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INVESTIGATING THE ECOLOGY AND BEHAVIOR OF THE INDIANA BAT AND TRI-COLORED BAT DURING FALL SWARMING AND SPRING STAGING

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I am submitting herewith a thesis written by Mallory E. Tate entitled "INVESTIGATING THE ECOLOGY AND BEHAVIOR OF THE INDIANA BAT AND TRI-COLORED BAT DURING FALL SWARMING AND SPRING STAGING." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

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INVESTIGATING THE ECOLOGY AND BEHAVIOR OF THE INDIANA BAT AND TRI-COLORED BAT DURING FALL SWARMING AND SPRING STAGING

A Thesis Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Mallory Elizabeth Tate

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DEDICATION

To my family, related and not.

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ABSTRACT

White-nose syndrome has devastated bat populations across North America since 2005. Due to declines in Indiana bat (*Myotis sodalis*) and tri-colored bat (*Perimyotis subflavus*) populations across the eastern United States, management prescriptions need to consider all seasons of these species annual cycles. However, data is severely lacking on the two seasons surrounding winter hibernation. These include fall swarming, a time period when bats are mating and preparing for hibernation, and spring staging, when bats are emerging from hibernation and preparing for spring migration. Both periods are critical for successful reproduction and survival following white-nose syndrome infection.

To investigate the timing of these two periods, I used Passive Integrated Transponders to detect bat activity at the entrances of caves from 2016–2019. We detected peak Indiana bat activity during fall swarming from September 10–October 2 and during spring staging from March 26–May 13th. For tri-colored bats, we detected increased activity from August 20–September 30 and February 19–April 22.

To understand roosting behavior and ecology of both species, we tracked bats to their diurnal roosts during fall swarming. We tracked 15 Indiana bats and 18 tri-colored bats from 2016–2019. For tri-colored bats, we were able to assess roost selection using AIC_c. Tri-colored bats selected roosts with less clutter and high solar exposure that were closer to caves. Due to small sample size, we were unable to assess selection for Indiana bat roosts. Indiana bats roosted in caves more often than in trees, and roosts were snags that were 108 ± 64.80 m ($\bar{x} \pm SE$) from caves.

The results from this thesis can be used to determine more efficient and timely management prescriptions and restrictions near caves during fall swarming and spring staging.

Further monitoring and research should investigate roosting ecology and behavior during spring staging, foraging ecology during both time periods, and the true sensitivity of bats to management activities during these critical times.

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LIST OF ABBREVIATIONS

GSMNP: Great Smoky Mountains National Park

NPS: National Park Service

Pd: *Pseudogymnoascus destructans*

PIT: Passive Integrated Transponder

TNC: The Nature Conservancy

TWRA: Tennessee Wildlife Resources Agency

U.S.: United States

USFWS: United States Fish and Wildlife Service

USGS: United States Geological Survey

WMA: Wildlife Management Area

WNS: White-nose Syndrome

CHAPTER 1: GENERAL INTRODUCTION

BACKGROUND AND NEED

Bats in the United States (U.S.) have faced many pressures over the past century. Habitat degradation, disturbance, wind energy development, pesticides, and, most recently, disease, currently pose devastating threats to many species (Voigt and Kingston 2016). In 2006, white-nose syndrome (WNS) was introduced to the eastern United States. This decimating disease has since killed more than 6 million cave hibernating bats in North America (U.S. Fish and Wildlife Service [USFWS] 2012), spread to at least 35 states and 7 Canadian provinces (USFWS 2020, U.S. Geological Survey [USGS] 2016, Texas Parks and Wildlife Department [TPWD] 2017) and caused bat population declines of 90 to 100% at some sites (Blehert et al. 2009, Frick et al. 2010a, Turner et al. 2011). While 16 bat species can carry *Psuedogymnoascus destructans* (*Pd*), the fungus that causes WNS, some are more susceptible to the disease than others (Bernard et al. 2017, Frick et al. 2017). The fungal pathogen can erode the epidermal tissue of hibernating bats and leads to disruption of homeostasis, respiratory acidosis, hypotonic dehydration, increased fat metabolism, and increased arousal from torpor during hibernation (Cryan et al. 2010, Warnecke et al. 2012, Warnecke et al. 2013, Cryan et al. 2013, Verant et al. 2014). Two of the bat species that have been found to be most susceptible and that have suffered the largest declines from WNS, being at risk of regional extinction, are the Indiana bat (*Myotis sodalis*) and the tri-colored bat (*Perimyotis subflavus*; Langwig et al. 2012, Thogmartin et al. 2013, Alves et al. 2014, Frick et al. 2015).

The Indiana bat was first listed as endangered under the Federal Endangered Species Act in 1973 due to habitat degradation and alteration, and hibernacula disturbance during winter that resulted in the death of large numbers of individuals (Silvis et al. 2016; USFWS 2017). In response to declines, the USFWS partnered with state agencies across the species range to

develop recovery plans that sought to improve habitat quality and availability and close critical hibernacula to increase bat survival (USFWS 2016). Managers and biologists hoped that improving and protecting habitat during the summer would not only increase reproductive rates, but provide greater opportunity to increase bat health and condition before entering winter torpor, reducing death tolls (USFWS 2017). However, the outbreak of WNS reversed recovery, causing declines in Indiana bat populations of up to 95% (Frick et al. 2015, Petit and O'Keefe 2017, Great Smoky Mountains National Park [GRSM] unpublished data).

The tri-colored bat is currently petitioned for federal listing (The Center for Biological Diversity and Defenders of Wildlife 2016) due to WNS-related population declines of up to 98% (Frick et al. 2015, O'Keefe et al. 2019). Before the introduction of *Pd*, the tri-colored bat was one of the most common bat species across its range, and very little research was done to understand its ecological needs and behaviors (NatureServe 2015).

Over the past decade, many agencies and institutions have worked to understand the ecology and behavior of the Indiana and tri-colored bat and the impact and effects of WNS on their populations. As defined by USFWS, the life cycle of a bat includes the summer maternity season, fall swarming, winter hibernation, and spring staging and migration (USFWS 2007). To date, studies across the range of each of these two species have focused heavily on their ecology and behavior during winter hibernation and the summer maternity seasons due to the timing of WNS susceptibility and reproduction (Loeb and Winters 201, Carpenter 2017, Jackson et al., unpublished data). However, an understanding of their ecology and behavior during other parts of their life cycle is needed for effective species management and conservation, particularly in the presence of WNS.

Winter and Summer Ecology

For bats in the eastern U.S., winter hibernation is a time of energy conservation, intermittent arousal for foraging when temperatures allow, and the onset of WNS (Reeder et al. 2012, Bernard and McCracken 2017, Bernard et al. 2017). Since copulation occurs most dominantly during the fall swarming season, this is also the period when female bats store sperm for delayed fertilization in spring (Racey and Entwistle 2000). Due to the sensitive nature of hibernation and the added stressors of WNS, this period is one with some of the highest mortality for bat species (Frick et al. 2017). During the summer, both focal species use diurnal tree roosts (O'Keefe et al. 2009, Carpenter 2017, O'Keefe and Loeb 2017, Cable et al. 2020). For females, this time period is dedicated to preparing for parturition, and birthing and rearing pups. Juvenile individuals become volant and begin foraging in late July (Tuttle 1976).

Indiana Bat

This species arrives to winter hibernacula from summer roosts later than most other eastern cave bats. Arrival at caves is documented to begin late September to early October (Jackson et al., unpublished data). Indiana bats are usually found in large clusters in select areas of the cave, and fidelity to caves and roost sites within the cave are high (LaVal et al. 1977). While Indiana bats do come out of torpor during this time period, they exit the cave to forage less and exhibit longer torpor bouts than some other cave dwelling southeastern bat species (Jackson 2019).

Indiana bats migrate to summer roosts an average of 164 km and as far as 532 km from winter hibernacula from April–May, with an average of 7 nights migrating (Roby et al. 2019). During the summer, this species roosts most often under the loose or sluffing bark of trees or snags in forested areas of lower canopy cover (55–78%; O'Keefe and Loeb 2017) They forage over closed forested and riparian areas with low clutter (Callahan et al. 1997, Murray and Kurta

2004). Females roost in large maternity colonies, birthing and rearing pups during this time period, while males tend to roost alone or in smaller bachelor groups (Menzel 2001).

Tri-colored Bat

Tri-colored bats tend to arrive at winter hibernacula earlier in the fall season, beginning as early as August (Jackson et al. unpublished data). This species uses a different hibernation strategy, most often roosting singularly toward cave entrances or areas of the cave where temperatures are more stable and humidity is greater (Kunz 1982). Additionally, though occasional band recoveries do occur, cave fidelity appears to be weaker for these bats (TWRA, unpublished data). Tri-colored bats emerge from hibernation during late hibernation season in Tennessee, exhibiting higher activity than other species at cave entrances and shorter torpor bouts during this time period (Jackson 2019).

Currently, the greatest documented distance travelled by this species from winter hibernacula to summer roosts is 52.8 km (Griffin 1940), though further investigation of spring migration by this species is ongoing by biologists with Arnold Engineering Development Complex, TN. During this time, both male and female tri-colored bats roost singularly, selecting clumps of dead leaves in living trees within forested tracks near stream corridors or large, open bodies of water (Carpenter 2017, Thames et al. unpublished data). Tree roost species is not selected, but the species of leaves where the roost is located appears to be, typically being oak or hickory (Thames et al. unpublished data). Foraging activity primarily occurs over those large bodies of water (Thames et al. unpublished data).

Fall Swarming and Spring Staging

While winter and summer ecology have been heavily studied, two extremely critical time periods in the life cycle of bats have yet to be investigated: fall swarming and spring staging. Fall

swarming was described by Poole et al. (1932) as the heightened activity at cave entrances, resulting in swarm-like behavior in and around caves. During this time period, bats are returning from summer roosts and gorging themselves on insects to prepare for winter hibernation, less frequent foraging events, lower insect abundance, and surviving the damaging effects of WNS (Ewing et al. 1970, Kunz et al. 1998, Jonasson and Willis 2011, Reeder et al. 2012, Bernard and McCracken 2017, Bernard et al. 2017). As mentioned, this is also the most important time period for copulation (Rivers et al. 2005).

Though spring staging is even less documented, it is understood to be a time period during which cave dwelling bats are most sensitive to stresses. Bats are emerging from hibernation at their lowest body weight and potentially infected with WNS (Jonasson 2011). Upon emerging they have to regain the energy reserves and hydration necessary to survive spring migration to summer roosts. During this time period, female bats ovulate and release stored sperm, although some copulation also occurs (Whitaker and Hamilton 1998).

Fall swarming and spring staging are two critically important periods for bat survival and reproductive success. However, we currently know very little about Indiana and tri-colored bat activity and habitat requirements during these vital periods. Without understanding ecology and behavior throughout the full life cycle of Indiana bats and tri-colored bats, we cannot make informed and effective management decisions to improve habitat quality and availability and maximize survival and reproduction of bats affected by WNS (Silvis 2016).

Current Management Restrictions

Though little research has been conducted to understand bat ecology and behaviors in fall and spring, the effects of many land management activities on bats during these periods have been

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assumed and restrictions on prescribed burns and tree harvest, and cave area closures have been put in place.

Managing forests with tree harvest and prescribed fire has been documented to benefit bat species, specifically the endangered Indiana bat, by improving foraging habitat and providing more available roosts with low canopy cover (Boyles 2006, Cox et al. 2016). Bat activity in forested stands that have been thinned and prescribed burned is higher due to lower forest clutter, which decreases interference with flight (Cox et al. 2016). Additionally, higher availability of nocturnal flying insect prey is documented in burned areas (Armitage and Ober 2012). However, in order to protect bats from disturbance and fatalities, management practices are limited within 1 mile of hibernacula (USFWS 2017).

On high-trafficked public lands, for example within GRSM in Tennessee and North Carolina, managers have implemented cave area closures around certain caves. During these closures, visitors are not permitted within 0.8 km of the cave from September–March. Closures are not backed by data on the landscape selection around hibernacula within these distances or during these times. Additionally, landscapes surrounding other critical hibernacula within the park are not protected by closures. Without knowledge of selection of foraging and roosting sites for Indiana bats and tri-colored bats throughout their entire life cycles, we may make uninformed management decisions that might restrict beneficial practices that are proven to increase habitat availability and quality, such as prescribed burning, and inefficiently and incorrectly implement those that might protect bats, such as cave area closures.

GOAL AND OBJECTIVES

The goal of our study is to understand the ecology and behavior of Indiana and tri-colored bats, two bat species threatened by WNS, during fall swarming and spring staging in Tennessee. Our findings will fill knowledge gaps on the requirements of these declining bat species during two critical stages and will be used to make informed management decisions. More specifically, are study objectives are to:

- Establish the timing of fall swarming/spring staging activity (e.g., start, peak, end) for Indiana bat and tri-colored bat.

- Identify day roost sites (i.e., trees and caves) used by Indiana bat and tri-colored bat during fall swarming and, as applicable, explore roost site selection.

- Determine distance travelled to roosts from cave hibernacula during fall swarming/spring staging.

Since each of our sites are surrounded by large forested tracks of land, we hypothesize that, during fall swarming, both Indiana bats and tri-colored bats will roost on the landscape surrounding winter hibernacula. Timing of fall swarming and activity at cave entrances will be concentrated in September and October. Each species will select roosts with characteristics similar to those selected as summer roosts. During spring staging we hypothesize bats will emerge caves and exhibit greater activity than during winter hibernation, but less activity than during fall swarming. The timing of spring activity will fall between late February and late April.

LITERATURE CITED

Aebischer, N.J., P.A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use
from radio-tracking data. Ecology 74:1313–1325.

Aldridge H.D., and R.M. Bringham. 1988. Load carrying and maneuverability in an
insectivorous bat: a test of the 5% rule of radiotelemetry. Journal of Mammology 69:379–
382.

Allen, A.A. 1921. Banding bats. Journal of Mammalogy 2:53–57.

Amelon, S. 2006. Conservation assessment: *Pipistrellus subflavus* (Eastern Pipistrelle) in the
Eastern United States. Pages 11–30 *in* F.R. Thompson, editor. Conservation assessments
for five forest bat species in the eastern United States. General Technical Report NC-260.
U.S. Forest Service, North Central Research Station, St. Paul, MN, USA.

Anthony, E.L.P. 1988. Age determination in bats. Pages 47–57 *in* T.H. Kunz, editor. Ecological
and behavioral methods for the study of bats. Smithsonian Institution Press, Washington,
D.C., USA.

Bernard, R.F., J.T. Foster, E.V. Willcox, K.L. Parise, and G.F. McCracken, G.F. 2015.
Molecular detection of the causative agent of white-nose syndrome on Rafinesque's big-
eared bat (*Corynorhinus rafinesquii*) and two species of migratory bats in the
Southeastern USA. Journal of Wildlife Diseases 51:519–522.

Bernard, R.F., and G.F. McCracken. 2017. Winter behavior of bats and the progression of
white-nose syndrome in the southeastern United States. Ecology and Evolution 7:1487–
1496.

Bernard, R.F., E.V. Willcox, K.L. Parise, J.T. Foster, and G.F. McCracken, G.F. 2017. White-

nose syndrome fungus, *Psuedogymnoascus destructans*, on bats captured emerging from

caves during winter in the southeastern United States. BMC Zoology 2:12.

https://doi.org/10.1186/s40850-017-0021-2.

Cable, A.B., J.M. O'Keefe, J.L. Deppe, T.C. Hohoff, S.J. Taylor, and M.A. Davis. 2020. Habitat

suitability and connectivity modeling reveal priority areas for Indiana bat (*Myotis*

sodalis) conservation in a complex habitat mosaic. Landscape Ecology.

https://doi.org/10.1007/s10980-020-01125.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and

habitat use by animals. Ecological Modelling 197:516–519.

Carpenter, G.M. 2017. Bat population status and roost selection of tri-colored bats in the

Great Smoky Mountains National Park in the era of white-nose syndrome. MS Thesis.

University of Tennessee, Knoxville, TN, USA.

Carter, T.C., M.A. Menzel, B.R. Chapman, and K.V. Miller. 1999. Summer foraging and

roosting behavior of an eastern pipistrelle, *Pipistrellus subflavus*. Bat Research News

40:5–6.

Carter T.C., and J.M. Menzel. 2007. Behavior and day-roosting ecology of North American

foliage-roosting bats. Pages 60–81 *in* M. J. Lacki, J. P. Hayes, and A. Kurta, editors. Bats

in forests: conservation and management. Johns Hopkins University Press, Baltimore,

Maryland, USA.

Cox, M.R.,. E. Willcox, P.D. Keyser, G. McCracken, A.L. Vander Yacht. 2016. Bat response to

prescribed fire and overstory thinning in hardwood forest on the Cumberland Plateau,

Tennessee. Forest Ecology and Management 359:221–223.

Cryan, P.M., and R.M.R. Barclay. 2009. Causes of bat fatalities at wind turbines: Hypotheses

and Prediction. Journal of Mammalogy 90:1330–1340.

Cryan, P.M., C.U. Meteyer, J.G. Boyles, and D.S. Blehert. 2010. Wing pathology of white-nose syndrome in bats suggests life-threatening disruption of physiology. BMC Biology 8:135. https://doi.org/10.1186/1741-7007-8-135.

Davis, W.H. 1959. Disproportionate sex ratios in hibernating bats. Journal of Mammalogy 40: 16–19.

Davis, W.H., and R.E. Mumford. 1962. Ecological notes on the bat *Pipistrellus subflavus*. American Midland Naturalist 68:394–398.

Ewing, W.G., E.H. Studier, and M.J. O'Farrell. 1970. Autumn fat deposition and gross body composition in three species of *Myotis*. Comparative Biochemistry and Physiology 36: 119–129.

