



Bats of Colonial National Historical Park Following White-nose Syndrome

Public Version

Natural Resource Report NPS/COLO/NRR—2023/2534



ON THE COVER

Tricolored bat (*Perimyotis subflavus*) captured at Yorktown, Virginia, Colonial National Historical Park
NPS/NICHOLAS KALEN

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Natural Resource Report NPS/COLO/NRR—2023/2534

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Contents

	Page
Figures.....	v
Tables.....	ix
Appendices.....	xiii
Abstract.....	xv
Acknowledgments.....	xvii
Introduction.....	1
Study Area	3
Methods.....	9
Acoustic Survey.....	9
Acoustic Data Modeling.....	11
Generalized Linear Mixed Model (GLMM)	11
Generalized Additive Model (GAM)	12
Capture Survey	12
Results.....	13
Big brown bat	21
Southeastern bat.....	22
Little brown bat	24
Northern long-eared bat.....	26
Indiana bat	28
Tricolored bat	30
Eastern red bat	32
Hoary bat	34
Silver-haired bat	36
Evening bat.....	38
Mexican free-tailed bat.....	40
Capture Survey	42

Contents (continued)

	Page
Discussion	47
Cave bats	48
Big brown bat	48
Southeastern bat.....	49
Little brown bat	50
Northern long-eared bat.....	51
Indiana bat	52
Tricolored bat	53
Tree bats	54
Eastern red bat	54
Hoary bat	55
Silver-haired bat	55
Evening bat.....	56
Mexican free-tailed bat.....	56
Conclusions.....	59
Literature Cited	61

Figures

	Page
Figure 1. Bat summer acoustic detector sites from 2019–2020 at Yorktown, Colonial National Historical Park, Virginia.	4
Figure 2. Bat summer acoustic detector sites from 2019–2020 at Jamestown Island, Colonial National Historical Park, Virginia.	5
Figure 3. Bat dormant season acoustic detector sites (yellow) and capture sites (red) from 2019–2021 at Yorktown, Colonial National Historical Park, Virginia.	6
Figure 4. Bat dormant season acoustic detector sites from 2019–2021 at Jamestown Island, Colonial National Historical Park, Virginia.	7
Figure 5. Representative acoustic detector deployment (COLO03D) in 2019 at Colonial National Historical Park, Virginia.	10
Figure 6. Big brown bat (<i>Eptesicus fuscus</i>) activity (mean passes/night and standard error) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia.	21
Figure 7. Predicted activity (mean passes per night and standard error) for big brown bats (<i>Eptesicus fuscus</i> , EPFU) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates habitat, distance to water (m), nightly precipitation (cm), and minimum temperature (°F).	22
Figure 8. Southeastern bat (<i>Myotis austroriparius</i>) activity (mean passes/night and standard error) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia.	23
Figure 9. Predicted activity (mean passes per night and standard error) for southeastern bats (<i>Myotis austroriparius</i> ; MYAU) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates: habitat and nightly precipitation (cm).	24
Figure 10. Little brown bat (<i>Myotis lucifugus</i>) activity (mean passes/night) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia.	25
Figure 11. Little brown bat (<i>Myotis lucifugus</i>) activity (mean passes/night and standard error) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia.	26
Figure 12. Northern long-eared bat (<i>Myotis septentrionalis</i>) activity (mean passes/night) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia.	27

Figures (continued)

	Page
Figure 13. Northern long-eared bat (<i>Myotis septentrionalis</i>) activity (mean passes/night and standard error) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia.....	28
Figure 14. Indiana bat (<i>Myotis sodalis</i>) activity (mean passes/night) at Colonial National Historical Park, Virginia as predicted by a generalized additive model of activity by Julian date.	29
Figure 15. Predicted activity (mean passes per night and standard error) for Indiana bats (<i>Myotis sodalis</i> , MYSO) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates habitat, distance top water (m), nightly precipitation (cm), and minimum temperature (°F).	30
Figure 16. Tricolored bat (<i>Perimyotis subflavus</i>) activity (mean passes/night) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia.	31
Figure 17. Predicted activity (mean passes per night and standard error) for tricolored bats (<i>Perimyotis subflavus</i> , PESU) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates habitat, distance to water (m), nightly precipitation (cm), and minimum nightly temperature (°F).	32
Figure 18. Eastern red bat (<i>Lasiurus borealis</i>) activity (mean passes/night) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia.	33
Figure 19. Predicted activity (mean passes per night and standard error) for eastern red bats (<i>Lasiurus borealis</i> , LABO) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates habitat, distance to water (m), nightly precipitation (cm), and minimum nightly temperature (°F).	34
Figure 20. Hoary bat (<i>Lasiurus cinereus</i>) activity (mean passes/night) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia.	35
Figure 21. Predicted activity (mean passes per night and standard error) for hoary bats (<i>Lasiurus cinereus</i>) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates habitat type, distance to water (m), nightly precipitation (cm), and minimum nightly temperature (°F).	36
Figure 22. Silver-haired bat (<i>Lasionycteris noctivagans</i>) activity (mean passes/night) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia.	37

Figures (continued)

Page

Figure 23. Predicted activity (mean passes per night and standard error) for silver-haired bats (<i>Lasionycteris noctivagans</i> , LANO) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates: habitat type distance to water (m), nightly precipitation (cm), and minimum nightly temperature (°F).....	38
Figure 24. Evening bat (<i>Nycticeius humeralis</i>) activity (mean passes/night) predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia.	39
Figure 25. Predicted activity (mean passes per night and standard error) for evening bats (<i>Nycticeius humeralis</i> , NYHU) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates: habitat type, distance to water (m), nightly precipitation (cm), and minimum nightly temperature (°F).....	40
Figure 26. Mexican free-tailed bat (<i>Tadarida brasiliensis</i>) activity (mean passes/night) predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia.	41
Figure 27. Predicted activity (mean passes per night and standard error) for Mexican free-tailed bat (<i>Tadarida brasiliensis</i> , TABR) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates: habitat type, distance to water (m), nightly precipitation (cm), and minimum nightly temperature (°F).....	42

Tables

	Page
Table 1. Mean nightly activity in number of echolocation passes per night of bat species at Colonial National Historical Park, Virginia during the summer period (April 16-September 15) in 2019–2020.	14
Table 2. Mean nightly activity of bat species at Colonial National Historical Park, Virginia during the fall period (September 16-November 30) during 2019 and 2020 in echolocation passes per night.	16
Table 3. Mean nightly activity of bat species at Colonial National Historical Park, Virginia during the winter period (December 1–February 28) in 2019–2021 in echolocation passes per night.	18
Table 4. Mean nightly activity of bat species at Colonial National Historical Park, Virginia during the spring period (March–April 14) in 2019–2021 in echolocation passes per night.	19
Table 5. Bat capture results by species, sex, and reproductive condition during mist-netting from 2019–2021 at Colonial National Historical Park, Virginia.	43
Table A-1. Crosswalk table for habitat classification, Colonial National Historical Park, Virginia.	71
Table B-1. Generalized linear mixed model (GLMM) parameter estimates of big brown bat (<i>Eptesicus fuscus</i>) activity at Colonial National Historical Park, Virginia.	73
Table B-2. Generalized additive model (GAM) parameter estimate of big brown bat (<i>Eptesicus fuscus</i>) activity at Colonial National Historical Park, Virginia.	73
Table B-3. Generalized linear mixed model (GLMM) parameter estimates of southeastern bat (<i>Myotis austroriparius</i>) activity at Colonial National Historical Park, Virginia.	73
Table B-4. Generalized additive model (GAM) parameter estimate of southeastern bat (<i>Myotis austroriparius</i>) activity at Colonial National Historical Park, Virginia.	73
Table B-5. Generalized linear mixed model (GLMM) parameter estimates of little brown bat (<i>Myotis lucifugus</i>) activity at Colonial National Historical Park, Virginia.	74
Table B-6. Generalized additive model (GAM) parameter estimate of little brown bat (<i>Myotis lucifugus</i>) activity at Colonial National Historical Park, Virginia.	74
Table B-7. Generalized linear mixed model (GLMM) parameter estimates of northern long-eared bat (<i>Myotis septentrionalis</i>) activity at Colonial National Historical Park, Virginia.	74

Tables (continued)

	Page
Table B-8. Generalized additive model (GAM) parameter estimate of northern long-eared bat (<i>Myotis septentrionalis</i>) activity at Colonial National Historical Park, Virginia.	74
Table B-9. Generalized linear mixed model (GLMM) parameter estimates of Indiana bat (<i>Myotis sodalis</i>) activity at Colonial National Historical Park, Virginia.	75
Table B-10. Generalized additive model (GAM) parameter estimate of Indiana bat (<i>Myotis sodalis</i>) activity at Colonial National Historical Park, Virginia.	75
Table B-11. Generalized linear mixed model (GLMM) parameter estimates of tricolored bat (<i>Perimyotis subflavus</i>) activity at Colonial National Historical Park, Virginia.	75
Table B-12. Generalized additive model (GAM) parameter estimate of tricolored bat (<i>Perimyotis subflavus</i>) activity at Colonial National Historical Park, Virginia.	75
Table B-13. Generalized linear mixed model (GLMM) parameter estimates of eastern red bat (<i>Lasiurus borealis</i>) activity at Colonial National Historical Park, Virginia.	76
Table B-14. Generalized additive model (GAM) parameter estimate of eastern red bat (<i>Lasiurus borealis</i>) at Colonial National Historical Park, Virginia.	76
Table B-15. Generalized linear mixed model (GLMM) parameter estimates of hoary bat (<i>Lasiurus cinereus</i>) activity at Colonial National Historical Park, Virginia.	76
Table B-16. Generalized additive model (GAM) parameter estimate of hoary bat (<i>Lasiurus cinereus</i>) activity at Colonial National Historical Park, Virginia.	77
Table B-17. Generalized linear mixed model (GLMM) parameter estimates of silver-haired bat (<i>Lasionycteris noctivagans</i>) activity at Colonial National Historical Park, Virginia.	77
Table C-18. Generalized additive model (GAM) parameter estimate of silver-haired bat (<i>Lasionycteris noctivagans</i>) activity at Colonial National Historical Park, Virginia.	77
Table B-19. Generalized linear mixed model (GLMM) parameter estimates of evening bat (<i>Nycticeius humeralis</i>) activity at Colonial National Historical Park, Virginia.	78
Table B-20. Generalized additive model (GAM) parameter estimate of evening bat (<i>Nycticeius humeralis</i>) activity at Colonial National Historical Park, Virginia.	78
Table B-21. Generalized linear mixed model (GLMM) parameter estimates of Mexican free-tailed bat (<i>Tadarida brasiliensis</i>) activity at Colonial National Historical Park, Virginia.	78

Tables (continued)

	Page
Table B-22. Generalized additive model (GAM) parameter estimate of Mexican free-tailed bat (<i>Tadarida brasiliensis</i>) at Colonial National Historical Park, Virginia.	79
Table C-1. Bat capture survey sites and net arrangements, Colonial National Historical Park, Virginia.	81

Appendices

	Page
Appendix A: Crosswalk Table for Habitat Classification	71
Appendix B: Bat Species Activity Model Parameters	73
Appendix C: Capture Survey Sites and Net Arrangements	81

Abstract

I conducted bat surveys at Colonial National Historical Park to assess the status of bat communities following potential impacts of white-nose syndrome (WNS) since its arrival in Virginia in 2009. This disease, caused by the fungus *Pseudogymnoascus destructans*, has severely reduced populations of several bat species in the eastern United States, threatening some with regional extirpation. In the East, most-affected species include the little brown bat (*Myotis lucifugus*), the federally-endangered northern long-eared bat (*Myotis septentrionalis*) and Indiana bat (*Myotis sodalis*) (USFWS 2007, USFWS 2022a), as well as the tricolored bat (*Perimyotis subflavus*), which has been proposed for endangered status (USFWS 2022b). I sampled sites in Yorktown and Jamestown Island with acoustic bat detectors from the spring of 2019 through the spring of 2021 and conducted capture surveys using mist nets in 2019 and 2021 to characterize seasonal occurrence of bat species with a focus on documenting WNS-imperiled species. Surveys also sought to document potential over-wintering of bats at COLO, especially northern long-eared bats, which occur year-round in the Coastal Plain of North Carolina. Acoustic results identified the presence of eleven bat species by echolocation calls: big brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), silver-haired bat (*Lasionycteris noctivagans*), southeastern bat (*Myotis austroriparius*), little brown bat, northern long-eared bat, Indiana bat, evening bat (*Nycticeius humeralis*), tricolored bat, and Mexican free-tailed bat (*Tadarida brasiliensis*). Acoustic results included diagnostic echolocation calls of little brown, northern long-eared, and Indiana bats, however, presence should be interpreted with caution due to similarities of call structures among *Myotis* spp. bats. Capture surveys documented seven species: big brown, eastern red, hoary, silver-haired, southeastern, evening, and tricolored bats. To examine habitat associations of bat species, I used generalized linear mixed models of a selection of variable candidates: habitat type, distance to water, minimum nightly temperature, and nightly precipitation to predict summer activity by significant predictors. Activity of hoary, silver-haired, little brown, evening, tricolored, and Mexican free-tailed bats was highest in open habitats. Big brown bat and Indiana bat identifications were most associated with forest habitats. Eastern red bat activity was high in both forest and open sites. Southeastern bat activity was highest in wetland sites and was largely confined to these habitats. Northern long-eared bat activity was not significantly different among habitat types. To examine seasonality in bat species occurrence, I modeled acoustic activity in passes/night by Julian date using generalized additive models. Activity of big brown, eastern red, hoary, little brown, northern long-eared, tricolored, evening, and Mexican free-tailed bats was highest during summer. Silver-haired bat activity was highest in March indicative of seasonal migration. Hoary and Mexican free-tailed bat also exhibited high activity on several nights in the spring suggestive of migratory movement. Dormant season results suggest some winter occurrence for all identified bat species except Indiana bats. Very few characteristic calls of northern long-eared bats were observed from December through February, suggesting they winter locally in far lower abundances than in the Coastal Plain of North Carolina to the south.

An internal NPS [version](#) of this document that includes an appendix with capture survey site coordinates is available and may be requested as needed.

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W. Mark Ford, Unit Leader of the U.S. Geological Survey Virginia Cooperative Fish and Wildlife Research Unit and Associate Professor of Fisheries and Wildlife Conservation at Virginia Tech guided this study and contributed greatly to this report. Dorothy Geyer, National Park Service Natural Resource Manager, provided assistance with field surveys.

Introduction

The introduction and spread of white-nose syndrome (WNS) in the eastern United States has caused precipitous declines in several formerly widespread and abundant cave-hibernating bat species (Coleman and Reichard 2014a, Frick et al. 2010, Turner et al. 2011, Langwig et al. 2015). WNS is an infectious disease caused by the invasive, cold-adapted fungal pathogen *Pseudogymnoascus destructans*. The fungus was initially introduced to North America in New York in 2006 and spread to Virginia in 2009 (Reynolds et al. 2016, Turner et al. 2011). *Pseudogymnoascus destructans* grows on hibernating bats where it breaches the epidermis, thereby causing arousal from torpor, resulting in dehydration, premature expenditure of fat reserves, and often death (Ford et al. 2011, Frick et al. 2015). Initial reports of regional population losses from hibernacula surveys in the Northeast and the Mid-Atlantic have been extremely high for several species: northern long-eared bat (*Myotis septentrionalis*, 98%), little brown bat (*Myotis lucifugus*, 91%), tricolored bat (*Perimyotis subflavus*, 75%), Indiana bat (*Myotis sodalis*, 72%; Turner et al. 2011). In Virginia, fall swarm survey and hibernacula counts have shown declines of 99% for little brown bats, 89.5% for tricolored bats, and 33.5% for Indiana bats (Powers et al. 2015). Summer mist-netting capture rates in Virginia have declined by 95% for northern long-eared bats (Reynolds et al. 2016). Signs of reduced recruitment have also been observed post-WNS including a 77% reduction in juvenile northern long-eared bat captures and a 66% reduction in juvenile little brown bats in Virginia (Francel et al. 2012, Reynolds et al. 2016). The effects of WNS have drastically altered bat communities in the eastern United States and threaten several species with regional extirpation, and potentially extinction (Frick et al. 2015, Kalen et al. 2022). In 2015, the United States Fish and Wildlife Service (USFWS) listed the northern long-eared bat as a threatened species following impacts from WNS and, in 2022, listed it as endangered (Federal Register § 81:1900-1922, USFWS 2022a). Tricolored bats have also recently been proposed for listing as endangered species (USFWS 2022b). The Indiana bat has been federally endangered since 1967 in response to declines associated with disturbances in hibernacula (USFWS 2007). The little brown bat is not federally protected presently but is under species status review and considered state endangered in Virginia (Straw et al. 2022, VDGIF 2016).

Historically, the eastern United States has supported a moderately diverse and abundant community of bats with two broad categories of species: “cave bats,” that generally migrate to caves or similar subterranean habitats to hibernate during the winter, and migratory “tree bats,” that generally migrate to tolerably warm climates in southern or coastal portions of their range during the winter. These long-distance migratory tree bats do not engage in extended periods of hibernation, and therefore, are believed to be unsusceptible to WNS. They are, however, prone to mortality from wind turbine collisions and barotrauma (Arnett et al. 2008). Species such as eastern red bat (*Lasiurus borealis*), hoary bat (*Lasiurus cinereus*), and silver-haired bat (*Lasionycteris noctivagans*) appear most affected by wind turbine mortality, however, deaths of other species including cave-hibernating bats have been observed (Arnett et al. 2008, Kunz et al. 2007).

Prior to WNS, most bat surveys in the eastern United States focused on identifying if endangered Indiana bats were present in forests during the summer or hibernacula in the winter within a regulatory monitoring and clearance context. As such, often little regard was given to assessing the

greater extant bat community. Accordingly, much remains unknown about most aspects of bat species' distribution, migration, and overall ecology in localities such as Colonial National Historical Park (COLO) where Indiana bats historically have been presumed absent. Surveys have increased significantly in frequency after the advent of WNS with greater focus on WNS-imperiled species that had previously received little attention. Recently, populations of northern long-eared bats have been observed year-round in the Coastal Plain of North Carolina, approximately 110 km south of COLO, where avoidance of cave hibernacula has allowed them to remain free of WNS impacts (Jordan 2020). Also in 2015, a maternity colony of Indiana bats was documented approximately 130 km northwest of COLO in Caroline County, Virginia beyond its previously known range in the Mid-Atlantic (St. Germain et al. 2017).

Following WNS impacts, there has been a great need to conduct large-scale, long-term monitoring of bat species communities to guide current and future conservation actions and to also gain understanding of bat community distributions and seasonal movements. Colonial National Historical Park may constitute significant high-quality bat habitat in a rapidly urbanizing portion of coastal Virginia and likely supports diverse species communities, including species imperiled by WNS. Investigating summer occurrences and, potentially, reproduction of imperiled bat species at localities such as COLO is essential to bat conservation following WNS. Furthermore, potential year-round occurrence of northern long-eared bats requires investigation. To evaluate bat species community composition at COLO, I conducted acoustic and capture surveys with specific focus on species most-impacted by WNS: little brown bat, northern long-eared bat, Indiana bat, and tricolored bat.

Study Area

Colonial National Historical Park (COLO) is located on the Lower Peninsula in coastal Virginia and comprises a total of 3,740 hectares, the majority of which is within two main parcels on opposing coasts of the peninsula: Yorktown, adjacent the York River, and Jamestown Island, along the James River (Figure 1 through Figure 4). COLO is in the Coastal Plain physiographic province. A little over half of the park area is forested, approximately one fourth is tidal and non-tidal wetlands, and the remaining lands are primarily managed open grasslands. Most forests are pine-oak with dominant tree species including: loblolly pine (*Pinus taeda*), white oak (*Quercus alba*), willow oak (*Q. phellos*), red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), mockernut hickory (*Carya tomentosa*), American holly (*Ilex opaca*), and tulip poplar (*Liriodendron tulipifera*). In wetlands, bald cypress (*Taxodium distichum*), swamp tupelo (*Nyssa biflora*) and green ash (*Fraxinus pennsylvanica*) are common. Yorktown is a diverse landscape that features pine-oak as well as, oak-hickory forest, cypress swamps, and open grasslands. It also encompasses several first and second order streams including Beaverdam Creek, Baptist Run, and Great Run, as well as a large approximately 6.5 hectare pond, Wormley Pond. Vernal pools and sinkholes are also abundant (Thornberry-Ehrlich 2016). Jamestown Island is primarily tidal marsh surrounding a central portion of pine-oak forest. Surrounding Yorktown, the approximately 3,100 hectare Newport News Park borders the south and 5,000 hectare Yorktown Naval Weapons Station borders the west combining to form a large, relatively undeveloped span of contiguous forest and wetlands. Beyond this, the peninsula is largely developed with Newport News to the south and Williamsburg to the northwest, which is also 12 kilometers northeast of Jamestown Island. Jamestown Island is 18 kilometers west of Yorktown.



Figure 1. Bat summer acoustic detector sites from 2019–2020 at Yorktown, Colonial National Historical Park, Virginia.

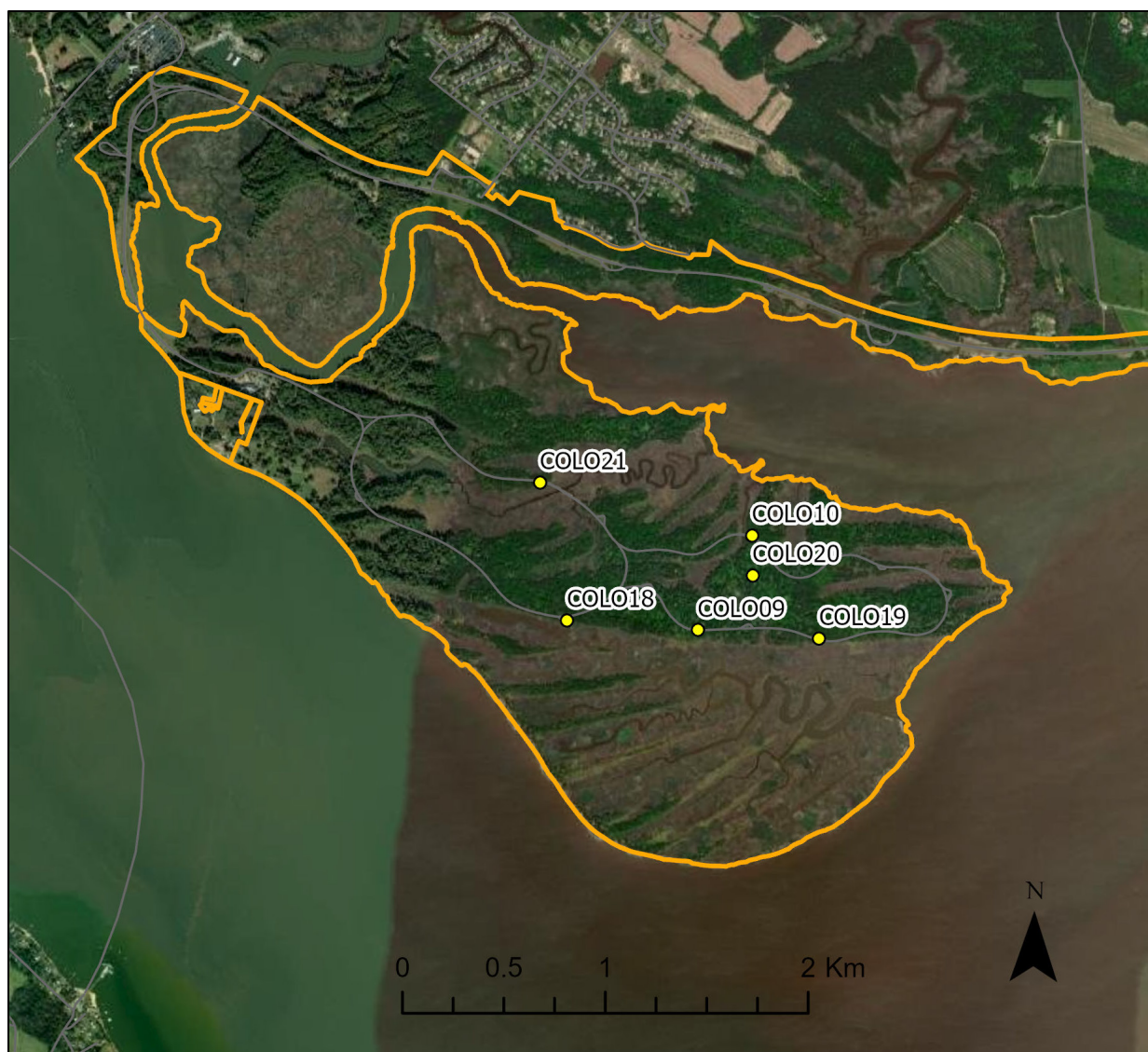


Figure 2. Bat summer acoustic detector sites from 2019–2020 at Jamestown Island, Colonial National Historical Park, Virginia.



