

Eastern Whip-poor-wills have larger nonbreeding home ranges in areas with more agriculture and forest fragmentation

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ABSTRACT

Migratory bird populations can be limited by events in disparate parts of the world. Birds wintering in tropical regions are facing rapid habitat loss, climate change, and intensive agricultural regimes, potentially contributing to population declines. However, an understanding of basic nonbreeding ecology of species, such as habitat and space use, is critical for determining if this is the case. Populations of the nocturnal/crepuscular Eastern Whip-poor-will (*Antrostomus vociferus*) have declined by 70% since the 1960's, yet data on the species are sparse outside of the breeding season. We extracted data from 41 archival GPS tags deployed on whip-poor-wills and estimated nonbreeding home ranges and land covers used. We used satellite imagery and stable carbon and nitrogen isotope values from claws grown during the nonbreeding season to analyze how land cover and habitat moisture impacted home range size and relative trophic level. Forest was by far the most prevalent land cover used by whip-poor-wills, occurring in all home ranges and accounting for >80% of diurnal roosting points. We found that less forest, the presence of agriculture, and more edge (irrespective of land cover) were associated with larger home ranges. Stable isotope values differed by broadscale ecoregion but not local land cover characteristics in our study, indicating that regional idiosyncrasies or broadscale processes can be more important in determining stable isotope ratios. Our findings suggest that the loss, fragmentation, and replacement of forest by agriculture in the core of the whip-poor-will's nonbreeding range may represent a threat to the species, as they rely heavily upon forest, and appear to alter space use in response to changes in forest cover.

Keywords: agriculture, Eastern Whip-poor-will, forest, fragmentation, full annual cycle ecology, home range, landscape composition, nightjar

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LAY SUMMARY

- Understanding threats and basic ecology throughout the full annual cycle is critical for effective conservation of migratory birds.
- We used GPS data with satellite imagery during the nonbreeding period to describe foraging and roosting habitat use in the declining Eastern Whip-poor-will. We combined these data with stable isotope values to analyze how land use and habitat moisture impacted home range size and relative trophic level.
- Whip-poor-will nonbreeding home ranges are small (mean: 1.86 ± 1.90 ha) compared to breeding home ranges, and all birds depended on forests for both foraging and roosting.
- Smaller, more fragmented forests were associated with increased home range sizes in whip-poor-wills, particularly when agriculture was present, potentially reflecting a reduced capacity for human-altered lands to meet habitat requirements.
- Minimizing the conversion of forest to agricultural lands, including the protection of small forest fragments, could prevent the loss of additional habitat for whip-poor-wills and other forest-dependent species.

Antrostomus vociferus tiene rangos de hogar no reproductivos más grandes en áreas con más agricultura y fragmentación forestal

RESUMEN

Las poblaciones de aves migratorias pueden verse limitadas por eventos en diferentes partes del mundo. Las aves que invernan en regiones tropicales se enfrentan a una rápida pérdida de hábitat, cambio climático y regímenes agrícolas intensivos, los cuales podrían contribuir a la disminución de sus poblaciones. Sin embargo, entender la ecología básica no reproductiva de las especies, como el uso del hábitat y del espacio, es fundamental para determinar si este es el caso. Las poblaciones de *Antrastomus vociferus*, una ave nocturna/crepuscular, han disminuido un 70% desde la década de 1960, pero los datos sobre la especie son escasos fuera de la temporada reproductiva. Extrajimos datos de 41 registradores GPS colocados en *A. vociferus* y estimamos los rangos del hogar no reproductivos y las coberturas de la tierra utilizadas. Usamos imágenes satelitales y valores de isótopos estables de carbono y nitrógeno de las garras que crecieron durante la temporada no reproductiva para analizar cómo la cobertura y la humedad del hábitat afectaron el tamaño del rango del hogar y el nivel trófico relativo. El bosque fue la cobertura más predominante utilizada por *A. vociferus*, presente en todos los rangos del hogar y representando > 80% de los puntos de descanso diurnos. Encontramos que menos bosque, presencia de agricultura y más borde (independientemente de la cobertura del suelo) estaban asociados con rangos de hogar más grandes. En nuestro estudio, los valores de isótopos estables diferían a gran escala según la ecorregión, pero no por las características locales de la cobertura, lo cual indica que idiosincrasias regionales o los procesos a gran escala pueden ser más importantes para determinar los valores de isótopos estables. Nuestros hallazgos sugieren que la pérdida, fragmentación y reemplazo de bosques por agricultura en el núcleo del área de distribución no reproductiva de *A. vociferus* puede representar una amenaza para la especie, ya que depende en gran medida del bosque, y parece alterar el uso del espacio en respuesta a los cambios en la cobertura del bosque.

Palabras clave: agricultura, *Antrastomus vociferus*, área de distribución, bosque, chotacabras, composición del paisaje, ecología de ciclo anual completo, fragmentación

INTRODUCTION

Migratory birds worldwide are in decline (Møller *et al.* 2008, Gilroy *et al.* 2016, Rosenberg *et al.* 2019), yet the basic natural history and ecology of most of these species outside of the breeding season remain poorly understood (Marra *et al.* 2015a). Understanding space and habitat use in the nonbreeding period, and throughout the diel cycle, is critical for informed conservation planning (Albert *et al.* 2020), as most migrants spend the majority of the year in these locations (La Sorte *et al.* 2017). Furthermore, land-use change has altered the distribution, quality, and quantity of habitat and food resources (Lawler *et al.* 2014), with important repercussions for biodiversity (Kennedy *et al.* 2019). Agriculture, which now covers roughly half of the earth's land mass (Kennedy *et al.* 2019), has displaced natural landscapes (Gibbs *et al.* 2010) and fragmented previously large tracts of forest (Lewis *et al.* 2015). Forest loss and fragmentation can lead to negative edge effects (Laurance *et al.* 2004, Ewers and Banks-Leite 2013) and arthropod declines (Attwood *et al.* 2008, Hallmann *et al.* 2017, Seibold *et al.* 2019), with implications for insectivorous birds (Bregman *et al.* 2014, Spiller and Dettmers 2019).

Changes in the amount and configuration of habitat can impact space use (Hinam and Clair 2008, Powell *et al.* 2016), which in turn has important local and downstream (i.e., carry-over effects) repercussions for population limitation (e.g., Marra *et al.* 1998, Akresh *et al.* 2019b, Powell *et al.* 2021). While food availability is perhaps the best-known determinant of space use (generally, the greater amount of food present, the smaller the area needed to meet metabolic needs; Smith and Shugart 1987, Mccloughlin and Ferguson 2000) in the stationary nonbreeding season (i.e., excluding migration), other factors such as competitive interactions (Powell *et al.* 2021), predator/prey dynamics (Harmange *et al.* 2021), amount of foraging habitat (Siffczyk *et al.* 2003, Hansbauer *et al.* 2008), habitat quality (Godet *et al.* 2018), and habitat needs throughout the diel cycle (Smith *et al.* 2008, Jirinec *et al.* 2011) can also impact space use. In particular, using distinct foraging and roosting locations (sometimes kilometers apart) can increase home range size, habitat types used, and functional connectivity requirements (e.g., Smith *et al.* 2008, Jirinec *et al.* 2011, Smetzer *et al.* 2021). Therefore, understanding nonbreeding space use and habitat requirements is critical to implementing effective conservation measures at

meaningful spatial scales (Nams *et al.* 2006, Boyd *et al.* 2008, Buchmann *et al.* 2013, Jirinec *et al.* 2018).

The link between increasing agriculture and insect declines (Attwood *et al.* 2008, Seibold *et al.* 2019) may be a key factor in the precipitous decline of aerial insectivores (Stanton *et al.* 2018, Spiller and Dettmers 2019, Rosenberg *et al.* 2019, Tallamy and Shriver 2021), as this guild is dependent on flying insects as a primary food source. While much research has focused on declines in insect abundance, changes in community composition may be equally important, as shifts in diet composition have been tied to reduced immune system function, body condition, and overall aerial insectivore declines (Nocera *et al.* 2012, Navarro-López *et al.* 2014). Insects at higher trophic levels seem to be particularly extinction-prone in the face of disturbance (e.g., Coleoptera; Didham *et al.* 1998, Attwood *et al.* 2008), suggesting birds residing in agricultural communities may feed at lower trophic levels. Because most temperate-zone aerial insectivores are migratory, the rapid conversion of forest for agricultural use (Hansen *et al.* 2008, Gibbs *et al.* 2010, Aide *et al.* 2013) and pesticide application on the nonbreeding grounds (e.g., Klemens *et al.* 2000, Cruz-Acevedo *et al.* 2020) likely pose significant threats to these species.

