

Korpach, A. M., V. von Zuben, K. C. Fraser, and C. M. Davy. 2025. High variation in Eastern Whip-poor-will home-range size and shape limits the effectiveness of one-size-fits-all habitat protection methods. *Avian Conservation and Ecology* 20(1):14. <https://doi.org/10.5751/ACE-02804-200114>
Copyright © 2025 by the author(s). Published here under license by the Resilience Alliance. Open Access. CC-BY 4.0

Research Paper

High variation in Eastern Whip-poor-will home-range size and shape limits the effectiveness of one-size-fits-all habitat protection methods

Alicia M. Korpach^{1,2,3} , Valerie von Zuben⁴ , Kevin C. Fraser¹  and Christina M. Davy^{1,4,5} 

¹University of Manitoba, Winnipeg, MB, Canada, ²University of Winnipeg, Winnipeg, MB, Canada, ³University of Regina, Regina, SK, Canada, ⁴Ontario Ministry of Natural Resources, Peterborough, ON, Canada, ⁵Carleton University, Ottawa, ON, Canada

ABSTRACT. Sustainable forestry harvest requires a balance between resource extraction and the habitat needs of wildlife. The breeding habitat of threatened birds is often delineated for protection by surveying sites for nesting pairs and applying fixed habitat-protection buffers around any observations. The buffers are then expected to provide sufficient habitat to complete breeding. Selecting appropriate buffer sizes requires accurate characterization of species' habitat requirements, but the accuracy of such data varies depending on the collection method. In harvested, public forests in Ontario, Canada, current buffers used to protect Eastern Whip-poor-wills (*Antrostomus vociferus*) are informed by estimates of territory and home-range size based on call surveys or radio-telemetry. To assess the effectiveness and efficiency of these buffer sizes, we GPS-tracked 32 male Whip-poor-wills during the breeding season and estimated home ranges using continuous-time movement models. Home ranges were highly variable in size and shape, ranging from 6.8 to 135.8 ha (mean 53.6 ha). We evaluated potential ecological determinants of home range size, and found that density of forest edge and density of neighboring birds were weakly negatively related to home-range sizes. Distance to wetland and primary productivity (NDVI) were weakly positively related. We also tested how well potential buffers would protect the empirically measured home ranges by overlaying an array of variously sized buffers around simulated Whip-poor-will observations. We found that circular buffers of 50 ha (approximately the mean home-range size) would protect about 60% of an actual average home range, and 100-ha buffers (twice the mean home-range size) would be required to achieve 80% protection. Conversely, over half of the area in the simulated 50- and 100-ha buffers would protect habitat (i.e., limit forestry activity) outside of the known home range. Our results highlight the challenges, and necessity, of creating evidence-informed, broadly applicable protection measures for threatened species that rely on forested landscapes.

La grande variabilité dans la taille et la forme des domaines vitaux de l'Engoulevent bois-pourri restreint l'efficacité des approches uniformes de protection de leur habitat

RÉSUMÉ. Une exploitation forestière durable repose sur un bon équilibre entre l'extraction des ressources et les besoins de la faune en termes d'habitat. L'aire de reproduction des oiseaux menacés est souvent délimitée en identifiant les emplacements des couples nicheurs et en assurant des zones tampons fixes autour des sites observés. Les zones tampons sont censées fournir un habitat suffisant pour la réussite de la reproduction. Le choix de zones tampons de taille suffisante requiert une caractérisation précise des besoins des espèces en matière d'habitat. Toutefois, la précision de ces données varie en fonction de la méthode de collecte. Dans les forêts publiques de l'Ontario (Canada), les zones tampons destinées à la protection de l'Engoulevent bois-pourri (*Antrostomus vociferus*) sont déterminées par des estimations de taille du territoire et d'aire de répartition, elles-mêmes renseignées par des enquêtes sur les cris et la radiotélémetrie. Pour évaluer l'efficacité de ces zones tampons, nous avons effectué un suivi GPS de 32 mâles d'Engoulevent bois-pourri pendant la saison de reproduction. Nous avons ainsi estimé les domaines vitaux à l'aide de modèles de déplacement en temps continu. La taille et la forme des domaines vitaux se sont avérés très variables, allant de 6,8 à 135,8 ha (moyenne de 53,6 ha). Nous avons évalué les déterminants écologiques potentiels de la taille du domaine vital et nous avons constaté que la densité de la lisière de la forêt et la densité des oiseaux voisins étaient liées faiblement et négativement à la taille du domaine vital. Les distances à la zone humide et de productivité primaire (IVDN) étaient liées faiblement et positivement. Nous avons également testé dans quelle mesure les zones tampons potentielles protégeraient les domaines vitaux mesurés de manière empirique en superposant un ensemble de zones tampons de différentes tailles autour des observations simulées de l'Engoulevent bois-pourri. Nous avons constaté que des zones tampons circulaires de 50 ha (approximativement la taille moyenne du domaine vital) assureraient une protection d'environ 60 % dans un domaine vital moyen réel, et que des zones tampons de 100 ha (deux fois la taille moyenne du domaine vital) seraient nécessaires pour une protection de 80 %. Inversement, plus de la moitié de la superficie des zones tampons simulées de 50 et 100 ha protégerait l'habitat (c.-à-d. limiterait l'activité forestière) en dehors du domaine vital connu. Nos résultats mettent en évidence les défis et la nécessité de créer des mesures de protection fondées sur des données probantes et largement applicables pour les espèces menacées qui dépendent des environnements forestiers.

Key Words: *aerial insectivore; avian conservation; forest management; kernel density estimators; nightjar; prey availability; species at risk*

INTRODUCTION

Effective and efficient management of breeding habitat relies on accurate information about how much space an animal needs to successfully complete a breeding cycle, and how space use varies with locally relevant ecological factors. Home-range size is influenced by characteristics of the available habitats (e.g., food availability and habitat structure) and of the species (e.g., life history traits, reproductive behavior, habitat selection, and territoriality; Rolando 2002). These factors, as well as individuality in movement patterns (Cain et al. 2023), make it difficult to predict the boundaries of an animal's home range. GPS tracking enables more accurate estimates of home-range sizes and shapes, which allows for more precise measurements of habitat characteristics, than can be derived from field observations (Stemle et al. 2022, Iverson et al. 2024). However, accurate and precise home-range data do not exist for most small-bodied and elusive species, leaving practitioners to make assumptions about the effectiveness of their management activities.

Food availability may be the most important ecological determinant of home-range size. Smaller home ranges are associated with greater food availability because less space is needed to meet an animal's food requirements (Rolando 2002, Marshall and Cooper 2004, Herfindal et al. 2005, Wilcox et al. 2021, Seigle-Ferrand et al. 2021). Food availability for predators is determined by prey accessibility and prey abundance. For animals that forage in edge habitat, home-range size may decrease as amounts of edge within an area increase, reflecting increased prey accessibility (Laundré and Loxterman 2007). Furthermore, theory predicts that higher prey abundance within available foraging habitats should also result in smaller home ranges (Zabel et al. 1995, Walton et al. 2017).

Prey abundance is challenging to quantify across an entire home range, but some habitat characteristics may provide proxies for the abundance of insect prey. Vegetation indices that represent primary productivity correlate well with flying and ground-dwelling arthropod biomass and thus potential prey for insectivores (Sweet et al. 2015, Fernández-Tizón et al. 2020, Traba et al. 2022). For insectivorous birds, the presence of highly productive land cover types like wetlands may also improve foraging opportunities that could influence home-range sizes. Wetlands are important breeding habitats for many insect species, providing habitat to developing larvae that then disperse as mature, volant individuals available to terrestrial predators (Schilke et al. 2020, Recalde et al. 2021). If wetlands create foraging habitat, the required home-range size for insectivores may be reduced when the home range contains wetland habitat. Alternatively, in areas where wetlands are less abundant, home ranges may increase in size as individuals commute between nesting and wetland foraging habitats, as seen in European Nightjar (*Caprimulgus europaeus*; Alexander and Cresswell 1990).

Competition is also likely to affect home range size. Ideal free distribution models and input matching rules, in their simplest forms, would predict that the number of equally competitive individuals in a habitat is proportional to the quality of the habitat (Fretwell and Lucas 1969, Parker and Sutherland 1986). Strongly territorial species can maintain per-capita productivity in lower-quality foraging habitat by using larger territories, thus lowering

the density of individuals in a landscape (Haché et al. 2013). If home-range size is mediated by competition or food availability, then conspecific density may have an indirect effect on home-range size (Elchuk and Wiebe 2003, Wilcox et al. 2021), and home-range size should decrease with the number of neighbors or nearest-neighbor distance.

Movement ecology research can directly support wildlife management and conservation; for example, status assessments for threatened species tend to consider movement data when they are available (Fraser et al. 2018). However, there are challenges to using home-range data in species-specific management and recovery plans. Accurate predictions of breeding home-range sizes are limited by the number of locations that can be collected with a given tracking method, by variation among individuals, and by uncertainty around the ecological determinants of home-range size and shape (Mitchell et al. 2019, Peris et al. 2020, Seigle-Ferrand et al. 2021). Incorrect assumptions about habitat requirements and minimum home-range sizes can waste limited resources if practitioners spend time, energy, and money to protect spaces that are ineffective at meeting the animals' needs, or are not used at all. Examples from marine reserve planning for coral reef fishes indicate that protected areas of at least twice the size of the focal species' home range are more likely to conserve populations (Kramer and Chapman 1999, Green et al. 2015). However, animal tracking is costly, and robust movement data are lacking for many threatened species (Fraser et al. 2018).

