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Research Paper

**Erratum:** Two in-text citations of reference Skinner et al. 2022 have been amended to Skinner et al. 2023; the latter reference has been added to the Literature Cited. The corrections were made on 3 February 2026.

## Home range size, overlap, and habitat selection of diurnally roosting Eastern Whip-poor-wills (*Antrostomus vociferus*) during the breeding season

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**ABSTRACT.** Eastern Whip-poor-will (*Antrostomus vociferus*) populations have declined considerably since 1970, primarily because of declines in insect prey and early successional forest breeding habitat. Previous studies on Whip-poor-wills have focused on tracking movements of adults on the breeding grounds and adults on the wintering grounds, tracking migratory pathways, and quantifying occupancy, yet few studies have focused on home range scale space use and habitat selection. We tracked 10 adult Whip-poor-wills from May–August 2022 at two Rhode Island, USA state management areas, Big River and Great Swamp, and five adult Whip-poor-wills (four of which were also tracked in 2022) from May–August 2023 at Great Swamp. We used diurnal locations to estimate home ranges for each individual and the extent of home range overlap for neighboring males, paired males and females, and the same males tracked in both years, as well as habitat selection at the home-range scale. Home range sizes of males and females were not different and averaged 18.05 ha. Home ranges of neighboring males minimally overlapped whereas paired males and females had a high degree of home range overlap. The four males that were tracked at Great Swamp in both years used very similar home ranges across years, suggesting that at least some individuals show site and home range fidelity. We found no support for selection for distance to any land cover types at the population level; however, 10 of 11 individuals selected for at least one land cover type and eight of 11 individuals selected for early successional forest openings (e.g., scrub and grassland), although the pattern of selection varied between individuals. These findings, when considered along with other published works on Whip-poor-will habitat selection and occupancy, underscore the importance of active forest management to maintain habitat mosaics on known Whip-poor-will breeding grounds.

### La taille du domaine vital, le chevauchement et la sélection de l'habitat de l'Engoulevent bois-pourri (*Antrostomus vociferus*) à perchage diurne pendant la saison de reproduction

**RÉSUMÉ.** Les populations d'Engoulevent bois-pourri (*Antrostomus vociferus*) ont considérablement diminué depuis 1970, principalement en raison du déclin des insectes proies et de l'habitat de reproduction dans les forêts en début de succession. Les études précédentes sur l'Engoulevent bois-pourri se sont concentrées sur le suivi des mouvements des adultes sur les aires de reproduction et d'hivernage, sur le suivi des voies migratoires et sur la quantification de l'occupation. Toutefois, peu d'études se sont penchées sur l'utilisation de l'espace à l'échelle du domaine vital et sur la sélection de l'habitat. Nous avons suivi 10 engoulevents bois-pourri adultes de mai à août 2022 dans deux zones de gestion de l'État du Rhode Island, États-Unis, Big River et Great Swamp, et cinq engoulevents bois-pourri adultes (dont quatre ont également été suivis en 2022) de mai à août 2023 à Great Swamp. Nous avons utilisé les localisations diurnes pour estimer les domaines vitaux de chaque individu et l'étendue du chevauchement des domaines vitaux pour les mâles voisins, les mâles et les femelles appariés, et les mêmes mâles suivis au cours des deux années, ainsi que la sélection de l'habitat à l'échelle du domaine vital. La taille des domaines vitaux des mâles et des femelles n'était pas différente et s'élevait en moyenne à 18,05 ha. Les domaines vitaux des mâles voisins se chevauchent très peu, tandis que les mâles et les femelles appariés présentent un degré élevé de chevauchement des domaines vitaux. Les quatre mâles qui ont été suivis à Great Swamp les deux années ont utilisé des domaines vitaux très similaires d'une année à l'autre, ce qui suggère qu'au moins certains individus restent fidèles au site et au domaine vital. Nous n'avons trouvé aucune preuve de la sélection de la distance par rapport à un type de couverture terrestre au niveau de la population. Toutefois, 10 des 11 individus ont sélectionné au moins un type de couverture terrestre et 8 des 11 individus ont sélectionné des ouvertures forestières de début de succession (p. ex. broussailles et prairies), bien que le schéma de sélection ait varié d'un individu à l'autre. Ces résultats, associés à d'autres travaux publiés sur la sélection et l'occupation de l'habitat de l'engoulevent bois-pourri, reflètent l'importance d'une gestion forestière active pour maintenir des mosaïques d'habitats sur les sites de reproduction connus de l'Engoulevent bois-pourri.