The use of stable isotope ratios in birds to obtain information remotely from disparate parts of the world has increased in recent decades (particularly following Marra *et al.* 1998), as stable isotope values can indicate habitat use and quality, trophic level, and geographic origin (Hobson and Wassenaar 2008). Bird claws in particular have been useful due to the slow turnover rates in claw tissue, and thus, samples obtained on the breeding grounds can be used to measure stable isotope ratios from the nonbreeding season (Bearhop *et al.* 2003, Hobson and Wassenaar 2008, Hahn *et al.* 2014). In terrestrial ecosystems, stable nitrogen isotope values ($\delta^{15}\text{N}$) are related to a bird's trophic level (Bearhop *et al.* 2003, English *et al.* 2018), whereas stable carbon isotope values ($\delta^{13}\text{C}$) vary based on moisture (e.g., Marra *et al.* 1998, Smith *et al.* 2010, Akresh *et al.* 2019a) and the photosynthetic pathway (C_3 vs. C_4) of the plants ingested by primary consumers (Post 2002); however, additional factors at both local (e.g., agricultural management practices) and large spatial scales (e.g., watershed) can also influence stable isotope ratios (e.g., Hobson 1999, Hobson *et al.* 2003, Ishikawa *et al.* 2012). It is unclear whether regional idiosyncrasies (González-Prieto and Hobson 2013) or large-scale drivers of stable carbon and nitrogen

TABLE 1. Tag deployment and recapture rates (numbers in parentheses represent the number of working tags), mean $\pm$ SD (sample size) of home range size (ha), and mean $\pm$ SD elevation (m), and range (minimum–maximum) of elevations (m) of whip-poor-will's first nonbreeding site in 2019–2020. Elevation data comes from 41 individuals.

Breeding site	Deployed	Recaptured	Average home range size (ha)	Mean $\pm$ SD elevation (m)	Range elevation (m)
Illinois	26	14 (12)	1.0 $\pm$ 0.4 (5)	589.3 $\pm$ 367.1	72–1250
Missouri	27	12 (11)	2.2 $\pm$ 0.9 (7)	769.4 $\pm$ 444.3	150–1568
N. Ohio	4	3	1.2 $\pm$ 0.9 (2)	575 $\pm$ 246.2	375–850
S. Ohio	10	4 (3)	5.4 $\pm$ 5.3 (2)	661.7 $\pm$ 575.5	10–1100
Wisconsin	27	14 (12)	1.5 $\pm$ 1.6 (9)	704.2 $\pm$ 362.6	40–1350
All sites	94	47 (41)	1.9 $\pm$ 1.9 (25)	675.5 $\pm$ 384.5	40–1568

isotope ratios could outweigh the local factors that are often assumed to influence isotopic patterns in birds (particularly relevant for birds with large nonbreeding ranges; [Boone et al. 2010](#), [Drake et al. 2014](#)).

The Eastern Whip-poor-will (*Antrostomus vociferus*; hereafter “whip-poor-will”) is a rapidly declining nightjar (70% population loss in the last 50 years; [Rosenberg et al. 2016](#)) that is largely non-vocal outside of the breeding season. On the breeding grounds, whip-poor-wills tend to use early-successional habitats; inhabiting regenerating forest and forest edge; cleared, barren, or burned areas; and wetlands at night; and roost in shrubland and deciduous forest ([Wilson and Watts 2008](#), [Tozer et al. 2014](#), [Akresh and King 2016](#), [Graham et al. 2021](#)). On the stationary nonbreeding grounds, single state GPS deployments by [Tonra et al. \(2019\)](#) and [Bakermans et al. \(2022\)](#) show that whip-poor-wills rely heavily on forests. Nevertheless, larger deployments across a greater swath of the whip-poor-will distribution are needed to understand variation in nonbreeding habitat use more fully. Furthermore, nothing is known of whip-poor-will diurnal roosting habits outside of the breeding season.

To better understand the impacts of land cover and habitat during the stationary nonbreeding period on whip-poor-wills, we deployed archival GPS tags at 5 breeding sites across 4 states in the Midwest U.S.A. to address 3 specific objectives. First, we calculated nonbreeding home range size, and then analyzed predictors of home range size at 3 spatial scales: within the home range, within the site (500-m radius buffer around home range centroids), and within the larger geographic region. As conversion of forest to agriculture reduces insect prey abundance/quality ([Attwood et al. 2008](#), [Seibold et al. 2019](#)) and increases the distance between habitat patches, we expected that whip-poor-wills in areas with substantial agricultural land cover would need more area to meet their metabolic needs, and thus have larger home ranges (as in [Buenestado et al. 2008](#)). Second, given that habitat use during breeding and nonbreeding seasons can differ (e.g., [Keast and Morton 1980](#)), we quantified land cover associated with whip-poor-will home ranges, the 500-m site, and diurnal roosting sites and qualitatively compare these results with patterns on the breeding grounds. We also quantified the spatial overlap between foraging home ranges and diurnal roosting locations. Finally, we tested the assumption that claw $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotopic values collected on the breeding grounds reflect land cover during the stationary nonbreeding season, despite claw synthesis occurring across a large nonbreeding range (northern Mexico to southern Nicaragua in our study). We predicted that whip-poor-wills in station-

ary nonbreeding sites with more agriculture would feed at a lower relative trophic level (i.e., lower $\delta^{15}\text{N}$ isotope values), and that agricultural or highly fragmented sites will be more xeric (i.e., more positive $\delta^{13}\text{C}$ isotope values) ([Camargo and Kapos 1995](#), [Kunert et al. 2015](#)).

METHODS

Study Sites

We captured whip-poor-wills in 5 breeding areas across 4 states in the midwestern U.S., spanning a latitudinal gradient of 9.49° (36.88°N to 46.37°N) and a longitudinal gradient of 8.81° (–91.21°W to –82.40°W). In the 5 breeding areas there were 9 breeding sites: Northern Ohio (41.47°N, –83.84°W), Southern Ohio (39.11°N, –82.40°W), Illinois (38.65°N, –88.77°W; 39.87°N, –90.93°W; 39.87°N, –90.93°W), Missouri (37.03°N, –91.15°W; 36.89°N, –91.21°W) and Wisconsin (46.10°N, –89.31°W; 46.37°N, –91.58°W). See figure 1 and the methods of [Skinner et al. \(2022a\)](#) for additional information on deployment locations.

Tag Deployment, Schedule, and Recovery

In May and June of 2019, birds were lured into mist nets by recorded calls of conspecifics. We aged and sexed individuals ([Pyle 1997](#)), took standard morphological measurements (e.g., mass, wing chord, tail length), collected claw samples (distal 3–5 mm of both central claws) for stable isotope ratio analysis, and marked all individuals with a U.S. Geological Survey aluminum band. We attached a 1.5-g archival GPS tag (model PinPoint-10; Lotek Wireless, Newmarket, Ontario, Canada; 2.3–3.2% of body mass) using a backpack-style leg-loop harness ([Rappole and Tipton 1991](#)) constructed from 0.7-mm bead cord (Stetch Magic) and 1.3-mm metal crimp beads. In 2020, we returned to the location where the bird was first caught and repeated the capture procedure. If the bird was not captured at the initial location, we expanded to the neighboring territories (within 500-m) and attempted to capture nearby vocalizing individuals.