The Eastern Whip-poor-will (*Antrostomus vociferus*) is a federally threatened species in Canada (Government of Canada 2024) whose breeding habitat overlaps with harvested forests on public and private lands. The Whip-poor-will provides an interesting case study for the challenges of managing harvested landscapes while supporting recovery of threatened wildlife. As one example, in Ontario, Canada, management plans for forests on public lands often protect Whip-poor-will nesting and foraging habitat by applying spatial buffers to Whip-poor-will observations. The buffer sizes are partly based on estimates from published literature and technical reports of breeding territories and home ranges derived from call survey observations or radio-tracking data (Ontario Ministry of the Environment, Conservation and Parks 2021). Territory-size estimates derived from call survey observations are approximately 4–10 ha (Fitch 1958, Hunt 2009, English et al. 2017a), but estimates derived using radio-tracking are much larger: 31 ha (50% core range sizes; Rand 2014). Home ranges, which are typically much larger than territories, have thus far only been estimated from radio-tracking data, and estimates range from 1 to 500 ha (means 25–136 ha; Wilson 2003, Garlapow 2014, Rand 2014). Home ranges and spatial buffers are often referred to either by area (i.e., hectares) or their radius (i.e., linear m); for reference, a 10-ha circular area has a radius of ~180 m, a 30-ha area ~300 m, and a 100-ha area ~560 m ($r = \sqrt{A * 10\,000 / \pi}$). It is unclear whether the high variation in estimates of Whip-poor-will territories and home ranges reflect differences in the methods used, or true variation in space use among individuals, and this uncertainty limits evaluation of the current habitat prescriptions. From a resource management perspective, the ideal buffer would be large enough to protect detected Whip-poor-will home ranges, without unduly limiting forestry activities beyond these areas.

In this study, we used GPS tracking of Whip-poor-wills to illustrate how improved home-range mapping can be used to clarify ecological determinants of home-range sizes for aerial insectivores, and to evaluate management prescriptions for this species. Whip-poor-wills typically breed in open mixed-wood or deciduous forest, with edge habitat that facilitates perch-and-sally foraging on aerial insects (Cink et al. 2020). Therefore, we hypothesized that characteristics that reflect varying food availability would influence home-range sizes. We predicted that home-range sizes would decrease with increased access to prey (edge density), prey abundance (productivity), and conspecific density (number of neighbors), and that home-range size would increase with increasing distance to wetland. The harvested forests that Whip-poor-wills use span a range of ecoregions, and we also compared home-range sizes among ecoregions.

Finally, to provide a tool that wildlife managers can use to compare the costs and benefits of potential management prescriptions, we simulated hypothetical protection buffers and quantified the extent to which each buffer size would protect the empirically estimated home ranges of the tracked individuals. Conversely, we also estimated the area in which each buffer size was likely to restrict harvest activities outside the mapped home ranges of the tracked Whip-poor-wills. Our results contribute to an understanding of home range use in aerial insectivores and can inform more refined conservation policies for Whip-poor-wills.

METHODS

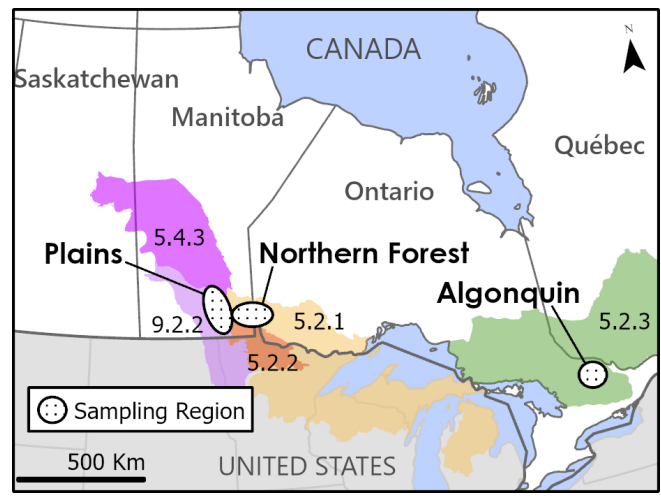
Study areas

We stratified study sites among categories of Level III North American Terrestrial Ecoregions (Wiken et al. 2011) in forested regions of Manitoba and Ontario, Canada. Level III ecoregions characterize locally distinct climate, hydrology, vegetation, and terrain, and are useful for regional-scale assessment and planning. We treated samples that fell near ecoregion borders, and had similar forest and landscape types, as being in the same ecoregion category. Combining data collected in ecoregions 5.2.1 and 5.2.2, and ecoregions 5.4.3 and 9.2.2, left us with home-range data from three main ecoregion categories: Plains; Northern Lakes and Forests (hereafter Northern Forest); and Algonquin/Southern Laurentians (hereafter Algonquin; Fig. 1, Table 1).

Bird capture and transmitter deployment

From May to July of 2018–2020, we used song lures and mist nets to capture 77 adult male Whip-poor-wills on their breeding territories between dusk and dawn. We banded and weighed each bird, and attached archival GPS tags (Lotek Pinpoint10 [18 tags; 1.5g] or Pathtrack NanoFix Mini [59 tags; 2g]) using leg-loop harnesses (Rappole and Tipton 1991) made of 0.75mm Teflon ribbon. The mass of the tag and harness equaled < 3.5% of body mass. We programmed the tags to collect multiple locations per night while the birds were on their breeding home ranges between June and September (Table 1). Typical sampling frequency was 0.5–4 hr, with some tags recording locations every 8–12 hr (Table 1). Each tag also collected one daily roost location between dawn and dusk. Sampling programs varied because of varying tag capacities and battery life, differences between tag models in the ability to customize programs, and some tags had been deployed

Fig. 1. Sampling regions in the breeding range of Eastern Whip-poor-will (*Antrostomus vociferus*), spanning three ecoregion categories (Plains, Northern Forest, and Algonquin) derived from Level III North American Terrestrial Ecoregions (Wiken et al. 2011).



as part of a longer-term project on migration (Korpach et al. 2024); breeding site data for the latter tags were collected incidentally. There was no evidence of a relationship between the duration (days) of data collection for each tag and home range size (Fig. S1), which allowed us to include tags with a range of tracking durations in the study.

Four individuals were tagged and tracked over two consecutive breeding seasons, which provided an opportunity to compare inter-annual variation in individual home-range size. When including these birds' data in statistical analyses of the determinants of home-range size, we only used the home range estimate from the year with the most GPS locations.

Home range estimation

We estimated home ranges as continuous-time stochastic processes using the *ctmmweb* app interface (v. 0.2.10; Dong et al. 2018), which was built upon the *ctmm* R package (Calabrese et al. 2016). Continuous-time stochastic processes are ideal for our data because they are robust to irregular sampling and can account for autocorrelation, which is a common feature of tracking datasets (Calabrese et al. 2016). We estimated both 95th (entire home range) and 50th (core home range) percentiles of the range distributions, with 95% confidence intervals (CI). Previous investigations into Whip-poor-will breeding space use have measured entire home ranges, core home ranges (territories), or both (Wilson 2003, Hunt 2009, Rand 2014). Our analyses were based only on the 95th percentile home ranges, but we report the results of the 50th percentile ranges to facilitate comparison to other studies on Whip-poor-will space use. Hereafter, “home range” refers to the 95th percentile estimates.

Our workflow required three steps: data preparation, model selection, and home-range estimation. To prepare the data, we excluded the lowest-accuracy GPS points by removing locations

Table 1. Summary of GPS data used to estimate home-range sizes for 32 Eastern Whip-poor-wills (*Antrostomus vociferus*), and continuous-time movement model results for 95% and 50% (core area) home-range estimates. CI = confidence interval. Tracking interval refers to frequency of data collected during nighttime hours. In most cases, one daily daytime roost location was also collected. Model type: IID = Independent and Identically Distributed; OU = Ornstein-Uhlenbeck; OUF/f = Ornstein-Uhlenbeck Foraging. Level 3 ecoregions: ASL = Algonquin/Southern Laurentians; LMLAP = Lake Manitoba and Lake Agassiz Plain; MBLIP = Mid-Boreal Lowland and Interlake Plain; NLF = Northern Lakes and Forests; NMW = Northern Minnesota Wetlands. Tracking start and end dates indicate the time first and last locations were collected, but high-frequency collection (as specified by tracking interval) occurred in main tracking months. Home Range IDs ending in four digits are from Lotek tags, and those ending in five digits are from Pathtrack tags.

