in a variety of habitats. Bats have been documented to occupy a large range of habitat types in various areas worldwide ranging from dry regions in Madagascar (Goodman et al. 2005), temperate forests in North America (Cryan 2003), montane landscapes in the Swiss Alps (Ashrafi et al. 2011), and rainforests in New Zealand (O'Donnell 2000).

Bats exhibit extreme plasticity in their habitat selection as they require various resources depending on life cycle stage and activity. Activities vary by hour and throughout the year, such as roosting, foraging, breeding, reproducing, torpor, and hibernating; these activities require a broad range of suitable habitat to be readily available. Regardless of the activity, bats will select habitats that improve their reproductive fitness and survival chances (Nkrumah et al. 2016).

Bats will readily select roosts with an intact social structure (Kerth and Reckardt 2003). Forest-roosting female bats form maternity colonies in the summer to birth and raise young. To combat energetic loss during reproduction, bats form social groups that allow energy expenditure to be minimized and decrease the cost of thermoregulation (Johnson et al. 2019). Specifically, reproductive females will select roosts based on temperature to aid in fetal development (Johnson et al. 2019). Males and non-reproductive females differ in their habitat selection during summer months because they have less extensive energetic requirements. During pregnancy, females will avoid torpor as it delays fetal development and milk production (Johnson et al. 2019), while males use torpor to conserve energy (Ancillotto et al. 2018).

Preferred summer roosting locations of more than half of North American bat species are commonly located within natural forest stands (Castleberry et al. 2020). Bats have also been

documented in other habitat types, such as caves (Smith et al. 2021), rock crevices (Chruszcz and Barclay 2002), tree cavities (Ruczyński and Bogdanowicz 2005), and tree canopy foliage (Perry et al. 2007). When available habitat is lacking or is of poor quality, some bat species may opt for secondary habitat within human-made structures, such as buildings and bridges. Habitat selection may be influenced by an area's ability to provide a place to rear young (Castleberry et al. 2020), offer protection from predators (Perry et al. 2007) and abiotic factors, such as temperature (Callahan et al. 1997, Perks and Goodenough 2020) and precipitation (Razgour et al. 2011).

Forest roosting locations are selected based on structural and climatic characteristics that provide desirable benefits (Castleberry et al. 2020). Forest characteristics such as vegetation density, stand volume, and stratification have been documented to directly influence bat activity and community composition (Silvis et al. 2016). Forest stands with lower basal areas and stem densities are more favorable for forest-dwelling bats due to the greater ability to navigate throughout corridors (Perry et al. 2007). Preferred roost tree attributes range between species but commonly are determined by diameter of breast height of the roosting tree (dbh), cavity availability, tree height, and canopy density (Grider et al. 2021). Larger tree diameters and trees that extend above the surrounding forest canopy allow bats to locate prior roost trees when returning from feeding bouts (Castleberry et al. 2020). Furthermore, taller trees also provide higher mobility as any vegetative clutter can be avoided when entering and leaving the roost. Taller trees with an open canopy also provide thermoregulatory benefits to bats as sunlight exposure is increased aiding in the maintenance of a high body temperature and reduction of energy expenditure (Bergeson et al. 2020). Trees in an advanced decay stage or dead (snags) are favorable as they provide structural safety from predators through peeling bark and cavities (Russo et al. 2017).

Insectivorous bats within temperate zones may also use caves and culverts as roosting habitat year-round or as a hibernaculum while overwintering. Caves can be split into three distinct groups: 1) warm caves during the summer that are used as maternity roosts, 2) winter hibernation caves, and 3) migratory caves used during swarming (Perry 2013, Zukal et al. 2016). Within caves, bats face environmental stressors that impact their survival including fluctuations in environmental conditions, disease, evaporative water loss, and predation (Newman et al. 2021). However, suitable caves offer long-term refuge and a microclimate that provides high humidity and stable temperatures that will protect against fluctuations in environmental conditions (Perry 2013).

Although cave systems may provide a stable temperature, climate conditions throughout the cave can be variable (Perry 2013). Specific habitat selection within caves can be dependent upon the individual but most North American bats require temperatures between 2 and 10°C for hibernation (Perry 2013). The low cave temperatures during hibernation are favorable as they facilitate the conservation of stored body fat resources, promote energy saving torpor, and influence metabolic rates and water balance (Ingersoll et al. 2010). In general, important structural characteristics for hibernaculum are size, airway flow, orientation, depth, and latitude. Briggler and Prather (2003) examined cave-dwelling bats in hibernaculum and found that caves with east-facing aspects were selected more regularly for thermal stability and held more bats. Depending on the orientation of caves, external temperatures can affect temperatures flowing into the cave system (Perry 2013).

Along with specific roost attributes, bats will commonly select roosting locations dependent on distances to nearest resources. With flight, bats have flexible access to scattered resources but still rely on proximity to resources (e.g., distance to road, distance to water,

distance to roost site) when selecting suitable habitats (Cryan 2003). Distance to resources from roost sites to forage locations ultimately depend upon forest composition for bat species. Roosting locations have been documented to occur a few dozen km away from foraging areas (Sparks et al. 2005, Rainho and Palmeirim 2011). Flight distance for feeding bouts is also dependent upon time of year and sex, specifically in the summer months when females are pregnant, lactating, or post-lactating (Henry et al. 2002). A consequence of traveling longer distances is extensive energetic loss which may impact reproductive success. To reduce commuting cost and energy constraints when foraging, bats will roost near bodies of water (Gonsalves et al. 2013). Forest vegetation limits flight ability (Castleberry et al. 2020), therefore, roost locations within reasonable distance to corridors that act as flight paths may be selected due to lower commuting costs. Foraging activity can also be reliant on water sources and riparian vegetation as rivers and streams provide channeled flight corridors with easier navigation and higher insect abundance (Brigham and Fenton 1991, Russo and Jones 2003, Hagen and Sabo 2011). Foraging decisions have been linked to the type of habitat and prey abundance (Nkrumah et al. 2016). While prey might be available, vegetation clutter within forest stands can reduce mobility and prohibit the reach of prey (Gonsalves et al. 2013). This implies that landscape resources are more important than roost tree resources in roost-site selection.

5 Causes of Bat Population Declines

North American bat species have been in decline for over a decade due to habitat loss (Foley et al. 2005, Maclean and Wilson 2011, Russo and Ancillotto 2015, Ripple et al. 2016), wind energy (Arnett and Baerwald 2013), and diseases (Frick et al. 2010). The cryptic nature of bats makes monitoring of populations difficult to properly evaluate population structure (Ingersoll et al. 2013). Mark-recapture efforts are commonly utilized but recapture of an animal

rarely occurs. There is an annual reliance on winter hibernaculum counts to provide a more accurate estimate of population trends and document well-known cavern habitat characteristics (O'Shea et al. 2003).

Bats are sensitive to human disturbances, with over a third of threatened bat species affected (Frick et al. 2020). Urbanization and destruction of forests have limited the availability of summer roosting sites utilized by forest-dwelling bat species. The destruction of summer habitat has led to the use of artificial structures as roosting sites, such as buildings and attics in suburban landscapes (Mering and Chambers 2014). The loss of summer habitat is likely one of the main reasons reproductive success in many forest bat species is declining (Brigham and Fenton 1986, Willis and Brigham 2004). Agricultural practices threaten bat populations through modification of land cover, directly reducing the availability of foraging and roost sites. Frick et al. (2020) suggests that implementing less intense agricultural practices may yield higher bat activity through organic farming and agroforestry. Some bat species are able to persist in fragmented habitats, such as Neotropical bats, and can benefit from a mosaic landscape structure due to their high mobility (Muylaert et al. 2016). Ripperger et al. (2013) suggests that despite bats' high mobility to access various resources, human disturbances across landscapes can still impact genetic diversity.