**Key Words:** *aerial insectivore; early successional forest; habitat management; space use sharing; territoriality*

## INTRODUCTION

The space use of breeding birds is influenced in part by their reproductive strategy (Lack 1968), which ranges from colonial nesting, where breeding pairs broadly share access to nesting areas and foraging locations (e.g., Cliff Swallows *Petrochelidon pyrrhonota*; Brown and Brown 1996), to solitary nesting, where individuals defend exclusive territories that encompass all necessary resources (e.g., Prairie Warblers *Setophaga discolor*;

Nolan 1978). For species that are solitary nesters, conspecific males typically do not share space and aggressively defend territories (Brown 1969, Stamps 1994) while sharing the territory with a mate during nesting and chick rearing (Lack 1968). Landscape composition and habitat availability also influence how individuals use space during the breeding season (Fretwell and Lucas 1969); thus, assessing the space use patterns of breeding birds is fundamental to understanding their habitat requirements.

Habitat selection is the process by which animals use habitat features (e.g., foraging, nesting, and roosting areas) disproportionately to their availability, which can influence the fitness of both breeding adults and their potential young (Manly et al. 2002, Northrup et al. 2022). There are various orders or scales at which habitat selection can be assessed, but one of the most common scales used by researchers and land managers is within the home ranges of individuals (third-order selection; Johnson 1980) in part because this is the scale at which habitat management practices are often implemented (e.g., habitat restoration or manipulation via cutting or burning). For species that depend on disturbance-maintained habitats such as early successional forests in the northeast United States (Harper 2007, Masse et al. 2015, Litvaitis et al. 2021), determining habitat selection at this home range scale is especially important because early successional forest is in decline as unused agricultural land and other open areas succeed into mature second growth forests (Buffum et al. 2021). Early successional forests support a variety of specialist bird species (e.g., Golden-winged Warbler *Vermivora chrysoptera*, Eastern Towhee *Pipilo erythrophthalmus*, Eastern Whip-poor-will *Antrostomus vociferus*, and Prairie Warbler), and the decline in this habitat has led to declines in the specialist species that rely on them (King and Schlossberg 2014). Targeted habitat management at biologically meaningful scales is essential for effective conservation of these declining species, and documenting habitat selection for a given species helps inform best management practices.

The Eastern Whip-poor-will (hereafter Whip-poor-will) is a nocturnal aerial insectivore that has declined throughout its range by approximately 70% since 1970 (Rosenberg et al. 2016), which is thought to be due primarily to the loss of early successional forest and declines of insect prey (Hallmann et al. 2014, Tozer et al. 2014, English et al. 2017, Spiller and Dettmers 2019). Male Whip-poor-wills establish and defend exclusive breeding territories that contain early successional forest openings as well as middle-aged or older trees that are used as nocturnal singing locations (Cink et al. 2020). Male and female Whip-poor-wills form monogamous pairs, with both actively involved in incubation and chick rearing (Corcoran et al. 2025), and there is evidence that pairs will continue to breed together for multiple years (Cink et al. 2020). Previous studies on Whip-poor-wills have focused on tracking movements of adults on the breeding grounds (e.g., Wilson 2003, Rand 2014, Spiller et al. 2022, Stewart 2023) and on the wintering grounds (e.g., Tonra et al. 2019, Bakermans et al. 2022, Skinner et al. 2023), tracking migratory pathways (e.g., English et al. 2017, Korpach et al. 2022, Skinner et al. 2022, Bakermans and Vitz 2023, Thompson 2023), and quantifying occupancy in relation to landscape features (e.g., Tozer et al. 2014, Slover and Katzner 2016, Farrell et al. 2017, 2019). Only two studies have quantified space use sharing of breeding adults (Rand 2014, Stewart 2023), and three studies have quantified habitat selection of Whip-poor-wills (Garlapow 2007, Rand 2014, Grahame et al. 2021). Only Garlapow (2007) has quantified habitat selection within individuals' breeding home ranges. Additional information is needed about how Whip-poor-wills share space and select habitat features at the home range scale, especially in southern New England forests where management for early successional species has been emphasized (King and Schlossberg 2014, Masse et al. 2014, Buffum et al. 2021, Litvaitis et al. 2021).

The objectives of our study of Whip-poor-wills during the breeding season were to (1) quantify the diurnal home ranges of breeding adults, (2) quantify the diurnal space use sharing of neighboring

adult males, (3) quantify the diurnal space use sharing of paired males and females, and (4) quantify home range-scale diurnal habitat selection of adults across two study sites. Given that Whip-poor-wills are monogamous, both sexes participate in incubation and chick rearing, and males defend exclusive territories, we predicted that diurnal home ranges of neighboring male Whip-poor-wills would not overlap, whereas diurnal home ranges of paired males and females would significantly overlap. Based on the land cover types commonly associated with Whip-poor-will roosting and nesting (e.g., Hunt 2013, Akresh and King 2016, Grahame et al. 2021, Spiller and King 2021), we predicted that individuals would select for areas closer to early successional forest openings (e.g., scrub and grasslands).