In May and June of 2019, we deployed 94 GPS tags ([Table 1](#); figure 1 in [Skinner et al. 2022a](#)) on male whip-poor-wills of the following ages: 12 second-year (SY) birds, 81 after-second year (ASY), one unaged (AHY). Data collection schedules varied throughout the nonbreeding period (2019–2020). The tags took points every 5 days before November 2; every 3 days (we increased fix frequency when individuals relocated to second home ranges in [Tonra et al. 2019](#)) from December 4 to January 1 and February 4 to March 1; and every 4 days from November 5 to December 1, January 5 to February

1, and March 5 to May 30, all at 2000 EST. We interpret these as foraging locations given that whip-poor-wills forage heavily around dusk (Cink *et al.* 2020, Souza-Cole 2021), although birds could also be resting or in transit. To identify diurnal roost locations, we programmed tags to take points every 21st day at 1300 EST from November 20 to March 5. Finally, from here onwards, reference to the “nonbreeding” season refers only to the stationary nonbreeding period (i.e., excluding migration).

Home Range Estimation

Ultimately, we had 25 nonbreeding home range estimates of whip-poor-will’s first nonbreeding site (5 individuals had multiple nonbreeding sites; see [Supplementary Material](#); Skinner 2021). We used area-corrected autocorrelated kernel density estimation (AKDE_c) in the *ctmm* package (Calabrese *et al.* 2016) in program R version 4.0.3 (R Development Core Team 2020). Principal steps in the generation of home range analysis were to (1) choose an appropriate error model based on the calibration data (Fleming *et al.* 2020), (2) identify and remove outliers, (3) determine if whip-poor-wills exhibit bounded home ranges (i.e., are range-residents), (4) select a continuous time movement model for each individual, and (5) use area-corrected autocorrelated kernel density estimation (Fleming *et al.* 2015, Fleming and Calabrese 2017) to delineate 95% utilization 2-dimensional (2D) home range polygons. A summary of these 5 steps follows; see [Supplementary Material Appendix 1](#) for additional details.

We determined an appropriate error model (Fleming *et al.* 2020) by assessing how different indicators of fix accuracy predicted error in the calibration data. Ultimately this error model is incorporated into home range estimates (i.e., real tracking data) by discounting the importance of fixes that are less reliable. In short, we performed error-model selection using calibration data ($n = 28$ tags; 20.68 ± 9.96 points per tag) from tags with known deployment location and the framework described in Fleming *et al.* (2020). We used Akaike’s Information Criterion corrected for small sample size (AIC_c) to select the combination of variables that best predicted error in the calibration data. The best model included 2 variables: the horizontal dilution of precision (HDOP) and a binary category indicating if the number of satellites was equal to 3 for a given fix. Thus, GPS fixes with high HDOP or 3 satellites were down weighted when estimating home range size.

We removed remaining outliers using a combination of horizontal and vertical distance from the geometric mean values (*outlie* function), removing 38 of 1,350 (2.8%) points. We inspected a pooled variogram (data quality prohibited inspection of individual variograms) and determined that, as a whole, individuals in our study exhibited range residency making these data appropriate for home range analyses (Calabrese *et al.* 2016). Individual variograms from other studies also suggest that whip-poor-wills demonstrate range-resident behavior on the nonbreeding grounds (Tonra *et al.* 2019, Bakermans *et al.* 2022). For each individual, the movement model with the lowest AIC_c score was selected ([Supplementary Material](#)) and used in AKDE_c calculation (*akde* function). We used the optimal weighting method to account for missing data, small effective sample sizes (i.e., degrees of freedom, *df*), and differences in sampling frequency throughout the nonbreeding period (Fleming *et al.* 2018). In

our study, 8 birds had *df* = 0 (making home range estimation impossible), and 7 individuals displayed error in location estimates larger than the home range size itself (particularly those with *df* < 2.5). Thus, we did not calculate home ranges for these 15 individuals (we excluded one additional individual that relocated very early in the nonbreeding period, see [Supplementary Material](#)), but we did analyze their site information based on the centroid of the points. This left us with 25 home ranges estimated from 26.48 ± 7.92 (range: 7–38; [Supplementary Material Figure 2](#)) GPS points per home range. We report 95% AKDE_c home range sizes and their associated 95% CIs.

Land Cover

The lead author (AAS) manually digitized land cover polygons (ArcGIS v 10.8; Esri) in a 78.5-ha site (i.e., a 500-m circular buffer; hereafter referred to as the “site”) around the centroid of each home range using aerial photographs from ESRI World Imagery and Google Earth (Google Earth 2001, Esri 2009). We selected a 500-m buffer as this was larger than all home ranges and offered a standardized size for comparing landscapes among individuals (Tonra *et al.* 2019). Only one ESRI image was available at each bird’s nonbreeding site, but Google Earth often provided multiple images via the “historical imagery” feature (7.05 ± 5.13 images; range: 1–24). Having a timeseries provided information on land-use change, which helped differentiate between land cover classes. We relied heavily on photos near the dates when whip-poor-wills were present on the nonbreeding grounds (roughly October 2019 to March 2020), and generally Google Earth imagery (mean nearest date: October, 2018 $\pm$ 2.17 years) and ESRI imagery (mean nearest date: December, 2017 $\pm$ 2.12 years) were available around that time. We digitized polygons corresponding to 6 land cover types: forest, scrub, agriculture, bare ground, developed, and water. Scrub included naturally scrubby habitats (e.g., on steep rocky slopes) or habitat regenerating after disturbance. Forest consisted of areas with high (>70%) forest cover > 10 years in age. If timeseries information was not available to determine the age since disturbance we used the apparent size, texture, and density of the satellite image to differentiate between forest and scrub. Bare ground included naturally barren areas and other areas dominated by herbaceous vegetation, but excluded pasture and other forms of agriculture. Developed land included anthropogenic structures or pavement. We did not include streams or rivers in the water class due to complications in landcover processing, but did include larger bodies of water (as in Tonra *et al.* 2019). Finally, we were conservative when delineating agriculture, but primarily used the following 3 criteria to differentiate between agriculture and bare ground or scrub: (1) the regularity of the polygons, (2) whether agriculture was present at a landscape scale, and (3) whether distinct row crops could be seen. Agriculture in the core of the whip-poor-will nonbreeding range (see Skinner *et al.* 2022a) is dominated by maize, beans, coffee, and sugarcane (FAO 2020).

We rasterized (1-m resolution) all polygons using the *raster* package (Hijmans 2020) in program R (R Development Core Team 2020), allowing for downstream processing in the *landscapemetrics* package (Hesselbarth *et al.* 2019). We calculated the proportion of each land cover type (*lsm_c_pland* function) in both the home range and site, patch richness (i.e., the number of unique patches present; *lsm_l_pr*) and total

edge in the site (*lsm_l_te*), and edge density (*lsm_l_ed*) in the home range. We define edge as the border between any two land cover types, and edge density as the amount of edge in relation to home range size. As we were particularly interested in agriculture's effect on our response variables, we also created a binary presence/absence agricultural variable at the scale of the home range, and a 3-level categorical variable at the level of the site (0%, 0–30%, and > 30%). This reduced collinearity and often allowed for agriculture to be included in models with other land cover variables at the home range and site scales. Given whip-poor-will dependence on forest on both the nonbreeding (Tonra *et al.* 2019, Bakermans *et al.* 2022) and breeding grounds (Vala *et al.* 2020, Grahame *et al.* 2021, Thompson III *et al.* 2022), and their use of early successional scrubby habitats on the breeding grounds (Wilson and Watts 2008, Tozer *et al.* 2014, Akresh and King 2016), we focused statistical analysis on forest, agriculture, and scrub, which were also the 3 most common land cover categories in the home range and site. Finally, we conducted a paired *t*-test comparing the proportion of forest in the home range and site.

Roosting Locations

To ensure accuracy of diurnal GPS locations, we removed all GPS fixes where the number of satellites equaled 3 or HDOP was greater than 10. We then determined (1) the land cover type at each roosting point; (2) for roosting points outside of forested land cover, the distance from the roosting point to the nearest forest patch; (3) the mean distance between roosting points and the centroid of the home range; and (4) the proportion of points that fell into the upper confidence level (UCL) of the 95% AKDE (or the 100% minimum convex polygon [MCP] for birds that did not have sufficient data for AKDE; $n = 10$) of nocturnal (foraging) home range estimates. We used the upper confidence level of home ranges as the data quality of GPS-location estimates likely negatively biased our estimates.

