

North American Tree Bat (Genera: *Lasiurus*, *Lasionycteris*) Migration on the Mid-Atlantic Coast—Implications and Discussion for Current and Future Offshore Wind Development

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ABSTRACT

In eastern North America, “tree bats” (Genera: *Lasiurus* and *Lasionycteris*) are highly susceptible to collisions with wind energy turbines and are known to fly offshore during migration. This raises concern about ongoing expansion of offshore wind-energy development off the Atlantic Coast. Season, atmospheric conditions, and site-level characteristics such as local habitat features (e.g., forest coverage) have been shown to influence wind turbine collision rates by bats onshore, and similar features may be related to risk offshore. In response to rapidly developing offshore wind energy development, I assessed the factors affecting coastal and offshore presence of tree bats. I continuously gathered tree bat nightly occurrence data using stationary acoustic recorders on five structures (four lighthouses on barrier islands and one light tower offshore) off the coast of Virginia, USA, across all seasons, 2012–2019. I used generalized additive models to describe nightly tree bat occurrence in relation to multiple factors. I found that sites either indicated maternity or migratory patterns in their seasonal occurrence pattern that were associated with local roosting resources (i.e., presence of forest). Across all sites, nightly occurrence was negatively related to wind speed and positively related to temperature and visibility. Using predictive performance metrics, I concluded that the model was highly predictive for the Virginia coast. My findings were consistent with other studies—tree bat occurrence probability and presumed mortality risk to offshore wind-energy collisions is highest on nights with low wind speed, high temperature and visibility during spring and fall. The high predictive model performance I observed provides a basis for which managers, using a similar monitoring and modeling regime, could develop an effective curtailment-based mitigation strategy.

Although information at fixed points is helpful for managing specific sites, large questions remain on certain aspects of tree bat migration, in part because direct evidence (i.e., tracking of individuals) has been difficult to obtain so far. For instance, patterns in fall behavior such as the timing of migration events, the existence of migratory pathways, consistencies in the direction of travel, the drivers of over-water flight, and the activity states of residents (or bats in stopover) remain unstudied in the mid-Atlantic. The recently established Motus Wildlife Tracking System, an array of ground-based receiver stations, provides a new technique to track individual bats via the ability to detect course-scale movement paths of attached very high frequency radio-tags. To reveal patterns in migration, and to understand drivers of over-water flight, I captured and radio-tagged 115 eastern red bats (*Lasiurus borealis*) and subsequently tracked their movements. For the bats with evidence of large movements, most traveled in a southwesterly direction whereby paths were often oriented interior toward the continental landmass rather than being oriented along the coastline. This observation challenges earlier held beliefs that bats closely follow linear landscape features, such as the coast, when migrating. I documented bats traveling across wide sections of the Chesapeake and Delaware bays confirming the species’ ability to travel across large water bodies. This behavior typically occurred in the early hours of the night and during favorable flying conditions such as low wind speeds, warm temperatures, and/or during sudden increases in temperature associated with the

passage of cold fronts. For bats engaging in site residency through the fall, the proportion of night-hours in which bats were in a resting state (and possibly torpor), increased with colder temperatures and the progression of the fall season. My study demonstrated that bats may be at risk to offshore wind turbine collisions off the mid-Atlantic, but that this risk might be minimal if most bats are migrating toward the interior landscape rather than following the coast. Nonetheless, if flight over large water bodies such as Chesapeake and Delaware bays is a viable proxy for over-ocean flight, then collision risk at offshore wind turbines may be somewhat linked to atmospheric, seasonal timing, or other effects, and therefore some level of predictable and manageable with mitigations options such as smart curtailment.

North American Tree Bat (Genera: *Lasiurus*, *Lasionycteris*) Migration on the Mid-Atlantic Coast—Implications and Discussion for Current and Future Offshore Wind Development

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GENERAL AUDIENCE ABSTRACT

In eastern North America on the mid-Atlantic and Northeast coasts, a group of bat species named “tree bats” engage in seasonal migrations—generally shifting north in spring and south in fall. On the East coast, it is known that eastern red bats and silver-haired bats will occasionally fly over the ocean during these periods. Although this behavior is somewhat hard to explain due to their reliance on trees for day-time roosting, it raises concern conservation concerns due to the current and future rapid development of offshore wind energy turbines. This is compounded by the fact that collision rates with turbines are high for this species group in general and highest in the fall migratory season. The fall period is also when bats may be attracted to tall structures such as turbines and when most offshore flight happens. Nevertheless, bats are sensitive to atmospheric conditions such as temperature and wind speed, and other factors influence their propensity to fly (and be at risk to turbine strikes). So, understanding these drivers may aid in understanding the conditions that present the highest risk to strike at offshore wind turbines.

In response to rapid offshore wind development in the Atlantic, I recorded bats in coastal Virginia, USA from 2012–2019, using acoustic monitors—devices that collect the echolocation vocalizations of bats. I found that tree bat visitation offshore or on barrier islands was associated with wind speed, temperature, visibility, and seasonality. Using statistical modeling, I developed a predictive tool to assess occurrence probabilities at varying levels of wind speed, temperature, and seasonality. Probability of occurrence and therefore assumed risk to collision was highest on high temperature and visibility nights, low wind speed nights, and during the spring and fall seasons. Therefore, I suggest a similar modeling regime could be used to predict the occurrence of bats at offshore wind sites to inform potential mitigation efforts.

Next, I attempted to answer broader questions about tree bat migratory behavior such as attempting to identify migratory pathways throughout the mid-Atlantic. The Motus Wildlife Tracking System gives researchers the ability to directly track individuals over long-distances with radio-transmitters and ground-based receiver stations. Using Motus, I captured and radio-tagged >100 tree bats, which were of majority eastern red bats and tracked their movements throughout the mid-Atlantic region. I found that movements were not oriented along the coastline, which challenged previously held beliefs that bats use the coast during migration. Tree bats also traversed large bodies of water, the Chesapeake and Delaware bays, confirming the ability for this group to fly over-water. Through statistical modeling, I found that these over-water bouts were early in the night and related to advantageous flying conditions such as low wind speeds, high temperatures, and during periods of sudden temperature increase (which could be linked to the passage of cold weather fronts). Offshore collision risk to tree bats may be somewhat minimal if most bats orient inland, rather than coastal for their migration movement. Nevertheless, for those bats that do fly over the ocean, if crossing large waterbodies is a viable proxy for over-ocean movement, then this behavior is linked to multiple factors, of which can be used to predict occurrences and even potentially predict and manage risk to collision.

Acknowledgements

It has been a quite an experience spending the past almost 3 years here at Virginia Tech. I have been surrounded by truly amazing people that helped me from the moment I loaded up the car to move to a state that I had never been to, to the point now, where I am putting these final marks on this thesis. Assistance from folks along the way came in many forms, and was certainly not limited to, original conceptualization for the project, physical help in the field, logistics behind the scenes, financial support for the project, emotional support, and all the teaching moments that have advanced my knowledge base and skillset as a wildlife biologist and statistician.

The original conceptualization for this project came primarily from Rick Reynolds at Virginia Department of Wildlife Resources whom had the foresight in 2011 to begin deploying acoustic detectors on barrier islands and offshore structures and more importantly, conceptualized the Motus section of the project. Moreover, it was Rick, that acquired nearly all the funding for the project via grants from the Virginia Department of Wildlife Resources and the U.S. Fish and Wildlife Service. Thank you so much, Rick, for putting trust in me to see this project to the finish line. In addition, I want to thank Ruth Boettcher for being an integral part in the operational management of the project and Jeremy Tarwater for his nautical skills navigating the team to acoustic detectors on the barrier islands.

Before I came to Virginia, aspects of my project were already underway and I need to thank Elaine Barr, Andrew Kniewski, Sara Sweeten, Katie Gorman, and Mike St. Germain for deploying, maintaining, and introducing me to the technical logistics of the four original Motus towers on Coastal Plain of Virginia. I also want to thank the Carnegie Museum of Natural History and Bird Studies Canada for hosting the Motus workshop that was vital for understanding the innerworkings of Motus. I continually bombarded Alison Fettermen, Jon Rice, and Todd Alleger with Motus questions after the workshop. In addition, thank you, Pam Loring, for donating tower parts, antennas, and cables for two additional deployments that were not originally planned.

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As this project progressed, it garnered some attention from other biologists who were also interested in the issue at hand. Naturally, some additional funding came through either in the form of additional grants or equipment. I want to thank Mona Khalil of the U.S. Geological Survey who helped contribute funding to underwrite my travel. In addition, a few other individuals purchased Motus tags from my use. MacKenzie Hall secured funding to tag extra tree bats in New Jersey which were added to our data pool. In addition, Cynthia Corsair of the U.S. Fish and Wildlife Service purchased additional tags with intention of tagging additional bats to

the north in Rhode Island. I made it up to Rhode Island which could not have happened if it were not for the help and assistance of Charlie Brown and his team at the Rhode Island Division of Fish and Wildlife. Thank you all.

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One must be surrounded by people that support them on a personal level. I want to thank the Fish and Wildlife Graduate Student Association (FIWGSA) for always being inclusive and ready to accept anyone no matter the background. When I first moved to Virginia, I knew one person (Dr. Mark Ford). I quickly made friends and those friendships I hope will last for years to come. Specifically, I want to shout out Hila Taylor, Katie Gorman, Nick Kalen, the rest of the Ford lab, Jon Low, Jeremy Jenrette, Brendan Shae, the entire Bachelorette crew, the bear trailer crew, and everyone else that was always down to grab a beer and just hang out for a bit. Moments with friends during this time in grad school will forever be seared into my memory. Last, I would not be alive, nor would I be the person I am today without the guidance, support, and love that I have received from all my family members and friends from back home on the Prairie. Thank you again to each one of you that made this all possible. It is very much appreciated.

To close this out, I have one last person to thank and that is of Dr. W. Mark Ford, who took a chance on me in 2019 as a full-time technician. I am told he asked Katie Gorman “he seems normal, right?” Little did he know I would be a somewhat pain-in-the-neck grad student due to my distracting addition of a separate degree and in accepting a part-time position before I graduated. I truly have never been more proud to work for, and with, an absolute badass scientist. Beyond his accolades, Dr. Ford always supported his students and even pretends to like us. It was refreshing to know a raconteur that I was actual friends with who I talked football with, enjoys a New Jersey bagel as much as I do, and effectively taught me how to hunt and quarter deer (with support Marcello Jorge and Emily Thorne of course). There was never a dull moment, particularly during fieldwork where Dr. Ford helped me discover my love of the simple things in life: Food Lion seltzer water, the State of Delaware, and drinking beers in a seedy motel gazebo in North Florida. Thank you, Mark, I really appreciate everything you have done for me.

Table of Contents

List of Figures	viii
List of Tables	xi
Preface.....	xii
Chapter 1: General Introduction	1
Figures.....	11
Literature Cited.....	12
Chapter 2: Monitoring and Modeling Tree Bat (Genera: <i>Lasiurus</i> , <i>Lasionycteris</i>) Occurrence Using Acoustics on Structures Off the Mid-Atlantic Coast—Implications for Offshore Wind Development.....	16
Abstract.....	16
Introduction.....	17
Materials and Methods.....	21
Study area.....	21
Acoustic data.....	21
Atmospheric conditions and other variables.....	22
Presentation of data and EDA.....	23
Modeling.....	24
Results.....	26
Discussion.....	29
Conclusions.....	33
Figures.....	36
Tables.....	42
Literature Cited.....	47
Chapter 3: Fall Migration, Oceanic Movement, and Site Residency Patterns of Migratory Bats on the Mid-Atlantic Coast with Emphasis on Eastern Red Bats (<i>Lasiurus borealis</i>).....	52
Abstract.....	52
Introduction.....	53
Methods.....	59
Study Area	59
Motus Tower Deployment, Mist-Netting, Nano-Tagging	61
Analysis.....	63
Overall patterns.....	63
Over-water behavior	64
Site residency daily activity patterns	67
Results.....	69
Overall patterns.....	69
Over-water behavior	72
Site residency daily activity patterns	73
Discussion.....	74
Figures.....	83
Tables.....	99
Literature Cited.....	103
Appendix A3-1.....	108

List of Figures

Figure 1-1. Offshore wind-energy lease areas (orange shapes) off the Northeast and Mid-Atlantic coast as of Aug 2, 2021. Most projects have gained site control and are applying for Federal permits in the near future (or have already) and are awaiting regulatory approval to begin construction (https://www.boem.gov/renewable-energy/mapping-and-data/renewable-energy-gis-data ; Accessed Oct 2, 2021).....	11
Figure 2-1. Acoustic detector sites (black points) on barrier islands and a light tower off the Eastern Shore of Virginia, USA, 2012–2019. Weather data was obtained from the nearest available National Oceanic and Atmospheric Administration (NOAA) weather stations (starred points) from the National Climatic Data Center (NCDC) online tool (Climate data online; https://www.ncdc.noaa.gov/cdo-web/ ; Accessed 2019-11-09).	36
Figure 2-2. Lighthouses and structures serving as infrastructure for acoustic detector deployment on Eastern Shore of Virginia, USA, 2012–2019. Acoustic detector microphone locations are indicated by the red circles. Locations are (a) Assateague Island (Assateague Lighthouse); (b) Cedar Island (inactive United States Coast Guard station); (c) Hog Island (inactive United States Coast Guard station); (d) Silver Beach (offshore navigation light structure), and (e) Smith Island (Cape Charles Lighthouse).	37
Figure 2-3. Site specific acoustic recording effort by ordinal date (day of the year). Effort (number of years monitored) is indicated as a heatmap of site vs. ordinal date such that lighter shades indicate lower effort (min = 1 year) and darker shades indicate higher effort (max = 8 years). Monitoring was conducted on the Eastern Shore of Virginia, USA, 2012-2019.....	38
Figure 2-4. Raw occurrence data (black points: occurrence, non-occurrence [1, 0]) from acoustic detectors deployed on the Eastern Shore of Virginia, USA, 2012-2019. Data is grouped by site for all years of data collection stacked on a 1–366 ordinal date calendar. The raw data is shown as semi-transparent to visualize the occurrence density across years. The general relationship of tree bat nightly occurrence vs ordinal date is represented by a 20-day two-sided moving average proportion of nightly occurrence (black line) and smoothed average using a generalized additive model (GAM) spline (blue line). Each site is labeled as containing viable day-roosting habitat (grey square) or limited day-roosting habitat (black square).....	39
Figure 2-5. Visualizations of all smooth effects, $f(x)$, in the final model fit using acoustic data off the Eastern Shore of Virginia, USA, 2012–2019. The fit (solid line) and 95% confidence intervals for the fit (black dotted line) are displayed. Smooths, $f(x)$, can be interpreted as the effect of the variable, x . Nightly occurrence probability is positively associated with larger smooth values along the range the of variable. The final model used smooth effects of nightly means of temperature (a), wind speed (b) visibility (c), and the ordinal date (c). The shape of the smooth effect was separated by roost availability, by limited (d) or viable (e).....	40
Figure 2-6. Confusion matrix of final model predictions compared to true values of test data collected off the Eastern Shore of Virginia, USA, 2012–2019. We used an 85% subset of the data to train the model ($n = 4,134$) and a 15% subset to test the model ($n = 730$). Values and percentages are displayed as true positives (top left), false positives (top right), false negatives (bottom right) and true negatives (bottom right). Shading indicates more frequency of any categorization—darker indicating more weight.....	41
Figure 3-1. A Motus tower located on the Eastern Shore of Virginia at the Virginia Tech Agriculture Research and Extension Center (VT AREC) property (37.59, -75.82). It was deployed in 2017 and equipped with three 9-element yogi antennas, a solar panel, and computational components (bin). Motus towers constantly scan and “listen” for (i.e., are tuned to	

a frequency) nanotags (coded very high frequency [VHF] transmitters) emitting a 166.38 MHz frequency registered to Motus (Taylor et al. 2017). 83

Figure 3-2. Motus (motus.org; [Taylor et al. 2017]) towers (yellow points) in the Delmarva peninsula and surrounding mid-Atlantic Coastal Plain active as of October 5, 2021. The Motus towers that I (or other Virginia Tech users) deployed are circled in blue. Motus towers are typically equipped with 2–4 5- or 9-element yagi antennas (black lines; see Figure 3-1) which are aimed at a certain bearing (black lines; 0–360°) and have a maximum detection distance of ~12 km (red points). If displayed towers do not have a bearing visualized with a black line it is equipped with an omnidirectional antenna. 84

Figure 3-3. A “nanotag” (top left, NTQB2-2, Lotek Wireless, www.lotek.com) is a uniquely coded very high frequency (VHF) transmitter tuned to the 166.38 MHz frequency of the Motus Wildlife Tracking System (motus.org; Taylor et al. 2017). I deployed nanotags by gluing the transmitter to the scapulae portion of tree bats (top right) in the fall periods of 2019 and 2021. I provide an example of a fully tagged eastern red bat (bottom; *Lasiurus borealis*) ready for release. 86

Figure 3-4. A flow chart of a typical two-state hidden Markov model (HMM) in ecology. In HMMs, an ecological time series $X_1 \dots X_T$ take on discrete latent (or “hidden”) states (i.e. “state 1” and “state 2”) which are directly unobservable at discrete time steps from $t = 1$ to $t = T$. State switching is determined by a 2×2 transition matrix, γ , such that it is a Markov process in which $\gamma_{i,j} = \Pr(X_{t+1} = j \mid X_t = i)$. Latent states give rise to a time series of observations in the data, $Y_1 \dots Y_T$. These observations are independent draws from a greater probability distribution such that $Y_t = f(y_t \mid X_t = N)$ for $N \in \{1, 2\}$. In the context of bats engaging in periods of site residency, which I tagged in the fall periods of 2019 and 2021 on the mid-Atlantic coast, bats are in discrete states of “rest” and “active” as part of the ecological process time series X , above, but is latent (i.e., unobservable directly). The transition matrix was regressed against and therefore mediated by a sinusoidally fluctuating time since sunset to mimic the diurnal and nocturnal patterns of active and rest states. The only observable time series, however, is Y , the hourly signal strength standard deviations at Motus towers. 87

Figure 3-5. Locations and dates of active bat netting and deployment of nanotags on tree bats (*Lasiurus* and *Lasionycteris*) in southern New Jersey and the Delmarva Peninsula in the late summer to early fall period of August 1 to October 15 in 2019 (left) and 2021 (right). Generally, over the two years I began netting efforts in southern New Jersey and continued down the coast to finish on the Eastern Shore of Virginia. Delaware was the last locality sampled in 2019. 88

Figure 3-6. The sex ratio of tree bats captured and tagged throughout southern New Jersey and the Delmarva Peninsula August–October 2019 and 2021. 89

Figure 3-7. The bearings of migrating bats from their point of origin to their final detected destination based on detections off towers in the Motus wildlife tracking system collected on eastern red bats in the mid-Atlantic during fall of 2019 and 2021. This is displayed as an angular (0–360°) histogram which shows the frequency of bearings in histogram bins (grey boxes). The raw data (arrows) are displayed showing the flight bearings. 90

Figure 3-8. Minimum site residency times related to the month tagged from Motus telemetry data on eastern red bats in the mid-Atlantic in the fall of 2019 and 2021. Minimum site residency time was generally longer for bats tagged in August than tagged in September. Bats tagged in October are not displayed as they could be misleading due to low sample sizes. 91

Figure 3-9. The density of long-distance migration events (blue curve) and over-water flights (green curve) and as they related to time of the year from Motus telemetry data on eastern red

bats in the mid-Atlantic in fall of 2019 and 2021. Over-water forays distinctly peaked in late August to early September while long distance migration events were sustained from late August to early October. These curves should be interpreted with caution because tagging events were not evenly distributed through this period, so some bias may be present..... 92

Figure 3-10. The migratory route of tagged bat #34845 (adult female eastern red bat [*Lasiurus borealis*]) displaying an over-water flight behavior. This map connects the coarse locations of individuals by connecting detections at Motus tower by line segmented arrows depicting the direction of travel which are colored by the time lag between detections (hours). The timeline of detections is displayed to assess the timing in these movements. This bat was tagged on September 10 on the Eastern Shore of Virginia and moved across the Chesapeake Bay in less than 3 hours on October 4, 2019..... 93

Figure 3-11. Selected marginal effects of the use-availability model of over-water flight given atmospheric conditions to visualize the effect of significant variables. Marginal effects are predictions of the relative probability of over-water flight of bats based on a single variable [each above] while holding all other variables at their means) The prediction estimate is displayed (black line) along with the 95% prediction interval (grey band)..... 94

Figure 3-12. The standard deviation of signal strength on an hourly basis individual bats chosen for hidden Markov modeling from Motus telemetry data on eastern red bats collected in the fall of 2019 and 2021. Boxplots of signal strength standard deviations are separated by hour of the day (0-23) and shaded by night (moon symbol) or day (sun symbol). Night and day are separated by dotted lines as the mean sunrise and sunset time over the of the duration of the study. Generally, the hourly standard deviation of signal strengths are larger for bats actively flying (i.e. in an “active” state) than those roosting, in torpor, or otherwise stationary (i.e. a “rest” state). This is evident as when most bats were (most likely) in rest (daylight hours) there was generally low signal strength standard deviations. When most bats were active (night hours) there was generally high signal strength standard deviations. There is some overlap, however indicating that bats could be in a rest state during the night or in an active state during the day (pre-sunset times)..... 95

Figure 3-13. A) The predicted state (rest [1], active [2]) of individual bats (n = 4; pink, green, orange, and blue points) from the hidden Markov model (HMMs) during night hours on hourly intervals versus date on a single calendar year from Motus telemetry data collected on eastern red bats in the fall of 2019 and 2021. Points are given a small amount of random variation for aid in visualization. A logistic regression line (black) shows the general trend from active to resting states as fall dates progress. **B)** A magnified version of the above showing Motus tag ID #34805 which undergoes a distinct period (between dotted lines) of rest states as temperature generally as temperatures (color bar) fall below 10°C in early November. Points are given a small amount of random variation for aid in visualization. A generalized additive logistic regression line (black) shows the smoothed proportion of active states from high to low (during the period between the dotted lines) and back to high as dates progress..... 97

Figure 3-14. The predicted state (rest [1], active [2]) of individual bats (n = 4; pink, green, orange, and blue points) from the hidden Markov models (HMMs) formulated from Motus telemetry data on eastern red bats on the Delmarva Peninsula in the fall seasons of 2019 and 2021. Individual points states at hourly intervals during the night versus atmospheric conditions (temperature and wind speed; top row) and hours after sunset (bottom left). Points are given a small amount of random variation for aid in visualization. Logistic regression lines (black) show the general trend in the state versus the variable of interest. 98

List of Tables

Table 2-1. A priori generalized additive models to evaluate the shape of the effect of seasonality (ordinal date) of tree bat occurrence at offshore/barrier island sites, Eastern Shore of Virginia, USA, 2012–2019. Three models are presented—one that only considers the ordinal date, one that considers local roosting availability, and one that considers site specifics 42

Table 2-2. 90%, 95%, and 99% quantiles representing the proportion of nights with tree bat occurrence under certain conditions of wind speed, temperature, and/or date ranges using acoustic data collected on the Eastern Shore of Virginia, USA, 2012–2019. 43

Table 2-3. A priori models ranked by Bayesian information criterion (BIC) from acoustic data collected off the Eastern Shore of Virginia, USA, 2012–2019. Displayed are the model names and numbers as referenced in Table 2-1, approximate degrees of freedom, $-\log(\text{Likelihood})$, BIC, and ΔBIC 44

Table 2-4. Top five competing post-hoc models ranked by Bayesian information criterion (BIC) from acoustic data collected off the Eastern Shore of Virginia, USA, 2012–2019. The model selection dredge contained all possible combinations of site (factor, 5 levels), smooth effects, $f(x)$, of ordinal date (1–365; one for each roost availability type [viable, limited]), and smooth effects of nightly mean pressure (mmHg), temperature (C), visibility (0-10 mi), and wind speed (m/s), total precipitation duration (hours), and change in pressure from the previous night. N/I indicates no inclusion in that particular model. We displayed the model degrees of freedom (df), BIC and ΔBIC 45

Table 2-5. Beta parameters names, estimates, standard errors, and p-values for site-specific intercept modifiers in the final model fit using acoustic data off the Eastern Shore of Virginia, USA, 2012–2019. Estimates of β_1 – β_4 should be added to the intercept (β_0) to interpret the intercept modifying effect of the specific locality correctly. 46

Table 3-1. The locations and species of tree bats (*Lasiurus*, *Lasionycteris*) captured and tagged in southern New Jersey, Delaware, and the Eastern Shore of Virginia (Figure 3-4) in the fall periods (August–October) of 2019 and 2021. In total we captured 116 eastern red bats (*Lasiurus borealis*), 2 silver-haired bats (*Lasionycteris noctivagans*), and 3 Seminole bats (*Lasiurus seminolus*). 99

Table 3-2. The variables, explanations, and expected associations used in modeling the relative probability of over-water flight by eastern red bats in the mid-Atlantic using data collected in southern New Jersey and the Delmarva Peninsula in the fall of 2019 and 2021..... 100

Table 3-3. Model selection table resulting from the dredge (comparison of all possible additive model combinations) using data collected from over-water movements by eastern red bats in the mid-Atlantic in the fall of 2019 and 2021. The first eleven columns represent β coefficient estimates in the logistic models as described in Table 3-2, of which each row is a unique model. Displayed are the competing models within $2 \Delta\text{AIC}_c$ points. I displayed the model degrees of freedom (df), negative log of the Likelihood ($-\log(\mathcal{L})$), AIC_c , and ΔAIC_c . I used R package *MuMIn* for all modeling and calculations which defines AIC_c as $-\log(\mathcal{L}) + 2K(K+1)/(n-K-1)$, where K is the number of parameters and n is the sample size (Barton 2020). 101

Table 3-4. The parameters, estimates, standard error, Z-statistic and approximate significance (p-value) of the top approximating model. The model was a use-availability logistic regression model (binary generalized linear mixed model) formulated from data on eastern red bats exhibiting over-water flight behaviors across the Chesapeake or Delaware Bays in the fall seasons of 2019 and 2021. 102

Preface

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Chapter 1: General Introduction

Interest in North American microbat (Family: Vespertilionidae) conservation has increased steadily since the 1960s and 1970s with the passage of the Endangered Species Act (ESA; 16 U.S.C. §§ 1531–1540) and listing of Indiana bats (*Myotis sodalis*) and grey bats (*Myotis grisecens*) as endangered. In more recent years, bat conservation concerns in eastern North America were exacerbated following the onset of White-nose Syndrome (WNS), a disease estimated to have killed millions of cave-hibernating bats since its discovery in 2006 (Jachowski et al. 2014; Frick et al. 2015). WNS has led to up to 99% reductions in population estimates for some species of *Myotis* (Blehert et al. 2009; Turner et al. 2011; Frick et al. 2015). Whereas WNS is primarily a threat to cave-hibernating bats (“cave bats”), collisions with wind-energy turbines at renewable energy facilities are a simultaneously expanding mortality concern to migratory “tree bats” (Genera: *Lasiurus* and *Lasionycteris*) in North America (Arnett et al. 2008b; Hein and Schirmacher 2016; Thompson et al. 2017). It is estimated that 500,000 bats are killed annually in the United States and Canada at wind-energy facilities (Arnett and Baerwald 2013; Hayes 2013; Smallwood 2013). Three species typically represent the large majority of bat mortalities at wind turbine facilities in the eastern United States—eastern red bats (*Lasiurus borealis*), hoary bats (*Lasiurus cinereus*), and silver-haired bats (*Lasionycteris noctivagans*—Kunz et al. 2007; Hein and Schirmacher 2016; Thompson et al. 2017).

To understand this, it is necessary to examine the phenological behavior of these species. In winter, tree bats do not hibernate in caves but rather day-roost in trees year-round (Cryan 2003; Mormann and Robbins 2007; Jorge et al. 2020). Therefore, in temperate regions North America, as a life history strategy, they are known to restrict their distribution to southern latitudes to overwinter (Cryan 2003; Wieringa et al. 2021). In the spring, they expand their

distributions to the north, establish maternity areas in summer to raise young, and then restrict their distribution again in the fall (Cryan 2003; Johnson et al. 2011b; Baerwald et al. 2014). To accomplish this, it is understood that tree bats, particularly at the northern edge of these seasonally fluctuating range limits, will migrate considerable distances during the spring and fall migratory periods (Perry 2018; Fleming 2019; Wieringa et al. 2021).

The tree bat mortality rate at wind-energy facilities (e.g., fatalities per megawatt) in eastern North America follows a seasonal pattern that mirrors the migratory habits of these species. The wind turbine collision rate is negligible in winter, elevates in spring, reduces slightly in summer, and dramatically peaks during late summer through fall (Kunz et al. 2007; Arnett et al. 2008; Thompson et al. 2017). Proximately, mortality at wind turbines has been attributed both to direct collisions (Horn et al. 2008; Grodsky et al. 2011) and barotrauma, the fatal damage to lung tissue due to pressure changes near the rotor zone (Baerwald et al. 2008, but see Schirmacher et al. 2018 and Lawson et al. 2020). The ultimate reasons for this seasonal pattern in fatalities, however, are not well understood, though evidence points toward a number of possibly interacting and additive, causes.

Cryan (2008) proposed that tree bats are adapted for selecting tall trees on the landscape for roosting, but also for mating sites. Since these species are generally solitary and wide ranging, it is hypothesized that males cluster upon and attempt to defend prominent landscape features, such as large trees. The females then, may orient toward these sites to find male suitors. This combination of behaviors may be indicative of a combination of resource defense polygyny and lekking strategies (Cryan 2008). For example, hoary bats have been seen in “rut”, gathering in large aggregations around cottonwood trees where males were observed fighting (Hall 1946), and female tree bats are known to mate with several males (Cryan 2008; Ammerman et al. 2019).

In addition, *Lasiurines* display characteristics associated with lekking such as spatial segregations often seen between male and female groups in fall (Cryan 2003; Perry et al. 2010) and sexual dimorphism in their size and coat color (Cryan 2008). Hence, tree bats may be attracted to tall structures mistaken for tall trees due to mating. Somewhat unique to tree bats is that a large proportion of juveniles are sexually mature in their first fall mating season (Cryan et al. 2012), whereby juveniles are subject to the same behaviors elicited in adults. Tree bats appear generally attracted to tall anthropogenic structures in general as indicated by their disproportionately high activity rates near them (Jameson and Willis 2014). Specifically at wind turbines, a concentration of investigative behaviors in fall seems to support the attraction hypothesis and its dependence on late summer to fall (Goldenberg et al. 2021).

Moreover, as the late summer to fall period progresses, the population density of tree bats increases as their distributions condense to the south (Cryan 2003). These populations are larger in fall relative to spring due to recent summer recruitment and volancy of summer juveniles (Nocera et al. 2019). In addition, an increase in space use in fall due to migration in general, to seek mates, or both, may also coincidentally increase mortality rates in fall (Cryan and Brown 2007; Cryan and Barclay 2009). These combined effects may coincidentally increase the collision rate as a larger proportion of the population are in proximity to turbine blades at more southerly latitudes, the population is larger, and there are heightened and more expanded movement patterns (Cryan and Barclay 2009). In all, some combination of mating behavior, fall explicit attraction to turbines, population density, and erratic movement may explain the fall specific peak mortality seen in these North American tree bats.

On the Atlantic Coast, Cryan (2003) noted a coastal concentration of migrating bats in fall, specifically of eastern red bats. Cryan and Brown (2007) speculated that hoary bats on the

Pacific coast use vision to orient themselves along the coastline, so the coast could be an important migratory corridor. The same may be true for Atlantic coast for southward-orienting eastern red bats. Tree bats are not only known to use coastlines during migration (Cryan 2008), but at times fly offshore during fall migration (Solick and Newman 2021). For several decades, visual observations from ships have documented anecdotal records of over-ocean flight by tree bats (Norton 1930; Brown 1935; Peterson 1970), providing support that over-ocean movement occurs, albeit with unknown frequency. Allen (1923) noted an eastern red bat capture on the island of Bermuda, more than 900 km from the North American coastline and fossil remains of eastern red bats are also known on the island (Grady and Olson 2006). More recently, in the mid-Atlantic coastal region, several studies documented coastal or offshore activity by tree bats. Hatch et al. (2013) noted several offshore visual observations of eastern red bats between 17 and 45 km east of the New Jersey, Delaware, and Virginia shorelines in the early fall of 2012. Similarly, Sjollema et al. (2014) equipped acoustic detectors aboard ships in spring and autumn of 2009 and 2010 and detected bats as much as 20 km offshore along the Atlantic Coast. Over 75% of these bat detections were identified as tree bats (mostly eastern red bats, followed by combined classifications of silver-haired/big brown bats [*Eptesicus fuscus*]). Onshore, Johnson et al. (2011a) recorded bats on the Assateague Island along the Maryland and Virginia border with notable peaks in spring and autumn. Smith and McWilliams (2016) concluded that bats migrate near or immediately offshore in southern New England and that activity levels are closely related to weather variables such as temperature (positive) and wind speed (negative). The Gulf of Maine also appears to contain some level of offshore use by bats (Peterson et al. 2014). In a recent review, Solick and Newman (2021) concluded that observations of tree bats offshore have

been documented from North Carolina to Nova Scotia during fall migration in eastern North America.

Collision risk to bats from wind-energy development in the offshore sector in the eastern U.S. is unknown. The reason, in part, is that very little wind energy development has been completed to-date, so monitoring has not been necessary. As of May 2021, two offshore wind facilities are operational in some capacity—the Block Island Wind Farm near Rhode Island and Dominion Energy’s Coastal Virginia Offshore Wind pilot project off the coast of Virginia Beach (Musial et al. 2021). These account for a relatively small amount of energy capacity as compared to wind-energy developed onshore—only 42 MW (Musial et al. 2021). For the future, however, the U.S. has 23 total GWs of capacity across many wind-energy projects that are either under a planning phase or already approved. These plans account for more than a 500-fold increase from current capacity. The development plans are concentrated primarily off the coasts of the wind resource-rich Northeast and Mid-Atlantic (Figure 1-1), close to localities in which tree bats have been observed over the ocean (Solick and Newman 2021). My research focuses on development in the mid-Atlantic, where multiple offshore wind turbine farms are currently in the site control or permitting phases in the Federal waters off the coasts of New Jersey, Delaware, Maryland, Virginia, and North Carolina. In these places, wind developers have obtained leases or are currently in the application phase from the U.S. Bureau of Ocean Management (BOEM). Specifically in Virginia, in April of 2020, the Virginia Clean Economy Act was enacted that created a production goal of 5.2 GW by 2034 (Musial et al. 2021). A similar act was passed in North Carolina. The states of New Jersey, Maryland, Virginia, and North Carolina have combined goals of 22.2 GW capacity by 2030–2040.

Because of this rapid potential increase in offshore wind development, and knowledge that bats may be at risk, basic information on the seasonal behaviors and drivers of offshore flight are needed as a first step in assessing risk to offshore wind collision. It has been shown that the relative activity of bats on shorter time scales (i.e., nightly or hourly) relates to multiple atmospheric conditions such as wind speed and temperature (Johnson et al. 2011b; Smith and McWilliams 2016; Muthersbaugh 2017; Gorman et al. 2021). Wind turbines require sustained wind speeds to operate and produce electricity, but a minimum sustained wind speed is necessary to do so, termed the “cut-in speed” (Manwell et al. 2009; Arnett et al. 2015). Typically, during non-generating periods, most production sites will feather rather than free-wheel wind turbines blades at wind speeds lower than the cut-in speed (Arnett et al. 2015). Bats are sensitive to wind speed and will decrease activity rates substantially at speeds generally >5 m/s (Johnson et al. 2011a; Gorman et al. 2021). However, it is known that considerable bat activity does occur at or above most cut-in speeds, thereby presenting the mortality risk (Solick et al. 2020). Operational curtailment, increasing cut-in speeds to avoid strike risk to bats, has proven to be successful at some wind-energy sites (Arnett et al. 2011, 2015; Martin et al. 2017).

Currently, the idea of “smart curtailment” is gaining acceptance in wind-energy policy and proposed management standards (Behr et al. 2017; Hayes et al. 2019; Farnsworth et al. 2021). This concept is geared toward minimizing the financial loss due to curtailment whereby subsequently minimizing mortality risk to bats by curtailing during periods of expected high bat activity or risk. Recently, in other regions, statistical models or algorithms developed to reduce collision risk by setting curtailment measures based on predicted bat activity have proven successful (Weller and Baldwin 2012; Behr et al. 2017; Martin et al. 2017; Peterson 2020). Statistical methods would be useful along the Atlantic Coast potentially, however regional

specific behavior (or estimates of parameters in a model) may differ, extending the need to develop a region-specific collection of data and modelling regimen.