## METHODS

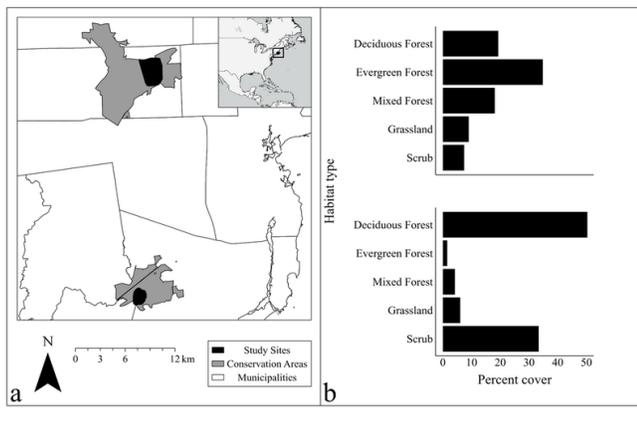
### Study sites

From May to August 2022 and 2023, we captured and tracked Eastern Whip-poor-wills at study sites within two state conservation areas in Rhode Island, USA: a 432-ha site (41.643996° N, 71.578277° W) within Big River Management Area (3367 ha) and a 152-ha site (41.45303° N, 71.59103° W) within Great Swamp Management Area (890 ha; Fig. 1a). These sites were actively managed to create or maintain early successional habitat and singing Whip-poor-wills were present. Both sites included stands with older second-growth forests (about 50–100 years old), early successional forest (about 5–20 years old) as well as areas with open grasslands, although the sites differed in the relative abundance of these stands (Fig. 1b) primarily because of past land-use history. The study site within Big River Management Area is a former sand and gravel quarry and so is a sparsely vegetated, managed grassland surrounded by second-growth forest. The study site within Great Swamp has never been developed and is maintained as different age stands of early successional forest by periodic selective cuts of forest as well as mowing and burning to maintain the grassland areas (Fig. 1b).

### Capture and tracking

We used singing surveys initiated 45 min after sunset the night prior to attempted captures to locate male Whip-poor-will singing perches. Prior to sunset the following night, we set up 60-mm mist nets and activated audio lures using conspecific playback (recording from *Xeno-canto*; Driver 2022) 45 min after sunset or when the first Whip-poor-will was heard singing to attract and capture these singing males. Subsequently, we tracked the tagged males at night to nests at which we used a spotlight and hand net to capture incubating females. All captured individuals were aged and sexed, measured (mass, tarsus length, wing chord, and tail length; Pyle 1997), and banded with a USGS aluminum leg band, and then an Advanced Telemetry Systems A1065 VHF transmitter weighing approximately 1.3 g (< 3% of body mass) was attached with a leg loop harness (Rappole and Tipton 1991) using Gutermann 4017 black elastic thread. We used a Telonics TR-8 handheld receiver and RA-23K antenna to track all tagged individuals directly to diurnal locations for males and females and nesting locations for females three to five times per week from capture until they departed the study areas to commence fall migration. This study was part of a larger multispecies spatial ecology study; due to logistical constraints we only tracked individuals during the diurnal period. In cases where individuals

**Fig. 1.** Details about study site locations. (a) Study site locations in Rhode Island, USA, from north to south: Big River Management Area (432.35 ha; 41.64400°N, -71.57828°W), Great Swamp Management Area (151.98 ha; 41.45303°N, 71.59103°W). (b) Percent cover of available land cover types within the home ranges of all tracked individuals that were included in the habitat selection models at Big River Management Area (top) and Great Swamp Management Area (bottom). Land cover types not included in the models (e.g. bare land, open water, etc.) were excluded, thus values do not add up to 100%.



were in inaccessible areas where we were unable to get exact locations, we used triangulation from three bearings to estimate the locations. We did not account for time between bearings given the low activity of Whip-poor-wills during the diurnal period and short times (< 30 min) between bearing recordings. Triangulations were calculated using the *razimuth* package (Peck 2017, Gerber et al. 2018) in R 4.1.0 (R Core Team 2021). We used the posterior mode from each triangulation and applied a criterion of < 0.5 ha for the 50% isopleth of each triangulation to exclude any points with large uncertainty, and we did not account for potential overlap of the 50% isopleth with multiple land cover types. All locations taken at nests during incubation were included despite the lack of movement because time was still an important component. Tracking data used for this analysis was from 4 May to 15 August, which encompassed the approximate end of birds arriving to the breeding grounds and the approximate end of the nesting period at our study areas, respectively (Corcoran et al. 2025).