Wind energy development is growing rapidly, but the trade-offs of renewable energy have been called into question. Bat fatalities at wind energy facilities are increasing and an estimated 500,000 bats are killed annually in North America (Frick et al. 2017). Many bat species engage in migratory behavior and excessive collision mortality in declining species with low reproductive outputs is concerning. Conservation approaches have been discussed to

alleviate the impacts from wind energy. Arnett et al. (2011) explores the possibility of increasing turbine cut-in speed, lowest wind speed generated by wind turbines, to decrease bat mortality.

North American bats are impacted through a new infectious disease causing many bat species to experience population declines. White-nose syndrome (WNS) is an emerging disease in North America caused by the fungal pathogen, *Pseudogymnoascus destructans* (Dzal et al. 2011). The first evidence of WNS in North America was documented in 2006 in New York State and the spread has led to the death of millions of bats (Blehert et al. 2009, Powers et al. 2015). *Pseudogymnoascus destructans* growth is temperature-dependent and relies on cool environments (Verant et al. 2012), such as cave hibernacula, used by many North American bat species. White-nose syndrome is associated with a cutaneous fungal infection that occurs on bats' muzzles, wings, and ears.

Twelve North American bat species have been confirmed with symptoms of WNS by the White-nose Syndrome Response Team (2021): the big brown bat (*Eptesicus fuscus*), the cave bat (*Myotis velifer*), the eastern small-footed bat (*Myotis leibii*), the fringed bat (*Myotis thysanodes*), the federally endangered gray bat (*Myotis grisescens*), the federally endangered Indiana bat (*Myotis sodalis*), the long-legged bat (*Myotis volans*), the federally threatened northern long-eared bat (*Myotis septentrionalis*), the western long-eared bat (*Myotis evotis*), the tri-colored bat (*Perimyotis subflavus*), and the yuma bat (*Myotis yumanensis*). Other North American species have been documented with *Pd* but with no WNS symptoms: the eastern red bat (*Lasiurus borealis*), the Mexican free-tailed bat (*Tadarida brasiliensis*), the Rafinesque's big-eared bat (*Corynorhinus rafinesquii*), the silver-haired bat (*Lasionycteris noctivagans*), the Townsend's big-eared bat (*Corynorhinus townsendii*), the Virginia big-eared bat (*Corynorhinus townsendii virginianus*), the Ozark big-eared bat (*Corynorhinus townsendii ingens*), and the western-small

footed bat (*Myotis ciliolabrum*). The eastern small-footed bat and the big brown bat have not been affected by WNS as severely (Langwig et al. 2012). The little brown bat, northern long eared bat, tri-colored bat, and Indiana bat have experienced sharp population declines since the introduction of *P. destructans*. Each of these species are still vulnerable to *P. destructans* because they use cave hibernacula during torpor in the winter. The reason for differences in severity between species is still unknown but Langwig et al. (2012) suggests that this could be linked to differences in roosting preference.

6 Conclusion

Habitat selection at multiple scales is now being preferred in recent years as a more adept way to interpret an organism's movement and choices. Management schemes are sought after to improve targeted mammalian populations but also enhance surrounding populations of different species as well (Johnson 2002). Bats are bioindicators that play a pivotal role in surrounding populations and sustaining ecosystem health. Multi-scale models allow the identification of key requirements for species at both broad and fine landscape levels. Landscape structural attributes need to be maintained across all scales to promote species diversity and ecosystem maintenance. No choice is confined to a single scale, as each attribute selected for is intertwined across scales. The presence of bats across landscapes is in deep decline and an accurate description of bat habitat relationships across multiple scales is necessary for conservation and understanding the decline of North American bat species. New forestry practices that promote the conservation of older trees, reduction of intense agricultural practices, and maintenance of natural water bodies and corridors should be taken into consideration to maintain habitat suitability.

CHAPTER TWO: SUMMER ROOST SITE SELECTION OF A DECLINING BAT SPECIES

1 Introduction

Understanding species-habitat relationships is relevant in relation to conservation and species restoration. Conserving bat populations is limited by the lack of information on habitat requirements across various species (Fenton 1997, Mager and Nelson 2001). Habitat selection models are a useful tool for understanding how land-use change can subsequently impact threatened and endangered species. Species at risk are especially susceptible to intensive forest management practices that alter the landscape and affect roost sites (Brigham et al. 1997). Forest conditions on multiple structural scales affect bat behavior, community composition, distribution, and resource selection (Silvis et al. 2016). Retaining suitable roost site locations is extremely important within the summer months, as bats enter one of the most critical life stages. Therefore, understanding habitat requirements and roost-site selection will be critical for successful conservation efforts.

Habitat selection studies provide information on key requirements needed for bat species. For instance, bat activity is directly influenced by connectivity of habitat patches (Li and Wilkins 2014), forest stand characteristics such as stand volume (Titchenell et al. 2011), stand age (Wright et al. 2021), forest stratification (Silvis et al. 2016), and structural forest characteristics, including vegetation density (Gonsalves et al. 2018), tree height (Müller et al. 2013), and canopy architecture (Froidevaux et al. 2016). Higher bat activity is associated with mature hardwood forests (Nelson and Gillam 2020), forest edges (Morris et al. 2010), and corridors (Hein et al. 2009). Silviculture practices, such as thinning (Cox et al. 2016), burning (Braun de Torrez et al.

2018), and timber harvests (Webala et al. 2011) have also been correlated with shifts in bat assemblages.

For many North American bat species, understanding specific habitat requirements is key to understanding what may negatively impact different species. For example, the federally endangered Indiana bat (*Myotis sodalis*) has a clear association with specific habitat requirements (Carter 2006, Bergeson et al. 2020). Other species, such as the big brown bat (*Eptesicus fuscus*), have shown more flexibility across urban and rural landscapes (Agosta 2002). Most North American bats exhibit variation in seasonal habitat requirements. In the summer, bats require habitats that involve both forage (Thomas et al. 2021) and cover resources (Dixon 2012), as well as areas for raising their young (Williams and Brittingham 1997). Additionally, prior studies document that summer habitat selection is centered on sites that are most advantageous towards metabolic processes, such as the maintenance of body temperature (Monarchino and Johnson 2020). Habitat variables, such as decay stage and tree species, are critical in the population restoration of the federally Endangered Indiana bat, a roost specialist (Carter 2006), and essential for providing optimal habitat for the little brown bat (*Myotis lucifugus*) throughout their range to prevent further population declines (Broders and Forbes 2004). However, we are still missing critical information for many bat species of concern such as accurate descriptions of bat habitat relationships which are necessary for conservation and the understanding of population declines throughout many bat species.

One declining bat species for which bat-habitat relationships have not been studied extensively is the tri-colored bat (*Perimyotis subflavus*). Tri-colored bats were once considered abundant throughout their range, therefore it remains well understudied. Tri-colored bat populations have severely declined after the introduction of the fungus *Pseudogymnoascus*

destructans, the causal agent of white-nose syndrome (WNS). WNS impacts bats by disrupting hibernation behavior, resulting in arousals becoming more frequent and thus depleting critical fat stores prematurely (Boyles and Willis 2010, Dzal et al. 2011). Increased energy expenditure due to WNS leads bats to emerge from hibernacula prematurely when no forage is readily available, ultimately leading to mortality (Blehert 2012, Reeder et al. 2012, Warnecke et al. 2012, Alves et al. 2014). Over the past ten years, tri-colored bat populations have declined up to 94% in parts of their range due to WNS impacts (Powers et al. 2015, Ingersoll et al. 2016, O’Keefe et al. 2019). The sharp declines of this species led the Center for Biological Diversity and Defenders of Wildlife to petition the U.S. Fish and Wildlife Service in 2016 to list the tri-colored bat as threatened or endangered under the Endangered Species Act (Center for Biological Diversity and Defenders of Wildlife 2016, USFWS 2016).