Stable Isotope Ratios

We collected the distal end of claws from 40 individuals on the breeding grounds between May 4th and June 8th (May 17th $\pm$ 9.7 days), although we removed the 5 individuals with multiple nonbreeding sites. On average, whip-poor-wills from our populations began spring migration on March 20th $\pm$ 7.2 days ($n = 13$; Skinner *et al.* 2022a), thus about 2 months passed from when an individual left the nonbreeding grounds to when the claw sample was collected on the breeding grounds. Unfortunately, we could not specify the exact dates that individual whip-poor-wills left the nonbreeding grounds in most cases ($n = 30$). However, we are confident that claws reflect nonbreeding grounds habitat 3–5 months earlier as whip-poor-wills have an elongated central pectinate claw that grows one barb per month (Cink *et al.* 2020) and we only collected the distal-most 2–3 barbs on each claw (see English *et al.* 2018). We sent claw samples to the UC Davis Stable Isotope Facility for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis using a continuous flow isotope ratio mass spectrometer. Stable isotope values are expressed as parts per thousand (‰) deviations from international standards, where $\delta X = \left\{ \left[\frac{R_{\text{unknown}}}{R_{\text{standard}}} \right] - 1 \right\} \times 1000$, X is either ^{13}C or ^{15}N , and R is either $^{13}\text{C}:^{12}\text{C}$ or $^{15}\text{N}:^{14}\text{N}$. Samples were repeatable within $\pm 0.09\text{‰}$ based on repeated measures of standards.

Of the 40 individuals, we collected claw samples in both 2019 and 2020 from 26 individuals and in only one year in 14 individuals. We conducted a paired *t*-test comparing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ collected in 2019 and 2020 and found that stable isotope values were not impacted by collection year ($\delta^{13}\text{C}$: $t = 0.05$, $df = 25$, $P = 0.96$; $\delta^{15}\text{N}$: $t = -1.19$, $df = 25$, $P = 0.25$). As our nonbreeding location data was collected from roughly October 2019 to March 2020, we used claw samples with isotopic values from that period (i.e., those collected in 2020) when available ($n = 22$). However, we used 2019 claw samples when 2020 was not available ($n = 13$), as there is evidence that nonbreeding site fidelity is high in this species (Bakermans *et al.* 2022, Skinner *et al.* 2022a; A. Korpach personal communication), suggesting that whip-poor-wills likely used the same nonbreeding location in both years, and the paired *t*-test results support this (as in Hjernerquist *et al.* 2009, Akresh *et al.* 2021).

Statistical Analyses

We examined predictors of home range size at 3 different scales (geographic region, site, and home range) using general linear models. At the home range scale, predictor variables included the proportion of forest, agriculture, and scrub; the presence/absence of agriculture; and edge density (m/ha). We also included body size (measured by unflattened wing chord), as body size can influence home range size (McLoughlin and Ferguson 2000, Jetz 2004). At the site scale, predictor variables included the proportion of forest, agriculture, and scrub; an ordinal factor of agriculture (0%, 0–30%, or > 30%); total edge; the number of distinct land cover classes; and claw $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. At the broadest geographic spatial scale, we included distance to the nearest ocean coast (km), the nonbreeding ecoregion, and the nonbreeding latitude and nonbreeding longitude. We included stable isotope values at the site scale as they reflect whip-poor-will prey (flying insects) and the animals/plants these insects have consumed; thus, these food webs may unfold at a scale larger than the home range but smaller than the geographic region. Nonbreeding ecoregions were delineated in Ríos and Raga (2018), and all whip-poor-wills had nonbreeding sites in one of 3 ecoregions: humid forest, dry forest, and sierras (Figure 1).

Given that our home range estimates were 2-dimensional (i.e., they did not account for changes in elevation), we examined the influence of rugosity, measured via the Terrain Ruggedness Index (hereafter “ruggedness”; calculated as the mean of the absolute value of the difference between the elevation [m] in the raster cell containing the centroid of an individual's home range and the 8 surrounding cells; *raster* package, Hijmans 2020). Ruggedness was marginally negatively related to home range size ($r^2 = 0.13$, $P = 0.07$, $\beta = -0.26$, $n = 25$; Figure 2A). Thus, we included ruggedness in all models to control for the 2D nature of our home range estimates. We compared all linear combinations of univariate and bivariate models plus ruggedness (i.e., 1 or 2 variables + ruggedness), resulting in 20 models at the home range scale, 26 models at the site scale, and 10 models at the scale of the geographic region (Supplementary Material Table 1). We $\log_{10}$ -transformed the response variable of home range size to meet assumptions of normality.

To explain variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, we ran general linear mixed-effects models using the *lmerTest* package (Kuznetsova *et al.* 2017) with $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ as the response

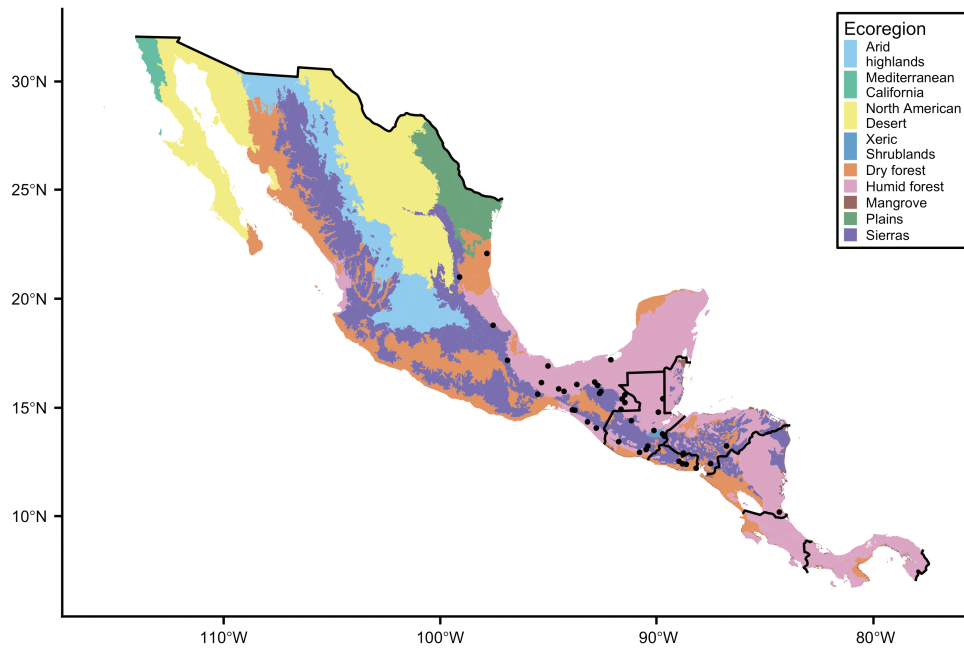


FIGURE 1. Forty-one whip-poor-wills had nonbreeding sites (black circles) in only 3 (of 9 possible) ecoregions in Mexico and Central America (delineated by [Ríos and Raga 2018](#)): dry forest (5 individuals), humid forest (21), and the sierras (15). The random effect used in the analysis of stable isotope ratios was created by intersecting country (black lines) with ecoregion, resulting in 10 ecoregion-country combinations.