### Home range size and spatial overlap of males and females

We used direct GPS location data and the posterior modes of triangulations to visually inspect each individual's variogram to confirm that range residency was achieved and individuals could thus be included in home range analyses (Calabrese et al. 2016). We fit continuous time movement models in the *ctmm* package (Calabrese et al. 2016) in R 4.1.0 (R Core Team 2021) using the functions *ctmm.guess* and *ctmm.select* to select and fit the best fitting movement models. We then calculated diurnal home ranges (hereafter home ranges) from the 95% auto-correlated kernel density estimates (AKDE) using the *akde* function for individuals with at least 32 locations during 4 May to 15 August. We used a

generalized linear model (GLM) in a Bayesian framework using the *brm* function in the *brms* package (Bürkner 2017) in R 4.1.0 (R Core Team 2021) to assess the influence of sex and location on home range size, including their interaction. The model was implemented using a Gaussian likelihood and estimated via a Markov Chain Monte Carlo (MCMC) algorithm with four parallel chains, each run for 10,000 iterations. The first 2000 iterations of each chain were used as warm-up and discarded, which resulted in a total of 32,000 posterior samples for inference. We specified weakly informative priors, setting a normal prior with mean 20 and standard deviation 10 for the intercept and normal priors with mean 0 and standard deviation 5 for the regression coefficients of the predictors. We checked for model convergence by visually inspecting the four parallel MCMC trace plots and considered the Gelman-Rubin diagnostic ( $\hat{R}$ ; Gelman et al. 2004) < 1.05 to indicate convergence. If individuals were tracked during multiple breeding seasons, we only used their first year of data to quantify the influences of sex and location on home range size. In order to get the mean home range size for each group (e.g., males, females, Big River, and Great Swamp), we generated the posterior draws for each individual using the *posterior\_epred* function in *brms*. We then averaged the posterior draws across individuals within each group and summarized the mean and 95% credible intervals for each group. We used Bayesian linear mixed models (LMM) with the same parameters specified above for the GLM to compare the home range sizes of paired males and females and across years for individuals tracked in both 2022 and 2023. Each LMM used a random effect for either pair (paired males and females) or for individual (same males tracked across years). We used the *ctmm* package and the code associated with Tilberg and Dixon (2021) to calculate the utilization distribution overlap index (UDOI, Fieberg and Kochanny 2005) and the area of shared space use ( $A_{1,2}$ ) of the home ranges for all neighboring male Whip-poor-wills and male and female pairs at each site to assess whether individuals shared diurnal areas. UDOI values can range from 0 (no home range overlap) to 1 (uniform space use, 100% home range overlap); values > 1 indicate nonuniform home ranges that have a higher degree of overlap than if they were uniform (Fieberg and Kochanny 2005).

### Habitat selection

We used the most recent land cover layer available in Rhode Island (Forest Habitat 2020, RIGIS 2020) to estimate the following continuous land cover covariates within each Whip-poor-will home range: distance to deciduous forest (m), distance to evergreen forest (m), distance to mixed forest (m), distance to scrub (m), and distance to grassland (m). We combined forested and scrub wetland cover into upland forest and scrub cover because we assumed roosting birds would use upland and wetland land cover types similarly. This land cover layer has a 1-meter resolution and was reprojected from NAD 1983 State Plane Rhode Island FIPS 3800 (US Feet) to NAD 83 UTM Zone 19N using the *Project Raster* tool in ArcGIS Pro 3.2.0. We generated the distance rasters for each land cover covariate using the *Euclidean distance* tool and then clipped these rasters to the extent of the home ranges of our tracked individuals using the *Clip Raster* tool.

We used a use-available framework to assess habitat selection by comparing used locations (tracking data) to a set of random available locations within each individual's home range (Manly

et al. 2002). We assessed whether any of the five land cover covariates were too highly correlated using a conservative Pearson correlation threshold of  $> 0.5$  (Dormann et al. 2013) and thus removed mixed forest from the models due to correlation with evergreen forest. Distance values to each land cover covariate for all used and available points were scaled to have a mean of 0 and standard deviation of 1 using the base R scale function. We determined the minimum number of available locations by sequentially randomly sampling 10, 100, 250, 500, 1000, and 2000 times the used locations (Northrup et al. 2013) and found that 100 times the used locations adequately produced stable estimates for each covariate. We fit separate logistic regression models for each individual in a Bayesian framework using the brms package (Bürkner 2017) in R 4.1.0 (R Core Team 2021). The models were implemented using a Bernoulli likelihood and estimated via a Markov Chain Monte Carlo (MCMC) algorithm with four parallel chains, each run for 10,000 iterations. The first 2000 iterations of each chain were used as warm-up and discarded, resulting in a total of 32,000 posterior samples for inference. We specified weakly informative priors, setting a normal prior with mean 0 and standard deviation 5 for the intercept and normal priors with mean 0 and standard deviation 2.5 for the regression coefficients of the predictors. We checked for model convergence by visually inspecting the four parallel MCMC trace plots and considered the Gelman-Rubin diagnostic ( $\hat{R}$ ; Gelman et al. 2004)  $< 1.05$  to indicate convergence. We included year as an additional predictor in models for individuals that were tracked in both 2022 and 2023. Population-level estimates were obtained by combining the full posterior distributions of each covariate from all individual models and summarizing them as means and 95% credible intervals. We assessed the support for each coefficient estimate from the models by examining whether its 95% credible intervals overlapped or included 0.