Tri-colored bats are a hibernating North American bat species that use forested landscapes during summer months before entering hibernacula over the winter. Such as in many North American bat species, multiple studies have discussed the important resources for winter hibernacula but lack information on summer needs (Vanderwolf et al. 2012, Leivers et al. 2019). Summer habitats are important to population persistence in this species as they are required for multiple life history activities, including maternity colonies, nursery sites, and foraging locations (Scott et al. 2010). This lack of information is crucial in the context of WNS due to the importance of obtaining adequate fat stores from the surrounding foraging habitats prior to hibernation (Cheng et al. 2019).

The objective of my study was to assess summer roost site selection of tri-colored bats. I am specifically interested in tree characteristics, such as height, canopy density, and decay stage. I tested three competing hypotheses of what drives roost site selection, represented by important

characteristics commonly selected for by different tree roosting bat species (Table 1). First, the environmental protection hypothesis suggests that canopy density, base density, decay stage, and roost tree height drive selection by providing an optimal microclimate that reduces energetic costs of torpor. The forest condition hypothesis suggests that stem density at the understory and overstory level will drive selection as cluttered areas can influence bat activity and accessibility to roosts. Finally, the landscape resources hypothesis suggests that roost distances to resources will drive selection due to their impact on commuting time needed to reach available foraging resources. I also used a combination of covariates, based on previous research, to explore different variations of potentially influential variables. I will also evaluate all explanatory variables individually as models to assess influence on roost site selection. Tri-colored bats are currently under review for listing under the Endangered Species Act and information from this study will provide a better understanding of roosting requirements for conservation and management plans.

2 Methods

2.1 | Study Area

I collected data from Fort Campbell Army Installation, KY from 15 May to 15 August in both 2020 and 2021. Fort Campbell is situated on approximately 105,000 acres of federally owned land, extending across 414 km making it one of the largest regions of natural land left in the Southeastern U.S. Roughly 86% of land on Fort Campbell is undeveloped, providing the opportunity to assess primarily undeveloped habitat (Fort Campbell 2020). Habitat on Fort Campbell consists of a mixture of forests, native prairies and grasslands, agriculture fields, and sub watersheds of the Cumberland River (Fort Campbell 2020). Forests occupy 46% of the installation and are composed of tree stands with two primary forest types; deciduous forests and

pine plantations. Fort Campbell has experienced dramatic changes within historic climatic variables, such as precipitation and temperature. Summer months in this region have an average temperature of 31.7 °C. Temperatures within this region have risen by 1.11 °C over the last century. In the last thirty years, annual precipitation for Fort Campbell has increased by 5% (Fort Campbell 2020). Mean annual precipitation is 49 cm and dispersed throughout the year. Elevation ranges from 397 to 718 m above sea level. The first sign of WNS was detected on Fort Campbell, Kentucky in February 2012 (Shelton 2013). Long term tri-colored population declines have been documented throughout its natural range, including TN and KY regions, since the emergence of WNS (Ingersoll et al. 2013, Powers et al. 2015, O’Keefe et al. 2019).

2.2 | Data Collection

To determine presence of tri-colored bats and aid in capture sites, I deployed acoustic bat detectors at 100 survey sites for 2 consecutive nights at each site (Figure 1). I recorded bat calls with Anabat Titley Scientific Anabat Express Passive Bat Detector and an omni-directional Ultrasonic Microphone (US-O V2) mounted at 3 m above the ground. Anabat deployment was consistent with Indiana Bat Summer 2020 Survey Guidance through U.S. Fish and Wildlife Service (USFWS 2020) and USGS regulations (Reichert et al. 2018). Sensors were launched for approximately 8 h and set to begin recording at sundown and end at sunrise. I digitized call files and analyzed them using Kaleidoscope Pro Analysis Software (Wildlife Acoustics, Inc.) to confirm tri-colored bat presence. The Kaleidoscope Pro Analysis Software uses an automatic species identification tool to identify species based on call sonograms.

I identified netting locations from tri-colored presence (> 50 calls per night) and by known forage behaviors (Scott et al. 2010). Bats were captured using Avinet Inc., 38 mm mesh 2.6 x 2.6, 4, 6, 9, and 12 m mist-nets placed across sources of water, old fire breaks, and roads

that act as flight corridors. The number of nets placed at each site was dependent upon water presence and presentable flight corridors. Nets were opened at sundown and were checked approximately every 10 min for 3-4 h. Captured bats were fitted with aluminum alloy 2.4 mm silver Split Metal Bat Rings (PORZANA) for future identification. In handling all bats, I followed protocols put forth by the Institutional Animal Care and Use Committee (APSU IACUC protocol 20.003R) and Association of Mammalogists Care and Use guidelines (Sikes and Mammalogists 2016). All handling occurred under Tennessee Wildlife Resources Agency state scientific collection permit (#2314), Kentucky Department of Fish and Wildlife Resources state educational wildlife collection permit (#SC2011006 and #SC2111014), and U.S. Fish and Wildlife Endangered Species permits (#TE80381A-2, #TE62026D-0, and #ES62026D-1).

Bats weighing more than 5 g and in good health received a 0.29 g VHF radio transmitter (Lotek Picopip, Ag337) with > 21-day battery life. I attached transmitters between the shoulder blades using Torbot Bonding Cement. I clipped fur using sewing scissors and an eyebrow brush to ensure skin was prepped and bare for transmitter attachment. A thin layer of the adhesive was applied on the back of the bat and transmitter. Baby powder was used over top of the transmitter and adhesive to avoid irritation and remove any tackiness left on the skin and fur was pressed over top the transmitter to ensure longevity of transmitter use. I tracked the tagged bats every day post-capture using a 3-Element Folding Yagi and Lotek Wireless BioTracker to their roost tree until the signal was lost for three consecutive days or a transmitter was found.

I completed a habitat survey for each visually confirmed roost tree, recording specific variables known to influence roost site selection for other tree-roosting bat species. I identified tree species, measured diameter at breast height (dbh; cm), determined the number of cavities and decay stage (classified by following Backhouse and Louiser 1991), estimated canopy density

(%), and recorded the geographic location. I used a clinometer to estimate tree height (m) and degree of slope ($^{\circ}$). Roost aspect was recorded from the trunk of the roost tree with a compass (SEENDA Orienteering Compass). Centered around each roost tree a 0.1 ha (17.85 m radius) circular plot was established to measure plot variables (Table 2). I estimated canopy density by measuring canopy volume with a densiometer (Concave Model C) at each cardinal direction at the base of the tree and along an 18 m transect at 2 m intervals. I then averaged these estimates to derive a mean value of canopy density for each roost tree. To describe stand density surrounding roost locations, I counted the number of overstory (> 9.5 cm in dbh) and understory (< 9.5 cm in dbh) stems per unit area (0.1 ha; Avery and Burkhart 1994).

To characterize the habitat surrounding roost trees, in each plot I recorded tree species composition and richness, habitat disturbance, vegetation cover, water presence and type, and distance to (m) and heights (m) of nearest and taller overstory trees. Habitat disturbance within each plot was defined by recent known management practices throughout my study area such as forest clear cut, partial cut, thinning, pruning, or prescribed burn. Vegetation cover surrounding identified roost trees was categorized into four general groups of vegetation cover type: hardwood, mix, softwood, or herbaceous/grass. Water presence was categorized as intermittent, ephemeral, and/or perennial water sources (stream, pond, wetland, lake). I used the measurement tool in ArcGIS (Version 2.8.3) to calculate distance from roosts to the nearest forest edge, water source, and gravel or paved road (in m).

To provide available habitat information, three random trees within the same forest stand were selected as habitat comparisons for each selected roost tree. These trees represented available roosting sites that were available but not readily used. To ensure each available tree was random, I generated a random azimuth from the roost tree and selected the first tree that

occurred along the transect at least 40 m from the roost tree and had a dbh > 9.5 cm. I then repeated the tree and plot measurements for the available tree as described above for selected roost trees.