Figure 3. Bat dormant season acoustic detector sites (yellow) and capture sites (red) from 2019–2021 at Yorktown, Colonial National Historical Park, Virginia.



Figure 4. Bat dormant season acoustic detector sites from 2019–2021 at Jamestown Island, Colonial National Historical Park, Virginia.

Methods

I conducted acoustic and mist-netting surveys at COLO with the objectives of assessing bat species communities and documenting locations where WNS-imperiled species occur with specific emphasis on the federally endangered northern long-eared bat. Work began in February of 2019 initiating acoustic monitoring during the non-reproductive, or dormant, season to examine over-wintering bat communities with specific focus on identifying if northern long-eared bats occurred year-round. Acoustic surveys were continued in the reproductive summer season of 2019, with dormant and summer sampling continuing through the spring of 2021. In addition to serving as the first sample approximation, I used data from acoustic sampling to guide subsequent mist-netting efforts to increase the likelihood of capturing northern long-eared bats, and potentially, monitoring reproduction and roosting.

Acoustic Survey

For acoustic survey, I deployed zero-crossing, frequency division bat detectors (Wildlife Acoustics, Concord, MA) at sites to sample for bat echolocation calls. All acoustic sampling occurred at passive acoustic sites (i.e., stationary) with detectors and microphones affixed to trees via cable lock (Figure 5). Acoustic bat detectors were set to record ultrasonic echolocation calls from dusk until dawn. Sampling methodology during the summer period, when bat activity is generally high, consisted of deploying detectors at many, non-repeating sites (COLO01-COLO21). Most summer acoustic sampling took place from May 15-August 15 to coincide with bat reproductive period (i.e., formation of maternity colonies through juvenile volancy) as defined the USFWS Indiana and northern long-eared bat survey guidelines (USFWS 2022c). However, for the purpose of presenting seasonal results, I extended this summer period to April 16-September 15 to better reflect bat activity patterns with respect to spring and fall. Summer sampling occurred from late May through mid-July in 2019, and from early July through mid-September in 2020. Outside of the summer reproductive season, hereafter referred to as the dormant season, I utilized long-term deployments of detectors at locations I considered to be optimal sites to record bat activity such as drinking sites or commuting corridors during traditionally low activity times of year (COLO01D-COLO24D). In some cases, dormant sites were in the same location as summer sites where high activity of bats, particularly *Myotis* spp., were observed (e.g. COLO03 and COLO15D, COLO05 and COLO04D). Sampling at several dormant sites was repeated over consecutive years, especially if focal species were identified. Additionally, many detectors stationed at dormant sites recorded through a portion of the summer season, and conversely, several summer site detectors continued recording through the fall in 2020. These acoustic data were included in the appropriate seasonal activity results. Some instances of equipment failure, battery depletion, or equipment disturbance did occur. Equipment failed at Jamestown summer sites COLO07 and COLO08, so there are no results for these sites.



Figure 5. Representative acoustic detector deployment (COL003D) in 2019 at Colonial National Historical Park, Virginia.

I selected individual acoustic sites to encompass a variety of habitat types and correspond with bat ecology. I targeted forest trails, riparian corridors, ponds, vernal pools, field edges, and interior forest gaps that represented suitable habitat for the foraging, commuting, drinking, and roosting behavior of eastern bats (Coleman et al. 2014a, Kunz and Kurta 1988, Murray et al. 1999, Silvis et al. 2016).

I used United States Fish and Wildlife Service and United States Geological Survey-approved software Kaleidoscope 5.3.9 (Wildlife Acoustics, Concord, MA) using 5.2.0 species classifiers to identify bat species activity by echolocation call classification. I chose species candidates for call identification analysis based on known distribution and recent and historic capture records that corresponded with the park location. Bat species considered for identification included cave bat species: big brown bat, southeastern bat (*Myotis austroriparius*), little brown bat, northern long-eared bat, Indiana bat, and tricolored bat; and tree bat species eastern red bat, hoary bat, silver-haired bat, evening bat (*Nycticeius humeralis*), and Mexican free-tailed bat (*Tadarida brasiliensis*). The Seminole bat (*Lasiurus seminolus*) and Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) were also considered for occurrence in initial analysis, but were ruled out as candidates based on results and distribution records in Virginia (VAFWIS 2022a-c). I used a maximum-likelihood estimator (MLE) p -value of 0.05 or less to qualify identification of bat species calls on a nightly basis to reduce reporting of misidentified bat calls. Kaleidoscope generates this MLE p -value for each sample night based on number of calls identified along with a confusion matrix of species error rates observed in test data. I performed visual validation on selected calls identified as northern long-eared bats, Indiana bats, and little brown bats to further evaluate identification accuracy. Selections for validation included calls from multiple sites from every season in which these species were identified, but results were not altered to reflect validation determinations. Systematic visual validation of all calls for these species was not performed due to large volume of call files (>50,000).

I tabulated mean nightly activity of species by summing total number of MLE-qualifying identified echolocation passes and dividing this by number of nights sampled. Results were tabulated seasonally over years for spring (March 1-April 15), summer (April 16-September 15), fall (September 16-November 30), and winter (December 1-February 28) with seasonal periods based on a generalized cave bat annual life cycle (Silvis et al. 2016). Spring, fall, and winter results are collectively included in the dormant season for the purposes of site naming convention.

Acoustic Data Modeling

Generalized Linear Mixed Model (GLMM)

To interpret bat activity relative to broadscale landscape and weather variables, I modeled summer nightly bat echolocation pass results by predictor covariates: habitat type, distance to water, nightly precipitation, and minimum temperature (Barr et al. 2021, Muthersbaugh et al. 2019, True et al. 2021). I classified habitat type at each acoustic site as: forest, open, and wetland based on U.S. National Vegetation Classification delineation classifications (Patterson 2008; Appendix A). As forests at COLO are predominately mixed pine and hardwood forest, I did not differentiate between deciduous and coniferous forest types. Open habitat comprises grasslands, agricultural fields, and shrubland habitats. Wetlands include open wetlands, estuarine tidal wetlands, riparian-zone forest, swamps, and bottomland hardwood swamps. I calculated distance to water source by calculating

distance from acoustic sites to streams and ponds in ArcGIS Pro 2.5.0 (Environmental Systems Research Institute, Inc., Redlands, CA) using US Geological Survey National Hydrology Dataset (USGS 2019). I obtained nightly weather data total rainfall and minimum temperature from the National Oceanic and Atmospheric Administration National Centers for Environmental Information (NOAA 2022).

Bat acoustic nightly activity data (passes/night) is often zero-inflated (i.e., datasets contain many zeros because many site-nights do not record species passes) and has very high variance because passes per night vary considerably by site and night. Accordingly, I modeled activity with zero-inflated Generalized Linear Mixed Models (GLMMs) using a negative binomial distribution with the package *glmmTMB* in Program R (Brooks et al. 2017, R Core Team 2017). I used backwards-stepwise selection to remove non-significant predictors, requiring a p -value of 0.10 or less for model inclusion. Resulting models varied by individual species and included all predictors that exceeded this significance threshold. I used models to predict fixed effects of each significant predictor on bat species activity using the *glmmTMB* package (Brooks et al. 2017).

Generalized Additive Model (GAM)

To evaluate seasonal fluctuations in bat activity, I used zero-inflated, negative binomial distribution Generalized Additive Models (GAMs) using package *mgcv* (Wood 2011) to predict species activity by Julian day in Program R (Guisan et al. 2002).

Capture Survey

I captured bats using 38 mm low-bag mist nets (Avinet Inc. Portland, Maine) of varying widths (4, 6, 9 and 12 m) and stacking configurations. Majority of sampling included multiple net stations with mist nets set across forest corridors, such as trails and unimproved roads, as well as, across streams and standing water where foliar clutter was such that it would surround mist nets to prevent free-flying bats from avoiding capture (Figure 3; Kunz and Kurta 1988, Kunz and Parsons 2009, Silvis et al. 2012). I used acoustic survey results to guide selection of mist-netting sites to improve the likelihood of captures, with specific regard to capturing northern long-eared bats and other WNS-imperiled species. I only mist-netted for bats on nights with optimal weather conditions, avoiding sampling during periods of high winds, substantial rain, or lightning (Loeb et al. 2015). I performed capture surveys on 16 nights from February through October in 2019, three nights in March 2020, and two nights in October 2021.

From captured bats, I recorded species, sex, age, reproductive condition, mass, and forearm length (Menzel et al. 2002a, Silvis et al. 2012). Age (i.e., adult or juvenile) was determined by backlighting the metacarpal-phalangeal joint to evaluate joint fusion (Kunz 1973). I determined reproductive condition in females by palpating the abdomen to detect pregnancy and examined mammary glands to detect lactation and post-lactation (Kunz 1973). I released all bats near the site of capture and all handling adhered to the guidelines of National Park Service and Virginia Tech Institutional Animal Care and Use Committee protocols, NNCR.NER_MultipleParks_Ford_Bats_2018.A2, 16-240, and 19-227, respectively.

Results

Acoustic detectors sampled for 4,853 detector-nights, 2,521 of which occurred during the summer period. Summer sampling included 19 summer sites in 2019 and 2020, as well as 15 dormant season sites that recorded during the summer period (Table 1). Sampling occurred at 22, 19, and 21 sites, over spring, winter, and fall, respectively, from 2019–2021, with several sites being resampled over this period (Tables 2-4). Equipment at sites COLO07, COLO08, and COLO12D failed to collect data during summer due to equipment failure so are not included in results. COLO11D failed in spring of 2019 but did record in the fall and winter of 2019 through 2020. Kaleidoscope software identified all eleven bat species considered for presence at qualifying MLE thresholds ($p \leq 0.05$, Table 2). Total numbers of bat passes identified by species were: big brown bat ($n = 100,723$), eastern red bat ($n = 67,950$), hoary bat ($n = 5,123$), silver-haired bat ($n = 3,268$), southeastern bat ($n = 6,078$), little brown bat ($n = 46,401$), northern long-eared bat (2,632), Indiana bat ($n = 2,758$), evening bat ($n = 29,966$), tricolored bat ($n = 36,932$), and Mexican free-tailed ($n = 6,719$). Bat species GLMM and GAM parameter estimates are presented in Appendix B.

Table 1. Mean nightly activity in number of echolocation passes per night of bat species at Colonial National Historical Park, Virginia during the summer period (April 16-September 15) in 2019–2020.

Site	Unit ¹	Year	EPFU ²	LABO ²	LACI ²	LANO ²	MYAU ²	MYLU ²	MYSE ²	MYSO ²	NYHU ²	PESU ²	TABR ²
COLO01	Y	2019	36.16	79.76	0.29	0.06	1.82	7.78	0.20	1.18	0.00	13.37	0.00
COLO02	Y	2019	52.82	8.61	3.61	0.24	0.69	0.06	0.27	0.04	33.82	31.45	0.76
COLO03	Y	2019	51.27	25.37	0.76	0.51	0.57	17.84	0.08	0.14	28.41	10.90	0.00
COLO04	Y	2019	35.45	62.10	1.08	0.55	1.71	8.92	1.31	3.61	0.00	1.22	0.00
COLO05	Y	2019	126.08	22.24	0.29	1.94	24.80	36.96	2.96	1.45	23.55	21.12	0.00
COLO06	Y	2019	51.63	139.51	0.39	0.27	1.22	6.18	0.16	1.94	96.14	60.88	0.18
COLO09	J	2019	109.09	60.57	5.12	2.69	1.45	42.76	0.01	0.04	81.25	16.68	0.00
COLO10	J	2019	137.51	36.43	10.32	0.00	0.26	2.87	0.00	0.00	65.28	3.84	0.88
COLO11	Y	2020	5.33	0.88	0.93	0.00	0.93	0.45	0.05	0.00	0.00	1.52	0.05
COLO12	Y	2020	39.95	45.58	0.09	2.49	0.16	21.74	0.00	0.00	26.65	25.33	12.70
COLO13	Y	2020	118.67	14.40	1.40	0.00	0.77	11.53	0.05	0.19	1.77	13.21	0.42
COLO14	Y	2020	148.00	57.50	0.00	0.00	0.00	4.85	0.90	0.65	51.75	43.55	0.25
COLO15	Y	2020	15.40	43.81	2.14	0.00	0.95	11.88	0.00	0.00	20.86	32.64	2.95
COLO16	Y	2020	0.10	0.00	0.00	0.10	0.00	0.00	0.20	0.00	0.00	0.00	0.00
COLO17	Y	2020	27.25	25.25	0.00	0.00	3.32	37.43	3.77	0.84	7.23	54.50	4.16
COLO18	Y	2020	79.00	2.94	0.00	0.00	0.00	1.15	0.00	0.00	5.29	3.29	6.00
COLO19	J	2020	9.39	5.42	0.00	0.39	0.52	5.61	0.00	0.06	0.00	0.82	1.85
COLO20	J	2020	87.52	38.65	0.65	0.00	1.55	1.74	0.00	0.00	19.29	25.97	0.00

¹ Y = Yorktown, J = Jamestown.

² EPFU = big brown bat (*Eptesicus fuscus*), LABO = eastern red bat (*Lasiurus borealis*), LACI = hoary bat (*Lasiurus cinereus*), LANO = silver-haired bat (*Lasionycteris noctivagans*), MYAU = southeastern bat (*Myotis austroriparius*), MYLU = little brown bat (*Myotis lucifugus*), MYSE = northern long-eared bat (*Myotis septentrionalis*), MYSO = Indiana bat (*Myotis sodalis*), NYHU = evening bat (*Nycticeius humeralis*), PESU = tricolored bat (*Perimyotis subflavus*), TABR = Mexican free-tailed bat (*Tadarida brasiliensis*).

³ Sites ending in “D” were dormant season sampling locations that also recorded during the summer.

Table 1 (continued). Mean nightly activity in number of echolocation passes per night of bat species at Colonial National Historical Park, Virginia during the summer period (April 16–September 15) in 2019–2020.

Site	Unit ¹	Year	EPFU ²	LABO ²	LACI ²	LANO ²	MYAU ²	MYLU ²	MYSE ²	MYSO ²	NYHU ²	PESU ²	TABR ²
COLO21	J	2020	19.30	11.70	0.00	0.07	0.00	6.26	0.00	0.00	0.00	0.93	0.59
COLO01D ³	Y	2019	2.49	2.33	6.57	17.61	0.13	10.36	8.70	3.71	1.61	0.13	12.88
COLO02D ³	Y	2019	4.50	0.20	0.15	0.00	0.03	0.03	0.08	0.04	0.00	0.04	0.22
COLO03D ³	Y	2019	4.57	1.32	0.38	3.11	0.00	0.15	0.00	0.06	2.51	5.22	0.36
COLO04D ³	Y	2019–2020	22.52	6.17	0.20	0.70	2.85	16.22	4.75	0.18	1.37	8.12	0.46
COLO05D ³	Y	2019–2020	20.85	55.47	1.64	0.23	1.81	45.15	0.29	1.34	2.82	14.88	4.39
COLO06D ³	J	2019–2020	3.68	2.20	0.79	1.05	0.05	3.95	0.39	0.25	0.00	0.53	0.51
COLO07D ³	J	2019–2020	4.55	11.33	0.14	1.40	0.10	1.98	0.00	0.00	24.00	5.24	4.00
COLO08D ³	J	2019–2020	1.29	3.38	0.07	3.00	0.12	2.05	0.00	0.00	1.45	0.07	1.52
COLO09D ³	J	2019–2020	1.67	5.85	0.43	0.28	0.02	0.77	0.00	0.02	6.95	1.10	0.77
COLO10D ³	J	2019	10.15	4.30	0.40	2.48	0.05	2.78	2.83	0.00	1.20	0.83	3.63
COLO11D ³	J	2020	35.56	39.95	9.21	0.00	0.21	24.84	0.00	0.00	7.84	2.40	7.71
COLO12D ³	J	2020	78.31	8.67	1.40	0.00	0.00	11.88	0.40	0.38	0.15	0.56	0.60
COLO13D ³	Y	2020	4.55	13.45	0.29	0.12	0.12	7.08	0.28	0.10	1.64	0.48	0.50
COLO14D ³	Y	2020	40.62	1.11	0.63	0.00	0.43	3.49	0.66	0.18	0.09	0.71	0.27
COLO15D ³	Y	2020	11.89	4.93	0.36	0.00	1.89	12.36	0.05	0.59	0.15	6.52	0.12

¹ Y = Yorktown, J = Jamestown.

² EPFU = big brown bat (*Eptesicus fuscus*), LABO = eastern red bat (*Lasiurus borealis*), LACI = hoary bat (*Lasiurus cinereus*), LANO = silver-haired bat (*Lasionycteris noctivagans*), MYAU = southeastern bat (*Myotis austroriparius*), MYLU = little brown bat (*Myotis lucifugus*), MYSE = northern long-eared bat (*Myotis septentrionalis*), MYSO = Indiana bat (*Myotis sodalis*), NYHU = evening bat (*Nycticeius humeralis*), PESU = tricolored bat (*Perimyotis subflavus*), TABR = Mexican free-tailed bat (*Tadarida brasiliensis*).

³ Sites ending in “D” were dormant season sampling locations that also recorded during the summer.

Table 2. Mean nightly activity of bat species at Colonial National Historical Park, Virginia during the fall period (September 16-November 30) during 2019 and 2020 in echolocation passes per night.

Site	Unit ¹	Year	EPFU ²	LABO ²	LACI ²	LANO ²	MYAU ²	MYLU ²	MYSE ²	MYSO ²	NYHU ²	PESU ²	TABR ²
COLO04D	Y	2019	7.60	2.76	0.03	0.00	3.45	8.67	0.00	0.33	0.06	3.19	1.49
COLO05D	Y	2019	3.94	8.23	0.18	0.02	0.75	6.75	0.06	0.56	0.00	20.43	0.17
COLO09D	J	2019	0.21	1.52	0.10	0.00	0.00	3.55	0.00	0.00	0.13	1.04	0.15
COLO11D	J	2019	1.00	0.58	0.03	0.03	0.34	5.88	0.00	0.00	0.00	1.57	0.32
COLO13D	Y	2019	0.29	0.28	0.34	0.00	0.05	1.26	0.00	0.00	0.00	0.48	0.17
COLO14D	Y	2019	1.00	0.00	0.07	0.00	0.58	1.14	0.16	0.43	0.00	0.81	0.00
COLO15D	Y	2019–2020	5.72	0.35	0.13	0.00	1.67	2.11	0.04	0.56	0.00	15.99	0.05
COLO16D	Y	2020	2.00	0.03	0.00	0.06	8.83	5.64	0.00	10.06	0.00	0.45	0.00
COLO17D	Y	2020	0.26	0.00	0.09	0.04	0.96	0.00	0.30	0.07	0.00	0.00	0.00
COLO18D	Y	2020	10.97	1.89	2.51	0.00	0.86	3.13	0.68	1.05	0.00	2.57	0.11
COLO19D	Y	2020	0.52	0.70	0.00	0.06	0.12	2.10	0.00	0.08	0.00	0.32	0.06
COLO20D	Y	2020	0.00	0.00	0.00	0.00	0.13	0.03	0.00	0.00	0.00	0.08	0.03
COLO21D	J	2020	1.48	0.06	0.17	0.27	1.14	0.86	0.45	3.18	0.00	0.00	0.08
COLO22D	J	2020	14.83	0.77	0.03	0.00	1.29	1.09	0.18	0.31	0.00	0.57	0.00
COLO23D	J	2020	2.94	0.06	0.03	0.00	0.16	1.33	0.00	0.05	0.05	0.86	0.00
COLO24D	J	2020	18.18	0.28	0.18	0.05	0.03	0.23	0.00	0.00	0.69	0.11	2.72
COLO11	Y	2020	10.50	0.00	3.20	0.00	1.40	0.00	0.00	0.00	0.00	0.00	0.00
COLO12	Y	2020	25.70	0.00	2.90	0.00	1.00	0.30	0.00	0.00	0.00	0.30	17.30
COLO13	Y	2020	16.30	0.60	2.40	0.00	0.00	0.20	0.00	0.00	0.00	0.60	0.00

¹ Y = Yorktown, J = Jamestown.

² EPFU = big brown bat (*Eptesicus fuscus*), LABO = eastern red bat (*Lasiurus borealis*), LACI = hoary bat (*Lasiurus cinereus*), LANO = silver-haired bat (*Lasionycteris noctivagans*), MYAU = southeastern bat (*Myotis austroriparius*), MYLU = little brown bat (*Myotis lucifugus*), MYSE = northern long-eared bat (*Myotis septentrionalis*), MYSO = Indiana bat (*Myotis sodalis*), NYHU = evening bat (*Nycticeius humeralis*), PESU = tricolored bat (*Perimyotis subflavus*), TABR = Mexican free-tailed bat (*Tadarida brasiliensis*).

Table 2 (continued). Mean nightly activity of bat species at Colonial National Historical Park, Virginia during the fall period (September 16-November 30) during 2019 and 2020 in echolocation passes per night.

Site	Unit ¹	Year	EPFU ²	LABO ²	LACI ²	LANO ²	MYAU ²	MYLU ²	MYSE ²	MYSO ²	NYHU ²	PESU ²	TABR ²
COLO18	Y	2020	73.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.40	1.70	5.20
COLO19	J	2020	1.00	1.60	1.10	0.00	3.60	7.40	0.00	0.00	0.00	0.00	1.40

¹ Y = Yorktown, J = Jamestown.

² EPFU = big brown bat (*Eptesicus fuscus*), LABO = eastern red bat (*Lasiurus borealis*), LACI = hoary bat (*Lasiurus cinereus*), LANO = silver-haired bat (*Lasionycteris noctivagans*), MYAU = southeastern bat (*Myotis austroriparius*), MYLU = little brown bat (*Myotis lucifugus*), MYSE = northern long-eared bat (*Myotis septentrionalis*), MYSO = Indiana bat (*Myotis sodalis*), NYHU = evening bat (*Nycticeius humeralis*), PESU = tricolored bat (*Perimyotis subflavus*), TABR = Mexican free-tailed bat (*Tadarida brasiliensis*).

Table 3. Mean nightly activity of bat species at Colonial National Historical Park, Virginia during the winter period (December 1–February 28) in 2019–2021 in echolocation passes per night.