Home Range ID	Tracking start date (dd-mm-yyyy)	Tracking end date (dd-mm-yyyy)	Main tracking months	Tracking interval (hrs)	Tracking duration (days)	No. GPS locations	Model type	Continuous time movement model results						Level 3 Ecoregion	Ecoregion Reclassification
								95% estimate; 95% CI			50% estimate; 95% CI				
								Area (ha)	Lower CI	Upper CI	Area (ha)	Lower CI	Upper CI		
123252703_20561	20-06-2019	28-09-2019	September	2	100.67	178	OU anisotropic	19.5	16.6	22.7	3.2	2.7	3.8	(5.2.3) ASL	Algonquin
123252705_2176	26-06-2018	01-07-2018	Late June	0.5	4.67	41	IID anisotropic	56.9	40.7	75.9	11.1	7.9	14.7	(5.2.3) ASL	Algonquin
123252708_20556	08-07-2018	04-10-2018	September	8	88	124	OUf anisotropic	27.5	22.6	32.8	3.3	2.7	4.0	(5.2.3) ASL	Algonquin
123252711_2189	15-09-2018	04-10-2018	September	12	19.5	39	IID anisotropic	48.5	16.3	98.0	8.2	2.7	16.5	(5.2.3) ASL	Algonquin
123252712_20597	26-04-2019	28-05-2019	May	8	32.5	120	OUf anisotropic	119.6	97.6	143.7	16.3	13.3	19.6	(5.2.3) ASL	Algonquin
123252713_20560	08-07-2018	04-10-2018	September	2	88.67	250	OU anisotropic	36.8	31.8	42.2	6.7	5.8	7.7	(5.2.3) ASL	Algonquin
123252720_20594	28-05-2019	15-07-2019	June July	0.5	48.87	767	OU anisotropic	29.2	26.9	31.7	6.0	5.5	6.5	(5.2.3) ASL	Algonquin
123252721_20595	28-05-2019	28-09-2019	September	4	123.5	112	OU anisotropic	72.4	58.8	87.5	16.3	13.2	19.7	(5.2.3) ASL	Algonquin
123252726_20602	20-06-2019	28-09-2019	September	2	100.67	191	OU anisotropic	24.9	20.9	29.3	4.4	3.7	5.1	(5.2.3) ASL	Algonquin
123252733_20593	27-06-2019	02-10-2019	September	2	97.67	207	OU anisotropic	26.9	22.4	31.7	6.3	5.3	7.5	(5.2.3) ASL	Algonquin
135268706_20568	17-06-2018	11-09-2018	September	2	86.75	89	OUf anisotropic	21.9	16.6	28.0	4.8	3.7	6.2	(5.4.3) MBLIP	Plains
135268707_20591	17-06-2018	11-09-2018	September	8	86.33	48	OUf anisotropic	72.0	50.8	96.7	14.5	10.3	19.5	(5.4.3) MBLIP	Plains
135268713_56109	10-06-2020	15-09-2020	September	2	102	93	OU isotropic	48.1	38.0	59.4	9.4	7.4	11.7	(9.2.2) LMLAP	Plains
135268716_20588	01-07-2018	11-09-2018	September	4	71.67	39	IID anisotropic	6.8	3.1	12.0	1.5	0.7	2.7	(5.4.3) MBLIP	Plains
135268721_20565	08-07-2018	19-09-2018	September	2	73.75	146	OUf anisotropic	122.7	94.8	154.2	22.4	17.3	27.9	(5.4.3) MBLIP	Plains
135268728_20588	26-05-2019	13-09-2019	June-Sept	8	110.17	406	IID anisotropic	65.1	58.9	71.6	13.3	12.0	14.6	(5.4.3) MBLIP	Plains
135268737_56175	10-06-2020	22-09-2020	September	2	105	149	OU anisotropic	52.0	42.2	62.7	12.3	10.0	14.8	(9.2.2) LMLAP	Plains
135268738_20591	14-06-2019	25-09-2019	September	2	103.83	170	OUf anisotropic	56.6	45.8	68.6	10.1	8.1	12.2	(9.2.2) LMLAP	Plains
135268740_20556	16-06-2019	21-09-2019	September	2	97.75	178	OU anisotropic	18.7	15.1	22.5	4.7	3.8	5.7	(5.4.3) MBLIP	Plains
135268743_56106	21-06-2020	17-09-2020	September	2	89	96	OU isotropic	18.5	14.5	22.9	4.5	3.5	5.6	(5.4.3) MBLIP	Plains
135268752_56139	16-06-2020	22-09-2020	September	2	99	154	OU anisotropic	70.0	55.0	86.7	13.7	10.7	17.0	(5.4.3) MBLIP	Plains
135268785_20557	09-07-2020	22-09-2020	September	2	76	154	OUf anisotropic	108.7	88.7	130.7	20.2	16.4	24.3	(5.4.3) MBLIP	Plains
135268786_20591	09-07-2020	23-09-2020	September	2	77	166	OU isotropic	30.4	25.0	36.4	5.2	4.3	6.2	(9.2.2) LMLAP	Plains
135268710_20600	30-05-2019	22-09-2019	September	2	115.08	147	OU anisotropic	115.8	94.8	138.9	15.7	12.8	18.8	(5.2.1) NLF	Northern Forest
135268724_20557	21-05-2019	19-06-2019	May June	0.25	29.86	903	OUf anisotropic	54.1	48.2	60.3	7.8	7.0	8.7	(5.2.2) NMW	Northern Forest
135268731_1700	15-06-2019	22-06-2019	June	0.5	6.67	66	OUf anisotropic	59.7	44.2	77.5	10.6	7.9	13.8	(5.2.1) NLF	Northern Forest
135268733_1844	15-06-2019	16-06-2019	June	0.5	0.29	15	IID isotropic	55.8	30.5	88.6	12.6	6.8	20.0	(5.2.1) NLF	Northern Forest
135268734_1709	15-06-2019	22-06-2019	June	0.5	6.67	65	IID anisotropic	27.8	21.5	34.9	7.5	5.8	9.5	(5.2.1) NLF	Northern Forest
135268735_20590	30-05-2019	22-09-2019	September	2	115.75	151	OU anisotropic	15.7	12.9	18.7	3.2	2.6	3.8	(5.2.1) NLF	Northern Forest
135268753_56148	03-07-2020	24-09-2020	September	2	83	145	OU anisotropic	33.5	27.6	39.9	5.3	4.3	6.3	(5.2.1) NLF	Northern Forest
135268760_20557	17-05-2020	30-05-2020	May	4	13	42	IID anisotropic	61.9	45.0	81.3	16.5	11.9	21.7	(5.2.2) NMW	Northern Forest
135268764_20594	06-06-2020	13-09-2020	September	2	100	69	OU anisotropic	135.8	94.6	184.3	35.2	24.4	47.7	(5.2.2) NMW	Northern Forest

with horizontal dilution of precision (HDOP) > 20 (Lotek tags), or that were estimated using < 5 satellites (Pathtrack tags), based on manufacturers' recommendations to minimize outliers related to satellite tracking error. GPS measurement error has little apparent effect on estimates of animal home ranges (Moser and Garton 2007). Weak relationships do exist between HDOP, number of satellites, and spatial error, indicating that lower-accuracy fixes should be assessed within the context of the study species, environment, and GPS tag used, but that aggressive filtering based solely on technical variables can lead to substantial loss of accurate and unbiased data (Adams et al. 2013, Ironside et al. 2017, Forrest et al. 2022). We verified that all lower-accuracy fixes were spatially clustered with the higher-accuracy fixes, and unlikely to exert extreme influence on the home-range sizes. Within *ctmmweb* (Dong et al. 2018), we also assigned a 10-m user equivalent range error to all datasets to account for typical telemetry error.

For the model selection step, we first visually assessed the variogram from each bird's tracking dataset to diagnose autocorrelation. Presence of a clear asymptote in a variogram indicated evidence of range-residency in the animal's movements, meaning the dataset was suitable for home range estimation (Calabrese et al. 2016). Each of our 32 datasets, with a range of 15–903 GPS points (Table 1), showed evidence of asymptote (Fig S1).

To identify the data process model for each dataset, *ctmmweb* (Dong et al. 2018) made initial estimates for the model parameter values. We manually adjusted the parameters where they did not closely match the lag features of the variogram. Based on those parameter values, several candidate models appropriate for correlated or uncorrelated data structures were fitted to the dataset. An independently and identically distributed (IID) process was assumed as the best-fitting model for datasets with no autocorrelation. In our data, IID models tended to be chosen for the datasets that had longer tracking intervals or shorter tracking durations, where autocorrelation was not obvious. Where we assumed autocorrelation in the positions of the data, an Ornstein-Uhlenbeck (OU) model was selected as the best candidate, and an OU-Foraging (OUF) movement model was selected where we assumed autocorrelation in positions and velocities of the data (Calabrese et al. 2016). Each candidate model was fitted in isotropic and anisotropic forms, which respectively model circular or non-circular home ranges, based on whether movement varied by direction. We compared candidate models for each dataset using Akaike's Information Criteria for small samples (AICc; Hurvich and Tsai 1989).

Once a model process was selected for each dataset, we used *ctmmweb* (Dong et al. 2018) to estimate home range boundaries using autocorrelated kernel density estimation (AKDE). Unlike conventional range estimators like KDE and minimum convex polygons, AKDE does not assume that tracking data points are independently sampled. Instead, it can account for and model the observed autocorrelation in the dataset. AKDE is often more accurate than conventional range estimators; for example, the IID process can severely underestimate home range areas when the locations are autocorrelated, especially when sample sizes are small (Noonan et al. 2019). However, when IID emerges as the selected model process for the dataset, AKDE and IID estimates are comparable.

For added confidence that we had sufficient data to produce accurate home range estimates, we compared the estimates and confidence intervals from our tags against home ranges estimated from test tags containing small sample sizes (< 15 GPS locations; Fig S1). We were satisfied that our smallest datasets performed markedly better than the low-sample test tags and were reasonably comparable to datasets with large sample sizes (> 100 locations).

Modelling determinants of home-range size

Covariates

(a) Normalized difference vegetation index (NDVI)

We assumed that NDVI, a measure of primary productivity, is associated with prey abundance for Whip-poor-wills, and predicted that home-range size should decrease as NDVI increases. This relationship is unlikely to be linear, because aerial prey produced in the home range may move out of the home range before being encountered by the Whip-poor-will, and we did not expect NDVI to be a strong predictor of home-range size. Nevertheless, in the absence of robust data on insect abundance at the home-range or landscape scale, we acknowledged that home range size likely varies with prey abundance, and tested our hypothesis using NDVI to explore such variation.

We downloaded 250m-resolution MODerate-resolution Imaging Spectroradiometer NDVI (Justice et al. 1998) raster datasets for every 16-day period between 1 June and 30 September, using the *MODIStools* package for R (Tuck et al. 2014). The NDVI data used for each home range corresponded to the same year in which the home range GPS data were collected (2018, 2019, or 2020).

We used the corresponding quality data for each NDVI dataset to clean the NDVI rasters by only keeping good (0) or marginal (1) pixels. This cleaning step removed approximately 3% of pixel dates. We then calculated the mean NDVI across the 26 Jun–14 Sep time series for each pixel. We overlaid the 95th percentile home-range polygons with the NDVI raster and calculated the mean NDVI within the home ranges.