2.3 | Statistical Analyses

To assess habitat variables that best describe roost-site selection, I fit a suite of mixed conditional logistic regression models (Table 1) based on hypotheses from characteristics known to influence roost-site selection for other bat species with the dependent variable of used versus available. I also fit individual variable models without additional covariates. I used ‘clogit’ in package *survival*, which compares used against available resources in a case-control design, allowing for the comparison of covariates at the resource and individual level. The random effect framework allows for individual variation associated with each bat and handles pseudoreplication associated with multiple measurements per bat. I centered all variables on the mean and scaled by the standard deviation. I dropped any correlated variables ($r > 0.60$; Fletcher and Hutto 2008) to align with the assumption of no multicollinearity. This analysis resulted in dbh being dropped from the models as it was correlated with roost tree height ($r = 0.66$). I used roost tree height instead of dbh in my models as previous literature suggests the importance of roost tree height as a habitat variable (O’Keefe and Loeb 2017). For the roost aspect and roost height variables, I generated random values from uniform distributions bounded by degrees and the random tree height, respectively. I took the median of roost aspect for trees that were used for multiple days.

To determine general trends of selected roost trees, I compared variables for used and available roost trees using a Student’s *t*-test. Variables included roost tree height, dbh, plot density, and base density. Normality was checked using the Shapiro-Wilk test and variances

compared by F-test; if data were not normal a Mann-Whitney test was performed. I compared the selected roost tree genera to the random sampled tree species using a Chi-squared goodness-of-fit test to determine which species were used more or less than expected.

I used a model selection framework using Akaike's information criterion modified for small sample sizes (AICc) to determine model parsimony (Burnham and Anderson 2002). Models were ranked through ΔAICc and Akaike weights (w_i ; Burnham and Anderson 2002). I determined the model with the lowest AICc score to be the best fit model for my available data (Table 2). I interpreted models within $< 2 \Delta\text{AICc}$ units to be acceptable alternative explanations (Burnham and Anderson 2002). I calculated odd ratios and 95% CI for variables included in the best models. To evaluate model accuracy, I applied k -folds cross-validation ($k=100$) for habitat selection models to evaluate prediction success within my top performing model (Boyce et al. 2002, Fortin et al. 2009, Hauser et al. 2017); this technique is more appropriate for use-availability studies as discussed in Boyce et al. (2002). I constructed a training data set using 75% of my data and withheld 25% as my test data set. I calculated the top model accuracy by comparing the observed values with the predicted; models with high accuracy were assumed to have high predictive abilities (Boyce et al. 2002, Fortin et al. 2009, Hauser et al. 2017). All analyses were performed in R v4.0.5 (R Core Team 2020).

3 Results

I conducted 62 nights of mist-netting, with a total of 239 net nights (# of nets opened per night). I captured 256 bats of 6 species, excluding recaptures and escapes from nets. I averaged 4.13 ± 4.55 SD captures per survey night. The capture rate for tri-colored bats was 0.37 bats each night (# individuals / # mist netting survey nights; range: 1 - 3) and 0.09 bats per net (# individuals / # net nights; range: 1 - 2) from 2020-2021. Over the span of two years, I captured

23 tri-colored bats (4 adult males, 4 juvenile males, 12 adult females, 3 juvenile females), attached transmitters to 20 tri-colored bats, and successfully tracked 15 individuals (3 adult males, 1 juvenile male, 8 adult females, 3 juvenile females). Three bats were too small to tag and five of the tagged bats were never located in the days following tagging. All successfully tracked radio-tagged bats changed roosts at least once and were tracked for an average of 7.8 ± 2.73 days. I tracked bats to 55 roost trees (mean = 3.4 ± 1.9 , minimum = 2, maximum = 8 trees per individual; Figure 2) and days between roost switches averaged 1.24 ± 0.28 days. Roosting height averaged 16.29 ± 5.23 m throughout the study. The average distance traveled between roosts was 167.9 ± 227.05 m. All bats roosted in the same forest stand for the duration of time tracked.

Overall, tri-colored bats were frequently tracked to oak trees (*Quercus spp.*) for roosts, followed by tulip poplars (*Liriodendron tulipifera*) and hickories (*Carya spp.*; Figure 3). Roost trees consisted of 1.8% pines and 98.2% hardwoods, including 23.6% tulip poplar (*Liriodendron tulipifera*), 7.3% green ash (*Fraxinus pennsylvanica*), 5.5% mockernut hickory (*C. tomentosa*), 3.6% shagbark hickory (*C. ovata*), 1.8% pignut hickory (*C. glabra*), 3.6% sweetgum (*Liquidambar styraciflua*), 1.8% red maple (*Acer rubrum*), and 1.8% sugar maple (*A. saccharum*). Oaks were the highest selected tree genera with 49.1% of roost trees occurring within the genus *Quercus*. Selected oak species consisted of 16.4% white oak (*Q. alba*), 10.9% southern red oak (*Q. falcata*), 10.9% northern red oak (*Q. rubra*), 3.6% shingle oak (*Q. imbricaria*), 1.8% swamp white oak (*Q. bicolor*), 1.8% chinkapin oak (*Q. muehlenbergii*), 1.8% post oak (*Q. stellata*), and 1.8% black oak (*Q. velutina*). No snags were used as a roost tree. Roosts were commonly found along dead branches and within knots, cracks, and cavities of trees. All individuals visually observed were documented roosting alone.

Roost tree species did not differ from expected given the general composition of trees in my study area ($X^2 = 1.07$, $df = 6$, $P = 0.98$; Figure 4). Tree height and dbh were correlated ($r = 0.66$, $p\text{-value} < 0.001$). Tree height was taller for selected roost trees than in random plots ($W = 3002$, $p\text{-value} < 0.0001$; Table 3). Dbh for roost trees was greater compared against random trees ($W = 2628$, $p\text{-value} = < 0.001$; Table 3). There was no difference among base canopy density and plot canopy density for selected and available trees (Base density, $W = 4696$, $p\text{-value} = 0.6991$; Plot density, $W = 4378.5$, $p\text{-value} = 0.6982$; Table 3). Distances to landscape features varied depending on the individual (for distance to water: mean = 256.97 ± 221.96 m, range 10.71 - 835.55 m; for distance to road: mean = 119.65 ± 77.07 m, range 3.37 - 305.22 m; for distance to edge: mean = 118.11 ± 68.91 m, range 12.73 - 282.81 m).

The top model of roost selection (used versus available trees) given the data contained only roost tree height ($AICc = 136.28$, $LL = -67.13$, $K = 1$, $wt = 0.93$; Table 4). All remaining models for roost and plot level characteristics received limited support ($\Delta AICc > 2$; Table 4). Odd ratios showed that bats were more likely to select taller trees (odds ratio = 1.06, $p\text{-value} = < 0.001$). For every 1 m increase in tree height, the relative probability of a tree being selected was 6% (Figure 5). The distribution of selected roost tree heights (m) followed a normal distribution (Figure 6). My top model of roost tree height had a predictive accuracy of 51%. Lower accuracy values are to be expected within case-controlled models as predicted and observed values are not unique (Boyce et al. 2002).

4 Discussion

Understanding tri-colored bat summer habitat use, and more specifically daytime roost selection, is critical to determining causal declines of this species across its range. I found that tree height was the best predictor variable of roost selection for tri-colored bats during the active

months. Tri-colored bats generally selected taller trees in relation to other available overstory trees. My results did not support the proposed hypotheses: environmental protection, forest condition, and landscape resources. This suggests that roost site selection is being driven by other factors, such as tree height.