## RESULTS

### Capture and tracking of radio-tagged males and females

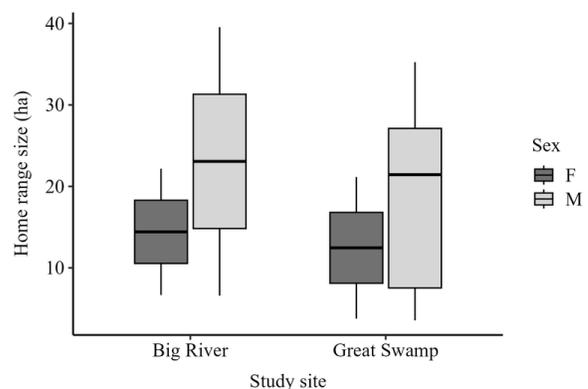
In 2022, we captured and tracked two males and two females at Big River and four males and two females at Great Swamp. Based on our singing surveys and the location of nests from May to August 2022, we believe that we tagged all individuals present at our site in Big River and all the males present at our site in Great Swamp. All captured and tracked females in 2022 were paired with radio-tagged males. At Great Swamp, we were unable to capture one female that was paired with a radio-tagged male, and we could not determine if the fourth radio-tagged male had a female mate. We confirmed the identity of male-female pairs by tracking males at night to nests that they were incubating where we subsequently captured the female mates. In 2023 at Great Swamp, we recaptured and tracked the same four males from 2022 plus one additional male that was not present the year before; therefore, four males have two years of tracking data. We also recaptured one female at Great Swamp from 2022, but she apparently left the study site before providing enough data to be included in our sample. In 2023 at Big River, we captured one new male, one new female, and recaptured a female from 2022; however, the recaptured female dropped her tag after three weeks and the other two individuals apparently left the study site before

providing enough data to be included in our sample. No other individuals were detected at Big River in 2023 so only individuals at Great Swamp were considered for this second year. In sum, the tracking dataset used for estimating home ranges and habitat selection included 11 individuals total, 10 from 2022 (six males, four females; four pairs) and five from 2023 (all males; four from both years, one from 2023 only) each with 32 to 45 diurnal locations per individual during the tracking period (4 May to 15 August). All individuals were tracked three to five times per week, so differences in total number of diurnal locations per individual are related to when a given bird was captured.

### Diurnal home range size and overlap between neighbors and breeding pairs

Given that the mean 50% isopleth for the triangulated points was  $< 1$  ha (mean = 0.58 ha, range = 0.06–0.94), we did not exclude any points when estimating home range size or overlap. For our GLM and LMMs, the MCMC trace plots indicated good mixing and  $\hat{R}$  values were  $< 1.05$  confirming model convergence. From our Bayesian GLM, we detected no differences in home range size of males (18.71 ha, 95% CI: 9.96, 27.44) and females (16.89 ha, 95% CI: 6.95, 27.13) across the two sites or within the same site (Fig. 2). Mean home range sizes at Big River and Great Swamp were 18.01 ha (95% CI: 7.97, 28.06) and 18.07 ha (95% CI: 9.42, 26.81), respectively. The overall mean home range size across sexes and sites was 18.05 ha (95% CI: 10.23, 26.11) with a range of 3.56–39.55 ha. The model was parameterized with females at Big River as the reference group (intercept: 17.22 ha, 95% CI: 6.18, 28.44). The coefficient for males at Big River ( $\beta = 1.68$ , 95% CI: -7.02, 10.23) represents the difference in home range size between males and females at Big River. The coefficient for Great Swamp ( $\beta = -0.57$ , 95% CI: -9.16, 8.06) represents the difference between females at Big River and females at Great Swamp. The interaction term ( $\beta = 0.43$ , 95% CI: -8.16, 9.06) represents how the difference between males and females at Great Swamp differs from Big River.

**Fig. 2.** Distribution of observed home range sizes of male and female Eastern Whip-poor-wills (*Antrostomus vociferus*) at Big River ( $n = 4$ ) and Great Swamp ( $n = 7$ ) management areas in 2022. The midline indicates the median, boxes show the interquartile range, and whiskers show the full range. No differences in home range size were detected between sexes or sites (GLM, see text for details).



From our Bayesian LMM for paired males and females, we detected no difference in home range sizes. The model was parameterized with females as the reference group (intercept: 15.05 ha, 95% CI: 5.11, 25.48), and the coefficient for males ( $\beta = 0.35$ , 95% CI: -7.44, 8.00) indicated no sex effect. The random intercept estimate (7.31 ha, 95% CI: 0.41, 18.19) indicated moderate variation between pairs. We also detected no difference in home range size for the same males across years. This LMM was parameterized with 2022 as the reference year (intercept: 18.10 ha, 95% CI: 6.48, 29.95), and the coefficient for 2023 ( $\beta = -1.49$ , 95% CI: -9.35, 6.71) indicated no year effect. The random intercept estimate (10.20 ha, 95% CI: 0.84, 24.26) indicated moderate variation between individuals.