(b) Edge density

Whip-poor-wills forage in edge habitats (Wilson and Watts 2008, Cink et al. 2020), so we predicted that home-range size would decrease as edge habitat (prey accessibility) increased. AMK manually digitized linear forest edges (the boundaries between continuous forest canopy and open areas) within each 95th percentile home-range polygon, using base satellite imagery in ArcGIS Pro version 2.9.3 (ESRI Inc 2022) as a reference. Edges were digitized at a 1:10000 on-screen map scale. We defined features with edges as patches larger than approximately 20 m in radius (e.g., the edge of a 15m x 15m meadow inside a forest, or forest patch within a clearing, would not be digitized). We then calculated the edge density for each 95th percentile home range by dividing the linear amount of edge (m) by the home-range area (ha).

(c) Distance to wetland

We predicted that, if wetlands correlate with prey abundance for Whip-poor-wills, then home ranges with more immediate access to wetland cover would be smaller. A comprehensive wetland dataset that fully covers our study sites was not available, so we merged and modified datasets from multiple public sources to ensure a standard of accuracy and precision (Manitoba

Department of Conservation 2002, Manitoba Habitat Heritage Corporation 2013, Ontario Ministry of Natural Resources and Forestry, Provincial Mapping Unit 2013). We chose datasets based on data age, resolution, visual comparisons with current satellite imagery, and our knowledge of the study sites. Scale and spatial resolution varied, but all datasets had a minimum mapping unit of 1 ha or a scale between 1:10000 and 1:250000, depending on the original source. Table S1 contains details of the source dataset characteristics, modifications, and data originators.

We modified the individual wetland datasets to create one standardized wetland layer for analyses. We removed open water classes, which Whip-poor-wills strongly avoid (Grahame et al. 2021), and retained only classes that could represent true wetlands (bog; fen; marsh; swamp; and shallow water). We chose the single best wetland layer that covered each of our study regions except northwestern Ontario, where we needed to overlay multiple datasets to ensure that all wetlands within or near the study sites were delineated. We then dissolved all wetland polygons together and filtered out polygons smaller than 1 ha to standardize the minimum mapping unit. Finally, we measured the distance from the centroid of each 50th percentile home-range polygon to the edge of the nearest wetland polygon.

(d) Neighbor density

We hypothesized that competition might limit home-range size, predicting that home ranges would be smaller in areas with higher concentrations of territorial birds. To test this prediction, we estimated the number of additional male Whip-poor-wills within one km of each 95% home-range boundary. Whip-poor-wills defending territories adjacent to tagged birds were detected either by capture as part of this study, or by song observations during normal field work activities. Each home range was visited at least once per year for two years. Increased time spent trapping and surveying near home ranges where multiple neighboring birds were included in the study, or where individual birds were included in the study for more than two years, may have resulted in inflated detection of neighbors at certain sites. We had no way to account for this potential observer effort bias, but we note it for transparency.

(e) Ecoregion

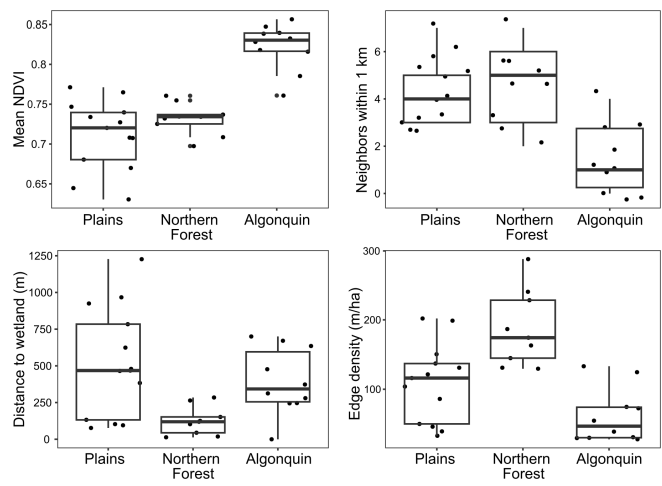
The landscape and climate characteristics that define the three ecoregions (Plains, Northern Forest, and Algonquin) in which our study sites were located also affect covariates like NDVI and edge density, and we therefore expected the covariates in each ecoregion to covary to a degree. However, we included ecoregion as an independent variable because it may explain additional variation in home-range sizes (i.e., from other factors such as vegetation types, soils and geographic features, and climate) that we were unable to test directly.

Statistical analysis

All statistical analyses were conducted in R software for statistical computing (version 4.0.3; R Core Team 2020). We log-transformed the dependent variable (home-range area, in hectares) to improve the distribution of residuals for meeting assumptions of normality and homogeneity of variance. All continuous independent variables were centered and scaled using R's `scale()` function.

The variation in ecological variables among ecoregions (Fig. 2) implied that the modeled effects of each variable on home-range size might vary by ecoregion, but we did not likely have sufficient ecoregion levels to fit a robust mixed-effects model. We therefore tested for interactions between each continuous variable and the ecoregion variable in separate models. We performed leave-one-out cross-validation on each model and compared it to the original model (without an interaction) with `loo_compare()` (package *brms*; Bürkner 2017). We also examined variation in effects via simple effect analyses (`hypothesis()` in *brms*) and interaction plots. We found no difference in predictive ability between the interaction models and the original model, and therefore no evidence that the interaction term (i.e., different effects by ecoregion) provided enough additional explanatory power to justify the added complexity of a mixed-effects model. The ecoregion variable was nonetheless included in the final model as a fixed effect.

Fig. 2. Ecoregion-level differences in measures of ecological variables in Whip-poor-will (*Antrostomus vociferus*) home ranges. Central lines are median values, box hinges are first and third quartiles, and whiskers show minimum and maximum values within 1.5 x the inter-quartile ranges.



We ruled out possible nonlinear relationships between the continuous independent variables and home-range area with a generalized additive model (package *mgcv*; Wood 2011), then fitted a Bayesian linear multiple regression model (package *brms*) using all covariates as fixed effects. The model was parameterized with: family = "gaussian"; chains = 4; warmup = 1000; iterations = 2000; and a weakly informative prior of normal(0, 1) for all fixed-effect coefficients (class = b). We confirmed model convergence by examining trace plots and posterior predictive checks to ensure acceptable model fit (i.e., that the model did an adequate job of predicting new data). Variance inflation factors were calculated with `check_collinearity()` in package *performance* (Lüdtke et al. 2021). We used `hypothesis()` in *brms* to conduct pairwise hypothesis tests (i.e., contrasts) between the ecoregion categories to assess the statistical probability that home-range size differed by ecoregion after controlling for other factors in the model.

We ran two additional models excluding either nearest neighbors or NDVI, because these two covariates were moderately negatively correlated ($r = -0.78$). Highly correlated variables in a model are inter-dependent, and their coefficients thus cannot be interpreted directly as independent effects. The results of these models are reported in Fig S3, and because exclusion of either of the two covariates did not alter the directions of effect, or our interpretation, we hereafter only consider the full model.

Habitat-protection buffer simulation

Within each of the estimated home-range polygons, we simulated 100 hypothetical Whip-poor-will observations (e.g., Whip-poor-will calls heard during a hypothetical call survey), using the Create Random Points tool in ArcGIS Pro 2.2.0 (ESRI Inc 2018). We then created a range of circular buffers (10, 30, 50, 70, 90, 110, 130, 150, 170, 190 hectares) centered on each simulated observation to represent potential habitat-protection buffers that might be applied (e.g., Fig 3a). This process resulted in 1000 potential buffers for each empirically estimated home-range polygon. We used 10 ha as a lower limit because it is similar to a current estimate of Whip-poor-will territory size in Ontario forests (9 ha; Ontario Ministry of the Environment, Conservation and Parks 2021), so smaller habitat-protection buffers are unlikely to be implemented. Thirty hectare and 50 ha approximate the mean sizes of territories (Rand 2014) and home ranges (this study) derived via radio-telemetry and GPS, and are useful benchmarks for exploring protection buffer options.

To quantify how effectively these buffers would protect the empirically estimated home ranges, we calculated the proportion of the home-range polygon captured within each buffer. To simplify the simulation, we did not generate any random points inside secondary polygons (e.g., Fig 3b), but we did include the secondary polygons in the calculation of the proportion of home-range area protected by the buffers. To understand the consequences to forestry of a mismatch between home ranges and protection buffers, we also calculated the proportion of each simulated habitat buffer that covered habitat outside of the known home-range polygons (Fig 3a). We used generalized additive models with a logit link in the beta regression family to model the effect of buffer size (independent variable) on the proportion of home range protected, as well as the proportion of buffer that falls outside of the home range (dependent variables).

The shape of a home range may influence the proportion of overlap possible with a circular habitat-protection buffer. We calculated a circularity index for each home range, which compares the home-range polygon to a circle ($\text{circularity} = 4\pi[\text{area}/\text{perimeter}^2]$). A perfect circle has a circularity index of 1.0, and the value decreases to 0.0 as the polygon becomes increasingly elongated (e.g., Figs 3c and 3d). We included the circularity index as a moderating factor (i.e., interaction) in a third generalized additive model to predict the proportion of home range protected by various buffer sizes at different levels of home-range circularity.