These results are consistent with other findings linking selection of taller trees to thermoregulation strategies in other species of bats (Bergeson et al. 2020). Bats often go into daily torpor during roosting to conserve energy, dropping their body temperature near environmental temperature; therefore, energetic costs are mediated by ambient conditions (Stawski and Geiser 2010). Taller trees provide a range of microclimate conditions (Vaughan and O'Shea 1976, Russo et al. 2004, Solick and Barclay 2007), providing flexibility in thermoregulatory behavior for bats. The vertical distribution of microclimates is influenced through vegetative and structural characteristics that can buffer environmental stressors. Specific tree life stages and certain tree species have been documented to retain heat longer than others (Nicolai 1986, Sedgeley and O'Donnell 1999). Dead trees or snags are not well insulated due to the decaying bark, suggesting that poorly insulated roosts show minimal thermal gradients, limiting the availability of various microclimates (Sedgeley and O'Donnell 1999). Whereas trees with large diameters can also provide a wide range of temperatures that support a suitable microclimate and protect against environmental stressors (Solick and Barclay 2007). Therefore, taller trees with a large diameter may provide insulation to support varying microclimates based on heat retention within the tree species.

Flexibility in thermoregulation has been documented within a wide variety of species (Nordberg and Schwarzkopf 2019, Basham and Scheffers 2020, Newman et al. 2021). Within bats, cave-dwelling species will alter their roosting sites within hibernaculum when microclimate

conditions become undesirable (Brack Jr. and Twente 1985, Boyles et al. 2007, 2017, Newman et al. 2021). Furthermore, rock and crevice roosting species have been documented to show flexibility within their thermoregulatory behavior by shifting their location to desirable microclimates (Solick and Barclay 2007). For tree roosting bats, vertical roosts provide the option to change their environment by shifting vertically on the roost tree (Chruszcz and Barclay 2002). Arboreal frog communities have displayed these types of vertical migrations along trees from the tree canopy to ground level to locate suitable microclimates dependent on environmental conditions (Basham and Scheffers 2020, De Frenne et al. 2021). Thus, my results suggest that plasticity in thermoregulatory and roosting behaviors during the summer is possible, but these behaviors have yet to be explicitly explored in tri-colored bats.

All roosts were live, healthy trees with a low decay stage, while available trees had a wide variety of decay stages. Forest structure across the study area was homogeneous, thus there was no difference in canopy density between used and available trees. General trends documented tri-colored bats using oak trees as roosts, however, my results for tree genera selection indicated that tri-colored bats did not select tree trees based on tree genus. There were no other discernible differences between characteristics measured. In other studies, landscape features were important for broader selection, influenced by foraging and energetic requirements (Thomas et al. 2021), but there was no preference for landscape features driving habitat selection within my study.

Tree characteristics selected for in my study were consistent with other reports within the southeastern United States. Individuals selected trees with canopy density (86.21%) and a dbh (51.98 cm) similar to other studies within the southeastern US (85% and 52.4 cm; Shute et al. 2021). Tree height (37.64 m) varied greatly from all other documentations reported by other

studies (16.5-19.3 m; O’Keefe et al. 2009; Poissant et al. 2010; Shute et al. 2021). Other forest dwelling bat species have been documented selecting roosts that optimize solar radiation and provide thermoregulatory benefits (Castleberry et al. 2020). The average roosting height for tri-colored bats was close to the canopy, suggesting that they may be in greater contact with wind, air temperatures, and solar radiation (Veilleux et al. 2004). Maintaining a high body temperature as the temperature lowers can be energetically costly for small mammals (Ruczyński and Bartoń 2020). Therefore, roosting high may have a thermal benefit that creates optimal microclimatic benefits. Future research is needed to evaluate tri-colored bats selection for tall tree height for thermoregulatory benefits.

Tri-colored populations have declined across their range since the introduction of WNS (Powers et al. 2015), with bat population declines attributed to increased fat expenditure during hibernation (Cryan et al. 2013, Pettit and O’Keefe 2017). A potential reduction of mortality due to WNS has been linked to higher fat stores accumulated within the summer months before entering hibernation (Cheng et al. 2019). This reduction in mortality may be because improved body condition from higher fat stores may allow recovery from a *P. destructans* infection. Bats require adequate summer forage and microclimates to build up and maintain pre-hibernation fat stores (Bernard et al. 2021). Facilitating greater forage availability in the summer and fall could result in higher fat consumption, thus leading to greater overwinter survival for bats experiencing WNS symptoms. Therefore, understanding what habitat resources are required for summer roosting is important. As bat populations continue to decline due to disease, habitat loss, and climate change, conservation and management of summer roost-site habitat will provide tri-colored bats a start at population recovery.

Due to tri-colored bats being a rare species in Tennessee (Powers et al. 2015), sample size for this study was limited. I was not able to compare differences in roost site selection between sex, reproductive condition, and age because of low numbers of each factor. Variations in sex, age, and reproductive stages of individuals were also unbalanced making comparisons difficult. Previous studies support that summer roost-site selection differs between males and females based on energetic demands, specifically related to reproductive stage and microclimate (Grinevitch et al. 1995). Females are energetically stressed during the summer months due to reproduction and need sufficient time and resources to meet their energetic needs. Barclay (1991) suggested that males may occupy different areas compared to females as their energy constraints are lower than females. My study area was dominated by females during the summer reproductive season; a higher capture rate of females may suggest that my study area provides suitable areas for maternity and nursery sites. Also, the high captures of reproductive females and late summer juvenile captures indicate that my study area is a suitable habitat that can yield reproductive success. The lack of male captures could be due to the occupation of unsuitable habitat, whereas survey efforts were focused in areas with adequate resources. Additionally, males have lower energetic demands and may reduce foraging activity, therefore altering their presence on the landscape.

In this study, radio telemetry was used to identify day roosting sites and movements across landscapes. A portion of individuals captured during this study were released without a transmitter attached because the addition would have exceeded 5% of their body weight (Animal Research Review Panel 2020), potentially harming the bat. However, long-term tracking of tri-colored bats can be difficult due to their small body size. Tracking duration is dependent on the battery size, which is limited due to the body size of the study species. Thus, tracking duration of

tri-colored bats within this study varied between individual (range 3 to 16 days). Variation within tracking duration can influence the number of roosts recorded for an individual, potentially causing uneven datasets. Home range estimation was not possible within my study but due to the variability of tracking duration and small sample size of roost trees identified per individual.

This study provided a distinct opportunity to study tri-colored bat summer roost site selection in a relatively undeveloped forested habitat. The objectives of this study were to assess summer roost site selection of tri-colored bats and the impacts of forest management. My results demonstrated that tri-colored bats had a preference for tree height in their summer roost site selection, which is commonly considered a limiting factor across forested landscapes (Ethier and Fahrig 2011). The maintenance of mature oak-hickory dominant forests has the greatest potential to support established and future roost sites. Landscape features may influence habitat selection but at larger scales not investigated within this study. Regardless, the conservation of summer habitats is important for overall survival and reproductive success of tri-colored bats.

5 Management Implications

Reports of tri-colored bats population declines have occurred since the arrival of WNS. Since the petitioning for listing under the Endangered Species Act in 2016 (USFWS 2016), there is a critical need to focus on summer habitats to promote reproductive success and facilitate the excess accumulation of fat stores before overwintering. Often roosting sites in this study were located within oak-hickory mature hardwood forests that had been managed through thinning and prescribed burns. These management practices are important for the restoration of oak-hickory forests and help to create a mosaic within forest stands. Connectivity brought throughout management practices will provide better access and movement across the landscape to

resources. Roosting sites utilized by tri-colored bats can be identified and future studies should focus on home range analyses to better describe larger selection.