Site	Unit ¹	Year	EPFU ²	LABO ²	LACI ²	LANO ²	MYAU ²	MYLU ²	MYSE ²	MYSO ²	NYHU ²	PESU ²	TABR ²
COLO01D	Y	2019	0.00	0.00	0.22	2.17	0.00	0.00	0.00	0.00	1.00	0.00	1.06
COLO02D	Y	2019	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
COLO03D	Y	2019	0.00	0.28	0.17	0.61	0.00	0.00	0.00	0.00	0.00	0.94	0.00
COLO04D	Y	2019	2.53	1.09	0.20	0.89	0.18	2.53	0.00	0.00	0.69	0.05	0.00
COLO05D	Y	2019–2020	2.41	1.91	0.20	0.28	0.67	6.47	0.00	1.14	0.00	0.38	0.27
COLO09D	J	2019–2020	0.03	0.16	0.64	0.06	0.00	2.69	0.00	0.00	0.00	0.78	0.24
COLO11D	J	2019–2020	0.00	0.06	3.38	0.02	0.08	1.64	0.00	0.05	0.00	0.13	0.64
COLO13D	Y	2019–2020	0.12	0.00	2.01	0.06	0.06	0.32	0.00	0.00	0.00	0.00	0.91
COLO14D	Y	2019–2020	0.72	0.00	0.15	0.00	0.28	1.18	0.22	0.24	0.00	0.00	0.00
COLO15D	Y	2019–2021	1.52	0.14	0.63	0.00	0.52	0.23	0.08	0.32	0.00	0.08	0.42
COLO16D	Y	2020–2021	0.12	0.35	0.00	0.00	3.35	0.00	0.65	5.18	0.00	0.41	0.00
COLO17D	Y	2020–2021	0.50	0.00	0.00	0.00	0.20	0.00	0.00	0.00	0.00	0.20	0.00
COLO18D	Y	2020–2021	0.64	0.50	0.00	0.00	0.21	1.71	0.29	0.43	0.00	0.14	0.14
COLO19D	Y	2020–2021	0.00	0.00	0.69	0.69	0.00	0.00	0.85	0.00	0.00	0.00	0.00
COLO20D	Y	2020–2021	2.57	0.00	0.00	0.14	0.00	0.00	0.21	0.36	0.00	0.00	2.57
COLO21D	J	2020–2021	0.00	0.00	0.25	0.17	0.25	0.00	0.00	0.25	0.00	0.00	0.00
COLO22D	J	2020–2021	0.00	0.00	2.26	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00
COLO23D	J	2020–2021	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
COLO24D	J	2020–2021	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.30	0.00	0.00

¹ Y = Yorktown, J = Jamestown.

² EPFU = big brown bat (*Eptesicus fuscus*), LABO = eastern red bat (*Lasiurus borealis*), LACI = hoary bat (*Lasiurus cinereus*), LANO = silver-haired bat (*Lasionycteris noctivagans*), MYAU = southeastern bat (*Myotis austroriparius*), MYLU = little brown bat (*Myotis lucifugus*), MYSE = northern long-eared bat (*Myotis septentrionalis*), MYSO = Indiana bat (*Myotis sodalis*), NYHU = evening bat (*Nycticeius humeralis*), PESU = tricolored bat (*Perimyotis subflavus*), TABR = Mexican free-tailed bat (*Tadarida brasiliensis*).

Table 4. Mean nightly activity of bat species at Colonial National Historical Park, Virginia during the spring period (March–April 14) in 2019–2021 in echolocation passes per night.

Site	Unit ¹	Year	EPFU ²	LABO ²	LACI ²	LANO ²	MYAU ²	MYLU ²	MYSE ²	MYSO ²	NYHU ²	PESU ²	TABR ²
COLO01D	Y	2019	2.38	0.36	10.69	27.90	0.00	0.62	1.67	0.67	2.21	0.21	20.36
COLO02D	Y	2019	1.20	0.00	0.24	0.00	0.04	0.04	0.00	0.00	0.00	0.07	0.04
COLO03D	Y	2019	6.04	0.84	0.16	4.07	0.00	0.24	0.00	0.04	2.20	5.58	0.44
COLO04D	Y	2019–2020	12.02	3.15	0.36	2.30	1.94	5.94	2.17	0.00	2.64	4.26	0.62
COLO05D	Y	2019–2020	17.77	17.48	0.57	0.39	2.45	47.57	0.71	0.21	0.21	6.03	3.95
COLO06D	J	2019–2020	1.87	0.58	0.10	2.55	0.00	2.00	0.29	0.00	0.00	0.74	1.03
COLO07D	J	2019	3.88	10.61	0.18	1.79	0.12	2.52	0.00	0.00	24.39	6.67	3.67
COLO08D	J	2019	1.30	1.85	0.00	3.67	0.09	1.39	0.00	0.00	1.33	0.09	1.27
COLO09D	J	2020	2.14	4.49	0.17	0.49	0.00	0.28	0.00	0.04	3.64	1.67	0.74
COLO10D	J	2019	5.94	1.03	0.52	3.19	0.06	1.39	0.00	0.00	0.00	1.06	0.84
COLO13D	Y	2020	3.35	3.11	0.28	0.30	0.00	5.76	0.26	0.11	0.00	1.02	0.65
COLO14D	Y	2020	33.26	0.52	0.43	0.00	0.43	1.87	0.74	0.28	0.15	1.09	0.00
COLO15D	Y	2020–2021	9.32	4.02	0.52	0.11	2.84	9.16	0.08	0.84	0.00	5.40	0.39
COLO16D	Y	2021	3.84	5.64	0.27	0.00	3.29	6.64	0.13	2.40	0.00	3.51	0.04
COLO17D	Y	2021	4.81	0.56	0.28	0.56	0.30	0.05	0.05	0.19	0.00	0.30	0.12
COLO18D	Y	2021	0.61	1.04	1.02	0.00	0.00	2.02	0.00	0.00	0.00	0.50	1.11
COLO19D	Y	2021	1.64	6.09	1.25	0.45	0.39	15.18	1.36	0.00	0.00	1.30	0.73
COLO20D	Y	2021	5.83	1.37	0.11	0.87	10.04	0.22	2.41	0.00	0.76	4.39	1.02
COLO21D	J	2021	2.02	0.39	0.30	5.70	0.09	0.27	0.00	0.05	1.34	0.00	1.00

¹ Y = Yorktown, J = Jamestown.

² EPFU = big brown bat (*Eptesicus fuscus*), LABO = eastern red bat (*Lasiurus borealis*), LACI = hoary bat (*Lasiurus cinereus*), LANO = silver-haired bat (*Lasionycteris noctivagans*), MYAU = southeastern bat (*Myotis austroriparius*), MYLU = little brown bat (*Myotis lucifugus*), MYSE = northern long-eared bat (*Myotis septentrionalis*), MYSO = Indiana bat (*Myotis sodalis*), NYHU = evening bat (*Nycticeius humeralis*), PESU = tricolored bat (*Perimyotis subflavus*), TABR = Mexican free-tailed bat (*Tadarida brasiliensis*).

Table 4 (continued). Mean nightly activity of bat species at Colonial National Historical Park, Virginia during the spring period (March–April 14) in 2019–2021 in echolocation passes per night.

Site	Unit ¹	Year	EPFU ²	LABO ²	LACI ²	LANO ²	MYAU ²	MYLU ²	MYSE ²	MYSO ²	NYHU ²	PESU ²	TABR ²
COLO22D	J	2021	1.67	3.55	1.05	1.21	0.05	2.21	0.21	0.12	0.00	1.17	1.48
COLO23D	J	2021	0.56	1.51	0.33	0.00	0.05	1.63	0.00	0.00	0.00	0.05	0.65
COLO24D	J	2021	54.79	8.12	0.00	1.10	0.50	3.14	0.31	0.17	4.76	2.74	0.00

¹ Y = Yorktown, J = Jamestown.

² EPFU = big brown bat (*Eptesicus fuscus*), LABO = eastern red bat (*Lasiurus borealis*), LACI = hoary bat (*Lasiurus cinereus*), LANO = silver-haired bat (*Lasionycteris noctivagans*), MYAU = southeastern bat (*Myotis austroriparius*), MYLU = little brown bat (*Myotis lucifugus*), MYSE = northern long-eared bat (*Myotis septentrionalis*), MYSO = Indiana bat (*Myotis sodalis*), NYHU = evening bat (*Nycticeius humeralis*), PESU = tricolored bat (*Perimyotis subflavus*), TABR = Mexican free-tailed bat (*Tadarida brasiliensis*).

Big brown bat

Big brown bat activity was highest of species identified at COLO, prevalent among most sample locations, and identified at all 34 summer sites (Tables 1-4). Activity was very high at several locations in the Yorktown (COLO05, COLO13, and COLO14) and Jamestown Island (COLO09 and COLO10) where mean passes per night exceeded 100 during the summer. Seasonally, big brown bat activity increased sharply in early April, peaked in the summer in mid-July, then declined through August (Figure 6). Activity was generally low in fall through winter and spring but did occur sporadically at most sites. The GLMM showed activity was relatively high among general habitat types and highest at forest sites. The GLMM included significant predictors: habitat type, distance to water, nightly precipitation, and minimum temperature (Figure 7).

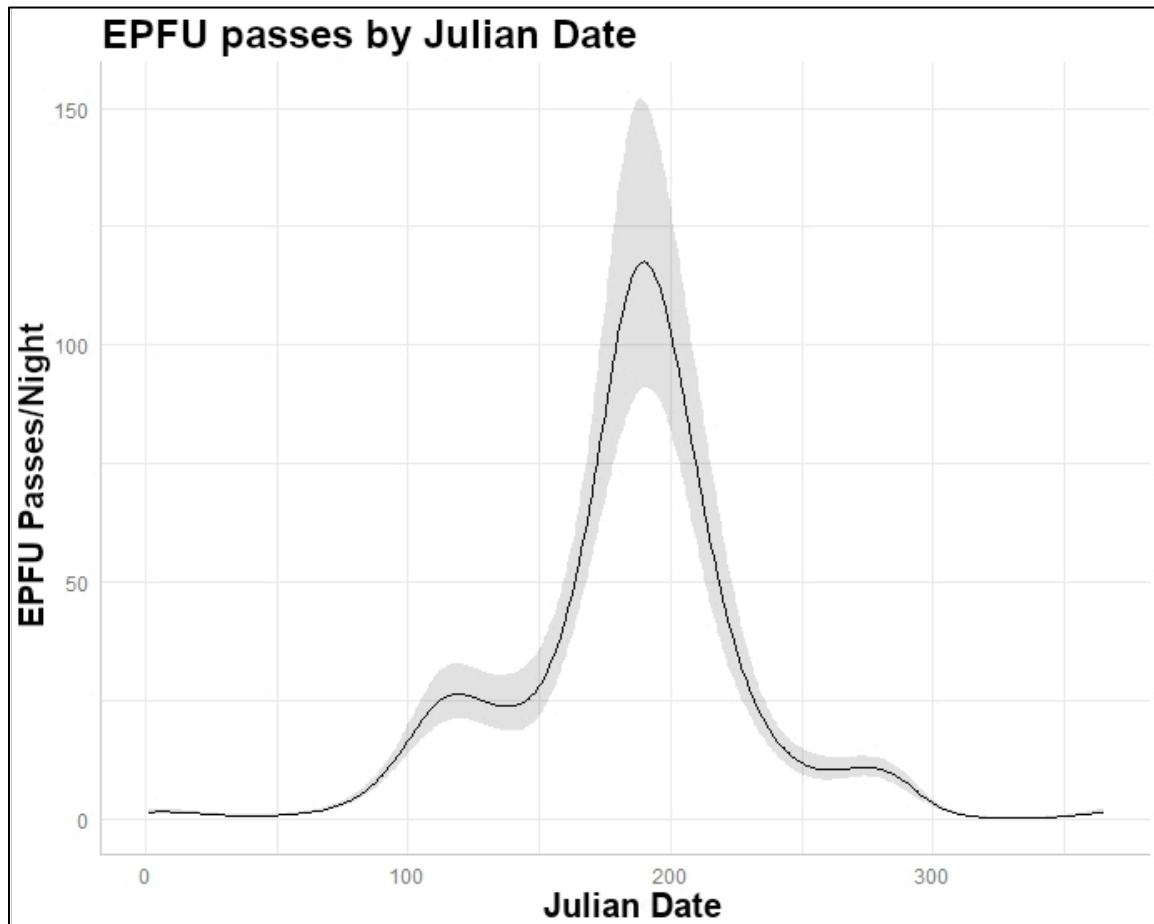


Figure 6. Big brown bat (*Eptesicus fuscus*) activity (mean passes/night and standard error) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia. Julian Day 100 = April 10; 200 = July 19; 300 = October 27.

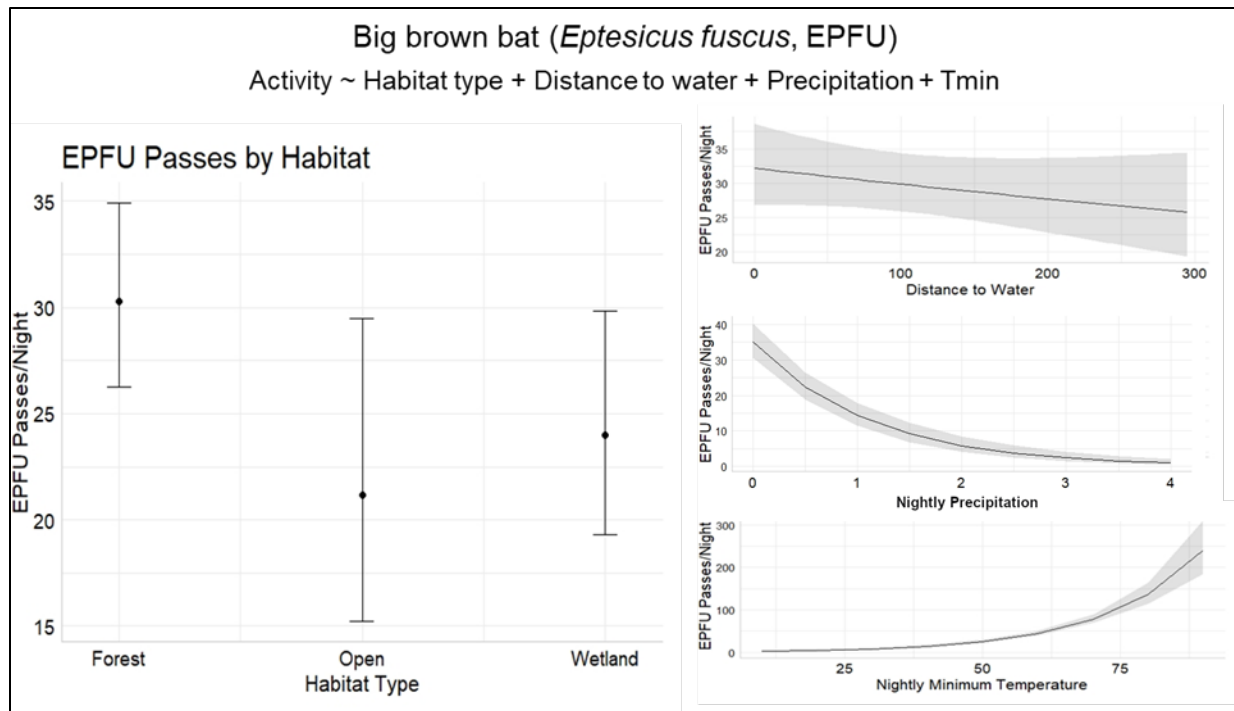


Figure 7. Predicted activity (mean passes per night and standard error) for big brown bats (*Eptesicus fuscus*, EPFU) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates habitat, distance to water (m), nightly precipitation (cm), and minimum temperature (°F).

Southeastern bat

Southeastern bat activity was identified at 28 of 34 summer sites at low levels except site COLO05 where moderate levels were identified. Seasonally, activity fluctuated among lower levels throughout the year with highest activity occurring in early July (Figure 8). The GLMM showed their activity was primarily observed in wetland habitat sites. The model included significant predictors: habitat type and nightly precipitation (Figure 9).

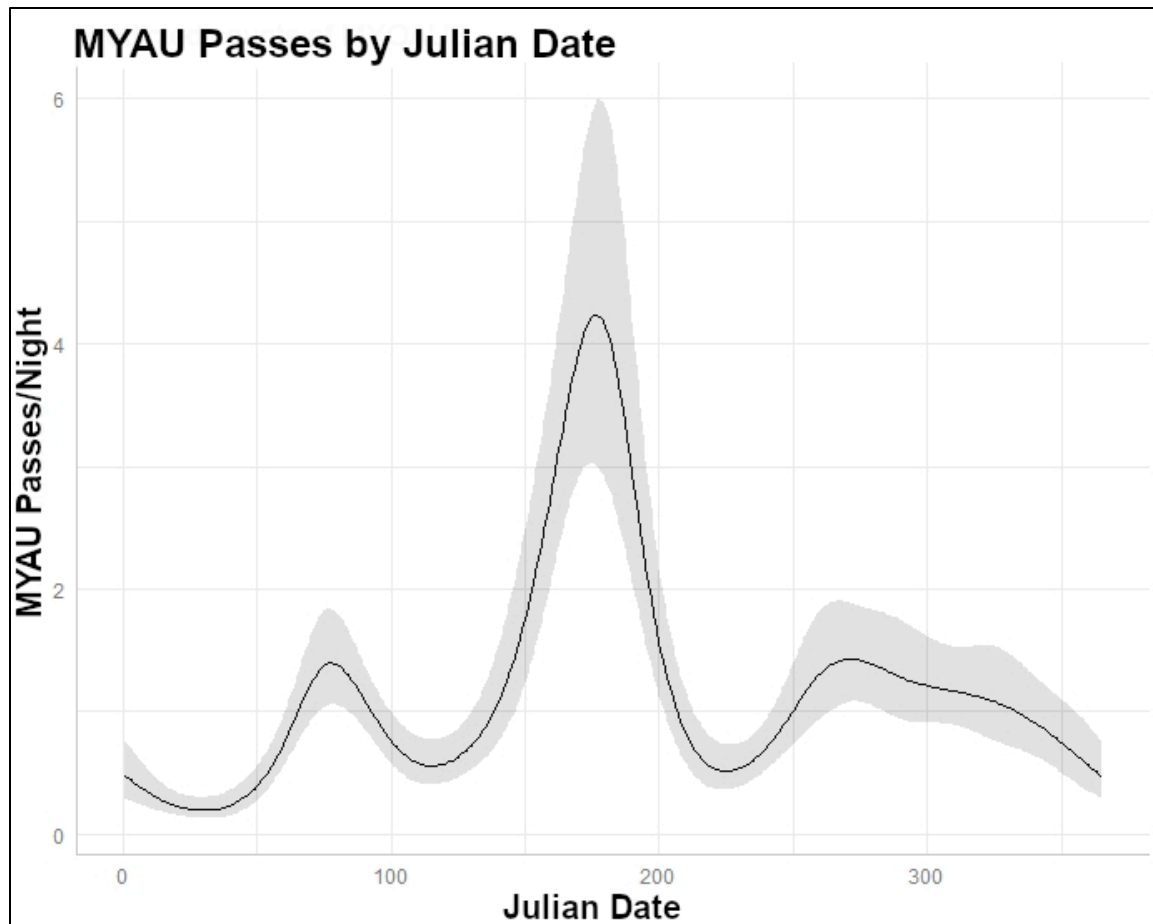


Figure 8. Southeastern bat (*Myotis austroriparius*) activity (mean passes/night and standard error) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia. Julian Day 100 = April 10; 200 = July 19; 300 = October 27.

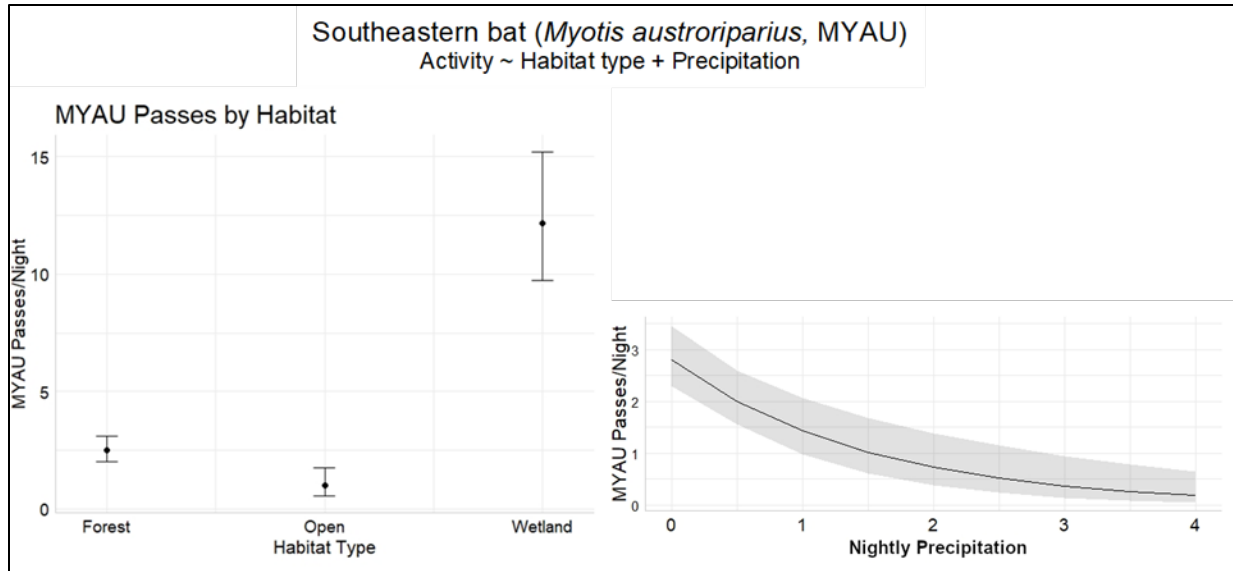


Figure 9. Predicted activity (mean passes per night and standard error) for southeastern bats (*Myotis austroriparius*; MYAU) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates: habitat and nightly precipitation (cm).

Little brown bat

Little brown bats were second most commonly identified among cave bats at COLO at 33 of 34 summer sites. Identified passes were widespread and occurred mostly at low to moderate levels. Highest activity levels were identified during summer from Yorktown sites (COLO05, COLO17, and COLO05D) and Jamestown Island site (COLO09). The GAM showed activity increasing in early April, peaking in mid-July, then declining through August (Figure 10). The GLMM showed activity to be most associated with open and forest habitats (Figure 11). However, visual validation of selected calls revealed many apparent misidentifications by software despite qualifying MLE values.