RESULTS

Home range estimation

We recaptured and retrieved tags from 37 of the 77 tagged birds in 2019, 2020, and 2021. After excluding five tags that malfunctioned and contained no data, we had a total of 32 tags (5 Lotek, 27 PathTrack) for use in analyses (13 from the Plains, 9 from the Northern Forest, and 10 from the Algonquin ecoregion; Table 1;

Fig. 3. Ninety-five percent home-range estimates (solid white lines) for four individual Eastern Whip-poor-wills (*Antrostomus vociferus*). Band ID numbers are in upper right. (a) An example of the simulation used to test overlap between estimated home ranges and potential circular habitat-protection buffers. White dots are 100 random points simulating whip-poor-will observations. Grey-scale dotted concentric circles represent three potential habitat-protection buffer sizes placed around one of the observations. Pink shading exemplifies habitat protection in a 10-ha buffer that falls outside of the known home range. (b) A “primary” home-range polygon and a smaller “secondary” polygon that includes wetland habitat (blue hatching). (c) and (d) Home ranges of similar area but different circularity indices (Circularity) may differ in the amount of home range protected (Protection, white shading) within a 50-ha circular habitat-protection buffer.

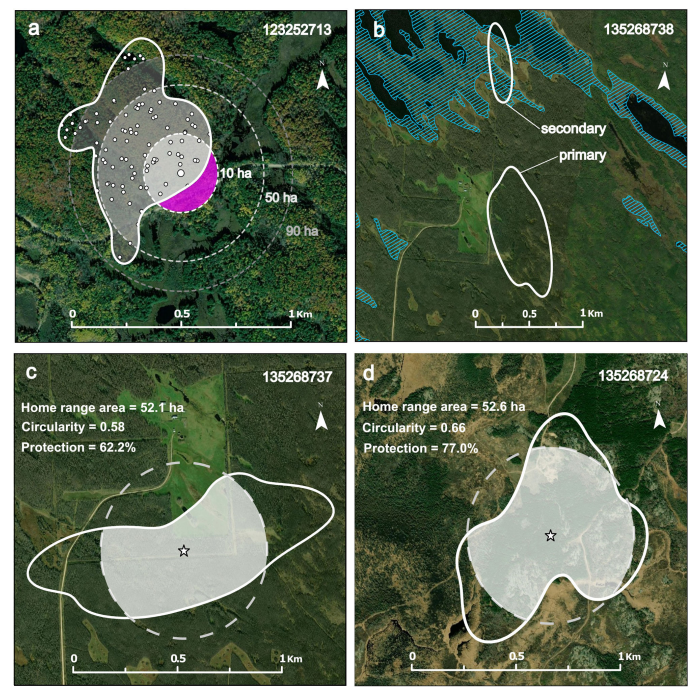
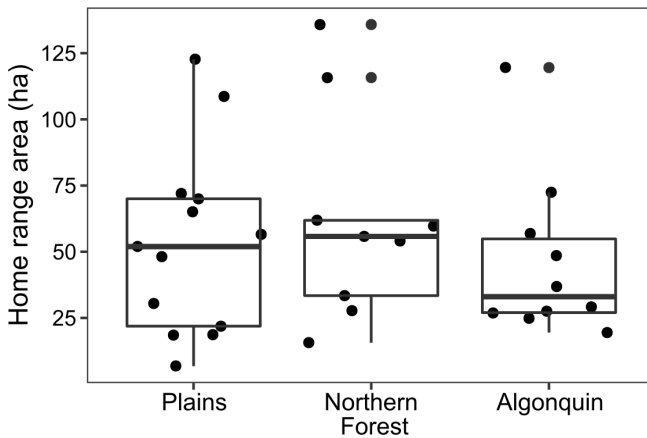


Fig 1). After filtering the GPS locations to remove the lowest-accuracy fixes, the dataset had 5520 (5294 Pathtrack, 226 Lotek) data points. Three Lotek fixes had HDOP > 10 (but < 20) and 19 Lotek fixes were 2D (but with low HDOP). Mean HDOP of Lotek fixes was 2.5. Mean number of satellites for Pathtrack and Lotek fixes were 6.4 and 6.0, respectively.

Home-range estimates (95th percentile [95% CI]) ranged from 6.8 ha (3.1–12.0) to 135.8 ha (94.6–184.3; Table 1). The overall mean home-range size across the 3 ecoregions was 53.6 ha \pm 34.6 standard deviation (SD) and the median size was 50.3 ha (equivalent to a circular area with a radius of \sim 400 m). Mean home-range size by ecoregion was 62.2 ha \pm 39.7 SD for Northern Forest (N = 9), 53.2 ha \pm 35.1 SD for Plains (N = 13), and 46.2 ha \pm 30.65 SD for Algonquin (N = 10; Fig. 4). Circularity indices for the home ranges ranged from 0.31 to 0.92 (mean 0.66 ± 0.15 SD). Repeat-tracking of four individual Whip-poor-wills over two breeding seasons suggested high repeatability in home-range size and shape (Fig. S2). These four birds re-used 65%, 68.5%, 75%, and 81% of their estimated home ranges in subsequent years.

Fig. 4. Eastern Whip-poor-will (*Antrostomus vociferus*) home-range sizes in three ecoregion categories.



Thirty-four percent (11/32) of estimated home ranges included one or two secondary polygons. These polygons ranged from 17 to 862 m from the closest edge of the primary polygon and were 0.9–25% of the size of the primary polygon. Some of the secondary polygons included a different habitat type than was available in the associated primary polygon. For example, the home-range estimates for four individuals included secondary polygons composed of mostly wetland, whereas the associated primary polygons contained no wetlands (e.g., Fig. 3b).

Determinants of home-range size

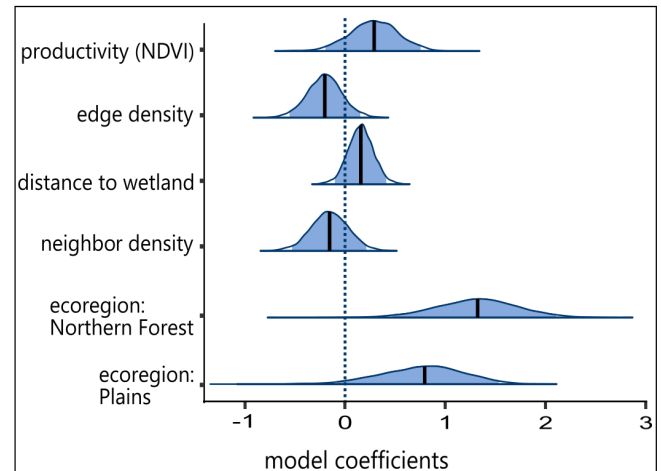
In the raw dataset, we found moderate correlation between NDVI and neighbor density ($r = -0.78$), between edge density and neighbor density ($r = 0.57$), and between productivity and edge density ($r = -0.56$). However, variance inflation factors for the multivariate model were all ≤ 5.64 (≤ 4.71 for all continuous variables), so we concluded that the covariates were sufficiently independent.

The Bayesian model results are median estimates and posterior probability distributions (Fig. 5 shows posterior probabilities within 95% credible intervals [CrI]). Model results (estimate, [lower CrI-upper CrI]) suggest weak probabilities that NDVI (0.28, [-0.20–0.75]) and distance to wetland (0.17, [-0.11–0.45]) had positive relationships with Whip-poor-will home-range size. The posterior probabilities for both edge density (-0.20, [-0.56–0.15]) and neighbor density (-0.15, [-0.53–0.21]) indicate weak probabilities of negative relationships with home-range size (i.e., an increase in either of these variables relates to a decrease in home-range size). Pairwise hypothesis tests (i.e., contrasts) between the three ecoregion categories indicated that, after controlling for the other covariates, home ranges in the Algonquin ecoregion were smaller than those in the Northern Forest ecoregion and in the Plains ecoregion with $> 95\%$ certainty. Home ranges in the Plains ecoregion were smaller than those in Northern Forest, but with $< 95\%$ certainty.

Habitat-protection buffer simulation

None of the simulated buffers would protect 100% of an average-sized home range in our sample of tracked Whip-poor-wills because of high variation in home-range size and shape and the

Fig. 5. Bayesian coefficients for the influence of ecological variables on Eastern Whip-poor-will (*Antrostomus vociferus*) home-range sizes. Blue areas are posterior probability distributions within 95% credible intervals; vertical bars are the median coefficient estimates. The Algonquin ecoregion is the reference category for the categorical ecoregion variable.



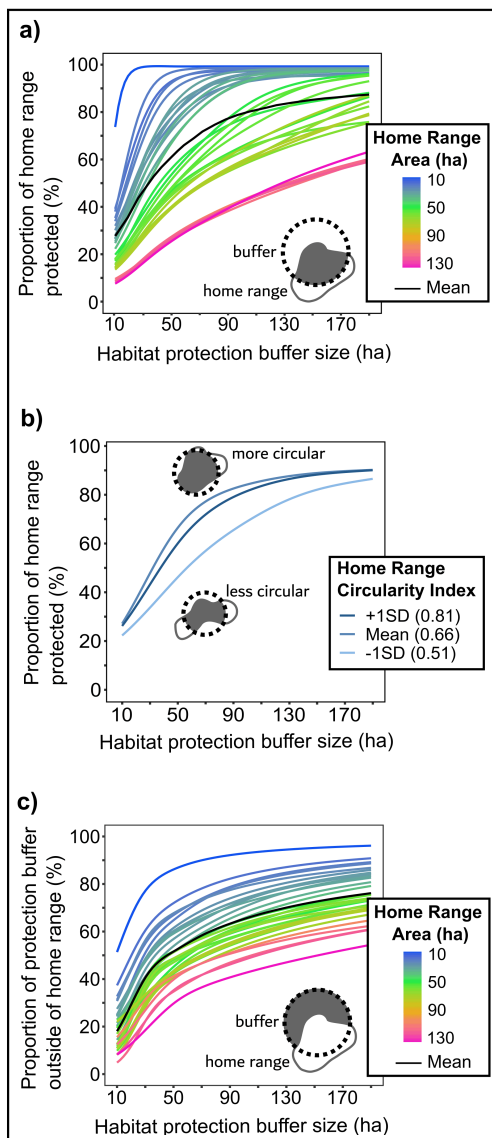
occurrence of secondary polygons. As the simulated buffer size increased, the proportion of overlap with the estimated home ranges (i.e., proportion that would be protected) also increased (Fig. 6a). However, the rate of increase was non-linear and varied with home-range size, such that small home ranges (10–30 ha) were well-protected once the buffer size exceeded ~ 50 ha, but even the largest simulated buffers protected only 50–80% of the larger home ranges. (Fig. 6a). The proportion of habitat-protection buffer falling outside of the estimated home ranges similarly increased non-linearly. In our simulations, 30–80% of the area in 50-ha buffers overlapped with habitat outside of the home ranges of the GPS-tracked Whip-poor-wills (Fig. 6c).