Male home ranges overlapped minimally with other males (Fig. 3), whereas the home ranges of each paired male and female had a high degree of overlap (Table 1). Home ranges of three of the four males that were tracked at Great Swamp in 2022 overlapped considerably with the home ranges they used in 2023 (Table 1), indicating that they were using similar areas in both years.

### Diurnal habitat selection of individuals

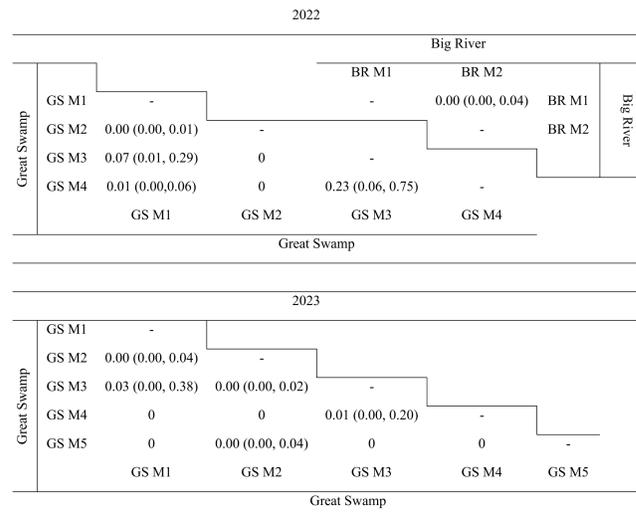
For our logistic regression models, the MCMC trace plots indicated good mixing and  $R$  values were  $< 1.05$  confirming model convergence. At the population level, the means and 95% credible intervals for all land cover covariates had zero overlap, indicating no support for selection to be closer to or farther from the land cover covariates that we considered. Population-level coefficient estimates for each land cover type are as follows: distance to deciduous forest ( $\beta = -0.52$ , 95% CI: -1.97, 0.32), distance to evergreen forest ( $\beta = -0.80$ , 95% CI: -6.01, 0.74), distance to scrub ( $\beta = -0.64$ , 95% CI: -4.00, 1.29), and distance to grassland ( $\beta = -0.49$ , 95% CI: -2.61, 0.70). At the individual level, 10 of 11 individuals selected to be closer to or farther from at least one land cover type (Fig. 4). More specifically, six of 11 individuals selected areas closer to deciduous forest, four of 11 individuals selected areas closer to evergreen forest while one selected areas farther from evergreen forest, four of 11 individuals selected areas closer to scrub, one selected areas farther from scrub, and six of 11 individuals selected areas closer to grassland.

## DISCUSSION

### Diurnal home range size

We detected no differences in diurnal home range size between males and females across sites or within the same site. The mean home range size of 18.05 ha across both study sites is smaller than those reported by other studies in North Carolina (Wilson 2003: 45 ha), Ontario (Rand 2014: 136.2 ha), Illinois (Stewart 2023: 45.6 ha), and across three ecoregions in Manitoba and Ontario (Korpach et al. 2025: 53.6 ha) but is similar in size to that reported by Garlapow (2007: 25 ha), which took place ~90 km from both of our sites in Massachusetts, USA. The wide variation in home range size that we documented (3.56–39.55 ha) is similar to that found in these other studies (Wilson 2003: 2.3–282.2 ha, Rand 2014: 19.6–499.5 ha, Stewart 2023: 5.3–158.7 ha, Korpach et al. 2025: 6.8–135.8 ha) but with our upper limit still much smaller than the upper limits of these other studies. The relatively smaller range of home range sizes that we report may be because our

**Fig. 3.** Utilization distribution overlap index (UDOI) values for all neighboring male (M) Eastern Whip-poor-wills (*Antrostomus vociferus*) in 2022 at both Big River (BR) Management Area and Great Swamp (GS) Management Area and in 2023 at only Great Swamp Management Area. UDOI values can range from 0 (no home range overlap) to 1 (uniform space use, 100% home range overlap) or greater than 1 (more likely to share space than if home ranges were uniform). 95% confidence intervals are in parentheses.



estimates of diurnal home range size do not capture the full extent of Whip-poor-will space use at our sites because they excluded the active nocturnal period, which is included in these other studies.