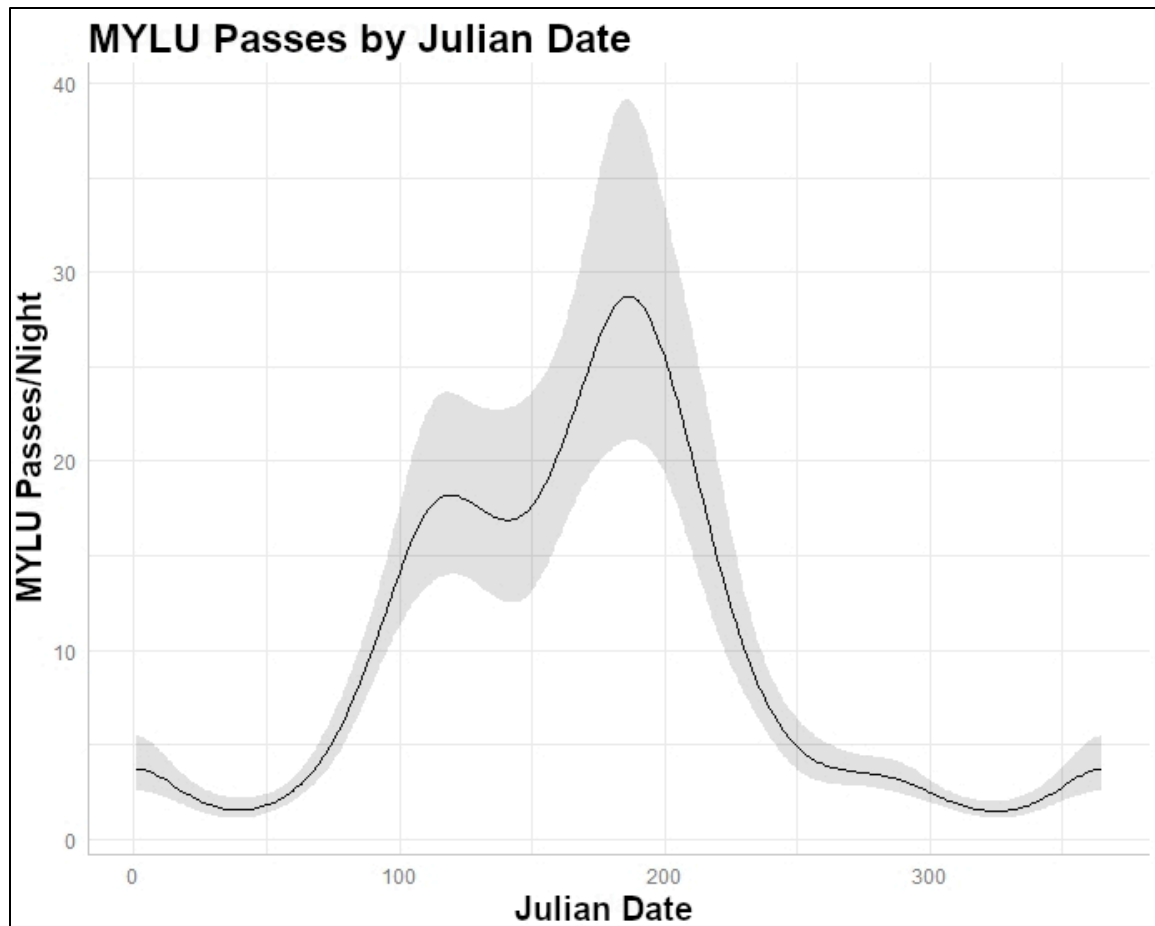


Figure 10. Little brown bat (*Myotis lucifugus*) activity (mean passes/night) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia. Julian Day 100 = April 10; 200 = July 19; 300 = October 27.

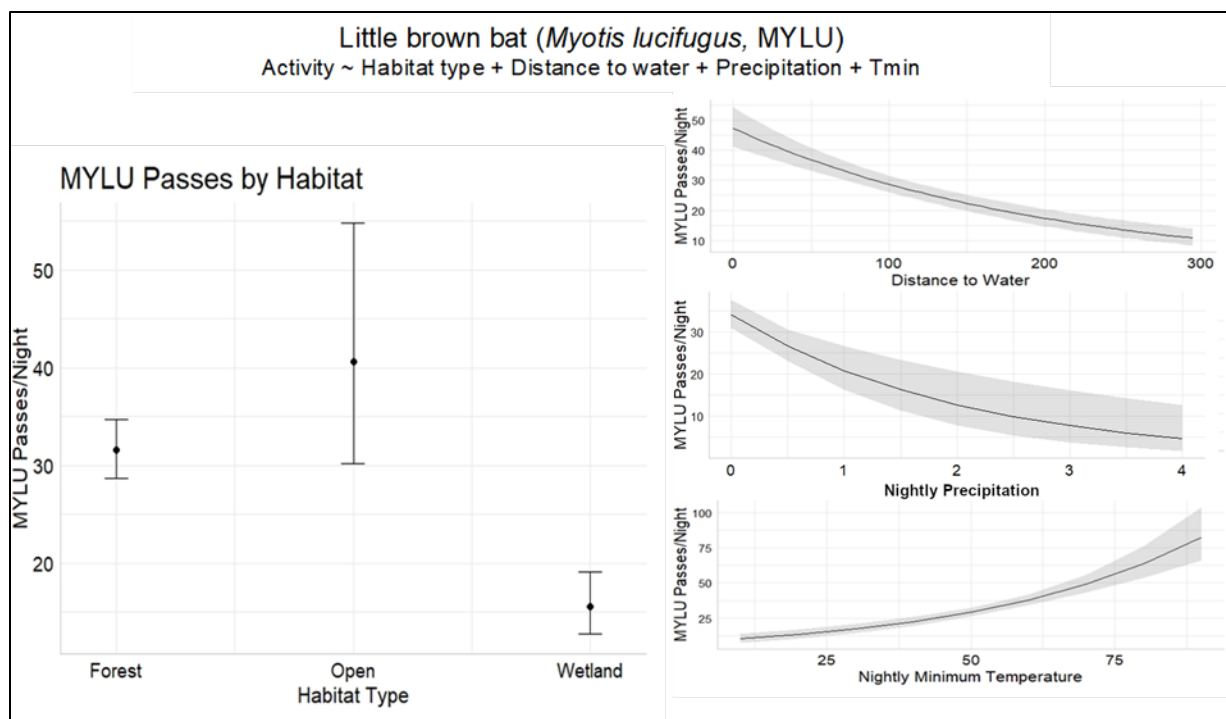


Figure 11. Little brown bat (*Myotis lucifugus*) activity (mean passes/night and standard error) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia. Julian Day 100 = April 10; 200 = July 19; 300 = October 27.

Northern long-eared bat

Northern long-eared bat calls were identified at low levels at 22 of 34 summer sites at Yorktown and Jamestown. Highest activity was recorded at Yorktown site COLO01D. Activity predicted by the GAM remained low throughout the year with a small increase from April through July (Figure 12). Northern long-eared bat activity was observed similarly among general habitat types and was somewhat negatively correlated with distance to water (Figure 13). Visual validation of calls from many sites revealed many to be misidentifications, while others appeared to be diagnostic or not ruled out. These included several passes recorded in January 2020 that suggest some individuals are wintering at or nearby COLO.

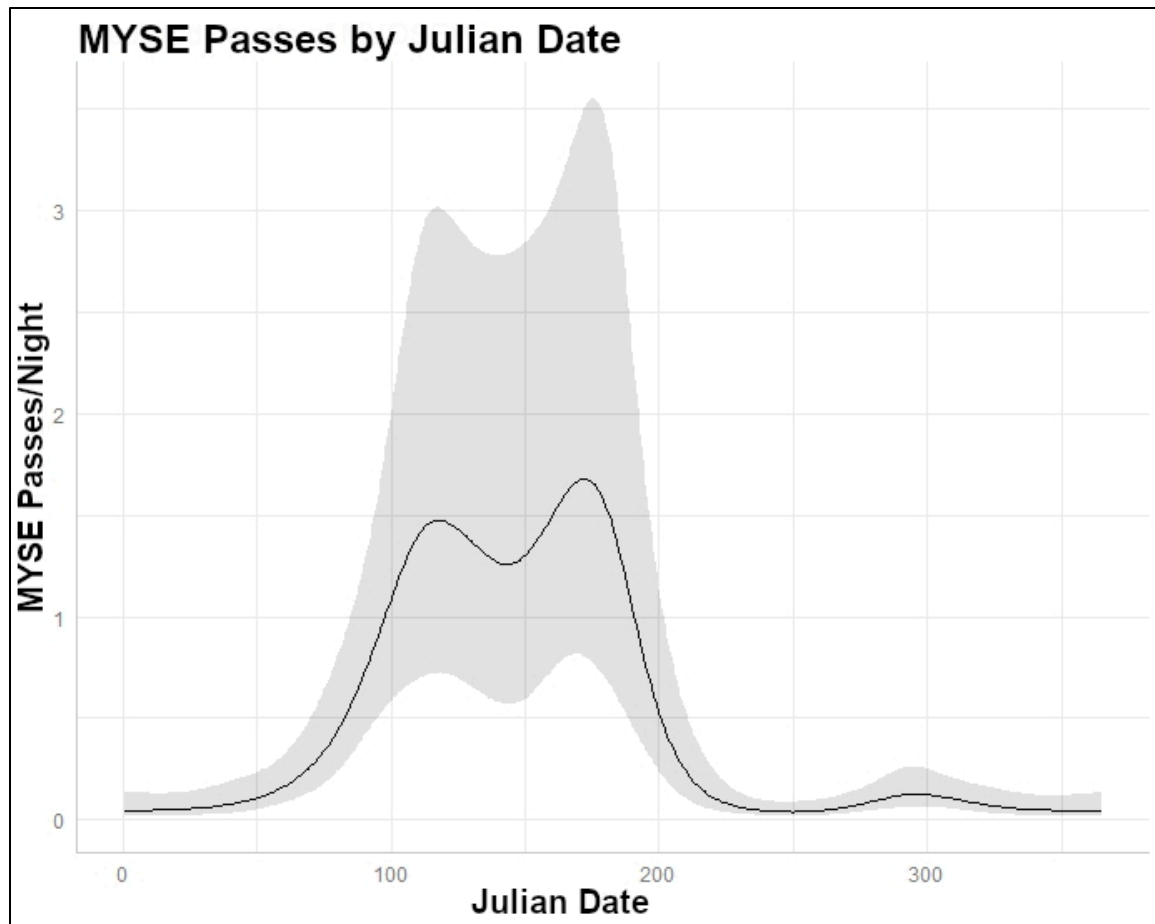


Figure 12. Northern long-eared bat (*Myotis septentrionalis*) activity (mean passes/night) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia. Julian Day 100 = April 10; 200 = July 19; 300 = October 27.

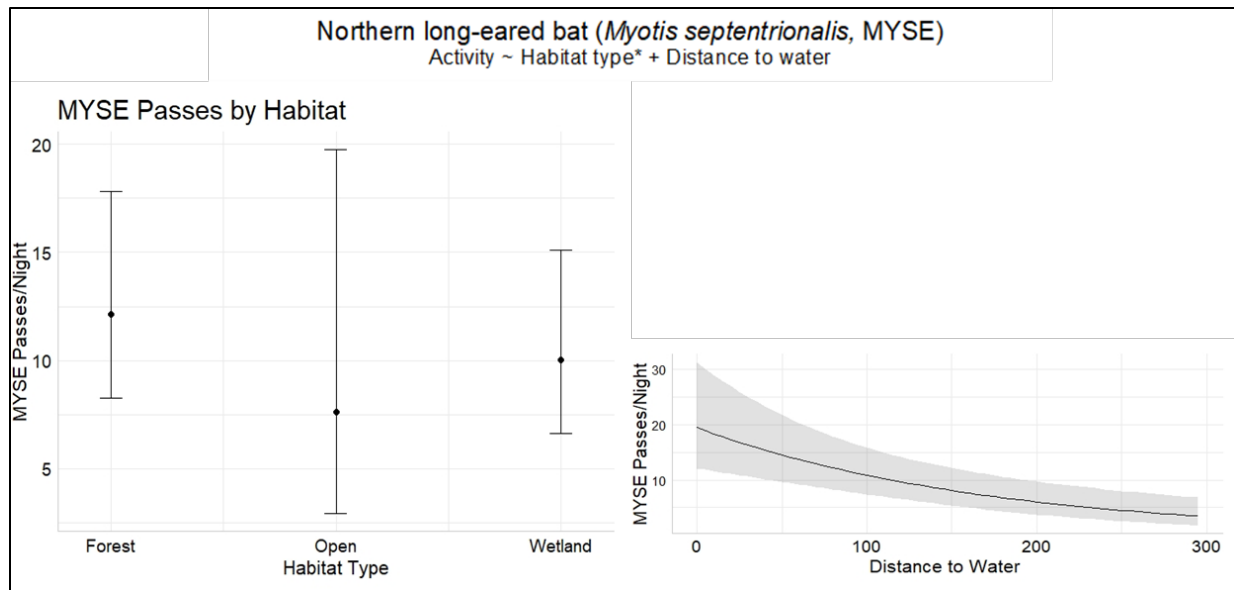


Figure 13. Northern long-eared bat (*Myotis septentrionalis*) activity (mean passes/night and standard error) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia. Julian Day 100 = April 10; 200 = July 19; 300 = October 27.

Indiana bat

Indiana bats were identified at 22 of 34 summer sample sites at low levels, with highest activity identified at sites COLO04 and COLO01D. Visual validation of a portion of calls found most identifications to be misidentifications. Some did appear to be diagnostic of Indiana bats or could not be ruled out. Outside of the summer season, very few passes were identified and no calls from the winter appeared to be plausible identifications. The GAM resulted in very low predicted activity with a mean remaining below 1.5 passes/night (Figure 14). The GLMM showed identified activity was most correlated with forest habitats (Figure 15).

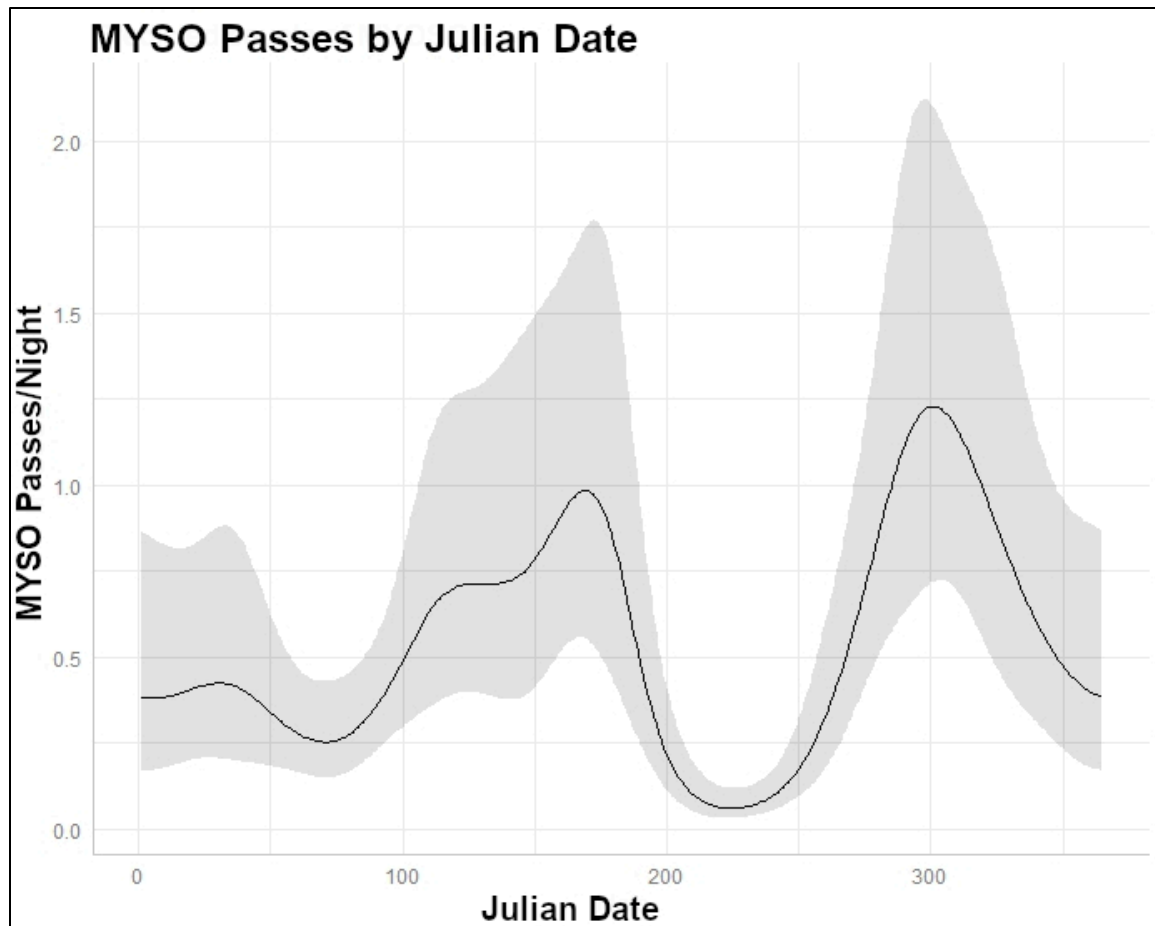


Figure 14. Indiana bat (*Myotis sodalis*) activity (mean passes/night) at Colonial National Historical Park, Virginia as predicted by a generalized additive model of activity by Julian date. Julian Day 100 = April 10; 200 = July 19; 300 = October 27.

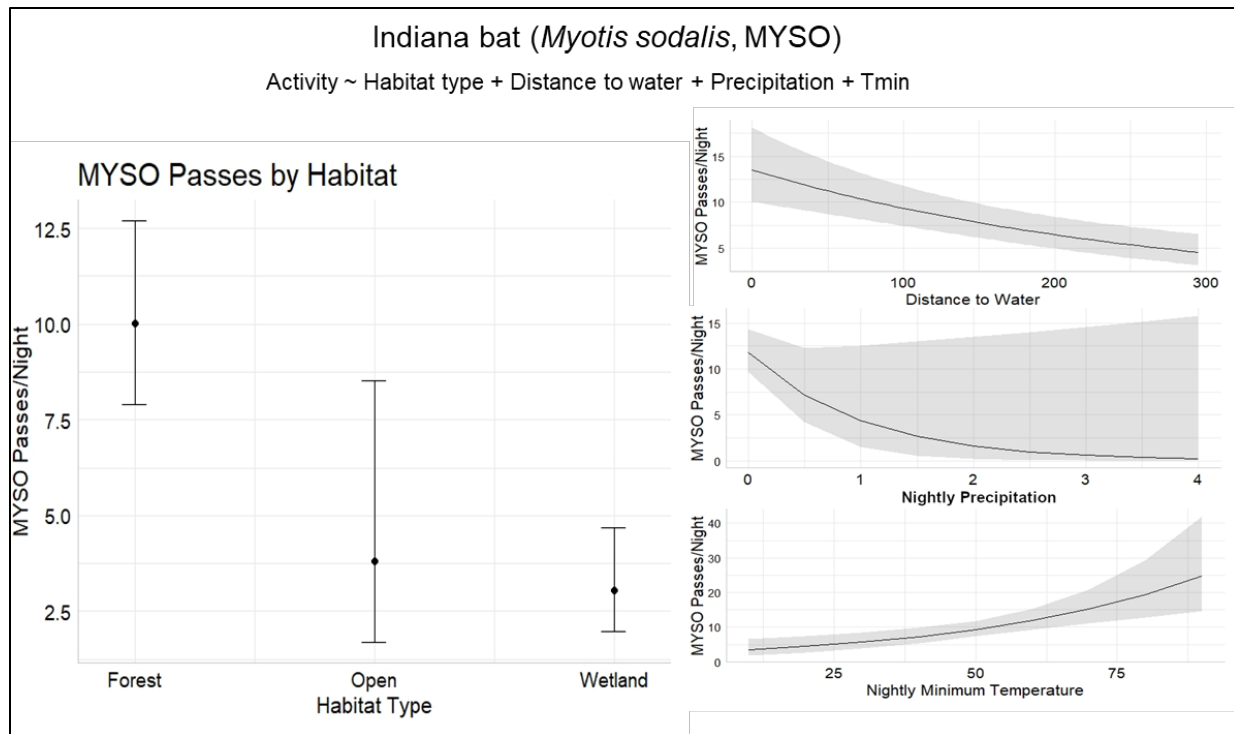


Figure 15. Predicted activity (mean passes per night and standard error) for Indiana bats (*Myotis sodalis*, MYSO) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates habitat, distance top water (m), nightly precipitation (cm), and minimum temperature (°F).

Tricolored bat

Tricolored bats were identified at 33 of 34 summer sites and were observed at moderate to high levels at many locations. Highest activity occurred at Yorktown sites COLO06, COLO17, and COLO14. The GAM showed that highest activity was observed from June through August (Figure 16). Activity continued through fall and passes were observed at several locations during winter. The GLMM found higher activity was associated with open and forest sites compared to wetland sites (Figure 17).

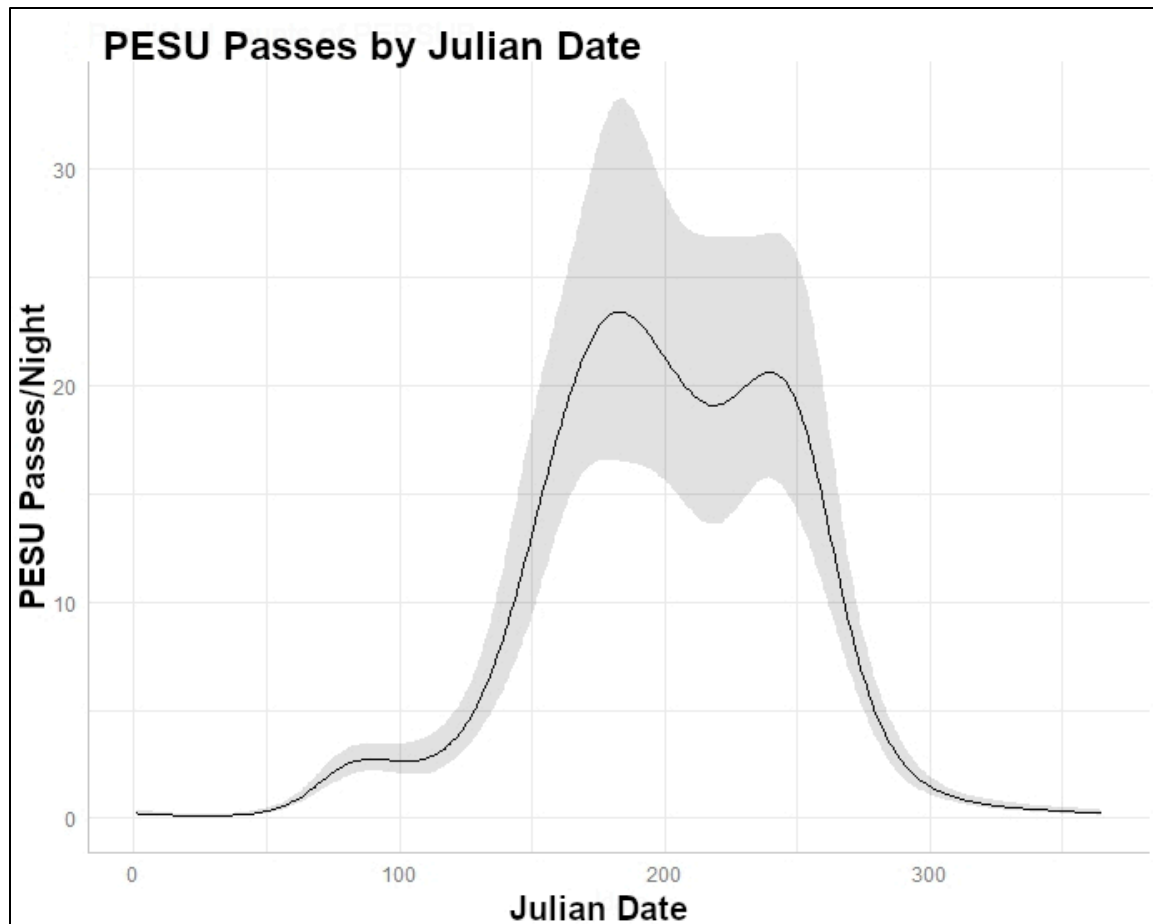


Figure 16. Tricolored bat (*Perimyotis subflavus*) activity (mean passes/night) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia. Julian Day 100 = April 10; 200 = July 19; 300 = October 27.