The proportion of protection provided by each buffer also varied with home-range circularity (Fig. 6b). For example, 50-ha-sized circular buffers were predicted to protect an average of 45.8% of the most oblong home ranges (at -1SD on the circularity index), 66.5% of home ranges with average circularity, and 59.7% of the most circular home ranges at (+1SD on the circularity index; Fig. 6b). The moderating effect of circularity differed between ecoregions, because of variation in the relationship between home-range size and circularity. Home-range size and circularity were weakly positively correlated in the Algonquin ecoregion ($r = 0.10$), but negatively correlated in the Plains and Northern Forest ecoregions ($r = -0.56$ and -0.45 , respectively; Figs. S4, S5).

DISCUSSION

Our study was designed to robustly quantify variation in male Whip-poor-will breeding home-range size, and to test the effectiveness of one approach to breeding habitat protection. Whip-poor-will home ranges were highly variable in size and shape, and size variation was not strongly explained by any of the factors that we hypothesized might affect food availability at the scale of the home range. The relationships between home-range size and edge density (negative), distance to wetland (positive),

Fig. 6. Effective management of Eastern Whip-poor-will (*Antrostomus vociferus*) habitat requires knowledge of home-range size and shape. (a) The estimated proportion of individual home ranges protected, based on 1000 simulations per individual, varies with circular habitat-protection buffers of different sizes. (b) When variation in home-range shape is included, a generalized additive model predicts the proportion of the average home range protected at different degrees of size and circularity. (c) Habitat-protection buffers are likely to encompass a substantial amount of habitat outside of a home range. A non-standard x-axis scale was chosen to ease comparison between commonly used metrics for habitat-protection areas for this species (e.g., 9 or 30 ha) and the average home-range size in this study (approximately 50 ha).



and neighbor density (negative) trended in the predicted directions, albeit weakly. Home-range size was also weakly related to NDVI, but contrary to our prediction, the relationship was positive. Overall, our results suggest that multiple factors, including unmeasured regional differences, are likely to influence home-range size.

From a conservation and management perspective, we found a mismatch between circular habitat-protection buffers centered on simulated call survey observations and the real GPS-estimated home ranges. Such buffers, even when they are the size of an average Whip-poor-will breeding home range (~ 50 ha), are unlikely to effectively protect entire home ranges, and overlap substantially with habitat outside the home range. Additional protection adjacent to the home range is likely to benefit Whip-poor-wills, but with the potential trade-off of greatly restricting forestry operations in forest that birds may not be using. Alternative paradigms of habitat protection are needed to facilitate forestry operations that do not endanger Whip-poor-wills, which are a classic case of the challenges of balancing resource extraction with recovery of threatened species.

Determinants of home-range size

We had expected increasing NDVI and edge density (as proxies for prey abundance and prey accessibility, respectively) would correlate with reduced home-range size. We found this association between home-range size and edge density, but not NDVI, which implies that edge habitat increases foraging opportunities for Whip-poor-wills and may be a more adequate measure of food availability than primary productivity is. This edge density hypothesis is supported by positive associations between breeding Whip-poor-will distribution and forest edges (Wilson and Watts 2008) and increased use of openings within forested home ranges during nighttime when foraging takes place (Grahame et al. 2021, Spiller et al. 2022). A related species, European Nightjar, disproportionately forages in young forest stands where foraging is easier, despite moth biomass being higher in older forest stands (Sharps et al. 2015). Suitable foraging habitat structure thus may impose a stronger constraint than prey abundance on foraging activities in nightjar species (Jetz et al. 2003). However, studies on Whip-poor-will home ranges at tropical wintering sites have associated larger home-range sizes both with a decrease (Tonra et al. 2019) and an increase (Skinner et al. 2023) in edge habitat, so a relationship may not be generalizable across landscapes or seasons, and may be especially dependent on habitat type (e.g., agriculture vs scrub; Skinner et al. 2023).

The unexpected weakly-positive relationship between home-range size and NDVI lead us to conclude that mean NDVI may not be an accurate spatial or temporal proxy for Whip-poor-will prey abundance at the fine spatial scale of the home range, and instead reflects a different process that is correlated with home-range size. NDVI sensitivity to land cover types and quantities varies by spatial scale (Martinez and Labib 2023), and a home range with a large area of mid-quality habitat could end up having a higher mean NDVI than a home range with a small area of high-quality habitat. Our study was focused on foraging needs, so relationships with primary productivity also would not capture well the habitat required for nesting. Despite inconclusive support

for an effect of prey abundance (as measured by NDVI) in our study, prey abundance must logically have some effect on Whip-poor-will foraging timing and success. Previous work shows that edge habitat and prey abundance can predict Whip-poor-will presence and abundance at multiple spatial scales larger than the home range (English et al. 2017a), and that moth abundance predicts Whip-poor-will associations with forest edges (Souza-Cole et al. 2022). Declining insect prey abundance is a potential factor in North American aerial insectivore population declines (Spiller and Dettmers 2019), and reliable methods to infer prey abundance at multiple spatial scales are needed to accurately assess habitat quality.

We used neighbor density as an alternate proxy for habitat quality because theory predicts that birds should establish smaller home ranges where resources are abundant and the landscape can support a higher density of individuals (Sells and Mitchell 2020). We did find that home ranges with higher neighbor densities tended to be smaller, after accounting for other variables in the model, even though the pattern was not apparent in the raw data at an ecoregion scale (i.e., the Algonquin home ranges were smallest, but also had the fewest neighbors). Potential interactions between population density, sociality, and food availability can influence home-range size (Adams 2001, Kjellander et al. 2004, Benson et al. 2006) and territorial behavior among conspecifics can limit breeding density, regardless of food supply (Krebs 1971). In such cases, it is difficult to say whether a measured home range represents the ideal amount of space for a breeding individual, or if it would have been larger in the absence of neighbors.

The presence of wetland habitat in or near the home range did not emerge as a strong predictor of home-range size. We had hypothesized that Whip-poor-wills would have smaller home ranges if they had ready access to productive wetland habitat, which could provide abundant and highly nutritious aquatic insects for aerial insectivores (Twining et al. 2016). Whip-poor-wills primarily forage on moths (Lepidoptera) and beetles (Coleoptera; Garlapow 2014, Cink et al. 2020, Souza-Cole et al. 2022), but aquatic and terrestrial invertebrates have different peak emergence timing, and terrestrial forest birds can subsidize their diet with aquatic-borne insects when terrestrial insect biomass is low (Nakano and Murakami 2001, Shipley et al. 2022). However, Whip-poor-wills may not take advantage of aquatic-borne insects if enough of their primary terrestrial prey are available (Souza-Cole et al. 2022). At a landscape scale, breeding home ranges of Whip-poor-wills and other nightjars are associated with wetlands (Alexander and Cresswell 1990, Ng 2009, Farrell et al. 2019, Vala et al. 2020, Knight et al. 2021). However, Whip-poor-wills associate with wetlands and drier open habitats at similar rates in boreal landscapes (Farrell et al. 2017), which suggests that the main ecological value of wetland may be to provide forest edge habitat for foraging, rather than an abundance of prey. Within a home range, Whip-poor-wills tended to avoid open water and wetlands directly during foraging, although they may use habitat adjacent to wetlands (Grahame et al. 2021). This may be because many wetlands do not contain suitable perches from which a perch-and-sally insectivore can hunt aerial insects, and does not imply that they do not benefit from wetland productivity. Some of our tracked birds appeared to expand their home ranges, via lesser-used secondary polygons, to include wetland habitat (Fig 3b); in three of the four cases, there was no wetland present in the

primary polygon. It is possible that the Whip-poor-wills opportunistically adjusted home range habitat use at fine spatial or temporal scales to include wetland, but it is unclear whether the benefit was aquatic insects, increased edge habitat, social factors, or something else.

It is perhaps unsurprising that we were unable to pinpoint a common habitat characteristic that relates to home-range size for all individuals of a species like the Whip-poor-will that uses a variety of forest habitats. Whip-poor-will home-range sizes in non-breeding areas likely depend on the suitability of specific open habitat types for foraging (Skinner et al. 2023), and home-range sizes of European Nightjars indicate trade-offs between habitat needs like availability of cleared habitat (smaller home ranges) and amount of open water (larger home ranges; Mitchell et al. 2020). Additionally, several unmeasured, or unmeasurable, characteristics likely influence home ranges. Demographic and other non-habitat characteristics (e.g., age, sex, body mass, species-specific behavior) have highly varied and complex relationships with home-range size (Rolando 2002, Ottaviani et al. 2006, Ofstad et al. 2016, Seigle-Ferrand et al. 2021). We assumed that all the adult male Whip-poor-wills in our study were in breeding pairs at the time of tracking and had similar resource needs. It is feasible that some of the birds we tracked were non-breeding, which might affect their home-range sizes. European Nightjar home-range sizes do not significantly differ between paired and unpaired males, although unpaired males tend to range farther from their song territories, reflecting potentially different movement needs like mate-finding (Sharps et al. 2015). The fact that home-range sizes and shapes in our dataset varied dramatically adds complexity to the problem of designing effective land-use prescriptions. However, once the variation in site-level ecological covariates was accounted for, our models revealed that home ranges in the Northern Forest are larger than those in the Algonquin ecoregion, and Plains home ranges are roughly in between. Broad ecoregional differences can be important for management planning, as practitioners can customize habitat-protection prescriptions in different regions.