Fenton, M.B. 1990. The foraging behavior and ecology of animal-eating bats. Canadian Journal of Zoology 68:411–422.

Forbes, G. 2012. Technical summary and supporting information for an emergency assessment of the tri-colored bat *Perimyotis subflavus.* Committee on the status of endangered wildlife in Canada. https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry/cosewic-assessments/tri-colored-bat-technical-summary-2012.html. Accessed 30 October 2020.

Fujita, M.S., and T.H Kunz. 1984. *Pipistrellus subflavus*. Mammalian species. 228:1–6.

Geluso, K., T.R. Mollhagen, J.T. Tigner, and M.A. Bogan. 2005. Westward expansion of the eastern pipistrelle (*Pipistrellus subflavus*) in the United States, including new records from New Mexico, South Dakota, and Texas. Western North American Naturalist 65:405–409.

Gould, E. 1955. The feeding efficiency of insectivorous bats. Journal of Mammalogy 36:399–407.

Griffin, D.R. 1940. Migrations of New England bats. Bulletin of the Museum of Comparative Zoology, Harvard University 86:217–246.

Harvey, M.J., J.S. Altenbach, and T.L. Best. 2011. Bats of the United States and Canada. John Hopkins University Press. Baltimore, Maryland, USA.

Hayes, M.A. 2013. Bats killed in large numbers at United States wind energy facilities. Bioscience 63: 975–979.

Hoofer, S.R., and R.A. Van Den Bussche. 2003. Molecular phylogenetics of the chiropteran family Vespertillionidae. Acta Chiropterologica 5 supplemental:1–63.

Horn, J.W., E.B. Arnett, and T.H. Kunz. 2008. Behavioral responses of bats to operating wind turbines. Journal of Wildlife Management 72:123–132.

Hoying, K.M., and T.H. Kunz. 1998. Variation in size at birth and post-natal growth in the insectivorous bat *Pipistrellus subflavus* (Chiroptera: Vespertilionidae). Journal of Zoology. 245:15–-27.

Jackson, R.T. 2019. Hibernation activity and susceptibility of Southeastern bats to *Pesudogymnoascus destructans*, the causal agent of white-nose syndrome. MS Thesis. University of Tennessee, Knoxville, TN, USA.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Jones, C., and J. Pagels.1968. Notes on a population of *Pipistrellus subflavus* in southern Louisiana. Journal of Mammalogy 49:134–139.

Jones, C., and R.D. Suttkus. 1973. Colony structure and organization of *Pipistrellus subflavus* in southern Louisiana. Journal of Mammalogy 54:962–968.

Jonasson, K.A., and C.K.R. Willis. 2011. Changes in body condition of hibernating bats support the thrifty female hypothesis and predict consequences for populations with white-nose syndrome. PLoS ONE 6:e21061. https://doi.org/10.1371/journal.pone.0021061.

Kunz, T.H., J.A. Wrazen, C.D. Burnet. 1998. Changes in body mass and fat reserves in pre-hibernating little brown bats (*Myotis lucifugus*). Ecoscience 5:8–17.

Kurta, A., L. Winhold, J.O. Whitaker, Jr., and R. Foster. 2007. Range expansion and changing abundance of the Eastern Pipistrelle (Chiroptera: Vespertilionidae) in the central Great Lakes region. American Midland Naturalist 157:404–411.

Lacki, M.J., and J.T. Hutchinson. 1999. Communities of bats (Chiroptera) in the Grayson Lake Region of northeastern Kentucky. Journal of the Kentucky Academy of Science 6:38–44.

Lacki, M.J., S.K. Amelon, and M.D. Baker. 2007. Foraging ecology of bats in forests. Pages 82–127 *in* M. J. Lacki, J.P. Hayes, and A. Kurta, editors. Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, Maryland, USA.

Langwig, K.E., W.F. Frick, J.T. Bried, A.C. Hicks, T.H. Kunz, and A.M. Kilpatrick. 2012. Sociality, density-dependence, and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. Ecology Letters 15:1050–1057.

Langwig, K.E., W.F. Frick, R. Reynolds, K.L. Parise, K.P. Drees, J.R. Hoyt, and A.M. Kilpatrick. 2015. Host and pathogen ecology drive the seasonal dynamics of a fungal disease, white-nose syndrome. Proceedings of the Royal Society B: Biological Sciences, 282:20142335. https://doi.org/10.1098/rspb.2014.2335.

Langwig K.E., Frick W.F., Hoyt J.R., Parise K.L., Drees K.P., Kunz T.H., Foster J.T., and

Kilpatrick A.M. 2016. Drivers of variation in species impacts for a multi-host fungal

disease of bats. Philosophical Transactions of the Royal Society B: Biological Sciences,

371:20150456. http://dx.doi.org/10.1098/rstb.2015.0456.

Langwig, K.E., J.R. Hoyt, K.L. Parise, W.F. Frick, J.T. Foster, and A.M. Kilpatrick. 2017.

Resistance in persisting bat populations after white-nose syndrome

invasion. Philosophical Transactions of the Royal Society B: Biological Sciences 372:

20160044. DOI:10.1098/rstb.2016.0044.

LaVal, R.K., R.L. Clawsonm, M.L. LaVal, and W. Caire. 1977. Foraging behavior and nocturnal

activity patterns of Missouri bats, with emphasis on the endangered species *Myotis*

grisescens and *Myotis sodalis*. Journal of Mammalogy 58:592–599.

Loeb, S.C., and J.M. O'Keefe. 2006. Habitat use by forest bats in South Carolina in relation to

local, stand, and landscape characteristics. Journal of Wildlife Management 70:1210–

1218.

MacDonald, K., E. Matsui, R. Stevens, and M.B. Fenton. 1993. Echolocation calls and field

identification of the eastern pipistrelle (*Pipistrellus subflavus* Chiroptera:

Vespertilionidae), using ultrasonic bat detectors. Journal of Mammalogy 75:462–465.

McNab, B.K. 1974. The behavior of temperate cave bats in a subtropical environmental. Ecology

55:943–958.

Menu, H. 1984. Revision of the status of *Pipistrellus subflavus* (F. Cuvier, 1832). A new generic

name is proposed: *Perimyotis* new genus. Mammalia 43:409–416.

Menzel, M.A., J.M. Menzel, J.C. Kilgo, W.M. Ford, T.C. Carter and J.W. Edwards. 2003. Bats

of the Savannah River Site and vicinity. General Technical Report SRS-68. U.S. Forest Service, Southern Research Station Asheville, NC, USA.

Miller, D.A., E.B. Arnett, and M.J. Lacki. 2003. Habitat management for forest-roosting bats of North America: a critical review of habitat studies. Wildlife Society Bulletin 31:30–44.

Minnis, A.M., and D.L. Lindner. 2013. Phylogenetic evaluation of *Geomyces* and allies reveals no close relatives of *Pseudogymnoascus destructans*, comb, nov., in bat hibernacula of eastern North America. Fungal Biology 117:638–649.

National Oceanic and Atmospheric Administration. 2016. National Oceanic and Atmospheric Administration National Climate Data Center. Local climatological data. http://www.ncdc.noaa.gov/most-popular-data#loc-clim. Accessed 30 October 2020.

NatureServe. 2015. NatureServe Explorer: An online encyclopedia of life [web application]. Version 7.1. NatureServe, Arlington, Virginia. http://explorer.natureserve.org. Accessed 30 October 2020.

Norberg, U.M., and J.M.V. Rayner. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London B 316:335–427.

O'Keefe J.M., S.C. Loeb, J.D. Lanham, and H.S. Hill Jr. 2009. Macrohabitat factors affect day roost selection by eastern red bats and eastern pipistrelles in the southern Appalachian Mountain, USA. Forest Ecology and Management 257:1757–1763.

O'Keefe, J.M., and S.C. Loeb. 2017. Indiana bats roost in ephemeral, fire-dependent pine snags in the southern Appalachian Mountains, USA. Forest Ecology and Management 391:264–274.

Perry, R.W., and R.E. Thill. 2007. Tree roosting by male and female eastern pipistrelles in a

    forested landscape. Journal of Mammalogy 88:974–981.

Pierson, E.D. 1998. Tall trees, deep holes, and scarred landscapes. Pages 309–325 *in* T.H. Kunz

    and P.A. Racey, editors. Bat biology and conservation. Smithsonian Institution Press.

    Washington D.C., USA.

Ploskey, G.R., and J.A. Sealer. 1979. Lipid deposition and withdrawal before and during

    hibernation in *Pipistrellus subflavus.* Southwestern Naturalist 24:71–78.

Powers, K.E., R.J. Reynolds, W. Orndorff, and C.S. Hobson. 2015. Post-white-nose syndrome

    trends in Virginia's cave bats, 2008–2013. Journal of Ecology and the Natural

    Environment 7:123–130.

Quinn, G.M., and H.G. Broders. 2007. Roosting and foraging ecology of eastern pipistrelle

    (*Perimyotis subflavus*) in SW Novia Scotia. Report prepared for Nova Scotia Department

    of Natural Resources. Halifax, Nova Scotia, Canada.

Racey, P.A. 1988. Reproductive assessment in bats. Pages 31–43 *in* T.H. Kunz, editor.

    Ecological and behavioral methods for the study of bats. Smithsonian Institution Press,

    Washington, D.C., USA.

Reeder, D.M., C.L. Frank, G.G. Turner, C.U. Meteyer, A. Kurta, E.R. Britzke, and D.D. Blehert,

    D.S. 2012. Frequent arousal from hibernation linked to severity of infection and

    mortality in bats with white-nose syndrome. PLoS ONE 7:e38920.

    https://doi.org/10.1371/journal.pone.0038920

Reichard J.D., and T.H. Kunz. 2009. White-nose syndrome inflicts lasting injuries to the wings

    of little brown myotis (*Myotis lucifugus).* Acta Chiropterologica 11:457–464.

Rivers, N.M., R.K. Butlin, and J.D. Altringham. 2005. Genetic population structure of Natterer's

bats explained by mating at swarming sites and philopatry. Molecular Biology 14:4299–4312.

Schirmacher, M.R., S.B. Castleberry, W.M. Ford, and K.V. Miller. 2007. Habitat associations of bats in south-central Virginia. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 61:46–52.

Seaman, D.E., J.J. Millspaugh, B.J. Kernohan, G.C. Brundige, K.J. Raedeke, and R.A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

The Tennessee Chapter of the Nature Conservancy. 2015. 2015 Tennessee bat population monitoring and white-nose syndrome investigation report. Final Report prepared for Tennessee Wildlife Resources Agency. Nashville, TN, USA.

Tennessee Wildlife Resources Agency. 2005. Tennessee's comprehensive wildlife conservation strategy. Tennessee Wildlife Resources Agency. Nashville, TN, USA.

Tennessee State Wildlife Action Plan Team. 2015. Tennessee State Wildlife Action Plan. Tennessee Wildlife Resources Agency. Nashville, TN, USA.

Texas Parks and Wildlife Department. 2017) Fungus that causes white-nose syndrome in bats detected in Texas. News Release. Retrieved from: https://tpwd.texas.gov/newsmedia/releases/?req=20170323c. Accessed 23 June 2019.

Turner, G., D. Reeder, and J. Coleman. 2011. A five-year assessment of mortality and geographic spread of white-nose syndrome in North American bats and a look to the future. Bat Research News 52:13–27.

U.S. Fish and Wildlife Service. 2007. Draft Indiana Bat Recovery plan.

https://www.fws.gov/midwest/endangered/mammals/inba/inba_drftrecpln16ap07.html.
Accessed 29 October 2020.

U.S. Fish and Wildlife Service. 2015. Endangered and threatened wildlife and plants; threatened
species status for the northern long-eared bat with 4(d) Rule. U.S. Federal Register 80:
17974–18033.

U.S. Fish and Wildlife Service. 2015a. New Jersey Species Being Evaluated for Possible Listing
under the Endangered Species Act.

http://www.fws.gov/northeast/njfieldoffice/pdf/Evaluated_Species.pdf. Accessed 30
October 2020.

U.S. Fish and Wildlife Service. 2017. Conservation Strategy for Forest-dwelling Bats in
Tennessee. https://www.fws.gov/southeast/pdf/strategy/conservation-strategy-for-forest-
dwelling-bats-in-tennessee.pdf. Accessed 18 November 2020.

U.S. Fish and Wildlife Service. 2020. Where is WNS Now.

https://www.whitenosesyndrome.org/where-is-wns. Accessed 30 October 2020.

U.S. Geological Survey. 2016. White-nose syndrome threatens the survival of hibernating bats
in North America. Retrieved from: www.fort.usgs.gov/ science-feature. Last accessed:
June 23, 2019.

Veilleux, J.P., J.O. Whitaker, and S.L.Veilleux. 2003. Tree-roosting ecology of reproductive
female eastern pipistrelles, *Pipistrelles subflavus,* in Indiana. Journal of Mammalogy 84:
1068–1075.

Verant, M.L., C.U. Meteyer, J.R. Speakman, P.M. Cryan, J.M. Lorch, and D.S. Blehert. 2014.

White-nose syndrome initiates a cascade of physiological disturbances in the hibernating bat host. BMC Physiology 14:10. https://doi.org/10.1186/s12899-014-0010-4.

Voight, C.C., and T. Kingston, editors. 2016. Bats in the Anthropocene: Conservation of Bats in a Changing World, Springer, NY, USA.

Walley, H.D., and W.L. Jarvis. 1971. Longevity record for *Pipistrellus subflavus.* Illinois Academy of Science 64:305.

Warnecke, L., J.M. Turner, T.K. Bollinger, V. Misra, P.M. Cryan, D.S. Blehert, G. Wibbelt, and C.K.R. Willis. 2013. Pathophysiology of white-nose syndrome in bats: A mechanistic model linking wing damage to mortality. Biology Letters 9:20130177. https://doi.org/10.1186/s12899-014-0010-4.

Whitaker, J.O. 1998. Life history and roost switching in six summer colonies of eastern pipistrelles in buildings. Journal of Mammalogy 79:651–659.

Whitaker, J.O., and W.J. Hamilton. 1998. Mammals of the Eastern United States. Cornell University Press. Ithaca, New York.

Winchell, J.M., and T.H. Kunz. 1996. Day-roosting activity budgets of the eastern pipistrelle bat, *Pipistrellus subflavus* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 74:431–441.

Wimsatt, W.A. 1945. Notes on breeding behavior, pregnancy, and parturition in some vespertilionid bats of the eastern United States. Journal of Mammalogy 26:23–33.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in homerange studies. Ecology 70:164–168.

CHAPTER 2: DETERMINING THE TIMING OF FALL SWARMING AND SPRING STAGING ACTIVITY OF INDIANA BAT (*MYOTIS SODALIS*) AND TRI-COLORED BAT (*PERIMYOTIS SUBFLAVUS*) USING PASSIVE INTEGRATED TRANSPONDER ANALYSIS

This chapter is modified from a paper in preparation: M.E. Tate, E.V. Willcox, J. Zobel, W.H. Stiver. *In prep.* Determining the timing of fall swarming and spring staging activity of Indiana bat (*Myotis sodalis*) and tri-colored bat (*Perimyotis subflavus*) using passive integrated transponder analysis. Planned submission to Journal of Mammalogy.

In this chapter I use the term "we" in reference to my co-authors and myself. The chapter is formatted for publication in the Journal of Mammalogy. I am responsible for all the following: (1) project design and data collection, (2) literature review, (3) statistical analyses, and (4) all writing. My co-authors advised on the design of the project, assisted with field work, and/or edited of the manuscript.

ABSTRACT

The Indiana bat and tri-colored bat populations have been severely impacted by white-nose syndrome (WNS). Management prescriptions and restrictions are implemented to help mitigate further declines but are not backed with data. In order to make informed management decisions, we must understand the timing of each life stage. Two time periods that have been neglected in historical studies include fall swarming and spring staging. These two time periods surround winter hibernation, the most concentrated time of fatalities from WNS. We used Passive Integrated Transponder tags to investigate the timing of increased activity at hibernacula for both species. We found that tri-colored bats arrive at hibernacula early in the fall swarming period (mid- August) and continue increased activity through the end of September. Indiana bats arrive mid-September and continue increased activity through mid-October. In the spring, tir-colored bats were active from February 19–April 22, while Indiana bats were active March 26–May13.

INTRODUCTION

Caves serve as critically important habitat for 8 of the 16 bat species in Tennessee (U.S. Fish and Wildlife Service [USFWS] 2016a). Bats use caves for fall swarming (i.e., diurnal roosting, mating, building calories for hibernation), hibernation (i.e., reserving energy and surviving winter and disease), and spring staging (i.e., preparing for migration and implanting pregnancy; Poole et al. 1932, Silvis et al. 2016). Two cave-dwelling bat species have been

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especially impacted by the devastating fungal disease white-nose syndrome (WNS; Langwig et al. 2016, U.S. Fish and Wildlife Service [USFWS] 2016), a disease caused by the fungal pathogen *Psuedogymnoascus destructans* (*Pd*) introduced to North America in 2005. The Indiana bat was federally listed as endangered in 1967 but, pre-WNS, populations were increasing, largely as a result of extensive management activities that conserved hibernacula and summer maternity habitat (Silvis et al. 2016). Since the introduction of WNS, Indiana bat populations have again experienced dramatic declines across the eastern U.S. and the species is now threatened with local extirpation across parts of its range (Thogmartin et al. 2012 and 2013, Langwig et al. 2016, Frick et al. 2017). In Great Smoky Mountains National Park (GRSM), research indicates summer capture rates of these species have declined by 95% (O'Keefe et al. 2019) and at one of the historically largest known Indiana bat hibernacula in the state of Tennessee, recent estimates indicate the number of hibernating individuals has dropped by 90% (GRSM unpublished data). Prior to WNS, the tri-colored bat was relatively common and locally abundant but, like the Indiana bat, has undergone significant population declines across the eastern U.S. that could result in local extirpations (Ford et al. 2011, Frick et al. 2015). Research conducted in GRSM suggests summer capture rates of tri-colored bats have declined by 73–77% post-WNS (Carpenter 2017, O'Keefe et al. 2019). Winter counts of tri-colored bats suggest up to 98% declines since the outbreak of the disease (GRSM unpublished data). As a result of declines across its range, the species was recently petitioned for federal listing (The Center for Biological Diversity and Defenders of Wildlife 2016).