Stationary acoustics have been relatively successful as the method of data collection as the means to measure bat activity and subsequently model the factors that influence either bat passage rates or occurrence patterns (Peterson et al. 2014, 2016; Smith and McWilliams 2016; Peterson 2020). To understand the factors that influence the occurrence of bats in offshore and coastal localities in Virginia, the Virginia Department of Wildlife Resources have, since 2012, continuously monitored bats using stationary acoustics on barrier islands and offshore structures in Virginia near a planned offshore wind turbine facility. Therefore, in chapter 2, I present these data and model the nightly occurrence of bats at distant barrier islands or offshore structures as they relate to seasonal, site characteristic, and nightly atmospheric condition effects. In addition, I used these variables in a predictive model framework and tested the predictive ability of the model. I present the conditions in which risk is most likely to occur (i.e., when bats are most likely to occur along barrier islands/offshore near the Eastern Shore of Virginia). Accordingly, with these metrics described, it might be feasible for wind-energy producers to use a similar monitoring and modeling regime to develop simple local site-specific models that would potentially reduce risk to bats if it is to occur.

Although acoustics are effective at monitoring site specific relationships for bats, many questions remain about the underlying migratory patterns of bats as it pertains to individuals and local populations. For instance, it is still generally unknown if actual migratory pathways exist (i.e., using the coastline as a topographic reference) for tree bats (Cryan 2003). It is suggested, however that tree bats do not necessarily migrate along specific flyways similar to birds because patterns on the documented travel paths vary substantially (Jonasson 2017; Dowling 2018).

Nevertheless, pathways of high density may still occur and hypotheses that bats use linear landscape features while migrating remain prevalent in the literature (Wieringa et al. 2021). These hypotheses should be more thoroughly tested to begin to assess the level of risk that offshore wind may pose to migrating tree bats.

As with birds (Shamoun-Baranes et al. 2017), atmospheric conditions effect the migratory behavior of bats (Weller et al. 2016; Jonasson 2017; Dowling 2018). For instance, birds and bats may use tail-winds, or the calm conditions following the passage of cold weather fronts as an energy expenditure reduction strategy (Cryan and Brown 2007; Smith and McWilliams 2016; Shamoun-Baranes et al. 2017). Therefore, it is feasible that, as with onshore activity rates, that the frequency of over-ocean travel in the mid-Atlantic reduces significantly during unfavorable atmospheric conditions such as high head-wind speeds, low temperatures and during cold fronts. In the Northeast, Dowling (2018) noted that migratory bouts were somewhat related to atmospheric conditions for a few select bat species. Further south in the mid-Atlantic, conditions that lead to overwater flight may be slightly altered as temperatures are warmer later in the year as fall progresses. Indeed, several other studies noted over-ocean bat activity in the mid-Atlantic and Northeast that reduced with atmospheric conditions associated with poor flying conditions (Johnson et al. 2011a; Sjollema et al. 2014; Peterson et al. 2016; Smith and McWilliams 2016; True et al. 2021).

In the mid-Atlantic, two large water bodies bracket the coastline—the Chesapeake Bay and the Delaware Bay. Similar to research from Ontario, Canada, where Lake Erie is a semi-permeable barrier for migration (McGuire et al. 2012; Jonasson 2017; Baloun and Guglielmo 2019), southbound migrating bats in southern New Jersey and Virginia are faced with waterbodies approximately 30–50 km wide. Therefore, bats that locate themselves north of these

localities must decide when, if at all, to cross these water bodies. These behaviors may be dictated by the atmospheric conditions. For example, a bat may select a night with a strong tailwind to cross the Chesapeake Bay when given some set of available nights. It is possible that these water body crossings also may serve as a proxy for over-ocean movement.

In chapter 3, using the Motus Wildlife Tracking System (Taylor et al. 2017), I captured and placed >100 transmitters on eastern red bats (and smaller samples of silver-haired bats and Seminole bats [*Lasiurus seminolus*]) in southern New Jersey, Delaware, and coastal Virginia and subsequently tracked their movements within the array of established Motus receiver stations. Herein, I performed a qualitative assessment of fall movement patterns including, but not limited to, direction of travel, timing of migration, identifying migratory pathways, and residency duration. I measured the atmospheric conditions and nightly timing in which over-water flight occurred (i.e., a bat travelled from one shoreline to the other shoreline of the Delaware or Chesapeake bays in one night) and used those instances of time as “used” versus a random selection of “available” instances in a use-availability logistic model. I used current and changes in atmospheric conditions to correlate over-water behaviors to these variables. Lastly, I used a measure of signal strength variability from local Motus towers that continuously recorded eastern red bats to infer the rest and active states of bats in relation to the progression of the season, temperature, wind speed, and time of night during the night hours. I discuss the implications of all above on the risk of bats at offshore wind turbine facilities in the mid-Atlantic.

Chapters 2 and 3 present relatively novel findings as the mid-Atlantic coast is relatively understudied compared to the Northeast and Great Lakes regions relative to tree bat migration. These chapters attempt to address questions about the biology of tree bats, but more importantly, the potential risk that offshore wind-energy development may pose to this group of species. I

concentrate primarily on atmospheric conditions and season as these are the most closely related to what we know about onshore wind turbine risk and holds promise as important factors that influence the offshore behavior of bats. With knowledge of the drivers affecting offshore behavior, researchers and managers may be better equipped to develop mitigation strategies to address periods of potential high collision risk.

Figures

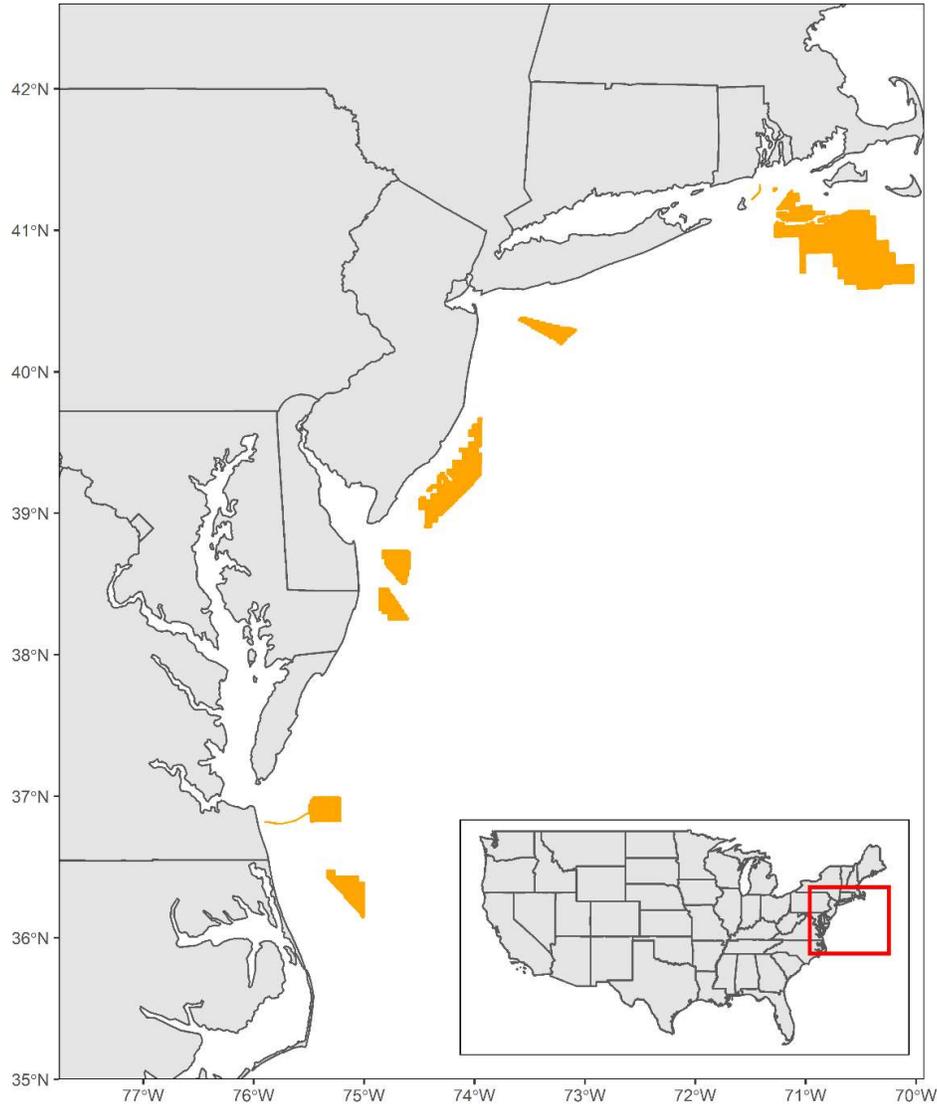


Figure 1-1. Offshore wind-energy lease areas (orange shapes) off the Northeast and Mid-Atlantic coast as of Aug 2, 2021. Most projects have gained site control and are applying for Federal permits in the near future (or have already) and are awaiting regulatory approval to begin construction (<https://www.boem.gov/renewable-energy/mapping-and-data/renewable-energy-gis-data>; Accessed Oct 2, 2021).

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Chapter 2: Monitoring and Modeling Tree Bat (Genera: *Lasiurus*, *Lasionycteris*) Occurrence Using Acoustics on Structures Off the Mid-Atlantic Coast—Implications for Offshore Wind Development

Abstract

In eastern North America, “tree bats” (Genera: *Lasiurus* and *Lasionycteris*) are highly susceptible to collisions with wind energy turbines and are known to fly offshore during migration. This raises concern about ongoing expansion of offshore wind-energy development off the Atlantic Coast. Season, atmospheric conditions, and site-level characteristics such as local habitat (e.g., forest coverage) have been shown to influence wind turbine collision rates by bats onshore, and therefore may be related to risk offshore. Therefore, to assess the factors affecting coastal presence of bats, we continuously gathered tree bat occurrence data using stationary acoustic recorders on five structures (four lighthouses on barrier islands and one light tower offshore) off the coast of Virginia, USA, across all seasons, 2012–2019. We used generalized additive models to describe tree bat occurrence on a nightly basis. We found that sites either indicated maternity or migratory seasonal occurrence patterns associated with local roosting resources, i.e., presence of trees. Across all sites, nightly occurrence was negatively related to wind speed and positively related to temperature and visibility. Using predictive performance metrics, we concluded that our model was highly predictive for the Virginia coast. Our findings were consistent with other studies—tree bat occurrence probability and presumed mortality risk to offshore wind-energy collisions is highest on low wind speed nights, high temperature and visibility nights, and during spring and fall. The high predictive model performance we observed provides a basis for which managers, using a similar monitoring and modeling regime, could develop an effective curtailment-based mitigation strategy.

Introduction

Collisions with wind turbines are an expanding conservation concern for bats (Arnett et al. 2015; Frick et al. 2017; Friedenbergs and Frick 2021). In North America, non-hibernating, migratory “tree bats” (Genera: *Lasiurus* and *Lasionycteris*) are particularly susceptible to collisions and are often the majority bat group in post-construction carcass surveys at wind energy facilities (Arnett et al. 2008; Arnett and Baerwald 2013; Hein and Schirmacher 2016; Thompson et al. 2017; Choi et al. 2020). The tree bat mortality rate at wind turbines appears to be highly correlated with the seasonal movements of these species (Cryan 2003, 2008; Cryan et al. 2004; Britzke et al. 2009; Cryan and Barclay 2009; Johnson et al. 2011b; Muthersbaugh 2017) whereby collisions are generally elevated in spring and maximized in fall migration periods (Arnett et al. 2008a; Thompson et al. 2017; AWWI 2020). Increased mortality counts during migration may be attributable to space-use increase due to fall mating and migration, erratic juvenile dispersal behavior, and general attraction to turbines (Cryan 2008; Horn et al. 2008; Cryan and Barclay 2009; Cryan et al. 2014).

North American tree bats are known to fly offshore with some regularity. This was first documented in anecdotal historical sightings from ocean vessels large distances off mainland coasts (Nichols 1920; Thomas 1921; Norton 1930) and observations of tree bats on the island of Bermuda (Allen 1923). In the eastern North America, recent research has discovered high-flying tree bats 8.4–44 km from the main shoreline (Hatch et al. 2013; Sjollema et al. 2014). The occurrence of tree bats offshore and along shorelines follows a similar seasonal activity pattern to wind turbine collisions—a general peak during spring and fall migration (Johnson et al. 2011a; Peterson et al. 2014, 2016; Sjollema et al. 2014; Smith and McWilliams 2016). The reason for this behavior remains unknown but some speculate that the coastline serves as a

topographic reference for navigation (Alerstam and Pettersson 1977) or that favorable wind conditions over open ocean may aid in long distance migration (Shamoun-Baranes et al. 2017). It is posited that the eastern shoreline acts as a topographic barrier, concentrating southward migrating tree bats along the coast during fall (Cryan 2003).

Wind energy in the eastern United States is expanding at an accelerating rate, particularly in the offshore sector (Beiter et al. 2017; Musial et al. 2019; Costoya et al. 2020). To date, two offshore wind turbine operations exist in the eastern United States that account for <50 MW capacity (Musial et al. 2019). However, an increasing number of offshore projects are now leased and in the beginning construction phases. It is projected that these projects will account for more than 20 GW of rated capacity (Musial et al. 2019), a 400-fold increase. Although projections indicate offshore wind facilities will likely be concentrated in the wind resource rich Northeast, some development is proposed off the mid-Atlantic coast along Virginia, Delaware, Maryland, and New Jersey (Musial et al. 2019). The impact this rapid development will have on bats is unknown, however, risk is certainly non-zero particularly for tree bats as they are the most susceptible bat group to collision (particularly during migration) and are the only bat group consistently seen at offshore localities (again, particularly during migration).

Onshore, extensive monitoring at wind facility sites post-construction have offered successful data driven conservation strategies to minimize bat mortality at turbines including, but not limited to, acoustic deterrents (Johnson et al. 2012; Lindsey 2017; Smotherman et al. 2019; Cooper et al. 2020; Schirmacher 2020; Weaver et al. 2020) and curtailment (Baerwald et al. 2009; Arnett et al. 2011; Behr et al. 2017; Hayes et al. 2019; Smallwood and Bell 2020). Curtailment is based on the knowledge that most bats generally avoid flying in overtly windy conditions, i.e., avoiding speeds generally above 5 m/s (Baerwald et al. 2009; Arnett et al. 2011).

Therefore, at low wind speeds below this (or other) threshold(s), turbine managers feather turbine blades, bringing rotor movement to a minimum, and thereby minimizing bat fatalities. There has been some success in the use of curtailment to reduce bat mortality while also minimizing financial loss (Arnett et al. 2011; Behr et al. 2017; Martin et al. 2017) through the development of “smart curtailment” algorithms (Hayes et al. 2019; Farnsworth et al. 2021). These are typically model based, multivariate approaches whereby curtailment is triggered by the expectation of high bat activity or probability of presence (Weller and Baldwin 2012; Behr et al. 2017; Peterson 2020). Although these strategies may hold promise for offshore wind energy impacts, unlike terrestrial systems, the factors that influence occurrence (and therefore the parameter values necessary to predict risk metrics) of bats offshore are poorly known.

Monitoring bat activity offshore is challenging. Passive acoustic monitoring over ocean waters requires some type of infrastructure (platforms, buoys, lighthouses, etc.) to support acoustic detectors. Barrier islands and offshore structures offer an alternative approach to collecting acoustic data in the near “offshore” environment if located a considerable distance from the mainland shoreline. Yet, these sites are accessible and feasible as detector deployment infrastructure. A few studies have approached the problem in this way, deploying acoustic detectors on islands, structures at sea, and on the coastline (Peterson et al. 2014, 2016; Smith and McWilliams 2016). However, most of this research has been concentrated in the Northeast. Further south in the mid-Atlantic, some degree of seasonally fluctuating barrier island use by bats has been observed (Johnson et al. 2011b) as has fall offshore flight (Hatch et al. 2013; Sjollema et al. 2014). However, temporally, and geographically limited sample sizes somewhat constrain generalizability and the development of predictive models to describe the factors

influencing bat use and to test the feasibility of a predictive curtailment algorithms in the near-offshore environment.

Our study sought to address these data gaps with a large sample of acoustic bat occurrence data off the Eastern Shore of Virginia (ESVA). From 2012 to 2019, the Virginia Department of Wildlife Resources deployed acoustic monitors at four barrier island sites and one offshore site. We used this large acoustic dataset to develop a model to describe migratory tree bat nightly occurrence relationships to season, atmospheric conditions, and site-specific characteristics. Our modeling served two purposes—description and prediction (Tredennick et al. 2021). We describe the parameters that reveal the effects of various potential drivers of nightly occurrence of tree bats. Then, we use the model as a predictive tool of bat occurrence and hence potential risk for regional wind turbine collisions once deployed.

We hypothesized that tree bat occurrence in mid-Atlantic coastal environments is closely related to season due to the seasonal fluctuations in which tree bats use coastal landscapes and oceanic space. We predicted strong positive effects in spring and fall, moderate effects in summer, and negative effects in winter. We also developed competing hypotheses that the seasonal effect is explained by either (1) unique sites, or (2) the availability of local day-roosting habitat and potentially important foraging habitat (e.g., trees/forests, fresh water). We predicted that if the seasonal pattern is best explained by site specifics that unique sites would have noticeably different occurrence relationships to season. If the seasonal pattern is best explained by roosting habitat, sites with limited roosting habitat would have similar occurrence relationships to season (e.g., peaks only during migration). Lastly, we hypothesized that tree bat occurrence is closely related to multiple atmospheric conditions. We predicted that occurrence would be negatively related to wind speed, positively related to nightly temperature.

Materials and Methods

Study area

We conducted acoustic monitoring on four barrier island sites and one offshore site off the ESVA (Figure 2-1 and Figure 2-2) 2012–2019. The ESVA is the southern portion of the Delmarva Peninsula, surrounded by the Chesapeake Bay to the west and the Atlantic Ocean to the east. Locally, the vegetation is mid-Atlantic Coastal Plain deciduous and evergreen (pine) mixed upland and bottomland forest in its interior and intertidal saltmarsh habitat along the coasts. On the eastern Atlantic boundary, a chain of barrier islands occur that are characterized by little physical relief above sea level with upland shrub thickets, scattered patches of forest and salt marsh (Fleming et al. 2021). On the eastern side of ESVA, we monitored on Assateague Island on the Assateague Lighthouse, Cedar Island on an inactive United States Coast Guard (USCG) station, Hog Island on an inactive USCG station, and Smith Island on the Cape Charles Lighthouse. Cedar Island, Smith Island, and Hog Island are similar in that they are primarily composed of saltmarsh and upland shrub thickets. Some overstory evergreen vegetation exists on Hog Island, however, it is extremely limited in extent. In contrast to other ESVA study sites, Assateague Island has considerable deciduous and evergreen forest habitat. Additionally, Assateague Island contains fresh water sources. On the western boundary, we conducted research near Silver Beach on a navigation light structure approximately 0.7 km off the western shore of the ESVA in the Chesapeake Bay.

Acoustic data

From 2012 to 2019, we collected acoustic data at the five ESVA sites named Assateague Island, Cedar Island, Hog Island, Smith Island, and Silver Beach (Figure 2-1 and Figure 2-2). We used frequency division/zero-crossing acoustic detectors (Anabat SD1 and SD2, Titley

Scientific, New Ballina, NSW) that record high frequency (15–150 kHz) echolocation pulses of bats. We placed the detectors on existing structures (lighthouses or similar) at heights of approximately 10–40 m. We collected data annually typically across three seasons—beginning in early spring and through late fall and recorded during the winter season at least once per site (Figure 2-3). We considered acoustic recordings on a nightly basis from sunset to sunrise.

The post processing data structure was composed of timestamped individual echolocation sequences of bats (hereafter “bat passes” or “passes”). Bat passes is defined as a distinct series of echolocation pulses, or “clicks”, which is identified to one bat as they pass within range of the detector (Brock 1970). We used Kaleidoscope 4.5.0 Bats of North America—4.2.0 classifier (Wildlife Acoustic, Inc., Maynard, MA, USA) to identify passes to species, unidentified bat passes (“no ID”), or noise. We tallied nightly pass counts by individual species, no ID, and noise. To minimize false positives, we manually inspected subsets of passes identified to species to confirm identification. Due to the context of the problem and realization that >85% of identified passes were tree bats, we placed particular emphasis on correct identification of eastern red bats (*Lasiurus borealis*), silver-haired bats (*Lasionycteris noctivagans*), and hoary bats (*Lasiurus cinereus*), and only used tree bat pass data in our analysis. In wind turbine collision risk studies, recent evidence suggests that the hourly or nightly passage rates of bats pre-construction are poor predictors of fatality rates post-construction (Solick et al. 2020) so to account for this, instead of using hourly or nightly tallies of bat passes as our response variable, we restructured the data to consider only the binary occurrence (or non-occurrence) of tree bat(s) on a nightly basis.

Atmospheric conditions and other variables

We compiled weather conditions from nearby National Oceanic and Atmospheric Administration (NOAA) weather stations on the ESVA (Climate data online;

<https://www.ncdc.noaa.gov/cdo-web/>; accessed 9 November 2019; Figure 2-1). We used the nearest available weather station to each site to approximate hourly weather conditions. We extracted hourly data on wind speed (m/s), wind gust speed (m/s), temperature (deg C), visibility (0–16.2 km), pressure (mmHg), precipitation duration (hours), precipitation (cm), and absolute humidity (mg/cm³). We filtered these data to reflect dates and hours in which the detector stations were active, i.e., reducing to a nightly basis between sunset and sunrise on active detector nights. We summarized each weather variable to reflect nightly conditions taking the nightly mean of wind speed, temperature, visibility, pressure, and relative humidity, the maximum wind gust speed, nightly cumulative sum of precipitation, and nightly cumulative number of hours precipitating. We also created a change in pressure variable calculated as the mean at the current night minus the mean of the previous night. Lastly, because bats may be more likely to be present at individual sites during different times of the year if they contain viable day-roosting habitat, we created a binary roosting habitat variable as has viable roost availability (forests) or, none or limited roost availability for each detector station. We also noted additional potentially relevant variables including ordinal date (day of year), site name, and year. We did not include the potentially relevant variable of detector height because we were limited by the number of unique heights ($n = 5$).

Presentation of data and EDA

We performed an exploratory data analysis (EDA) to visualize the effect of wind speed, temperature, and seasonality. At each site, we noted tree bat occurrence or non-occurrence and calculated a 20-day moving average on the ordinal date (day of the year [1–365]). We also fit a smoothing line (generalized additive model [GAM] spline; Wood 2020) to aid in visualization. We calculated 90%, 95%, and 99% quantile values in which 90%, etc. of all nights with tree bat

occurrence were less than a wind speed threshold, greater than a temperature threshold, or between spring or fall date ranges. We calculated these quantiles for wind speed only, temperature only, and a mix of wind speed and temperature or a spring and fall date range.

Modeling

We used generalized additive models (GAMs; Hastie and Tibshirani 1990; Wood 2017) with a binomial distribution (logit link function) to model the relationship between binary nightly occurrence of tree bats and the variables. GAMs are an extension of generalized linear models (GLMs; Nelder and Wedderburn 1972) such that the expected response is a link transformed summation of an intercept and the product of slope coefficients and variables, however, some or all variable effects may be specified as semi- or non-parametric real functions denoted as splines (hereafter “smooths” or “ $f(x)$ ”; Hastie and Tibshirani 1990; Wood 2003, 2004, 2011, 2017; Wood et al. 2016). Smooths are created by a series of coefficient scaled basis functions “tied” together at knots—evenly spaced segments along the variable range. These smooths then, can take on complex, non-parametric shapes in the relationship between the variable effect and the variable as opposed to the generally linear, or parametric relationships in GLMs that may not reflect actual biological patterns. We performed all analysis in program R (R Core Team 2021) and fit GAMs using the R package *mgcv* (Wood 2020).

To test our first hypothesis and the subsequent competing hypotheses, we used a model selection process that tested three a priori models to select the appropriate model that best accounted for a potentially nonlinear seasonal effect. These three models contained smooth non-parametric function(s) of the ordinal date that took on factor level-specific shapes depending on the factor provided in the model. We supplied one model with no factor variable, one with roosting habitat availability that varied its intercept with site, and one with site only (Table 2-1).

We used the minimum change in Bayesian information criterion (ΔBIC ; Schwarz 1978) as the basis for model selection because BIC outperforms Akaike's information criterion (AIC) when n is large ($n > 3000$; Burnham and Anderson 2004) and tends to select more parsimonious models because the penalty for complexity is larger than AIC (for $n > e^2$). We calculated each a priori model BIC using Schwarz's method of $\text{BIC} = -2 \log(\mathcal{L}) + K \log(n)$ implemented in the *model.sel* function of the R package *MuMIn* (Barton 2020).

We used the top a priori model structure in all further models as a baseline (i.e., this model structure was nested within any other further competing model). To include atmospheric conditions into the model, we first reduced variables by omitting those of high correlation (Pearson correlation coefficient > 0.7). We then created a global model that included all variables as smooth functions. We performed a dredge (i.e., fit all possible additive model combinations). We compared these models by BIC. We considered models < 2 BIC points competing models in which we selected the top model by biological feasibility and interpretability (Burnham and Anderson 2004).

To test predictive performance, we performed a series of diagnostic tests on the final model. First, to assess general performance, we conducted a Monte-Carlo cross validation (MCCV; Xu and Liang 2001) on the area under the receiver operating characteristic (AUC; Hanley and McNeil 1982). The AUC is a threshold dependent, sensitivity and specificity dictated metric of predictive performance for binary data such that an AUC of 0.5 is no better than random and an AUC of 1 is perfect prediction. To perform the MCCV, we (1) randomly selected 85% of the data for training and 15% of the data for testing the model, (2) fit the model and predicted on the withheld data, and (3) measured and saved the AUC using the R package *pROC* (Robin et al. 2011, 2020). We repeated those steps for 1000 iterations. We calculated the mean of

the AUCs, and a 95% confidence interval by taking 2.5% and 97.5% quantiles of those 1000 iterations.

As a second metric of predictive performance, we again divided the data into 85% training and 15% testing groups. Using the training group, we fit the final model, then predicted occurrence probabilities from 0 to 1 on the testing group. We selected an optimal “cut-off” threshold using the Youden index (Youden 1950) to categorize occurrence. We used these categorizations to compare to their true occurrence values. Therein, we calculated a confusion matrix and values for sensitivity (true positive rate; true positives/true positives + false negatives) and specificity (true negative rate; true negatives/true negatives + false positives; Murtaugh 1996; Manel et al. 2001; Fu et al. 2019). We used various other R packages for data manipulation, cleaning, processing (Wickham et al. 2019, 2020b; Wickham 2020), and visualizations and mapping (Fasiolo et al. 2018; Tennekes 2018, 2020; Kassambara 2020; Wickham et al. 2020a).

Results

We recorded acoustic data over eight years (2012–2019) resulting in a total of 5735 nights of recording across all detectors. We recorded at Silver Beach across four years (762 nights), Assateague Island and Smith Island across five years (791 and 1328 nights, respectively), Hog Island across six years (1268 nights), and Cedar Island across all eight years (1586 nights). Per year, effort was primarily centered on warmer months of spring to autumn, however, winter effort existed 1–2 years per site resulting in nearly entire year effort across all sites (Figure 2-3). We detected tree bats on a total of 39.26% of recorded nights, which varied by site (min = 29.89% at Hog Island, max = 71.30% at Assateague Island).

With respect to the exploratory data analysis, tree bats appeared to occur at sites with strong relationships to season (Figure 2-4). At Assateague Island, we detected nightly occurrence with a unimodal shape—low occurrence in winter, increase in spring, a peak in summer, and a decrease in fall. For all other localities, we detected bimodal effect shapes with respect to season—low occurrence in winter, a small peak in spring, a slight decrease in summer, then an increase and larger peak in fall. Sites showing a bimodal shape contained limited roosting habitat and probably limited foraging habitat.

The proportion of nights with tree bat occurrences appear related to wind speed and temperature as 90% of occurrences were on nights where wind speed averaged below 4.06 m/s and average temperatures were above 12.66 °C (Table 2-2). As an additive effect to these atmospheric conditions, the spring and fall months appeared to carry a large proportion of positive occurrence nights as 90% of occurrences occur during either wind speeds below 4.5 m/s, above 12 °C, or were between the dates of 28 April–14 May or 16 August–1 September.

Through model selection, the top approximating a priori model via minimum Δ BIC was model 2—the ordinal date shaped by roosting habitat model (Table 2-3). In post-hoc, our atmospheric variables reduced from seven to six potentially relevant variables by omitting nightly maximum wind gust (m/s) due to multicollinearity with nightly mean wind speed (m/s). We argue that nightly mean wind speed more closely relates to the wind conditions throughout an entire sampling night. We encountered missing values from weather stations that forced us to reduce the total number of nights from 5735 to 4864 so that each model used the same data in calculating model selection metrics.

Our global model included all remaining terms as additive smooths. The model selection dredge resulted in 128 models from which we selected the top model via BIC (Table 2-4). This

top model included an intercept, site as a factor, a smooth effect of ordinal date based on day-roosting habitat, and smooth effects of nightly mean temperature, wind speed, and visibility.

The smooth effect of temperature and visibility was generally positive along the range of variable values, however, plateaus at higher values of each were evident (Figure 2-5). The smooth effect of wind speed was linear and negative along the range of variable values. The smooth effect of ordinal date was different for each roost availability type. For sites with limited roost availability the ordinal date effect was generally low in winter, locally maximized in spring at around ordinal date 125 (~May 5), lower in summer, and maximized in fall at around ordinal date 235 (~August 22). For sites with viable roosting habitat, the ordinal date effect generally increased from winter to spring, peaked in summer at around ordinal date 200 (~July 17), and decreased in fall (Figure 2-5). The intercept of the model was modified based on site. The greatest positive effect was Assateague Island ($\beta_0 + \beta_1$), the only site with viable roosting habitat (Table 2-5). The lowest effect was at Hog Island ($\beta_0 + \beta_2$; Table 2-5), the most distant barrier island from the ESVA mainland.

Our final model was highly predictive. It contained a mean MCCV AUC value of 0.852–95% CI (0.828, 0.877). The optimal cutoff for predicting occurrence or non-occurrence was 0.393, which we used as a threshold to predict on withheld data. The model appeared to correctly predict occurrences as indicated by the confusion matrix (Figure 2-6). Therein, the number of false positives and false negatives were generally low (117 and 65 out of 730 data points). Sensitivity (true positive rate) and specificity (true negative rate) values were 0.826 and 0.671, respectively.

Discussion

Our hypotheses were generally supported by our analysis. First, tree bats do occur at offshore barrier island sites, but occurrence is most related to season. This became apparent as peaks in the occurrence rate over ordinal date contained local maximums in spring and fall. This seasonal effect is demonstrated in the EDA (Figure 2-4), the smoothed ordinal effects of the model (Figure 2-5), and in that 90 and 95% of occurrence nights fell within either nights of certain wind speed and temperature conditions or somewhat narrow spring or fall date ranges (Table 2-2). These seasonal effects undoubtedly are related to the migratory behavior of tree bat species' (Cryan 2003; Cryan and Brown 2007; Britzke et al. 2009; Johnson et al. 2011b; Muthersbaugh 2017; Fleming 2019). Why tree bats traverse large bodies of water seasonally remains speculative, however, it could be explained by a simple increase in space use during migration or favorable conditions for long-distance flight occurring offshore (Shamoun-Baranes et al. 2017). Curiously, while both fall and spring seasons contain local peaks in occurrence, fall occurrence rates are higher than spring. This could be explained by the fact that fall is mating season and tree bats are more active in searching for mates and thereby more likely to explore more space (Cryan 2008; Cryan et al. 2012). This appears consistent as female eastern red bats are known to have multiple mates in a single season (Ammerman et al. 2019). These effects are compounded, too, by additional volant juveniles navigating long distances for the first time. Moreover, these effects occur at a time when the species' population should be at a level higher following summer parturition and juvenile volancy than winter and spring which could incidentally cause a higher rate of occurrence in fall as compared to spring (Ford et al. 2011).

Another obvious effect on occurrence was the presence or absence of viable roosting habitat (forests), which seemed to influence the shape of the seasonal pattern. The unimodal

seasonal activity pattern observed at Assateague Island, which contained forests available for roosting habitat, was more typical of onshore sites—bats arrive in spring, activity peaks in mid-summer which corresponds to maternity activity, and bats settle into reduced activity states (cave hibernation [cave bats] or intermittent torpor [tree bats]) in fall and then winter (Johnson et al. 2011b). The other survey sites that contained little or no forest patches seemed to be visited consistently in just spring and fall—an indication of vagrant, rather than maternity, use. These sites contained lower activity in general, suggesting that without quality roosting habitat, bat occurrence and residency time was low, aside from the spring and fall season. Therefore, our results support the latter of our competing hypothesis—the pattern of seasonal use is best explained by the availability of local day-roosting habitat. This point also supports that siting for offshore wind turbines should consider increasing distance to viable roosting habitat to reduce curtailment needs during the summer. A similar study also observed this (Peterson et al. 2016), that bat activity decreases with increasing distance from mainland and decreasing forest coverage.

Next, including nightly atmospheric conditions greatly improved the model. It was not surprising that wind speed had negative effects on occurrence and conversely temperature and visibility had positive effects on occurrence. For example, we found that ~95% of nights that contained positive tree bat occurrence were $< \sim 5$ m/s (~ 11 mi/hr) and $> \sim 10$ °C (50 °F). High wind speeds and low temperatures greatly increase the energy costs associated with flying (Popa-Lisseanu and Voigt 2009) which may be particularly true at distant barrier islands where we speculate that the nightly origin of these bats was most likely non-local, i.e., from the ESVA mainland. We understand that a multitude of atmospheric conditions relate to the activity states of bats (Smith and McWilliams 2016) and the migratory behavior of birds (Shamoun-Baranes et

al. 2017). Indeed, many observations of over-ocean flying bats have been during calm conditions (Solick and Newman 2021). We were initially surprised that visibility was selected as a relevant variable considering that bats rely on audible cues to navigate during flight via echolocation. However, it is intuitive to assume that bats use visual cues when flying above the ocean and/or when traveling to the islands and structures that we detected them nearby. Bats are known to echolocate while traveling over the ocean, particularly when close enough to detect them with acoustics (e.g., Ahlen et al. 2007; Sjollem et al. 2014), however, hoary bats (*Lasiurus cinereus*) sometimes forgo echolocation when traveling, and therefore rely solely on visual clues intermittently (Corcoran and Weller 2018). It is not beyond the realm of possibility that over-ocean flying bats use vision when there are no reflective surfaces for echolocation (e.g., at high altitudes) and therefore are unlikely to engage in over-ocean flights when visibility is low. The negative relationship of occurrence to visibility could also be explained by poor conditions for flying in general (rain, wind, low temperatures) as poor visibility is generally associated with those poor weather conditions, which, require more energy to fly in (e.g., rain, Voigt et al. 2011).

Our modeling effort increased our understanding of the pattern of occurrence of migratory tree bats at barrier island sites in the mid-Atlantic. Importantly, this dataset revealed the conditions whereby occurrence along the coast is more or less likely. Whether inland or coastal, it is established that site characteristics, seasonality, and atmospheric conditions influence the activity rates of bats (Johnson et al. 2011a; Peterson et al. 2014, 2016; Smith and McWilliams 2016). These effects are reinforced with our findings at the more southerly latitude of the ESVA. The occurrence of bats offshore was highly predictable when using the model. Our large AUC values from the MCCV indicated that, on average, given site specifics, day of the year, and atmospheric conditions, the occurrence probability of migratory tree bats is very

accurate for the ESVA sites. We also argue that our study continues a trend of consistency across studies. Tree bats appear to use offshore areas on the East coast during a certain set of conditions—calm and warm weather, during fall (and to some extent spring), and nearer to shorelines or forest coverage than far (Peterson et al. 2016; Solick and Newman 2021). Therefore, we believe our results are fairly generalizable to the surrounding region of the mid-Atlantic coastline.

Nonetheless, our study is not without limitations. First, observing bats via acoustics contain potential biases in that the physics of ultrasonic sound (bat echolocation pulses) change with atmospheric conditions (Voigt et al. 2021). This, plus the fact that non-occurrence does not necessarily equate to absence (i.e., detection probability is not reliably 1; Hamilton et al. 2012), may over or underestimate probabilities of occurrence depending on the conditions, time of year, among other factors. Additionally, acoustic activity of bats and wind turbine collision risk are not always analogous (Solick et al. 2020). Regardless, these issues largely concern the correct detection of absence rather than presence of bats. In our research, nights of known occurrence follow patterns that are consistent (i.e., prediction accuracy is high on withheld data when trained on multiple years of data). Lastly, our study was limited in the number of sites to support our results. As we were limited in detector deployment infrastructure and accessibility, we were restricted to only five sites which could restrict generalizability and could contain bias. As just mentioned however, our study does not differ in major ways from other studies. Even with just five sites, patterns of occurrence follow associations with atmospheric conditions, site specifics, and seasonality in a largely nonunique manner which, as a standalone study may suffer with site limitations, but in the greater literature is in support of what has previously been known (Ahlen et al. 2007; Johnson et al. 2011a; Peterson et al. 2016).