Management applications of habitat-protection buffer simulation

Multiple factors inform policy for management of harvested forests, and clear information on potential outcomes and their consequences can help to focus the decision-making process (Mills and Clark 2001). Policy makers and resource managers are often asked to create and implement management guidelines despite substantial uncertainty about target species' movements and habitat requirements (Ferraz et al. 2021). In this study, we addressed one source of uncertainty by quantifying the likelihood that potential habitat-protection buffers can effectively and efficiently protect the full breeding home ranges of individual Whip-poor-wills. We introduced one management region (Ontario, Canada) as an example of how habitat-protection buffers are developed and applied for Whip-poor-wills, but our results are relevant to any region that uses individual-based protection guidelines for a species that has highly varied home-range sizes and shapes.

We had hoped to identify a habitat-protection buffer size that would strike a balance between protecting detected Whip-poor-will home ranges and minimizing additional restrictions on

proposed forestry operations. However, we found that even extremely large buffers (> 170 ha) could not capture 100% of an average-sized and -shaped home range of the 32 individuals tracked in this study and would substantially limit forestry activities outside the home range (Fig. 6a–c).

Whip-poor-wills present a complex case for habitat protection, because fully restricting forestry activities in their habitat is unlikely to benefit them at a broad landscape scale. Whip-poor-wills prefer heterogeneous forest with edges that provide foraging habitat (Cink et al. 2020), and very old, dense forests do not provide optimal habitat for this species. This habitat preference could provide an opportunity for “win-win” management outcomes. Some harvest methods create patches of mature forest next to small, harvested areas that Whip-poor-will can use (Tozer et al. 2014, Farrell et al. 2017, Spiller et al. 2022), and quantitative targets for forest management plans to conserve breeding Whip-poor-wills are emerging (Spiller and King 2021).

The goal of managing habitat at the scale of the home range is typically to protect a nest and ensure that the foraging needs of the breeding pair are met. However, female Whip-poor-wills are cryptic and nests are extremely well camouflaged, so few studies focus on female movements or nesting ecology (English et al. 2017b, 2018, Grahame et al. 2021). Most Whip-poor-will studies rely on limited data collected from males because logistical constraints restrict nocturnal bird surveys to roadside call surveys of territorial males (Hannah 2021), and males are easier to capture for use in telemetry studies (e.g., this study, Bakermans and Vitz 2023). This approach presents two caveats. First, call survey observations of males are not likely to identify the centers of their home ranges, their nesting partner’s home range, nor their nest. Second, even if call surveys were adequate to identify the centers of home ranges, the assumption that protecting the core defended territory will protect all required resources has not been tested (e.g., in the manner of Gardiner et al. 2019). Reduction in home-range size can have negative impacts on individuals beyond those of direct damage to the nest.

Identifying an alternate habitat-protection strategy for Whip-poor-wills is beyond the scope of this paper. Ideally, our results can inform the future development and testing of effective alternatives to circular, standard-sized, habitat-protection buffers. Until we know how individual birds tolerate disturbance during breeding, and how critical the habitat is in different areas of the home range to the survival of the individual, we assume that full home range protection is necessary for a breeding pair to successfully complete breeding and raise offspring. Targeted research is required to assess whether female Whip-poor-will home ranges differ from those of their male mates; where nests are located within the home range and relative to the locations of singing males detected during call surveys; and how both males and females respond to partial destruction of their home range through forest harvest or other activities. Whip-poor-wills are strongly faithful to their breeding sites, and the four repeat-tracked birds in this study had substantial, but not complete, overlap between their home ranges across two years (65–85%, Fig. S2), suggesting that home range boundaries can shift over time and potentially with shifting resource availability. However, it is crucial to track individuals over multiple years, ideally in experimental studies where their responses to nearby harvest activities can be assessed, as well as further study individual responses to inter-annual changes in habitat condition. Finally, it is essential to monitor the

long-term consequences of management decisions about individual home ranges to the health of Whip-poor-will populations. Working relationships between resource managers, industry, and researchers provide the best opportunities for moving forward on applied questions.

Author Contributions:

AMK, CD, KCF, and VV conceived of the study and designed analyses. AMK, VV, and CD conducted fieldwork and collected the data. AMK and VV performed the analyses and drafted the manuscript. All authors contributed substantially to edits and approved the final manuscript.

Acknowledgments:

For their field assistance or logistical support, we thank: Lucy Brown, Josh DeClerke, Maryse Gagné, Len Gal, Claire Heidenreich, Pete Hettinga, Alexandra Hjort-Toms, Jennifer Hoare, Lauren Hooten, Dan Hughes, Kaylyn Kalupar, Alison Lake, Alex Legere, Chris Martin, Tim Teetaert, Stephanie Thompson, and Abigail Warren. Dana Kinsman provided helpful information about forest management in Ontario. Nature Conservancy Canada supported our work at the Manitoba Tall Grass Prairie Preserve and the Swan Lake Wetland-Parkland Complex. This research was funded by the University of Manitoba (KCF and AMK), Carleton University (CMD), NSERC Discovery Program (KCF and CMD), Government of Ontario (VVZ, CMD), Canadian Foundation for Innovation John R Evans Leaders Fund (KCF), the American Ornithological Society (AMK), the Connie Holland Bird Study Fund (AMK), and a Mitacs Accelerate Internship (AMK) in partnership with Weyerhaeuser Company Limited, EACOM Timber Corporation, Interfor, Resolute Forest Products, and Domtar Inc. This study was created to address key needs identified by partners in the forestry industry and government. The authors independently designed the study, collected the data, and interpreted the results of the analysis.

LITERATURE CITED

- Adams, A. L., K. J. M. Dickinson, B. C. Robertson, and Y. van Heezik. 2013. An evaluation of the accuracy and performance of lightweight GPS collars in a suburban environment. *PLoS ONE* 8:e68496. <https://doi.org/10.1371/journal.pone.0068496>
- Adams, E. S. 2001. Approaches to the study of territory size and shape. *Annual Review of Ecology, Evolution, and Systematics* 32:277-303. <https://doi.org/10.1146/annurev.ecolsys.32.081501.114034>
- Alexander, I., and B. Cresswell. 1990. Foraging by Nightjars *Caprimulgus europaeus* away from their nesting areas. *Ibis* 132:568-574. <https://doi.org/10.1111/j.1474-919X.1990.tb00280.x>
- Bakermans, M. H., and A. C. Vitz. 2023. Hot stops: timing, pathways, and habitat selection of migrating Eastern Whip-poor-wills. *Journal of Avian Biology* 2024:e03142. <https://doi.org/10.1111/jav.03142>