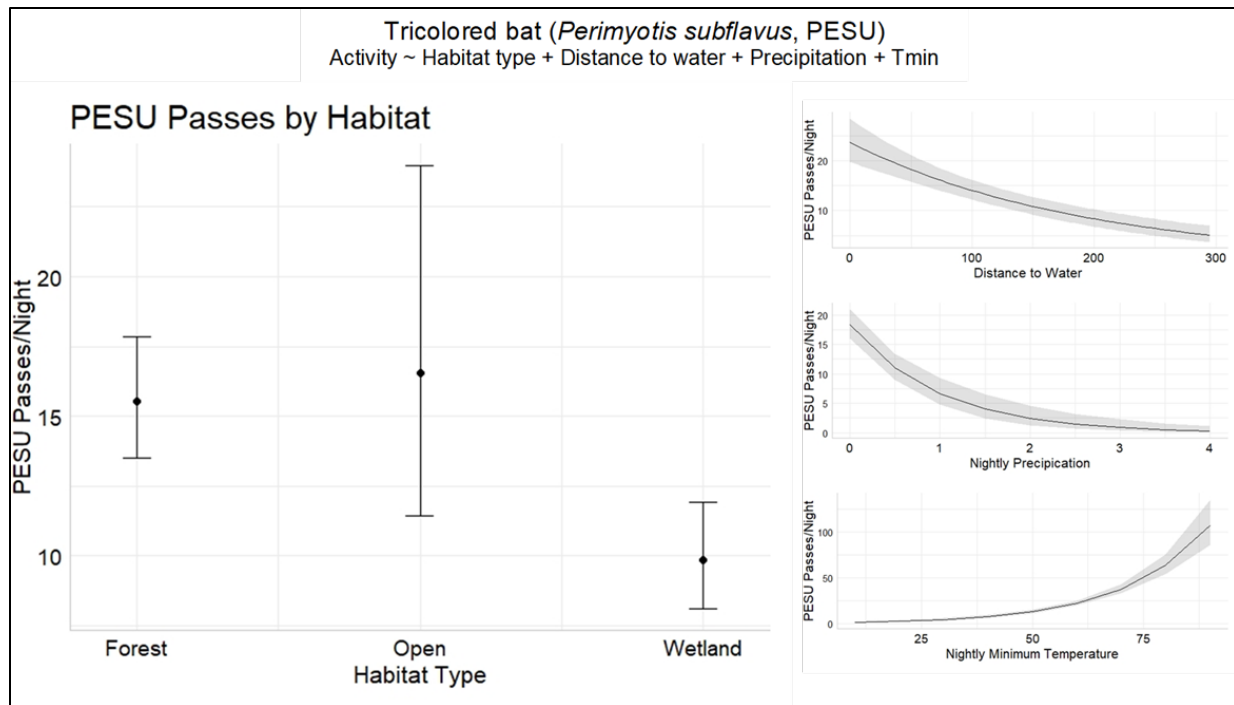


Figure 17. Predicted activity (mean passes per night and standard error) for tricolored bats (*Perimyotis subflavus*, PESU) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates habitat, distance to water (m), nightly precipitation (cm), and minimum nightly temperature (°F).

Eastern red bat

Eastern red bat activity was the highest among tree bat species and second highest among all bats. They were identified at 33 of 34 summer sites, and activity appeared generally high at both Yorktown and Jamestown during summer. Highest activity was identified at COLO01, COLO04, COLO06, COLO14, and COLO05D. The GAM showed that activity was highest from mid-April through late July, peaking in early July (Figure 18). Activity persisted at lower levels in the fall and most Yorktown sites recorded some eastern red bat passes in the winter. The GLMM indicated higher activity levels were observed at forest and open locations compared to wetland habitats (Figure 19).

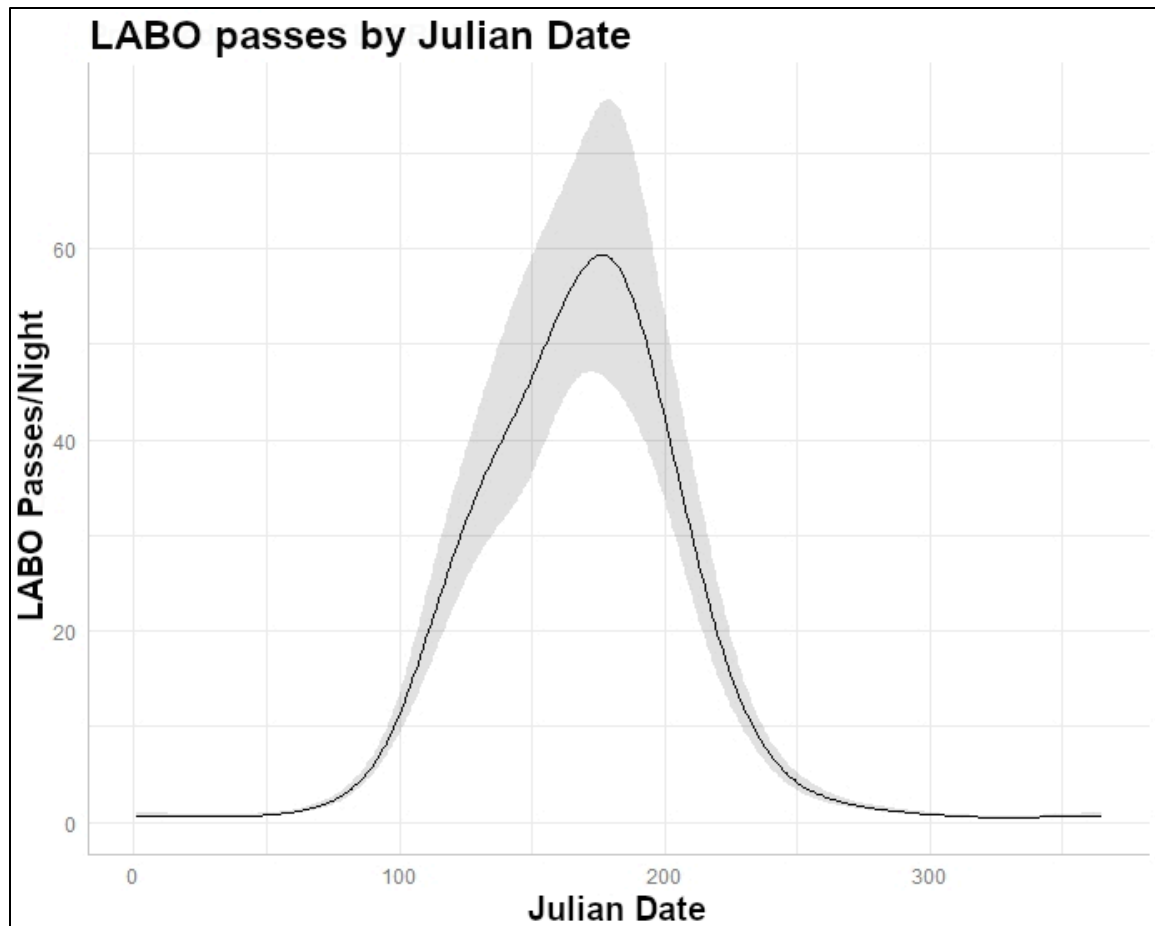


Figure 18. Eastern red bat (*Lasiurus borealis*) activity (mean passes/night) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia. Julian Day 100 = April 10; 200 = July 19; 300 = October 27.

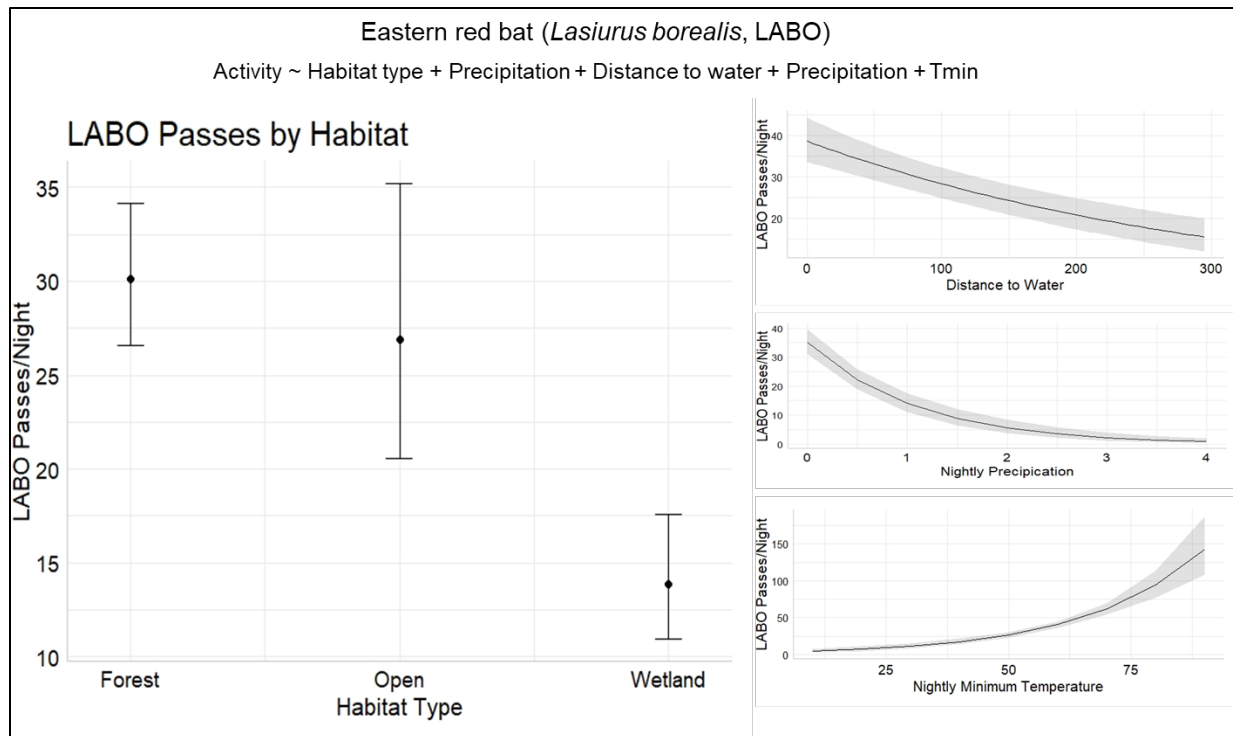


Figure 19. Predicted activity (mean passes per night and standard error) for eastern red bats (*Lasiurus borealis*, LABO) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates habitat, distance to water (m), nightly precipitation (cm), and minimum nightly temperature (°F).

Hoary bat

Hoary bat passes were identified at 28 of 34 summer sites at low levels, with the exception of several nights of high activity in mid-March at site COLO01D; late June at COLO06 and COLO10; and in early July at site COLO11D. Passes were identified through December and January at both Yorktown and Jamestown. The GAM showed activity was highest in mid-July (Figure 20). Highest activity was associated with open habitats compared to forest and wetlands (Figure 21).

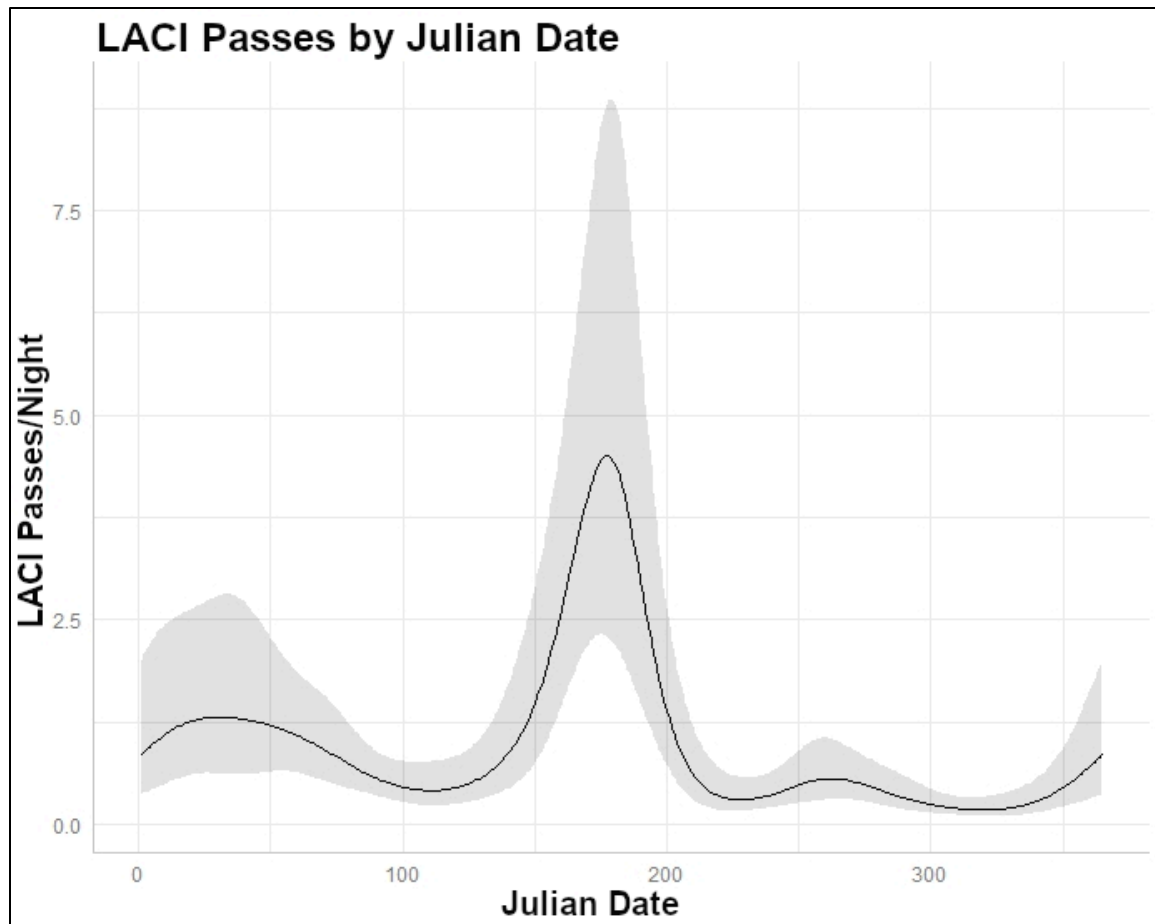


Figure 20. Hoary bat (*Lasiurus cinereus*) activity (mean passes/night) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia. Julian Day 100 = April 10; 200 = July 19; 300 = October 27.

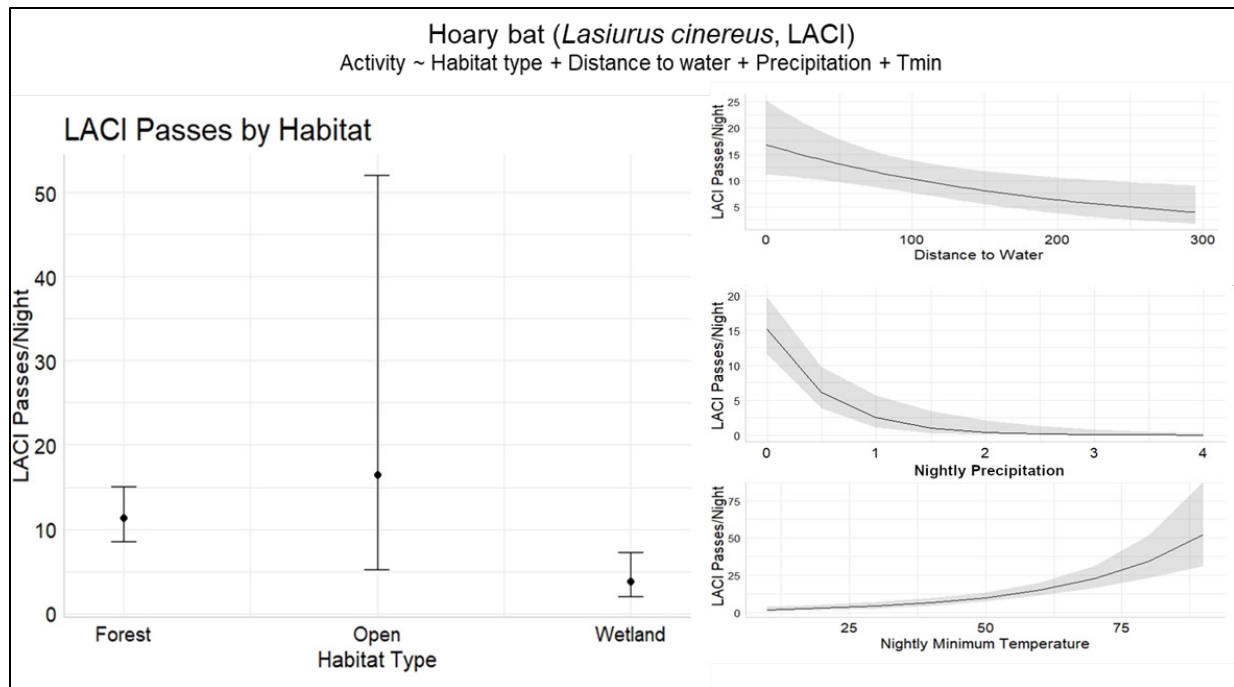


Figure 21. Predicted activity (mean passes per night and standard error) for hoary bats (*Lasiurus cinereus*) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates habitat type, distance to water (m), nightly precipitation (cm), and minimum nightly temperature (°F).

Silver-haired bat

Silver-haired bats were identified at 21 of 34 of summer sample sites at low levels. Highest activity occurred at COLO01D at Wormley Pond during the spring, in which over 100 calls were identified on one night in mid-March. Activity was otherwise low outside of summer but did persist through the winter, especially at site COLO01D. The predicted activity of the GAM followed these observations, showing generally very low activity with a peak in March (Figure 22). The GLMM showed higher activity was associated with open habitats, which was reflective of the few sites that recorded nights of high activity (Figure 23).

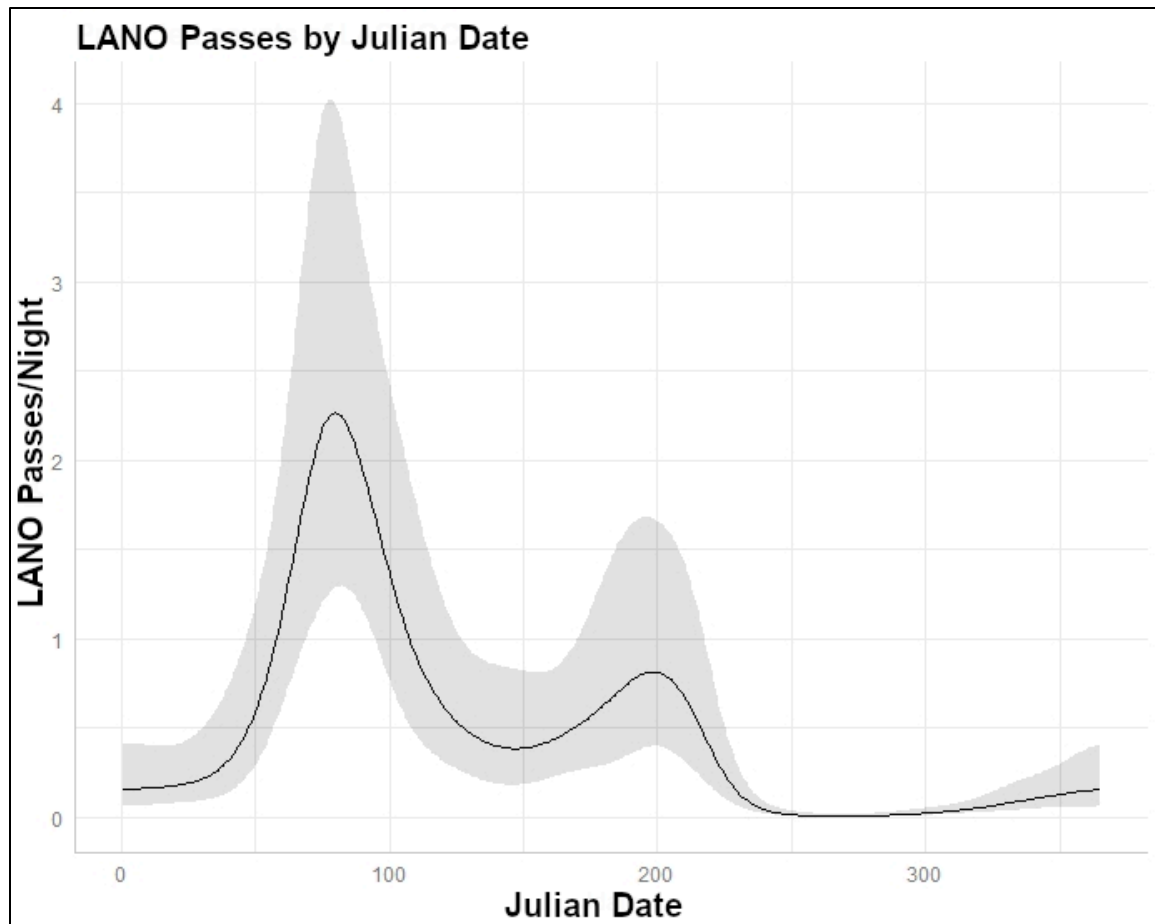


Figure 22. Silver-haired bat (*Lasionycteris noctivagans*) activity (mean passes/night) as predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia. Julian Day 100 = April 10; 200 = July 19; 300 = October 27.

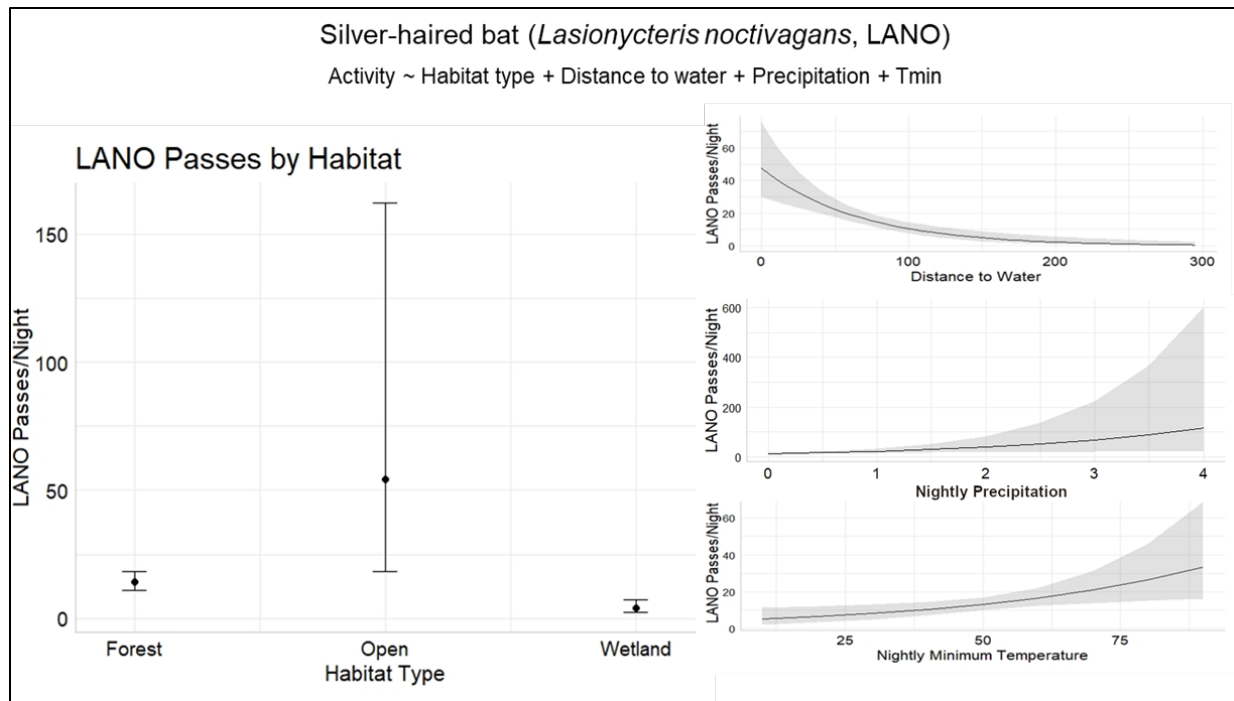


Figure 23. Predicted activity (mean passes per night and standard error) for silver-haired bats (*Lasionycteris noctivagans*, LANO) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates: habitat type distance to water (m), nightly precipitation (cm), and minimum nightly temperature (°F).