The development and deployment of predictive smart curtailment algorithms is currently underway onshore and may be a viable method to reducing bat collisions at offshore wind farms. While additional research is warranted to assess collision risk at project-level localities, these data and this analysis helps identify a starting-point in assessing the temporal and climatic conditions when tree bats may be most susceptible to impacts from wind turbines offshore in the Mid-Atlantic region. If nightly occurrence does indeed generally correlate to offshore wind strike risk, a similar algorithm or model could be used to predict when risk is more likely. Even more simply, if managers were to implement simple standards, such as curtailing on nights with average wind speeds <5 m/s, temperatures >10 °C, and/or during the spring and (especially) the fall, most bat occurrence (and potential risk) could be avoided. It appears that curtailment using a combination of variables as these could be a relatively inexpensive (Dowling 2018) and effective (Arnett et al. 2011; Farnsworth et al. 2021) way to reduce bat fatalities at offshore wind facilities.

Conclusions

Although we do not suggest using our specific model as a smart curtailment tool per se, this framework provides a viable starting point for creating curtailment regimens in the Mid-Atlantic. Our model was highly predictive and parsimonious which may suggest generalizability. Our results suggest that tree bat occurrence, and therefore a potential for risk is most likely under general and definable conditions—during the spring and fall seasons and on nights with low wind speeds, high temperatures, and high visibility. As such, it would be feasible for wind energy managers to collect acoustic data pre- and post-construction, assess the frequency of visitation at their specific sites, use site specific effects, atmospheric conditions, and seasonality in a modeling framework, and test the predictive ability of the model for specific locations. Using this approach, managers could have some basis for understanding which conditions

influence nightly occurrence and when and where bat collision risk is non-zero or high as a guide to curtailment or other mitigation practices to minimize bat mortality.

Author Contributions

Conceptualization, R.J.R. and W.M.F.; methodology, M.C.T., R.J.R. and W.M.F.; formal analysis, M.C.T.; resources, R.J.R.; data curation, M.C.T.; writing—original draft preparation, M.C.T.; writing—review and editing, R.J.R. and W.M.F.; visualization, M.C.T.; supervision, R.J.R. and W.M.F.; project administration, R.J.R. and W.M.F.; funding acquisition, R.J.R. and W.M.F. All authors have read and agreed to the published version of the manuscript.

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Informed Consent Statement

Not applicable.

Data Availability Statement

Cleaned data (nightly values of occurrence or non-occurrence and their associated predictor variables) and supporting R scripts to run all analyses are provided at a github repository (github.com/mtrue/vacoastalbats; accessed on 29 September 2021). Raw acoustic data is available upon request. E-mail the corresponding author for details.

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Conflicts of Interest

The authors declare no conflict of interest.

Figures

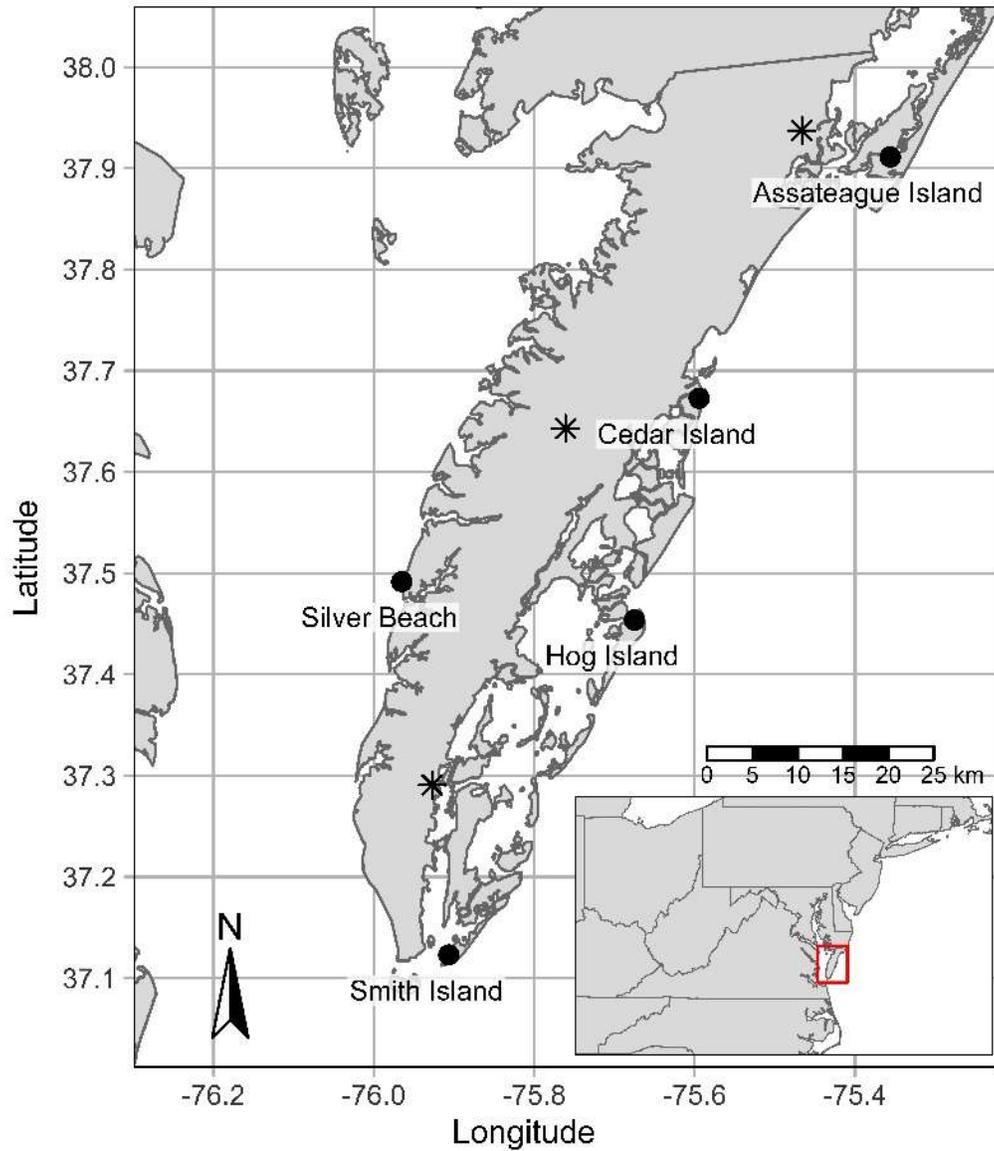


Figure 2-1. Acoustic detector sites (black points) on barrier islands and a light tower off the Eastern Shore of Virginia, USA, 2012–2019. Weather data was obtained from the nearest available National Oceanic and Atmospheric Administration (NOAA) weather stations (starred points) from the National Climatic Data Center (NCDC) online tool (Climate data online; <https://www.ncdc.noaa.gov/cdo-web/>; Accessed 2019-11-09).



Figure 2-2. Lighthouses and structures serving as infrastructure for acoustic detector deployment on Eastern Shore of Virginia, USA, 2012–2019. Acoustic detector microphone locations are indicated by the red circles. Locations are (a) Assateague Island (Assateague Lighthouse); (b) Cedar Island (inactive United States Coast Guard station); (c) Hog Island (inactive United States Coast Guard station); (d) Silver Beach (offshore navigation light structure), and (e) Smith Island (Cape Charles Lighthouse).

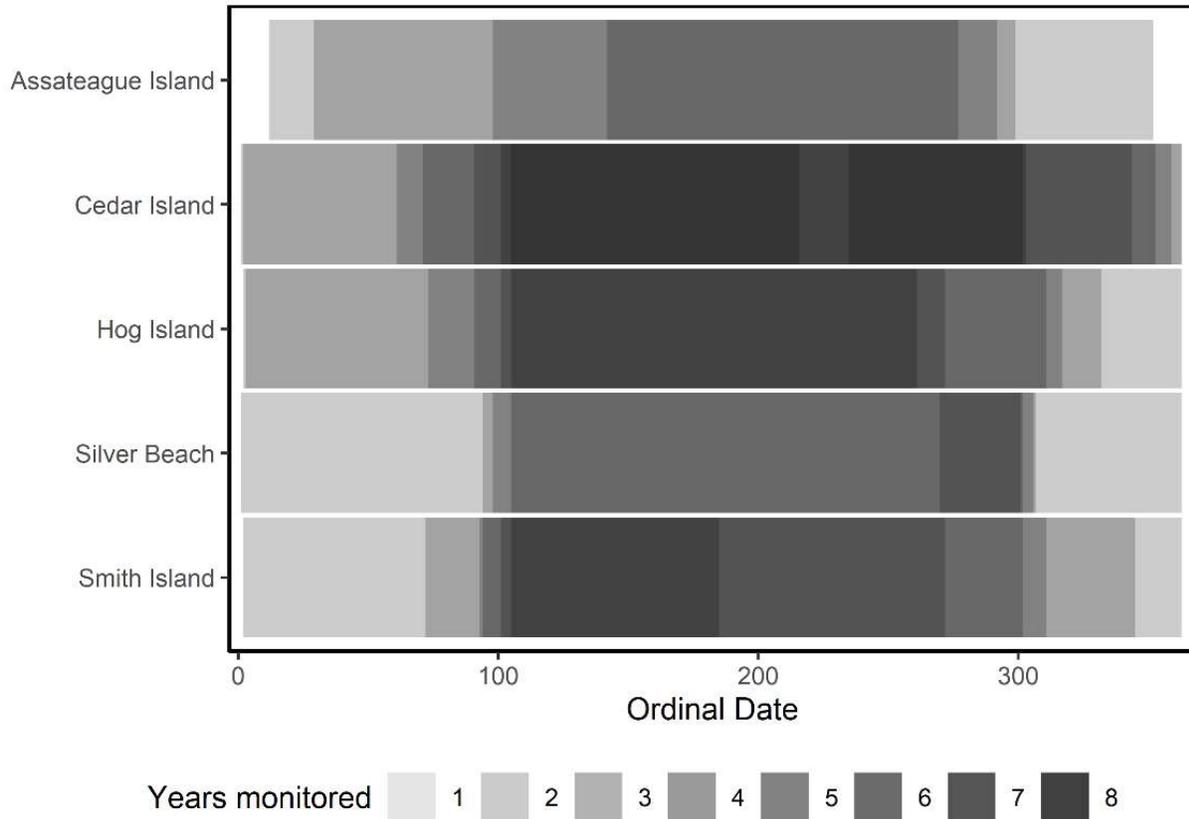


Figure 2-3. Site specific acoustic recording effort by ordinal date (day of the year). Effort (number of years monitored) is indicated as a heatmap of site vs. ordinal date such that lighter shades indicate lower effort (min = 1 year) and darker shades indicate higher effort (max = 8 years). Monitoring was conducted on the Eastern Shore of Virginia, USA, 2012-2019.

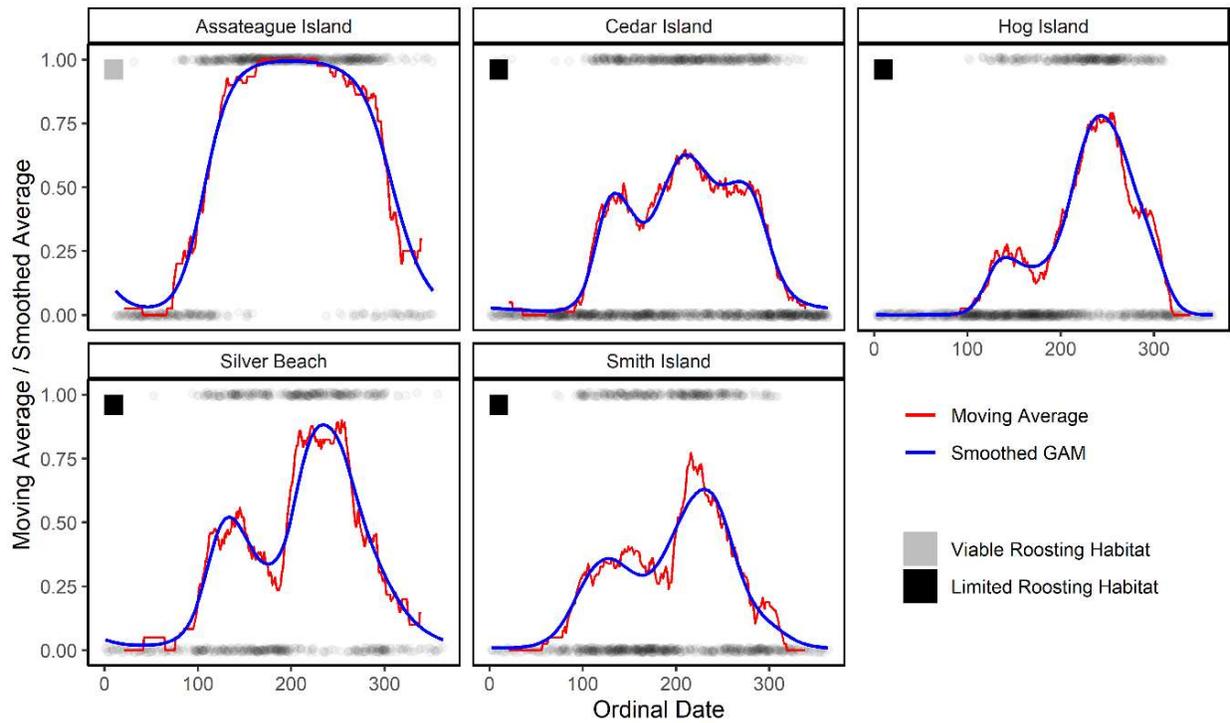


Figure 2-4. Raw occurrence data (black points: occurrence, non-occurrence [1, 0]) from acoustic detectors deployed on the Eastern Shore of Virginia, USA, 2012-2019. Data is grouped by site for all years of data collection stacked on a 1–366 ordinal date calendar. The raw data is shown as semi-transparent to visualize the occurrence density across years. The general relationship of tree bat nightly occurrence vs ordinal date is represented by a 20-day two-sided moving average proportion of nightly occurrence (black line) and smoothed average using a generalized additive model (GAM) spline (blue line). Each site is labeled as containing viable day-roosting habitat (grey square) or limited day-roosting habitat (black square).

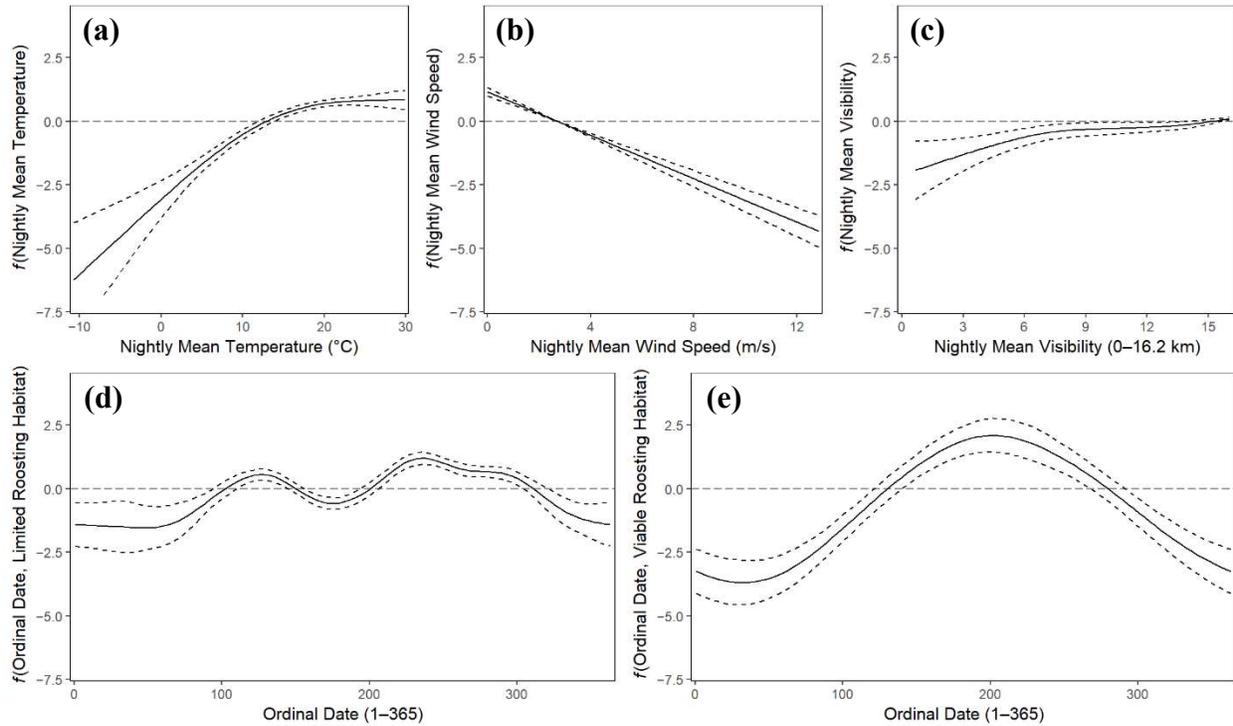


Figure 2-5. Visualizations of all smooth effects, $f(x)$, in the final model fit using acoustic data off the Eastern Shore of Virginia, USA, 2012–2019. The fit (solid line) and 95% confidence intervals for the fit (black dotted line) are displayed. Smooths, $f(x)$, can be interpreted as the effect of the variable, x . Nightly occurrence probability is positively associated with larger smooth values along the range the of variable. The final model used smooth effects of nightly means of temperature (a), wind speed (b) visibility (c), and the ordinal date (c). The shape of the smooth effect was separated by roost availability, by limited (d) or viable (e).

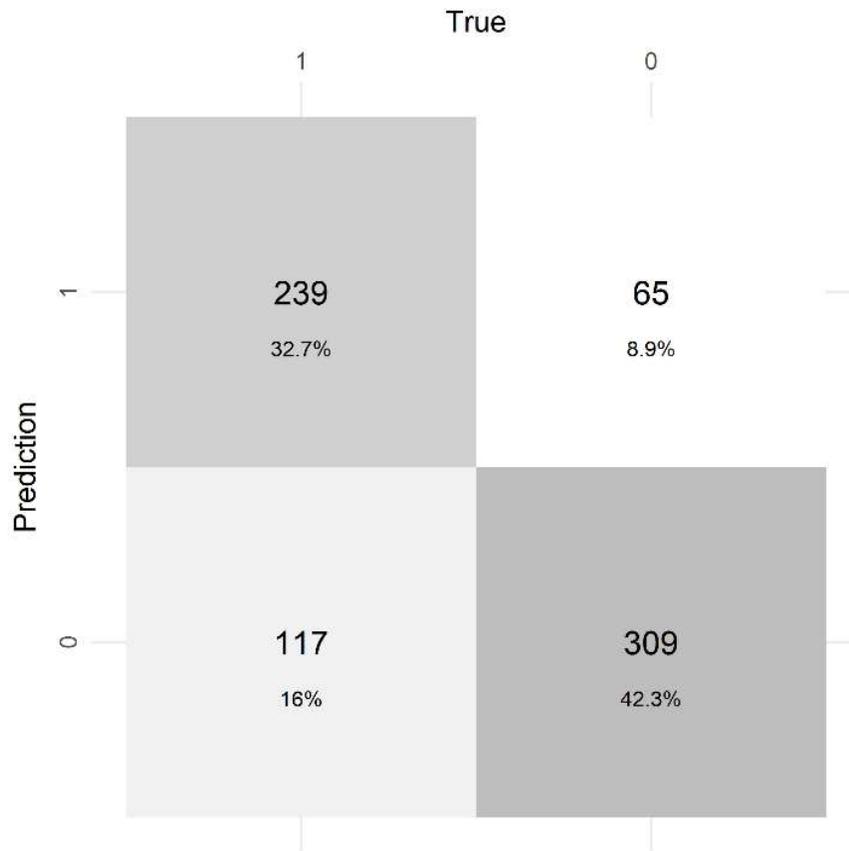


Figure 2-6. Confusion matrix of final model predictions compared to true values of test data collected off the Eastern Shore of Virginia, USA, 2012–2019. We used an 85% subset of the data to train the model ($n = 4,134$) and a 15% subset to test the model ($n = 730$). Values and percentages are displayed as true positives (top left), false positives (top right), false negatives (bottom left) and true negatives (bottom right). Shading indicates more frequency of any categorization—darker indicating more weight.

Tables

Table 2-1. A priori generalized additive models to evaluate the shape of the effect of seasonality (ordinal date) of tree bat occurrence at offshore/barrier island sites, Eastern Shore of Virginia, USA, 2012–2019. Three models are presented—one that only considers the ordinal date, one that considers local roosting availability, and one that considers site specifics

Model Name (Model Number)	Explanation	Biological Significance
Ordinal date only (1)	Nightly tree bat occurrence is explained by a smoothed effect of the ordinal date.	Tree bat visitation of barrier islands is related to the day of the year (ordinal date) because of the seasonal offshore habits of tree bats during migration.
Ordinal date by roosting habitat (2)	Nightly tree bat occurrence is explained by a smoothed effect of the ordinal date, but two shapes exist—one for viable roosting habitat, one for limited roosting habitat. Additionally, an intercept modifier exists for each site.	Tree bat visitation of barrier islands is related to the day of the year (ordinal date) because of the seasonal offshore habits of tree bats during migration. For sites with viable roosting habitat, the effect of ordinal date is likely highest in mid-summer, indicating maternity use. For sites with limited roosting habitat the effect of ordinal date is likely highest in spring and fall, indicating migratory use only. While the effect shapes are roost-availability specific, occurrence rates may differ between sites for some unknown reason, so the intercept is free to fluctuate between sites.
Ordinal date by site (3)	Nightly tree bat occurrence is explained by smooth effects of the Ordinal date—one for each site.	Tree bat visitation of barrier islands is related to the day of the year (ordinal date) and this relationship is specific to each site. For instance, some sites may be migration only, some sites may be for some migration and summer use, and many other minute differences between sites.

Table 2-2. 90%, 95%, and 99% quantiles representing the proportion of nights with tree bat occurrence under certain conditions of wind speed, temperature, and/or date ranges using acoustic data collected on the Eastern Shore of Virginia, USA, 2012–2019.

Percent of positive occurrence nights with conditions	Conditions	Values
0.90	Wind Speed	< 4.06 m/s
0.95	Wind Speed	< 4.90 m/s
0.99	Wind Speed	< 7.28 m/s
0.90	Temperature	> 12.66 °C
0.95	Temperature	> 10.31 °C
0.99	Temperature	> 5.43 °C
0.90	Wind Speed and Temperature or Date Range	< 4.5 m/s and > 12 °C or within either Apr 28–May 14 or Aug 16–Sept 1
0.95	Wind Speed and Temperature or Date Range	< 4.5 m/s and > 12 °C or within either Mar 23–June 11 or July 11–Oct 7
0.99	Wind Speed and Temperature or Date Range	< 4.5 m/s and > 12 °C or within Feb 24–Nov 3

Table 2-3. A priori models ranked by Bayesian information criterion (BIC) from acoustic data collected off the Eastern Shore of Virginia, USA, 2012–2019. Displayed are the model names and numbers as referenced in Table 2-1, approximate degrees of freedom, $-\log(\mathcal{L})$, BIC, and ΔBIC .

Model Name (Model Number)	df	$\log(\mathcal{L})$	BIC	ΔBIC
Ordinal date by roosting habitat (2)	18	-2798.92	5758.08	0.00
Ordinal date only (1)	14	-2834.04	5794.93	36.85
Ordinal date by site (3)	44	-2760.76	5906.33	148.25

Table 2-4. Top five competing post-hoc models ranked by Bayesian information criterion (BIC) from acoustic data collected off the Eastern Shore of Virginia, USA, 2012–2019. The model selection dredge contained all possible combinations of site (factor, 5 levels), smooth effects, $f(x)$, of ordinal date (1–365; one for each roost availability type [viable, limited]), and smooth effects of nightly mean pressure (mmHg), temperature (C), visibility (0-10 mi), and wind speed (m/s), total precipitation duration (hours), and change in pressure from the previous night. N/I indicates no inclusion in that particular model. We displayed the model degrees of freedom (df), BIC and Δ BIC.

Intercept	Site	$f(\text{Ordinal, by Roost Habitat})$	$f(\text{Press})$	$f(\text{Temp})$	$f(\text{Visib})$	$f(\text{Wind Spd})$	$f(\text{Precip Duration})$	$f(\Delta\text{Press})$	df	BIC	Δ BIC
-1.149	+	+	N/I	+	+	+	N/I	N/I	23	4557.7	0.00
-1.149	+	+	N/I	+	+	+	+	N/I	24	4563.8	6.09
-1.136	+	+	N/I	+	N/I	+	N/I	N/I	20	4567.5	9.82
-1.134	+	+	N/I	+	N/I	+	+	N/I	21	4569.1	11.37
-1.149	+	+	+	+	+	+	N/I	N/I	28	4579.8	22.12

Table 2-5. Beta parameters names, estimates, standard errors, and p-values for site-specific intercept modifiers in the final model fit using acoustic data off the Eastern Shore of Virginia, USA, 2012–2019. Estimates of β_1 – β_4 should be added to the intercept (β_0) to interpret the intercept modifying effect of the specific locality correctly.

β parameter	Estimate	Standard Error	Z-score	p-value
β_0 (Intercept, Cedar Island)	-1.170	0.086	-13.69	<0.05
β_1 (Assateague Island)	3.133	0.209	14.96	<0.05
β_2 (Hog Island)	-0.444	0.101	-4.38	<0.05
β_3 (Silver Beach)	0.311	0.113	2.74	<0.05
β_4 (Smith Island)	-0.335	0.104	-3.21	<0.05

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Chapter 3: Fall Migration, Oceanic Movement, and Site Residency Patterns of Migratory Bats on the Mid-Atlantic Coast with Emphasis on Eastern Red Bats (*Lasiurus borealis*)

Abstract

North America migratory tree bats (Genera: *Lasiurus* and *Lasionycteris*) are of increasing conservation concern due to wind-energy mortality threats. The mortality pattern is apparently seasonal as collision rates typically peak in fall during mating and southern migrations. Along the mid-Atlantic and Northeast coastline, large concentrations of eastern red bats (*Lasiurus borealis*) appear during fall migration and have been documented flying over the Atlantic Ocean that potentially could be vulnerable to rapidly expanding offshore wind-energy development. However, in the mid-Atlantic region where offshore wind-energy development is planned, little is known about most aspects of tree bat migration, in part because direct evidence (i.e., the tracking of individuals) has been difficult to obtain. Therefore, patterns in the migratory behavior during fall such as the timing of migration events, the existence of migratory pathways, consistencies in the direction of travel or relationship to atmospheric conditions remain speculative. However, the recently established Motus Wildlife Tracking System, an array of ground-based receiver stations on the Atlantic Coast, provides a new technique to track a large number of individual bats over long distances. To reveal patterns in migration, and understand drivers of over-water flight, I captured and radio-tagged 115 eastern red bats and subsequently tracked their movements throughout the mid-Atlantic region using the Motus system. For the bats with documented large movements, most traveled in a southwesterly direction whereby path vectors were often oriented interior toward the continental landmass rather than being oriented along the coastline. This observation challenges earlier beliefs that bats follow linear landscape features, such as the coast, when migrating. I documented bats traveling across wide sections of

the Chesapeake and Delaware bays confirming the species' ability to travel across large water bodies. This over-water flight behavior typically occurred in the early hours of the night and during favorable flying conditions such as low wind speeds, warm temperatures, and/or during sudden increases in temperature associated with the passage of cold fronts. For bats engaging in site residency through the fall, the proportion of night-hours in which bats were in a resting state (and possibly torpor), increased with colder temperatures and the progression of the fall season. My study demonstrated that bats potentially may be at risk to offshore wind turbine collisions off the mid-Atlantic, but that this risk might be minimal if bats are migrating toward the interior landscape rather than following the coast. Nonetheless, if flight over large water bodies such as Chesapeake and Delaware bays is a viable proxy for over-ocean flight, then collision risk at offshore wind turbines may be linked nightly to warm temperatures that occur early in the fall season. Risk, then, may be somewhat predictable and therefore manageable with mitigations options linking wind-energy operation to weather conditions and seasonality.

Introduction

Impacts to migratory “tree bats” (Genera: *Lasiurus*, *Lasionycteris*) from wind-energy development continue to be a conservation concern as this group comprises the majority of bat fatalities at wind turbine facilities in North America (Arnett and Baerwald 2013; Hein and Schirmacher 2016). There are population viability concerns for some tree bat species under continued wind-energy expansion scenarios (Frick et al. 2017). However, data on tree bats continues to be lacking, particularly in the study of movement ecology (Fleming 2019). Though they are varied in their continental distributions, the tree bats of eastern North America (eastern red bats [*Lasiurus borealis*], hoary bats [*Lasiurus cinereus*], Seminole bats [*Lasiurus seminolus*], and silver-haired bats [*Lasionycteris noctivagans*]) engage in northward movements in spring to

maternity areas and southward movements in fall to overwintering habitats (Cryan 2003; Johnson et al. 2011b; Perry 2018; Wieringa et al. 2021). Mortality from wind turbine collision generally shows this same pattern whereby mortality is elevated during spring migration (April–May) but dramatically peaks during late summer into the fall migration and mating period (late July–October; Arnett et al. 2008; Arnett et al. 2015; Thompson et al. 2017).

On the mid-Atlantic and Northeast coasts, eastern red bats appear to congregate in high numbers during fall as the Atlantic coastline is believed to be a migratory pathway for the species (Cryan 2003; Smith and McWilliams 2016; Dowling 2018; Wieringa et al. 2021). It is plausible that similar to birds, the coastline acts as topographic reference for navigation or that favorable atmospheric conditions lessen the energetic costs associated with traveling long distances (Alerstam and Pettersson 1977; Richardson 1990b; Shamoun-Baranes et al. 2017). Alternatively, or in conjunction, the coastline may serve as mating grounds for eastern red bats as Cryan (2008) noted that easily identifiable landmarks such as the coastline are used as breeding areas. Conversely, the fall increase in density may simply be coincidental as the geography of the Northeast restricts directed southern movement due to the position of the Atlantic Ocean to the east and south and the position of the Appalachian Mountains nearby to the west whereby migrating bats are funneled along the Coastal Plain during fall migration (Cryan 2003; Johnson et al. 2011a; Dowling 2018; Wieringa et al. 2021). As fall approaches winter, eastern red bats that spend the summer in the Northeast may only need to travel as far south as the mid-Atlantic Coastal Plain for over-winter habitat (Cryan 2003; Wieringa et al. 2021). Overwintering for eastern red bats is known and common in coastal Virginia (Whitaker et al. 1997; Reynolds and Fernald 2021), and (with increasing rarity) the higher latitudes of Maryland (Edward 2008), Delaware (H. Niederriter, Delaware Division of Fish and Wildlife, personal

comm.), New Jersey (Wieringa et al. 2021), and Long Island, New York (Gorman et al. 2021). As such, eastern red bats may only need to position themselves at or below these latitudes to survive the winter (Griffin 1970; Fleming 2019). Regardless, migratory activity occurs along the coastline in fall from the Northeast south to the mid-Atlantic.

Previously, most information about seasonal movements of bats has been based on banding studies or accumulations of anecdotal observations (Anthony 1923; Griffin 1970; Fleming 2019). Today, migration in bats is studied in three major ways: inferred seasonal movement of individuals using stable isotope analysis (Cryan et al. 2004; Britzke et al. 2009; Baerwald et al. 2014), the “active” tracking of individuals along migration routes via aircraft, drones, or ground-based vehicles using traditional very high frequency (VHF) radio transmitters attached to bats (e.g., Roby 2019; Roby et al. 2019), or the “passive” tracking of individuals along migration routes via stationary receivers using coded radio transmitters attached to bats (Jonasson 2017; Taylor et al. 2017; Dowling 2018; Jonasson and Guglielmo 2019). North American bat migration and movements are difficult to obtain because nearly all species do not weigh enough to attach modern GPS tracking devices that would enable timestamped location information on individuals to describe movement patterns. Although some work has been done with the larger bodied hoary bat (Weller et al. 2016), the lightest available GPS technologies still require transmitter reacquisition to download data. The long-distance flights that these bats can make and the unlikely recapture rate or dropped transmitter discovery effectively negates the utility of this approach even with large sample sizes.

The Motus Wildlife Tracking System (hereafter, "Motus"; Taylor et al. 2017) offers a novel approach to studying small animal migration as the system uses radio-transmitters, hereafter, “nanotags” (Lotek Wireless, ww.lotek.com; Cellular Tracking Technologies [CTT],

celltracktech.com) that are light enough (<1g) to affix to small bodied animals (e.g., birds, bats, and insects), and are relatively inexpensive (\$175-\$200 USD) compared to GPS tags. This multi-partner, collaborative approach uses an array of ground-based VHF receiver-stations (hereafter, “towers”) to detect the VHF-pulse-emitting nanotags that are coded, enabling the ability to uniquely identify individual tags. These towers are typically tall structures with one or multiple (usually 2–4) directional antennas and a receiving electronic device (“receivers”) to log data. Therefore, as tagged animals fly within towers’ antenna ranges, the towers will record the tag, the timestamp, and the tag signal strength. If tagged animals fly within range of multiple towers, some inference can be made on the course-scale movement paths that were travelled (Baldwin et al. 2018). Researchers have demonstrated the utility of using this approach for bats as direct evidence of migration and their associated patterns have been described for silver-haired bats in the Great Lakes region (McGuire et al. 2012; Jonasson 2017; Jonasson and Guglielmo 2019) as well as eastern red bats in the Northeast (Dowling 2018).

The impetus for this study, however, is the knowledge that eastern red bats, as well as hoary bats and silver-haired bats have been anecdotally observed engaging in over-ocean flight during fall migration (Norton 1930; Peterson 1970; Cryan and Brown 2007; Smith and McWilliams 2016; Solick and Newman 2021). This is a potential conservation issue as offshore wind development is rapidly expanding and is predicted to increase 500-fold in total capacity off the mid-Atlantic and Northeast coasts in the coming years (Musial et al. 2021). There has been some investigation into the atmospheric factors that are associated with over-ocean flight to optimize migration strategies in both bats and birds (Hedenström 2009; Shamoun-Baranes et al. 2017). Instances of ocean-flying bats have been associated with the passage of weather fronts (Cryan and Brown 2007) and weather conditions such as warm temperatures, low (or profitable,

i.e., in the direction of travel) wind speeds, and minimal precipitation (Johnson et al. 2011; Sjollem et al. 2014; Smith and McWilliams 2016; True et al. 2021b). Oceanic bat flight has been shown to be somewhat predictable given the association with these conditions (Smith and McWilliams 2016; True et al. 2021b). Importantly, understanding the conditions that are optimal for over-ocean flight and hence potential collisions with offshore wind turbines could facilitate the creation of mitigation strategies such as a seasonal or condition specific “smart curtailment” strategy, demonstrated as potentially effective in other studies (Behr et al. 2017; Dowling 2018; Hayes et al. 2019).

The mid-Atlantic Coast remains an understudied region relative to tree bat migration during the fall season. Unknown factors that potentially can be addressed by Motus include but are not limited to: 1) the proportion of tree bats that engage in long-distance migration during the fall 2) the directions (i.e., bearings) of travel or the existence of migratory pathways in the region and 3) the seasonal timing of migration events as opposed to site residency or stopover. Additionally, the mid-Atlantic is unique in geography in that it contains two large water bodies, the Chesapeake and Delaware bays, that potentially impede the travel of bats. These water bodies are relatively wide (≥ 30 km) at many points and therefore, the drivers associated with transiting across (hereafter, “over-water flight”) may serve as a viable proxy for understanding drivers of over-ocean movement. Motus provides the ability to infer points in time that bats engage in over-water flight if a tagged individual is detected on one shoreline and then subsequently detected on the opposite shoreline in a short time period. Therefore, the atmospheric conditions and within-night timing drivers of over-water flight behavior can be linked to this behavior.

In addition to migration and over-water flight observations potentially gathered from Motus, a third, more localized approach may be possible if a tagged bat maintains a longer

residency within range of an individual Motus tower that allows for continual data recording. Accompanied with detections are time-stamped signal strengths. Therefore, if a bat is in active flight state, then, the angle, distance, and any obstructions between the tag antenna and the Motus tower are constantly changing, providing large variations of signal strengths per unit time. In this way, Motus also allows the inference of the underlying activity states (i.e., resting, or actively foraging) during site residency (Schofield et al. 2018). Understanding the underlying behavioral states of individuals as they relate to time of night or other atmospheric conditions along the Atlantic coastline would be particularly useful. For instance, if temperatures reduce, or storm conditions persist, bats may use intermittent torpor during the night to reduce energy expenditure during the migratory season (Baloun and Guglielmo 2019). The frequency of nighttime rest states may also increase as the season progresses. An increase in frequency of resting states during the night may indicate less risky times for bats resident along the coastline during fall.