Rand (2014) and Stewart (2023) also found no differences in male and female home range sizes, although these and other studies have not directly compared space use between multiple sites. This consistency in home range size between males and females suggests that sex may not be a primary driver of variation in Whip-poor-will space use, because both males and females likely have similar resource demands during the breeding season. Stewart (2023) also found that both males and females increased their home range sizes during chick rearing, and that home range sizes changed with the time of day (i.e., larger during the crepuscular period and smaller at night). This temporal variation in home range size suggests that accounting for different times of the day and stages of the breeding season provides a more complete representation of an individual's space use patterns. For example, figure 1 in Grahame et al. (2021) reported both diurnal and nocturnal tracking locations, with diurnal locations consistently falling close to nocturnal points. Additionally, Skinner et al. (2023) found that 87.5% of diurnal roost locations fell within the nocturnal home range of Whip-poor-wills in the non-breeding season. Thus, although our results only represent home ranges derived from diurnal locations, these locations are likely near areas used for foraging as well as singing perches used for territorial defense.

**Table 1.** Utilization distribution overlap index (UDOI) and area of shared space use (A 1,2) values for the home ranges of paired male (M) and female (F) Eastern Whip-poor-wills (*Antrostomus vociferus*) tracked at Big River (BR) Management Area and Great Swamp (GS) Management Area in 2022 and the same males tracked at Great Swamp Management Area in 2022 and 2023. UDOI values typically range from 0 (no home range overlap) to 1 (uniform space use, 100% home range overlap) with values greater than 1 indicating that individuals are more likely to share space than if home ranges were uniform. The A 1,2 value is the spatial area in hectares (ha) that a pair of individuals share. 95% confidence intervals are in parentheses.

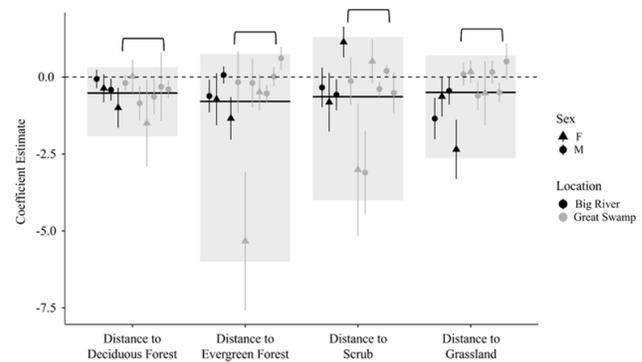
2022 Pairs		
Pair	UDOI	A 1,2 (ha)
GS M1, GS F1	0.82 (0.10, 2.09)	2.25 (1.56, 3.27)
GS M2, GS F2	1.04 (0.22, 1.43)	8.86 (5.06, 11.35)
BR M1, BR F1	0.67 (0.11, 1.55)	11.12 (7.66, 15.51)
BR M2, BR F2	0.79 (0.56, 2.22)	24.30 (14.42, 35.63)
2022, 2023 Same Males		
Male	UDOI	A 1,2 (ha)
GS M1	0.76 (0.33, 1.74)	2.20 (1.65, 2.85)
GS M2	1.06 (0.52, 1.80)	7.18 (4.23, 10.22)
GS M3	1.04 (0.40, 1.77)	2.52 (1.86, 3.27)
GS M4	0.38 (0.25, 0.98)	32.63 (16.83, 34.71)

### Diurnal home range overlap

Consistent with our predictions, we showed that neighboring male home ranges minimally overlapped whereas paired males and females shared a significant amount of space. Neighboring males likely shared minimal space due to territorial behavior during the breeding season and paired males and females likely shared a significant amount of space because of the shared nesting responsibilities of monogamous pairs. Rand (2014) and Stewart (2023) also showed that male and female pairs were more likely to share a significant amount of space than neighboring males. In addition, Stewart (2023) reported that neighboring males regularly shared space especially during the crepuscular foraging period but also throughout the night, which is inconsistent with our findings and those reported in Rand (2014). We acknowledge that our estimates of diurnal home range overlap do not capture the full extent of Whip-poor-will space use and thus limit our interpretations, especially given the temporal variation in home range size reported by Stewart (2023).

The home ranges of three of the four males tracked at Great Swamp in both 2022 and 2023 overlapped significantly, indicating that those males not only showed site fidelity, but also fidelity to their home ranges within the site. One male (GS M4 in Table 1) showed a lower degree of overlap likely due to three roosting locations in 2022 that were 750 to 800 m from the main cluster of roosting locations, which greatly expanded the 2022 home range size, but the majority of roosting locations were in very similar areas in both years. Korpach et al. (2025) also report repeat tracking of four breeding males across two years in which these males reused 65–81% of their previous home ranges. Bakermans et al. (2022) reported a similar pattern of site fidelity of nine Whip-

**Fig. 4.** Habitat selection coefficient estimates for each tracked individual (n = 11: males n = 7, females n = 4) in 2022–2023 at two study sites, Big River (black) and Great Swamp (gray), in Rhode Island, USA. Mean population-level estimates calculated from the posterior distributions of all individuals are represented by the black lines, with the 95% CIs represented by the shaded areas. The two paired males and females at each study area are the first eight individuals with pairs adjacent to each other. The brackets encompass the four males that were tracked at Great Swamp in both 2022 and 2023 (both years were included together, see methods for details). Support for selection closer to (negative) or farther from (positive) each land cover covariate is shown if the 95% CIs do not overlap 0.



poor-wills across two years on their wintering grounds. Although more studies are needed, evidence to date suggests that there may be high site and home range fidelity of both breeding and non-breeding adult Whip-poor-wills.