Evening bat

Evening bats were identified at 26 of 34 summer sites at varying levels of activity. Highest activity was identified during summer at Yorktown COLO06 and Jamestown COLO09 and COLO10. The GAM of activity showed a great increase during summer, peaking in late June, then declining through late July (Figure 24). Evening bats were observed at low levels from fall through spring and a few sites observed passes during winter. The GLMM showed higher activity was observed at forest and open sites compared to wetlands (Figure 25).

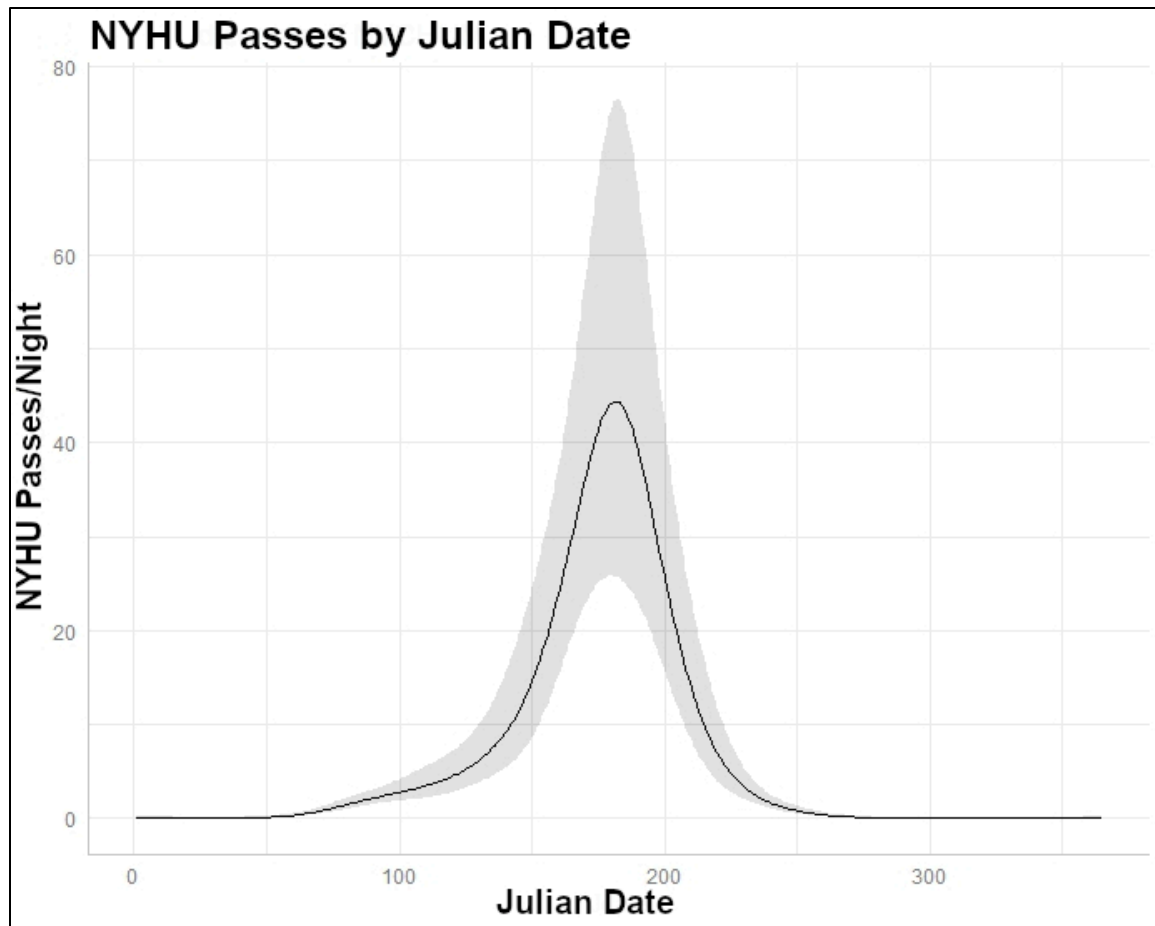


Figure 24. Evening bat (*Nycticeius humeralis*) activity (mean passes/night) predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia. Julian Day 100 = April 10; 200 = July 19; 300 = October 27.

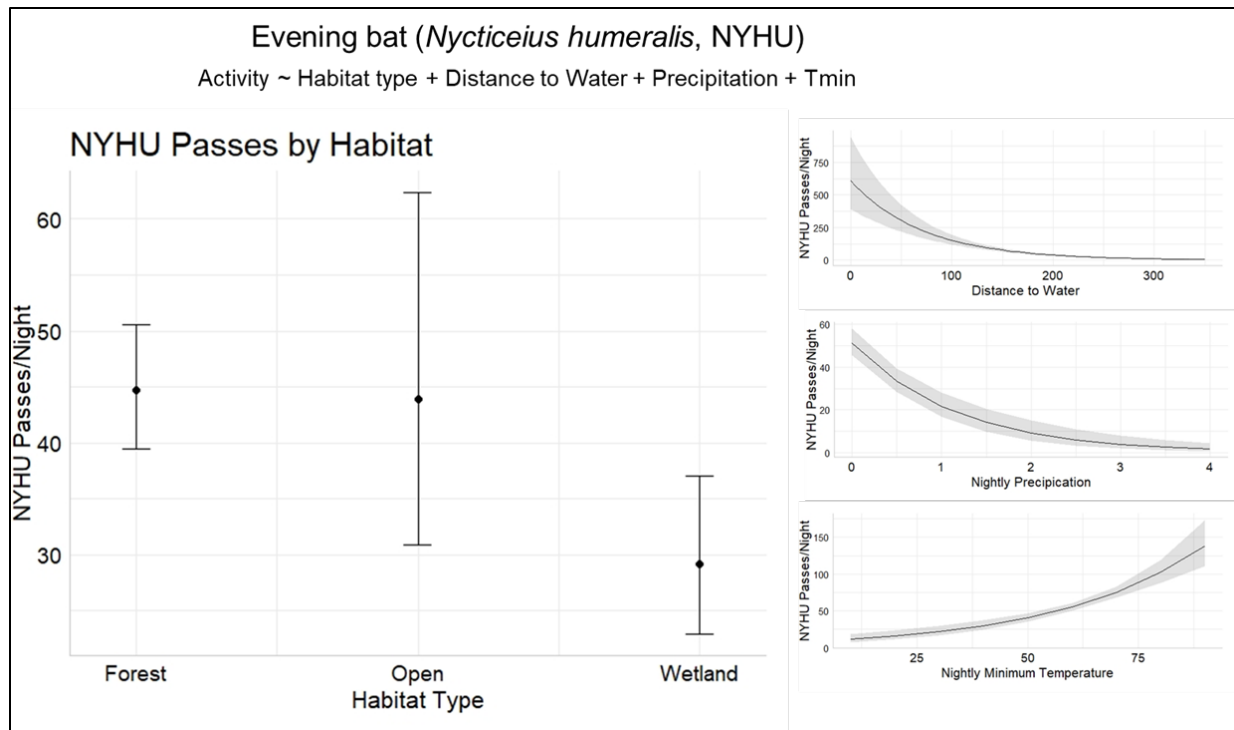


Figure 25. Predicted activity (mean passes per night and standard error) for evening bats (*Nycticeius humeralis*, NYHU) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates: habitat type, distance to water (m), nightly precipitation (cm), and minimum nightly temperature (°F).

Mexican free-tailed bat

Mexican free-tailed bats were identified at 27 of 34 summer sites at low levels but did appear to occur regularly at COLO01D. High activity was identified sporadically on several nights in March and April at COLO01D and COLO05D. Passes were consistently observed at COLO12 in August and September. The GAM predicted activity to be low overall with increases in the spring and late summer (Figure 26). The GLMM found activity to be highest in open habitats (Figure 27).

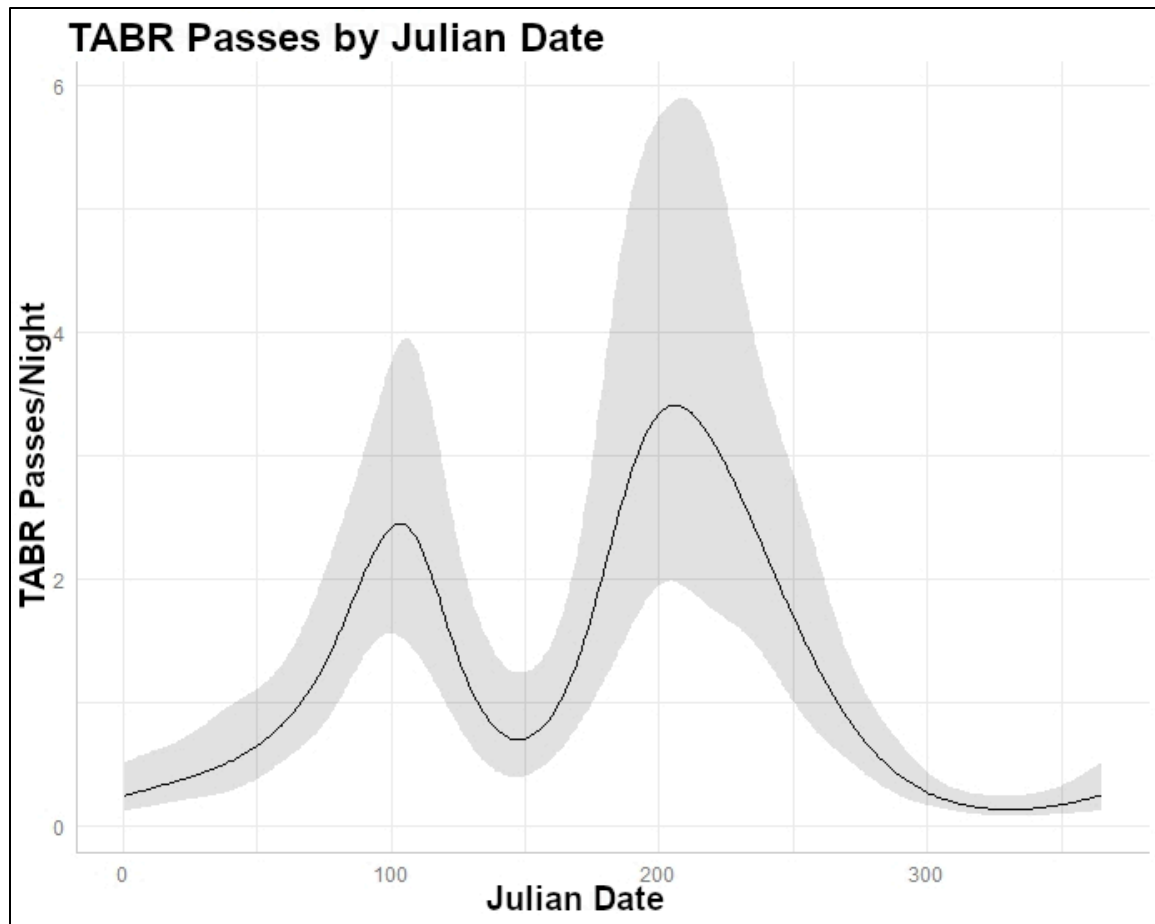


Figure 26. Mexican free-tailed bat (*Tadarida brasiliensis*) activity (mean passes/night) predicted by a generalized additive model of activity by Julian date at Colonial National Historical Park, Virginia. Julian Day 100 = April 10; 200 = July 19; 300 = October 27.

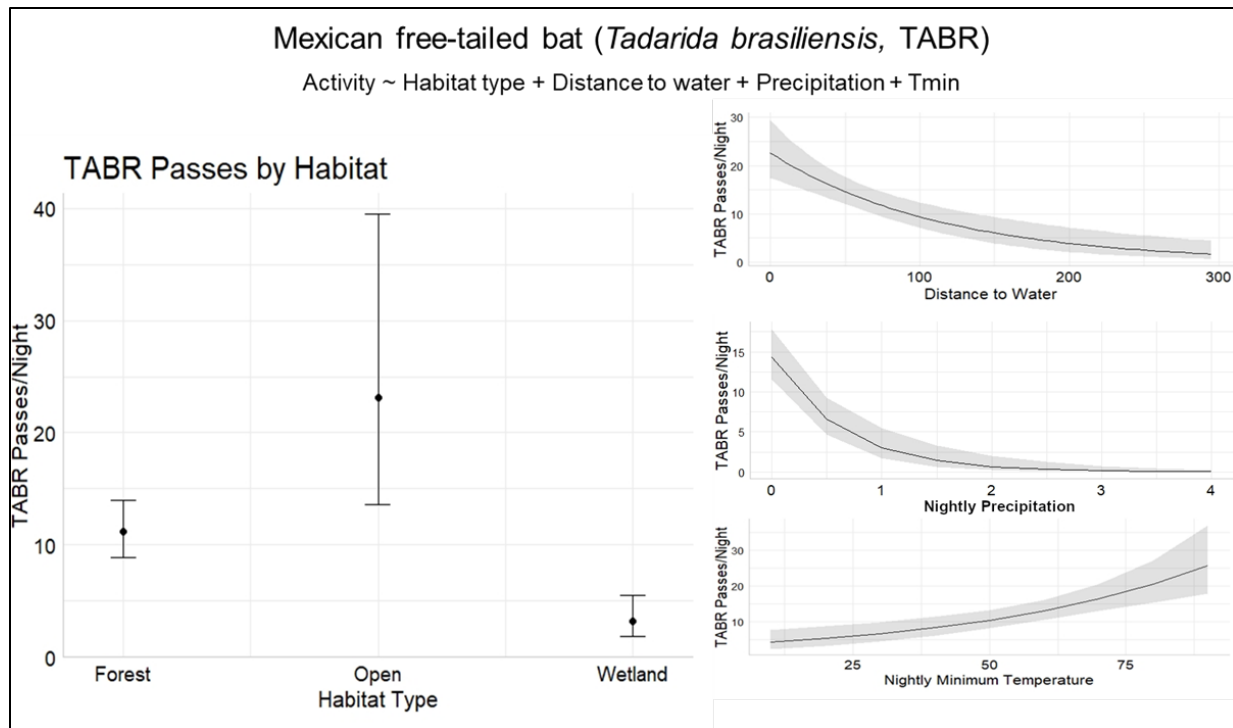


Figure 27. Predicted activity (mean passes per night and standard error) for Mexican free-tailed bat (*Tadarida brasiliensis*, TABR) by generalized linear mixed model during summer at Colonial National Historical Park, Virginia by covariates: habitat type, distance to water (m), nightly precipitation (cm), and minimum nightly temperature (°F).

Capture Survey

I captured seven bat species: big brown, eastern red, hoary, silver-haired, southeastern, evening, and tricolored bats at COLO during mist-netting in 2019 and 2021 (Table 5; Appendix D). Capture surveys could not be completed past March in 2020 due to a national moratorium on bat capture surveys due to the potential transmission of COVID-19 to native bats. Bat capture was permitted in 2021 with the use of protective equipment. I conducted mist-netting capture surveys on 22 nights at six sites targeting locations where higher levels of acoustic activity of *Myotis* species (i.e. southeastern, little brown, Indiana, and northern long-eared bats) were identified when possible (Figure 4). All mist-netting took place in Yorktown, where bat activity was higher, especially of *Myotis* bats and habitats were more mature, heterogeneous, and better-suited for mist-netting.

I captured eastern red and big brown bats on most occasions, totaling 34 and 26 bats, respectively. Evening bats were also commonly captured totaling 29 bats. Reproductive females (i.e. pregnant, lactating, or post-lactating) of all three species were documented, indicating maternity colonies were present or nearby. I captured three silver-haired bats in early February and a single hoary bat in October. I captured two southeastern bats in March and September, which were the only *Myotis* spp. encountered.

Table 5. Bat capture results by species, sex, and reproductive condition during mist-netting from 2019–2021 at Colonial National Historical Park, Virginia.

Net Site	Date	EPFU ¹		LABO ¹		LACI ¹		LANO ¹		MYAU ¹		NYHU ¹		PESU ¹	
		# Captured	Age & Sex ²	# Captured	Age & Sex ²	# Captured	Age & Sex ²	# Captured	Age & Sex ²	# Captured	Age & Sex ²	# Captured	Age & Sex ²	# Captured	Age & Sex ²
COLO-N01	2/8/19	0	–	1	AM, NR	0	–	3	AM, NR	0	–	0	–	0	–
COLO-N02	3/12/19	0	–	0	–	0	–	0	–	1	AM, NR	0	–	0	–
COLO-N02	3/14/19	0	–	0	–	0	–	0	–	1	AM, NR	0	–	0	–
COLO-N01	3/15/19	1	AF, U	1	AM, NR	0	–	0	–	0	–	1	AM, NR	0	–
COLO-N01	3/24/19	0	–	1	AM, NR	0	–	0	–	0	–	0	–	0	–
COLO-N03	3/29/19	0	–	4	AM, NR	0	–	0	–	0	–	0	–	0	–
COLO-N01	4/10/19	0	–	3	AM, NR	0	–	0	–	0	–	0	–	0	–
	4/10/19	0	–	1	U, U*	0	–	0	–	0	–	0	–	0	–
COLO-N04	4/11/19	3	AM, NR	1	AM, NR	0	–	0	–	0	–	0	–	0	–
	4/11/19	1	AF, U	0	–	0	–	0	–	0	–	0	–	0	–
COLO-N02	4/12/19	1	AM, NR	5	AM, NR	0	–	0	–	0	–	0	–	1	AM, NR
	4/12/19	0	–	1	AF, U	0	–	0	–	0	–	0	–	0	–
COLO-N06	7/9/19	1	AF, P	2	AF, L	0	–	0	–	0	–	0	–	0	–
	7/9/19	1	AF, NR	0	–	0	–	0	–	0	–	0	–	0	–
COLO-N02	7/10/19	3	AM, NR	2	AF, L	0	–	0	–	0	–	10	AM, NR	1	AF, NR
	7/10/19	1	AF, L	1;	AF, NR	0	–	0	–	0	–	1	AF, L;	1	AM, NR
	7/10/19	0	–	1	AM, NR	0	–	0	–	0	–	1	AF, U	0	–
	7/10/19	0	–	0	–	0	–	0	–	0	–	2	JF, NR	0	–
COLO-N05	8/14/19	1	AF, NR	2	AF, NR	0	–	0	–	0	–	1	AF, NR	0	–
	8/14/19	0	–	2	AM, NR	0	–	0	–	0	–	0	–	0	–
COLO-N05	8/15/19	0	–	0	–	0	–	0	–	1	AF, U	1	AF, PL	0	–
	8/15/19	0	–	0	–	0	–	0	–	1	AM, NR	0	–	0	–
COLO-N05	10/1/19	2	AM, D	3	AM, D	1	AM, D	0	–	0	–	4	AM, D	0	–
	10/1/19	1	AM, NR	1	AF, NR	0	–	0	–	0	–	3	AF, NR	0	–
	10/1/19	1	AF, NR	0	–	0	–	0	–	0	–	0	–	0	–
COLO-N01	10/3/19	1	AM, D	0	–	0	–	0	–	0	–	0	–	0	–
COLO-N05	10/15/19	0	–	1	AM, NR	0	–	0	–	0	–	2	AM, D	0	–
COLO-N02	3/9/20	0	–	0	–	0	–	0	–	0	–	0	–	0	–
COLO-N05	3/10/20	2	AF, U	1	AM, NR	0	–	0	–	0	–	1	AM, NR	0	–
COLO-N01	3/11/20	0	–	0	–	0	–	0	–	0	–	0	–	0	–
COLO-N06	3/12/20	0	–	0	–	0	–	0	–	0	–	0	–	0	–
COLO-N03	10/12/21	1	AM, D	0	–	0	–	0	–	0	–	0	–	0	–
	10/12/21	1	AM, NR	0	–	0	–	0	–	0	–	0	–	0	–

¹ Species: EPFU = big brown bat (*Eptesicus fuscus*), LABO = eastern red bat (*Lasiurus borealis*), LACI = hoary bat (*Lasiurus cinereus*), LANO = silver-haired bat (*Lasionycteris noctivagans*), MYAU = southeastern bat (*Myotis austroriparius*), NYHU = evening bat (*Nycticeius humeralis*), PESU = tricolored bat (*Perimyotis subflavus*);

² Age and sex: AM = adult male, AF = adult female, JM = juvenile male, JF = juvenile female; Reproductive condition: NR= non-reproductive, D= descended testes, P= pregnant, L= lactating, PL= post-lactating, and U=unknown.

Table 5 (continued). Bat capture results by species, sex, and reproductive condition during mist-netting from 2019–2021 at Colonial National Historical Park, Virginia.

Net Site	Date	EPFU ¹		LABO ¹		LACI ¹		LANO ¹		MYAU ¹		NYHU ¹		PESU ¹	
		# Captured	Age & Sex ²	# Captured	Age & Sex ²	# Captured	Age & Sex ²	# Captured	Age & Sex ²	# Captured	Age & Sex ²	# Captured	Age & Sex ²	# Captured	Age & Sex ²
COLO-N05	10/13/21	4	AM, D	0	–	0	–	0	–	0	–	1	AF, NR	0	–
	10/13/21	0	–	0	–	0	–	0	–	0	–	1	AM, D	0	–

¹ Species: EPFU = big brown bat (*Eptesicus fuscus*), LABO = eastern red bat (*Lasiurus borealis*), LACI = hoary bat (*Lasiurus cinereus*), LANO = silver-haired bat (*Lasionycteris noctivagans*), MYAU = southeastern bat (*Myotis austroriparius*), NYHU = evening bat (*Nycticeius humeralis*), PESU = tricolored bat (*Perimyotis subflavus*);

² Age and sex: AM = adult male, AF = adult male, JM = juvenile male, JF = juvenile female; Reproductive condition: NR= non-reproductive, D= descended testes, P= pregnant, L= lactating, PL= post-lactating, and U=unknown.

Tricolored bats were the only WNS-imperiled species captured, including two adult males and one female that did not show signs of reproduction. I radio-tagged the tricolored bat male captured on April 12 and tracked it to the neighboring Newport News Park. I also radio-tagged and attempted to track the female tricolored bat captured on July 10, but I could not obtain a signal from it following its release, indicating it left the area.

Discussion

Acoustic results identified a community of eleven species of bats that occur at COLO. Capture surveys confirmed the presence of seven of these species: big brown, eastern red, hoary silver-haired, southeastern, evening, and tricolored bats, while little brown, northern long-eared, Indiana, and Mexican free-tailed bats were only identified acoustically. Misidentifications of acoustic calls were problematic for *Myotis* species: little brown, northern long-eared, and Indiana bats. Echolocation calls of the southeastern bat did not appear to be falsely identified but were rather misidentified as other *Myotis* species.