During the fall of 2019 and 2021, I tagged 120 tree bats, mostly eastern red bats, with Motus nanotags along the mid-Atlantic Coastal Plain with efforts concentrated in southern New Jersey, Delaware, and eastern Virginia. In this study I had three objectives:

1. Categorize and summarize the movement behaviors of eastern red bats throughout the region by measuring: the proportion of bats that I gathered evidence of migration from, the bearings and pathways (inland or coastal) of migration, the minimum duration of residency post-capture, and the seasonal timing and demographic effects of each.
2. Measure the influence of atmospheric conditions and other potentially relevant variables on over-water flight behaviors of eastern red bats.

3. Measure the activity patterns of eastern red bat site residents throughout the fall season in relation to these relevant variables.

I restricted all formal analysis to the large sample of eastern red bats I gathered, but I described movements of other species as anecdotes. I hypothesized that eastern red bats migrating along the mid-Atlantic coast would travel in a southwest direction for fall migration and use the coastline to navigate through the region, but most bats would not travel long distances because much of the region is suitable for over-wintering or still occupiable in the early fall. As such, I predicted that bats would move along the coast, but that some bats would not engage in migratory flight and/or their site residency times will be generally longer than those observed at more northern latitudes. I also hypothesized that eastern red bats would at times move across large bodies of water, but that their movements would minimize energy costs associated with this behavior. I predicted that bat over-water bat flight would occur during favorable atmospheric conditions such as of low wind speeds, warm temperatures, and during periods after cold fronts had passed. Lastly, I hypothesized that tree bats would engage in increasing frequencies or lengths of time of prolonged rest states as the fall season progresses or during unfavorable weather events to minimize energy expenditure during prey-scarcities. I predicted that the frequency of rest states increases with the coming of winter, and during periods of high wind speeds and low temperatures.

Methods

Study Area

I conducted this study in the mid-Atlantic Coastal Plain regions of southern New Jersey and the Delmarva Peninsula in the late summer to fall periods (late July to mid-October) in 2019 and 2021. I refer to “southern New Jersey” as the portion that borders the Atlantic Ocean to the

east and the Delaware Bay to the west/southwest of Cape May, Atlantic, and Cumberland counties. This area is comprised of two primary ecoregions, both considered Coastal Plain, the Atlantic pine barrens and mid-Atlantic Coastal Plain (Woods et al. 2007). The pine barrens are relatively forested dominated by pitch pine (*Pinus rigida*) or mixed pine-hardwood forest types. Adjacent to the Atlantic Ocean and Delaware Bay shorelines, the landscape is dominated by intertidal salt marsh habitat that contains understory shrub-scrub habitat above the tidal zone. The chain of barrier islands that lines the Atlantic Coast in New Jersey largely is developed but tidal salt marsh systems are common. Interior towards the Delaware Bay, mid-Atlantic Coastal Plain habitat also is dominated by an admixture of mixed pine-hardwoods in the uplands and swamp forests in the bottomlands. A similar intertidal saltmarsh habitat exists along the shoreline of the Delaware Bay (Woods et al. 2007). To the south in Delaware, eastern Maryland and the Eastern Shore of Virginia, the Delmarva peninsula is the landscape that is bracketed by the Delaware and Chesapeake bays. Though largely dominated by agricultural land use, natural habitats on the Peninsula is comprised of habitats of warm-temperate upland and bottomland mixed pine-hardwood forest, including considerable acreage of managed plantation loblolly pine (*Pinus taeda*). Similar to New Jersey, a string of barrier islands exists on its Atlantic coast, but south of Ocean City, Maryland, development is limited and habitats are dominated coastal shrub-scrub and intertidal salt marshes (Woods et al. 1999).

Climatically, this portion of the mid-Atlantic region is characterized by hot summers, and cool/cold winters which are generally colder at increasing latitudes. The region has a maritime influence due to proximity to the Atlantic Ocean meaning the annual temperature minima and maxima are less extreme relative to more inland, continental portions of the region (Odom and Ford 2020). Average winter temperatures in the coldest month of January are generally above

freezing at 0–3°C for southern New Jersey and the Maryland and Delaware portions of the Delmarva, and generally warmer at 3–6°C for the Eastern Shore of Virginia and the Virginia coast (Hart and Bell 2015). These temperatures are comparable to temperatures experienced by eastern red bats where they are resident in winter at inland, continental sites (Mormann and Robbins 2007).

Motus Tower Deployment, Mist-Netting, Nano-Tagging

The typical Motus tower is a tall structure or tripod system which is comprised of 2–4 antennas at the top and a receiver and other electrical parts at the base (Figure 3-1; Taylor et al. 2017). Antennas are typically 9-element, 5-element, or omni-directional and are tuned to detect very high frequency (VHF) emissions from radio transmitters usually at 166.38 MHz (Taylor et al. 2017). These small (<1g) radio transmitters (hereafter, “nanotags”) are attached to animals, emit this frequency, and are therefore detectable by Motus towers “listening” for this frequency (Taylor et al. 2017). Nanotags are uniquely coded transmitters that emit VHF pulses on 5, 7, or 10 second pulse intervals (i.e., the time between pulse emissions). These codes are unique in the timing of four sub-pulses that occur at microsecond intervals within each main pulse. Therefore, animals with nanotags are uniquely identified when they come within detection range of a tower (Taylor et al. 2017). Calibration studies suggest an average detection range of up to 12km for the 9-element Yagi antennas that most towers have (Mills et al. 2011; Taylor et al. 2011).

Motus is collaborative in that users of the network may access any user-deployed tag detections from towers that are deployed by other users. Motus towers are distributed throughout North America and the array is dense in the mid-Atlantic (Figure 3-2). In 2017, the region was well covered by towers along the coast, at inland sites, and surrounding the Delaware Bay, but coverage was less dense in Virginia, specifically at localities surrounding the Chesapeake Bay.

To increase my ability to detect movements, particularly cross-water transits in the southern portion of my study area, I deployed an additional seven towers in Virginia on the eastern and western shores of the Chesapeake Bay in 2017 and 2019 (Figure 3-2).

I captured bats in the late summer to fall periods (August–October) of 2019 and 2021 on a nightly basis from sunset to 3–5 hours after sunset as weather permitted. I used mist-nets (Avinet, Dryden, New York) of 4, 6, 9, and 12m lengths in double and triple high net set configurations (i.e., heights of around 10 and 15m respectively) over unimproved trails or roads. In 2019, I spent 10 nights in southern New Jersey from August 14–30, 10 nights on the Eastern Shore of Virginia during September 10–23, and 4 nights in coastal Delaware during October 10–15. In 2021, I spent 5 nights in southern New Jersey from August 2–5 and September 3 and 10 nights on the Eastern Shore of Virginia August 16–31 and September 1–3. I typically netted for bats as close as possible to active Motus towers, typically <12 km away, to maximize detection probability of bats post-release to measure the activity patterns of eastern red bat site residents.

During active netting nights, I identified bats to a species and sex. I used degree of epiphyseal fusion of the metacarpal-phalangeal joint to assign an age (adult or juvenile). I recorded other standard measurements such as weight (g), and length of forearm (mm; Kunz et al. 2009). I attached a nanotag (NTQB2-1 or 2-2, Lotek Wireless, Newmarket, ON, CAN), to all tree bats captured. I used a surgical cement (Perma-type surgical cement; Perma-Type, Plainville, CT) to glue the nanotag between the scapulae directly to the skin by parting any obstructing hair down the middle (Figure 3-3). Weight of the attached transmitter was always < 5% of body mass as recommended by Aldridge and Brigham (1988). All tagged bats were then released unharmed. All netting activities occurred under the approval of the Virginia Polytechnic

Institute and State University Institutional Animal Care and Use (IACUC) protocol #19-227 and all necessary State and Federal scientific collecting permits.

Analysis

Once all deployed nanotags were suspected to be depleted of battery and users of the Motus network had uploaded data to the database, I acquired all Motus tower detection data of deployed nanotags by using the R package *motus* (R Core Team 2021; Brzustowski and LePage 2020) and followed the data acquisition and cleaning methods of Crewe et al. (2018). The data structure was comprised of individual timestamped detections of pulse emissions from nanotags which were attached to bats. These observations were accompanied by the signal strength, the antenna that detected the tag, the antenna bearing, the tower location, and the tower name. I filtered out potential false-positive detections by reducing the dataset to retain detection run lengths (i.e., the number of sequential tag detections at a tower) that were > 3 . I considered detections from stations $> 1,000$ km away from either the point of release or subsequent Motus detections as false positives, and in doing so only used detections within the general mid-Atlantic region for inference on movements. I also visually inspected all paths for plausibility and filtered out detections whereby bats were calculated to travel at improbable speeds. I ensured that nanotags did not simply drop off bats near towers by manually inspecting signal strength versus time. I excluded the ends of deployment sections where the signal strength remained steady through time and had appeared to have fallen off.

Overall patterns

I began the analysis by describing the overall patterns of movement throughout the region. First, I noted the number of bats captured by species, sex, and age and described any temporal trends within. Then, I reported the proportion of bats that were detected at a Motus

tower post-release. Of those bats that were detected, I noted the proportion of bats that displayed evidence of migration. I defined evidence of migration as detection at one Motus tower (or release point) followed by detection at a different Motus tower >50 km away without the return to the original or nearby detection location as this is the threshold for non-sedentary behavior (Fleming 2019). For those bats that migrated, I described the general direction of movement by summarizing the bearing of travel (by recording the range, and mean, and visualized graphically). I then attempted to show evidence of the coastline as a migratory pathway by comparing the proportion of migration paths along the coastline to migration toward the interior landscape.

I assessed the proportion of bats that demonstrated site residency or migrated long distances or both. I defined evidence of site residency as detections from Motus towers that were <12 km away from the release point which contained subsequent daily detections as the bat remained in that local site >1 night. I defined minimum site residency time as the total days between the tagging date and the last date of detection at that tower. I summarized minimum residency times by examining the mean and 95% quantiles. I described migratory movement and minimum site residency time in relation to seasonal timing and demographics by visualization. I noted any novel, unique, or otherwise unexpected movement patterns observed in the movement paths or site residency behaviors. I calculated all of the above for eastern red bats, however due to sample size constraints, I only noted the migration paths or site residency times for other tree bat species as anecdotes.

Over-water behavior

I defined evidence of over-water flight as detections on one or more Motus towers that were separated in space by either the Chesapeake or Delaware bays, and in time by less than 9

hours. In these cases, I was reasonably certain that a bat flew above (i.e., did not transit around) either the Delaware or Chesapeake bays, and did this action within a single night. I compared the temporal trends of over-water flight and long-distance movements as over-water flight may have not necessarily been a migratory behavior by my definitions above. I considered the mid-point time between across-water departures and arrivals as instances of over-water flight. I used nearest whole hour and date as the resolution for positive instances of over-water crosses. I considered these instances as “used” (i.e., positive) points in a resource selection (use-availability) framework (Lele 2009). I used a random selection ($10\times$ the number of “used” points) that were available to individual bats to be used as background, “available” (i.e., negative) points. These points were restricted to instances of time between release and 40 days post-release to be reasonably certain that these instances were truly available.

Atmospheric conditions or the passage of weather fronts can influence the costs or benefits for bird and bats to engage in long-distance travel during migration (Cryan and Brown 2007; McGuire et al. 2012; Shamoun-Baranes et al. 2017), or in this case, across large bodies of water. Therefore, for both used and available points, I calculated the potentially relevant variable of hours since sunset (Gorman et al. 2021). In addition, I calculated the local atmospheric conditions which were a mix of instantaneous conditions (e.g., the current wind speed, temperature) or changes in conditions (i.e., an increase in pressure indicating the passage of a weather front). Because of potentially small sample sizes, I selected a relatively small amount of variables known or suspected to influence over-water flight in bats to ensure model convergence (Cryan and Brown 2007; Smith and McWilliams 2016). I selected instantaneous (hourly averages) conditions of wind speed (m/s), temperature ($^{\circ}\text{C}$), visibility (0–16 km), precipitation (accumulated cm), the longitudinal component of wind speed and direction (m/s), the latitudinal

component of wind speed and direction (m/s) and one-hour and 24-hour changes in these (Table 3-2). I selected these instantaneous conditions as they are believed to influence the activity of bats, specifically along the coast (Johnson et al. 2011; Smith and McWilliams 2016; True et al. 2021b). I also considered a set of variables calculated as the change from 1 or 24 hour increments including the 1 hour change in wind speed (m/s), the 1 hour change in temperature (°C), and the 24 hour change in pressure (Δ kPa). These variables could indicate the passage of weather fronts (Richardson 1990a). For instance, a wind speed reduction, temperature increase, and a more gradual pressure increase may indicate a cold front had passed, that might therefore be associated with favorable flying conditions (Cryan and Brown 2007; Smith and McWilliams 2016; Shamoun-Baranes et al. 2017). For all measurements of atmospheric condition variables, I used the nearest available weather station available on Visual Crossing (visualcrossing.com/weather-data; Visual Crossing, Hamburg, Germany; accessed October 1, 2021).

To test the influence of within-night timing, current atmospheric conditions, and the passage of weather fronts on the over-water flight of eastern red bats, I used generalized linear mixed models (Nelder and Wedderburn 1972; Gilmour et al. 1985) in the R package *lme4* (Bates et al. 2015), using the binary response of “used” instances of over-water flight and “available” instances of suspected non-flight. This model was generalized in that it contained a logit link function. I treated the variables of hours since sunset and the atmospheric variables as fixed effects and a unique nanotag ID as a random effect. I performed a “dredge” using R package *MuMIn* (Barton 2020), which created a large set of independent models composed of all possible combinations of variables and ranked each model by AICc (Burnham and Anderson 2004). I retained all models within $< 2 \Delta$ AICc points as competing models. Within this set, I selected the

top model (where $\Delta AICc$) unless it could not be interpreted biologically (Burnham and Anderson 2004). To visualize the relative probability of over-water flight by tree bats, I calculated marginal effects for variables included in the top model. Marginal effects are predictions (and 95% predictive intervals) of the relative probability given a range of values for an explanatory variable while keeping all other variables at their means. I plotted these effects and visualized them graphically.

Site residency daily activity patterns

I defined site residency as detections at one or more Motus towers semi-continuously for multiple days. Therefore, this data provided consistent timestamped information on signal strengths (i.e., power detected from the tag) when the bat engaged in site residency. Signal strength readings from towers generally increase when a tagged bat decreases distance to a tower or when the butt end of the tag is pointing toward (rather than away) from the tower. Therefore, when a resident tagged bat was actively flying, the variability in the signal strength was expected to be higher because the attached transmitter was changing angles, heights, and distances in relation to the receiving tower and antennas (Schofield et al. 2018). In contrast, when the bat is remaining still (i.e., in rest or torpor), the variability of the signal strength readings was expected to be lower because the tagged bat is at a constant position, angle, and height in relation to the tower and antennas. Considering this, a tagged bat's daily activity patterns (i.e., the underlying "rest" versus "active" states) could be inferred based on the variability of the signal strength measurements.

To provide insights on the daily and seasonal activity patterns of bats that retain site residency throughout the fall, I reduced the entire dataset to contain only bats that retained site residency for >20 days, had consistent readings on a tower (i.e., very short and rare periods

without continuous detections), and had no major lags in data collection (i.e., > 2 sequential days without detection and signal strength readings). I scaled signal strength readings by dividing tower- and antenna-specific data by their standard deviations for consistent scales across towers. I then binned signal strength readings of individual by hour and calculated the hour-by-hour standard deviations of scaled signal strengths across individual antennas. If the bat was recorded on multiple antennas, I averaged the signal strength standard deviations across all antennas that recorded the bat. I required at least 20 individual detections within any hour and antenna to calculate these standard deviations. Therefore, for each bat within the subset, I created a discrete time series of hour-by-hour signal strength standard deviations.

To estimate the underlying state (i.e., “resting” or “active”) during the time series of detections for each bat I used hidden Markov models (HMMs; McClintock et al. 2020). In ecology, HMMs attempt to decouple the relationship between an underlying ecological process (e.g., a time series of discrete states such as “rest” or “active”) and the potentially noisy observations that result due to those processes (e.g., a time series of continuous observations such as signal strength standard deviations; Figure 3-4). The time series of ecological states are unobservable directly such that the states are inferred as hidden or latent based on the observations (Figure 3-4). In a two-state system, a 2×2 transition matrix dictates the switching of states between discrete time steps which contains the probability of transitioning from state 1 to state 2, state 2 to state 1, or staying in the same state (Figure 3-4). I used the R package *depmixS4* to create 2-state HMMs (Visser and Speekenbrink 2010). The HMMs in this R package are refined such that the transition matrix can be regressed (i.e., generalized logistic with a logit link function) against time-varying covariates. In this case, the probability of transitioning between

active and resting states should vary with the diurnal cycle of arousal during or around sunset and then resting/roosting at some time before sunrise for nocturnal bats (Nocera et al. 2019).

Because each bat and tower are unique and the model cannot incorporate random effects, I modelled each bat individually. I fit each model using signal strength standard deviations as the response and used transition matrix covariates of a cyclical transformed hours since sunset (0–23), which was both sine and cosine transformations that varied sinusoidally from -1 to 1 on a 24-hour period. I used this variable to increase model stability which would mimic the diurnal pattern of rest and nocturnal pattern of rest for bats. However, this would not negate the ability for the model to detect periods of rest during the night or alternatively, but perhaps more rarely, periods of activity during the day. Once the models were fit, I predicted the underlying states for each hour using the function *posterior* in *depmixS4* which makes use of the Viterbi algorithm to predict the most likely state given the data (Forney 1973). I then filtered the data to contain night hours only and plotted each hourly state prediction against variables of date, hours since sunset, wind speed, and temperature, to visualize the conditions in which bats are most likely active or resting during night hours.

Results

Overall patterns

In the late summer to fall period (August–October) of 2019 and 2021, I caught and tagged 120 tree bats throughout southern New Jersey and the Delmarva Peninsula (Figure 3-4 and Table 3-1). In 2019, I tagged 22 eastern red bats in southern New Jersey, 19 eastern red bats and 1 Seminole bat on the Eastern Shore of Virginia, and 4 eastern red bats and 1 Seminole bat in Delaware (Table 3-1). In 2021, I tagged 40 eastern red bats and 2 silver-haired bats in southern New Jersey, and 30 eastern red bats and 1 Seminole bat on the Eastern Shore of

Virginia (Table 3-1). Over both years, I tagged 31 (26%) bats from August 1–14, 55 (46%) bats from August 15–31, 13 (10%) bats from Sept 1–14, 15 (12.5%) bats Sept 15–30, and 6 (5%) bats in October (Table 3-1).

Eastern red bats

I caught and tagged 115 eastern red bats during the study that accounted for ~ 95% of the total tree bat captures. The sex ratio (males to females) increased temporally through the tagging periods (Figure 3-6). Generally, I captured more males (75; 65%) than females (40; 35%). Most bats were adults (74; 64%) as opposed to juveniles (39; 34%) or unknown (2; 2%). In the region, 95 bats (83%) were detected post-release at at least one Motus tower in the region. Detection probability was related to proximity to a Motus tower as 83 (93%) bats were detected when released near a tower. In contrast, only 12 (46%) were detected when released >12 km from the nearest Motus tower.

Of the 95 eastern red bats detected, 29 (31%) displayed some migration behavior as indicated by deployment and subsequent detection >50 km away. The direction of migration was generally southwesterly as the mean bearing of travel was 230° (min = 179, max = 319; Figure 3-6). Bearings were concentrated in a southwesterly direction, but some directly south and northwest bearings of travel existed (Figure 3-6). Bats displayed both inland and coastal orienting when moving through the region. Most bats that migrated displayed the former approach such that 17 bats (58%) took an inland route whereas 12 bats (42%) took a coastal route. Three bats tagged in southern New Jersey appeared to have circumvented the Delaware Bay by travelling north along the Delaware Bay coastline instead of crossing the bay and travelling south. The last detection location of individual bats that showed evidence of migration ranged from coastal North Carolina (n = 2; 6%), Eastern Shore of Virginia (n = 6; 19%), west of

the Chesapeake Bay in Virginia or Maryland (n = 14; 45%), on the Delmarva Peninsula in Maryland or Delaware (n = 7; 23%), and New Jersey (n = 2; 6%).

For most bats, however, I did not find evidence of migratory behavior during the study period. For bats that were tagged near Motus towers, 84 (89%) were residents post-release as indicated by remaining at the capture site for more than one night. Mean minimum site residency time was 15 days (0.05 and 0.95 quantiles [2, 32]). Site residency time appeared to be related to the month in which the bats were tagged as mean residency time was lower for bats tagged in September (11.3 days) versus those tagged in August (15.5 days; Figure 3-8). There were no obvious trends in migratory status or minimum residency time in relation to sex or age in our sample of tagged bats as the proportions were relatively even for each documented behavior. I observed a novel behavior in some bats whereby a small proportion engaged in long distance travel (>30 km), were documented on multiple non-local Motus towers, and some days later returned to the original tagging site. This behavior was documented in 7 bats (6%).

Silver-haired bats and Seminole bats

For the two other species I captured, Seminole bats (n = 3, adult females) and silver-haired bats (n = 2, adult females), I documented some degree of migratory and site residency behavior. One silver-haired bat was tagged and released on September 3, 2021 and was never detected upon release in southern New Jersey at Peaslee Wildlife Management Area (WMA), Cumberland County, New Jersey (39.398, -74.907). One silver-haired bat was tagged and released on October 13, 2021 in southern New Jersey in Ducktown, Atlantic County, New Jersey (39.363, -74.433) and moved along the Atlantic coastline and across the Delaware Bay eventually transiting inland to Maryland by late October. Two Seminole bats were tagged on September 21, 2019, and August 31, 2021, on the Eastern Shore of Virginia at Savage Neck

Natural Area Preserve, Northampton County, Virginia (37.329, -76.008) and Chincoteague National Wildlife Refuge, Accomack County, Virginia (37.999, -75.279), respectively. However, there was no evidence of a migratory behavior. These bats displayed site residency for 8 and 17 days respectively, before contact was lost. One Seminole bat was captured on October 10, 2019, in southeastern Delaware at Assawoman Wildlife Management Area, Sussex County, Delaware (38.489, -75.077) and migrated south along the Atlantic coastline on the evening of October 28, 2019.

Over-water behavior

I detected numerous instances of eastern red bats transiting across the Chesapeake and Delaware bays, the behavior indicated by a Motus detection on one shoreline of either the Chesapeake or Delaware bays and subsequent detection on the opposite shoreline with a time lag of less than 9 hours (i.e., single night flights). Of the 99 bats that were detected at Motus towers, 31 bats (31%) displayed an over-water behavior as indicated by subsequent detections across water less than 9 hours apart. These movements were not necessarily migratory as some bats crossed the body of water, then returned to the originally detection locality either the same night or some night after. This over-water flight, as opposed to explicit migratory behavior, appeared to be loosely seasonally dependent as over-water behaviors peaked in the late August to early September whereas explicit migration events occurred relatively evenly throughout August to October (Figure 3-9).

I detected 39 instances of over-water flight to use as “used” or “positive” instances in the use-availability logistic models. I used 390 “available” or “negative” instances for potential non-use. No variable reductions were necessary due to multicollinearity. I compared 1,024 individual models from the dredge and found that 10 models were within 2 Δ AICc points (Table 3-3). I

selected the top model via minimum AICc, because every variable that was included could be explained biologically. For instance, my top model included effects of wind speed and hours since sunset which were negatively associated with use and included effects of longitudinal (x) component of wind speed and direction, latitudinal (y) component of wind speed and direction, and 1-hr change in temperature which were positively associated with use. Similar effects have been seen in other studies (Cryan and Brown 2007; Johnson et al. 2011; Smith and McWilliams 2016; True et al. 2021b) except for northeasterly winds, however these wind direction components were included in every competing model, and it was appropriate to include both latitudinal and longitudinal components of wind speed and direction. Over-water travel was positive and significantly ($\alpha \leq 0.05$) related to temperature, 1-hour change in temperature, and the latitudinal (y) component of wind speed and direction. Over-water travel was negative and significantly ($\alpha \leq 0.05$) related to wind speed, and hours since sunset. Upon using the model to produce marginal effects, I produced visualizations indicating a generally negative association between over-water flight and wind speed and hours since sunset (Figure 3-11). In contrast, I produced visualizations indicating a generally positive association between use and temperature and the change in temperature over a 24-hr period (Figure 3-11).

Site residency daily activity patterns

I documented four individual bats that retained site residency for long durations of time (≥ 14 days) and there was a constant collection of timestamped signal strengths from a nearby Motus tower. Two of these bats were tagged in 2019 and two were tagged in 2021. All bats were adult male eastern red bats. The data on timestamped signal strengths were recorded at the Motus tower at Savage Neck Natural Area Preserve, Northampton County, Virginia (37.329, -76.008) beginning on September 21, 2019 (for one bat) and August 18, 2021 (for two bats) and at the

Motus tower at Cape Henlopen State Park, Sussex County, Delaware (38.772, -75.086) beginning on October 14, 2019 (for one bat).

After I aggregated signal strengths on an hourly basis, the standard deviation of hourly signal strengths appeared to have reasonable degrees of separation between times I inferred that bats were in a rest state versus in an active state (i.e., during daylight hours, the standard deviation of signal strengths was lower than during night hours; Figure 3-12). However, some signal strength deviations were low during night hours, indicating possible rest states during night hours (Figure 3-12)

All four HMM models converged. When considering only nighttime hours when bats were suspected to be active, I found a general decreasing trend in the proportion of predicted hourly active versus rest states as time progressed from August to November (Figure 3-13A). The bats tagged in August were predicted to be active on nearly every night hour over the life of the nanotags. Conversely, the bats tagged in late September and October were predicted to be active at a lower proportion of night hours over the life of the nanotags (Figure 3-13A). I noted a short period of decreased proportion of night hours predicted to be an active state which coincided directly with temperatures falling from ~15–20°C to <10°C (Figure 3-13B). Generally, when considering only night hours, the proportion of active to rest states increased with temperature and decreased with hours after sunset and wind speed (Figure 3-14), though the effect of wind speed was not convincing. The most obvious effect therein was that of temperature which reduced the probability of being in an active state dramatically.

Discussion

This study marks the largest effort to date to study eastern red bat migration patterns along the mid-Atlantic coast with automated telemetry. It was the first to provide direct evidence

of migrating eastern red bats in the mid-Atlantic region that revealed patterns of fall movements. Throughout, my hypotheses were generally supported in that eastern red bats move throughout the region in a common southwesterly direction most likely to avoid cooler temperatures of northerly latitudes. However, when some bats migrated, other bats displayed lengthy site residency durations often the entire duration of the expected tag life or time to tag shed. This may suggest that in the mid-Atlantic, there is a delayed urgency or no need to migrate at least in the early to mid-fall period. This is at least true for the months of August and September when these bats were tracked. So, this hypothesis in the months of October and November remain untested with an appreciable sample. I documented that eastern red bats will readily travel across both the Chesapeake and Delaware bays, but as hypothesized, they do so relative to atmospheric conditions and within-night timing potentially to reduce energy expenditure. Lastly, I provided evidence that bats that engage in site residency will, at times during the night, switch to rest states (and perhaps torpor bouts) during periods of low temperatures similar to stop-over bouts of silver-haired bats in the Great Lakes region (Baloun and Guglielmo 2019; Jonasson and Guglielmo 2019). Proportion of the night in resting states also increased as the fall season progressed pointing toward an overall reduction in activity and energy expenditure as the fall continued toward winter.

Eastern red bats along the mid-Atlantic behaved in similar, but at times, contrasting ways than that of a similar study on the species that occurred at higher latitudes of the Northeast (Dowling 2018). For instance, in my study and that of Dowling (2018), eastern red bats engaged in long-distance migration, however the direction of travel, the timing, and the pathway of travel were highly variable. I found that a very similar proportion of bats that displayed evidence of migration compared to Dowling (2017), about 30%. I would have expected the bats tagged in

this study to show a lower proportion of migration because of the more southerly latitude and known over-wintering residency within the study area. However, the ratio of bats that displayed evidence of migration for both studies should be interpreted carefully as the combined probability of migrating and being detected while migrating is unknown and these probabilities could be different across the two studies because of Motus tower densities differences and the seasonal timing of tagging events.

For the eastern red bats showing evidence of migration, they did so with some degree of consistency. Some bats moved slightly north and west, presumably to avoid crossing large sections of either bay, however most bats moved through the region in a southwest direction. These observations also were consistent with Dowling (2018) in that bats from the Northeast travelled in a southwesterly direction albeit with some north bound outliers. My study contrasted, however, with Dowling (2018) who noted a more consistent coastline orientation of travel whereas the bats in this study used the coast at a lower rate. This effect could be explained by the fact that the geographic distance between two potential barriers, the coastline and the Appalachian Mountains, are closer in proximity in Northeast than that of the mid-Atlantic. Therefore, migrating bats may be able to disperse more widely (i.e., have a wider range of possible bearings of travel) once they reach southern New Jersey or the Delmarva Peninsula because the distance between the movement-restricting coast and mountains is larger. In other words, the eastern Coastal Plain and Piedmont provides a path of least resistance between the mountains and sea, which in the mid-Atlantic is larger in extent than the Northeast, therefore migrating bats can fly in a wide array of directions once in the mid-Atlantic. In addition, the lack of coastal movements in the mid-Atlantic may suggest that the Northeast coastline is used by a higher proportion of the regional population of eastern red bats than the mid-Atlantic coastline.

Accordingly, it is possible that tree bat population viability is most at risk due to collisions with Northeast offshore wind turbine facilities than those planned for the mid-Atlantic.

Less than half of bats that were documented migrating used the mid-Atlantic coastline as a migration route. This challenges traditional assumptions that bats use linear features as a reference for migration. Recent studies have also refuted this assumption and concluded that inland bats do not necessarily use linear features such as rivers to the degree previously thought (Krauel et al. 2017; Cortes and Gillam 2020). Yet, because of seasonal increases in activity larger than expected along the mid-Atlantic coast (Johnson et al. 2011; True et al. 2021b), this assumption remains operative (Wieringa et al. 2021). Nevertheless, eastern red bat use of the shoreline on the Northeast may be higher proportionately than the mid-Atlantic because the mid-Atlantic offers a larger landscape and different landscape configuration suitable for migration that in turn may lead to a more widely distributed population in fall.

Eastern red bats in my study did show much higher average minimum site residency times, (15 days) than the bats in the Northeast (6.9 days) reported in Dowling (2017) whom also tagged most bats close to Motus towers to measure minimum site residency time. This finding may support the point that, at the more southerly latitude of southern New Jersey and the Delmarva, the need to migrate simply is less critical, or that large-scale movements happen at later dates than when we tracked bats. Certainly, the region is warmer, and is more suitable for over-winter use than that of the Northeast (Wieringa et al. 2021), so it could be either that migration is not necessary, or that bats engaging in lengthy site residency times when I tagged them (in August and September) would travel a southwesterly distance later in the year.

Irrespective of the lack of migration routes along the coast and long residency times, I showed eastern red bats have the ability to travel over large areas of water suggesting some level

of risk at offshore wind turbines if this flight behavior is similar in timing and frequency to oceanic flight behavior. First, over-water flight appeared influenced positively by warm temperatures and low wind speeds which was expected as these are two atmospheric conditions that influence activity rates, specifically offshore, in bats (Sjollema et al. 2014; Peterson et al. 2016; Smith and McWilliams 2016; True et al. 2021b). In addition, the nightly timing of these events was informative as over-water flight behavior occurred typically in the hours following sunset. This effect is seen typically with bat activity onshore in that peak activity occurs directly following sunset (e.g Gorman et al. 2021). For bats offshore, there are more mixed results including activity occurring before sunset (Smith and McWilliams 2016) and in the early daylight hours (Hatch et al. 2013). Additionally, it was unexpected that eastern red bats disproportionately selected winds blowing from the southwest to the northeast (head winds) to fly over water. It is possible that some over-water flight is accidental due to disorientation in young migrants that is sometimes observed in young birds referred to as the “coastal effect” (Ralph 1978). Therefore, winds from the southwest blowing to the northeast could sweep unsuspecting bats out to sea. This is plausible as the opposite is true for westerly winds directing hoary bats over the Pacific (Cryan and Brown 2007). Nevertheless, it is known that birds will fly with a headwind if other conditions are otherwise suitable for migration (Shamoun-Baranes et al. 2017), so this wind direction observation could have been extraneous and irrelevant due to other prevailing calm conditions. In addition, the wind direction conditions at local weather towers could differ from the wind directions experienced by bats flying over water depending on the elevation of the flight path. I did not find pressure change (a proxy to the passage of a cold weather front) to be an informative predictor in the model as was noted by Cryan and Brown

(2007), however, it could be interpreted that the variable of the 1-hour change in temperature may be indicative of the clearing of cold fronts as associated with over-water flight.

The seasonal timing of over-water events generally peaked in late August to early September, whereas directed, explicit migration events were relatively evenly distributed throughout September when individual bats were equally able to demonstrate either, or both. On the Eastern shore of Virginia's barrier islands, True et al. (2021b) observed a similar effect in that barrier island visitation (which implies some degree of over-water flight) explicitly peaks in the late summer (~August 19). Similarly, in the same area, the over-ocean observations of eastern red bats in Hatch et al. (2013) occurred generally in early September. This effect could be simply a product of the generally warmer period of fall in August rather than late September. Indeed, I demonstrated that the proportion of night hours in a foraging, or "active" state generally decreases as the season progresses to October and November, so it is plausible that over-water flights would peak seasonally during periods when insect prey was still abundant and able to support the caloric demands of over-water flight. In addition, energetic costs associated with over-water flight might also be minimized by the generally warm period of late August.

Nevertheless, it remains to be unknown whether over-water movement over the Chesapeake or Delaware bays is a viable proxy for over-ocean movement. But, my results are somewhat consistent with the observations of other studies (Cryan and Brown 2007; Johnson et al. 2011; Peterson et al. 2016; Smith and McWilliams 2016; True et al. 2021b). It is believed that some combination of low wind speeds, high temperatures, after the passage of storm fronts, and/or early in the fall season is associated with high probabilities of bats engaging in open water flight (Solick and Newman 2021). Accordingly, wind turbine collision by bats may be highest during these conditions. As such, operational curtailment (i.e., the increasing of minimum wind

speed thresholds to rotate wind turbine blades), to avoid or reduce the number of bat fatalities annually may be effective for offshore facilities as demonstrated for inland facilities (Weller and Baldwin 2012; Arnett et al. 2015; Dowling 2018; Smallwood and Bell 2020). Informed and focused curtailment during periods of expectations of high risk, or “smart curtailment,” increasingly is being employed (Behr et al. 2017; Hayes et al. 2019; Farnsworth et al. 2021). For instance, at its simplest implementation, a wind operator may curtail during the fall as it is the highest collision risk seasonal period. A more complicated curtailment algorithm may include temperature or other weather conditions in setting nightly or weekly curtailment. At offshore wind facilities, then, managers could use the conditions that I found informative of over-water flight in eastern red bats to set curtailment standards at periods of expected risk in a relatively cost-efficient manner (Dowling 2018). However, my study did not explicitly assess risk to collision strike at project localities, and therefore, I suggest wind turbine managers first monitor for bats at project specific localities. Nevertheless, my study provides the likely conditions in which over-water flight is possible that can serve as a starting point for when wind-energy managers could focus monitoring efforts and potentially what to expect for the atmospheric, within-night, and within-season influences on collisions risk at offshore wind facilities in the mid-Atlantic.

I was not able to describe the overall patterns of migration with respect to timing, direction, and degree of over-water flight for other species of tree bats due to low capture rates. However, I did capture 3 Seminole bats and 2 silver-haired bats and tagged them as anecdotal information. Seminole bats are not common in mid-Atlantic region as their range is thought to be largely restricted to southeast Virginia (Perry 2018). However, I captured Seminole bats as far north as southern Delaware. True et al. (2021a) observed that the mid-Atlantic coast may be

more suitable for the species during the active season than previously thought. The observations and hypotheses of Perry (2018) which point to Seminole bats exhibiting migratory behaviors are corroborated by the evidence of a southward transiting Seminole bat along the Atlantic coast in late October. I was only successful in capturing two silver-haired bats, which was a surprise considering they are a species sometimes noted offshore along the Atlantic Coast (second only to eastern red bats; Solick and Newman 2021), the Eastern Coast is suitable for the species during the fall (Wieringa et al. 2021), and they historically have been observed in the region during the fall and winter (Cryan 2003). However, my capture effort was focused primarily in August and September, so it is possible that silver-haired bats may have not have arrived in appreciable numbers south of their maternity grounds when I netted. Anecdotally, it appears that the population increases in New Jersey in late fall due to emigrants as an annual influx of silver-haired bats are reported to rehabilitators in October (MacKenzie Hall, New Jersey Department of Fish and Wildlife Resources, personal comm.). The bulk of silver-haired bat winter distribution is predicted to be slightly more northerly, too (Cryan 2003; Wieringa et al. 2021). This might therefore explain the limited catches as the population density in the mid-Atlantic in early fall may be smaller in comparison to a more northerly latitude. Considering this, offshore wind collision risk, at least in the mid-Atlantic, may be lower or delayed for silver-haired bats compared to that of eastern red bats. However, I documented migration and an over-water flight behavior in one silver-haired bat in late October tagged along the New Jersey-Atlantic coast, so risk cannot be discounted.