The majority of research on Indiana bats and tri-colored bats has historically focused on the winter hibernation and summer maternity seasons and neglected fall swarming and spring staging. During fall swarming, the period that falls between the end of the summer maternity

season and beginning of the winter hibernation season, there is a drastic increase in bat activity around cave hibernacula. One of the primary reasons for this increase in activity is mating (Poole et al. 1932, Rivers et al. 2005, Lowe et al. 2012). During this period, bats also increase their foraging activity on the landscape and individuals gorge themselves on insects to increase energy reserves prior to going into prolonged bouts of torpor (Poole et al. 1932). Eventually, fall swarming activity tapers off as bats enter hibernation, a time of decreased foraging activity and increased torpor and energy conservation (Jonasson et al. 2011). The effects of WNS include dehydration, disruption of metabolic processes, more frequent arousal from torpor, and, often, increased emergence from cave hibernacula (Reeder et al. 2012, Cryan et al. 2013, Verant et al. 2014). These effects frequently lead to mortality during the hibernation season (Reichard et al. 2014, Maslo et al. 2015). However, not every individual infected with WNS dies. Infected bats that survive winter hibernation emerge in the spring still suffering from the effects of the disease, including dehydration, emaciation, and overall poor physiological condition (Fuller et al. 2011, Meteyer et al. 2012, Reichard et al. 2014, Maslo et al. 2015). In addition to fighting remaining effects of WNS, bats are replenishing depleted energy in preparation for the spring migration journey (Meierhofer et al. 2018) during this time period. Because females are implanting pregnancy during this time, reproductive efforts in the spring and summer are likely negatively impacted by the resulting poor body condition and stress, leading to lower recruitment in already declining populations (Davy et al. 2016, Wilcox and Willis 2016).

As our understanding of the importance of fall swarming and spring staging in relation to energetic maintenance, the survival of bats infected with WNS, and eventual population recruitment becomes further understood, so does the need to know the specific timing of arrival

at hibernacula, increased behavior around cave entrances, the entering of hibernation, spring emergence and activity around cave entrances, and the start of spring migration.

Due to the listing of the Indiana bat, USFWS placed tree harvest restrictions including and surrounding the maternity period. These protections currently limit harvest to the hibernation period, allowing cuts to take place only from November 15–March 31 (USFWS 2020). More recently and in response to WNS driven declines and as an effort to protect affected and imperiled bat species, state and federal managers placed recreational and management restrictions on areas surrounding hibernacula to protect these two species. Restrictions include, but are not limited to, cave area closures and restriction of hazard tree removal, mechanical management, and prescribed fire practices. Some of these management practices may benefit imperiled bat species (e.g., prescribed fire and forest stand basal area reduction; Boyles 2006 Cox et al. 2016). Due to a lack of complete life history data and research on most impacted species, these restrictions were not backed by data. There is also no consistency across either the Indiana bat or tri-colored bat range when addressing restrictions (B. Stiver, personal communication, February 2019). Therefore, a detailed timeline of bat activity at cave entrances combined with data on roost proximity to hibernacula would allow for more informed and consistent management decisions.

The goal of our study was to determine activity patterns of Indiana bats and tri-colored bats during fall swarming and spring staging. Specifically, our objective was to define the timeline for hibernacula arrival, peak of fall swarming activity, beginning of hibernation, peak of spring emergence and staging, and beginning of spring migration. Based on acoustic data collected by Muthersbaugh et al. (2019), we predicted that bat activity would begin at cave entrances in September and taper off by the beginning of November, signaling the start of

hibernation. While Muthersbaugh et al. (2019) found emergence to begin mid-March, we predicted a slightly earlier emergence in March based on Jackson (2019) finding emergence activity increasing in late winter. Furthermore, we predicted that spring migration would begin at the end of March.

METHODS AND MATERIALS

Study Area

Our study was conducted at three cave hibernacula in East Tennessee: Blount Cave, Campbell Cave, and White Cave (Figure 2.1). Caves were selected by highest number of Indiana bat and tri-colored bat hibernacula counts over the past years with cave entrances that were less than 10 m^2 to fit the length of the PIT tag antenna. Blount Cave is located in GRSM and is managed by NPS. Prior to WNS, Blount Cave was the largest known Indiana bat hibernaculum in the state. A population census conducted in February 2019 indicated Indiana bat numbers at this site have declined from ~8,000 to ~750 since it was confirmed WNS positive in the winter of 2009/10. Tri-colored bats also exhibit relatively high use of this cave. Campbell Cave, managed by Tennessee Wildlife Resources Agency (TWRA) and The Nature Conservancy (TNC), contains approximately 1,000 bats, including ~60 Indiana bats and between 60–150 tri-colored bats annually. White Cave, managed by TWRA, contains approximately 400 bats, including ~70 Indiana bats and between 30–200 tri-colored bats annually.

Bat Capture

During fall swarm (September 1–October 31) 2016–2019 and spring emergence (March 1–April 30) 2016–2019, we used mist nets (Avinet Inc., Dryden, NY; mesh diameter: 75/2, 2.6m high, 4 shelves, 4–9 m wide) to capture bats flying at cave entrances. During fall swarm, we mist-netted at each cave 1–3 times per week. We opened mist nets 30 minutes before civil sunset and left them open for 2–5 hours, or until temperatures fell below 0°C. We recorded species, sex,

reproductive status, wing damage index (Reichard and Kunz 2009), and age (by degree of epiphyseal fusion; Kunz 1988) of each bat captured, as well as forearm length (mm) and weight (g). We fitted each bat with a uniquely identifiable 2.4 mm or 2.9 mm (depending on species) forearm band (Porzana, Ltd., Icklesham, East Sussex, UK) and 12 mm passive integrated transponder (PIT) tag (HDX12 Preloaded, Biomark, Inc., Boise, ID). We implanted PIT tags subcutaneously, just below the shoulder blades in the interscapular region (O'Shea et al. 2010, Britzke et al. 2012, Johnson et al. 2012.) using an implant gun (MK25, Biomark, Inc., Boise, ID). We only implanted PIT tags in bats with a body mass ≥ 4.5 g and no obvious health issues to reduce potential stress from handling bats preparing for hibernation. All bats were released at the site of capture. We followed decontamination procedures outlined by the U.S. Fish and Wildlife Service (Shelley et al. 2013). Capture, handling, sample collection, radio-transmitter application, and PIT tagging protocols were approved by the University of Tennessee Institutional Animal Care and Use Committee (IACUC 2253-0317), as developed by the American Society of Mammalogists (Sikes et al. 2016) and authorized under scientific collection permits from the USFWS (TE35313B-3), NPS (GRSM-2018-SCI-1253), and TWRA (3742).

Passive Integrated Transponder Tag Data Collection

Passive integrated transponders are uniquely coded tags that are detected within 2 m of an associated antenna and reader, providing an opportunity to collect long-term monitoring and movement information without the need for recapture (Gibbons and Andrews 2004, Rigby et al. 2011). We deployed a 15 m long PIT tag cable antenna, attached to a PIT tag data-logger with an external power source, around the entrance of each cave (IS1001 Cord Antenna System, Biomark, Inc., Boise, ID). We placed the PIT tag data logger outside caves to minimize disturbance during data downloads and equipment checks. We downloaded data from each

receiver weekly, when possible, and at a minimum biweekly. Data loggers ran from August 15–

May 25, beginning in August 2016 and ending in February 2020. Due to the life span of the

battery systems, extreme weather events, or other technical difficulties, our PIT tag systems did

not run continuously. Systems were down for a maximum of 4 consecutive days during our

sampling periods.

Statistical Analysis

Passive integrated transponder tag detections were recorded every 300th of a second. To identify

actual bat activity and remove cases of bats roosting near the antenna, we excluded any

detections that were less than 0.10 seconds apart. We conducted a nonparametric Kruskal-Wallis

test to test that there were no differences in start and end dates of increased activity across caves

due to geographical locations. As there were no difference among caves, we combined data for

all caves and all years for analysis. Due to low capture rates of females, we analyzed data by

species without separating by sex.

In order to isolate the timing of fall swarming and spring emergence, we used

changepoint detection analysis. This statistical technique is commonly used in time-series

applications to identify the moments when a stream of data significantly diverges from the

previous pattern (e.g., Gallagher et al. 2013; Costa et al. 2016). When applied to our longitudinal

activity data, changepoint detection identifies the time points when bat activity spikes in the

spring and fall.

The segment neighborhood algorithm was selected for determining multiple changepoints

(Auger and Lawrence 1989). The method essentially conducts a hypothesis test comparing the

maximum log-likelihood across all possible changepoints (alternative hypothesis) to the log-

likelihood assuming no changepoints (null hypothesis). A significant difference identifies a

changepoint. The method continues searching for additional changepoints through an optimization routine (dynamic programming), ultimately listing all significant points. We used this technique to determine the starting and ending week of spring emergence and fall swarming, respectively, and their associated ranges and confidence intervals (across all caves and all years). Significant changepoints were determined using an Akaike Information Criterion (AIC) penalty and a normal test statistic (Akaike 1974, Killick and Eckley 2014, Hinkley 1970). In addition, when multiple changepoints were detected coinciding with traditional peak activity, these points were checked against observed trends to select the most reasonable estimates. For more information on changepoint analysis and associated methods, see Killick and Eckley (2014) and Tartakovsky et al. (2014). Results are displayed as an average of PIT tag detections for all years at all caves by Julian week. All analyses were conducted in R (R Core Team 2018) and the 'changepoint' package (Killick et al. 2016).

RESULTS

Bat Capture

We conducted 122 nights of netting (10,536.5 net hours) across our 3 study cave hibernacula. We captured 1072 bats, 725 of which were our two focal species. We captured 445 Indiana bats (41.5% of total bat captures) and 280 tri-colored bats (26.1% of total bat captures). Only 4% (n = 18) of Indiana bats and 12% (n = 34) of tri-colored bats captured were female.

Passive Integrated Transponder Tags

Overall bat activity did not differ across caves. Timing of fall swarming and spring staging increased activity for all bat species (Figure 2.2, Figure 2.3, and Figure 2.4).

Indiana Bat

We implanted 382 Indiana bats with PIT tags. We detected 89% of all PIT tagged Indiana bats at least once over the course of the study. Using changepoint analysis, we identified two time

periods of increased Indiana bat activity at cave entrances during fall swarming and spring staging (Figure 2.5). Individuals began arriving at the beginning of September. We detected the start of increased activity September 10, with the highest peak in activity the first week of October. Increased swarming activity continued through October 21, with little to no activity beginning the first week of November. We then detected emergence in the spring beginning March 26 with peak activity the last week of April. The increase in Indiana bat spring behavior ended May 13. We had 5000–25,000 PIT tag detections in the fall and 2500 PIT tag detections in the spring.

Tri-colored Bat

A total of 221 tri-colored bats received PIT tags. Seventy-six percent of PIT tagged tri-colored bats were detected at least once throughout the study. Similar to Indiana bat activity, there were two time periods of increased activity at cave entrances in fall and spring (Figure 2.6). We detected the start of increased tri-colored bat fall swarming activity on August 20. Peak activity occurred immediately and lasted about two weeks. Overall increased activity continued through the end of September, tapering off by September 30. Though not detected as significantly increased, activity did persist through the beginning of November before almost completely ceasing. We detected the initial increase in activity post-hibernation in late February, with spring activity continuing through mid-April, ceasing by May. We collected an average of 270–800 PIT tag detections during the fall and 10–160 PIT tag detections during the spring.

DISCUSSION

This is the first study to use PIT tag technology to investigate the fall swarming and spring staging behavior of caverniculous bat species. Our data defines the timeline of each period as well as peaks in overall bat activity outside of caves.

Indiana bats arrived at our cave sites in mid-September. This differs from pre-WNS fall swarming data showing Indiana bats arriving a hibernacula throughout August in South Dakota, where weather differences may require earlier arrival (Cope and Humphrey 1977). While fall migration data is lacking, spring migration of the Indiana bat shows an average of 7.3 nights of migration (Roby et al. 2019). If we assume similar fall migration lengths, this means Indiana bats are leaving summer maternity areas as early as the beginning of September. The largest peak in Indiana bat activity at cave entrances throughout the year occurred during the first week in October, indicating that this time period holds the greatest risk of human-bat interaction at cave entrances.

Jackson et. al (2019) found that only 10% of Indiana bats emerge from caves during winter season, highlighting the importance to individuals of boosting fat reserves prior to entering hibernation (Frick et al. 2017). An acoustic study by Muthersbaugh et al. (2019) found bat activity tapering off mid-October in the Appalachians, which only slightly differs from our findings that detected continued activity through the first week of November. Disparities may lie in detection methods and locations (PIT tag at cave entrance vs. acoustic detector on the landscape). Our data emphasize an importance in the final week of October and first of November, as these likely provide the last major foraging opportunities for several months. Activity this late into the fall swarming season could provide extra time foraging and increased fat stores (Kunz et al. 1998, Frick et al. 2017, Cheng et al. 2019), explaining lower arousal frequency during hibernation (Thomas et al. 1990, Park et al. 2000, Jackson et al. 2019). Therefore, our findings indicate that in relation to Indiana bat protections, the USFWS timber harvest start date of November 15th is appropriate to reduce arousing bats in tree roosts on the landscape.

While studies have found that some Indiana bats were active in February (Jackson 2019), we did not detect a significant increase in activity until the last week of March, signifying the beginning of emergence from hibernation. The highest peak in activity during the spring was in the last week of April and tapered off by the middle of May, confirming the USFWS accepted start of the maternity season on May 15th. The cut-off date of March 31st may need to be shifted to mid-March to include protections for all increased spring activity. These protections may be imperative to the survival of individuals that emerge from hibernation sick and weakened from white-nose syndrome (Turner et al. 2011, Meierhofer et al. 2018).

While historically accepted shorter migration routes were once used to explain early hibernacula arrival, tri-colored bat migration has recently been documented as long as 243 km straight line distance (Samoray et. al 2019). Because we detected increased tri-colored bat activity in the middle of August, this species may leave summer maternity areas earlier than other caverniculous species. The largest peak in activity was immediately after arrival, though we detected increased activity through the end of September. Fall swarming activity occurring and tapering off earlier may affect fat reserves entering and throughout hibernation (Cheng et al. 2019) due to less foraging activity and a longer hibernation period, which could contribute to lower survival of hibernation and WNS.

Studies show that since the onset of WNS, tri-colored bats begin arousing from torpor more frequently throughout late hibernation, likely due to depleted fat reserves (Reeder et al. 2012, Bohn et al. 2016, Langwig et al. 2016, Bernard et al. 2017, Jackson et al. 2019). Early spring emergence could be the result of sickness (Reeder et al. 2012, Bohn et al. 2016, Langwig et al. 2016). We detected increased spring staging activity beginning mid to late February and continuing through mid to late April. Therefore, pending federal listing results, the USFWS

timber harvest start date would include fall activity protections, but neglect spring emergence. In order to reduce topor disruption, potential forced roost switching, and additional disturbance post-emergence and when they are potentially at the weakest, most sick stage of WNS (McAlpine et al. 2012, Reeder et al. 2012, Carr et al. 2014, Langwig et al. 2016, Bernard et al. 2017), the cutoff date would need to be shifted to mid-February. While Samoray et al. (2019) tracked one female tri-colored bat during spring migration beginning April 27th, our data suggests the majority of tri-colored bats leave cave areas and begin migration earlier. This could suggest earlier arrival a maternity sites and earlier implantation and birth of tri-colored bat pups than previously thought.

For both species, we detected lower activity at cave entrances in spring compared to fall. This suggests less time swarming at the cave entrance, less time attempting to mate in the spring, and quickly initiating migration (Hall 1962). Reduced swarming activity also reduces human-bat interaction risk during this time period. Additionally, peaks in spring activity appeared to be less defined than those in fall, likely due to ambient temperatures substantially impacting bat activity in the spring and not in the fall (Muthersbaugh et al. 2019).

We have outlined the timeline for Indiana bats and tri-colored bat at hibernacula during fall swarming and spring staging, two time periods neglected in previous studies. Our study only explored activity at cave entrances, limiting knowledge of movements across the landscape during this time period. Roost locations and selections should be investigated (Chapter 3), as well as foraging site selection by both species to determine accurate protective buffer zones. Additionally, more specific impacts of roost site or foraging site disturbances on bats and their ability to survive WNS should be assessed.

ACKNOWLEDGMENTS

LITERATURE CITED

Allen, A.A. 1921. Banding bats. Journal of Mammalogy 2:53–57.

Amelon, S. 2006. Conservation assessment: *Pipistrellus subflavus* (Eastern Pipistrelle) in the Eastern United States. Pages 11–30 *in* F.R. Thompson, editor. Conservation assessments for five forest bat species in the eastern United States. Gen. Tech. Rep. NC- 260. U.S. Forest Service, North Central Research Station, St. Paul, MN, USA.

Anthony, E.L.P. 1988. Age determination in bats. Pages 47–57 *in* T.H. Kunz, editor. Ecological and behavioral methods for the study of bats. Smithsonian Institution Press, Washington, D.C., USA.

Aldridge H.D., and R.M. Bringham. 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5% rule of radiotelemetry. Journal of Mammology 69:379–382.