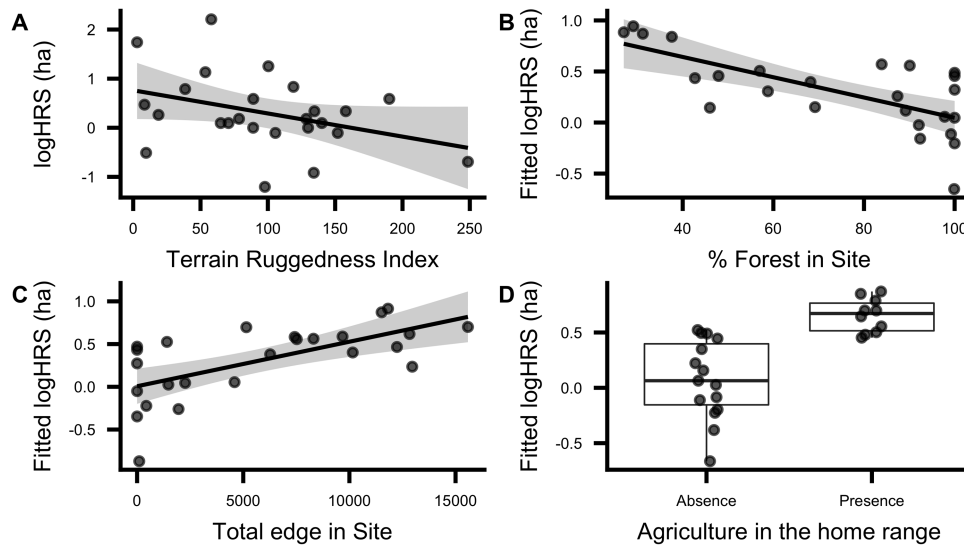


FIGURE 2. Relationship of important predictor variables across multiple spatial scales and $\log_{10}$ -transformed home range size (HRS). Panel (A) shows the negative relationship between ruggedness and the $\log_{10}$ -transformed home range size. Panels (B–D) show relationships between important configuration or composition metrics and the fitted values (y-axis) of a bivariate model $\log\text{HRS} \sim \text{variable} + \text{terrain ruggedness index}$.

variable, the same site-level habitat composition and configuration variables discussed above as fixed effects, and ecoregion by country as a random intercept ([Figure 1](#)). We also included body size, and $\delta^{13}\text{C}$ (when $\delta^{15}\text{N}$ was the response variable) as predictor variables. We included $\delta^{13}\text{C}$ as a predictor of $\delta^{15}\text{N}$, but not vice versa, as habitat moisture could predict trophic level through impacts on insect communities ([Studds and Marra 2007](#), [Smith et al. 2011](#)), but the reverse (prey community influencing habitat moisture) was not logical. An exploratory analysis of variance (ANOVA) was used to test for differences in baseline isotope levels by ecoregion ($\delta^{15}\text{N}$: $F_{2,32} = 4.5$, $P = 0.02$; $\delta^{13}\text{C}$: $F_{2,32} = 6.5$, $P = 0.004$; [Figure 3](#)). We also ran a Tukey post-

hoc test to determine which ecoregions were driving this difference. As isotopes did differ by ecoregion, we created a random effect by intersecting the broadscale nonbreeding ecoregions ([Ríos and Raga 2018](#)) and nonbreeding country, producing 10 ecoregions by country combinations (e.g., Mexico * humid forest; [Figure 1](#)). We examined 34 models in the analysis of $\delta^{15}\text{N}$, and 18 models for $\delta^{13}\text{C}$ ([Supplementary Material Table 2](#)).

For the analysis of home range size and stable isotope values we compared models using AIC_c , and conducted natural averaging to obtain parameter estimates for parameters in models with a $\Delta\text{AIC}_c \leq 4$ ([Burnham and Anderson 2004](#), [Burnham et al. 2011](#)). We scaled and centered all predictor variables

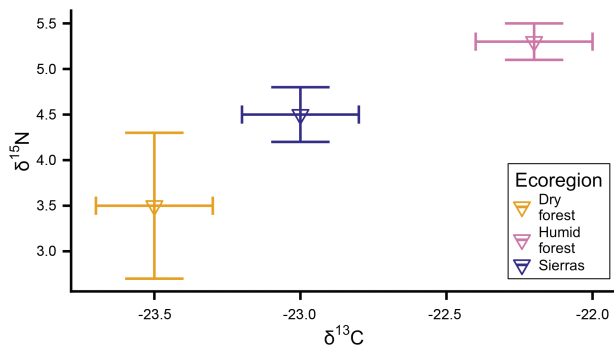


FIGURE 3. Mean (bars represent standard errors) stable carbon ($\delta^{13}\text{C}$) and stable nitrogen ($\delta^{15}\text{N}$) isotope values ($n = 35$) obtained from whip-poor-will pectinate claws synthesized on the nonbreeding grounds differed at broad spatial scales (by ecoregion; [Ríos and Raga 2018](#)), as shown by an ANOVA.

to facilitate model averaging and calculated 90% unconditional confidence intervals using parameter estimates and unconditional standard errors. We used a 90% cutoff as we had small sample sizes and potentially noisy data, and thus, low statistical power. We considered confidence intervals that did not include 0 as evidence of important relationships between predictors and the response variable. We did not examine any interactions or models with > 3 variables due to small sample sizes. We did not include any highly correlated ($|r| > 0.7$) predictor variables in the same model. All models had variance inflation factors < 2.9 suggesting collinearity was not an issue ([Zuur et al. 2009](#)). Finally, to assess goodness-of-fit we compared the top model of each set of candidate models to the null model (i.e., with only ruggedness in home range analyses or only the random effect in stable isotope analyses) using a likelihood ratio test, and visually assessed model fit using standard model diagnostic plots of the most parsimonious models that included an important parameter ([Zuur 2009](#)). Across all objectives, we report results as mean $\pm$ standard deviation (SD).

RESULTS

Tag Recovery Rates

We recovered 47 of the 94 tags we deployed (50.0%). Recapture rates varied by site, ranging between 40% and 75% ([Table 1](#)). Six tags did not collect usable data. Of the 41 birds with tags containing extractable data, 4 were second-year (SY) birds, 36 were after-second year birds (ASY), and 1 was not aged (AHY).

Predictors of Home range Size

Whip-poor-wills had small (1.86 ± 1.90 ha) but variable (range: 0.3–9.1 ha) home ranges ([Figure 4](#)). Outside of terrain ruggedness, which was important across all spatial scales (home range β_{avg} : -0.24 , 90% CI: -0.47 to -0.04 ; site β_{avg} : -0.29 , 90% CI: -0.51 to -0.06 ; and region β_{avg} : -0.25 , 90% CI: -0.48 to -0.02), only variables at the home range and site scales were important in predicting home range size ([Figures 2 and 5](#)).

There was substantial model-selection uncertainty at the home range scale, as the top model had only 14% of the weight. The top model included only presence/absence of agriculture and terrain ruggedness, but the amount of

scrub, forest, and agriculture as well as wing length and edge density were present in competing models ($\Delta\text{AIC}_c \leq 4$) ([Table 2A](#)). Home ranges were larger when agriculture was present (β_{avg} : 0.55 ; 90% CI: 0.09 – 1.02 ; [Figures 2 and 5](#)). The confidence intervals for all other parameter estimates at the home range scale overlapped zero. The top model fit the data better than the null model ($\delta^2 = 4.75$, $\text{df} = 1$, $P = 0.03$).

There was also model-selection uncertainty at the site scale, with the top model having 30% of the weight. This model included the total amount of edge and terrain ruggedness. The amount of forest, scrub, and agriculture as well as $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and number of land cover types were present in competing models ($\Delta\text{AIC}_c \leq 4$) ([Table 2B](#)). Home ranges with more total edge were larger (β_{avg} : 0.36 ; 90% CI: 0.10 – 0.62 ; [Figures 2 and 5](#)), and home ranges with more forest were smaller (β_{avg} : -0.30 ; 90% CI: -0.02 to -0.57 ; [Figures 2 and 5](#)). Confidence intervals for all other parameter estimates overlapped zero. Total edge and % forest in the site were negatively correlated ($r = -0.85$, $P < 0.001$), helping explain the similar effect sizes but opposite directions of their effects on home range size. The model including total edge was $2.8 \times$ more likely to be the best model than the forest model. The top model fit the data better than the null model ($\delta^2 = 5.49$, $\text{df} = 1$, $P = 0.02$). Finally, at the scale of the broader geographic region ([Table 2C](#)), the null model was the best supported model and the confidence intervals of all parameters except terrain ruggedness overlapped zero.