The Motus Wildlife Tracking System is a viable and cost-effective approach to studying the migratory behaviors of animals that do not weigh enough for available GPS technologies. The system and its users certainly benefit in the form of cost-savings, and data sharing abilities

through the collaborative nature of the system. The system does suffer, however, from relatively course migration paths that result in unknown detection (and non-detection) probabilities. Additionally, I found that battery or computational failures occurred somewhat commonly which furthered my concern of somewhat unknown non-detection probabilities. Nevertheless, it comprises the best available technology for this and/or similar applications and therefore I encourage its use. As wind turbine development progresses offshore, the need to better understand the underlying biological drivers and patterns of movements throughout the continent for migratory bats is apparent (Goldenberg et al. 2021), as some species may become imperiled due to wind-energy development (Frick et al. 2017; Friedenber and Frick 2021). Although my study made some progress documenting migratory patterns, the development and execution of similar studies here and in other regions in the United States experiencing rapid wind turbine development is needed to inform the conservation and management of tree bat species.

Figures



Figure 3-1. A Motus tower located on the Eastern Shore of Virginia at the Virginia Tech Agriculture Research and Extension Center (VT AREC) property (37.59, -75.82). It was deployed in 2017 and equipped with three 9-element yagi antennas, a solar panel, and computational components (bin). Motus towers constantly scan and “listen” for (i.e., are tuned to a frequency) nanotags (coded very high frequency [VHF] transmitters) emitting a 166.38 MHz frequency registered to Motus (Taylor et al. 2017).

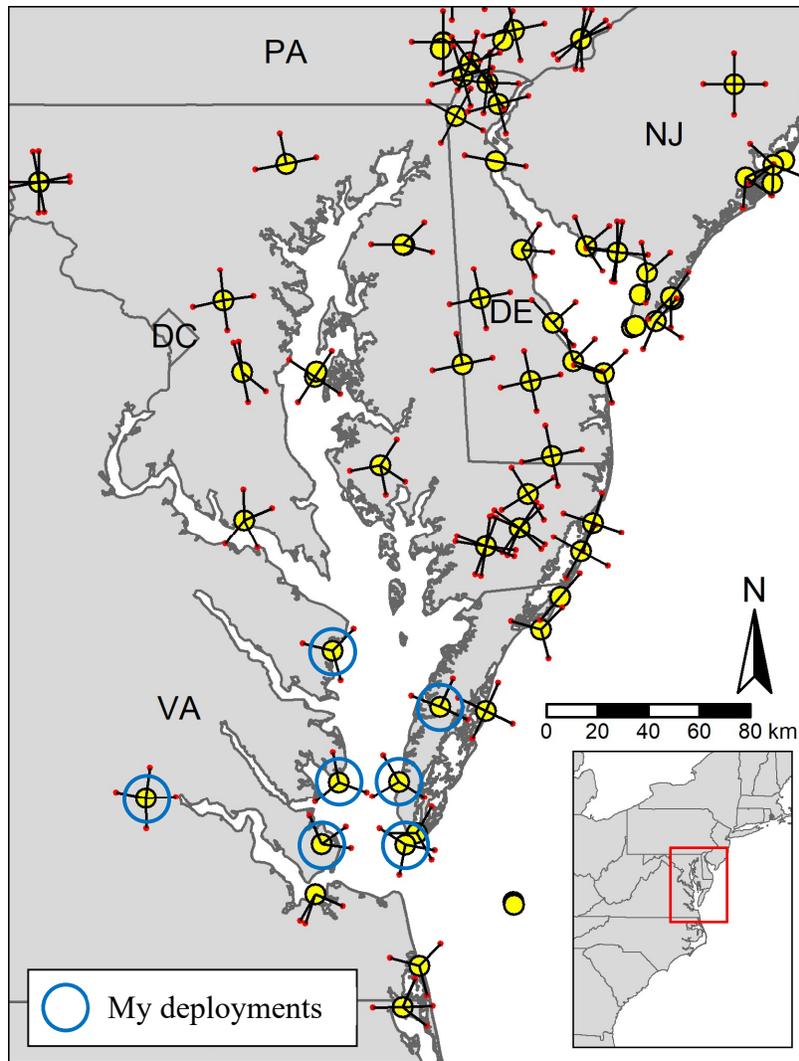


Figure 3-2. Motus (motus.org; [Taylor et al. 2017]) towers (yellow points) in the Delmarva peninsula and surrounding mid-Atlantic Coastal Plain active as of October 5, 2021. The Motus towers that I (or other Virginia Tech users) deployed are circled in blue. Motus towers are typically equipped with 2–4 5- or 9-element yagi antennas (black lines; see Figure 3-1) which are aimed at a certain bearing (black lines; 0–360°) and have a maximum detection distance of ~12 km (red points). If displayed towers do not have a bearing visualized with a black line it is equipped with an omnidirectional antenna.



Figure 3-3. A “nanotag” (top left, NTQB2-2, Lotek Wireless, www.lotek.com) is a uniquely coded very high frequency (VHF) transmitter tuned to the 166.38 MHz frequency of the Motus Wildlife Tracking System (motus.org; Taylor et al. 2017). I deployed nanotags by gluing the transmitter to the scapulae portion of tree bats (top right) in the fall periods of 2019 and 2021. I provide an example of a fully tagged eastern red bat (bottom; *Lasiurus borealis*) ready for release.

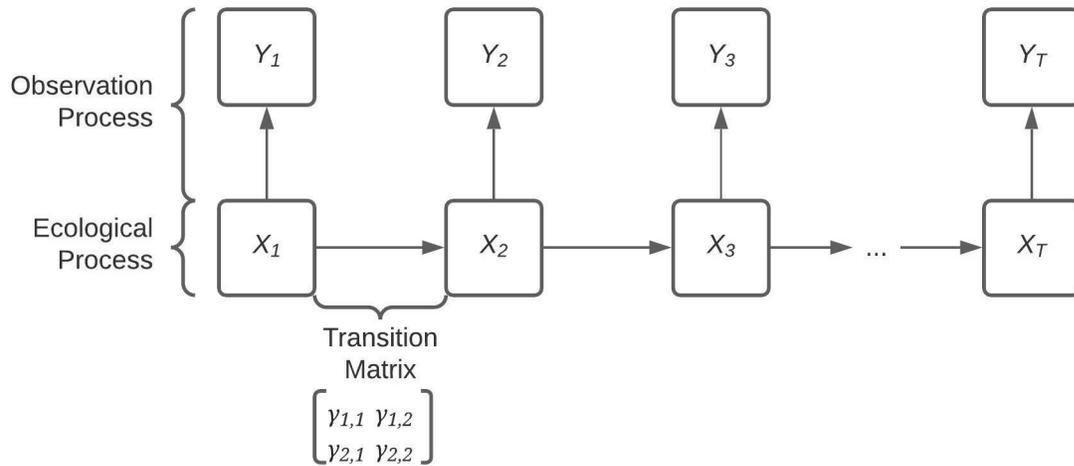


Figure 3-4. A flow chart of a typical two-state hidden Markov model (HMM) in ecology. In HMMs, an ecological time series $X_1 \dots X_T$ take on discrete latent (or “hidden”) states (i.e. “state 1” and “state 2”) which are directly unobservable at discrete time steps from $t = 1$ to $t = T$. State switching is determined by a 2×2 transition matrix, γ , such that it is a Markov process in which $\gamma_{i,j} = \Pr(X_{t+1} = j \mid X_t = i)$. Latent states give rise to a time series of observations in the data, $Y_1 \dots Y_T$. These observations are independent draws from a greater probability distribution such that $Y_t = f(y_t \mid X_t = N)$ for $N \in \{1, 2\}$. In the context of bats engaging in periods of site residency, which I tagged in the fall periods of 2019 and 2021 on the mid-Atlantic coast, bats are in discrete states of “rest” and “active” as part of the ecological process time series X , above, but is latent (i.e., unobservable directly). The transition matrix was regressed against and therefore mediated by a sinusoidally fluctuating time since sunset to mimic the diurnal and nocturnal patterns of active and rest states. The only observable time series, however, is Y , the hourly signal strength standard deviations at Motus towers.

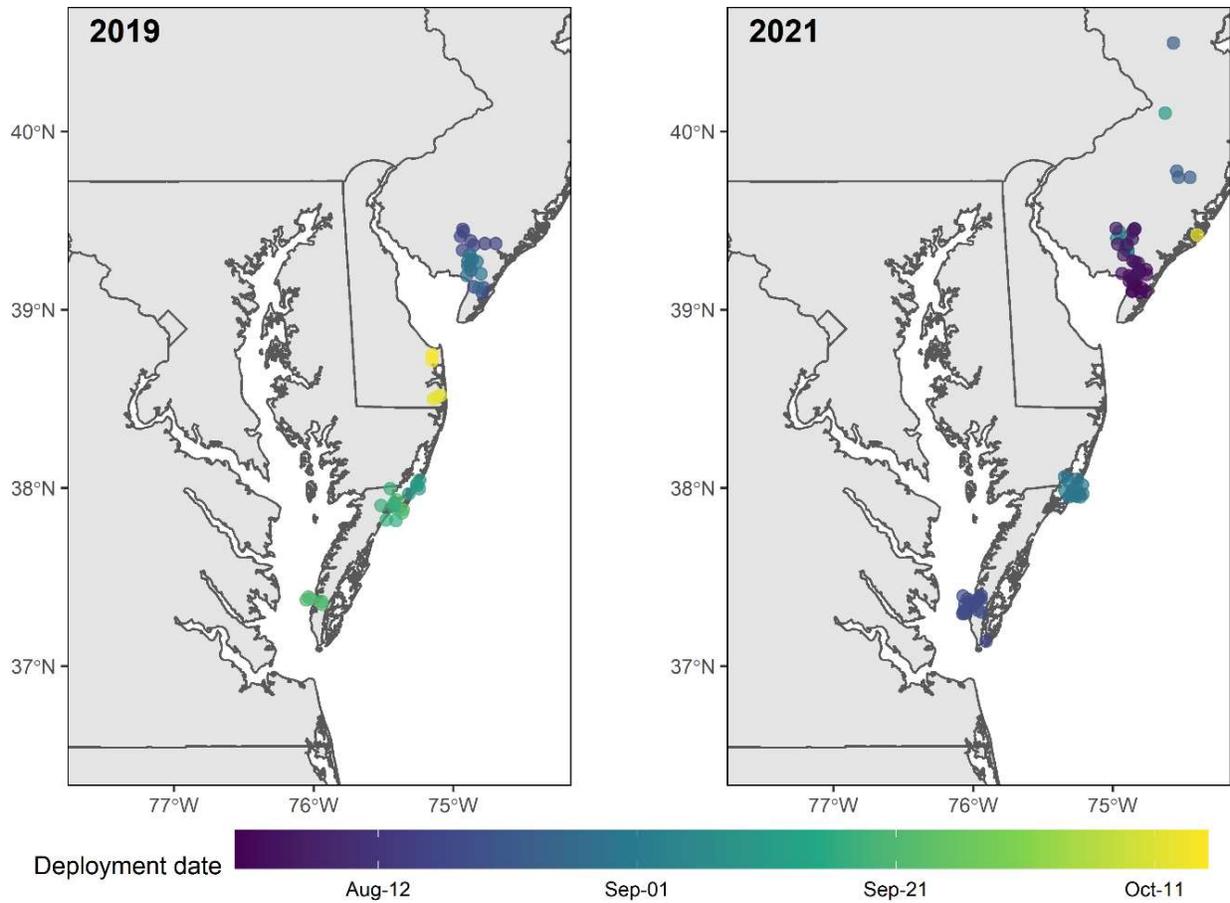


Figure 3-5. Locations and dates of active bat netting and deployment of nanotags on tree bats (*Lasiurus* and *Lasionycteris*) in southern New Jersey and the Delmarva Peninsula in the late summer to early fall period of August 1 to October 15 in 2019 (left) and 2021 (right). Generally, over the two years I began netting efforts in southern New Jersey and continued down the coast to finish on the Eastern Shore of Virginia. Delaware was the last locality sampled in 2019.

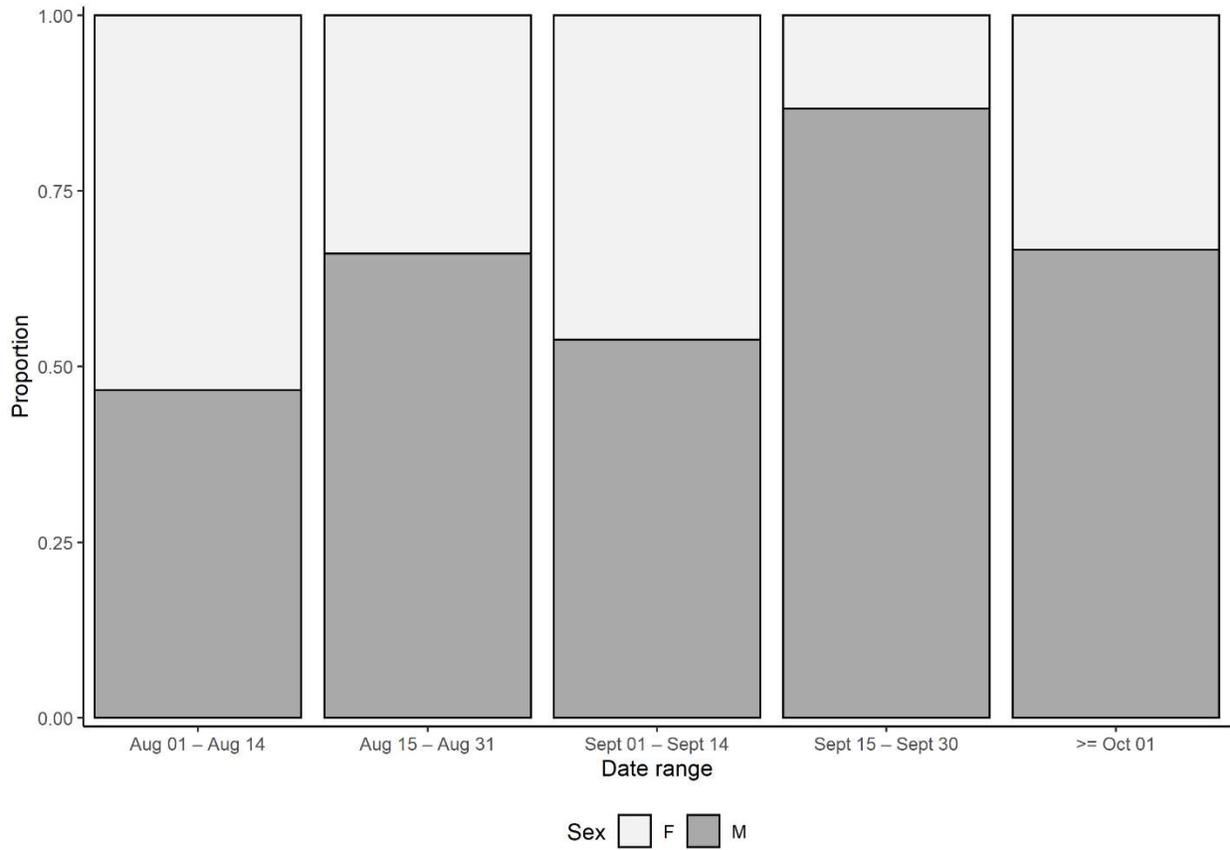


Figure 3-6. The sex ratio of tree bats captured and tagged throughout southern New Jersey and the Delmarva Peninsula August–October 2019 and 2021.

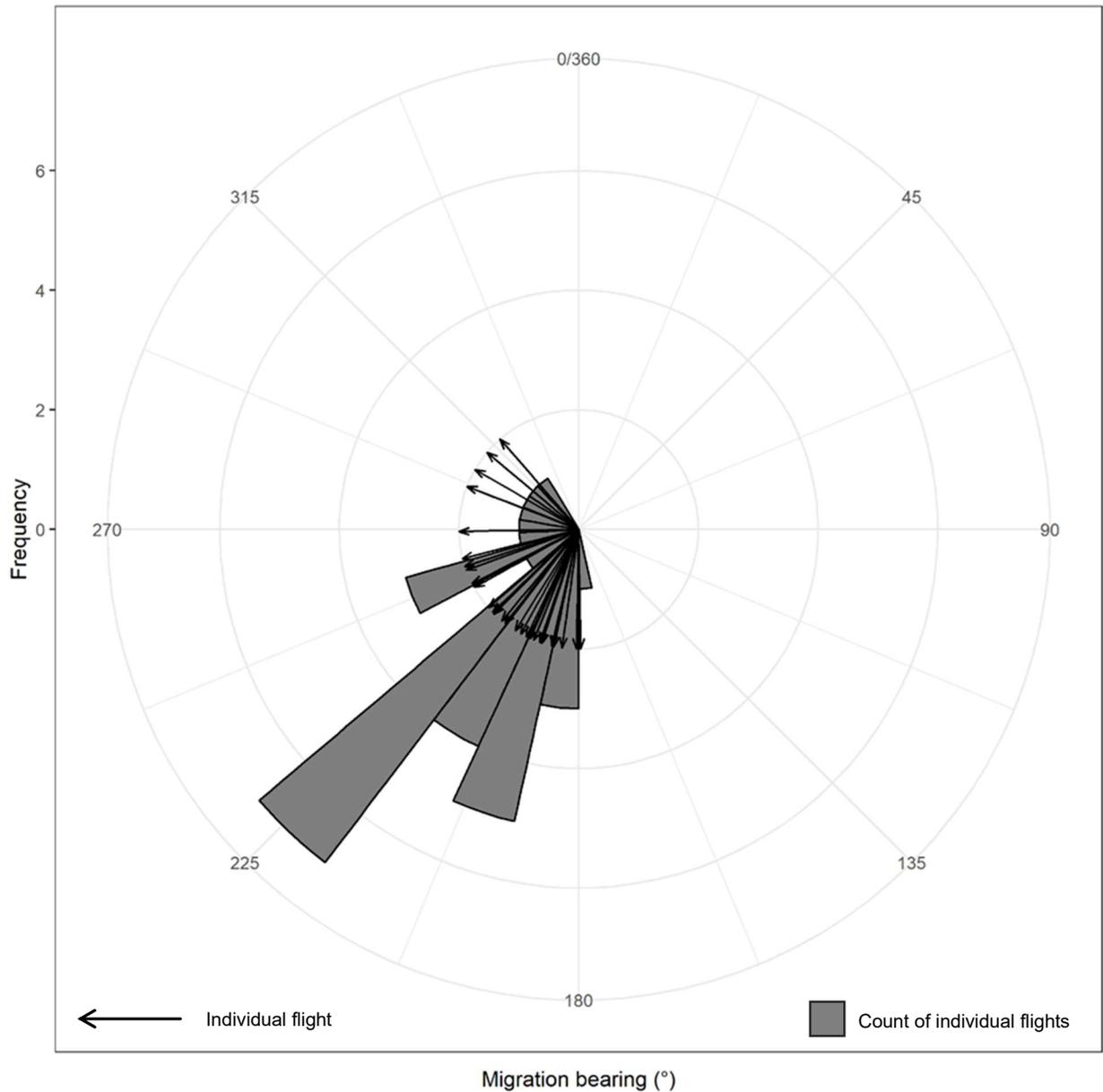


Figure 3-7. The bearings of migrating bats from their point of origin to their final detected destination based on detections off towers in the Motus wildlife tracking system collected on eastern red bats in the mid-Atlantic during fall of 2019 and 2021. This is displayed as an angular (0–360°) histogram which shows the frequency of bearings in histogram bins (grey boxes). The raw data (arrows) are displayed showing the flight bearings.

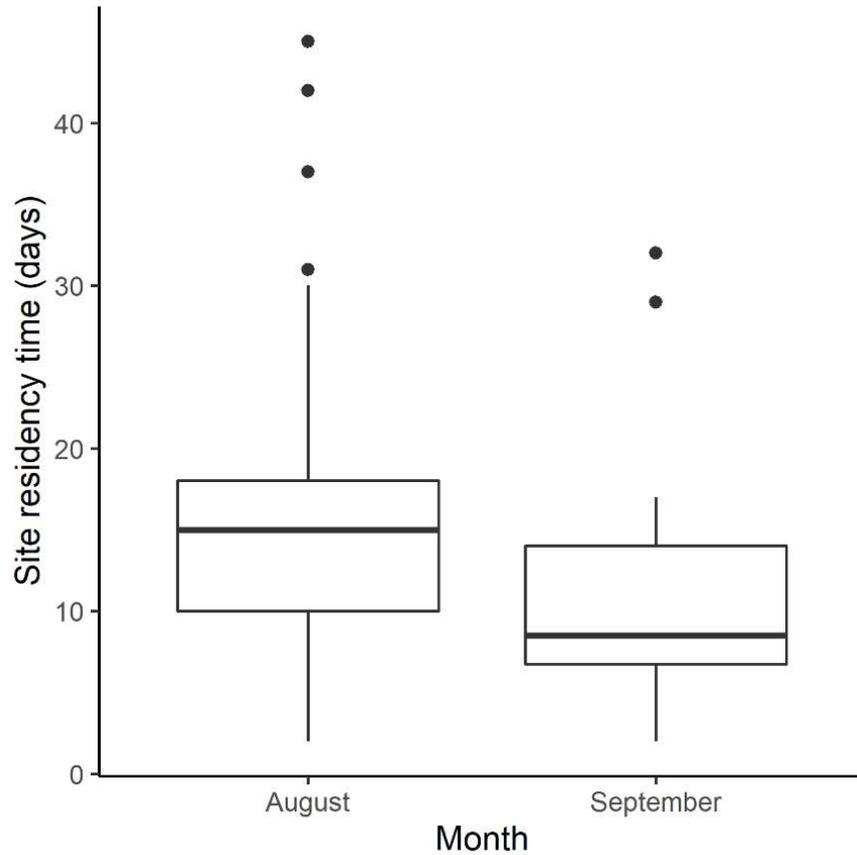


Figure 3-8. Minimum site residency times related to the month tagged from Motus telemetry data on eastern red bats in the mid-Atlantic in the fall of 2019 and 2021. Minimum site residency time was generally longer for bats tagged in August than tagged in September. Bats tagged in October are not displayed as they could be misleading due to low sample sizes.

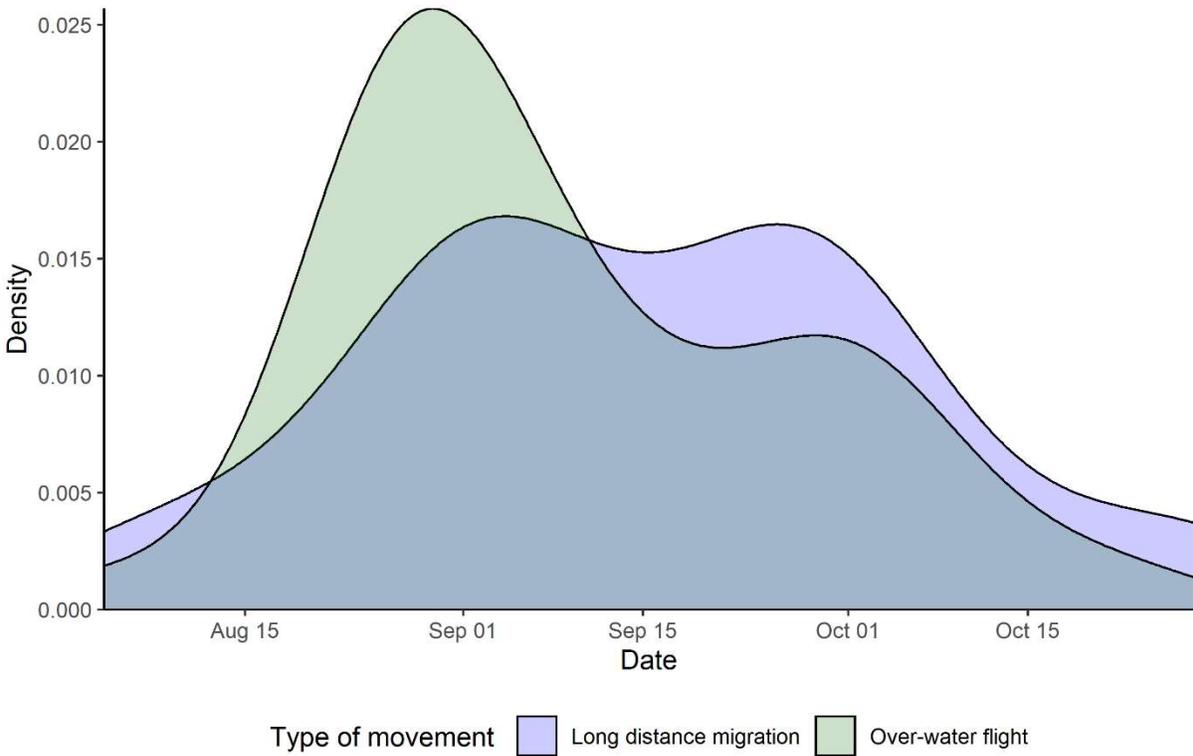


Figure 3-9. The density of long-distance migration events (blue curve) and over-water flights (green curve) and as they related to time of the year from Motus telemetry data on eastern red bats in the mid-Atlantic in fall of 2019 and 2021. Over-water forays distinctly peaked in late August to early September while long distance migration events were sustained from late August to early October. These curves should be interpreted with caution because tagging events were not evenly distributed through this period, so some bias may be present.

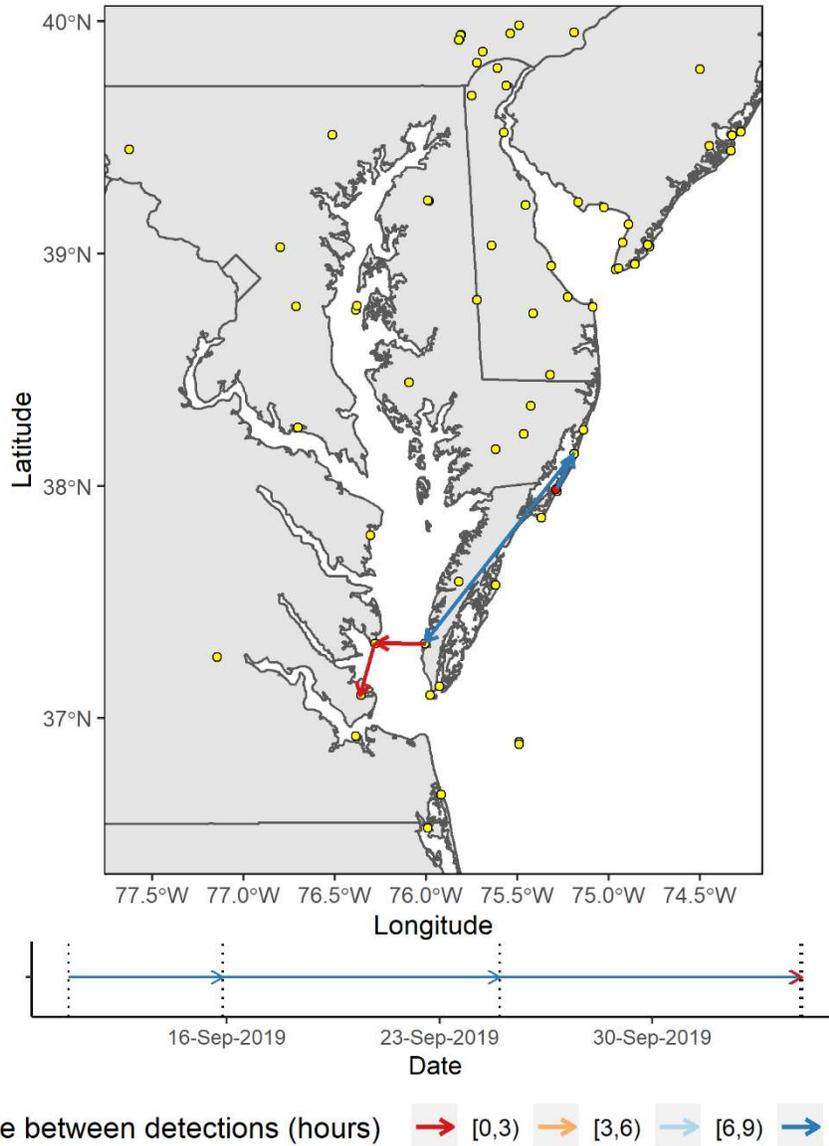


Figure 3-10. The migratory route of tagged bat #34845 (adult female eastern red bat [*Lasiurus borealis*]) displaying an over-water flight behavior. This map connects the coarse locations of individuals by connecting detections at Motus tower by line segmented arrows depicting the direction of travel which are colored by the time lag between detections (hours). The timeline of detections is displayed to assess the timing in these movements. This bat was tagged on September 10 on the Eastern Shore of Virginia and moved across the Chesapeake Bay in less than 3 hours on October 4, 2019.

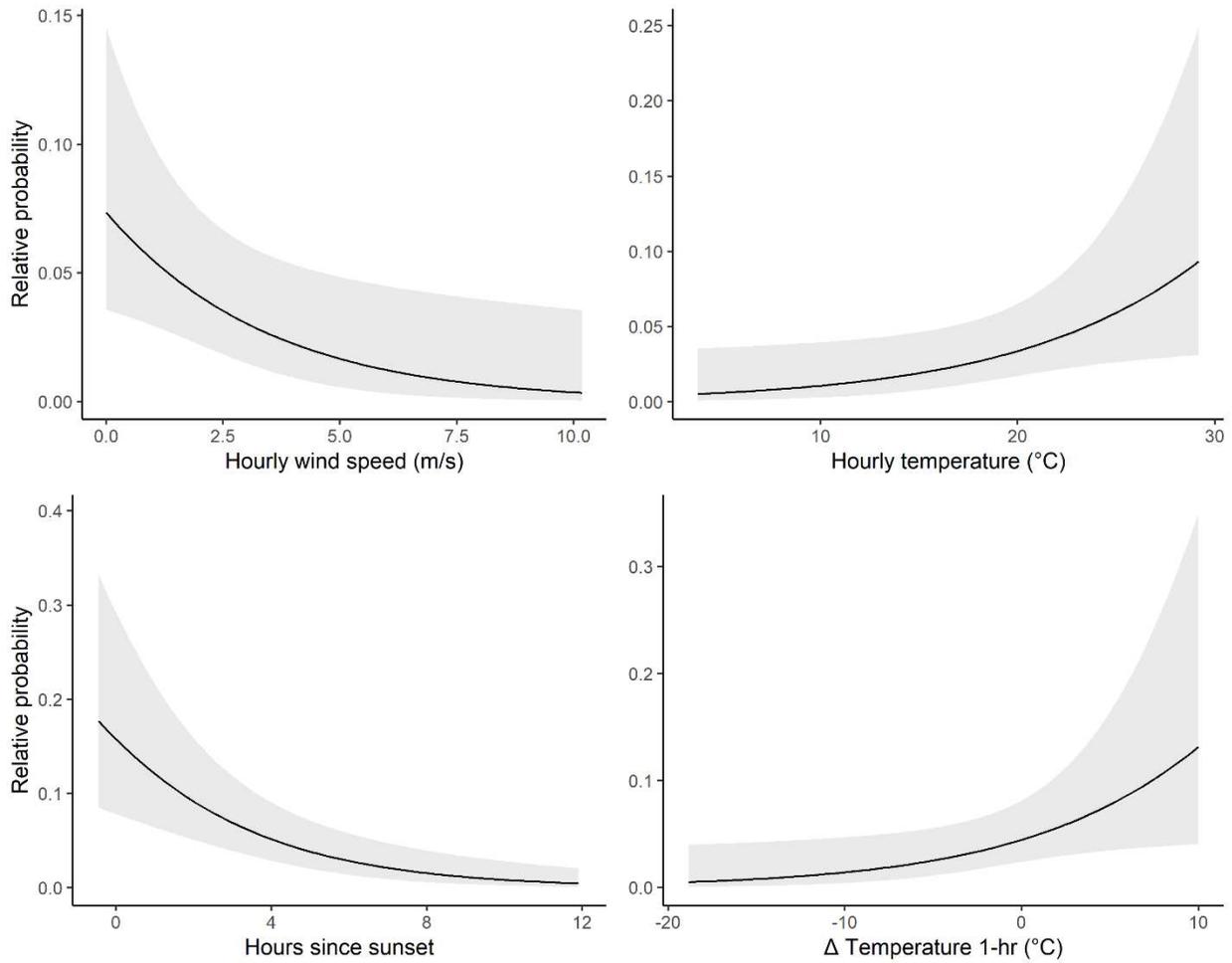


Figure 3-11. Selected marginal effects of the use-availability model of over-water flight given atmospheric conditions to visualize the effect of significant variables. Marginal effects are predictions of the relative probability of over-water flight of bats based on a single variable [each above] while holding all other variables at their means) The prediction estimate is displayed (black line) along with the 95% prediction interval (grey band).

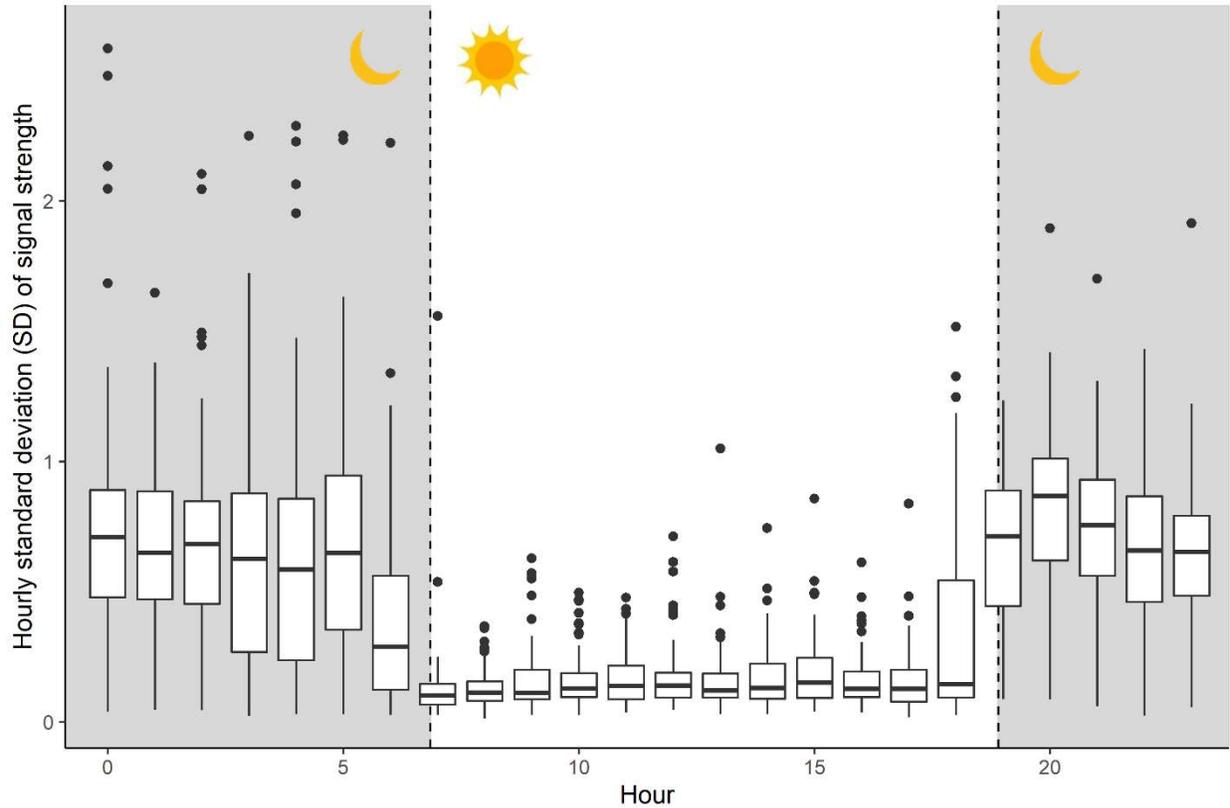


Figure 3-12. The standard deviation of signal strength on an hourly basis individual bats chosen for hidden Markov modeling from Motus telemetry data on eastern red bats collected in the fall of 2019 and 2021. Boxplots of signal strength standard deviations are separated by hour of the day (0-23) and shaded by night (moon symbol) or day (sun symbol). Night and day are separated by dotted lines as the mean sunrise and sunset time over the of the duration of the study.