Bernard, R.F., Foster, J.T., Willcox, E.V., Parise, K.L., and McCracken, G.F. 2015. Molecular detection of the causative agent of white-nose syndrome on Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) and two species of migratory bats in the Southeastern USA. Journal of Wildlife Diseases, 51: 519–522.

Bernard, R.F., and G.F. McCracken, G.F. 2017. Winter behavior of bats and the progression of white-nose syndrome in the southeastern United States. Ecology and Evolution 7:1487–1496.

Bernard, R.F., E.V. Willcox, K.L. Parise, J.T. Foster, and G.F. McCracken. 2017. White-nose syndrome fungus, *Psuedogymnoascus destructans*, on bats captured emerging from caves during winter in the southeastern United States. BMC Zoology, 2: doi.org/10.1186/s40850-017-0021-2.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling, 197:516–519.

Carpenter, Grace Marie. 2017. Bat population status and roost selection of tri-colored bats in the Great Smoky Mountains National Park in the era of white-nose syndrome. MS Thesis. University of Tennessee, Knoxville, TN, USA.

Carr, J.A, R.F. Bernard, and W.H. Stiver. 2015. Unusual bat behavior during winter in Great Smoky Mountains National Park. Southeastern Naturalist 13:N18–N21.

Carter T.C., and J.M. Menzel. 2007. Behavior and day-roosting ecology of North American foliage-roosting bats. Pages 60-81 *in* M. J. Lacki, J. P. Hayes, and A. Kurta, editors. Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, Maryland, USA.

Carter, T.C., M.A. Menzel, B.R. Chapman, K.V. Miller. 1999. Summer foraging and roosting behavior of an eastern pipistrelle, *Pipistrellus subflavus*. Bat Research News. 40:5–6.

Cheng, T.L., A. Gerson, M.S. Moore, J.D. Reichard, J. DeSimone, C.K. Willis, and A.M. Kilpatrick. 2019. Higher fat stores contribute to persistence of little brown bat populations with white-nose syndrome. Journal of Animal Ecology 88:591–600.

Costa, M., A.M.P. Gonçalves, and L. Teixeira. 2016. Change-point detection in environmental time series based on the informational approach. Electronic Journal of Applied Statistical Analysis. 9:267–296. DOI:10.1285/i20705948v9n2p267.

Cox, M.R.,. E. Willcox, P.D. Keyser, G. McCracken, A.L. Vander Yacht. 2016. Bat response to prescribed fire and overstory thinning in hardwood forest on the Cumberland Plateau, Tennessee. Forest Ecology and Management 359:221–223.

Cryan, P.M., and R.M.R. Barclay. 2009. Causes of bat fatalities at wind turbines: Hypotheses and Prediction. Journal of Mammalogy 90:1330–1340.

Cryan, P.M., C.U. Meteyer, J.G. Boyles, and D.S. Blehert. 2010. Wing pathology of white-nose syndrome in bats suggests life-threatening disruption of physiology. BMC Biology 8:135.

Davis, W.H. 1959. Disproportionate sex ratios in hibernating bats. Journal of Mammalogy 40:16–19.

Davis, W.H., and R.E. Mumford. 1962. Ecological notes on the bat *Pipistrellus subflavus*. American Midland Naturalist 68:394–398.

Davy, C.M., M.E. Donaldson, C.K. Willis, B.J. Saville, L.P. McGuire, H. Mayberry, A. Wilcox, G. Wibbelt, V. Misra, T. Bollinger, and C.J. Kyle. 2017. The other white-nose syndrome transcriptome: Tolerant and susceptible hosts respond differently to the pathogen *Pseudogymnoascus destructans*. Ecology and Evolution 7:7161–7170. https://doi.org/10.1002/ece3.3234.

Fenton, M.B. 1990. The foraging behavior and ecology of animal-eating bats. Canadian Journal of Zoology 68:411–422.

Forbes, G. 2012. Technical Summary and Supporting Information for an Emergency Assessment of the Tri-colored Bat *Perimyotis subflavus.* Committee on the status of endangered wildlife in Canada. https://www.registrelepsararegistry.gc.ca/virtual_sara/files/cosewic/ca_pipistrelle_tricolored_bat_0212_e.pdf. Accessed 22 December 2015.

Ford, W.M., E.R. Britzke, C.A. Dobony, J.L., Rodrigue, and J.B. Johnson. 2011. Patterns of acoustical activity of bats prior to and following white-nose syndrome occurrence. Journal of Fish and Wildlife Management, 2:125–134.

Frick, W.F., J.F. Pollock, A.C. Hicks, K.E. Langwig, D.S. Reynolds, and G.G. Turner, G.G. 2010. An emerging disease causes regional population collapse of a common North American bat species. Science 329:679–682.

Frick, W.F., D.S. Reynolds, T.H. and Kunz. 2010. Influence of climate and reproductive timing on demography of little brown myotis *Myotis lucifugus*. Journal of Animal Ecology 79: 128–136.

Frick, W.F., S.J. Puechmaille, J.R. Hoyt, B.A. Nickel, K.E. Langwig, J.T. Foster, and A.M. Kilpatrick. 2015. Disease alters macroecological patterns of North American bats. Global Ecology and Biogeography 24:741–749.

Frick, W.F., E.F. Baerwald, J.F. Pollock, R.M.R. Barclay, J.A. Szymanski, T.J. Weller, A.L. Russell, S.C. Leob, R.A. Medellin, and L.P. McGuire. 2017. Fatalities at wind turbines may threaten population viability of a migratory bat. Biological Conservation 209:172– 177.

Fujita, M.S., and T.H Kunz. 1984. *Pipistrellus subflavus*. Mammalian species. 228:1–6

Gallagher, C., R. Lund, and M. Robbins. 2013. Changepoint detection in climate time series with long-term trends. Journal of Climate 26:4994–5006.

Geluso, K., T.R. Mollhagen, J.T. Tigner, and M.A. Bogan. 2005. Westward expansion of the eastern pipistrelle (*Pipistrellus subflavus*) in the United States, including new records from New Mexico, South Dakota, and Texas. Western North American Naturalist 65:405–409.

Gibbons, W.J., and Andrews, K.M. 2004. PIT tagging: simple technology at its best. Bioscience, 54:447–454.

Gould, E. 1955. The feeding efficiency of insectivorous bats. Journal of Mammalogy 36:399–

407.

Griffin, D.R. 1940. Migrations of New England bats. Bulletin of the Museum of Comparative

Zoology 86:217–246.

Hall, J. 1962. A life history and taxonomic study of the Indiana bat, *Myotis sodalis*. Reading

Public Museum and Art Gallery Publication 12:1–68.

Harvey, M.J., J.S. Altenbach, and T.L. Best. 2011. Bats of the United States and Canada. John

Hopkins University Press. Baltimore, MD, USA.

Hayes, M.A. 2013. Bats killed in large numbers at United States wind energy facilities.

Bioscience 63:975–979.

Hoofer, S.R. and R.A. Van Den Bussche. 2003. Molecular phylogenetics of the chiropteran

family Vespertillionidae. Acta Chiropterologica Supllemental 5:1–63.

Horn, J.W., E.B. Arnett and T.H. Kunz. 2008. Behavioral responses of bats to operating wind

turbines. Journal of Wildlife Management 72:123–132.

Hoying, K.M. and T.H. Kunz. 1998. Variation in size at birth and post-natal growth in the

insectivorous bat *Pipistrellus subflavus* (Chiroptera: Vespertilionidae). Journal of

Zoology. 245:15–27.

Humphrey, S. R., J.B. Cope. 1977. Survival rates of the endangered Indiana bat, *Myotis sodalis*.

Journal of Mammalogy 58:33–36.

Jackson, R.T. 2019. Hibernation activity and susceptibility of Southeastern bats to

Pesudogymnoascus destructans, the causal agent of white-nose syndrome. MS Thesis.

University of Tennessee, Knoxville, TN, USA.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating

resource preference. Ecology 61:65–71.

Johnson, J.S., M.J. Lacki, S.C. Thomas, and J.F. Grider. 2012. Frequent arousals from winter

    torpor in Rafinesque's big-eared bat (*Corynorhinus rafinesquii*). PLoS ONE,

    https://doi.org/10.1371/journal.pone.0049754.

Jonasson, K. A., & Willis, C. K. 2011. Changes in body condition of hibernating bats support the

    thrifty female hypothesis and predict consequences for populations with white-nose

    syndrome. PLoS ONE 6: e21061. https://doi.org/10.1371/journal.pone.0021061

Jones, C. and J. Pagels. 1968. Notes on a population of *Pipistrellus subflavus* in southern

    Louisiana. Journal of Mammalogy 49:134–139.

Jones, C. and R.D. Suttkus. 1973. Colony structure and organization of *Pipistrellus subflavus* in

    southern Louisiana. Journal of Mammalogy 54:962–968.

Kunz, T.H., editor. 1988. Ecological and behavioral methods for the study of bats. Smithsonian

    Institution Press, Washington, DC, USA.

Kurta, A., L. Winhold, J.O. Whitaker, Jr., and R. Foster. 2007. Range expansion and changing

    abundance of the Eastern Pipistrelle (Chiroptera: Vespertilionidae) in the central Great

    Lakes region. American Midland Naturalist 157:404–411.

Lacki, M.J., and Hutchinson, J.T. 1999. Communities of bats (Chiroptera) in the Grayson Lake

    Region of northeastern Kentucky. Journal of the Kentucky Academy of Science 60: 38–

    44.

Lacki, M.J., S.K. Amelon, and M.D. Baker. 2007. Foraging ecology of bats in forests. Pages 82-

    127 *in* M.J. Lacki, J.P. Hayes, and A. Kurta, editors. Bats in forests: conservation and

    management. Johns Hopkins University Press, Baltimore, Maryland, USA.

Langwig, K.E., W.F. Frick, J.T. Bried, A.C. Hicks, T.H. Kunz, and A.M. Kilpatrick. 2012.

    Sociality, density-dependence and microclimates determine the persistence of

populations suffering from a novel fungal disease, white-nose syndrome. Ecology
Letters 15:1050–1057.

Langwig, K.E., W.F. Frick, R. Reynolds, K.L. Parise, K.P. Drees, J.R. Hoyt, and A.M.
Kilpatrick, A. M. 2015. Host and pathogen ecology drive the seasonal dynamics of a
fungal disease, white-nose syndrome. Proceedings of the Royal Society B: Biological
Sciences 282. https://doi.org/10.1098/rspb.2014.2335.

Langwig K.E., W.F. Frick, J.R. Hoyt, K.L. Parise, K.P. Drees, T.H. Kunz, J.T. Foster, and A.M.
Kilpatrick A.M. 2016. Drivers of variation in species impacts for a multi-host fungal
disease of bats. Philosophical Transactions of the Royal Society B: Biological Sciences
371. https://doi.org/10.1098/rstb.2015.0456.

Langwig, K.E., J.R. Hoyt, K.L. Parise, W.F. Frick, J.T. Foster, and A.M. Kilpatrick. 2017.
Resistance in persisting bat populations after white-nose syndrome
invasion. Philosophical Transactions of the Royal Society B: Biological Sciences 372.
DOI:10.1098/rstb.2016.0044.

Loeb, S.C., and J.M. O'Keefe. 2006. Habitat use by forest bats in South Carolina in relation to
local, stand, and landscape characteristics. Journal of Wildlife Management 70:1210–
1218.

Lowe, A. J. 2012. Swarming behaviour and fall roost-use of little brown (Myotis lucifugus), and
northern long-eared bats (Myotis septentrionalis) in Nova Scotia, Canada.

MacDonald, K., E. Matsui, R. Stevens, and M.B. Fenton. 1993. Echolocation calls and field
identification of the eastern pipistrelle (*Pipistrellus subflavus* Chiroptera:
Vespertilionidae), using ultrasonic bat detectors. Journal of Mammalogy 75:462–465.

McAlpine, D.F., K.J. Vanderwolf, J.F. Graham, and D. Malloch. 2011. Consumption of bats
(M*yotis* spp.) by raccoons (*Procyon lotor*) during an outbreak of white-nose syndrome in
New Brunswick, Canada: implications for estimates of bat mortality. Canadian Field
Naturalist 125:157–160.

McNab, B.K. 1974. The behavior of temperate cave bats in a subtropical environmental. Ecology
55:943–958.

Meierhofer, M. B., Johnson, J. S., Field, K. A., Lumadue, S. S., Kurta, A., Kath, J. A., & Reeder,
D. M. 2018. Bats recovering from white-nose syndrome elevate metabolic rate during
wing healing in spring. Journal of Wildlife Diseases 54:480–490.

Menu, H. 1984. Revision of the status of *Pipistrellus subflavus* (F. Cuvier, 1832). A new generic
name is proposed: *Perimyotis* new genus. Mammalia 43:409–416.

Menzel, M.A., J.M. Menzel, J.C. Kilgo, W.M. Ford, T.C. Carter and J.W. Edwards. 2003. Bats
of the Savannah River Site and vicinity. U.S. Forest Service, Southern Research Station.
General Technical Report SRS-68. Asheville, NC, USA.

Miller, D.A., E.B. Arnett, and M.J. Lacki. 2003. Habitat management for forest-roosting bats of
North America: a critical review of habitat studies. Wildlife Society Bulletin 31:30–44.

Minnis, A.M., and D.L. Lindner. 2013. Phylogenetic evaluation of *Geomyces* and allies reveals
no close relatives of *Pseudogymnoascus destructans*, comb, nov., in bat hibernacula of
eastern North America. Fungal Biology 117:638–649.

Muthersbaugh, M.S., W.M. Ford, K.E. Powers, and A. Silvis. 2019. Activity patterns of bats
during the fall and spring along ridgelines in the Central Appalachians. Journal of Fish
and Wildlife Management 10:180–195.

National Oceanic and Atmospheric Administration. 2016. National Oceanic and Atmospheric

41

Administration National Climate Data Center. Local climatological data. http://www.ncdc.noaa.gov/most-popular-data#loc-clim. Accessed 13 January 2016.

NatureServe. 2015. NatureServe Explorer: An online encyclopedia of life [web application]. Version 7.1. NatureServe, Arlington, Virginia. http://explorer.natureserve.org. Accessed 22 December 2015.

Norberg, U.M., and J.M.V. Rayner. 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): Wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London B 316:335–427.

O'Keefe J.M., S.C. Loeb, J.D. Lanham and H.S. Hill Jr. 2009. Macrohabitat factors affect day roost selection by eastern red bats and eastern pipistrelles in the southern Appalachian Mountain, USA. Forest Ecology and Management 257: 1757–1763.

O'Keefe, Petit, Loeb. 2019. White-nose syndrome dramatically altered the summer bat assemblage in a temperate Southern Appalachian Forest. Mammalian Biology 98:146–153.

O'Shea, T.J., M.A. Bogan, and L.E. Ellison. 2003. Monitoring trends in bat populations of the United States and territories: Status of the science and recommendations for the future. Wildlife Society Bulletin 31:16–29.

Park, K.J., G. Jones, and R.D. Ransome. 2000. Torpor, arousal and activity of hibernating greater horseshoe bats (*Rhinolophus ferrumequinum*). Functional Ecology 14:580–588.

Perry, R.W. and R.E. Thill. 2007. Tree roosting by male and female eastern pipistrelles in a forested landscape. Journal of Mammalogy 88: 974–981.

Pierson, E.D. 1998. Tall trees, deep holes, and scarred landscapes. Pages 309-325 *in* T.H. Kunz and P.A. Racey, editors. Bat biology and conservation. Smithsonian Institution Press. Washington D.C., USA.

Ploskey, G.R. and J.A. Sealer. 1979. Lipid deposition and withdrawal before and during

> hibernation in *Pipistrellus subflavus.* Southwestern Naturalist 24:71–78.

Poole, E.L. 1932. A survey of the mammals of Berks County, Pennsylvania. Bull. Reading

> Public Museum andnd Art Gallery 13:5–74.

Powers, K.E., R.J. Reynolds, W. Orndorff, and C.S. Hobson. 2015. Post-white-nose syndrome

> trends in Virginia's cave bats, 2008–2013. Journal of Ecology and the Natural
>
> Environment 7:123–130.

Quinn, G.M., and H.G. Broders. 2007. Roosting and foraging ecology of eastern pipistrelle

> (*Perimyotis subflavus*) in SW Novia Scotia. Report prepared for Nova Scotia Department
>
> of Natural Resources. Halifax, Nova Scotia, Canada.

Racey, P.A. 1988. Reproductive assessment in bats. Pages 31-43 *in* T.H. Kunz, editor.

> Ecological and behavioral methods for the study of bats. Smithsonian Institution Press,
>
> Washington, D.C., USA.

Reeder, D.M., Frank, C.L., Turner, G.G., Meteyer, C.U., Kurta, A., Britzke, E.R., and Blehert,

> D.S. (2012). Frequent arousal from hibernation linked to severity of infection and
>
> mortality in bats with white-nose syndrome. PloS ONE 7.
>
> https://doi.org/10.1371/journal.pone.0038920

Reichard J.D. and T.H. Kunz. 2009. White-nose syndrome inflicts lasting injuries to the wings of

> little brown myotis (*Myotis lucifugus).* Acta Chiropterologica 11:457–464.

Reichard, J.D, N.W. Fuller, and T.H. Kunz. 2011. Condition of wings is an important criterion of

> bat health: a response to Francl et al. Journal of Wildlife Diseases 47:1050–1051.

Richter, A.R., S.R. Humphrey, J.B. Cope, and V. Brack, Jr. 1993. Modified cave entrances: thermal effect on body mass and resulting decline of endangered Indiana bats (*Myotis sodalis*). Conservation Biology 7:407– 415.