Land Cover

Forest, agriculture, and scrub were the most common land cover types at both the home range and site scale ([Figure 6](#)). Forest was the only land cover type found in both the home range ($n = 25$) and site ($n = 41$) scales for all birds. There is weak evidence that forest cover was greater in the home range ($82.3 \pm 28.5\%$; range: 4–100.0%) relative to the site ($66.9 \pm 29.7\%$; range: 13.4–100.0%; $t = -1.98$, $\text{df} = 24$, $P = 0.06$; [Figure 6](#)). Nine whip-poor-wills (36%) had only forest in their home range, while 11 birds (44%) had 2 land cover types and 5 birds (20%) had 3 land cover types ([Supplementary Material Figure 2](#)). At the scale of the site and home range, respectively, forest was 3.6 and 8.9 times more prevalent on average than agriculture ([Figure 6](#)). Agriculture was found in 40.0% of home ranges and 73.2% of sites. Of birds with agriculture present in the home range ($n = 10$ of 25) or site ($n = 30$ of 41), it accounted for $25.5\% \pm 18.9\%$ (overall range: 0.0–80.3%) and $23.2 \pm 25.8\%$ (overall range: 0.0–67.7%) of land cover, respectively ([Figure 6](#)).

Diurnal Roosting Locations

GPS tags took 96 temporally independent roosting points across 35 individuals, resulting in 2.7 ± 1.6 roosting points per bird. Seventy-eight of these points were in forests (81.3%), 7 were in agriculture (7.3%), and 11 were in scrub (11.5%). For non-forest points ($n = 18$, across 10 individuals), the mean distance to the nearest forested patch was 19.2 ± 14.3 m. Mean distance between roosting points and the centroid of the home range was 47.3 ± 39.2 m (range: 1.7–199.1 m). Finally, 87.5% of diurnal roosting points fell within the nocturnal MCP or the UCL of the 95% AKDE_c estimate.

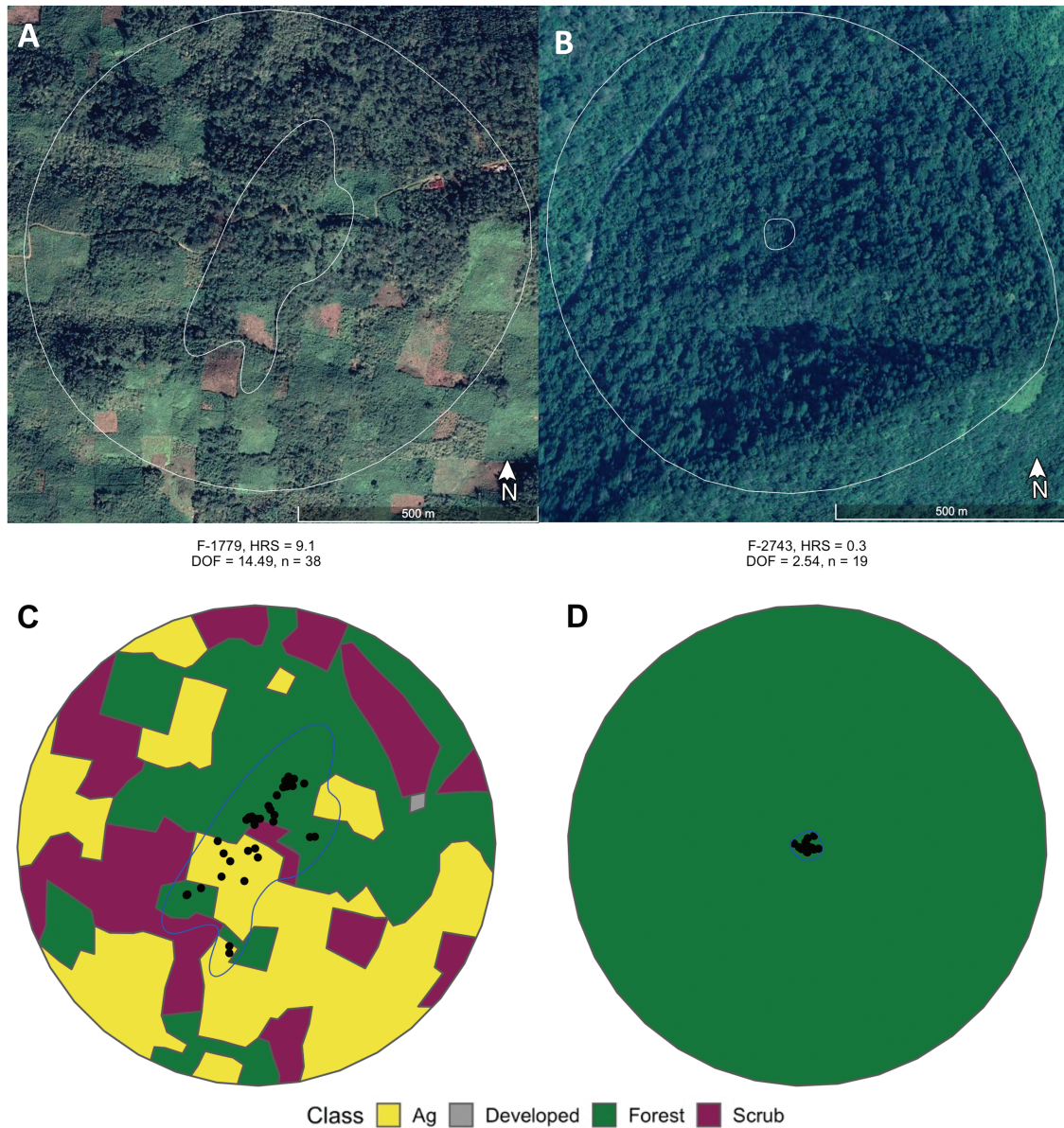


FIGURE 4. We used satellite imagery to manually digitize the land cover within the home range and site (500-m radius buffer around the centroid of the home range) for 41 whip-poor-wills on the nonbreeding grounds. In panels (C) and (D), black points represent the predicted (after error modeling) GPS locations (n = sample size; DOF = effective sample size) used to generate the 95% home range size estimates (HRS; blue polygons). Panels (A) and (C) depict the individual with the largest (9.1 ha) nonbreeding home range, in a highly fragmented landscape with agriculture present; panels (B) and (D) depict the individual with the smallest (0.3 ha) nonbreeding home range, in a tract of continuous forest. Scale is consistent across all 4 panels.

Predictors of Stable Isotope Values

Stable isotope ratios showed variation by ecoregion, with humid forest having greater $\delta^{13}\text{C}$ values than dry forest ($P = 0.03$, mean difference = 1.30, 95% CI: 0.09–2.51) and the sierras ($P = 0.01$, mean difference = 0.85, 95% CI: 0.15–1.55), and greater $\delta^{15}\text{N}$ values than dry forest ($P = 0.03$, mean difference = 1.76, 95% CI: 0.12–3.40) (Figure 3). There was also greater variation in $\delta^{15}\text{N}$ than $\delta^{13}\text{C}$ values ($\delta^{15}\text{N}$: 4.85 ± 1.18 , range: 2.61–6.74, %CV = 24.4; $\delta^{13}\text{C}$: -22.59 ± 0.91 , range: -24.40 to -20.23, %CV = 4.0). In models predicting $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values, the null model including only the random effect (ecoregion by country) was always the best supported model (Table 3), and confidence intervals for all parameter estimates overlapped zero.

DISCUSSION

We obtained previously undocumented nonbreeding habitat use and home range information for the Eastern Whip-poor-will, a rapidly declining, cryptic nocturnal aerial insectivore. We found that whip-poor-wills both foraged and roosted within heavily forested sites, and that their home ranges contained higher percentages of forest than the site. Home range size was larger in sites with less forest, more edge, and when agriculture was present in the home range. The predominant trend of landscape transformation in the Neotropics (conversion of forest to agriculture) likely increases space use in whip-poor-wills, which has important implications for the conservation and management of this species.

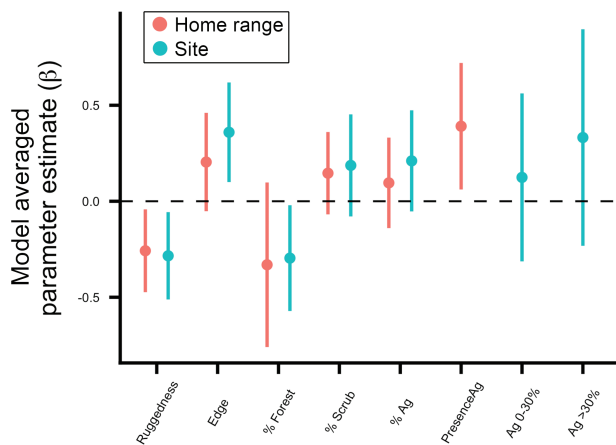


FIGURE 5. Total edge (scale = site), percent forest (site), and the presence of agriculture (home range) were important predictors of home range size ($n = 25$), as the 90% unconditional confidence intervals of the model averaged coefficient estimates did not overlap 0. Landscape composition and configuration metric abbreviations are as follows: Ruggedness = terrain ruggedness index, PresenceAg = binary variable indicating if agriculture is present, Ag 0–30% = a categorical representation of sites with 0–30% agriculture, Ag > 30% = a categorical representation of sites with > 30% agriculture. Edge refers to the total edge (m) at the scale of the site, or edge density (m ha^{-1}) at the scale of the home range.