Generally, the hourly standard deviation of signal strengths are larger for bats actively flying (i.e. in an “active” state) than those roosting, in torpor, or otherwise stationary (i.e. a “rest” state).

This is evident as when most bats were (most likely) in rest (daylight hours) there was generally low signal strength standard deviations. When most bats were active (night hours) there was generally high signal strength standard deviations. There is some overlap, however indicating that bats could be in a rest state during the night or in an active state during the day (pre-sunset times).

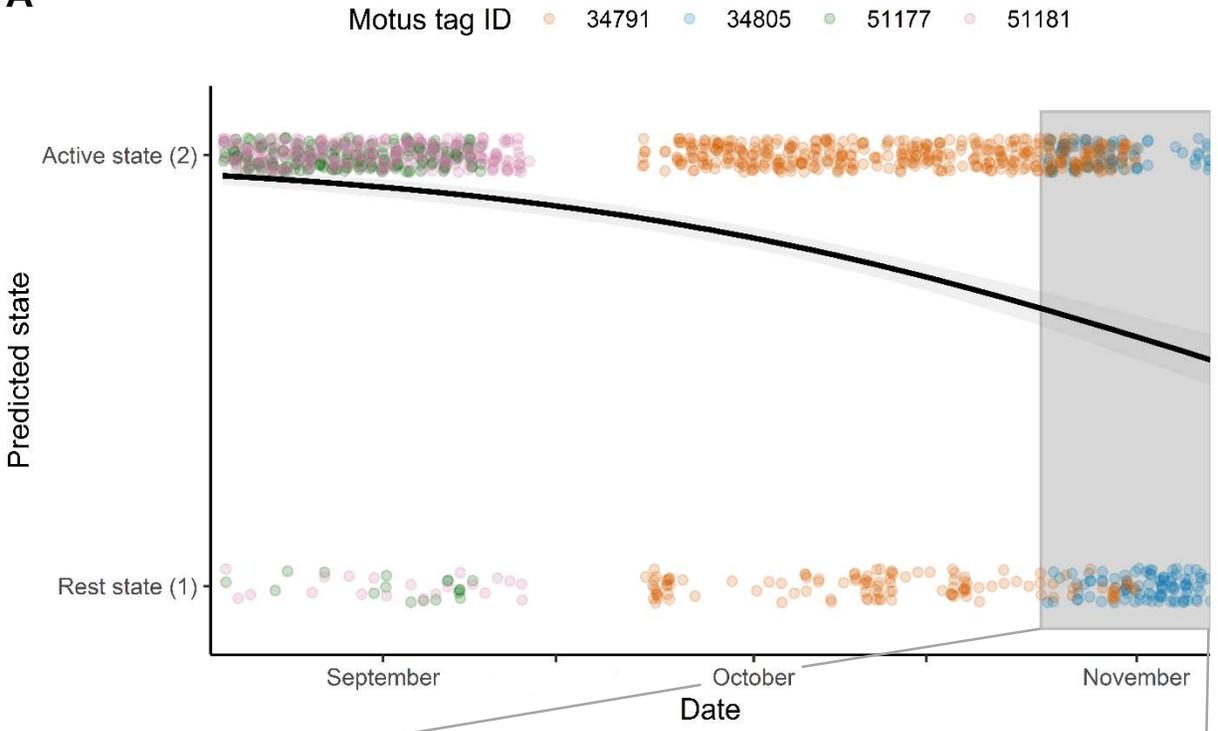
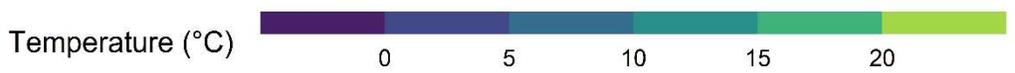
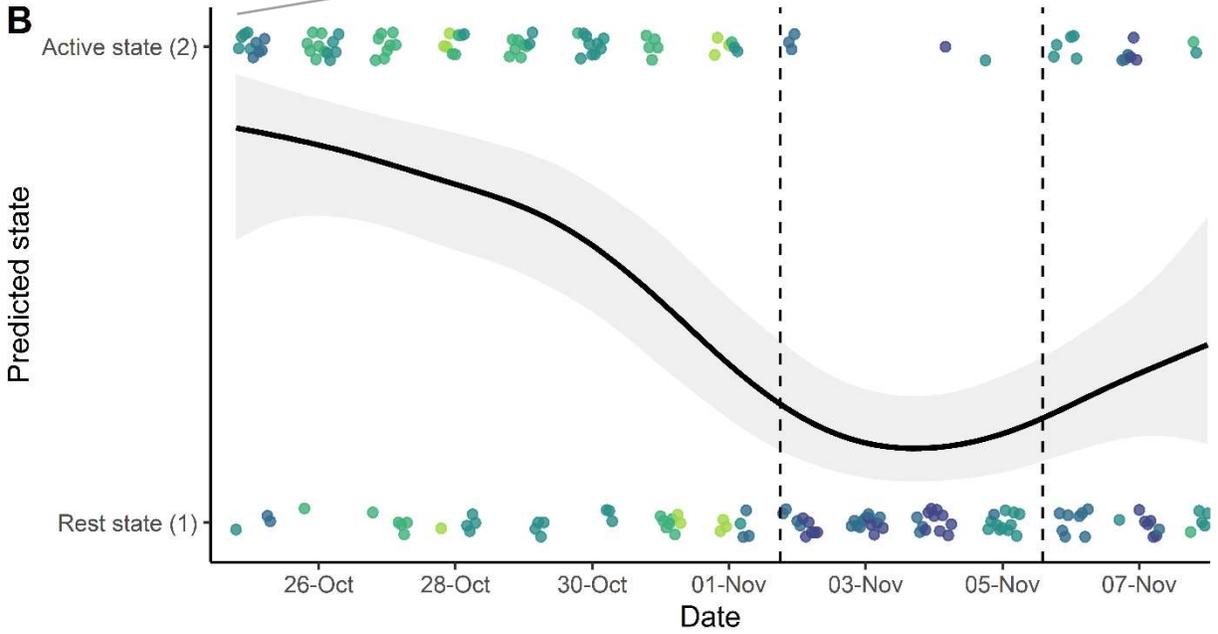
A**B**

Figure 3-13. A) The predicted state (rest [1], active [2]) of individual bats ($n = 4$; pink, green, orange, and blue points) from the hidden Markov model (HMMs) during night hours on hourly intervals versus date on a single calendar year from Motus telemetry data collected on eastern red bats in the fall of 2019 and 2021. Points are given a small amount of random variation for aid in visualization. A logistic regression line (black) shows the general trend from active to resting states as fall dates progress. **B)** A magnified version of the above showing Motus tag ID #34805 which undergoes a distinct period (between dotted lines) of rest states as temperature generally as temperatures (color bar) fall below 10°C in early November. Points are given a small amount of random variation for aid in visualization. A generalized additive logistic regression line (black) shows the smoothed proportion of active states from high to low (during the period between the dotted lines) and back to high as dates progress.

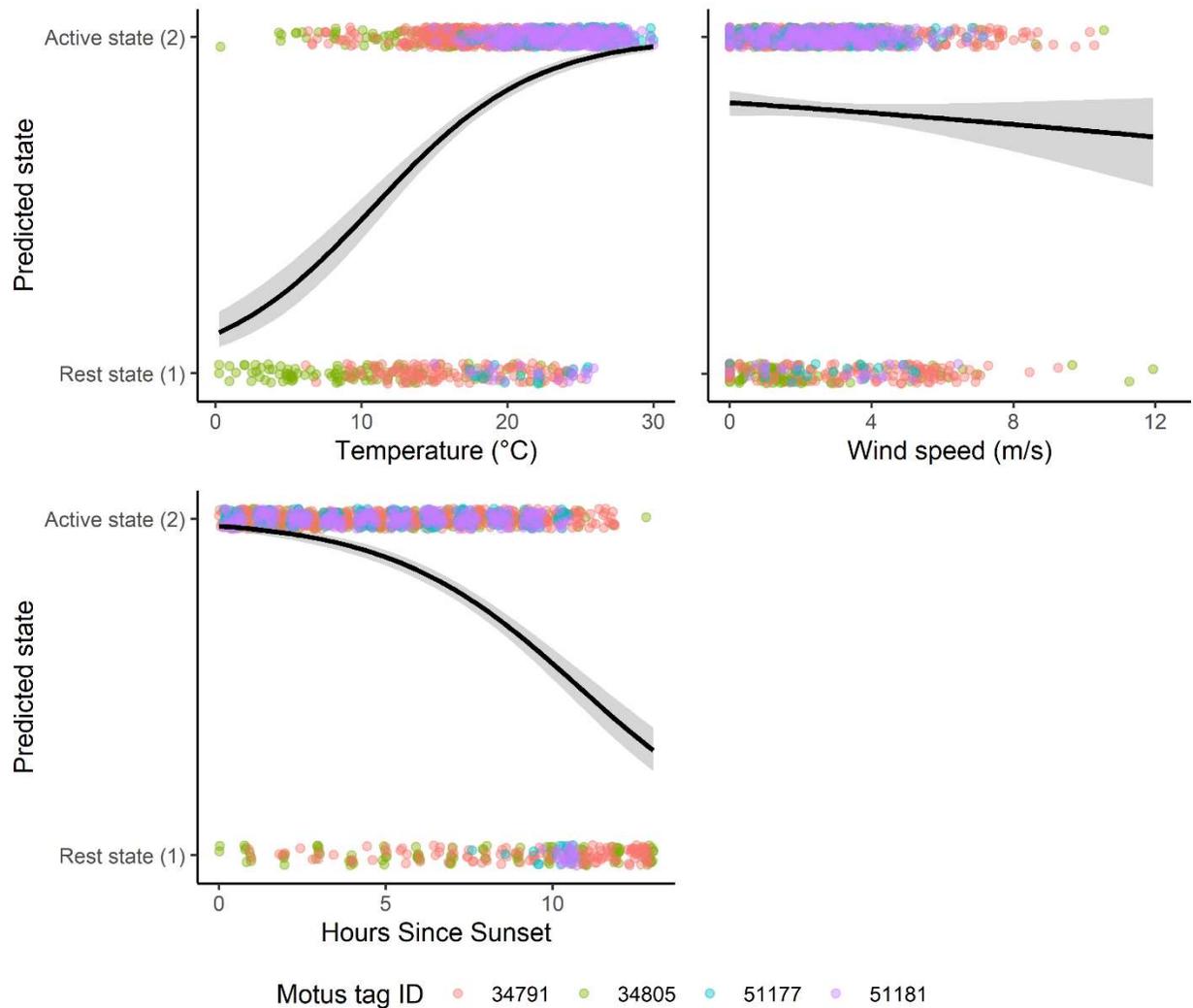


Figure 3-14. The predicted state (rest [1], active [2]) of individual bats ($n = 4$; pink, green, orange, and blue points) from the hidden Markov models (HMMs) formulated from Motus telemetry data on eastern red bats on the Delmarva Peninsula in the fall seasons of 2019 and 2021. Individual points states at hourly intervals during the night versus atmospheric conditions (temperature and wind speed; top row) and hours after sunset (bottom left). Points are given a small amount of random variation for aid in visualization. Logistic regression lines (black) show the general trend in the state versus the variable of interest.

Tables

Table 3-1. The locations and species of tree bats (*Lasiurus*, *Lasionycteris*) captured and tagged in southern New Jersey, Delaware, and the Eastern Shore of Virginia (Figure 3-4) in the fall periods (August–October) of 2019 and 2021. In total we captured 116 eastern red bats (*Lasiurus borealis*), 2 silver-haired bats (*Lasionycteris noctivagans*), and 3 Seminole bats (*Lasiurus seminolus*).

Year	Location	Number of bats tagged by species
2019	So. New Jersey	22 eastern red bats
	Coastal Delaware	4 eastern red bats; 1 Seminole bat
	Eastern Shore of Virginia	19 eastern red bats; 1 Seminole bat
2019 Total	All	48 eastern red bats; 2 Seminole bats
2021	So. New Jersey	40 eastern red bats; 2 silver-haired bats
	Eastern Shore of Virginia	30 eastern red bats; 1 Seminole bat
2021 Total	All	70 eastern red bats; 2 silver-haired bats; 1 Seminole bat
Grand total	All	116 eastern red bats; 2 silver-haired bats; 3 Seminole bats

Table 3-2. The variables, explanations, and expected associations used in modeling the relative probability of over-water flight by eastern red bats in the mid-Atlantic using data collected in southern New Jersey and the Delmarva Peninsula in the fall of 2019 and 2021.

Variable	Explanation	Expected Association
Wind speed	Hourly wind speed (m/s)	–
Temperature	Hourly dry bulb temperature (°C)	+
Precipitation	Hourly precipitation accumulated (cm)	–
Visibility	Hourly visible distance (0–16km).	+
Pressure	Hourly Barometric pressure (kPa)	
Longitudinal component of wind speed and direction	The longitudinal (<i>x</i>) component of the hourly wind speed (m/s) and direction (0–360°) vector. Positive values are easterly winds, negative values are westerly winds	–
Latitudinal component of wind speed and direction	The latitudinal (<i>y</i>) component of the hourly wind speed (m/s) and direction (0–360°) vector. Positive values are northerly winds, negative values are southerly winds	–
Δ Wind speed 1-hr	The change in wind speed (m/s) from the previous hour to the current hour	–
Δ Temperature 1-hr	The change in temperature (°C) from the previous hour to the current hour	+
Δ Pressure 24-hr	The change in nightly pressure average (Δ kPa) from the previous night to the current night	+

Table 3-3. Model selection table resulting from the dredge (comparison of all possible additive model combinations) using data collected from over-water movements by eastern red bats in the mid-Atlantic in the fall of 2019 and 2021. The first eleven columns represent β coefficient estimates in the logistic models as described in Table 3-2, of which each row is a unique model. Displayed are the competing models within 2 ΔAIC_c points. I displayed the model degrees of freedom (df), negative log of the Likelihood ($-\log(\mathcal{L})$), AIC_c , and ΔAIC_c . I used R package *MuMIn* for all modeling and calculations which defines AIC_c as $-\log(\mathcal{L}) + 2K(K+1)/(n-K-1)$, where K is the number of parameters and n is the sample size (Barton 2020).

Intercept	Hours Since Sunset	Wind Speed	Temperature	Visibility	Pressure	Lon. Comp. Speed	Lat. Comp. Speed	Δ Temperature 1-hr	Δ Wind Speed 1-hr	Δ Pressure 24-hr	df	$-\log(\mathcal{L})$	AIC_c	ΔAIC_c
-2.92	-0.31	-0.31	0.12	N/I	N/I	0.18	0.46	0.12	N/I	N/I	8	-95.69	207.73	0.00
-2.92	-0.32	-0.23	0.12	N/I	N/I	N/I	0.45	0.12	N/I	N/I	7	-97.08	208.43	0.70
-55.96	-0.32	-0.24	0.12	N/I	0.05	N/I	0.48	0.12	N/I	N/I	8	-96.19	208.73	1.00
-1.13	-0.32	-0.31	0.11	-0.11	N/I	0.18	0.44	0.12	N/I	N/I	9	-95.21	208.88	1.15
-3.20	-0.31	-0.26	0.12	N/I	N/I	0.17	0.47	0.12	-0.07	N/I	9	-95.37	209.19	1.46
-3.80	-0.32	N/I	0.13	N/I	N/I	N/I	0.39	0.12	-0.14	N/I	7	-97.47	209.22	1.49
-28.22	-0.31	-0.30	0.12	N/I	0.02	0.14	0.47	0.12	N/I	N/I	9	-95.54	209.53	1.80
-59.41	-0.34	-0.25	0.12	-0.13	0.06	N/I	0.46	0.12	N/I	N/I	9	-95.55	209.54	1.81
-1.09	-0.34	-0.23	0.11	-0.11	N/I	N/I	0.43	0.12	N/I	N/I	8	-96.60	209.55	1.82
-3.27	-0.33	-0.17	0.12	N/I	N/I	N/I	0.46	0.12	-0.09	N/I	8	-96.67	209.70	1.97

Table 3-4. The parameters, estimates, standard error, Z-statistic and approximate significance (*p*-value) of the top approximating model. The model was a use-availability logistic regression model (binary generalized linear mixed model) formulated from data on eastern red bats exhibiting over-water flight behaviors across the Chesapeake or Delaware Bays in the fall seasons of 2019 and 2021.

Parameter	Estimate	Std. Error	Z-value	<i>p</i> -value
β_0 (Intercept)	-2.92	1.36	-2.14	0.032
β_1 (Hours since sunset)	-0.31	0.08	-3.08	<0.001
β_2 (Wind speed)	-0.31	0.14	-2.26	0.024
β_3 (Temperature)	0.11	0.06	2.11	0.035
β_4 (Longitudinal component of wind speed and direction)	0.17	0.11	1.62	0.104
β_5 (Latitudinal component of wind speed and direction)	0.46	0.12	3.94	<0.001
β_6 (Δ Temperature 1-hr)	0.12	0.55	2.15	0.031

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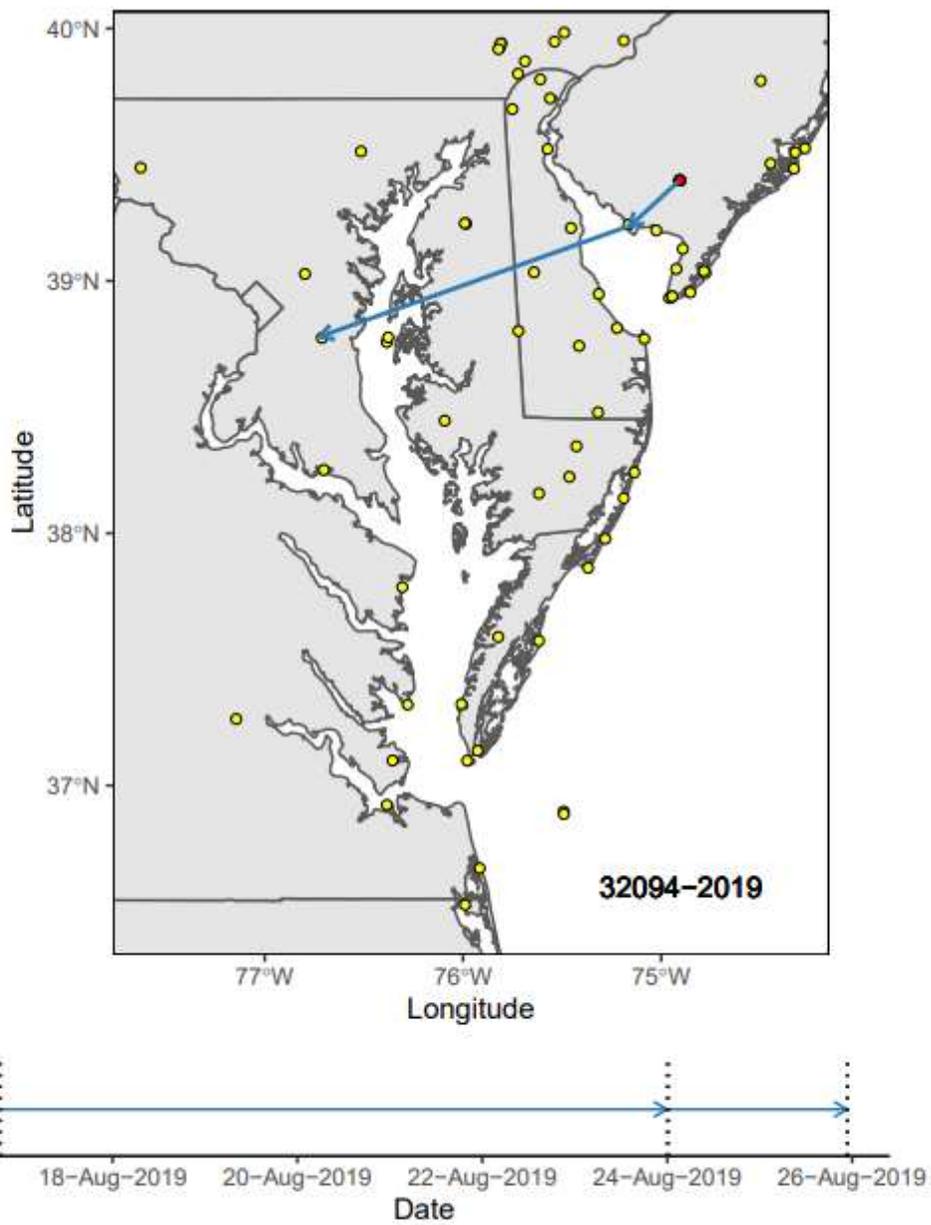
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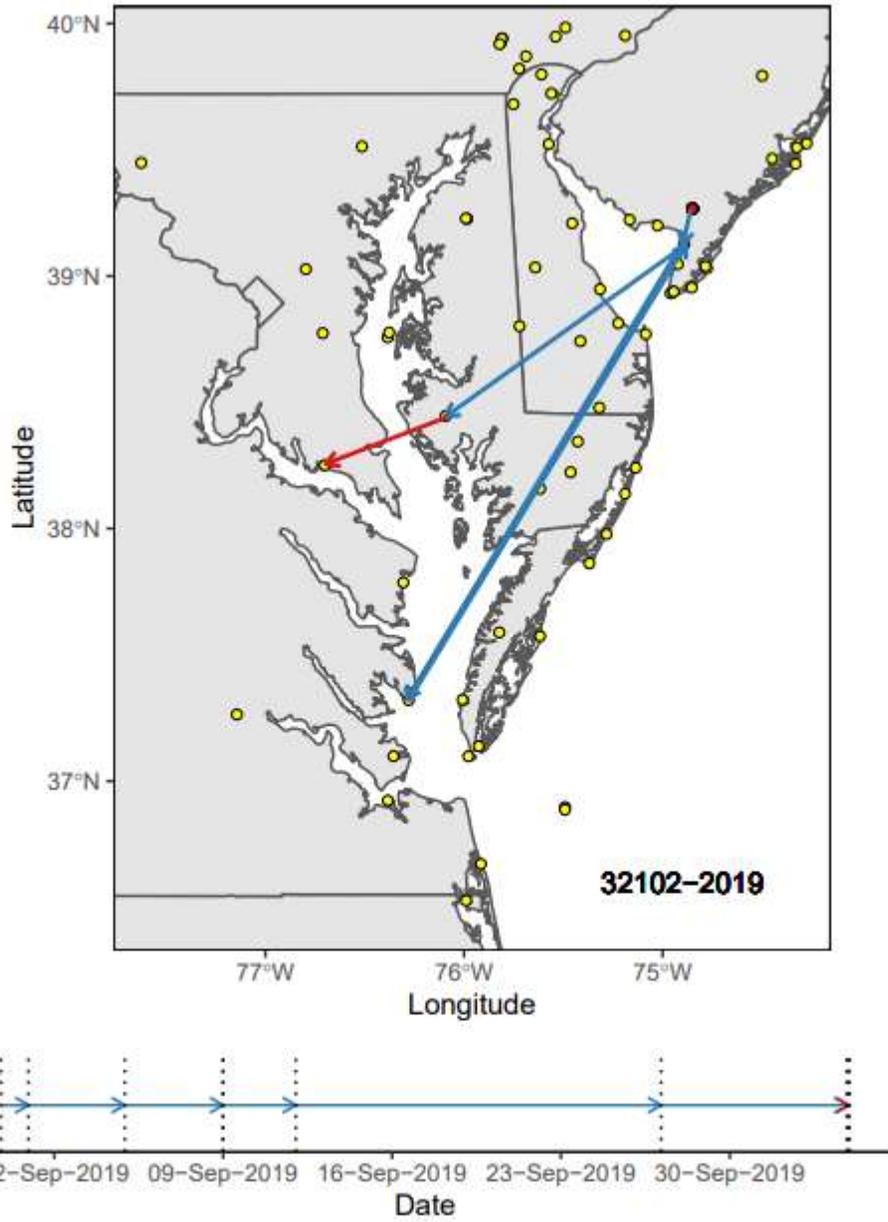
Appendix A3-1

This appendix displays each recorded migratory path by tree bats that were tagged in this study that contained evidence of migration using the Motus Wildlife Tracking System. Each map indicates dates and timing of movements, the lag in detections (by color; hours between detections), the sex and species of bat, and the Motus tag ID #. As a general warning, some false positive detections of bats may still exist after the filtering described in the methods, so some erratic movements should be interpreted cautiously.



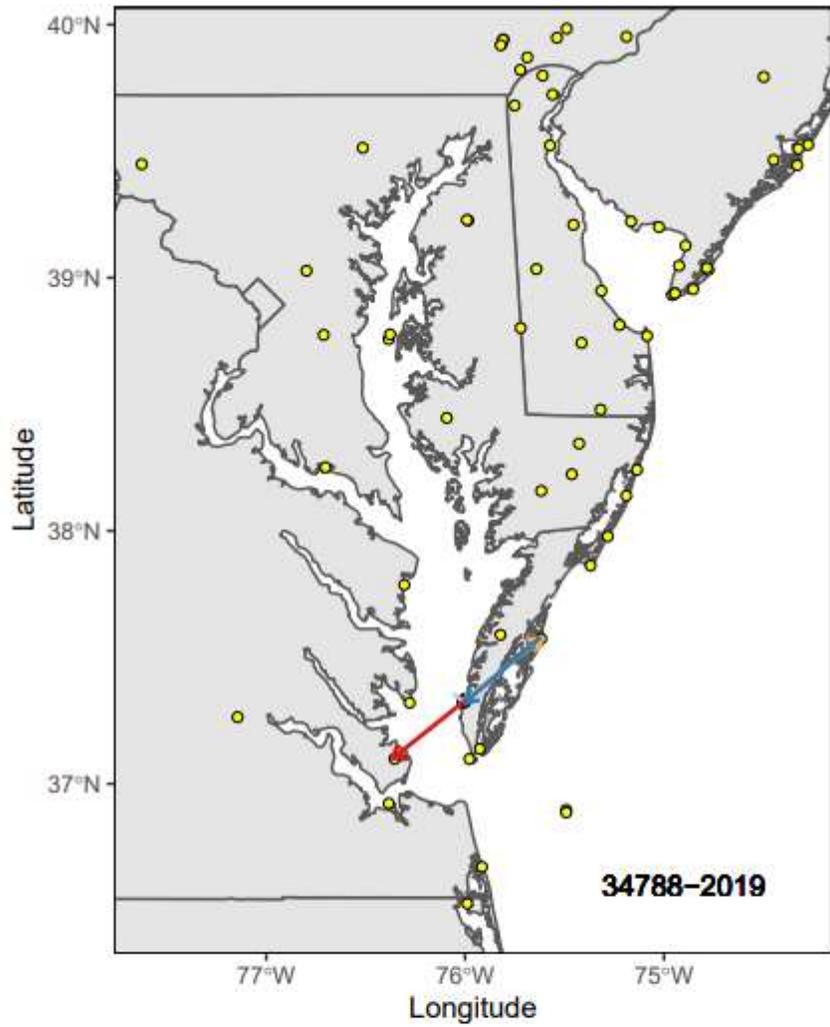
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Female, eastern red bat (*Lasiurus borealis*), Motus tag ID #32094



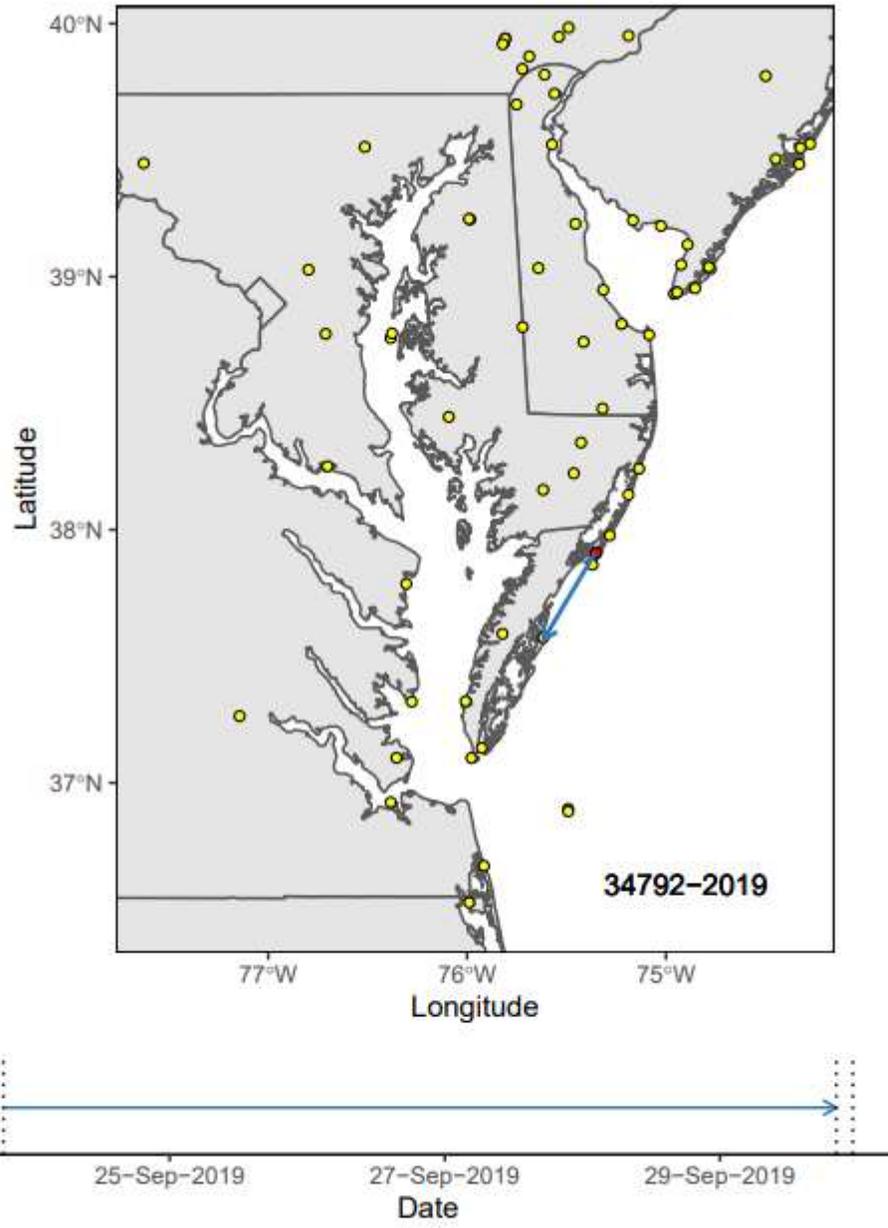
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Female, eastern red bat (*Lasiurus borealis*), Motus tag ID #32102



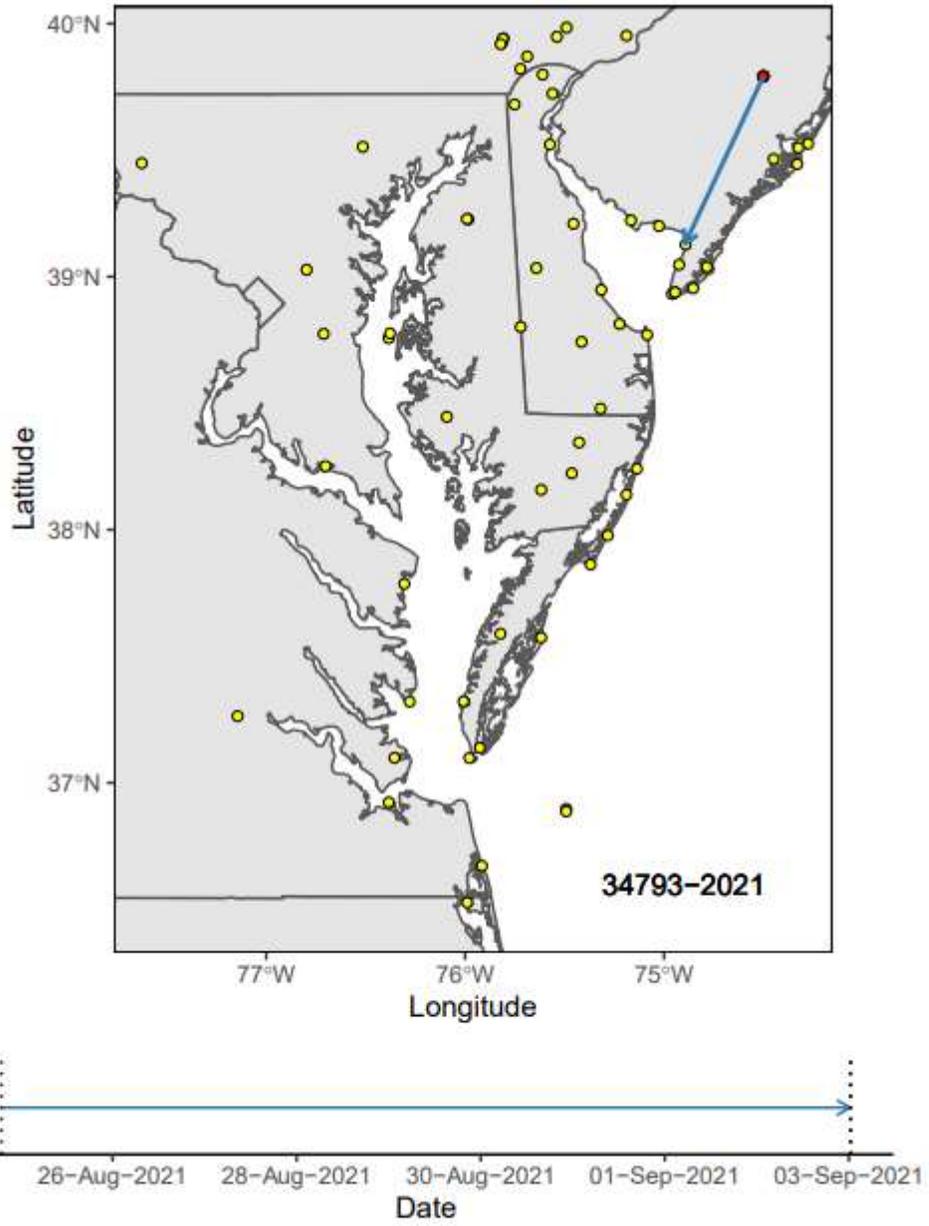
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Male, eastern red bat (*Lasiurus borealis*), Motus tag ID #34788



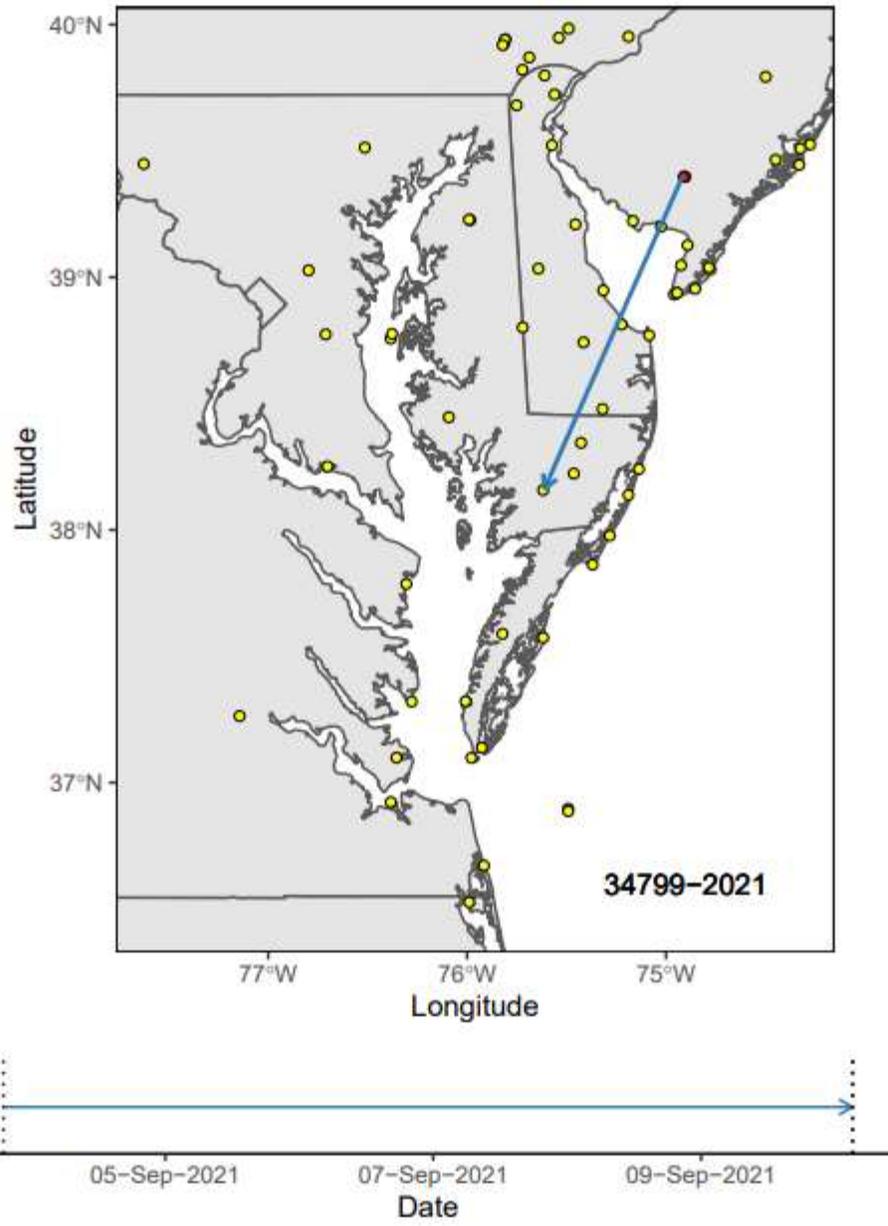
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Female, eastern red bat (*Lasiurus borealis*), Motus tag ID #34792