Generally, cave bat species: big brown, little brown, northern long-eared, and tricolored bats had increasing nightly activity in March and April, highest activity in June or July, which is generally associated with reproduction (Deeley et al. 2022), then declines in activity in August–October. Southeastern bats also appeared to have highest activity in the summer, but were relatively more active in spring and fall. Eastern red and evening bats had the highest activity among migratory species with significantly greater activity in mid-summer. Hoary bats and Mexican free-tailed bats had low activity overall and their GAM-predicted annual activity trends were primarily driven by individual site-nights with high activity in spring and summer. Silver-haired bats similarly exhibited sporadic high activity site-nights in the spring, but had low activity in the summer, indicating COLO may be more important as a migratory stopover, rather than for summer maternity habitat. All bat species except Indiana bats appeared to occur in January through February, albeit most at very low levels, indicating at least some individuals winter locally. Winter occurrences of big brown, eastern red, hoary, silver-haired, southeastern, northern long-eared, evening, and tricolored bats at COLO are supported by findings of by Grider *et al* (2016), who also acoustically observed these species wintering south of COLO in the Coastal Plain of northeastern North Carolina. Tree bat species eastern red, hoary, and silver-haired bat have historically been documented during the winter in the Coastal Plain of Virginia in museum records (Cryan 2003). These tree bat species are known to roost among foliage or leaf litter during the winter (Jorge et al. 2021a). Other species may be winter-roosting in bottomland hardwood swamps as northern long-eared bats have been documented using these habitat types for winter day-roosts in eastern North Carolina (Jordan 2020). Winter occurrences may also be linked to use of anthropogenic structures (e.g. houses, bridges).

Activity in passes per night is often used as an indication of abundance, but it is not a direct measure of species abundance (Ford et al. 2011). Bats are elusive and difficult to capture, especially bat species that have suffered extreme declines following WNS, so often acoustic activity is the best attainable measure of their occurrence. Bat species occurrences should not be considered limited to sites of acoustic detections because nightly home ranges of bats are large and can exceed the area of Yorktown and Jamestown (Coleman et al. 2014b, Menzel et al. 2005, Morris et al. 2011, Owen et al. 2003). Also, acoustic detections are not necessarily reflective of bat day-roosting sites.

Acoustic survey results were highly variable by night, site, and within broad habitat categories. Despite extremely high variance in the dataset, species GLMMs provided interpretable associations among habitat types for several species, several of which were consistent with previous findings of

others. When distance to water was a significant covariate in species models, its inclusion improved model fit because it was representative of trends in results at COLO. Positive relationships between species activity and distance to water should not necessarily be interpreted as behavioral avoidance of streams and riparian habitats altogether because a small number of sites that recorded very high activity away from a water course can overrepresent the relationship of activity and distance to water in such a highly variable dataset. Minimum nightly temperature acted as a seasonal temporal smoother when it was significant by offering improved fit when highest activity occurred during warmer nights of the summer (Muthersbaugh et al. 2019, True et al. 2021a). When nightly precipitation was significant, it was representative of finer scale nightly variance that correlated with rain events, which are known to reduce bat activity (Gorman et al. 2021).

Cave bats

Big brown bat

Big brown bats are a cave-hibernating species also known to overwinter in man-made structures and are commonly associated with urbanized environments (Boyles et al. 2006, Johnson et al. 2008, Kurta and Baker 1990). Big brown bats are the largest among cave-hibernating species present with adult total length ranging from 87–138 mm, wingspan of averaging near 330 mm, and weight from 11–23 g (Kurta and Baker 1990). Their diet includes a range of insects, but they specialize in preying on beetles (Agosta 2002). Big brown bats will naturally day-roost in tree cavities and under sloughing bark, but they are largely now associated with an array of anthropogenic structures as day-roosts in current environments (Agosta 2002, Whitaker and Gummer 1992). Tree roost studies have observed them using silver maple (*Acer saccharinum*), black locust (*Robinia pseudoacacia*), and oak in Missouri and Maryland (Agosta 2002, Timpone et al. 2006).

Prevalence and amount of acoustic detections and captures throughout COLO indicate an abundant population persists that has not been severely impacted by WNS. This corresponds with findings throughout the East in which WNS mortality of big brown bats have been low compared to other species and acoustic and capture surveys indicate stable and even increasing populations (Barr et al. 2021, Deeley et al. 2021, Ford et al. 2011, Frank et al. 2014). Big brown bats appear to exhibit resistance to the effects of WNS that are thought to be attributable to amassing greater percentages of body fat before hibernation and undergoing shorter bouts of torpor than other species (Frank et al. 2014).

Sharp increases in activity in early April suggest the end of their hibernation period and increased activity by local residents and regional migrants. Sustained activity through fall, winter, and spring months at Yorktown suggests at least some individuals remain nearby and utilize areas of the park. Big brown bats are known to hibernate in anthropogenic structures so winter occurrences at Yorktown where surroundings are urbanized may indicate they are wintering in buildings or other anthropogenic structures (Agosta 2002, Boyles et al. 2006). Peak activity in July is likely related to reproduction based on capture results (Deeley et al. 2022).

Spatially, the GLMM of activity found it to be high among all three general habitat types but highest at forest sites. This is somewhat contrary to their reputation as an open-adapted foraging species

(Barr et al. 2021, Duchamp et al. 2004, Ford et al. 2005). However, they are also considered to be a habitat generalist likely to occur in all habitats (Agosta 2002, Duchamp et al. 2004).

Big brown bats were commonly captured during capture surveys and were documented on most netting occasions. One pregnant female was captured on July 9, 2019 at Beaverdam Creek (COLO-N02) and a lactating female was captured the following night on July 10, 2019 at Surrender Field (COLO-N06). These captures demonstrate maternity colonies with active recruitment occur at or nearby COLO and that partition takes place in early July. Results indicate big brown bats are maintaining abundant populations following WNS at COLO that utilize habitats year-round.

Southeastern bat

Southeastern bats exhibit different wintering behavior in different portions of their range. In northern portions, such as Illinois and Indiana, they hibernate in caves, mines, or beneath buildings, sometimes roosting in caves year-round; whereas in the southern portion of their range, such as Louisiana or Florida, they remain active throughout much of the winter, entering states of torpor or semi-torpor during colder weather and roost either in caves or in tree cavities (Jones and Manning 1989, Zinn and Humphrey 1981). Their seasonal movements remain poorly understood and it is unknown if they migrate long distances (Lacki and Bayless 2013). They are relatively small bats, approximately 80–97 mm in length, 240–270 mm in wingspan, and 5–8 grams in weight (Jones and Manning 1989, Lacki and Bayless 2013). Southeastern bats are most commonly associated with permanent water sources and bottomland hardwood habitats (Lacki and Bayless 2013). They have been observed forming very large maternity colonies of hundreds to thousands of individuals in caves, under bridges, and in hollowed trees depending on location (Jones and Manning 1989, Lacki and Bayless 2013). Tree summer day roosts are most commonly mature, live hollowed trees with large basal openings. Roost species include: black gum (*Nyssa sylvatica*), water tupelo (*N. aquatica*), American sycamore (*Platanus occidentalis*), sweetgum (*Liquidambar styraciflua*), water oak (*Quercus nigra*), bald cypress (*Taxodium distichum*), pignut hickory (*Carya glabra*), red maple, and American beech (Lacki and Bayless 2013). Southeastern bats appear to be generalists with regard to prey taxa but have demonstrated preference for mosquitos, moths, and beetles and affinity for foraging over water (Zinn and Humphrey 1981).

Very little is known about the effects of WNS on southeastern bats. The fungus that causes WNS has been observed on southeastern bats but without evidence of tissue damage or mortality (Turner et al 2011). Beyond that, the impacts of WNS on southeastern bats remains unknown. Southeastern bats at COLO likely behave similarly to those observed in other southeastern coastal portions of their range, in which torpor occurs in shorter periods (Zinn and Humphrey 1981), so winter arousal and foraging bouts may sustain bats and reduce effects from fungal infection.

Southeastern bat activity was commonly observed at COLO including dormant season activity suggestive of year-round residence. Importantly, southeastern bat activity is underrepresented in results because many calls falsely identified as other *Myotis* spp. appeared to actually be southeastern bat calls due to similarities of vocalizations among the genus. Examined calls that were identified as southeastern bats by software did appear to be authentic, so their seasonal trends do reflect species activity patterns despite being underrepresented overall. Annual activity trends included higher

activity in mid-March and early July. Southeastern bats have been found to birth young earlier than most other species, with parturition usually occurring in late April through mid-May and young becoming volant in late June or early July (Lacki and Bayless 2013). So, elevated activity in early July may correspond with juvenile volancy. Southeastern bats remained fairly active through the fall especially at site COLO05D, supporting their continued residence at COLO. In winter, activity was highest at site COLO16D near Wormley Pond.

Spatially, southeastern bat activity was strongly associated with wetland and riparian habitats, which is consistent with its previously observed affinity for bottomland forests and foraging over water (Jones and Manning 1989, Zinn and Humphrey 1981).

Presence of southeastern bats was confirmed by capture of three males and one female. Although reproductive females were not documented, acoustic activity trends are suggestive that reproduction occurs locally.

Little brown bat

Little brown bats are a hibernating species and are known to primarily use caves and mines forming clusters along ceilings (Fenton and Barclay 1980). They are a smaller-bodied bat with adult total length averaging between 80–95 mm, weight ranging from 4 to 9 grams, and wingspan typically ranges from 220–270 mm (Harvey et al. 2011). This highly maneuverable species is considered a generalist in regard to habitat, but has been most associated with foraging in both open and forested riparian habitats feeding on a variety of small-bodied insects (Fenton and Barclay 1980). During summer, they are known to day-roost in anthropogenic structures (e.g. attics, barns), tree cavities, and rock outcrops (Bergeson et al. 2015, Fenton and Barclay 1980). In Indiana, little brown bats were found to roost in cavities and under exfoliating bark in oaks, maples (*Acer* spp.), and hickories (*Carya* spp.; Bergeson et al. 2015).

Previously one of the most abundant bat species in the eastern United States, little brown bats have experienced an approximately 90% population decline based on winter hibernacula counts (Turner et al. 2011). Little brown bats are not currently federally protected but are under review for potential federal listing and are considered state endangered in Virginia (Straw et al. 2022, VDGIF 2016). Acoustic survey results included high levels of identified little brown bat activity, however, manual validation of selected calls showed a significant portion of identified activity was misidentified. Unfortunately, this high level of misidentification imparts inaccuracy to results and analysis, so I suggest strong caution in interpreting results for little brown bats. Specifically, validation of calls found many misidentifications to actually be calls of eastern red bats, in particular “feeding buzzes,” whereby bats display high frequency, high slope, and high rate pulses as they approach and consume prey that, in red bats, mimic the normal search phase echolocation pulses of *Myotis* bat species. Another portion of misidentifications appeared to be misidentifications of southeastern bats. I did document many diagnostic little brown bat echolocation calls, so they likely occur at COLO, but at lower levels of abundance than indicated by acoustic results. Both Yorktown and Jamestown should be considered areas of use from a conservation perspective, and winter occurrence of little brown bats at the Yorktown is likely. Little brown bats have not been observed wintering in bottomland forests in the Coastal Plain as have northern long-eared bats (Jordan 2020), so it is more likely that

they would be hibernating in anthropogenic structures if they remain locally in the winter (Brown et al. 2007).

Analysis of identified passes of little brown bats by GLMM found them to be more associated with open and forested habitats during summer, which correspond with previous observations of little brown bats (Fenton and Barclay 1980, Ford et al. 2005). Temporally, increase in activity in early April suggests arrival of migrants whether local or from karst landscapes in western Virginia. The peak in early July is likely associated with reproduction, and declines through September suggests departure of migrants (Francl et al. 2012).

Northern long-eared bat

Northern long-eared bats are a small-bodied, cave hibernating bat similar in morphology to little brown bats. Adult body length is typically 85–95 mm, weight is between 5–8 g, and wingspan is 230–260 mm (Barbour and Davis 1969, Caceres and Barclay 2000). Highly maneuverable and capable of hawking (i.e., aerial capture) and gleaning (i.e., capturing from leaves) prey. Northern long-eared bats are known to predate moths, flies, and beetles (Lee and McCracken 2004). They most commonly hibernate in caves and mines individually or in small groups, usually in deep crevices (Caceres and Barclay 2000). During summer, they day-roost in cavities and sloughing bark in a wide variety tree species, but have shown preference for black locust, red maples (*Acer rubrum*), and oaks in the Mid-Atlantic and commonly use dead and dying trees, often with high solar exposure (Kalen et al. 2022, Silvis et al. 2016). Though uncommon in the Mid-Atlantic, they may day-roost in anthropogenic structures (Caceres and Barclay 2000, Silvis et al. 2016). However, they have been found to readily use “rocket-box” style bat houses in in the upper Ohio Valley of West Virginia and Ohio (De La Cruz et al. 2018).

Northern long-eared bats were very common in the East prior to WNS, and similar to little brown bats, they have suffered extreme population declines following the disease, with regional mortality estimates exceeding 90% and facing potential extirpation (Frick et al. 2015, Reynolds et al. 2016, Turner et al. 2011). Recent discoveries of northern long-eared bats wintering along the coast of North Carolina have increased interest in investigating potential winter occurrence, as these anomalous coastal wintering populations do not appear to show signs or impacts from WNS (Jordan 2020). Therefore, exploring potential winter occurrences of northern long-eared bats at COLO was an important objective in this study.

Northern long-eared bat activity was identified at low to moderate levels. Review of identified calls did reveal diagnostic calls of northern long-eared bats, but also found many to be misidentifications of eastern red, southeastern, or little brown bats. High rates of misidentifications and lack of captures indicates the presence, distribution, and activity trends of northern long-eared bats at COLO remain equivocal. Although I was unable to capture them with targeted effort, northern long-eared bats have proven difficult to capture following WNS, even where they are known to be present (Kalen et al. 2022). Positive identifications of northern long-eared bats including captures in the region support their potential occurrence at COLO. In the fall of 2021, a northern long-eared bat was captured in Sussex County, VA approximately 40 miles southwest of COLO (J. L. De La Cruz, Virginia Tech, personal communication). They have also been documented post-WNS in Virginia by capture and

maternity colonies were observed in recent surveys at Rock Creek Park in the District of Columbia, Prince William Forest Park, and Shenandoah National Park (Deeley et al. 2021, Kalen et al. 2022). Additionally, recent findings suggest genetic similarities between northern long-eared bats captured at Rock Creek Park in Washington DC and the North Carolina coast, indicating they may be linked (Hoff et al. 2022), in which case their migratory route could pass through COLO. Based on these regional occurrences and levels of diagnostic calls recorded, northern long-eared bats most likely occur sporadically at COLO in low abundances during the summer, but maternity colonies are unlikely. Relatively few positively identified calls during winter indicate northern long-eared bats may occur then, but COLO is not being used as a wintering site to the degree that has been documented in the North Carolina Coastal Plain (Jordan 2020). Wintering northern long-eared bats could be using tree roosts (Jordan 2020), or they could be hibernating in anthropogenic structures (Brown et al. 2007, Dowling and O'Dell 2018).

Indiana bat

Indiana bats are similar in size and ecology to northern long-eared bats and little brown bats, with a typical adult Indiana bat total body length measuring around 85 mm, wingspan measuring 240–270 mm, and weighing 6–9 g (Thomson 1982). They have a similar diet to northern long-eared bats, preferring moths (Lee and McCracken 2004). They hibernate in caves and mines in clusters along ceilings in the winter (Silvis et al. 2016). In the summer, Indiana bats day-roost in a variety of tree species and have shown preference for roosting under exfoliating bark of snags in positions with high solar exposure (St. Germain et al. 2017, Silvis et al. 2016). Tree species summer day roost use is diverse and includes selection for pine snags including loblolly pine in the Mid-Atlantic Coastal Plain (St. Germain et al. 2017) and hickories, maples, and ash (*Fraxinus* spp.) in the Appalachians (Silvis et al. 2016).

Although Indiana bats were much less common than northern long-eared and little brown bats in the Mid-Atlantic prior to WNS, they have also experienced significant population declines following WNS (Silvis et al. 2016). Already a federally endangered species prior to WNS, high additive mortality from the disease threatens them with extirpation over portions of their range (Thogmartin et al. 2013).

Similar to northern long-eared bats, Indiana bats were identified sporadically at many sites throughout the summer, but most examined identifications appeared to be misidentifications of southeastern, little brown, and eastern red bats. Nonetheless, some calls did seem authentic, so presence at COLO is possible. Indiana, little brown, and southeastern bat calls are the most similar of the bat community at COLO and are very difficult to distinguish, making confident identification of Indiana bats through acoustic survey extremely difficult where they co-occur. Highest Indiana bat activity was identified from sites COLO01 and COLO05D during summer and COLO16D in the fall. Although most of these passes appeared to be misidentifications of southeastern bat and eastern red bat calls, several could not be ruled out as potentially being from Indiana bats. Diagnostic calls indicate Indiana bats may occur at COLO during summer and fall. Identified passes recorded during winter ruled out as misidentifications. The nearest capture of Indiana bats occurred in Caroline

County, VA where an active maternity colony was identified in 2015 approximately 80 miles northwest of COLO (St. Germain et al. 2017).

Tricolored bat

Tricolored bats are considered a hibernating species that uses caves, but they are also known to overwinter and roost in tree cavities, foliage, and bridges in the southern portion of their range (Newman et al. 2021). They are the smallest bat present at COLO and are typically 77–89 mm long, weigh between 4–8 g, and have a wingspan of 210 to 260 mm (Fujita and Kunz 1984, Harvey et al. 2011). They generally hibernate singly or in smaller groups in caves, mines, and man-made structures (Fujita and Kunz 1984). During the summer they most often day-roost in tree foliage and, to a lesser extent, man-made structures (Silvis et al. 2016). Day-roost selection is not well understood, but tricolored bats have been observed roosting in oaks in Indiana, South Carolina, and Arkansas, as well as shortleaf pine (*Pinus echinate*) in Arkansas and sweetgum in South Carolina (Shute et al. 2021, Silvis et al. 2016). They move by slow, fluttery flight and forage by hawking and gleaning a variety of small-bodied insects including flies, beetles, aphids, leafhoppers, and moths (Fujita and Kunz 1984).

Tricolored bats were previously common throughout the East and have sustained large declines from WNS that threaten extirpation over portions of their range, particularly where they engage in long-duration hibernation (Frick et al. 2015, Silvis et al. 2016). Tricolored bats have been proposed for listing as an endangered species in response to mortality from WNS and are currently listed as state endangered in Virginia (USFWS 2022b, VDGIF 2016).

Identification of tricolored bat calls by Kaleidoscope is generally highly accurate, so results and analysis are more reliable for this species. They were identified at most sample sites at both Yorktown and Jamestown during the summer and were observed at moderate to high levels of activity at several sites indicating COLO is important summer habitat for persisting populations in the region.

Tricolored bats have most often been observed foraging over waterways and ponds and have been associated with wetland and riparian habitats (Ford et al. 2005, Fujita and Kunz 1984). However, the GLMM found higher activity was observed at open and forested sites compared to wetland and riparian sites. Lack of greater association of tricolored bats with wetland and riparian sites could be attributable to the fact that several sites that documented highest activity were classified as open and forest (e.g. COLO06, COLO14, and COLO17) were also close to permanent streams, which may have factored in greater tricolored bat activity there.

The GAM predicted increasing activity in late April which correlates with previously recorded timing of formation of maternity colonies (Silvis et al. 2016). The activity peak in early July could be associated with reproduction, specifically either increased foraging during lactation or increased abundance from juvenile volancy (Fujita and Kunz 1984). Activity declined in early September, but sites COLO05D and COLO15D continued to document them consistently through the fall. Passes recorded from December through February suggest some individuals are wintering nearby. Tricolored bats are known to hibernate in a variety anthropogenic structures and have been observed

wintering in Caroline County, VA approximately 80 miles northwest of COLO in an abandoned concrete culvert (W. M. Ford, USGS, personal communication, Silvis et al. 2016). Tricolored bats could be using similar structures to winter in near COLO.

Captures of three tricolored bats including one female were notable considering the proposal for their listing as an endangered species (USFWS 2022b). All three captures took place at Beaverdam Creek (COLO-N02). I radio-tagged and attempted to track the male captured on April 12, 2019 and the female captured on July 10, 2019. I located the male day-roosting at the adjacent Newport News Park, but could not obtain a radio signal for the female indicating it left the area following release. Acoustic results and captures suggest widespread and fairly abundant occurrence of tricolored bats at COLO.

Tree bats

Eastern red bat

Eastern red bats are a migratory tree bat species that generally migrate to southern or coastal portions of their range to winter in tree foliage or in leaf litter, entering torpor in cold temperatures and periodically emerging in warm temperatures (Cryan 2003, Mormann and Robbins 2005, Shump and Shump 1982a). They are a medium-sized bat generally measuring 100–130 mm long, weighing 7–15 g, with wingspan of 280–330 mm (Harvey et al. 2011, Shump and Shump 1982a). They have relatively long, pointed wings adapted for fast flight and moderate maneuverability (Shump and Shump 1982a). They prey on a variety of insects including moths, beetles, flies, and crickets (Shump and Shump 1982a). During the summer they disperse throughout their range and day-roost in tree foliage, shrubs (Mormann and Robbins 2007, Shump and Shump 1982a). Red bats have been reported roosting in a variety of tree species including oaks, pines, red maple, tulip poplar, sweetgum, and blackgum in Maryland, South Carolina, and Florida (Jorge et al. 2021a, Limpert et al. 2005, Menzel et al 2002b). They appear to roost and raise young individually but often congregate to forage and migrate (Mormann and Robbins 2007, Shump and Shump 1982a).

Eastern red bats were the second most commonly identified species in acoustic surveys and were the most commonly captured species during capture surveys. Captures occurred from early February through mid-October. Lactating females were captured July 9 and 10, 2019 at Beaverdam Creek (COLO-N02) and Surrender Field (COLO-N06).

The GLMM for eastern red bats showed activity was higher in forests and open habitats compared to wetland and riparian habitats. This corresponds with other findings of eastern red bats being more associated with open and moderately-cluttered habitats, as forested sites were along roads, trails, and forest gaps (Ford et al. 2005, Shump and Shump 1982a).

Seasonally, the GAM showed activity rose sharply in early April and peaked in late June, which aligns with the lactation phase based on capture results from various locations in Virginia, as well as at lactating females observed at COLO in early July (Deeley et al. 2022). GAM-predicted activity decreased greatly by early September, suggesting some summer residents emigrated during this time. Fall, winter, and spring activity indicated some individuals wintered locally to Yorktown, which is consistent with previous observation of eastern red bats wintering in coastal Virginia (Cryan 2003).

Hoary bat

Hoary bats are the largest bat species at COLO and are a migratory tree bat that winters in tree foliage along the Atlantic and Gulf coasts in the East (Cryan 2003, Jorge et al. 2021a, Shump and Shump 1982b). Though overall migratory habits are poorly understood, they appear to vary regionally and by sex, with females more likely to migrate greater distances (Cryan 2003). They are believed to be generally solitary but migrate long distances in large flocks to summer locations where they day-roost in foliage of a variety of tree species (Cryan 2003, Shump and Shump 1982b). Day-roosting observations include use of oaks and pines in Arkansas and Florida (Jorge et al. 2021a, Perry and Thill 2007), eastern hemlock (*Tsuga canadensis*) in New Hampshire (Veilleux et al. 2009), and white spruce (*Picea glauca*) in Saskatchewan (Willis et al. 2005). Adults are typically 130–150 mm long, weigh 20–35 g, and have a wingspan of approximately 430 mm (Harvey et al. 2011, Shump and Shump 1982b). They have long, high-loaded wings adapted for fast flying, facilitating efficient migration and open and above canopy foraging (Menzel et al. 2005, Shump and Shump 1982b). They predate moths, beetles, flies, grasshoppers, dragonflies, and wasps (Shump and Shump 1982b).