Rigby, E.L., J. Aegerter, M. Brash, and J.D. Altringham. 2011. Impact of PIT tagging on recapture rates, body condition, and reproductive success of wild Daubenton's bats (*Myotis daubentonii*). Veterinary Record 170:101. DOI:10.1136/vr.100075.

Rivers, N. M., Butlin, R. K., & Altringham, J. D. 2005. Genetic population structure of Natterer's bats explained by mating at swarming sites and philopatry. Molecular Ecology 14:4299– 4312.

Roby, P.L., M.W. Gumbert, and M.J. Lacki. 2019. Nine years of Indiana Bat (*Myotis sodalis*) spring migration behavior. *Journal of Mammalogy* 100:1501–1511.

Samoray, S.T., S.N. Cotham, and M.W. Gumbert. 2019. Spring migration behavior of a *Perimyotis subflavus* (tri-colored bat) from Tennessee. Southeastern Naturalist 18. https://doi.org/10.1656/058.018.0302.

Schirmacher, M.R., S.B. Castleberry, W.M. Ford, and K.V. Miller. 2007. Habitat associations of bats in south-central Virginia. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 61:46–52.

Seaman, D.E., J.J. Millspaugh, B.J. Kernohan, G.C. Brundige, K.J. Raedeke, and R.A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

Shelley, V., S. Kaiser, E. Shelley, T. Williams, M. Kramer, and K. Haman. 2013. Evaluationof strategies for the decontamination of equipment for *Geomyces destructans*, the causative agent of the white-nose syndrome (WNS). Journal of Cave Karst Studies

75:1–10.

Silvis, A., R.W. Perry, and W.M. Ford. 2016. Relationships of three species of bats impacted by white-nose syndrome to forest condition and management. Forest Service Research and Development Southern Research Station. General Technical Report SRS-214.

Sikes, R. S., and Animal Care and Use Committee. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy, 97:663–688.

The Tennessee Chapter of the Nature Conservancy. 2015. 2015 Tennessee bat population monitoring and white-nose syndrome investigation report. Final Report prepared for Tennessee Wildlife Resources Agency. Nashville, TN, USA.

Thomas, D.W., M. Dorais, and J. Bergeron. 1990. Winter energy budgets and cost of arousals for hibernating little brown bats, *Myotis lucifugus*. Journal of Mammalogy, 71:475–479.

Thomas, D.W., and F. Geiser. 1997. Periodic arousals in hibernating mammals: is evaporative water loss involved? Functional Ecology, 11:585–591.

Tennessee Wildlife Resources Agency. 2005. Tennessee's comprehensive wildlife conservation strategy. Tennessee Wildlife Resources Agency. Nashville, TN, USA.

Tennessee State Wildlife Action Plan Team. 2015. Tennessee State Wildlife Action Plan. Tennessee Wildlife Resources Agency. Nashville, TN, USA.

Thogmartin, W.E., C.A. Sanders-Reed, J.A. Szymanski, P.C. McKann, L. Pruitt, R.A. King, and R.W. Russell. 2013. White-nose syndrome is likely to extirpate the endangered Indiana bat over large parts of its range. Biological Conservation 160:162–172.

Turner, G., D. Reeder, and J. Coleman. 2011. A five-year assessment of mortality and

geographic spread of white-nose syndrome in North American bats and a look to the future. Bat Research News 52:13-27.

U.S. Fish and Wildlife Service. 2015. Endangered and threatened wildlife and plants; threatened species status for the northern long-eared bat with 4(d) Rule. U.S. Federal Register 80: 17974–18033.

U.S. Fish and Wildlife Service. 2015a. New Jersey Species Being Evaluated for Possible Listing under the Endangered Species Act. <http://www.fws.gov/northeast/njfieldoffice/pdf/Evaluated_Species.pdf>. Accessed February 16 2016.

U.S. Fish and Wildlife Service. 2016. Current WNS occurrence map (updated March 21,2016). <https://www.whitenosesyndrome.org/about/where-is-it-now>. Accessed 31 March 2016.

U.S. Fish and Wildlife Service. 2020. Range-wide Indiana bat survey guidelines. <https://www.fws.gov/midwest/endangered/mammals/inba/surveys/pdf/FINAL%20Range-wide%20IBat%20Survey%20Guidelines%203.23.20.pdf> Accessed October 29 2020.

Veilleux, J.P., J.O. Whitaker, and S.L.Veilleux. 2003. Tree-roosting ecology of reproductive female eastern pipistrelles, *Pipistrelles subflavus,* in Indiana. Journal of Mammalogy 84:1068–1075.

Verant, M.L., C.U. Meteyer, J.R. Speakman, P.M. Cryan, J.M. Lorch, and D.S. Blehert. 2014. White-nose syndrome initiates a cascade of physiological disturbances in the hibernating bat host. BMC Physiology 14:10.

Walley, H.D. and W.L. Jarvis. 1971. Longevity record for *Pipistrellus subflavus.* Illinois Academy of Science 64:305.

Warnecke, L., J.M. Turner, T.K. Bollinger, V. Misra, P.M. Cryan, D.S. Blehert, G. Wibbelt, and

  C.K.R. Willis. 2013. Pathophysiology of white-nose syndrome in bats: A mechanistic model

  linking wing damage to mortality. Biology Letters 9. DOI:10.1098/rsbl.2013.0177.

Whitaker, J. O. 1998. Life history and roost switching in six summer colonies of eastern

  pipistrelles in buildings. Journal of Mammalogy 79:651–659.

Whitaker, J.O., and W.J. Hamilton. 1998. Mammals of the Eastern United States. Cornell

  University Press. Ithaca, New York.

Wilcox, A., and Willis, C. K. 2016. Energetic benefits of enhanced summer roosting habitat for

  little brown bats (*Myotis lucifugus*) recovering from white-nose syndrome. Conservation

  Physiololgy 4:cov070. DOI:10.1093/conphys/cov070.

Winchell, J.M., and T.H. Kunz. 1996. Day-roosting activity budgets of the eastern pipistrelle bat,

  Pipistrellus subflavus (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 74:431–

  441.

Wimsatt, W.A. 1945. Notes on breeding behavior, pregnancy, and parturition in some

  vespertilionid bats of the eastern United States. Journal of Mammalogy 26:23–33.\

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in homerange

  studies. Ecology 70:164–168.

APPENDIX

Figure 2. 1 Map of Tennessee with counties of study sites indicated by blue stars.
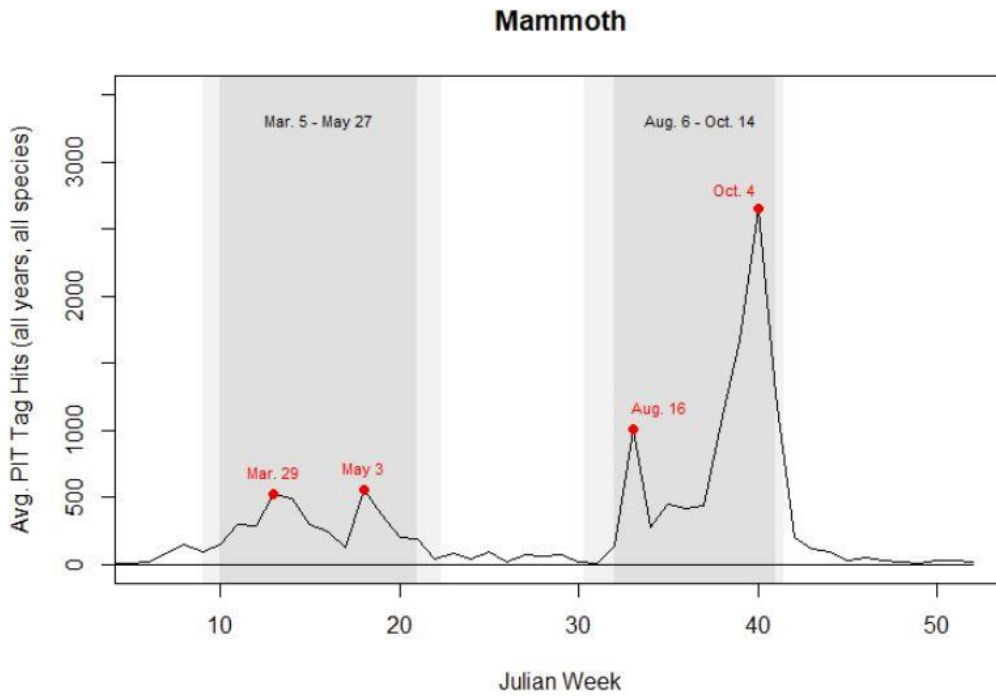
Figure 2. 2 Changepoint analysis showing peaks in activity of bats with passive integrated transponder tags at Campbell Cave, TN, 2016–2019. Darker shading represents average and lighter shading represents standard error.
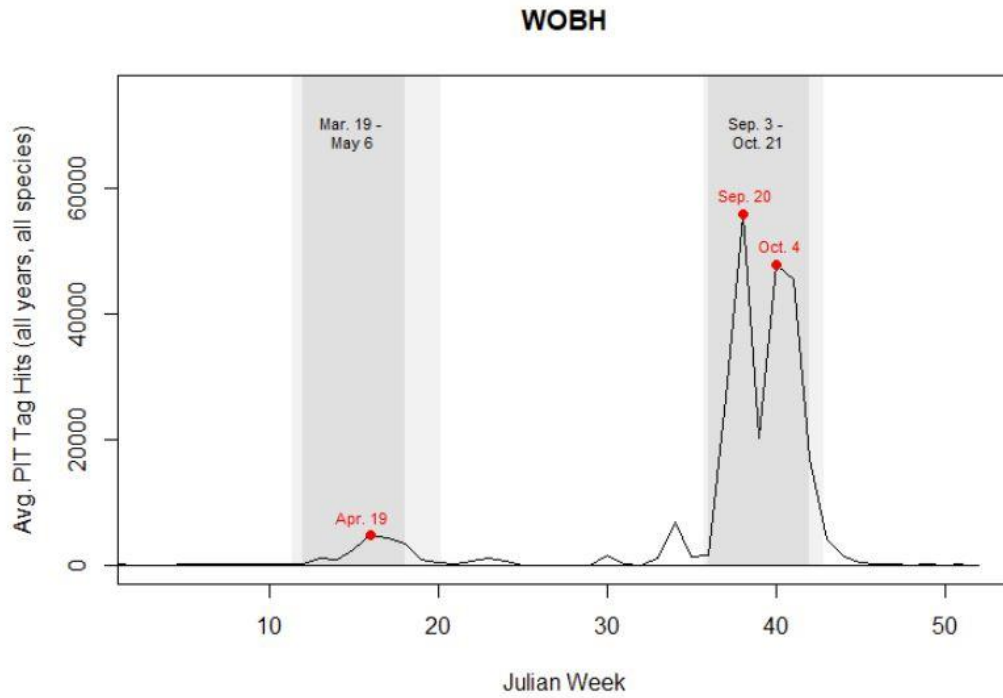
Figure 2. 3 Changepoint analysis showing peaks in activity of bats with passive integrated transponder tags at Blount Cave, TN, 2016–2019. Darker shading represents average and lighter shading represents standard error.
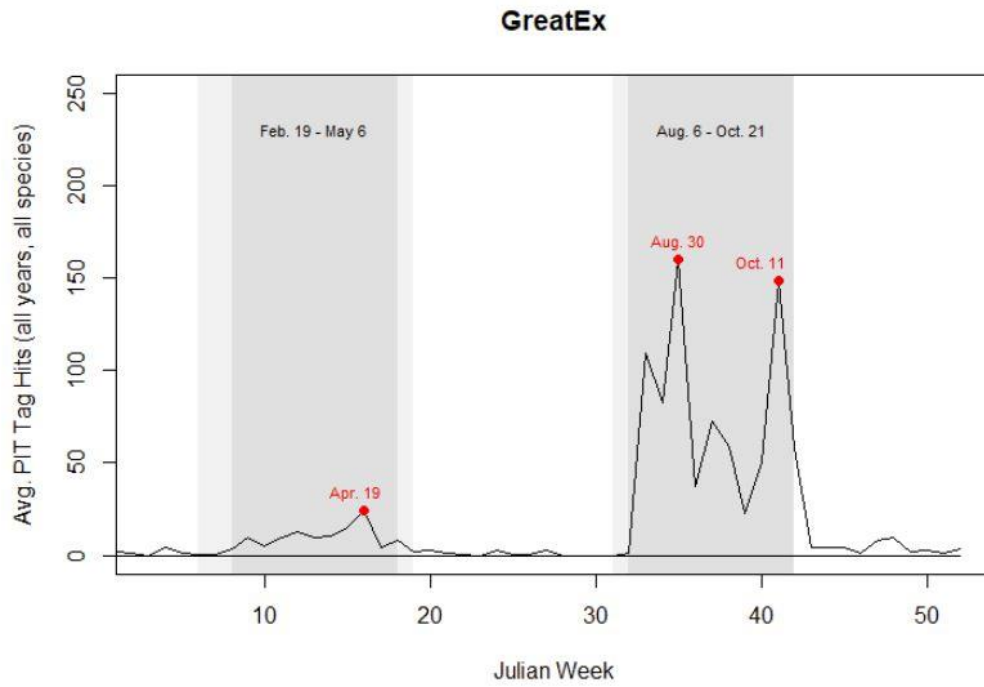
Figure 2. 4 Changepoint analysis showing peaks in activity of bats with passive integrated transponder tags at White Cave, TN, 2016–2019. Darker shading represents average and lighter shading represents standard error.
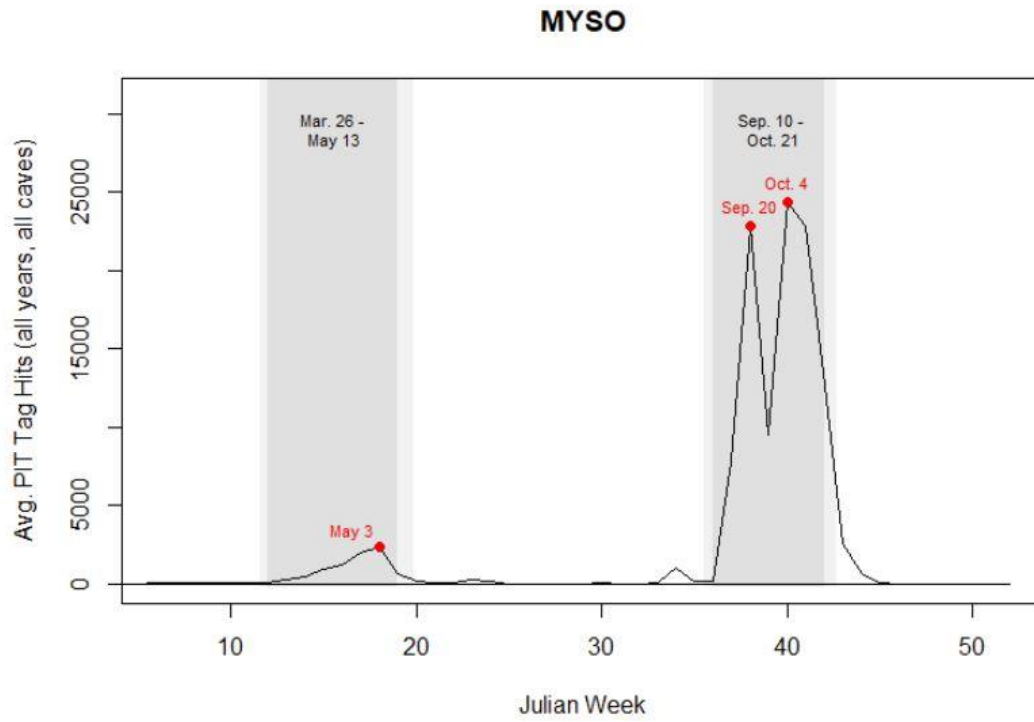
Figure 2. 5 Changepoint analysis of all Indiana bat PIT tag hits at all 3 caves over all years. TN, 2016–2019. Darker shading represents average and lighter shading represents standard error.
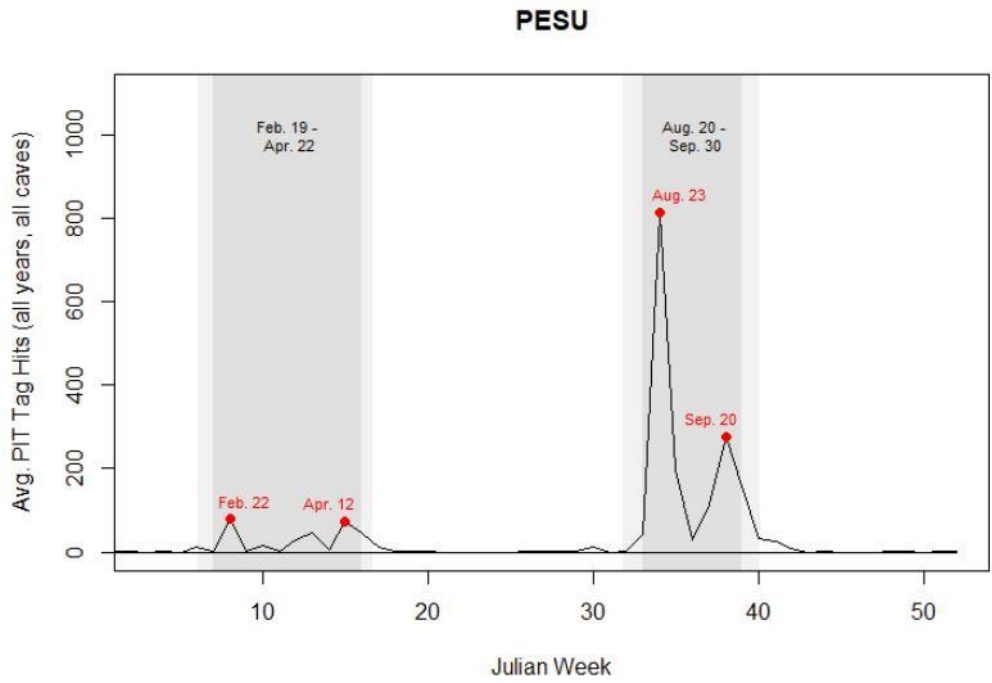
Figure 2. 6 Changepoint analysis of all tri-colored bat PIT tag hits at all 3 caves over all years.