Variation in Home Range Size

Whip-poor-wills had small, but highly variable home ranges (as in [Mitchell et al. 2020](#), [Bakermans et al. 2022](#)). Birds with more edge and less forest in the site, and with agriculture present in the home range, had larger home ranges. These 3 important predictor variables were collinear, making it difficult to disentangle the principal determinant of increased space use (see [Fahrig 2003](#)), although it is worth noting that the replacement of forest by scrub did not impact home range size (suggesting agriculture may be more impactful). Agriculture may increase home range size if it negatively influences the quantity or quality of insect prey ([Attwood et al. 2008](#), [English et al. 2018](#), [Seibold et al. 2019](#)), forcing whip-poor-wills to use more space to meet metabolic needs ([McLoughlin and Ferguson 2000](#)). Alternatively, the loss or fragmentation of forest may result in more dispersed foraging habitat, necessitating larger home ranges ([Haskell et al. 2002](#), [Siffczyk et al. 2003](#), [Hansbauer et al. 2008](#)). Fragmentation can reduce survival in forest-dependent birds ([Ruiz-Gutiérrez et al. 2008](#)) with particularly deleterious long-term effects for insectivorous populations (e.g., [Sekercioglu et al. 2002](#)). Future work understanding the degree of edge affiliation in whip-poor-wills during the nonbreeding season ([Pfeifer et al. 2017](#)), as well as documenting prey composition and abundance across land-use gradients will be critical. Irrespective of the mechanism, land transformation appears to increase the space used by nonbreeding whip-poor-wills. This could have important repercussions if density-dependent processes influence body condition or survival ([Marra et al. 2015b](#)), which could ultimately lead to a reduction in the carrying capacity for habitat of a given size ([Lamb et al. 2018](#)) or carryover effects ([Marra et al. 1998](#), [Akresh et al. 2019b](#)). This possibility is particularly concerning given that forest is being lost at alarming rates in the whip-poor-wills' core nonbreeding range ([Hansen et al. 2008](#), [Aide et al. 2013](#), [Skinner et al. 2022a](#)).

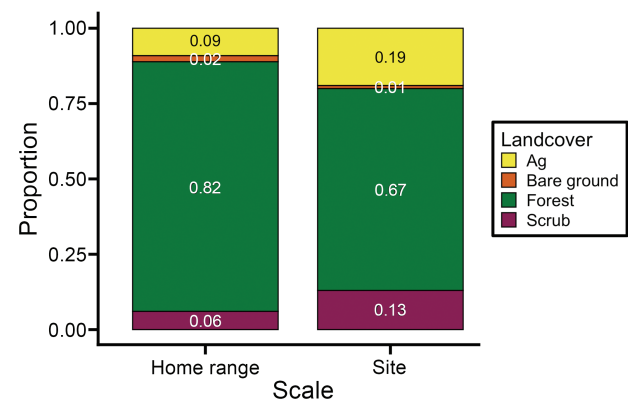


FIGURE 6. Whip-poor-wills used forest > agriculture > scrub > bare ground land covers in the nonbreeding home range ($n = 25$) and site ($n = 41$; a 500-m radius buffer around the centroid of each home range). Each home range was weighted equally irrespective of home range size when calculating the proportion of each land cover at the home range scale. The proportions of water and developed land covers were too small to see (rounded to 0.0) at the site scale and were not present in any home ranges.

[Tonra et al. \(2019\)](#) and [Bakermans et al. \(2022\)](#) conducted similar studies (both studies used AKDE in the *ctmm* package and report 95% home range estimates) on small samples of whip-poor-wills from Ohio and Massachusetts, respectively, although [Bakermans et al. \(2022\)](#) did not look at predictors of space use. Our home range size estimate was very similar to [Bakermans et al. \(2022\)](#), who report a median home range size of 1.95 ha ($n = 19$). However, [Tonra et al. \(2019\)](#) found relatively larger nonbreeding home ranges (mean = 5.24 ha) and a negative relationship between total edge in the site and home range size. We believe that the present findings more likely reflect drivers of whip-poor-will space use as we controlled for the 2D-nature of home ranges produced from the *ctmm* package (the terrain ruggedness variable was important at all spatial scales), and modeled tag error ([Fleming et al. 2020](#)). Modeling tag error discounts the importance of unreliable fixes by bringing them towards the home range center (helping to explain the smaller home ranges we observed as well). We acknowledge that data quality was higher in [Tonra et al. \(2019\)](#), likely obviating the need for error modeling ([Supplementary Material Appendix 1](#)). In fact, we reanalyzed their home ranges using the present methodology, and found similar estimated sizes in most cases (mean = 4.27 ha; Skinner personal communication). Finally, [Tonra et al. \(2019\)](#) acknowledged the tenuous nature of the relationship between total edge and home range size, which depended on the exclusion of a potential outlier. Our analysis had a greater sample size and included populations from a much wider swath of the breeding range, providing more robust examination of ecological predictors.

Land Cover

While many species of migratory birds are expected to use similar habitats in the nonbreeding and breeding season (e.g., [Keast and Morton 1980](#)), this appears to be only moderately true in whip-poor-wills. They are perhaps more highly dependent on forest in the nonbreeding season: all individuals in this study had forest in the home range and site, the average forest cover was > 80% in the home range, and we found marginal evidence that the amount of forest in the home range is

TABLE 2. Top models ($\Delta AIC_c < 4$) explaining home range size ($n = 25$; $\log_{10}$ -transformed) with predictors across 3 spatial scales. Models are ranked by differences in Akaike's information criterion corrected for small sample size (ΔAIC_c). K is the number of model parameters and w_i is the model weight. Independent variable abbreviations are as follows: Ruggedness = terrain ruggedness index, PresenceAg = binary variable indicating if agriculture is present, Ag3Levels = categorical representation of agriculture amount, $\delta^{13}C$ = stable carbon values, $\delta^{15}N$ = stable nitrogen values.

Model	k	ΔAIC_c	w_i	-2 Log-likelihood
(A) Home range				
PresenceAg + Ruggedness	4	0.00 ^a	0.14	-24.12
PresenceAg + %Scrub + Ruggedness	5	0.33	0.12	-22.71
PresenceAg + Wing + Ruggedness	5	1.09	0.08	-23.09
Wing + Ruggedness	4	1.44	0.07	-24.84
EdgeDensity + PresenceAg + Ruggedness	5	1.57	0.07	-23.33
EdgeDensity + Ruggedness	4	1.66	0.06	-24.95
%Forest + Ruggedness	4	1.73	0.06	-24.99
PresenceAg + %Forest + Ruggedness	5	1.73	0.06	-23.41
Ruggedness	3	1.89	0.06	-26.50
%Forest + Wing + Ruggedness	5	2.39	0.04	-23.74
EdgeDensity + Wing + Ruggedness	5	2.42	0.04	-23.76
%Scrub + Ruggedness	4	2.66	0.04	-25.45
%Ag + Ruggedness	4	3.17	0.03	-25.71
%Scrub + Wing + Ruggedness	5	3.31	0.03	-24.20
%Ag + Wing + Ruggedness	5	3.72	0.02	-24.40
(B) Site				
TotalEdge + Ruggedness	4	0.00 ^b	0.28	-23.14
%Forest + Ruggedness	4	2.14	0.10	-24.20
PatchRichness + Ruggedness	4	2.51	0.08	-24.39
Ruggedness	3	2.59	0.08	-25.88
$\delta^{13}C$ + TotalEdge + Ruggedness	5	2.96	0.06	-23.00
$\delta^{15}N$ + TotalEdge + Ruggedness	5	3.17	0.06	-23.11
%Ag + Ruggedness	4	3.37	0.05	-24.82
%Scrub + Ruggedness	4	3.56	0.05	-24.92
(C) Region				
Ruggedness	3	0.00 ^c	0.35	-26.5
Longitude + Ruggedness	4	1.23	0.19	-25.69
DistanceCoast + Longitude + Ruggedness	5	2.16	0.12	-24.57
Latitude + Ruggedness	4	2.19	0.12	-26.17
DistanceCoast + Ruggedness	4	2.37	0.11	-26.26
DistanceCoast + Latitude + Ruggedness	5	3.5	0.06	-25.24

^a AIC_c value of best model = 58.25.