### Diurnal habitat selection

The Whip-poor-will is generally considered a disturbance-dependent species that consistently occupies open canopy forest and open land cover types like grasslands and shrublands. Many studies have identified edge as an important feature for Whip-poor-wills (e.g., Wilson 2003, Hunt 2013, Tozer et al. 2014, Akresh and King 2016, English et al. 2017, Stewart 2023). We found no support for selection of any land cover types at the population level but found support for selection of certain land cover types at the individual level (Fig. 4). Specifically, we found that 10 of 11 individuals selected for distance to at least one land cover type, although selection varied across individuals. Consistent with our second prediction, 8 of 11 individuals selected for areas closer to early successional forest openings (e.g., scrub or grasslands). There were no clear patterns of selection within either sex, either site, or within male and female pairs. Garlapow (2007) and Rand (2014) also found no population-level selection of any land cover types or features available in their study areas, although Garlapow (2007) did not consider discrete land cover types like Rand (2014) and our study. Grahame et al. (2021) compared land cover types used by Whip-poor-wills to land cover types available within a minimum bounding polygon encompassing all locations from 44 adult Whip-poor-wills at their study site rather than within home ranges and included both diurnal and nocturnal locations. They

found that Whip-poor-wills selected for deciduous forest and shrubland areas during the day and deciduous forest, mixed forest, rock barrens, and shrublands at night. Both Garlapow (2007) and Rand (2014) and our study included  $\leq 15$  individuals in our habitat selection analyses. These small sample sizes may have limited the ability to parse out population-level selection patterns. Space use and habitat selection of Whip-poor-wills may differ between the active nocturnal foraging period and the less active diurnal period (Grahame et al. 2021, Stewart 2023); thus, a complete understanding of habitat selection requires tracking individuals throughout the day and at night. In general, our use of only diurnal locations for this habitat selection analysis and our small sample size ( $n = 11$ ; male  $n = 7$ , female  $n = 4$ ) limits our inference and thus our results should be interpreted with this in mind. Despite these limitations, diurnal locations are still an important component of a bird's daily activities and offer important insights because birds rely on these locations to provide adequate cover for predator avoidance as well as for optimal thermoregulation throughout the day, both of which influence an individual's fitness (Walsberg 1986, Körtner and Geiser 1999, Fisher et al. 2004, Bock et al. 2013).

## Conservation implications and future directions

Given that paired males and females shared home ranges—on average  $\sim 18$  ha but as high as  $\sim 40$  ha—that were exclusive from other pairs, a sufficiently large area that contains early successional forest openings as well as middle-aged or older trees (Cink et al. 2020) is required to sustain a local breeding population. Additionally, the site and home range fidelity observed in four of our males and the individuals described in Korpach et al. (2025) indicates that at least some individuals return to their same breeding home ranges across years. Thus, management efforts that focus on known breeding grounds may help to support stable local populations. Whereas our findings demonstrated no support for selection of any land cover types at the population level, 8 of 11 individuals showed support for selection of early successional forest (e.g., scrub and grassland). These results, in addition to the existing body of literature on Whip-poor-will habitat selection (Garlapow 2007, Rand 2014, Grahame et al. 2021) and occupancy (e.g., Tozer et al. 2014, Slover and Katzner 2016, Farrell et al. 2017, 2019), underscore the importance of managed landscapes that maintain disturbance-driven habitat mosaics of forest, edges, and scrub. Because these land cover types depend on periodic disturbance, active management practices such as selective or clearcutting, prescribed burning, and mowing are essential for sustaining suitable conditions for Whip-poor-wills (Hunt 2014).

Future studies should aim to collect tracking data across the full 24-hour period at multiple sites throughout the breeding season to better capture habitat selection patterns at the home range scale and ensure that conservation strategies address all aspects of Whip-poor-will habitat needs. Additionally, the movement patterns and habitat selection of juvenile Whip-poor-wills have largely been ignored, yet they are crucial for understanding post-fledging survival, dispersal, and the identification of critical areas for young birds.

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### Author Contributions:

*Liam Corcoran: conceptualization, methodology, software, validation, formal analysis, investigation, data creation, writing (original draft, review, and editing), visualization, supervision, project administration. Scott McWilliams: conceptualization, writing (review and editing), supervision, funding acquisition, project administration.*

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