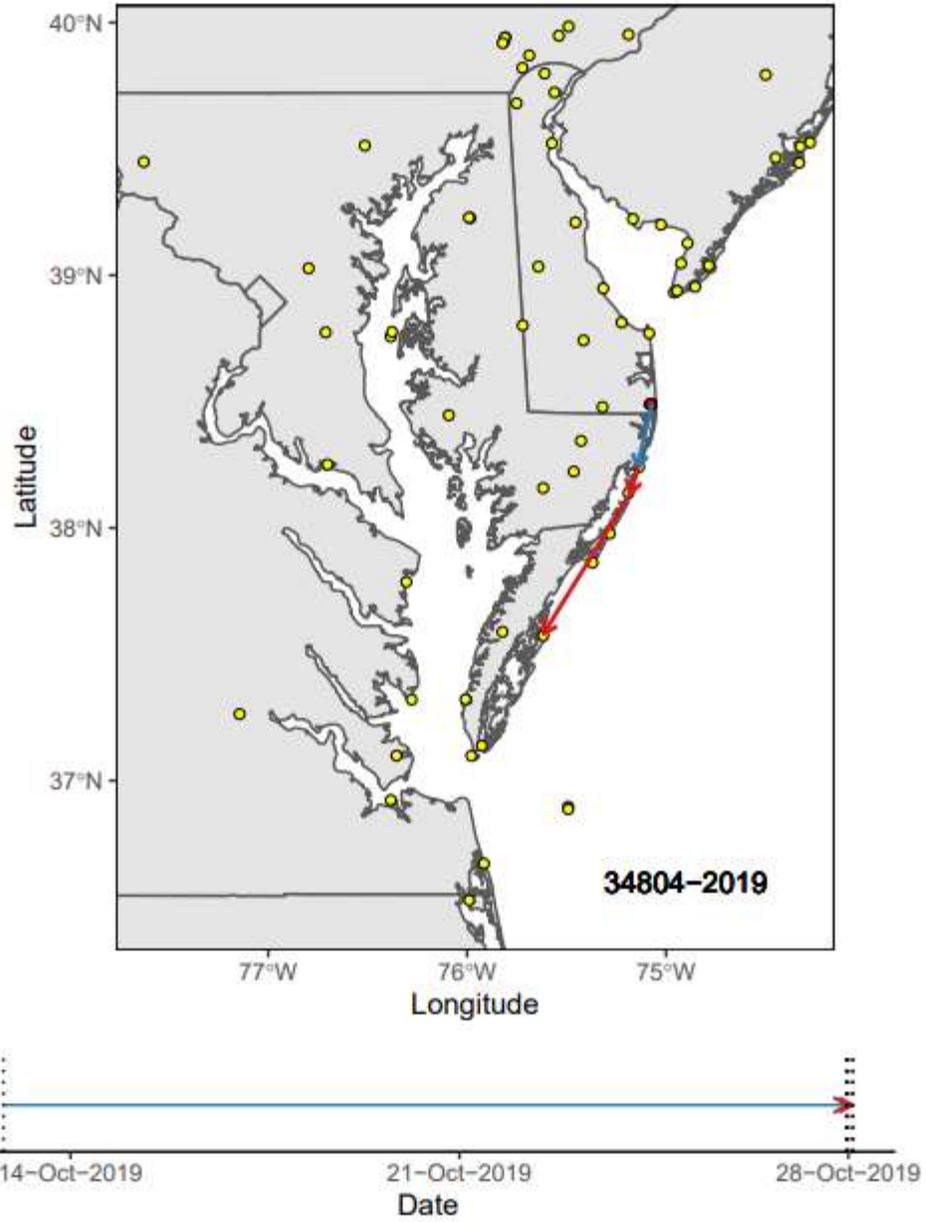
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Female, eastern red bat (*Lasiurus borealis*), Motus tag ID #32094



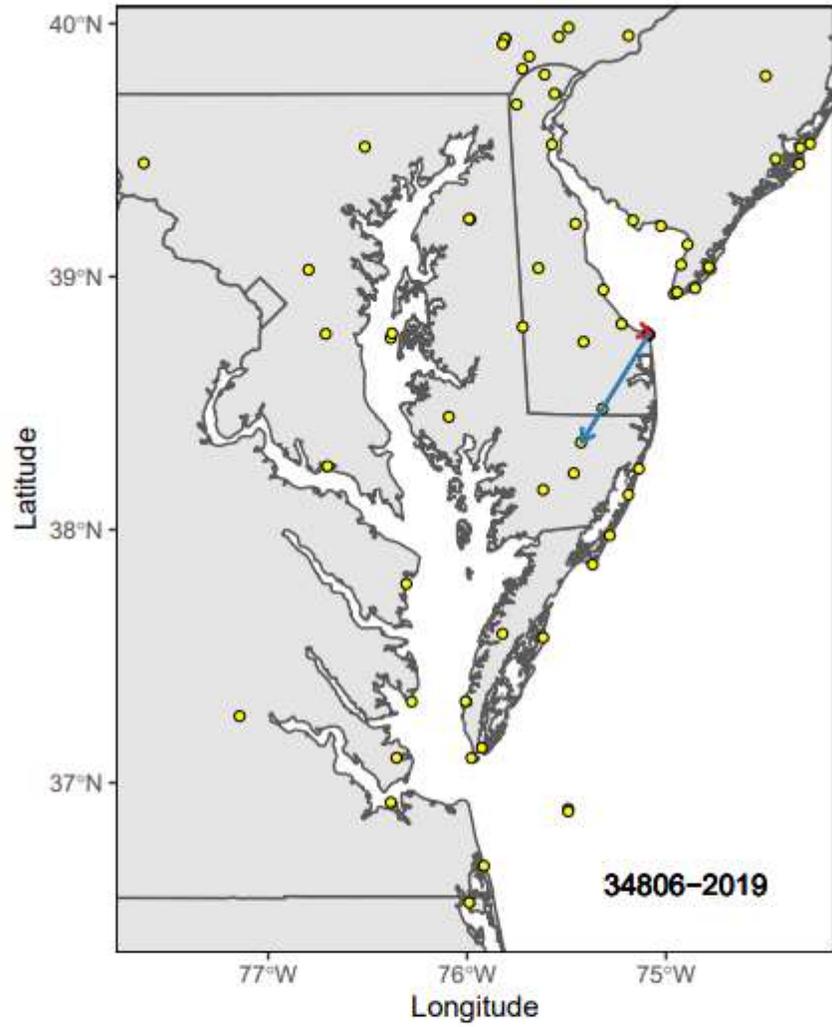
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Male, eastern red bat (*Lasiurus borealis*), Motus tag ID #34799



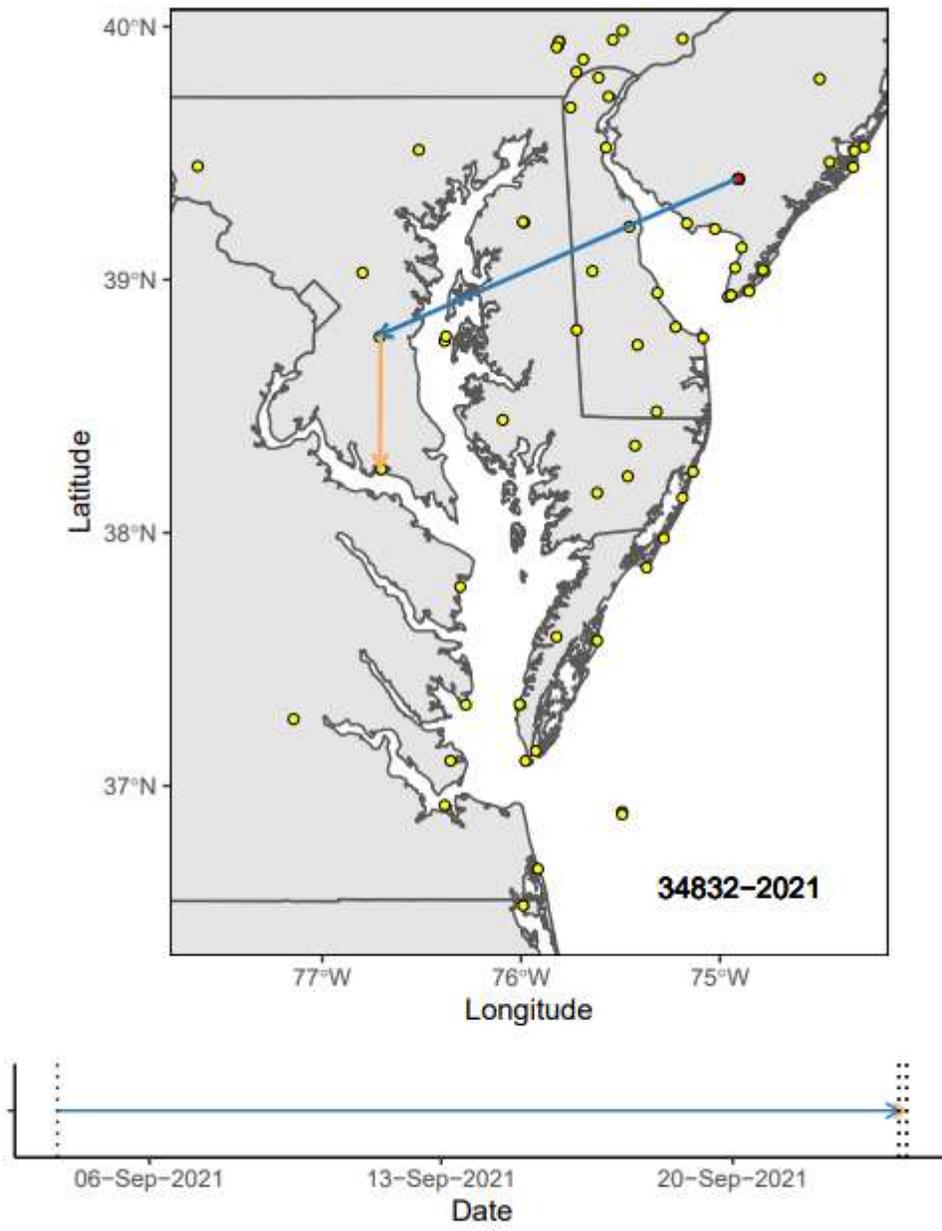
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Female, Seminole bat (*Lasiurus seminolus*), Motus tag ID #34804



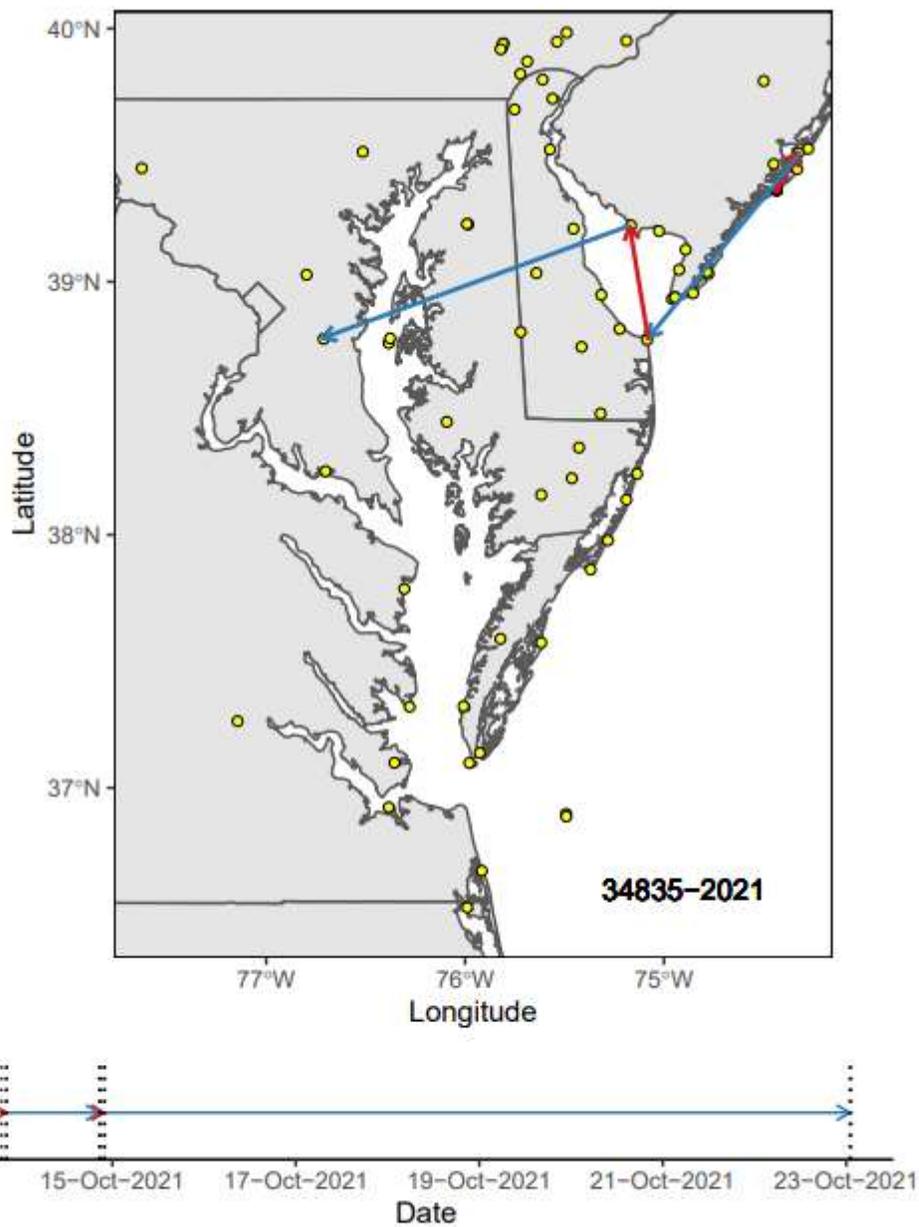
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Male, eastern red bat (*Lasiurus borealis*), Motus tag ID #34806



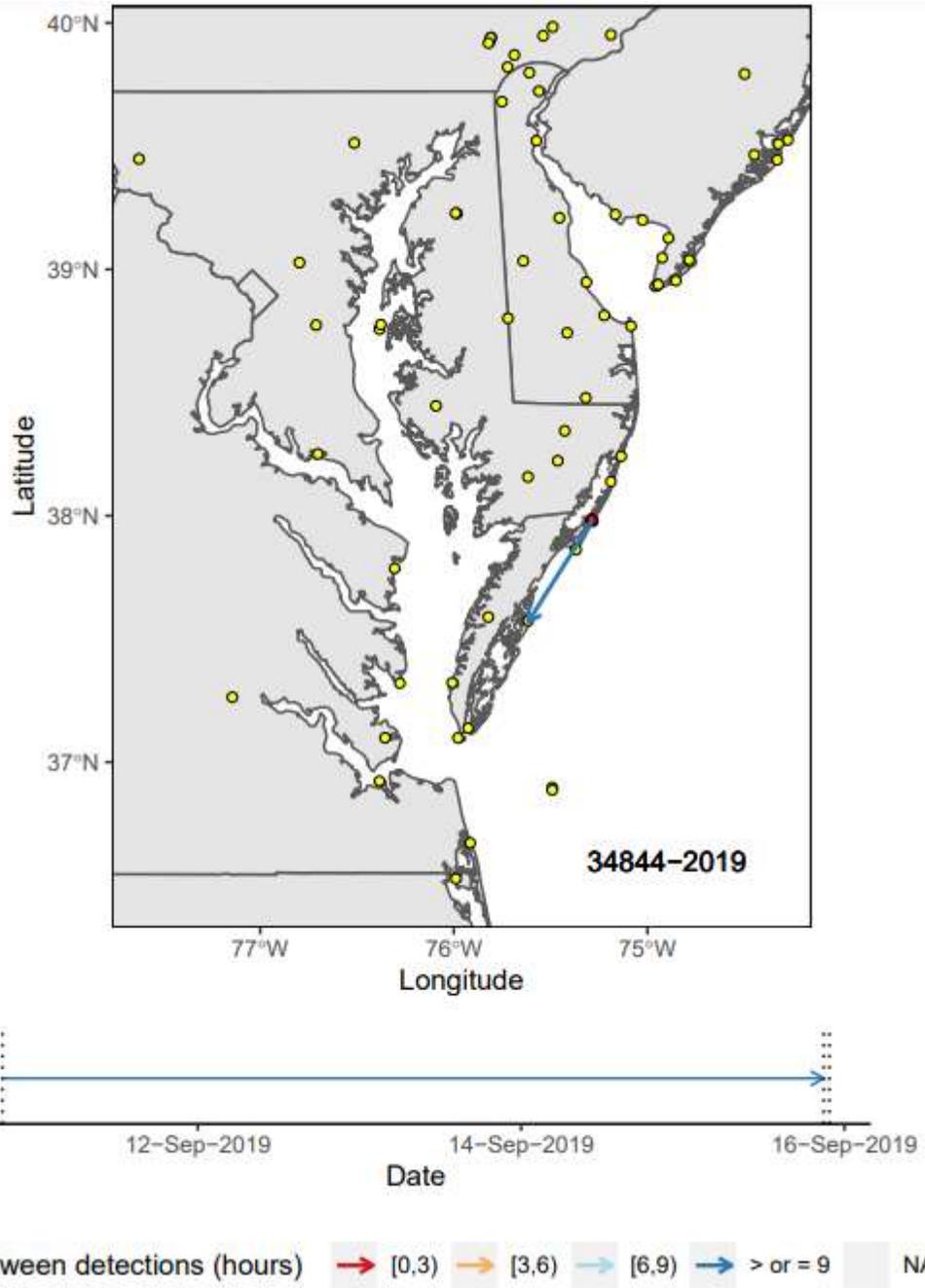
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Male, eastern red bat (*Lasiurus borealis*), Motus tag ID #34832

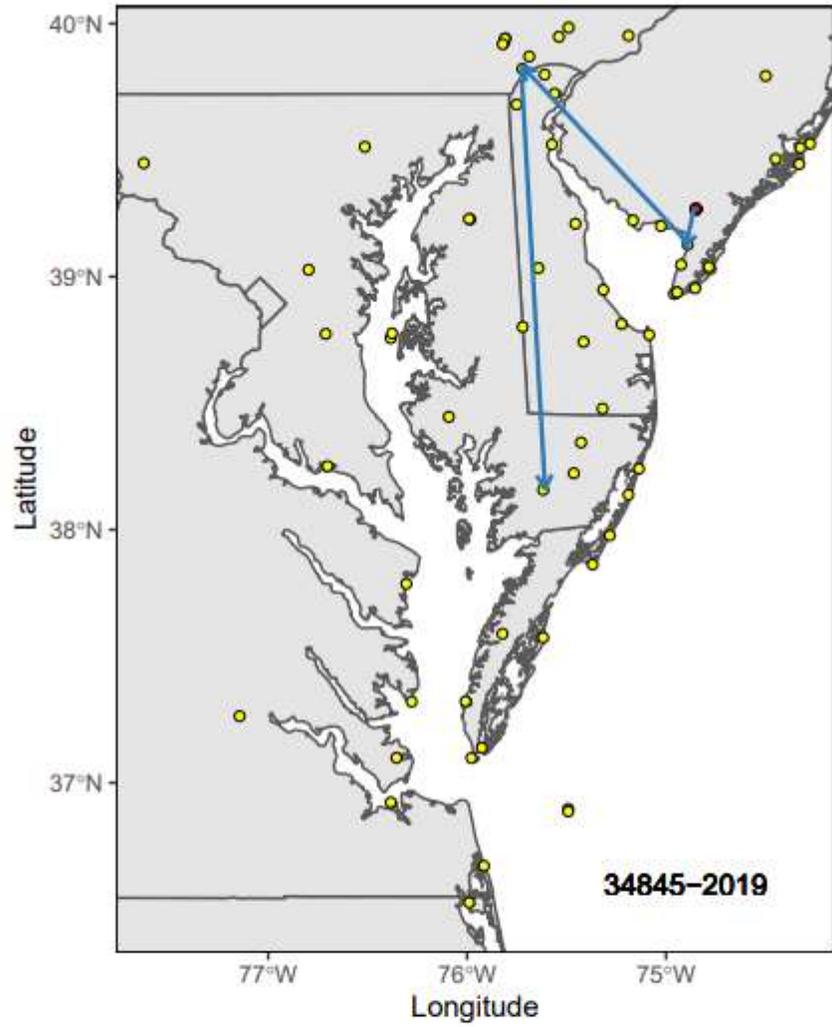


Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Female, silver-haired bat (*Lasionycteris noctivagans*), Motus tag ID #34835

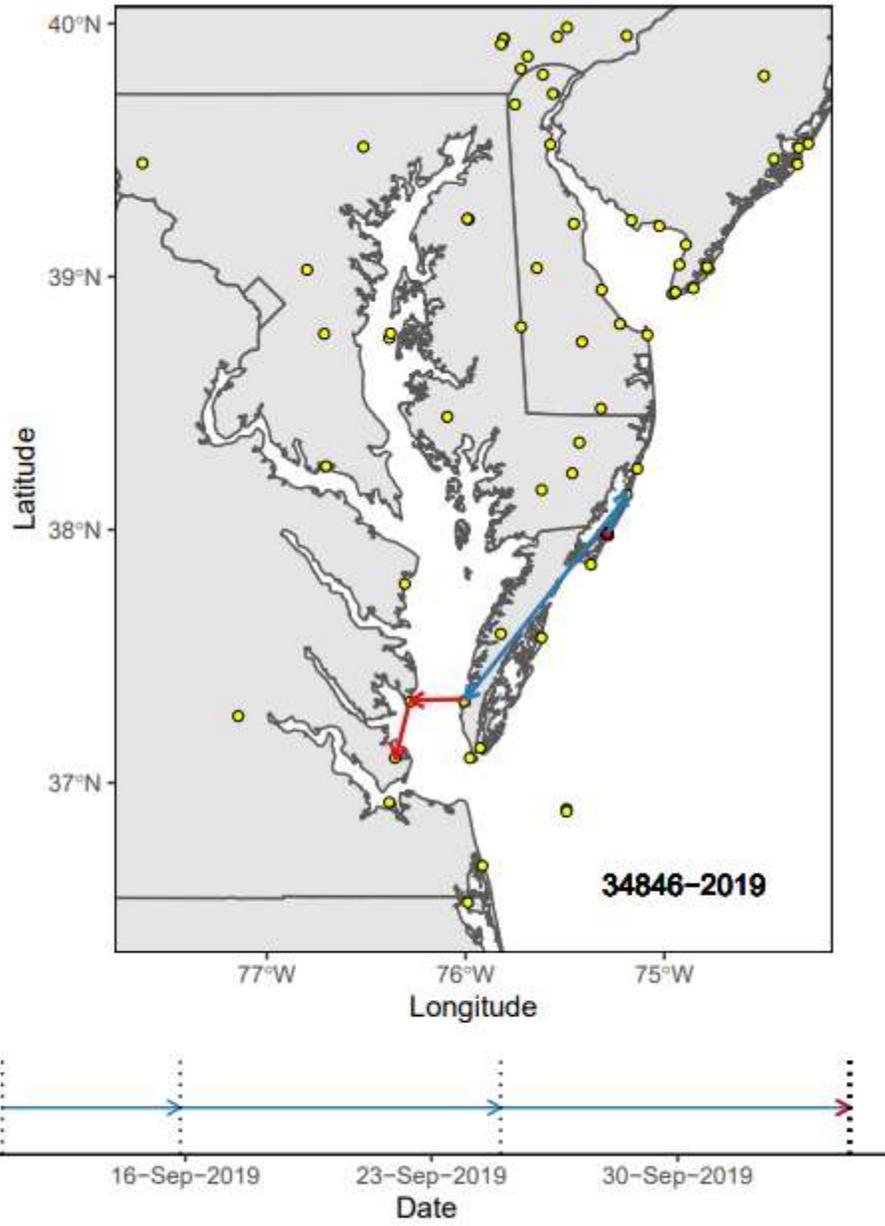


Female, eastern red bat (*Lasiurus borealis*), Motus tag ID #34844



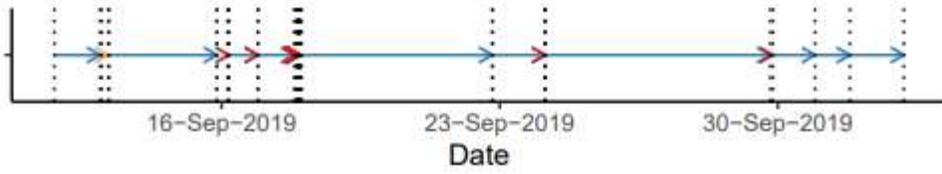
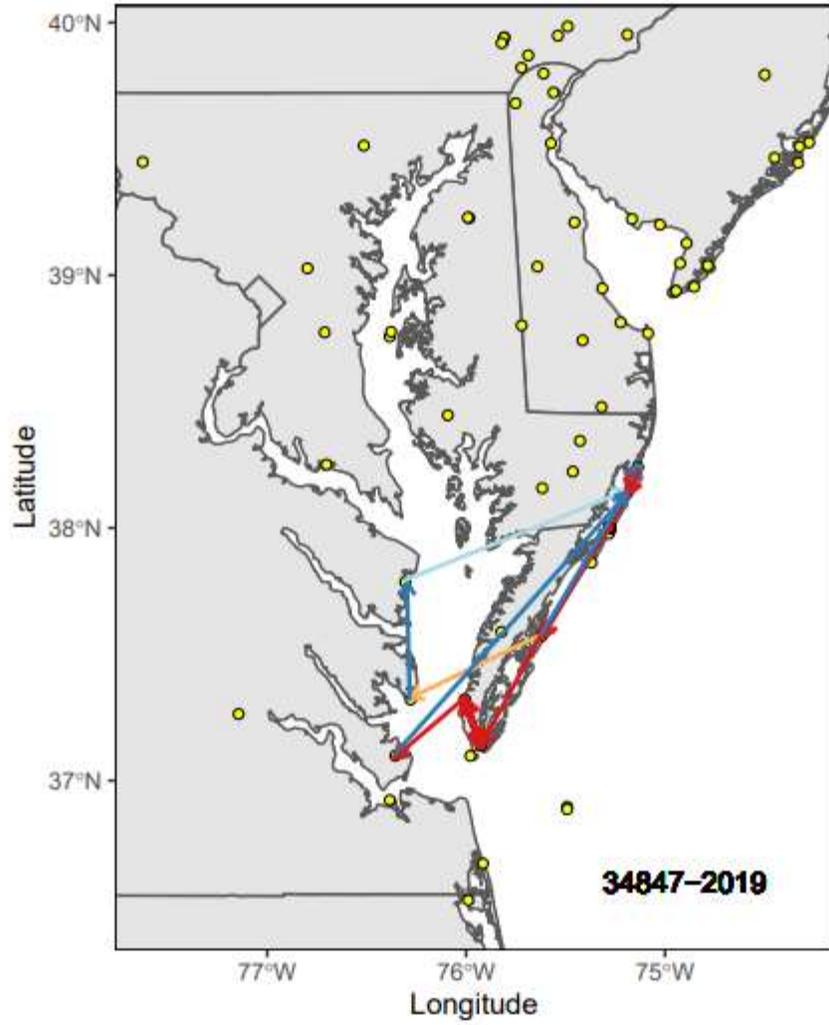
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Female, eastern red bat (*Lasiurus borealis*), Motus tag ID #34845



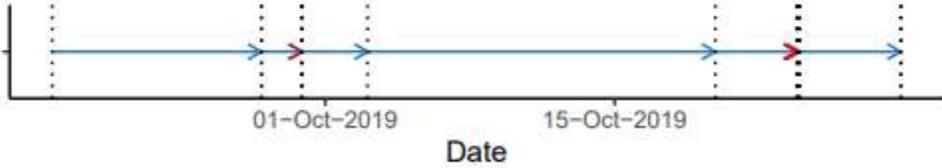
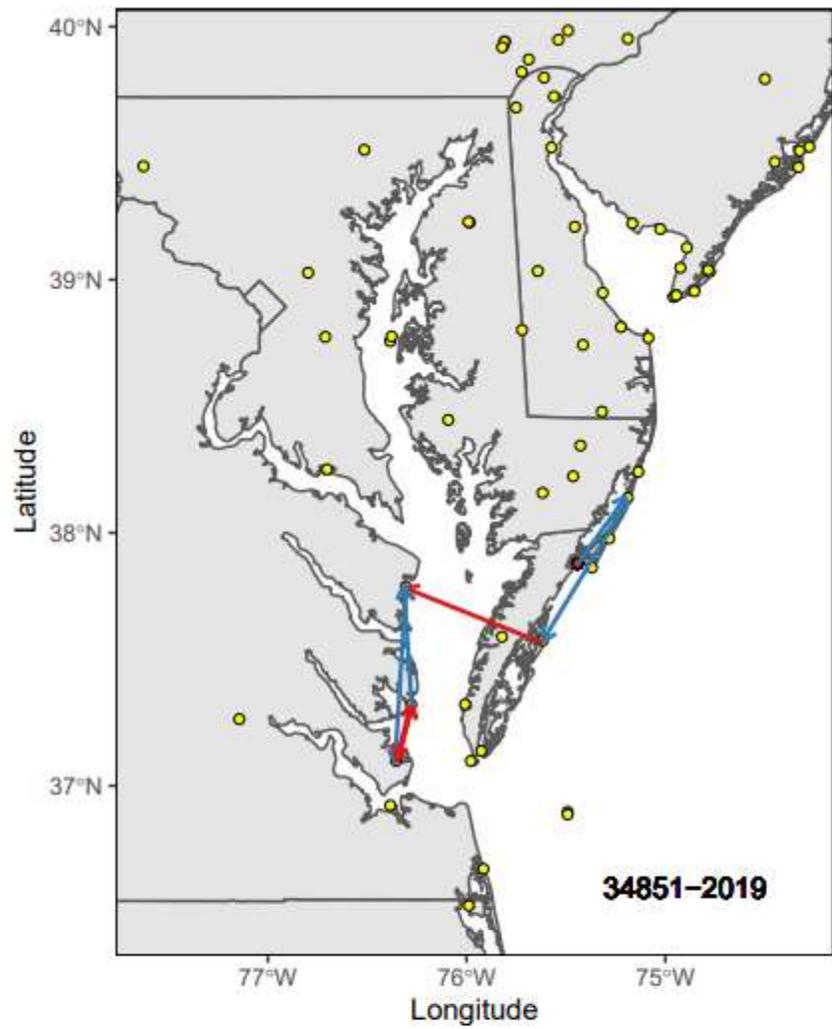
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Female, eastern red bat (*Lasiurus borealis*), Motus tag ID #34846



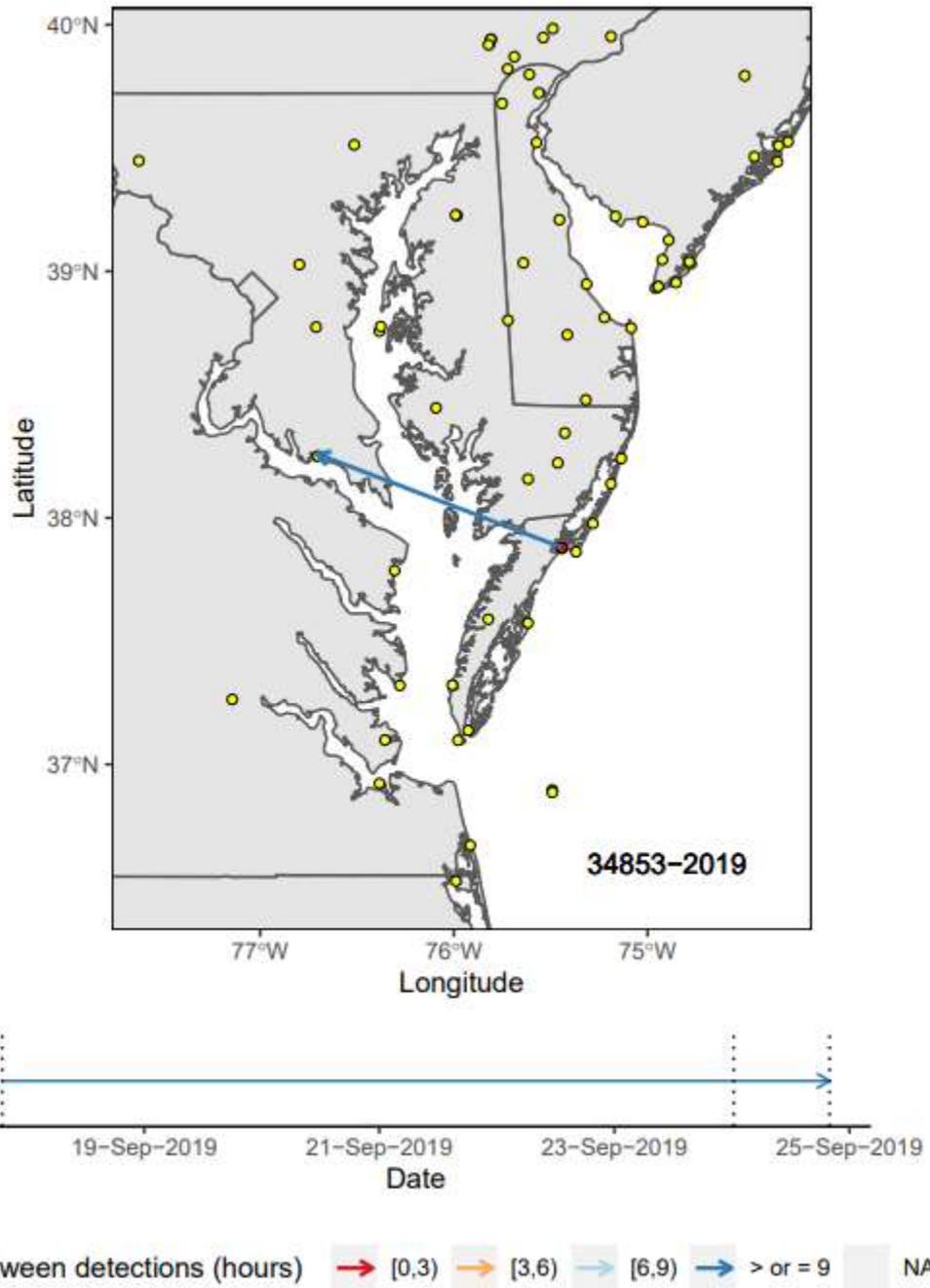
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 → NA