^b AIC_c value of best model = 56.38.

^c AIC_c value of best model = 60.14.

greater than that in the site, potentially indicating selection of more forested habitat patches (as demonstrated by [Bakermans et al. 2022](#)). Additionally, nonbreeding home ranges of 36% of individuals were entirely in forest, a slightly higher percentage than a smaller sample of birds tracked from Ohio ([Tonra et al. 2019](#)). Although previously documented, this behavior is somewhat surprising, as whip-poor-wills are thought to prefer early-successional habitats often near forested habitat on the breeding grounds ([Tozer et al. 2014](#), [Akresh and King 2016](#), [Grahame et al. 2021](#), [Spiller et al. 2022](#)). Documenting the structure (e.g., tree density, presence of an understory or treefall gaps) and composition (e.g., broadleaf vs. coniferous) of the forests, along with foraging strategies whip-poor-wills employ on the nonbreeding grounds (e.g., foraging above the canopy) are critical next steps. Also surprising was the lack of wetlands or water in either the home range or site (only 2 individuals had water present in the site), which was the

primary predictor of occupancy in some breeding grounds studies ([Farrell et al. 2019](#), [Vala et al. 2020](#), but see [Grahame et al. 2021](#)). Other migratory species use different habitats throughout the annual cycle, the Common Nighthawk (*Chordeiles minor*) being of particular note, as it is another Neotropical nightjar that is highly associated with water features on the breeding grounds ([Farrell et al. 2019](#), [Vala et al. 2020](#)) but not on the nonbreeding grounds ([Ng et al. 2018](#)). Spatial scale may be an important factor as whip-poor-wills avoid wetlands at small spatial scales ([Grahame et al. 2021](#)) yet are affiliated with wetlands at large spatial scales (5-6 km) in some studies on the breeding grounds ([Farrell et al. 2019](#), [Vala et al. 2020](#)). A publicly available, high-resolution, accurate land cover database for the Neotropics would greatly expand the types of ecological questions that could be answered and would advance our understanding of how land use affects ecology throughout the full annual cycle.

TABLE 3. Top models ($\Delta AIC_c < 4$) from AICc model selection explaining variation of $\delta^{13}C$ and $\delta^{15}N$ isotope values ($n = 35$). All models include a random intercept of ecoregion by country, and all other variable abbreviations are the same as in Table 2.

Model	<i>k</i>	ΔAIC_c	w_i	–2 Log likelihood
(A) Stable carbon ($\delta^{13}C$)				
Random-intercept only	3	0.00 ^a	0.27	–44.63
PatchRichness	4	2.18	0.09	–44.44
Wing	4	2.30	0.09	–44.50
TotalEdge	4	2.49	0.08	–44.59
%Scrub	4	2.53	0.08	–44.61
%Forest	4	2.53	0.08	–44.61
%Ag	4	2.56	0.08	–44.63
Ag3Levels + PatchRichness	6	3.84	0.04	–42.43
(B) Stable nitrogen ($\delta^{15}N$)				
Random-intercept only	3	0.00 ^b	0.14	–54.40
PatchRichness	4	1.26	0.07	–53.75
TotalEdge	4	1.50	0.07	–53.87
Wing	4	1.72	0.06	–53.98
%Ag	4	1.75	0.06	–53.99
Ag3Levels + PatchRichness	6	1.75	0.06	–51.16
$\delta^{13}C$	4	2.03	0.05	–54.13
Ag3Levels	5	2.09	0.05	–52.79
%Forest	4	2.42	0.04	–54.32
%Scrub	4	2.54	0.04	–54.39
PatchRichness + Wing	5	2.96	0.03	–53.23
TotalEdge + Wing	5	3.45	0.03	–53.48
$\delta^{13}C$ + PatchRichness	5	3.56	0.02	–53.53
Ag3Levels + PatchRichness + Wing	7	3.67	0.02	–50.54
%Ag + Wing	5	3.68	0.02	–53.59
$\delta^{13}C$ + TotalEdge	5	3.90	0.02	–53.70
%Ag + $\delta^{13}C$	5	3.92	0.02	–53.71
PatchRichness + %Scrub	5	3.92	0.02	–53.71

^aAIC_c value of best model = 96.03.^bAIC_c value of best model = 115.57.

Diurnal Roosting Ecology

Roosting ecology is an important but understudied aspect of habitat use in ecology. Whip-poor-wills primarily roosted in the same forested areas where they forage, but also used shrubby habitats (as on the breeding grounds; Akresh and King 2016, Grahame *et al.* 2021) and agriculture. All non-forest roosts were close to forests, suggesting that proximity to forest edges may be desirable. Overlap in foraging and roosting areas is common in territorial species (Brown and Sherry 2006, Grahame *et al.* 2021), and greatly simplifies conservation planning (Brown and Sherry 2006).

Stable Isotope Ratios

Stable carbon and stable nitrogen isotope ratios from claw samples collected on the breeding grounds were best predicted by broadscale geographic patterns on the nonbreeding grounds and not local-scale factors related to nonbreeding habitat composition or configuration. Furthermore, in a post-hoc analysis we found that elevation negatively influenced stable carbon isotope values (see Hobson *et al.* 2003 as well). This is an important reminder for ornithologists that $\delta^{13}C$ and $\delta^{15}N$ values can vary with

large-scale hydrological, geological, climatological, and biological processes (Bowen 2010). Thus, we attempted to control for broadscale factors influencing stable isotope values by using a spatial random effect, but local differences in baseline isotope values (e.g., due to different agricultural management practices; Hobson 1999), as well as broadscale variation may have masked effects of local land cover (see Ohkouchi *et al.* 2017 for an alternative approach). Additional analyses within regions may have been insightful but we did not have adequate sample sizes. While stable isotopes are certainly an important tool for ornithologists, explicitly recognizing the spatial scale of a bird's nonbreeding distribution, as well as the (unmeasured) local and broadscale factors that can influence stable isotope values is critical for study planning and interpretation of results (Inger and Bearhop 2008, Hobson 2011).

CONCLUSIONS

We identified predictors of whip-poor-will space use across multiple spatial scales during the nonbreeding season. Whip-poor-wills depended heavily upon forest throughout the diel

cycle, and are less associated with habitat heterogeneity than they are on the breeding grounds (Wilson 2003, Tozer *et al.* 2014, English *et al.* 2017). Given that agriculture and increased edge (or less forest) increased home range size, minimizing additional conversion of forest to agriculture and promoting agricultural systems that incorporate forest could benefit whip-poor-wills and other forest-dependent Neotropical migrants in the nonbreeding season (Rosenberg *et al.* 2016). However, significant knowledge gaps persist regarding basic nonbreeding ecology (particularly for juveniles and females), including whip-poor-will diet, fine-scale (e.g., forest structure/composition) foraging habits, and whether there are fitness consequences for variation in habitat and space use (Bakermans *et al.* 2022). These gaps must be addressed before effective conservation plans can be implemented across the full annual cycle.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

This research was conducted under the Ohio State University Institutional Animal Care and Use Protocol (No. 201500000028-R2) and permit No. 23941 from the Bird Banding Lab.

Author contributions

All authors contributed to study design, acquiring funding, field data collection, and manuscript editing. A.A.S. conducted data analysis and wrote the original draft of the manuscript.

Datadeposits

Raw GPS location data is archived in Movebank (Skinner *et al.* 2022b). The analyses reported in this article can be reproduced using the data provided by (Skinner *et al.* 2022c).

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