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APPENDIX A: TABLES

Table 1. Suite of competing hypotheses and subsequent explanatory variables tested to explain tri-colored bat (*Perimyotis subflavus*) roost site selection in Fort Campbell, KY, during the summers of 2020 and 2021. All explanatory variables will be examined as models separately to assess influence of roost site selection. Overstory trees are trees with diameter at breast height > 9.5 cm while understory are < 9.5 cm.

Hypothesis	Explanatory Variables
Environmental Protection	Canopy density (%) Base density (%) Decay stage (Backhouse and Lousier 1991) Tree height (m)
Forest Condition	Overstory stem density (# trees/plot) Understory stem density (# trees/plot) Overstory species diversity Understory species diversity
Landscape Resources	Distance to edge (m) Distance to water (m) Distance to road (m)
Global Roost Model	Combination of model covariates; environmental protection, degree of slope (°), and roost aspect (°)
Global Landscape Model	Combination of model covariates; landscape resources, forest condition, percent of snags (%), and percent of conifers (%)

Table 2. Variables measured at summer roosts and random available trees of tri-colored bats (*Perimyotis subflavus*) in Fort Campbell, KY, 2020-2021.

Roost characteristics		
Tree characteristics	Plot characteristics	Landscape characteristics
Tree height (m)	Distance to nearest overstory tree (m)	Distance to nearest water (m)
Diameter at breast height (m)	Distance to nearest taller overstory tree (m)	Distance to nearest road (m)
Decay Stage (Backhouse and Lousier 1991)	Height of nearest overstory tree (m)	Distance to nearest forest edge (m)
Number of cavities	Height of nearest taller overstory tree (m)	
Degree of slope (°)	Overstory stem density	
Base canopy density (%)	Understory stem density	
	Plot canopy density (%)	
	Percent of snags (%)	
	Percent of conifers (%)	
	Overstory species diversity	
	Understory species diversity	
	Habitat disturbance	
	Vegetation cover	
	Water presence	
	Water type	

Table 3. Mean and standard deviations (SD) of habitat variables describing summer roost trees used by tri-colored bats (*Perimyotis subflavus*) and random available trees in summers 2020 and 2021 on Fort Campbell, KY.

Habitat Variable	Roost Trees		Random Trees	
	Mean	SD	Mean	SD
Tree height (m)	37.64	7.63	30.91	11.84
Diameter at breast height (cm)	51.98	17.02	38.78	18.87
Average roosting height (m)	16.29	5.23	14.84	11.39
Decay stage ¹ (1-5)	1.45	-	1.47	-
Roost aspect ¹ (°)	191	-	207	-
Degree of slope (°)	5.78	5.35	4.99	4.28
Base canopy density (%)	88.53	6.63	87.89	9.30
Plot canopy density (%)	86.21	8.71	84.11	13.00
Distance to nearest overstory tree (m)	2.75	1.70	3.11	2.26
Distance to nearest taller overstory tree (m)	7.50	4.76	6.65	5.78
Height of nearest overstory tree (m)	22.99	11.16	24.70	12.64
Height of nearest taller overstory tree (m)	43.00	7.83	39.49	10.64
Percent snags (%)	6.80	5.23	7.99	5.49
Percent conifers (%)	6.49	12.47	7.03	15.13
Total understory trees in plot	65.26	37.83	67.03	43.15
Total overstory trees in plot	39.00	13.71	38.84	17.37
Understory diversity	11.71	5.16	10.88	4.66
Overstory diversity	10.53	3.20	10.48	3.42
Distance to water (m)	256.97	221.96	271.49	229.75
Distance to road (m)	119.65	77.07	126.30	81.59
Distance to edge (m)	118.11	68.91	130.67	106.16

¹ Due to decay stage and roost aspect being discrete variables, median is reported with no standard deviation.

Table 4. Top performing models ranked from Akaike's information criterion corrected for small sample size (AICc), Δ AIC, log likelihoods (LL), number of parameters (K), and AIC weights (w_t) predicting tri-colored bat (*Perimyotis subflavus*) activity in relation to individual tree and plot-scale habitat selection in Fort Campbell, KY. Models include the competing hypotheses and top 5 subsequent explanatory variables.

Model	Δ AICc	LL	K	w_t
Tree height	0.00	-67.13	1	0.93
Environmental protection	5.60	-66.85	4	0.06
Global roost model	9.21	-66.55	6	0.01
Height of nearest taller overstory tree	12.16	-73.21	1	0.00
Distance to water	13.70	-73.98	1	0.00
Landscape resources	14.38	-72.27	3	0.00
Plot density	15.57	-74.92	1	0.00
Snag percent	15.84	-75.05	1	0.00
Global landscape model	17.71	-67.57	9	0.00
Forest condition	19.93	-74.02	4	0.00

APPENDIX B: FIGURES

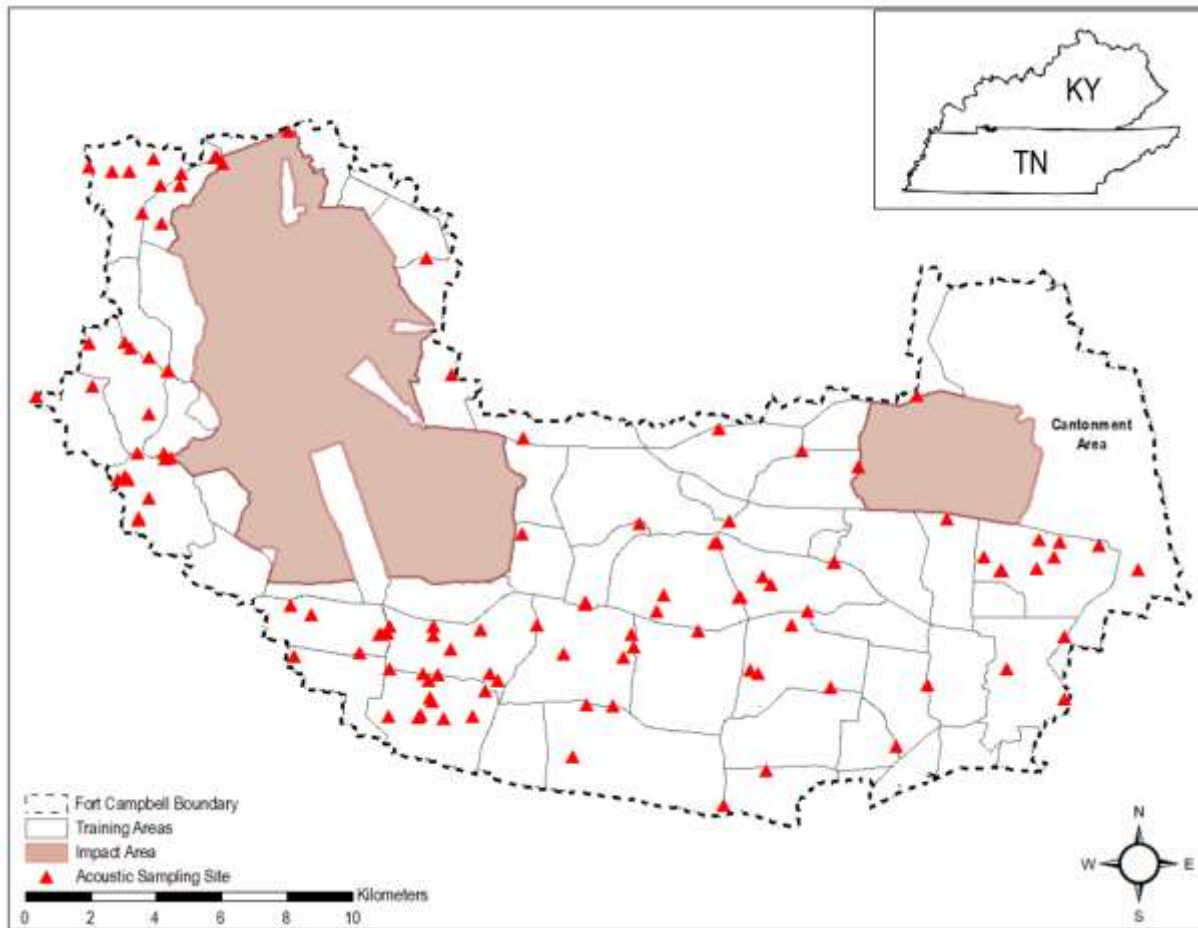


Figure 1. Site locations of Anabat Titley Scientific Express Passive Bat Detectors deployed across Fort Campbell, KY to assess tri-colored bat (*Perimyotis subflavus*) occurrence from 2020-2021. Sampling was prohibited within the areas designated as Impact Areas due to safety concerns.