Activity of hoary bats was generally very low except for some nights in mid-March, late June, and early July. Individual nights of high activity in mid-March are indicative of large, passing migratory groups (Cryan 2003, Shump and Shump 1982b). Increased activity of migratory hoary bats in spring is consistent with acoustic observations from the southern and central Appalachians, as well coastal Virginia (Diggins et al. 2022, True et al. 2021a). Sporadic nights of high activity in late June and early July may be associated with reproduction (Cryan 2003). Otherwise activity remained low through the summer. Low levels of activity were also recorded through the fall and winter indicating some individuals winter locally, which corresponds to previous records of hoary bats wintering in coastal Virginia (Cryan 2003). Higher activity was associated with open habitats in the GLMM, which is consistent with previous observations (Ford et al. 2005).

Hoary bats often fly high above forest canopies and open areas, which may contribute to low levels of acoustic detection (Menzel et al. 2005). Additionally, hoary bats have been found to use “micro” echolocation pulses that are undetectable by ultrasonic bat detectors and even navigate without using echolocation in some instances, which could potentially contribute to underrepresentation in acoustic results (Corcoran and Weller 2018).

Silver-haired bat

Silver-haired bats are a migratory tree species that are believed to overwinter in the Mid-Atlantic, but their migratory habits and distribution are not well understood (Cryan 2003, Kunz 1982). They are medium-bodied with an approximate total length of 90–155 mm, wingspan of 270–310 mm, and weight of 8–11 grams (Harvey et al. 2011, Kunz 1982). They are known to roost in tree cavities and are considered a solitary species but do form maternity colonies (Harvey et al. 2011). They have been observed roosting in shortleaf pine, blackgum, and oaks in Arkansas (Perry et al. 2010). They are a slower flying species adapted for consuming smaller insects (Kunz 1982).

Silver-haired bat activity was generally very low, but similar to hoary bats, a few incidences of high activity occurred in March that were likely the result of passing migrants (Cryan 2003). Lack of

persisting activity during the summer suggests very few individuals remain locally through the reproductive season, which is consistent with findings of others (Diggins et al. 2022, True et al. 2021a). Also, summer calls identified as silver-haired bats may in fact be misidentifications of big brown bats (Austin et al. 2020). The GLMM predicted higher activity in open habitats, although this was due to isolated nights of high activity at Wormley Pond (COLO01D) and was not a broadly observed trend.

Evening bat

Evening bats are believed to be moderate to short distance migrants and year-round residents in much of their distribution (Watkins 1972). They are known to overwinter in trees and in buildings (Boyles et al. 2006). During the summer, they form maternity colonies and day-roost in a variety of trees and anthropogenic structures (Menzel et al. 2001, Watkins 1972). They were found to prefer longleaf pine (*Pinus palustris*) in South Carolina, loblolly pine in Georgia, and used silver maple, oaks, and hickories in Missouri but roost tree selection is otherwise poorly understood (Menzel et al. 2001, Miles et al. 2006, Timpone et al. 2006). They are a smaller-bodied bat with an approximate total length of 88–105 mm, wingspan of 260–280 mm, and weight of 8 g (Harvey et al. 2011, Watkins 1972). They prey on moths, beetles, leaf hoppers, and flies among other insects (Whitaker and Clem 1992).

Evening bats were common at COLO. Activity was increased in early April through August. A sharp decline in acoustic activity in the fall suggests most summer inhabitants migrate away from COLO to winter. However, there were some passes identified at a few sites during winter that suggests some individuals may remain year-round. Similar to big brown bats, evening bats may be wintering in buildings nearby (Boyles et al. 2006). The GLMM showed activity was fairly high among habitat types except wetland and riparian forest habitats where it was lowest.

Evening bats were captured from March through October, supporting their year-round occurrence. At Beaverdam Creek 15 bats were captured on July 10 including one lactating female and two juvenile females, indicating active local recruitment. This timing of juvenile volancy and female lactation coincided with highest acoustic activity and indicates partition occurs sometime from late May to early June.

Mexican free-tailed bat

Mexican free-tailed bats are known to be long-distance migrants, but migration varies significantly by region (McCracken et al. 2018, Wilkins 1989). They generally move to warmer climates in winter and are not considered a true hibernator, though they may undergo torpor for short periods (Wilkins 1989). They are a medium-sized bat with an approximate length of 90–105 mm, wingspan of 290–350 mm, and weight of 9–15 g (Harvey et al. 2011, Wilkins 1989). They have long, narrow wings that enable fast flight and foraging (Wilkins 1989). They most commonly roost in a variety of anthropogenic structures, but can also roost trees (Wilkins 1989). Mexican free-tailed bats have recently expanded their range into Virginia (McCracken et al. 2018).

Activity of Mexican free-tailed bats was generally low, suggesting they occur at low abundances. Higher activity identified on several nights in March and April at COLO01D and COLO05D may

have been associated with migration (McCracken et al. 2018). During summer, passes occurred with some consistency at sites COLO12 and COLO01D. Activity was also low during fall except at site COLO12. Some passes did occur during winter, suggesting some Mexican free-tailed bats winter locally. Wintering in the area is supported by a record of a Mexican free-tailed bat in February 2015 from Henrico County, Virginia, approximately 65 miles northwest of COLO (McCracken et al. 2018). Spatially, activity was most associated with open habitats in the GLMM, which corresponds with their morphology and acoustic results from Tennessee (McCracken et al. 2018, Wilkins 1989).

Conclusions

COLO still supports a diverse and abundant community of bats. Species big brown, eastern red, and evening bats were especially common in both acoustic and capture results. Tricolored bats were commonly documented acoustically and three bats were documented during capture surveys. COLO also supports hoary, silver-haired, and Mexican free-tailed bats that occur less frequently but did exhibit nights of high activity indicative of passing migratory groups. Southeastern bats likely occur more so than indicated by acoustic results, as their calls appear to account for many misidentifications as other *Myotis* species. Unfortunately, the occurrence of little brown, northern long-eared, and Indiana bats remains uncertain as no bats were captured to confirm their presence and acoustic identification of these species remains unreliable, especially with the presence of southeastern bats. Diagnostic calls of all three species were observed, yet uncertainty of acoustical identification among the genus precludes certainty in individual species presence, even when visually validated. If northern long-eared bats do occur at COLO, it is in low abundances, with few individuals remaining through the winter.

Relative to WNS impacts, the widespread occurrence and moderate activity levels of tricolored bats is especially significant given their dramatic declines from the disease and potential for listing as an endangered species (USFWS 2022b). Fall and winter activity of tricolored bats are indicative of year-round occurrence, especially at Yorktown (COLO05D and COLO15D).

Considerations for future bat research should include further investigation of tricolored bats and their potential for recruitment at COLO. Although I did attempt to track two of the three tricolored bats captured, they were not a focal species in this study. Generally, I targeted areas of higher *Myotis* spp. activity attempting to document northern long-eared and Indiana bats, and inability to conduct capture surveys in 2020 hindered capture effort overall. The potential for listing tricolored bats as an endangered species increases the importance of their conservation, as well as the potential for their presence to impact park activities. Future research should also include continued effort to confirm the occurrence of little brown, northern long-eared, and Indiana bats by capture. Other future considerations for COLO include the potential occurrence of the Seminole bat and Rafinesque's big-eared bat, which did not occur during my surveys but do have potential to colonize to COLO (VAFWIS 2022a-c). The Seminole bat appears to be expanding its range northward coastally and was recently captured in the Delmarva Peninsula (True et al. 2021b, VAFWIS 2022c). Rafinesque's big-eared bats have been historically reported in the southeastern coast of Virginia and also have potential to occur at COLO (VAFWIS 2022a,b).

The forests and natural habitats preserved in COLO are important bat habitats, especially in the case of the Yorktown, where surroundings are becoming increasingly urbanized. Management practices should include consideration for bat species use of these diverse habitats. Forests are important for foraging and/or roosting of all bat species that occur. Open habitats and forest edges are also commonly utilized by big brown, eastern red, hoary, evening, silver-haired and Mexican free-tailed bats. Wetland, riparian, and pond habitats support southeastern bats and are important as water sources and for supporting insect prey. Standing snags should be retained where safe because many

species, including federally protected northern long-eared and Indiana bats, have shown preference for roosting in dead and decaying trees (Silvis et al. 2016). Prescribed fire aids in creating and improving such roosts, as well as reducing forest clutter, which is beneficial to foraging (Austen et al. 2020, Jorge et al. 2021b, Ford et al. 2016). Tree-clearing should be avoided if possible from May 15-August 15 to prevent take of federally-protected species during the maternity season. Management practices during the dormant season should be considerate of potential fall, spring, and winter occurrences of bats. Due to potential overwinter forest use by northern long-eared and tricolored bats, tree removal activity outside of the maternity season should include assessment of tree species and condition and investigation for evidence of recent or current bat use including: inspecting cavities for guano, searching for inhabiting bats, watching for emerging bats at dusk, or acoustic surveys at the removal site prior to action.

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Appendix A: Crosswalk Table for Habitat Classification

Table A-1. Crosswalk table for habitat classification, Colonial National Historical Park, Virginia.

U.S. National Vegetation Classification Habitat Class¹	General Habitat Class
Acidic Oak - Hickory Forest	Forest
Beaches	Open
Coastal Plain / Piedmont Small-Stream Floodplain Forest	Wetland
Coastal Plain Calcareous Seepage Swamp	Wetland
Coastal Plain Depression Wetland (Red Maple - Sweetgum - Willow Oak Type)	Wetland
Coastal Plain Depression Wetland (Swamp Tupelo Type)	Wetland
Coastal Plain Dry Calcareous Forest	Forest
Coastal Plain Loblolly Pine - Oak Forest	Forest
Coastal Plain Mesic Calcareous Ravine Forest	Forest
Cultural Meadow	Open
Dense Hardwood Regeneration	Forest
Disturbed Calcareous Forest	Forest
Disturbed Depressional Wetland	Wetland
Disturbed Seepage Swamp	Wetland
Disturbed Tidal Hardwood Swamp	Wetland
Golden Bamboo Shrubland	Open
Grass	Open
Industrial and Commercial Complexes	Open
Loblolly Pine Plantation	Forest
Mesic Mixed Hardwood Forest	Forest
Mixed Urban or Built-up Land	Open
Non-Riverine Saturated Forest	Forest
Other Urban or Built-up Land	Open
Piedmont / Coastal Plain Oak - Beech / Heath Forest	Forest
Piedmont / Low Elevation Mixed Oak / Heath Forest	Forest
Residential	Open
Salt Scrub	Open
Semipermanent Impoundment	Wetland
Successional Black Walnut Forest	Forest
Successional Mixed Scrub	Open
Successional Sweetgum Forest	Forest
Successional Tree-of-Heaven Forest	Forest
Successional Tuliptree - Loblolly Pine Forest	Forest

¹ U.S. National Vegetation Classification Habitat Class used in Patterson 2008

Table A-1 (continued). Crosswalk table for habitat classification, Colonial National Historical Park, Virginia.

U.S. National Vegetation Classification Habitat Class¹	General Habitat Class
Tidal Bald Cypress Forest / Woodland	Forest
Tidal Freshwater Marsh	Wetland
Tidal Mesohaline and Polyhaline Marsh	Wetland
Tidal Oligohaline Marsh	Wetland
Tidal Shrub Swamp (Wax Myrtle Type)	Wetland
Transportation, Communications, and Utilities	Open

¹ U.S. National Vegetation Classification Habitat Class used in Patterson 2008

Appendix B: Bat Species Activity Model Parameters

Big brown bat (*Eptesicus fuscus*; EPFU)

Table B-1 and Table B-2 show the activity model parameters for big brown bat.

Table B-1. Generalized linear mixed model (GLMM) parameter estimates of big brown bat (*Eptesicus fuscus*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Forest)	0.6520	0.2920	2.233	0.0256
Habitat – Open	-0.3575	0.1514	-2.361	0.0182
Habitat – Wetland	-0.2325	0.1140	-2.039	0.0415
Distance to Water	-0.000747	0.00064	-1.175	0.2401
Precipitation	-0.8953	0.086	-10.41	< 0.0001
Minimum Temperature	0.05594	0.0045	12.42	< 0.0001

Table B-2. Generalized additive model (GAM) parameter estimate of big brown bat (*Eptesicus fuscus*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Julian Date)	1.9980	0.0375	53.29	< 0.0001

Southeastern bat (*Myotis austroriparius*, MYAU)

Table B-3 and Table B-4 show the activity model parameters for little brown bat.

Table B-3. Generalized linear mixed model (GLMM) parameter estimates of southeastern bat (*Myotis austroriparius*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Forest)	1.0316	0.1050	9.821	< 0.0001
Habitat – Open	-0.9330	0.2747	-3.397	0.0007
Habitat – Wetland	1.5770	0.1365	11.550	< 0.0001
Precipitation	-0.6757	0.1564	-4.319	<0.0001

Table B-4. Generalized additive model (GAM) parameter estimate of southeastern bat (*Myotis austroriparius*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Julian Date)	1.5669	0.0630	24.87	< 0.0001

Little brown bat (*Myotis lucifugus*, MYLU)

Table B-5 and Table B-6 show the activity model parameters for little brown bat.

Table B-5. Generalized linear mixed model (GLMM) parameter estimates of little brown bat (*Myotis lucifugus*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Forest)	2.5558	0.1744	14.65	< 0.0001
Habitat – Open	0.2538	0.1552	1.636	0.1020
Habitat – Wetland	-0.7026	0.1101	-6.381	< 0.0001
Distance to Water	-0.0050	0.0006	-8.530	< 0.0001
Precipitation	-0.4933	0.1265	-3.899	< 0.0001
Minimum Temperature	0.0260	0.0031	8.398	< 0.0001

Table B-6. Generalized additive model (GAM) parameter estimate of little brown bat (*Myotis lucifugus*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Julian Date)	1.8280	0.0451	40.49	< 0.0001

Northern long-eared bat (*Myotis septentrionalis*, MYSE)

Table B-7 and Table B-8 show the activity model parameters for northern long-eared bat.

Table B-7. Generalized linear mixed model (GLMM) parameter estimates of northern long-eared bat (*Myotis septentrionalis*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Forest)	2.968	0.2416	12.285	< 0.0001
Habitat – Open	-0.4661	0.4950	-0.942	0.346
Habitat – Wetland	-0.1909	0.2855	-0.669	0.504
Distance to Water	-0.0058	0.0015	-4.009	< 0.0001

Table B-8. Generalized additive model (GAM) parameter estimate of northern long-eared bat (*Myotis septentrionalis*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Julian Date)	-1.4760	0.141	-10.48	< 0.0001

Indiana bat (*Myotis sodalis*, MYSO)

Table B-9 and Table B-10 show the activity model parameters for Indiana bat.

Table B-9. Generalized linear mixed model (GLMM) parameter estimates of Indiana bat (*Myotis sodalis*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Forest)	1.4722	0.3487	4.221	< 0.0001
Habitat – Open	-0.9704	0.4134	-2.348	0.0189
Habitat – Wetland	-1.1929	0.2403	-4.964	< 0.0001
Distance to Water	-0.0037	0.00081	-4.566	< 0.0001
Precipitation	-0.9960	0.5493	-1.813	0.0698
Minimum Temperature	0.0244	0.0066	3.674	0.0002

Table B-10. Generalized additive model (GAM) parameter estimate of Indiana bat (*Myotis sodalis*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Julian Date)	-0.8373	0.1066	-7.857	< 0.0001

Tricolored bat (*Perimyotis subflavus*, PESU)

Table B-11 and Table B-12 show the activity model parameters for tricolored bat.

Table B-11. Generalized linear mixed model (GLMM) parameter estimates of tricolored bat (*Perimyotis subflavus*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Forest)	0.5532	0.2435	2.272	0.0231
Habitat – Open	0.0634	0.1764	0.359	0.7193
Habitat – Wetland	-0.4565	0.1094	-4.172	< 0.0001
Distance to Water	-0.0052	0.0007	-7.543	< 0.0001
Precipitation	-1.0580	0.1631	-6.226	< 0.0001

Table B-12. Generalized additive model (GAM) parameter estimate of tricolored bat (*Perimyotis subflavus*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Julian Date)	1.1450	0.0522	21.95	< 0.0001

Eastern red bat (*Lasiurus borealis*, LABO)

Table B-13 and Table B-14 show the activity model parameters for eastern red bat.

Table B-13. Generalized linear mixed model (GLMM) parameter estimates of eastern red bat (*Lasiurus borealis*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Forest)	1.5758	0.2730	5.772	< 0.0001
Habitat – Open	-0.1125	0.1382	-0.814	0.4160
Habitat – Wetland	-0.7747	0.1093	-7.086	< 0.0001
Distance to Water	-0.0031	0.0005	-6.447	< 0.0001
Precipitation	-0.9151	0.0982	-9.322	< 0.0001
Minimum Temperature	0.0421	0.00457	9.212	< 0.0001

Table B-14. Generalized additive model (GAM) parameter estimate of eastern red bat (*Lasiurus borealis*) at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Julian Date)	1.4480	0.0391	36.98	< 0.0001

Hoary bat (*Lasiurus cinereus*, LACI)

Table B-15 and Table B-16 show the activity model parameters for hoary bat.

Table B-15. Generalized linear mixed model (GLMM) parameter estimates of hoary bat (*Lasiurus cinereus*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Forest)	0.9187	0.4188	2.194	0.0283
Habitat – Open	0.3786	0.6031	0.628	0.5301

Table B-15 (continued). Generalized linear mixed model (GLMM) parameter estimates of hoary bat (*Lasiurus cinereus*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
Habitat – Wetland	-1.0820	0.3284	-3.294	0.0010
Distance to Water	-0.0049	0.0018	-2.669	0.0076
Precipitation	-1.8100	0.4161	-4.350	< 0.0001
Minimum Temperature	0.0415	0.0070	5.904	< 0.0001

Table B-16. Generalized additive model (GAM) parameter estimate of hoary bat (*Lasiurus cinereus*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Julian Date)	-0.4513	0.1106	-4.081	< 0.0001

Silver-haired bat (*Lasionycteris noctivagans*, LANO)

Table B-17 and Table B-18 show the activity model parameters for silver-haired bat.

Table B-17. Generalized linear mixed model (GLMM) parameter estimates of silver-haired bat (*Lasionycteris noctivagans*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Forest)	2.5310	0.4231	5.984	< 0.0001
Habitat – Open	1.3530	0.5984	2.261	0.0237
Habitat – Wetland	2.0992	0.3293	6.374	< 0.0001
Distance to Water	-0.0151	0.0032	-4.734	< 0.0001
Precipitation	0.5470	0.2306	2.372	0.0177
Minimum Temperature	0.0234	0.0091	2.566	0.0103

Table C-18. Generalized additive model (GAM) parameter estimate of silver-haired bat (*Lasionycteris noctivagans*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Julian Date)	-1.5450	0.1354	-11.42	< 0.0001

Evening bat (*Nycticeius humeralis*, NYHU)

Table B-19 and Table B-20 show the activity model parameters for evening bat.

Table B-19. Generalized linear mixed model (GLMM) parameter estimates of evening bat (*Nycticeius humeralis*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Forest)	2.4100	0.2618	9.207	< 0.0001
Habitat – Open	0.0971	0.1684	0.577	0.5642
Habitat – Wetland	-0.6211	0.1291	-4.811	< 0.0001
Distance to Water	-0.00263	0.0007	-3.750	0.0018
Precipitation	-0.9107	0.1232	-7.393	< 0.0001
Minimum Temperature	0.0324	0.0041	7.906	< 0.0001

Table B-20. Generalized additive model (GAM) parameter estimate of evening bat (*Nycticeius humeralis*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Julian Date)	-1.6120	0.0540	29.87	< 0.0001

Mexican Free-tailed bat (*Tadarida brasiliensis*, TABR)

Table B-21 and Table B-22 show the activity model parameters for Mexican free-tailed bat.

Table B-21. Generalized linear mixed model (GLMM) parameter estimates of Mexican free-tailed bat (*Tadarida brasiliensis*) activity at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Forest)	2.1770	0.3057	7.122	< 0.0001
Habitat – Open	0.7312	0.3235	2.261	0.0238
Habitat – Wetland	-1.2530	0.2402	-5.216	< 0.0001
Distance to Water	-0.0088	0.0019	-4.519	0.0018
Precipitation	-1.5480	0.2867	-5.398	< 0.0001
Minimum Temperature	0.0226	0.0054	4.140	< 0.0001

Table B-22. Generalized additive model (GAM) parameter estimate of Mexican free-tailed bat (*Tadarida brasiliensis*) at Colonial National Historical Park, Virginia.

Parameter	Estimate	Standard Error	Z Value	P-Value
(Intercept – Julian Date)	-0.1068	0.0964	-1.108	0.027

Appendix C: Capture Survey Sites and Net Arrangements

Table C-1. Bat capture survey sites and net arrangements, Colonial National Historical Park, Virginia.

Date	Site	Description	# of Nets	Placement
2/8/2019	COLO-N01	Mixed forest road adjacent open field and stream	2	Triple high 12m across road; double 9m across trail
3/12/2019	COLO-N02	Wetland stream	2	Triple high 12m across stream, triple high 9m adjacent stream
3/14/2019	COLO-N02	Wetland stream	2	Triple high 12m across stream, double high 9m across road
3/15/2019	COLO-N01	Mixed forest road adjacent open field and stream	3	Triple high 12m across road, double high 6m across trail, single high 6m across stream
3/28/2019	COLO-N01	Mixed forest roads adjacent open field and stream	1	Triple high 12m across road
3/29/2019	COLO-N03	Mixed forest trail	1	Triple high 9m across trail
4/10/2019	COLO-N01	Mixed forest road adjacent open field and stream	2	Triple high 12m across road, triple high 9m in open field
4/11/2019	COLO-N04	Mixed forest road	2	Triple high 12m and triple high 9m across road
4/12/2019	COLO-N02	Wetland stream	2	Triple high 12m across stream, triple high 9m across road
7/9/2019	COLO-N06	Mixed forest road adjacent open field	2	Triple high 6m and double high 6m across road
7/10/2019	COLO-N02	Wetland stream	2	Triple high 12m across stream, triple high 9m across road
8/14/2019	COLO-N05	Mixed forest stream	1	Triple high 12m across stream
8/15/2019	COLO-N05	Mixed forest stream	1	Triple high 12m across stream
10/1/2019	COLO-N05	Mixed forest stream	2	Triple high 18m across stream, double high 9m across road
10/3/2019	COLO-N01	Mixed forest road adjacent open field and stream	2	Triple high 12m and triple high 9m across road
10/15/2019	COLO-N05	Mixed forest stream	1	Triple high 18m across stream
3/9/2020	COLO-N02	Mixed forest road adjacent open field and stream	1	Triple high 9m across road
3/10/2020	COLO-N05	Mixed forest stream	1	Triple high 18m across stream
3/11/2020	COLO-N01	Mixed forest road adjacent open field and stream	1	Triple high 12m across road
3/12/2020	COLO-N06	Mixed forest road adjacent open field	1	Triple high 12m across road
10/12/2021	COLO-N03	Mixed forest trail	2	Double high 9m and double high 6m across road
10/13/2021	COLO-N05	Mixed forest stream	2	Triple high 9m across road, double high 12m across stream

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