TN, 2016–2019. Darker shading represents average and lighter shading represents standard error.

CHAPTER 3: ROOST SELECTION BY INDIANA BAT (MYOTIS SODALIS) AND TRI-COLORED BAT (PERIMYOTIS SUBFLAVUS) DURING FALL SWARMING SEASON IN TENNESSEE

This chapter is modified from a paper in preparation: M.E. Tate, E.V. Willcox, and W.H. Stiver. *In prep.* Determining the timing of fall swarming and spring staging activity of Indiana bat (*Myotis sodalis*) and tri-colored bat (*Perimyotis subflavus*) using passive integrated transponder analysis. Planned submission to Forest Ecology and Management.

In this chapter I use the term "we" in reference to my co-authors and myself. The chapter is formatted for publication in Forest Ecology and Management. I am responsible for all the following: (1) project design and data collection, (2) literature review, (3) statistical analyses, and (4) all writing. My co-authors advised on the design of the project, assisted with field work, and/or edited of the manuscript.

ABSTRACT

Roosting ecology and behavior of the Indiana bat (*Myotis sodalis*) and tri-colored bat (*Perimyotis subflavus*) is unknown for the critical time period, known as fall swarming, that precedes winter hibernation. During this time period, bats are mating and increasing energy reserves in preparation for longer torpor bouts and decreased foraging activity during the winter. In order to make informed and efficient management decisions, an understanding of roost site selection during this time period is critical to the conservation of these imperiled species. Tri-colored bats roost in trees on the landscape more often than in caves. Tree roosts are in live trees in stands with greater solar exposure and decreased clutter. Tri-colored bats roost within 198 ± 72.4 m of caves. Indiana bats roost in caves more often than in trees on the landscape. When roosting on the landscape, Indiana bats roost in snags within 108 m ± 64.80 m of caves.

INTRODUCTION

Like many North American wildlife species, bats are facing threats from habitat loss and degradation (Voigt and Kingston 2016). Adding to declines resulting from these disturbances, bat populations are facing further pressures from wind energy development, which is expanding across North America, specifically along migratory routes of several species (Frick et al. 2017). Further, in 2005, the fungal pathogen *Psuedogymnoascus destructans* (*Pd*), the causal agent of

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the disease white-nose syndrome (WNS), was introduced to North America (USFWS 2012). Bats

infected with WNS experience disruption to their torpor and metabolic processes, specifically

during hibernation (Verant et al. 2014). As torpor is continually disrupted, energy reserves are

depleted, often leading to mortality. An estimated 6.7 million North American bats have been

killed by WNS since 2006 (Gargas et al. 2009, Lorch et al. 2011, Minnis and Linder 2013). Of

particular threat from this disease are Indiana bats (*Myotis sodalis*) and tri-colored bats

(*Perimyotis subflavus*; Frick et al. 2015).

Before the introduction of WNS, the Indiana bat was federally listed as an endangered

species under the Endangered Species Act due to habitat loss and degradation and hibernacula

disturbances (USFWS 2006). As WNS spread throughout the Indiana bat range, devastating

population declines were reported (Langwig et al. 2016, Frick et al. 2017), with hibernacula

experiencing up to 94% population losses (Langwig et al. 2015, Frick et al. 2017).

In contrast to the Indiana bat, the tri-colored bat was so abundant and common

throughout its range that it was minimally surveyed, much less studied at depth before WNS.

However, the disease WNS resulted in rapid tri-colored bat declines, with some populations

experiencing up to 98% loss (O'K9eefe et al. 2019, Frank and Davis 2019). Following rapid

declines across its range, the Center for Biological Diversity and Defenders of Wildlife (2016)

petitioned the tri-colored bat for federal listing and protection under the Endangered Species Act.

Understanding roosting strategies and selection of roost characteristics by bats is crucial

to their management and conservation. Bats use different roost types during different periods of

their life cycle (Fraser et al. 2012), which include the maternity season, fall migration, fall

swarming, hibernation, spring staging, and spring migration. The selection of roosts affects the

distance to resources such as prey and water (Barclay and Kurta, 2007). Roost characteristics

selected may also influence body temperature, risk of predation, protection from extreme elements, and risk of exposure to fungal and bacterial pathogens (Barclay and Kurta 2007).

Due to the incredible importance of successful reproduction in threatened bat populations, most research has focused on understanding the ecology and behavior of bats during the maternity season (May 15–August 15; USFWS 2009, Fraser et al. 2012, Jachowski et al. 2016, O'Keefe and Loeb 2017, Carpenter 2017, Cable et. al 2020). During this time period, female bats feed and prepare for, birth, and raise pups. For the duration of the maternity period, Indiana bats roost in large maternity colonies, under the sloughing bark of large snags or shagbark hickories (Britzke et al. 2003, O'Keefe and Loeb 2017). They select trees in forested stands with lower basal area, ranging 1-2 m^2/0.1 ha (Carter 2004, Kurta 2004, O'Keefe and Loeb 2017). Because decreased basal area increases solar exposure, this likely suggests the importance of thermoregulation for Indiana bats during the maternity period. In the southeastern part of their range, tri-colored bats have been found to select clumps of both live and dead foliage hanging in live deciduous trees throughout the summer (Carpenter 2017, Thames et al. unpublished data). Tri-colored bats tend to select forest stands with lower clutter related characteristics, including stem density, percent of coniferous trees, and basal area. Additionally, bodies of water including streams, wetlands, ponds, or reservoirs were often within 4km of the roost (O'Keefe and Loeb 2009, Carpenter 2017, Thames et al. unpublished data). These findings suggest that proximity to optimal foraging areas might influence roost selection during the maternity season.

As the mechanisms of WNS are investigated further, specifically the metabolic and energetic impacts, we are only beginning to understand the importance of bats entering winter hibernation at peak health. During this time period, known as fall swarming, bats engage in swarming behavior at the entrances of hibernacula where mating occurs (Poole et. al 1932). This

is also a time period of increased foraging across the landscape, due to bats gorging themselves on insects, consuming large amounts of calories in preparation for winter hibernation, a time period of decreased arousal and foraging events (Poole et. al 1932). This suggests the importance of prime forging opportunities and limited torpor disturbances, especially disturbances by humans, during this time. Fall swarming has primarily been investigated using acoustic surveys, where with bat activity was heightened around hibernacula but reduced on the landscape, suggesting bats may select cave roosts over landscape roosts (Muthersbaugh et. al 2019). However, two other cave-dwelling species, little brown bat (*Myotis lucifugus*) and northern long-eared bat (*Myotis septentrionalis*) have been recorded roosting in trees, snags, emergent rocks, and human structures on the landscape in the fall (Brack 2006; Lowe et. al 2012). Still, data on the roosting ecology of Indiana and tri-colored bats during fall is limited and likely varies from that of the little brown bat and northern long-eared bat, as the summer roosting behavior varies (Shivley et al. 2017, Carpenter 2017, Cable et al. 2020). Even so, management restrictions have been implemented in cave areas in an effort to protect bat species. These restrictions are not backed with data and research in regards to time nor distance from hibernacula, and may be restricting management practices that benefit imperiled bat species (B. Stiver, personal communication, March 2017). Additionally, USFWS prohibits timber harvest between November 15–March 31 (USFWS 2020). This time period is thought to restrict harvest to a time period that bats are not on the landscape, though data justifying these dates is lacking. Without an understanding of the ecology and behavior of the Indiana bat and tri-colored bat during fall swarming, we cannot make informed management decisions to increase survival and reproduction of individuals (Silvis 2016).

The objective of our study was to characterize roost selection by both Indiana bats and tri-colored bats at the microhabitat and landscape levels in Tennessee during the fall swarming season. Due to Indiana bats largely selecting snags as summer roosts in this part of their range (O'Keefe and Loeb 2017), we predicted that fall diurnal roosts on the landscape would be under sloughing bark in snags. As studies of Indiana bats show selection at the microhabitat level based on thermoregulation (Hammond 2013, O'Keefe 2017), we hypothesized that Indiana bats would roost in forested areas with lower basal area. At the landscape level, we hypothesized that Indiana bats would select roosts closer in proximity to limited resources such as forested foraging areas, water sources, and hibernacula (DuChamp et al. 2007). For tri-colored bats, we predicted that roosts would primarily consist of dead clumps of leaves (Thames et al. unpublished data). Roosting ecology studies conducted in the southeast suggest that tri-colored bats do not select for microhabitat level characteristics (Farrow et al. 2011, O'Keefe et al. 2009, Thames et al. unpublished data). However, Carpenter (2017) conducted a similar roosting ecology study in the Great Smoky Mountains National Park (GRSM), an area with high density of eastern hemlock and eastern white pine, and found variables impacting stand clutter and thermoregulation variables can predict roost selection. Therefore, we hypothesized that tri-colored bats would select areas with lower clutter and greater solar exposure for improved thermoregulation. Based on previous findings of limiting resources influencing tri-colored bat roost selection, we predicted that proximity to open bodies of water (foraging sites; O'Keefe et. al 2009), roads (flight corridors), and hibernacula (DuChamp et al. 2007) would determine roost selection of tri-colored bats during fall swarming. Finally, based on studies investigating other North American *Chiroptera* during the fall season, we predict that both species will roost on the landscape more often than in caves (Lowe 2012).

METHODS AND MATERIALS

Study Area

Our study sites consisted of 4 caves and the surrounding landscapes in eastern Tennessee. Caves were selected by highest number of Indiana bat and tri-colored bat hibernacula counts over the past years with cave entrances that were less than 10 m^2 (Figure 3.1). Three caves were located within the boundaries of the GRSM in Blount County. The park ranges from 267 m–2075 m in elevation, though all caves fall in the lower elevation areas of the park (NPS 2020). The areas covered in this project are dominantly pine-and-oak forests. The forest consists of oaks and evergreens (primarily white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), and American holly (*Ilex opaca*), with intermittent maples and hickories (NPS.gov). All three of the caves are on the outskirts of the national park, with human development within <10 miles of each. Our fourth cave was on a Tennessee Wildlife Resource Agency (TWRA) owned and managed Wildlife Management Area along the Cumberland Plateau in White County. Forest composition is similar to that of GRSM, with oaks, hickories, and evergreens as the primary tree species. The elevation ranges from 156 m–897 m. Both areas are surrounded by pastures, ex-urban housing, and multiple streams (NLCD 2020).

Radiotelemetry

From late August–late October of 2017–2019, we used radio telemetry to track Indiana bats and tri-colored bats to their diurnal roosts to determine roost selection. Bats were captured using 4 m or 6 m long single high mist nets (75 denier, 2-ply; Avinet, Dryden, New York) at the entrances of the four study site caves. We recorded species, sex, reproductive status, wing damage index (Reichard and Kunz 2009), and age (by degree of epiphyseal fusion; Kunz 1988) of each bat captured, as well as forearm length and weight. We fitted the heaviest bats captured each night with a VHF radio transmitter (BD-2X, Holohil Systems, Ltd., Ontario, Canada) weighing 0.26g–

0.35 g, with transmitter weight not exceeding 5% of body weight (Silvis et al. 2012, Kurta and

Murray 2002). To attach each transmitter, the fur between the scapula was trimmed and a small

amount of surgical glue was placed directly on the exposed skin (Perma–Type, Plainville, CT).

The transmitter was then placed and held securely to the bat for 8–12 mins to allow time for the

glue to dry completely. Each bat was released in under 30 minutes from the time of capture.

We tracked each bat for 5 consecutive days or until the signal was lost, with the

assumption that this indicated bats transitioning from roosting on the landscape to roosting

within the cave and potentially beginning the hibernation period. However, this also could have

indicated bats leaving the area. We tracked bats to their daytime roosts using 3- and 5-element

Yagi antennae, Telonics TR-5 receivers (Telonics, Inc., Mesa, AZ) and Wildlife Materials

receivers (Wildlife Materials, Murphysboro, IL) by vehicle and on foot. Once a roost tree was

located, we used binoculars to locate and confirm the specific roosting location of each bat. This

was done by lying on the forest floor and searching for the transmitter protruding from roost

substrates. In some instances, we were able to confirm bats within a cave using telemetry. If we

could not confirm cave roosts using telemetry during the day, emergence counts were conducted

and radio telemetry was used to detect the bats exiting caves at night. If roosts could not be

confirmed, we did not include them in analysis. Our methods were approved by the University of

Tennessee Animal Care and Use Committee (IACUC 2253) and research was conducted under

state and federal scientific collection and recovery permits (USFWS, TE353135-3; NPS, GRSM-

01228; TWRA, 3742).

Roost Characteristics

We collected microhabitat data within a 0.1 ha plot surrounding each confirmed roost tree. Data

for each roost included the substrate the bat was roosting in (roost type; dead/live foliage, bark,

free-hanging from branch), species, and height above ground (m). Additionally, we measured percent clutter (%) above and below the roost location using a spherical densiometer (Model-C, Forest Densiometers, Rapid City, SD), and roost azimuth. Data collected on the roost tree included species, height (m), canopy area (canopy length x canopy width; m^2) and diameter at breast height (DBH; cm). Presence of clumps of dead and live foliage and percentage of sloughing bark (%) was also recorded for each roost tree. For non-roost trees that fell within the 0.1 ha plot, we determined species, DBH (cm), and tree height (m). Stand basal area (10 factor prism), overstory height (m, average of tallest tree each cardinal direction), and percent canopy closure (%) at 10 m from the roost tree were also measured. We took all height measurements using a Suunto PM5 clinometer (Suunto, Helsinki, Finland). Finally, we measured stem density within each plot (stems/0.1 ha^2) with stems including any tree below 7 cm DBH and over 1 m tall. To determine diurnal roost selection of both tri-colored bats and Indiana bats, we collected the same measurements at random trees, excluding those that were roost specific. We paired each roost tree with a random tree, which was selected by walking a randomly generated distance between 50–200m at a randomly generated azimuth. The range of 50–200 m was selected to ensure that random trees did not fall within the 0.1 ha plot of the roost tree but were within the same forest stand.

We also measured landscape level variables, specifically those related to fall swarming activities, to determine the importance of various features to roost selection by Indiana bats and tri-colored bats. We used a handheld GPS (Garmin International, Olathe, KS, USA) to determine locations of roost trees, and ArcMap 10.7 (ESRI, Inc., Redlands, CA) along with shapefiles from the NPS (2020) and National Land Cover Dataset (Homer et al. 2015) to create maps of potential selection variables including hydrological features, roads, and hibernacula locations. We

measured the distance from a roost tree to streams, roads, bodies of water, and hibernacula (m). To ensure that random landscape locations were available to bats, random points were generated within the distance of the home ranges for each species. Because home ranges are unknown for the fall swarming period, average maximum distances from roost to foraging sites during the summer were used. Random locations were within 4 km for Indiana bats (USFWS 2008) and 11.4 km for tri-colored bats (Thames et al. unpublished data). Distance between random roost and hibernacula, road, stream, and open bodies of water (km) was then calculated.

Data Analysis

Tri-colored Bat Roosts

As tri-colored bats are known to switch day roosts often, we assumed that all day roosts selected by individuals were independent of each other, hence we included all observations as experimental units (Lewis 1995). Due to low capture rates of females, we analyzed all data together without factoring sex. We used Program R 3.3.2 (R Core Development Team, 2010) to conduct all statistical analyses outlined below. We used a Fisher's exact test to examine selection of roost tree species compared to available overstory. We calculated mean characteristics of all identified roost trees, and used an information theoretic approach to determine characteristics of roost trees that best predicted bat presence. We totaled the number of days bats roosted in trees and days bats roosted in caves, and calculated the percentages of days spent in each roost type. An information-theoretic approach using Akaike information criterion (AIC) has been recommended to determine selection of bat roosts, as biologically valuable characteristics could be removed from models in null hypothesis testing (Anderson et al. 2000; Burnham and Anderson 2002). Therefore, we developed *a priori* linear regression models for the microhabitat and landscape-levels, which we used to investigate the differences between selected and

available microhabitat and landscape-level variables (e.g., tree species, dbh, height, basal area etc.). Due to our small sample size, we tested these models using AIC_c, a variation of AIC developed specifically for small sample sizes. (Anderson et al. 2002). We created models using microhabitat variables and landscape variables. We tested variables for correlation, and none were highly correlated (Pearson r >0.70). To ensure no biologically significant variables were removed, we included variables in our models that had a very high alpha value (P >0.35). This resulted in the removal of the deciduous density, height to base of crown, and distance to nearest stream. Our microhabitat global model had 8 variables including roost tree height, roost height, roost tree canopy volume, average height of plot, % canopy closure at 10 m from roost tree, tree density, coniferous density, and stem count (Table 3.1). Our landscape level global model included distance to hibernacula, distance to nearest open body of water, and distance to road (Table 3.2).

Our models were grouped to explain microhabitat and landscape level selection based on our hypotheses. Microhabitat level variables were broken into two categories: those related to clutter and those related to thermoregulation. The landscape level variables were run as independent models, as each explains proximity to unrelated limiting resources. Using AICc scores and model weights (wi; Burnham and Anderson 2002), we examined differences between candidate models, with best models represented by lowest scores and highest weights. AIC weight can be interpreted as the probability that a candidate model is the best among potential models. We considered models within 2 AICc units of the top model to be indicative of bat presence in roosts. For models in the confidence set, we calculated model-averaged parameter estimates and unconditional standard errors to assess the relative importance of each variable and account for model uncertainty (Burnham and Anderson 2002). To avoid reporting spurious

effects, we considered only parameters with 95% confidence intervals not including 0 to be informative (Payton et al. 2003). We used AICcmodavg and MuMln packages in Program R 3.3.2 (R Core Development Team, 2010) to conduct statistical analyses.