Figure 2. Roost tree locations selected by 15 tri-colored bats (*Perimyotis subflavus*) that were successfully tracked to 55 roost trees across Fort Campbell, KY from 2020-2021. Roost tree locations on map are the centroid location of the roost area per bat if multiple roost trees were selected in the area.

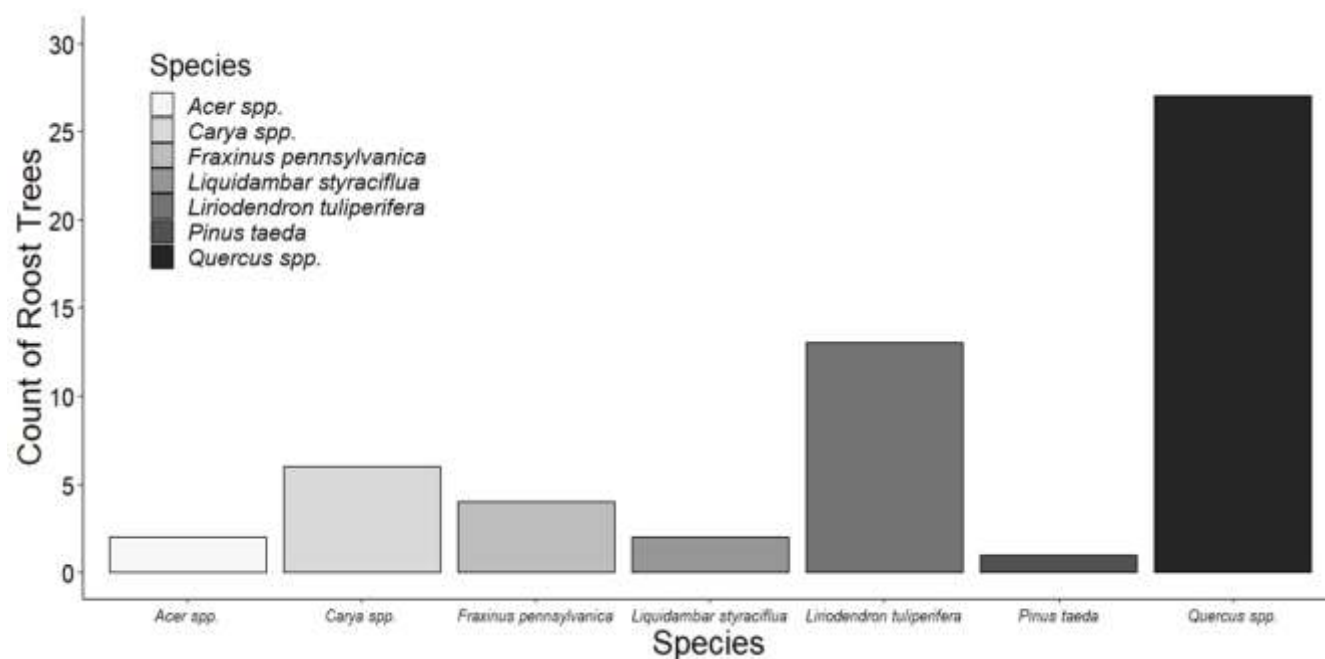


Figure 3. Total count of tree species selected as roost trees by tri-colored bats (*Perimyotis subflavus*) on Fort Campbell, KY from 2020-2021.

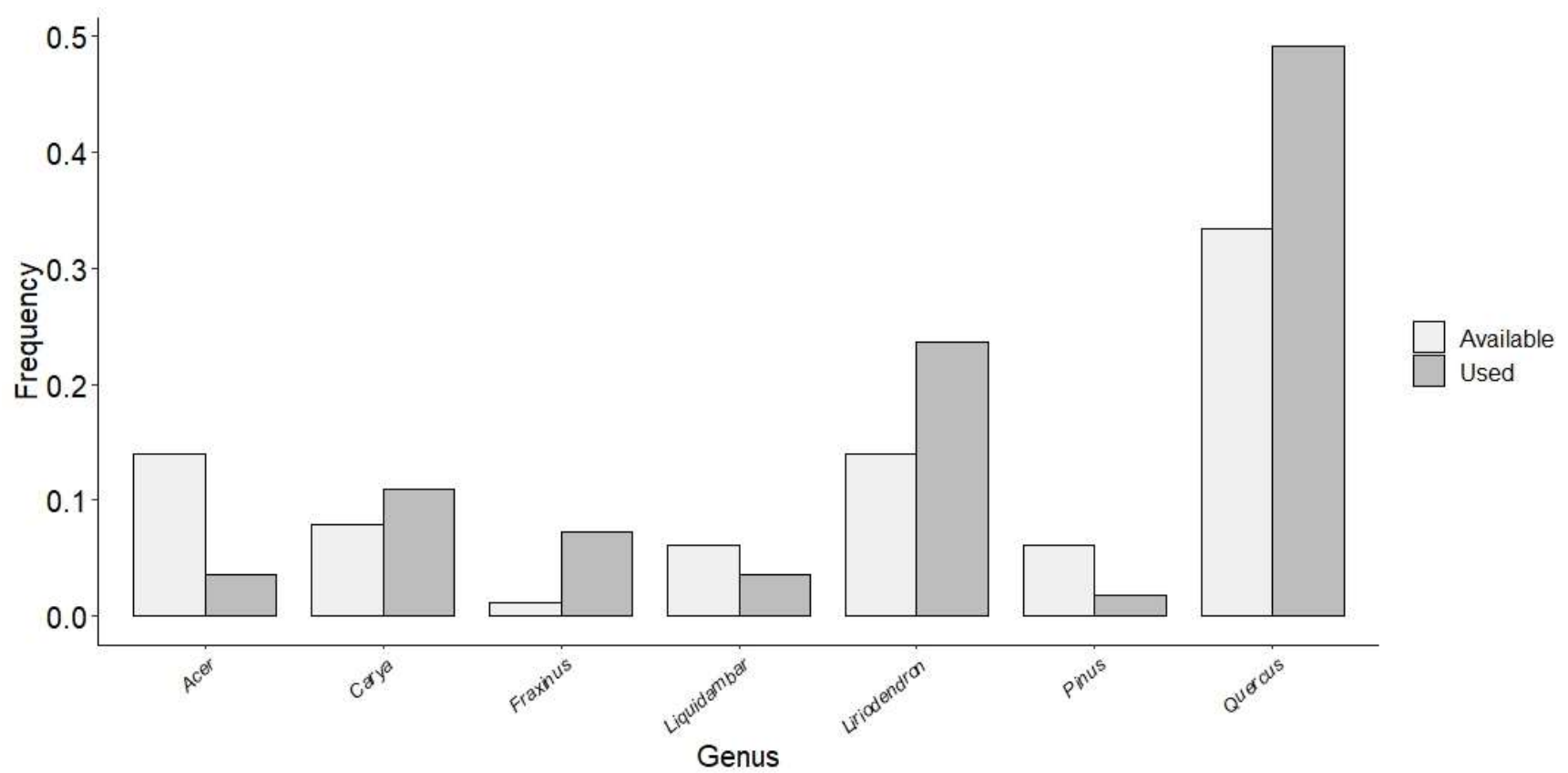


Figure 4. Frequency of tree genera selected as roost trees by tri-colored bats (*Perimyotis subflavus*) and the frequencies of available trees sampled as a comparison on Fort Campbell, KY from 2020-2021.