Male, eastern red bat (*Lasiurus borealis*), Motus tag ID #34847

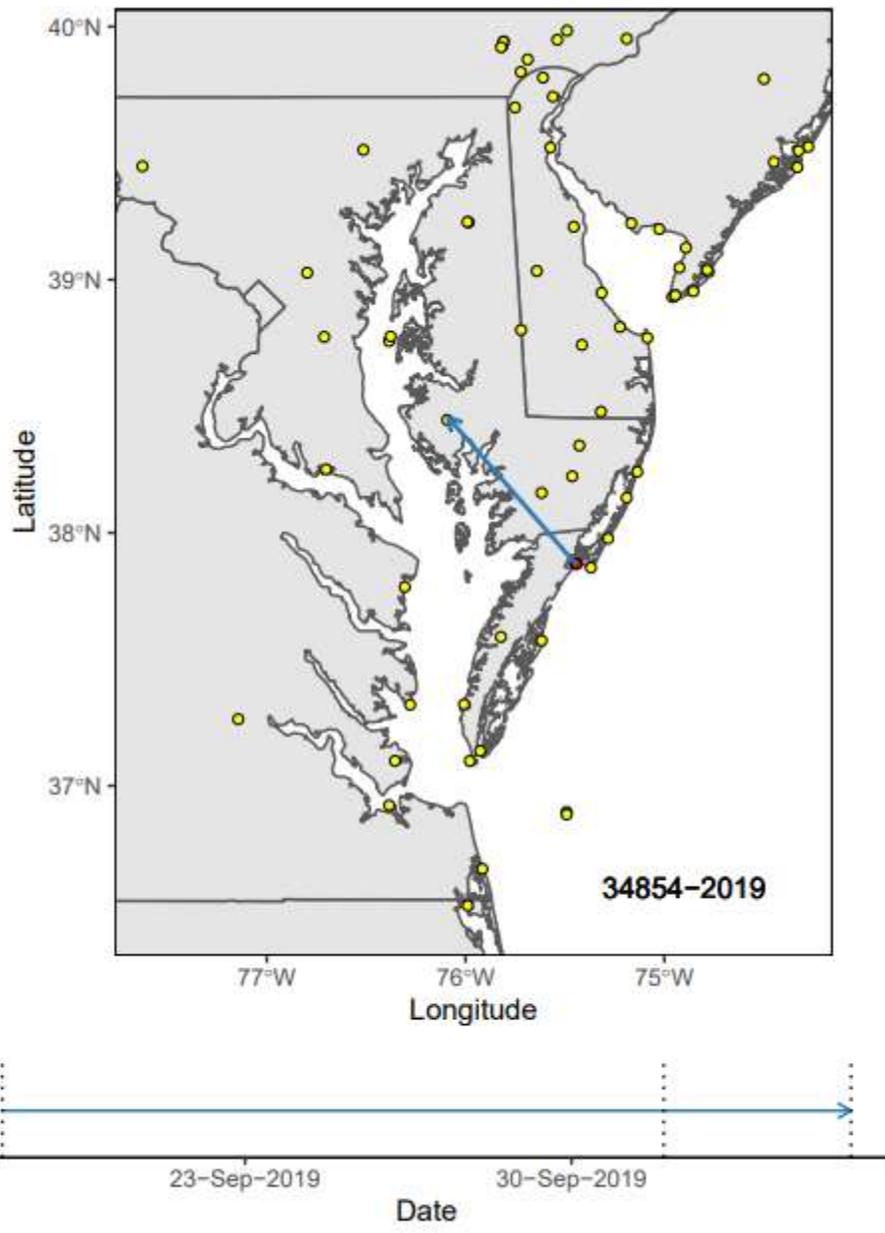


Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Male, eastern red bat (*Lasiurus borealis*), Motus tag ID #34851

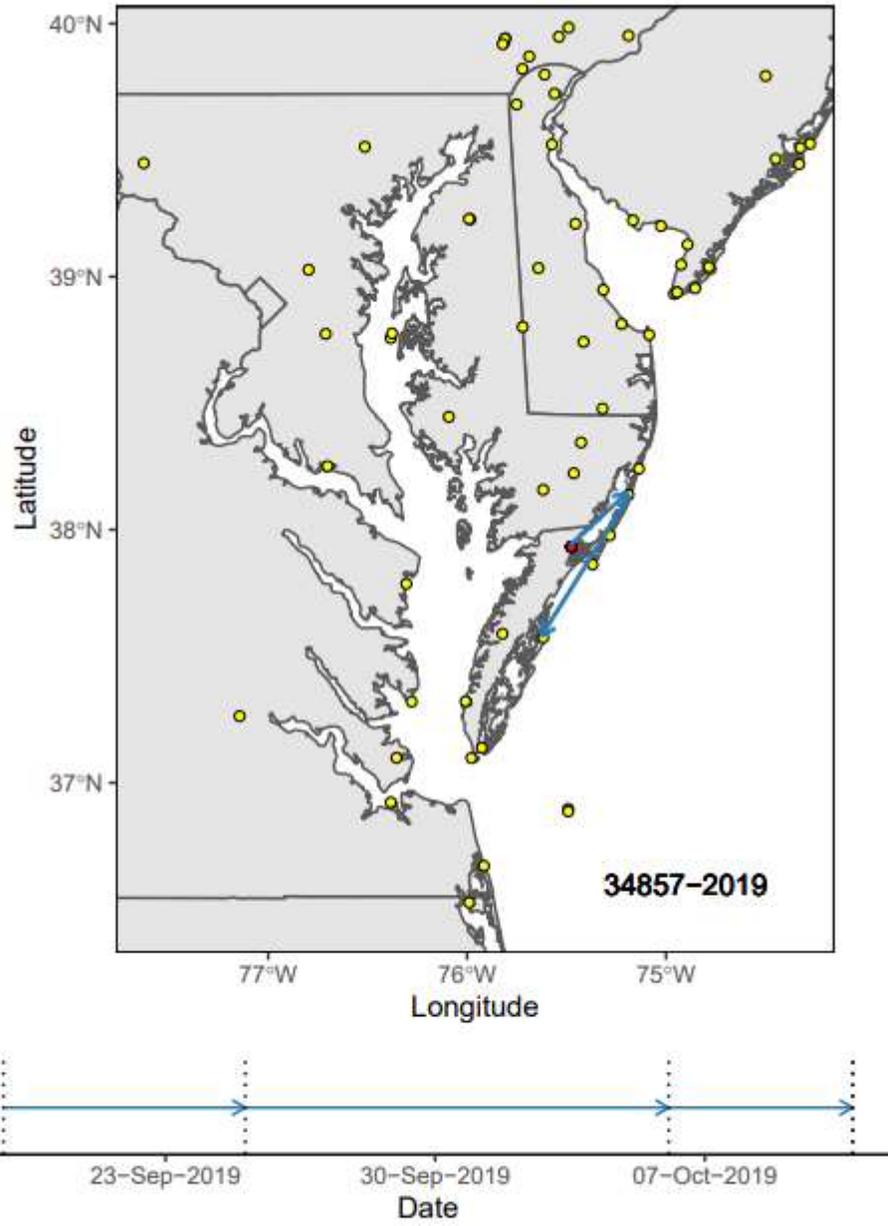


Male, eastern red bat (*Lasiurus borealis*), Motus tag ID #34853



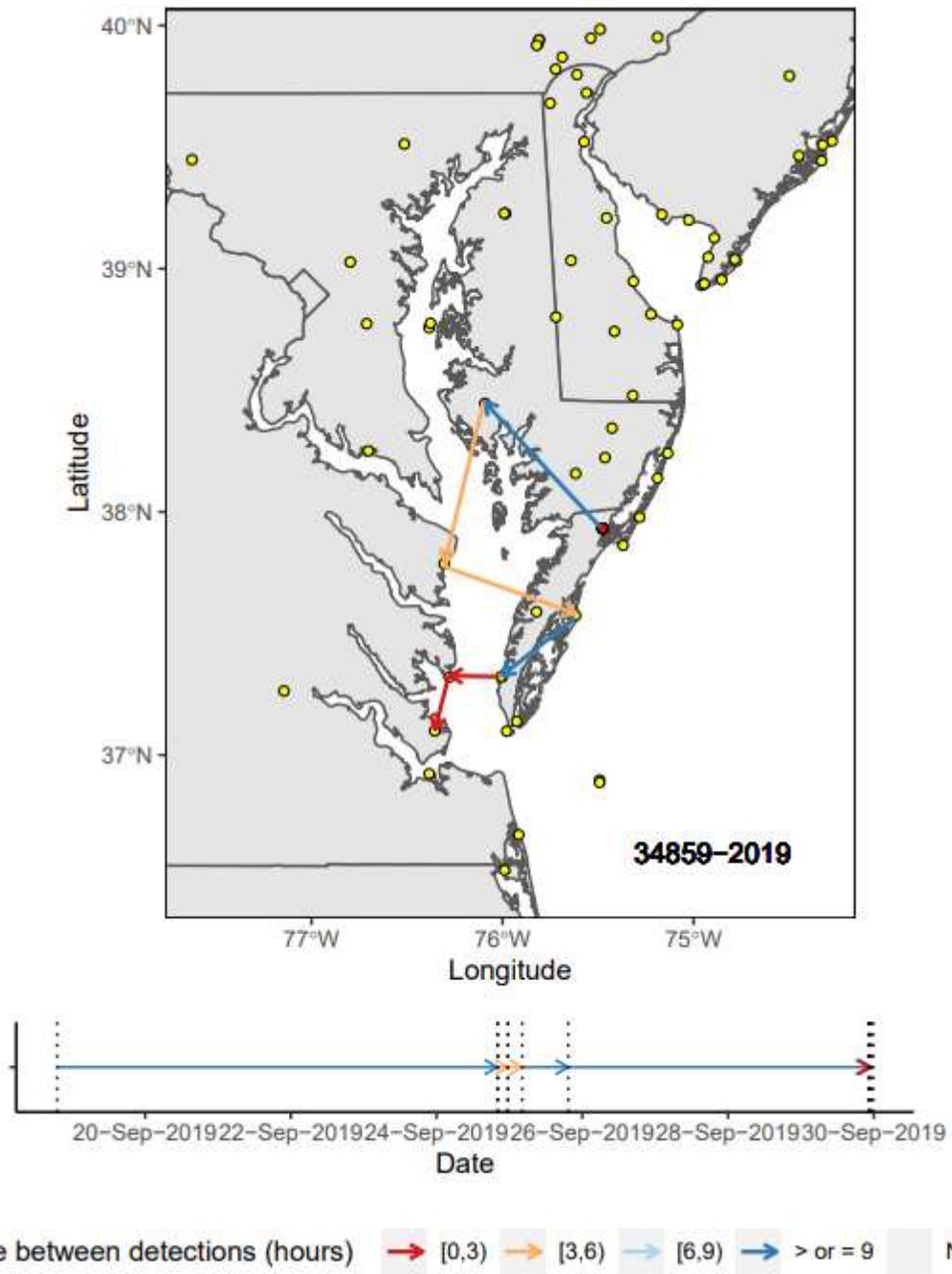
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Male, eastern red bat (*Lasiurus borealis*), Motus tag ID #34854

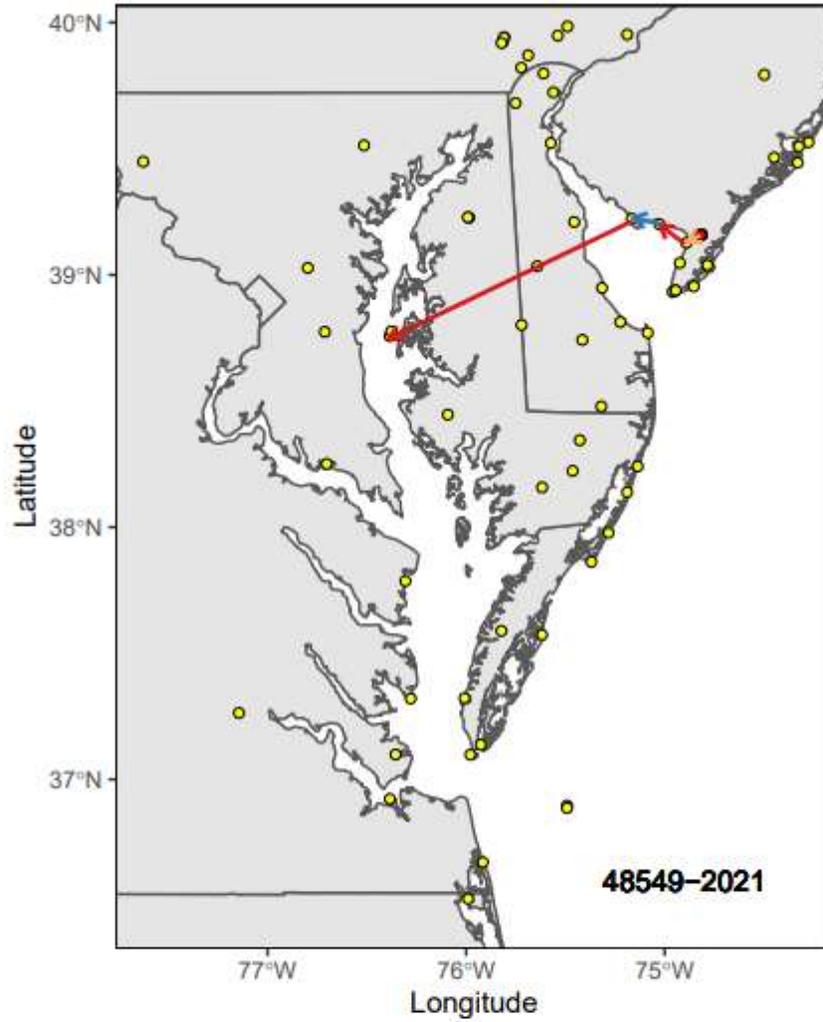


Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Male, eastern red bat (*Lasiurus borealis*), Motus tag ID #34857

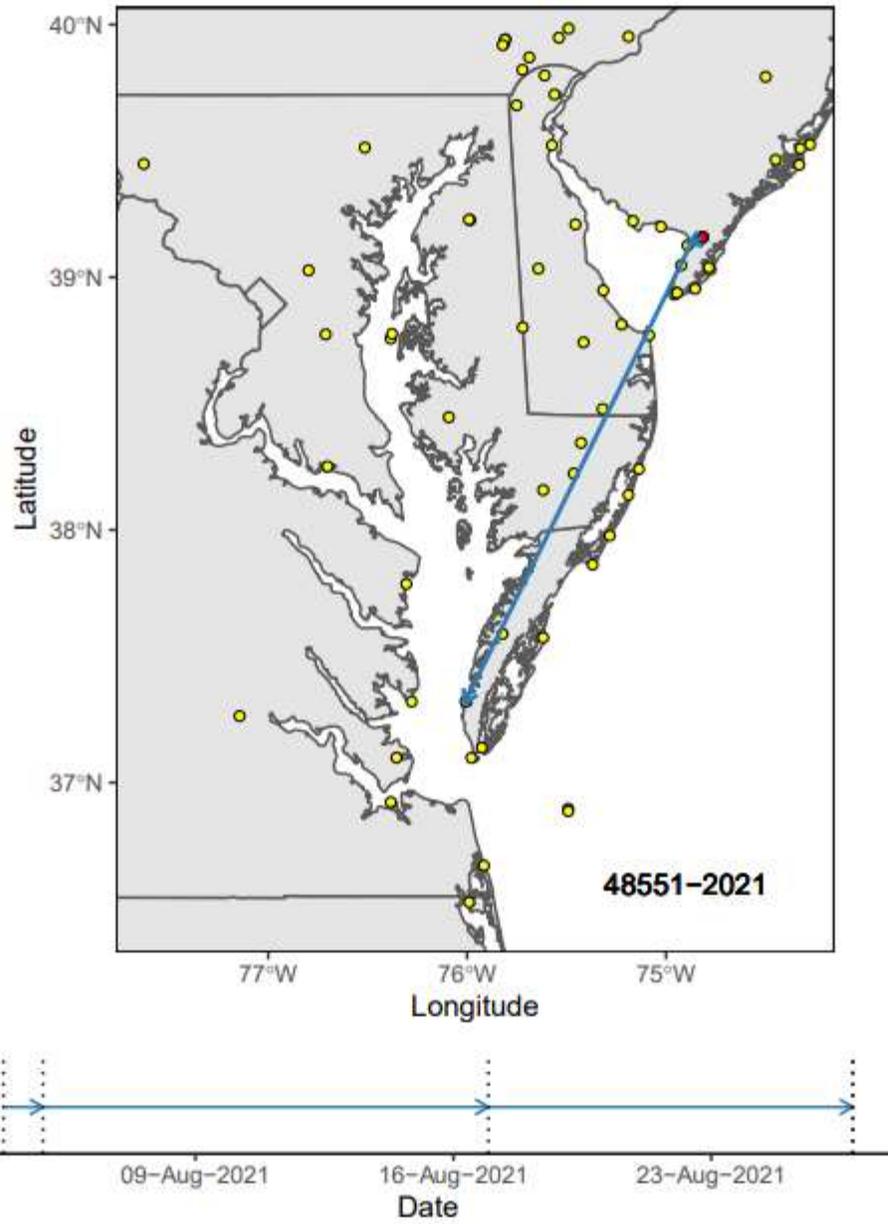


Male, eastern red bat (*Lasiurus borealis*), Motus tag ID #34859



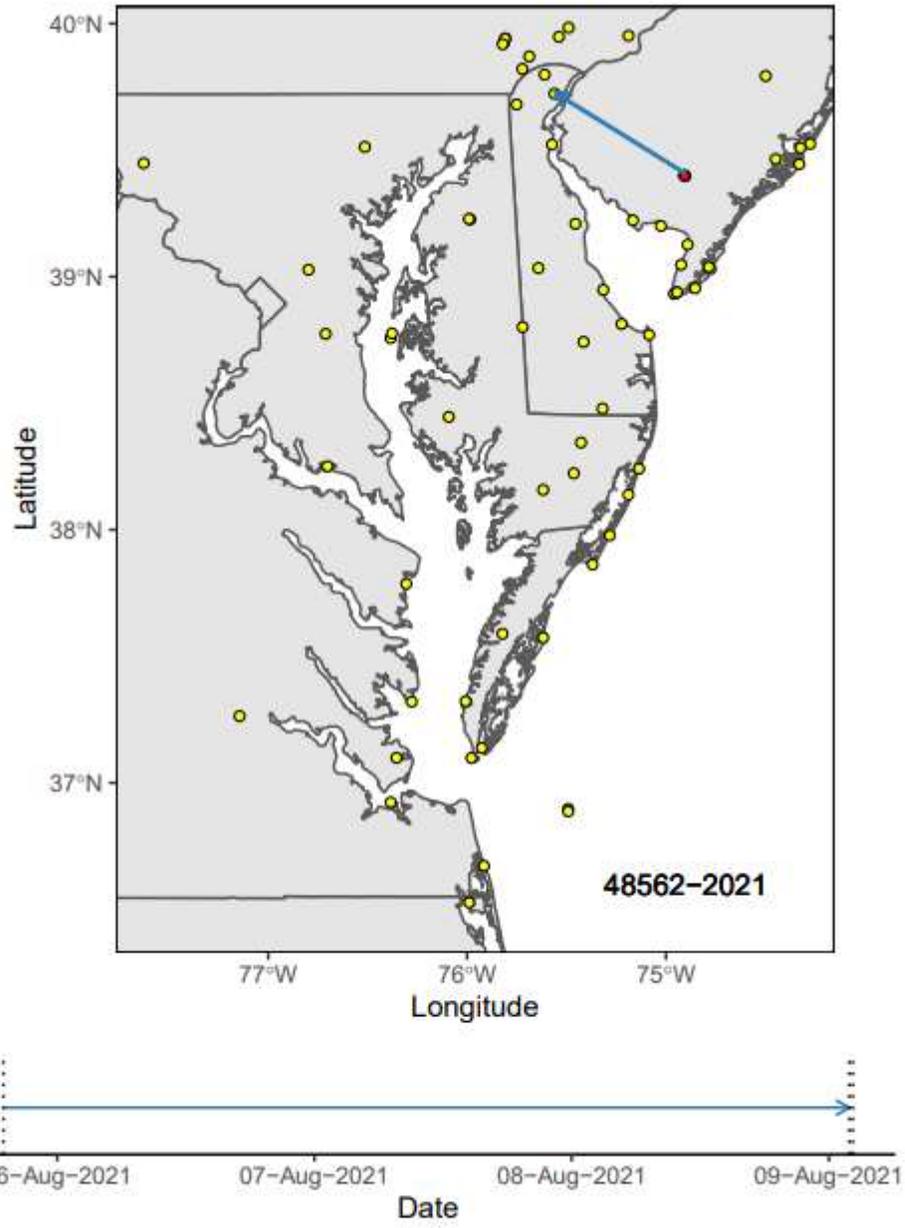
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Male, eastern red bat (*Lasiurus borealis*), Motus tag ID #48549



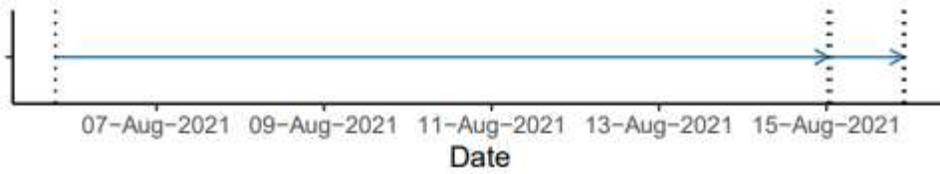
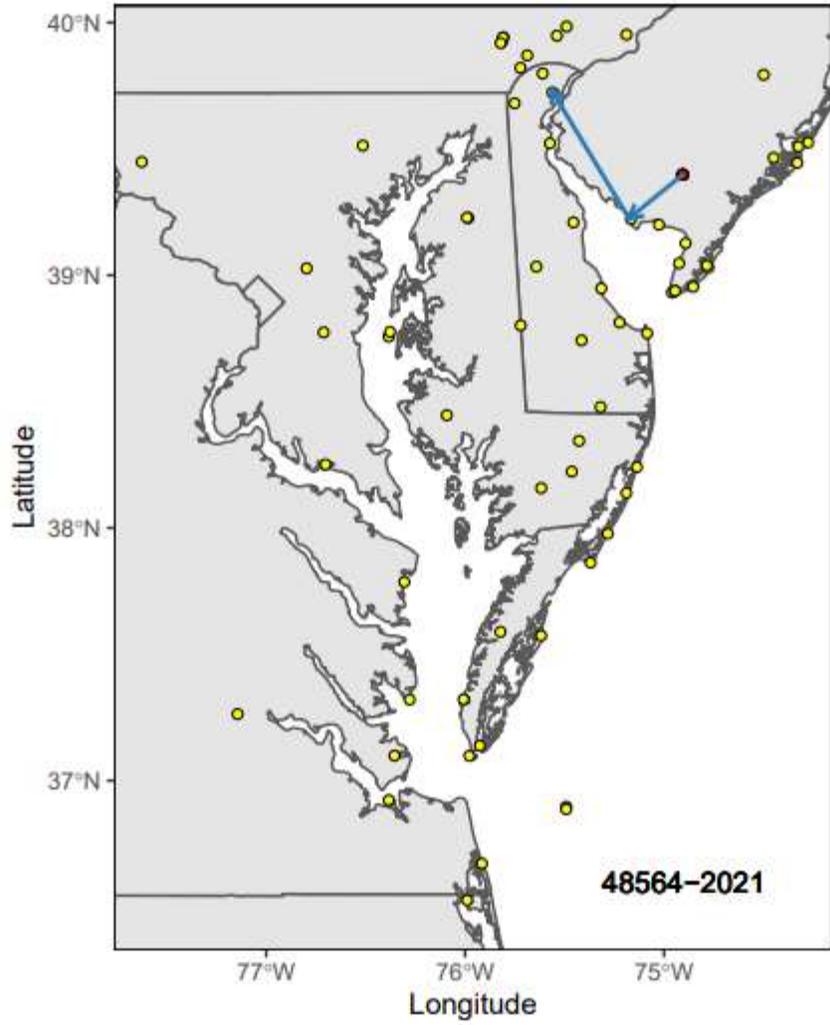
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Male, eastern red bat (*Lasiurus borealis*), Motus tag ID #48551



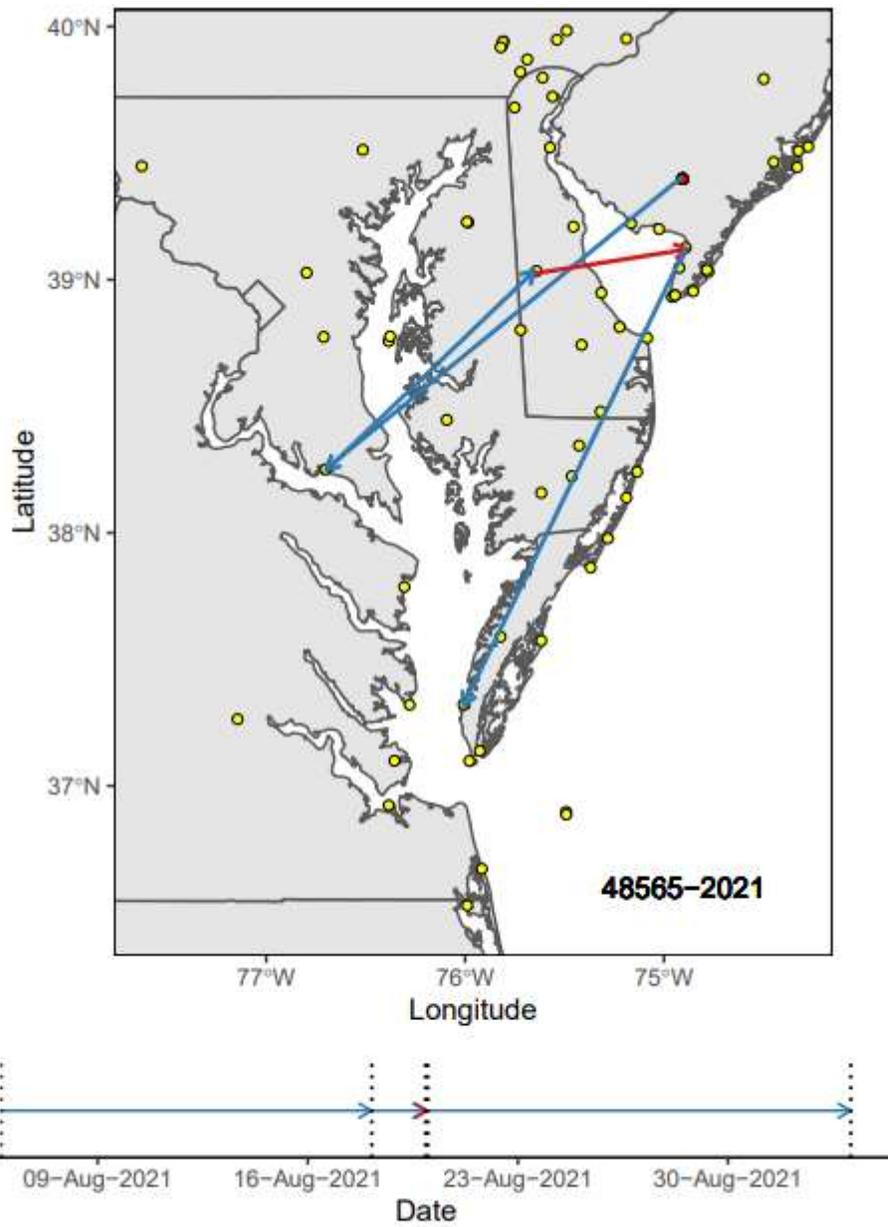
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Male, eastern red bat (*Lasiurus borealis*), Motus tag ID #48562



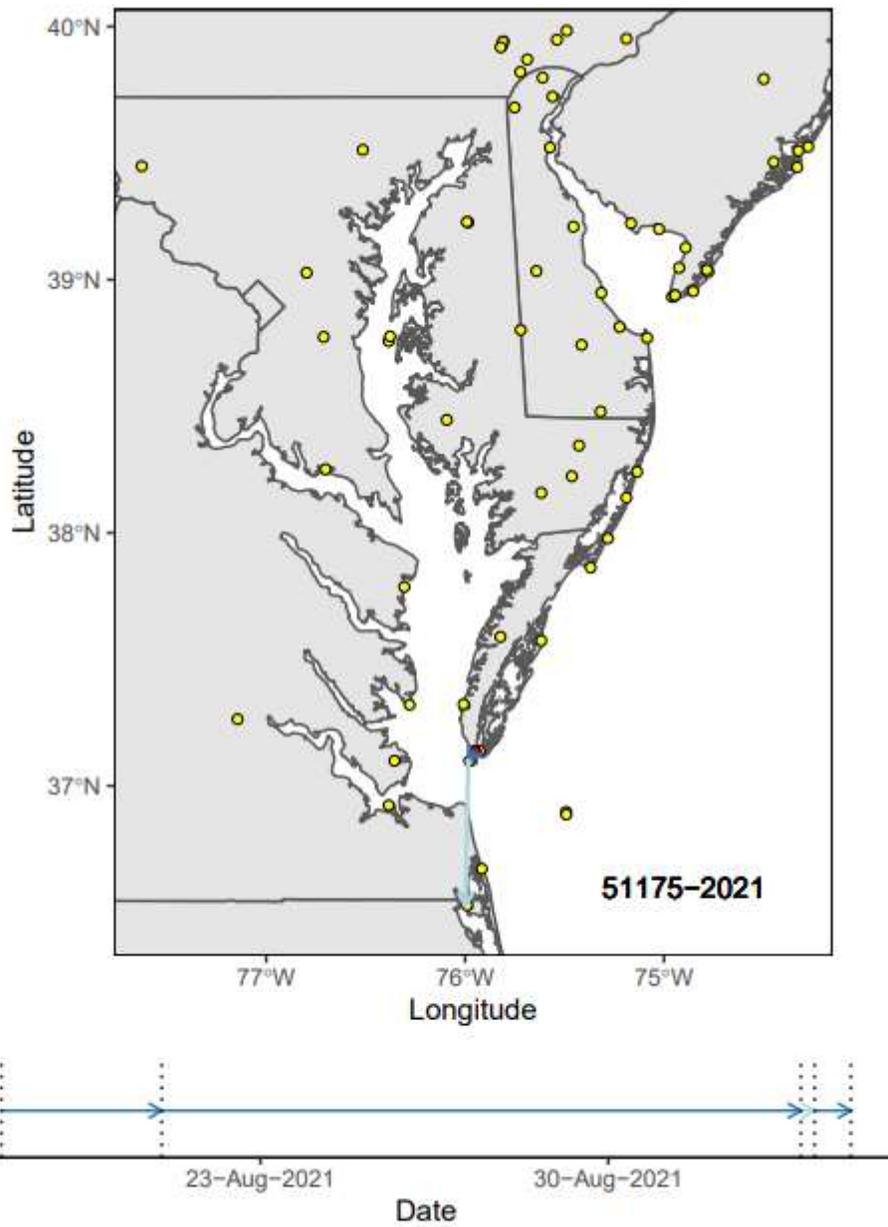
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Male, eastern red bat (*Lasiurus borealis*), Motus tag ID #48564



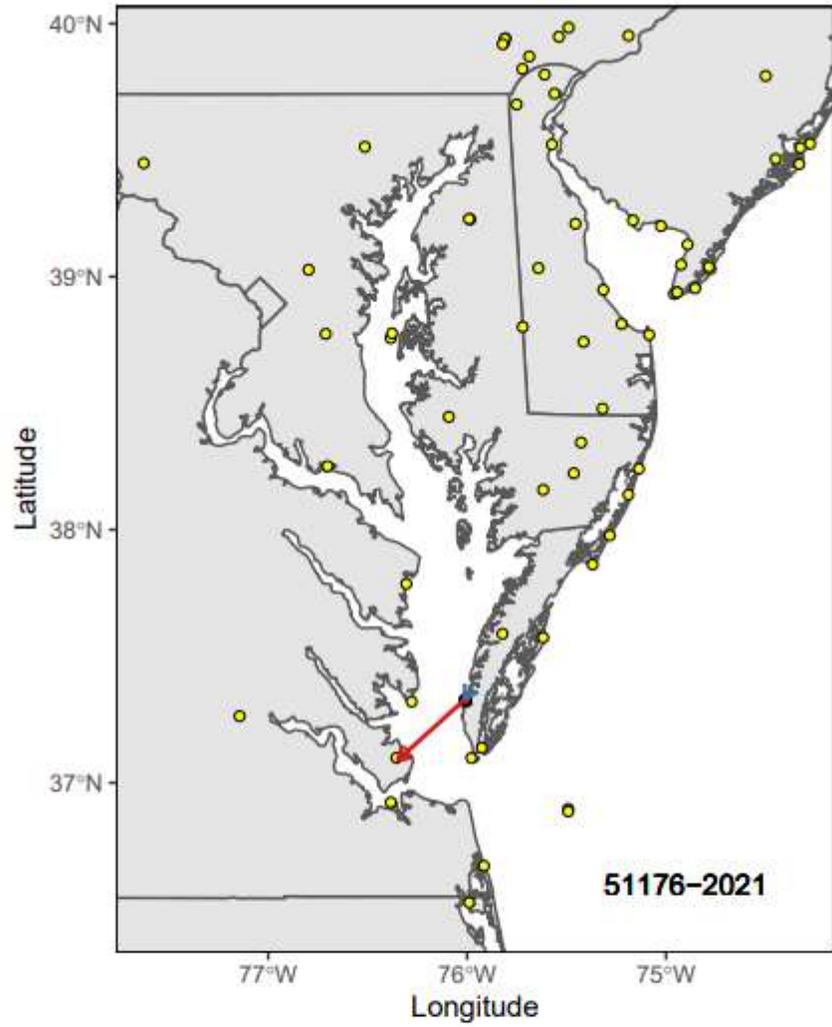
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Female, eastern red bat (*Lasiurus borealis*), Motus tag ID #48565



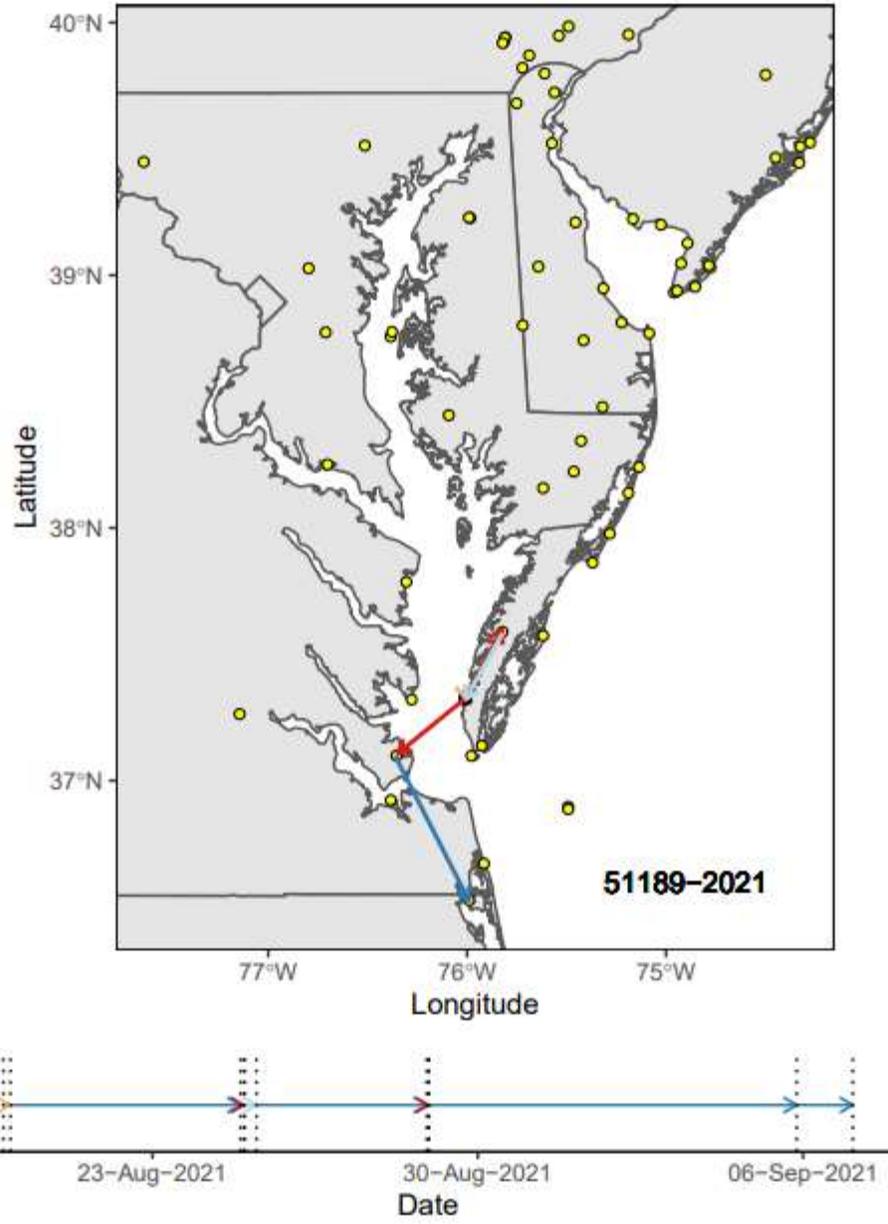
Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Male, eastern red bat (*Lasiurus borealis*), Motus tag ID #51175



Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Male, eastern red bat (*Lasiurus borealis*), Motus tag ID #51176



Time between detections (hours) → [0,3) → [3,6) → [6,9) → > or = 9 NA

Male, eastern red bat (*Lasiurus borealis*), Motus tag ID #51189