Indiana Bat Roosts

Due to exceptionally low Indiana bat landscape roosts, we were unable to run selection analysis. In order to define Indiana bat roost characteristics during fall swarming, we calculated the mean and standard error of each microhabitat and landscape level variable. Total days that Indiana bats roosted in caves and days roosted in trees were also calculated as percentages.

RESULTS

Tri-colored Bats

We applied radio transmitters to 22 tri-colored bats during the fall swarming season of 2017–2019. We successfully tracked 18 (4 female, 14 males) individuals for 84 days to a total of 46 roost trees. Bats we were unable to track likely left the area or roosted in areas of caves that we could not detect via radio telemetry. Tri-colored bats roosted in caves 17% (n = 14 days) of the time and trees 83% (n = 70 days) of the time. All tree roosts were in dead foliage hanging in living deciduous trees (42% oak, 26% hickory, 32% maple and American hornbeam) with DBH of 18.68 ± 9.24 cm . Roost locations were an average 6.2 m ± 2.8 m from the ground. Roost trees were 198 m ± 72.4 m from caves (Range = 26.2 m – 428.8 m). Distance from roost to open body of water was 5069.5 m ± 128.3 (Range 4891.6 m – 6124.3 m). The distance to the nearest road was 1169.17 ± 79.3 m (Range = 88.23 m – 5876 m). Our tri-colored bats were detected roosting on the landscape through the beginning of November. All bats that roosted in caves were in the hibernacula of capture.

We tested 20 candidate microhabitat level models examining clutter and thermoregulation related characteristics. Two models were within 2 AIC_c units of the top model, indicating that these were best at predicting roost from random trees. Two models were from the clutter category, while the final indicative model was in the thermoregulation category (Table 3.3). The sum of the AIC_c weights for these three models was 0.502, indicating a 50.2% chance that they are the true predicting models of whether a tree was roost or random.

Model averaging results indicated coniferous density and canopy closure at 10m from tree, were the only informative explanatory variables (i.e., confidence intervals did not cross 0; Table 3.4). Odds of bat presence in a roost tree decreased by 7.3% for each additional coniferous tree in each 1 ha plot (estimated odd ratio = 0.927) and decreased 5.6% (estimated odd ratio = 0.944) as canopy closure at 10 m increased by 1%. Our roost plots had 14.1% less coniferous trees than random and 12% less canopy closure at 10 m than random.

At the landscape level, our top model included distance to closest cave only (Table 3.5). No other landscape level models fell within 2 AIC_c units of the top model. On average, our selected roost trees were 3,271 m closer to caves than our random landscape level roosts.

Indiana Bats

We applied radio transmitters to 18 Indiana bats during the fall swarming seasons of 2017–2019. We successfully tracked 15 (1 female, 14 males) of these individuals for a total of 50 days to a total of 4 roosts. The individuals we were unable to track likely left the area or were roosting in areas of hibernacula we could not detect via radio telemetry. Indiana bats roosted in caves 78% (n = 39/50) of the time and trees 22% (n=11/50) of the time. Only 5 bats roosted in trees and only used 4 trees total, with DBH of 58.75 ± 8.25 cm. All bats roosted in the caves at which they

were captured, with the exception of one bat roosting at a separate cave 843 m away from the capture site.

When in trees, Indiana bats roosted under the sloughing bark of eastern hemlock snags. Roost height was 9.89 m $\pm$ 1.58 m with roost tree height of 27.58 m $\pm$ 10.22 m. Stands had low overstory tree density, with 230.00 trees/ha $\pm$ 27.30 trees/ha. Canopy closure around each roost was extremely low at 13.75% $\pm$ 10.68/ha. Coniferous species comprised 13% of the overstory trees. Selected stands also had low stem counts of an average 292.5 stems/ha. Roosts were 108.00 m $\pm$ 64.80 m from caves. Distance from roost to open body of water was 5,069.50 m $\pm$ 706.17 m. Distance to the nearest road was 1169.17 $\pm$ 360.72 m.

DISCUSSION

This is one of the first studies to investigate roosting behavior and ecology of the Indiana bat and tri-colored bat post-WNS during the fall swarming season. Our findings show the importance of hibernacula during this critical time period.

Indiana bats largely roosted in caves during this time period. This differs from previous findings of similar *Myotis* species that detected bats roosting on the landscape more often (Lowe 2012), and emphasizes the importance of cave protections. While we were unable to analyze roost selection by Indiana bats, our results show that when roosting on the landscape, Indiana bats remain near hibernacula, likely due to the importance of swarming and mating behavior at the entrance of caves (Poole et al. 1932, Davis and Hitchcock 1965, Lowe 2012, Muthersbaugh et al. 2019). However, when roosting on the landscape, roost trees were only dead eastern hemlocks that were similar to those confirmed during summer Indiana bat roost studies within the GSMNP (O'Keefe and Loeb 2017). Additionally, roost trees exceeded the 12.7 cm DBH requirements for Indiana bat protections (USFWS 2017). Since the average roost DBH was

58.75 cm (minimum 22 cm), this supports raising the DBH requirements for harvest and allowing larger trees to be cut.

Similar to summer roost selection, tri-colored bats roost within the foliage of living trees during fall swarming (Loeb & O'Keefe 2011, Thames et al. unpublished data). On the microhabitat level, our top models supported variables that relate to clutter and thermoregulation. Because bats use this time period to gain as much energy as possible, they are likely selecting areas with lower clutter to reduce energy expenditures via flight (Sleep et al. 2003). Bats may also select for lower clutter to optimize efficiency of echolocation during this time period (Falk et al. 2014). Solar exposure levels may be critical during this time period to reduce energy expenditures on thermoregulation to ensure the highest reserves available for the hibernation period (Geiser et al. 2003, Turbill et al. 2018).

As open bodies of water are selected as foraging sites during the summer by this species (Thames et al. unpublished data), we expected distance to the nearest open body of water to be a significant variable in roost selection. However due to our findings, proximity of roost to hibernacula seems to be a more important factor during this time period. This suggests, similar to Indiana bats, an emphasis of the importance of hibernacula to tri-colored bats for mating behavior.

When examining the timing of fall behavior (Chapter 2) and roosting ecology of our two target species, recreational and management practices should potentially be limited within 200 m of caves from August 15–November 15. This would protect the average distance from hibernacula to roost during the most active time period, protecting bats from disturbances and reducing the risk of human-bat interaction.

Our study only characterizes roosting ecology of Indiana bats and tri-colored bats near caves during the fall swarming time period. Because all bats were captured at hibernacula, this study is limited when making management decisions (timber harvest restrictions, hazard tree removal, etc.) to protect these two species in areas that are not near caves. Additionally, greater sample sizes are needed to assess fall roost selection of Indiana bats. Finally, because foraging data during the fall swarming period is nonexistent, we are unable to claim that the suggested cave area barrier includes all areas used by these two species.

ACKNOWLEDGMENTS

LITERATURE CITED

Aldridge H.D. and R.M. Bringham. 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5% rule of radiotelemetry. Journal of Mammalogy 69:379–382.

Amelon, S. 2006. Conservation assessment: *Pipistrellus subflavus* (Eastern Pipistrelle) in the Eastern United States. Pages 11–30 *in* F.R. Thompson, editor. Conservation assessments for five forest bat species in the eastern United States. General Technical Report NC-260. U.S. Forest Service, North Central Research Station, St. Paul, MN, USA.

Anderson, D. R., and K.P. Burnham, K. P. 2002. Avoiding pitfalls when using information-theoretic methods. The Journal of Wildlife Management 912–918.

Anderson, D.R., K.P. Burnham, and W.L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. The Journal of Wildlife Management, 912–923.

Anthony, E.L.P. 1988. Age determination in bats. Pages 47–57 *in* T.H. Kunz, editor. Ecological and behavioral methods for the study of bats. Smithsonian Institution Press, Washington, D.C., USA.

Barclay, R.M.R., and A. Kurta. 2007. Ecology and behavior of bats roosting in tree cavities and under bark. Pages 17–59 *in* M.J. Lacki, J.P. Hayes, and A. Kurta, editors. Bats in forests: conservation and management. John Hopkins University Press, Baltimore, MD, USA.

Bernard, R.F., and G.F. McCracken. 2017. Winter behavior of bats and the progression of white-nose syndrome in the southeastern United States. Ecology and Evolution 7:1487–1496.

Brack, V. (2006). Autumn activity of *Myotis sodalis* (Indiana bat) in Bland County, Virginia. Northeastern Naturalist 13:421–434.

Britzke, E.R., M.J. Harvey, and S.C. Loeb,2003. Indiana bat, *Myotis sodalis*, maternity roosts in

the southern United States. Southeastern Naturalist 2:235–242.

Carpenter, G.M. 2017. Bat population status and roost selection of tri-colored bats in the

Great Smoky Mountains National Park in the era of white-nose syndrome. MS Thesis.

University of Tennessee, Knoxville, TN, USA.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and

habitat use by animals. Ecological Modelling, 197:516–519

Carter, T.C. 2004. Summer habitat use of roost trees by the endangered Indiana bat (*Myotis*

sodalis) in the Shawnee National Forest of southern Illinois. PhD Dissertation. Southern

Illinois University, Carbondale, IL, USA.

Carter T.C., and J.M. Menzel. 2007. Behavior and day-roosting ecology of North American

foliage-roosting bats. Pages 60–81 *in* M. J. Lacki, J. P. Hayes, and A. Kurta, editors. Bats

in forests: conservation and management. Johns Hopkins University Press, Baltimore,

MD, USA.

Carter, T.C., M.A. Menzel, B.R. Chapman, K.V. Miller. 1999. Summer foraging and roosting

behavior of an eastern pipistrelle, *Pipistrellus subflavus*. Bat Research News 40:5–6.

Cryan, P.M., and R.M. R. Barclay. 2009. Causes of bat fatalities at wind turbines: hypotheses

and prediction. Journal of Mammalogy 90:1330–1340.

Cryan, P.M., C.U. Meteyer, J.G. Boyles, and D.S. Blehert. 2010. Wing pathology of white-nose

syndrome in bats suggests life-threatening disruption of physiology. BMC Biology 8:135.

https://doi.org/10.1186/1741-7007-8-135.

Davis, W.H. 1959. Disproportionate sex ratios in hibernating bats. Journal of Mammalogy

40:16–19.

Davis, W.H. and R.E. Mumford, R.E. 1962. Ecological notes on the bat *Pipistrellus subflavus*.

American Midland Naturalist 68:394–398.

Davis, W.H., and H.B. Hitchcock. 1965. Biology and migration of the bat, *Myotis lucifugus*, in New England. Journal of Mammalogy 46:296–313.

Duchamp J.E., D.W. Sparks, and J.O. Whitaker. 2007. Foraging-habitat selection by bats at an urban–rural interface: comparison between a successful and a less successful species. Canadian Journal of Zoolology 82:1157–1164.

Falk, B., L. Jakobsen, A. Surlykke, and C.F. Moss. 2014. Bats coordinate sonar and flight behavior as they forage in open and cluttered environments. Journal of Experimental Biology, 217:4356–4364.

Farrow, L.J., and H.G. Broders. 2011. Loss of forest cover impacts the distribution of the forest-dwelling tri-colored bat (*Perimyotis subflavus*). Mammalian Biology 76:172–179.

Fenton, M.B. 1990. The foraging behavior and ecology of animal-eating bats. Canadian Journal of Zoology 68:411–422.

Forbes, G. 2012. Technical Summary and Supporting Information for an Emergency Assessment of the Tri-colored Bat *Perimyotis subflavus.* Committee on the status of endangered wildlife in Canada. https://www.canada.ca/en/environment-climate-change/services/species-risk-public-registry/cosewic-assessments/tri-colored-bat-technical-summary-2012.html. Accessed 30 October 2020.

Frank, C.L., A.D. Davis and C. Herzog. 2019. The evolution of a bat population with white-nose syndrome (WNS) reveals a shift from an epizootic to an enzootic phase. Frontier in Zoology 16:40. https://doi.org/10.1186/s12983-019-0340-y.

Fraser, E.E., L.P. McGuire, J.L Eger, F.J., Longstaffe, and M.B. Fenton, M. B. 2012. Evidence of latitudinal migration in tri-colored bats, *Perimyotis subflavus*. PLoS ONE 7:e31419.

DOI:100.1371/journal.pone.0031419.

Frick, W.F., J.F. Pollock, A.C. Hicks, K.E. Langwig, D.S. Reynolds, and G.G. Turner. 2010. An emerging disease causes regional population collapse of a common North American bat species. Science 329:679–682.

Frick, W.F., D.S. Reynolds, T.H. and Kunz. 2010. Influence of climate and reproductive timing on demography of little brown myotis *Myotis lucifugus*. Journal of Animal Ecology 79: 128–136.

Frick, W.F., S.J. Puechmaille, J.R. Hoyt, B.A. Nickel, K.E. Langwig, J.T. Foster, and A.M. Kilpatrick. 2015. Disease alters macroecological patterns of North American bats. Global Ecology and Biogeography 24:741–749.

Frick, W.F., E.F. Baerwald, J.F. Pollock, R.M.R. Barclay, J.A. Szymanski, T.J. Weller, A.L. Russell, S.C. Leob, R.A. Medellin, and L.P. McGuire. 2017. Fatalities at wind turbines may threaten population viability of a migratory bat. Biological Conservation 209:172–177.

Fujita, M.S., and T.H Kunz. 1984. *Pipistrellus subflavus*. Mammalian species. 228:1–6

Gargas, A., M.T. Trest, M. Christensen, T.J. Volk, and D.S. Blehert. 2009. *Geomyces destructans* sp. nov., associated with bat white-nose syndrome. Mycotaxon 108:147–154.

Geluso, K., T.R. Mollhagen, J.T. Tigner, and M.A. Bogan. 2005. Westward expansion of the eastern pipistrelle (*Pipistrellus subflavus*) in the United States, including new records from New Mexico, South Dakota, and Texas. Western North American Naturalist 65:405–409.

Geiser, F., and R.L. Drury. 2003. Radiant heat affects thermoregulation and energy expenditure during rewarming from torpor. Journal of Comparative Physiology B 173:55–60.

Gould, E. 1955. The feeding efficiency of insectivorous bats. Journal of Mammalogy 36:399–407.

Griffin, D.R. 1940. Migrations of New England bats. Bulletin of the Museum of Comparative Zoology, Harvard University 86:217–246.

Harvey, M.J., J.S. Altenbach, and T.L. Best. 2011. Bats of the United States and Canada. John Hopkins University Press. Baltimore, MD, USA.

Hayes, M.A. 2013. Bats killed in large numbers at United States wind energy facilities. Bioscience 63: 975–979.

Hoofer, S.R., and R.A. Van Den Bussche. 2003. Molecular phylogenetics of the chiropteran family Vespertillionidae. Acta Chiropterologica, 5 supplemental:1–63.

Horn, J.W., E.B. Arnett, and T.H. Kunz. 2008. Behavioral responses of bats to operating wind turbines. Journal of Wildlife Management 72:123–132.

Hoying, K.M. and T.H. Kunz. 1998. Variation in size at birth and post-natal growth in the insectivorous bat *Pipistrellus subflavus* (Chiroptera: Vespertilionidae). Journal of Zoology. 245:15–27.

Jachowski, D.S., C.T. Rota, C.A. Dobony, W.M. Ford, and J.W. Edwards. 2016. Seeing the forest through the trees: Considering roost-site selection at multiple spatial scales. PLoS ONE 11(3):e0150011. https://doi.org/10.1371/journal.pone.0150011.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Jones, C. ,and J. Pagels. 1968. Notes on a population of *Pipistrellus subflavus* in southern Louisiana. Journal of Mammalogy 49:134–139.

Jones, C., and R. D. Suttkus. 1973. Colony structure and organization of *Pipistrellus subflavus* in

southern Louisiana. Journal of Mammalogy 54:962–968.

Kurta, A. 2004, November. Roosting ecology and behavior of Indiana bats (*Myotis sodalis*) in summer. Pages 29–42 in K.C. Vories and A. Harrington, editors. Indiana bat and coal mining: a technical interactive forum. US Department of Interior, Office of Surface Mining, Alton, IL and Coal Research Center, Southern Illinois University, Carbondale, IL, USA.

Kurta, A., L. Winhold, J. O. Whitaker, Jr., and R. Foster. 2007. Range expansion and changing abundance of the Eastern Pipistrelle (Chiroptera: Vespertilionidae) in the central Great Lakes region. American Midland Naturalist 157:404–411.

Lacki, M.J., and J.T, Hutchinson. 1999. Communities of bats (Chiroptera) in the Grayson Lake Region of northeastern Kentucky. Journal of the Kentucky Academy of Science 60:38–44.

Lacki, M.J., S.K. Amelon and M.D. Baker. 2007. Foraging ecology of bats in forests. Pages 82–127 *in* M.J. Lacki, J.P. Hayes, and A. Kurta, editors. Bats in forests: conservation and management. Johns Hopkins University Press, Baltimore, MD, USA.

Langwig, K.E., W.F. Frick, J.T. Bried, A.C. Hicks, T.H. Kunz, and A.M. Kilpatrick. 2012. Sociality, density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. Ecology Letters 15:1050–1057.