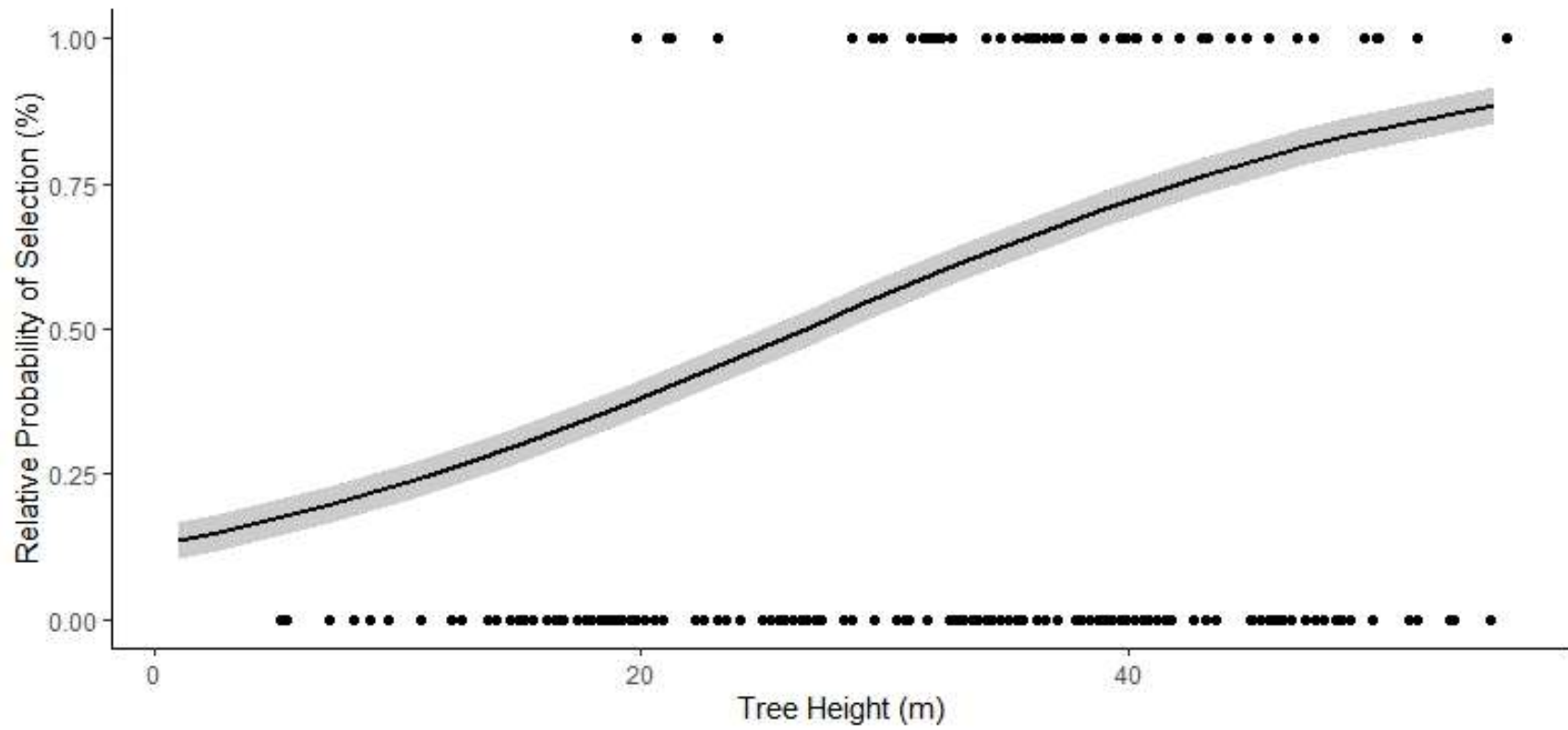


Figure 5. Predicted relative probability (with 95% confidence intervals) of roost tree selection of tri-colored bats (*Perimyotis subflavus*) in accordance to height of tree (m) in Fort Campbell, KY. Measured tree height of used (top points) and available heights (bottom points) are also reported.

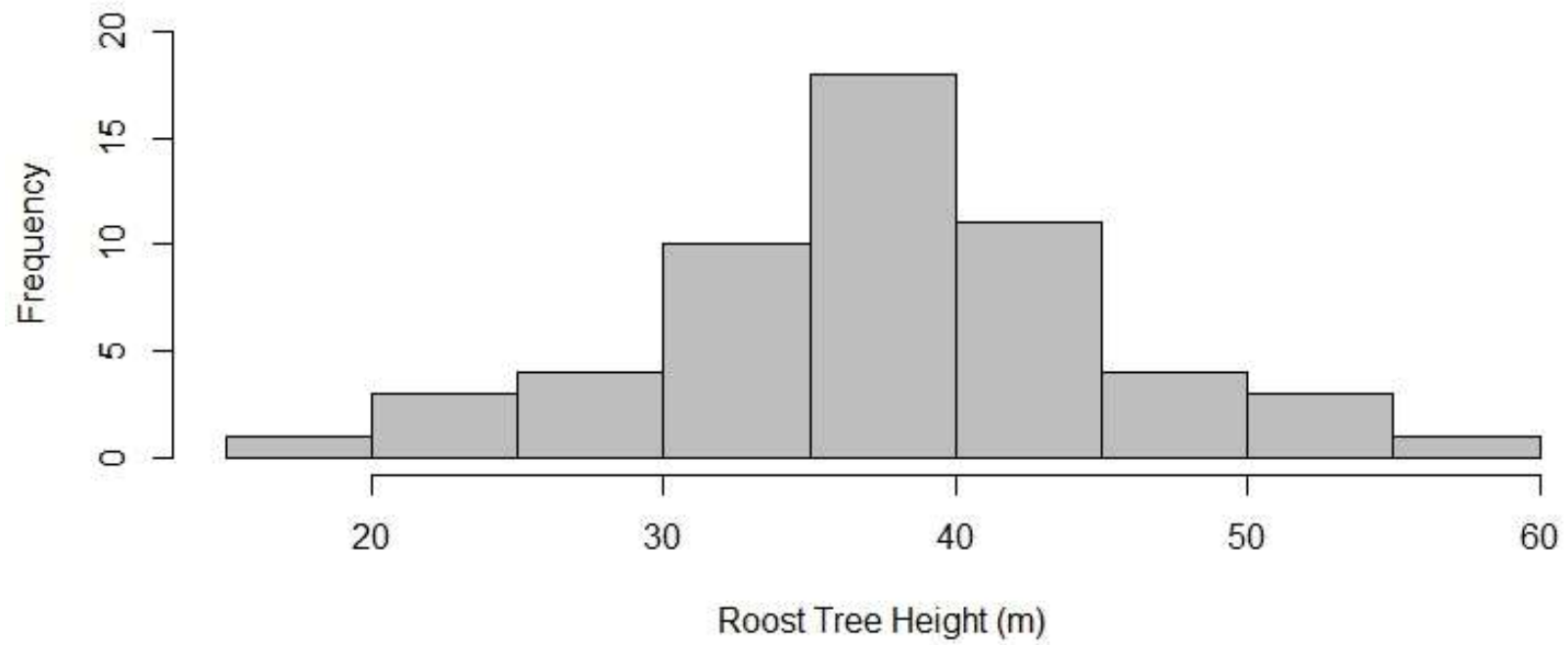


Figure 6. Frequency distribution of roost tree heights (m) selected by tri-colored bats (*Perimyotis subflavus*) in Fort Campbell, KY from 2020-2021.