Langwig K.E., W.F. Frick, J.R. Hoyt, K.L. Parise, K.P. Drees, T.H. Kunz, J.T. Foster, and A.M. Kilpatrick A.M. 2016. Drivers of variation in species impacts for a multi-host fungal disease of bats. Philosophical Transactions of the Royal Society B: Biological Sciences 371: 20150456. https://doi.org/10.1098/rstb.2015.0456.

Langwig, K.E., J.R. Hoyt, K.L. Parise, W.F. Frick, J.T. Foster, and A.M. Kilpatrick. 2017.

Resistance in persisting bat populations after white-nose syndrome

invasion. Philosophical Transactions of the Royal Society B: Biological Sciences 372:

20160044. DOI:10.1098/rstb.2016.0044.

Lewis, S.E. 1995. Roost fidelity of bats: a review. Journal of Mammalogy 76:481–496.

Loeb, S.C., and J.M. O'Keefe. 2006. Habitat use by forest bats in South Carolina in relation to

local, stand, and landscape characteristics. Journal of Wildlife Management 70:1210–

1218.

Lorch, J.M., C.U. Meteyer, M.J. Behr, J.G. Boyles, P.M. Cryan, A.C. Hicks, A.E. Ballman,

J.T.H. Coleman, D. N. Redell, D.M. Reeder, and D.S. Blehert. 2011. Experimental

infection of bats with *Geomyces destructans* causes white-nose

syndrome. Nature, 480:376–378.

Lowe, A.J. 2012. Swarming behavior and fall roost-use of little brown (*Myotis lucifugus*), and

northern long-eared bats (*Myotis septentrionalis*) in Nova Scotia, Canada. MS Thesis. St

Mary's University, Halifax, Nova Scotia, Canada.

MacDonald, K., E. Matsui, R. Stevens, and M.B. Fenton. 1993. Echolocation calls and field

identification of the eastern pipistrelle (*Pipistrellus subflavus* Chiroptera:

Vespertilionidae), using ultrasonic bat detectors. Journal of Mammalogy 75:462–465.

McNab, B.K. 1974. The behavior of temperate cave bats in a subtropical environmental. Ecology

55: 943–958.

Menu, H. 1984. Revision of the status of *Pipistrellus subflavus* (F. Cuvier, 1832). A new generic

name is proposed: *Perimyotis* new genus. Mammalia 43:409–416.

Menzel, M.A., J.M. Menzel, J.C. Kilgo, W.M. Ford, T.C. Carter, and J.W. Edwards. 2003. Bats

of the Savannah River Site and vicinity. General Technical Report SRS-68. U.S. Forest

Service, Southern Research Station, Asheville, NC, USA.Miller, D.A., E.B. Arnett, and M.J.

    Lacki. 2003. Habitat management for forest-roosting bats of

    North America: a critical review of habitat studies. Wildlife Society Bulletin 31:30–44.

Minnis, A.M., and D.L. Lindner. 2013. Phylogenetic evaluation of *Geomyces* and allies reveals

    no close relatives of *Pseudogymnoascus destructans*, comb, nov., in bat hibernacula of

    eastern North America. Fungal Biology 117:638–649.

Muthersbaugh, M.S., W.M. Ford, A. Silvis, and K.E. Powers. 2019. Activity patterns of

    cave-dwelling bat species during pre-hibernation swarming and post-hibernation

    emergence in the Central Appalachians. Diversity11:159.

National Oceanic and Atmospheric Administration. 2016. National Oceanic and Atmospheric

    Administration National Climate Data Center. Local climatological data.

    http://www.ncdc.noaa.gov/most-popular-data#loc-clim. Accessed 30 October

NatureServe. 2015. NatureServe Explorer: An online encyclopedia of life [web application].

    Version 7.1. NatureServe, Arlington, Virginia. http://explorer.natureserve.org. Accessed

    30 October 2020.

Norberg, U.M. and J.M.V. Rayner. 1987. Ecological morphology and flight in bats (Mammalia;

    Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation.

    Philosophical Transactions of the Royal Society of London B 316:335–427.

O'Keefe J.M., S.C. Loeb, J.D. Lanham, and H.S. Hill Jr. 2009. Macrohabitat factors affect day

    roost selection by eastern red bats and eastern pipistrelles in the southern Appalachian

    Mountain, USA. Forest Ecology and Management 257:1757–1763.

O'Keefe, J.M., and S.C. Loeb. 2017. Indiana bats roost in ephemeral, fire-dependent pine snags in the southern Appalachian Mountains, USA. Forest Ecology and Management 391:264–274.

O'Keefe, J.M, J.L. Petit, and S.C. Loeb. 2019. White-nose syndrome dramatically altered the summer bat assemblage in a temperate Southern Appalachian Forest. Mammalian Biology 98: 146–153.

Perry, R.W., and R.E. Thill. 2007. Tree roosting by male and female eastern pipistrelles in a forested landscape. Journal of Mammalogy 88:974–981.

Pierson, E.D. 1998. Tall trees, deep holes, and scarred landscapes. Pages 309–325 *in* T.H. Kunz and P.A. Racey, editors. Bat biology and conservation. Smithsonian Institution Press. Washington D.C., USA.

Ploskey, G.R., and J.A. Sealer. 1979. Lipid deposition and withdrawal before and during hibernation in *Pipistrellus subflavus.* Southwestern Naturalist 24:71–78.

Poole, E.L. 1932. A survey of the mammals of Berks County, Pennsylvania. Bulletin Reading Public Museum and Art Gallery 13:5–74.

Powers, K.E., R.J. Reynolds, W. Orndorff, and C.S. Hobson. 2015. Post-white-nose syndrome trends in Virginia's cave bats, 2008–2013. Journal of Ecology and the Natural Environment 7:123–130.

Quinn, G.M., and H.G. Broders. 2007. Roosting and foraging ecology of eastern pipistrelle (*Perimyotis subflavus*) in SW Novia Scotia. Report prepared for Nova Scotia Department of Natural Resources. Halifax, Nova Scotia, Canada.

Racey, P.A. 1988. Reproductive assessment in bats. Pages 31–43 *in* T.H. Kunz, editor.

Ecological and behavioral methods for the study of bats. Smithsonian Institution Press, Washington, D.C., USA.

Reichard J.D., and T.H. Kunz. 2009. White-nose syndrome inflicts lasting injuries to the wings of little brown myotis (*Myotis lucifugus).* Acta Chiropterologica 11:457–464.

Schirmacher, M.R., S.B. Castleberry, W.M. Ford, and K.V. Miller. 2007. Habitat associations of bats in south-central Virginia. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 61:46–52.

Seaman, D.E., J.J. Millspaugh, B.J. Kernohan, G.C. Brundige, K.J. Raedeke, and R.A. Gitzen. 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife Management 63:739–747.

Sleep, D.J., and R.M. Brigham. 2003. An experimental test of clutter tolerance in bats. Journal of Mammalogy 84:216–224.

Shively, R., P. Barboza, P. Doak, and T.S. Jung. 2018. Increased diet breadth of little brown bats (*Myotis lucifugus*) at their northern range limit: a multimethod approach. Canadian Journal of Zoology 96:31–38.

Silvis, A., R.W. Perry, and W.M. Ford. 2016. Relationships of three species of bats impacted by white-nose syndrome to forest condition and management. General Technical Report SRS-214. Forest Service Research and Development Southern Research Station, Asheville, NC, USA.

The Tennessee Chapter of the Nature Conservancy. 2015. 2015 Tennessee bat population monitoring and white-nose syndrome investigation report. Final Report prepared for Tennessee Wildlife Resources Agency. Nashville, TN, USA.

Tennessee Wildlife Resources Agency. 2005. Tennessee's comprehensive wildlife conservation

strategy. Tennessee Wildlife Resources Agency. Nashville, TN, USA.

Tennessee State Wildlife Action Plan Team. 2015. Tennessee State Wildlife Action Plan. Tennessee Wildlife Resources Agency. Nashville, TN, USA.

Turbill, C., G. Körtner, and F. Geiser. 2008. Timing of the daily temperature cycle affects the critical arousal temperature and energy expenditure of lesser long-eared bats. Journal of Experimental Biology 211:3871–3878.

Turner, G., D. Reeder, and J. Coleman. 2011. A five-year assessment of mortality and geographic spread of white-nose syndrome in North American bats and a look to the future. Bat Research News 52:13–27.

U.S. Fish and Wildlife Service. 2015. Endangered and threatened wildlife and plants; threatened species status for the northern long-eared bat with 4(d) Rule. U.S. Federal Register 80: 17974–18033.

U.S. Fish and Wildlife Service. 2015a. New Jersey Species Being Evaluated for Possible Listing under the Endangered Species Act. http://www.fws.gov/northeast/njfieldoffice/pdf/Evaluated_Species.pdf. Accessed 30 October 2020.

U.S. Fish and Wildlife Service. 2017. Conservation Strategy for Forest-dwelling Bats in Tennessee. https://www.fws.gov/southeast/pdf/strategy/conservation-strategy-for-forest-dwelling-bats-in-tennessee.pdf. Accessed 18 November 2020.

U.S. Fish and Wildlife Service. 2020. Where is WNS Now. https://www.whitenosesyndrome.org/where-is-wns. Accessed 30 October 2020.

U.S. Fish and Wildlife Service. 2020. Range-wide Indiana bat survey guidelines.

https://www.fws.gov/midwest/endangered/mammals/inba/surveys/pdf/FINAL%20Range-wide%20IBat%20Survey%20Guidelines%203.23.20.pdf. Accessed 29 October 2020.

Veilleux, J.P., J.O. Whitaker, and S.L.Veilleux. 2003. Tree-roosting ecology of reproductive female eastern pipistrelles, *Pipistrelles subflavus,* in Indiana. Journal of Mammalogy 84: 1068–1075.

Verant, M.L., C.U. Meteyer, J.R. Speakman, P.M. Cryan, J.M. Lorch, and D.S. Blehert. 2014. White-nose syndrome initiates a cascade of physiological disturbances in the hibernating bat host. BMC Physiology 14:10. https://doi.org/10.1186/s12899-014-0010-4.

Voight, C.C., and T. Kingston, editors. 2016. Bats in the Anthropocene: Conservation of Bats in a Changing World, Springer, NY, USA.

Walley, H.D., and W.L. Jarvis. 1971. Longevity record for *Pipistrellus subflavus.* Illinois Academy of Science 64:305.

Warnecke, L., J.M. Turner, T.K. Bollinger, V. Misra, P.M. Cryan, D.S. Blehert, G. Wibbelt, and C.K.R. Willis. 2013. Pathophysiology of white-nose syndrome in bats: A mechanistic model linking wing damage to mortality. Biology Letters 9:20130177. https://doi.org/10.1186/s12899-014-0010-4.

Whitaker, J.O. 1998. Life history and roost switching in six summer colonies of eastern pipistrelles in buildings. Journal of Mammalogy 79:651–659.

Whitaker, J.O., and W.J. Hamilton. 1998. Mammals of the Eastern United States. Cornell University Press. Ithaca, New York.

Winchell, J.M., and T.H. Kunz. 1996. Day-roosting activity budgets of the eastern pipistrelle bat, *Pipistrellus subflavus* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 74:431–441.

Wimsatt, W. A. 1945. Notes on breeding behavior, pregnancy, and parturition in some

    vespertilionid bats of the eastern United States. Journal of Mammalogy 26:23–33.

Worton, B.J. 1989. Kernel methods for estimating the utilization distribution in homerange

    studies. Ecology 70:164–168.

APPENDIX

Figure 3. 1 Map of Tennessee with counties of study sites indicated by blue stars.

Table 3. 1 Microhabitat variables used in candidate models to determine roost selection by tricolored bats (*Perimyotis subflavus*) captured at caves in Tennessee, (August – November) USA, 2017–2019.

Model Variable	Definition
t.den	Total tree density in plot
sw.den	Total coniferous density in plot
can.close	Canopy closure at 10 m from roost tree (%)
stem	Stem count in plot
roost.ht	Height of roost (m)
rt.ht	Height of roost tree (m)
ov.ht	Average overstory height (m)
can.vol	Area of roost tree canopy (m^2)

Table 3. 2 Landscape variables used in candidate models to determine roost selection by tri-colored bats (Perimyotis subflavus) captured at caves in Tennessee, USA, (August-November) 2017–2019.

Variable	Definition
dist.cave	Distance from roost tree to nearest cave
dist.water	Distance from roost tree to nearest open body of water
dist.road	Distance from roost tree to nearest road

Table 3. 3 Best candidate models predicting roost selection at the microhabitat by tri-colored bats captured at caves in Tennessee, USA, 2017–2019. We present the number of parameters in the model (K), the Aikake's Information Criterion score (AICc), difference in in AIC from top model sore (ΔAIC), and relative weight for each model (w).

Model	Model	K	AIC$_c$	AIC	W
clutter1	t.den+sw.den+can.close+stem+roost.ht	6	129.9956	0.00	0.210
clutter2	t.den+sw.den+can.close+stem	5	130.2134	0.22	0.163
therm1	rt.ht+roost.ht+can.close+can.vol+ov.ht	6	131.0679	1.07	0.129
clutter3	t.den+sw.den+can.close	4	140.1790	10.18	0.108
therm2	roost.ht+can.close+can.vol+ov.ht	5	141.4963	11.50	0.078
clutter4	t.den+sw.den	3	146.2215	16.23	0.053
therm3	roost.ht+can.close+can.vol	4	153.0904	23.09	0.048
clutter5	t.den+can.close	3	154.0724	23.58	0.056
clutter4	t.den+stem	3	154.0832	23.42	0.088
therm4	ov.ht+can.close+can.vol	4	155.0612	24.01	0.067
Null	.	1	161.1592	31.16	0.00

Table 3. 4 Model-averaged 95% confidence intervals and odds ratios for variables of models within 2 IAC units of the top model explaining microhabitat selection in tri-colored bats captured at caves in Tennessee, USA, 2017–2019.

Variable	Lower CI	Upper CI	Estimate odds
Clutter			
t.den	-0.328	0.107	0.687
sw.den	-0.053	-0.114	0.927

Table 3. 5 Best candidate models predicting selection of landscape variables by tri-colored bats captured at caves in Tennessee, USA, 2017–2019. We present the number of parameters in the model (K), the Aikake's Information Criterion score (AICc), difference in AIC from top model sore (ΔAIC), and relative weight for each model (w).

Model	Model	K	AIC$_c$	AIC	W
landscape5	dist.cave	2	140.1551	0.00	0.216
landscape2	dist.cave+dist.water	3	142.9164	2.7613	0.162
landscape1	dist.cave+dist.water+dist.road	4	152.4566	12.3015	0.112
landscape3	dist.cave+dist.road	3	153.1455	12.9904	0.079
landscape4	dist.road+dist.water	3	153.9486	13.7935	0.066
landscape6	dist.water	2	155.4523	15.2972	0.052
Null	.	1	175.1512	34.9961	0.00

Table 3. 6 Microhabitat level roost characteristics summarized for Indiana bats (*Myotis sodalis*) captured at caves in Tennessee, USA, 2017–2019.

Variable	Mean $\bar{X}$	Min	Max	SE
Roost height	9.83	12.19	8.84	1.58
Roost tree height (m)	27.58	21.94	42.67	10.22
Stand density (tree/(0.1 ha)	23	19	31	2.73
Canopy closure 5m from roost (%)	13.75	0	45	10.68
Average stand height (m)	28.80	24.99	33.53	1.80
Roost tree canopy volume (m^2)	3.25	1	8	1.60
Coniferous Density	3	1	4	0.71
Stem count	29.25	16	45	6.18
Roost DBH	58.75	22	86	8.25

Table 3. 7 Landscape level roost characteristics summarized for Indiana bats (*Myotis sodalis*) captured at caves in Tennessee, USA, 2017-2019.

Variable	Mean $\bar{X}$	Min	Max	SE
Distance to cave	108.32	32.68	300.61	64.80
Distance to water	5069.50	2954.21	5876.20	706.17
Distance to road	1169.17	88.23	1564.07	360.72

CHAPTER 4: CONCLUSIONS

In this thesis, I investigated the timing of the fall swarming and spring staging behavior of the Indiana bat and tri-colored bat at caves in Tennessee. I found that tri-colored bats arrive to hibernacula early in the fall swarming period, around mid-August. Increased activity continues through the end of September. Indiana bats arrive at hibernacula mid-September and continue increased Activity through the first week of November.

I also explored the roosting ecology of these two WNS sensitive species during fall swarming. Tri-colored bats use roosts on the landscape more than cave roosts. At the microhabitat level, roosts were selected based on clutter and thermoregulation related variables on the microhabitat level. Tri-colored bats selected roosts at the landscape level that were close in proximity to hibernacula. Indiana bats use cave roosts more than landscape roosts. This species roosted in snags close to hibernacula.

The findings of this thesis can be used to make more informed management decisions near hibernacula during the fall and spring seasons. Further research should explore foraging behavior of each species during these times, as well as impacts of management prescriptions and restrictions on bat species.

VITA

Mallory was born and raised in Rosemark, Tennessee. She grew up enjoying outdoor recreation of all varieties, where her love of understanding the natural world began. She moved to Knoxville, Tennessee in the fall of 2012 to begin her undergraduate degree in Animal Science. After studying abroad and participating in wildlife research projects in New Zealand, Mallory switched her major to Wildlife and Fisheries Science. While working toward her bachelors, she volunteered with Tennessee Wildlife Resources Agency and the Willcox Lab at the University of Tennessee. Working with these two groups, Mallory began focusing on non-game and bat specific research.

She graduated with a Bachelor's of Science in Wildlife and Fisheries in May 2017, and accepted a Master's position under Dr. Emma Willcox in August 2017. After completion of her Master's thesis defense, she will work as a Wildlife Diversity Survey Manager 1 for Tennessee Wildlife Resources Agency.