- Benson, J. F., M. J. Chamberlain, and B. D. Leopold. 2006. Regulation of space use in a solitary felid: population density or prey availability? *Animal Behaviour* 71:685-693. <https://doi.org/10.1016/j.anbehav.2005.08.005>
- Bürkner, P.-C. 2017. brms : An R Package for Bayesian multilevel models using Stan. *Journal of Statistical Software* 80:1-28. <https://doi.org/10.18637/jss.v080.i01>
- Cain, S., T. Solomon, Y. Leshem, S. Toledo, E. Arnon, A. Roulin, and O. Spiegel. 2023. Movement predictability of individual barn owls facilitates estimation of home range size and survival. *Movement Ecology* 11:10. <https://doi.org/10.1186/s40462-022-00366-x>
- Calabrese, J. M., C. H. Fleming, and E. Gurarie. 2016. ctm : an R package for analyzing animal relocation data as a continuous-time stochastic process. *Methods in Ecology and Evolution* 7:1124-1132. <https://doi.org/10.1111/2041-210X.12559>
- Cink, C. L., P. Pyle, and M. A. Patten. 2020. Eastern Whip-poor-will (*Antrostomus vociferus*), version 1.0. In P. G. Rodewald, editor. *Birds of the world*. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.whip-p1.01>
- Dong, X., C. H. Fleming, M. J. Noonan, and J. M. Calabrese. 2018. ctmweb: A shiny web app for the ctm movement analysis package.
- Elchuk, C. L., and K. L. Wiebe. 2003. Home-range size of Northern Flickers (*Colaptes auratus*) in relation to habitat and parental attributes. *Canadian Journal of Zoology* 81:954-961. <https://doi.org/10.1139/z03-077>
- English, P. A., A. M. Mills, M. D. Cadman, A. E. Heagy, G. J. Rand, D. J. Green, and J. J. Nocera. 2017b. Tracking the migration of a nocturnal aerial insectivore in the Americas. *BMC Zoology* 2:5. <https://doi.org/10.1186/s40850-017-0014-1>
- English, P. A., J. J. Nocera, and D. J. Green. 2018. Nightjars may adjust breeding phenology to compensate for mismatches between moths and moonlight. *Ecology and Evolution* 8:5515-5529. <https://doi.org/10.1002/ece3.4077>
- English, P. A., J. J. Nocera, B. A. Pond, and D. J. Green. 2017a. Habitat and food supply across multiple spatial scales influence the distribution and abundance of a nocturnal aerial insectivore. *Landscape Ecology* 32:343-359. <https://doi.org/10.1007/s10980-016-0454-y>
- ESRI Inc. 2018. ArcGIS Pro. Environmental Systems Research Institute, Inc., Redlands, California, USA.
- ESRI Inc. 2022. ArcGIS Pro. Environmental Systems Research Institute, Inc., Redlands, California, USA.
- Farrell, C. E., L. Fahrig, G. Mitchell, and S. Wilson. 2019. Local habitat association does not inform landscape management of threatened birds. *Landscape Ecology* 34:1313-1327. <https://doi.org/10.1007/s10980-019-00843-6>
- Farrell, C. E., S. Wilson, and G. Mitchell. 2017. Assessing the relative use of clearcuts, burned stands, and wetlands as breeding habitat for two declining aerial insectivores in the boreal forest. *Forest Ecology and Management* 386:62-70. <https://doi.org/10.1016/j.foreco.2016.11.026>
- Fernández-Tizón, M., T. Emmenegger, J. Perner, and S. Hahn. 2020. Arthropod biomass increase in spring correlates with NDVI in grassland habitat. *Science of Nature* 107:42. <https://doi.org/10.1007/s00114-020-01698-7>
- Ferraz, K. M. P. M. de B., R. G. Morato, A. A. A. Bovo, C. O. R. da Costa, Y. G. G. Ribeiro, R. C. de Paula, A. L. J. Desbiez, C. S. C. Angelieri, and K. Traylor-Holzer. 2021. Bridging the gap between researchers, conservation planners, and decision makers to improve species conservation decision-making. *Conservation Science and Practice* 3:e330. <https://doi.org/10.1111/csp2.330>
- Fitch, H. S. 1958. Home ranges, territories, and seasonal movements of vertebrates of the Natural History Reservation. University of Kansas Publications Museum of Natural History 11:63-326.
- Forrest, S. W., M. R. Recio, and P. J. Seddon. 2022. Moving wildlife tracking forward under forested conditions with the SWIFT GPS algorithm. *Animal Biotelemetry* 10:19. <https://doi.org/10.1186/s40317-022-00289-9>
- Fraser, K. C., K. T. A. Davies, C. M. Davy, A. T. Ford, D. T. T. Flockhart, and E. G. Martins. 2018. Tracking the conservation promise of movement ecology. *Frontiers in Ecology and Evolution* 6:150. <https://doi.org/10.3389/fevo.2018.00150>
- Fretwell, S. D., and H. L. Lucas Jr. 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16-36. <https://doi.org/10.1007/BF01601953>
- Gardiner, R., K. Proft, S. Comte, M. Jones, and C. N. Johnson. 2019. Home range size scales to habitat amount and increasing fragmentation in a mobile woodland specialist. *Ecology and Evolution* 9:14005-14014. <https://doi.org/10.1002/ece3.5837>
- Garlapow, R. M. 2014. Whip-poor-will prey availability and foraging habitat: implications for management in pitch pine / scrub oak barrens habitats. Thesis. University of Massachusetts Amherst, Amherst, Massachusetts, USA.
- Government of Canada. 2024. Species at Risk Act, SC 2002, c 29. Government of Canada, Ottawa, Ontario, Canada. <https://canlii.ca/t/56fds>
- Grahame, E. R. M., K. D. Martin, E. A. Gow, and D. R. Norris. 2021. Diurnal and nocturnal habitat preference of Eastern Whip-poor-wills (*Antrostomus vociferous*) in the northern portion of their breeding range. *Avian Conservation and Ecology* 16(2):14. <https://doi.org/10.5751/ACE-01929-160214>
- Green, A. L., A. P. Maypa, G. R. Almany, K. L. Rhodes, R. Weeks, R. A. Abesamis, M. G. Gleason, P. J. Mumby, and A. T. White. 2015. Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews* 90:1215-1247. <https://doi.org/10.1111/brv.12155>
- Haché, S., M.-A. Villard, and E. M. Bayne. 2013. Experimental evidence for an ideal free distribution in a breeding population of a territorial songbird. *Ecology* 94:861-869. <https://doi.org/10.1890/12-1025.1>
- Hannah, K. 2021. Ontario Nightjar survey instruction manual. Ontario Breeding Bird Atlas, Port Rowan, Ontario, Canada.

- Herfindal, I., J. D. C. Linnell, J. Odden, E. B. Nilsen, and R. Andersen. 2005. Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). *Journal of Zoology* 265:63-71. <https://doi.org/10.1017/S0952836904006053>
- Hunt, P. D. 2009. Whip-poor-will territory mapping at two New Hampshire sites. New Hampshire Audubon, Concord, New Hampshire, USA.
- Hurvich, C. M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. *Biometrika* 76:297-307. <https://doi.org/10.1093/biomet/76.2.297>
- Ironside, K. E., D. J. Mattson, T. R. Arundel, and J. R. Hansen. 2017. Is GPS telemetry location error screening beneficial? *Wildlife Biology* 2017:1-7. <https://doi.org/10.2981/wlb.00229>
- Iverson, A. R., D. L. Humple, R. L. Cormier, T. P. Hahn, T. A. Block, D. Shizuka, B. E. Lyon, A. S. Chainé, E. J. Hudson, and E. M. Hull. 2024. Winter GPS tagging reveals home ranges during the breeding season for a boreal-nesting migrant songbird, the Golden-crowned Sparrow. *PLoS ONE* 19:e0305369. <https://doi.org/10.1371/journal.pone.0305369>
- Jetz, W., J. Steffen, and K. E. Linsenmair. 2003. Effects of light and prey availability on nocturnal, lunar and seasonal activity of tropical nightjars. *Oikos* 103:627-639. <https://doi.org/10.1034/j.1600-0706.2003.12856.x>
- Justice, C. O., E. Vermote, J. R. G. Townshend, R. Defries, D. P. Roy, D. K. Hall, V. V. Salomonson, J. L. Privette, G. Riggs, A. Strahler, W. Lucht, R. B. Myneni, Y. Knyazikhin, S. W. Running, R. R. Nemani, Z. Wan, A. R. Huete, W. van Leeuwen, R. E. Wolfe, L. Giglio, J. Muller, P. Lewis, and M. J. Barnsley. 1998. The moderate resolution imaging spectroradiometer (MODIS): land remote sensing for global change research. *IEEE Transactions on Geoscience and Remote Sensing* 36:1228-1249. <https://doi.org/10.1109/36.701075>
- Kjellander, P., A. J. M. Hewison, O. Liberg, J.-M. Angibault, E. Bideau, and B. Cargnelutti. 2004. Experimental evidence for density-dependence of home-range size in roe deer (*Capreolus capreolus* L.): a comparison of two long-term studies. *Oecologia* 139:478-485. <https://doi.org/10.1007/s00442-004-1529-z>
- Knight, E. C., R. M. Brigham, and E. M. Bayne. 2021. Specialist or generalist? It depends. Context-dependent habitat relationships provide insight into forest disturbance effects for a boreal bird species. *Forest Ecology and Management* 502:119720. <https://doi.org/10.1016/j.foreco.2021.119720>
- Korpach, A. M., C. M. Davy, A. M. Mills, and K. C. Fraser. 2024. Lunar synchrony, geography, and individual clocks shape autumn migration timing in an avian migrant. *Behavioral Ecology* 35: arae001. <https://doi.org/10.1093/beheco/arae001>
- Kramer, D. L., and M. R. Chapman. 1999. Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes* 55:65-79. <https://doi.org/10.1023/A:1007481206399>
- Krebs, J. R. 1971. Territory and breeding density in the Great Tit, *Parus Major* L. *Ecology* 52:2-22. <https://doi.org/10.2307/1934734>
- Laundré, J. W., and J. Loxterman. 2007. Impact of edge habitat on summer home range size in female pumas. *American Midland Naturalist* 157:221-229. [https://doi.org/10.1674/0003-0031\(2007\)157\[221:IOEHOS\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2007)157[221:IOEHOS]2.0.CO;2)
- Lüdecke, D., M. S. Ben-Shachar, I. Patil, P. Waggoner, and D. Makowski. 2021. performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software* 6:3139. <https://doi.org/10.21105/joss.03139>
- Manitoba Department of Conservation. 2002. 1:20 000 Water Bodies - polygons. Manitoba Department of Conservation, Winnipeg, Manitoba, Canada.
- Manitoba Habitat Heritage Corporation. 2013. MHHC Wetland Inventory 2013. Manitoba Habitat Heritage Corporation, Winnipeg, Manitoba, Canada.
- Marshall, M. R., and R. J. Cooper. 2004. Territory size of a migratory songbird in response to caterpillar density and foliage structure. *Ecology* 85:432-445. <https://doi.org/10.1890/02-0548>
- Martinez, A. de la I., and S. M. Labib. 2023. Demystifying normalized difference vegetation index (NDVI) for greenness exposure assessments and policy interventions in urban greening. *Environmental Research* 220:115155. <https://doi.org/10.1016/j.envres.2022.115155>
- Mills, T. J., and R. N. Clark. 2001. Roles of research scientists in natural resource decision-making. *Forest Ecology and Management* 153:189-198. [https://doi.org/10.1016/S0378-1127\(01\)00461-3](https://doi.org/10.1016/S0378-1127(01)00461-3)
- Mitchell, L. J., T. Kohler, P. C. L. White, and K. E. Arnold. 2020. High interindividual variability in habitat selection and functional habitat relationships in European nightjars over a period of habitat change. *Ecology and Evolution* 10:5932-5945. <https://doi.org/10.1002/ece3.6331>
- Mitchell, L. J., P. C. L. White, and K. E. Arnold. 2019. The trade-off between fix rate and tracking duration on estimates of home range size and habitat selection for small vertebrates. *PLoS ONE* 14:e0219357. <https://doi.org/10.1371/journal.pone.0219357>
- Moser, B. W., and E. O. Garton. 2007. Effects of telemetry location error on space-use estimates using a fixed-kernel density estimator. *Journal of Wildlife Management* 71:2421-2426. <https://doi.org/10.2193/2007-003>
- Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America* 98:166-170. <https://doi.org/10.1073/pnas.98.1.166>
- Ng, J. W. 2009. Habitat use and home range characteristics of Common Nighthawks (*Chordeiles minor*) in mixed-grass prairie. Thesis. University of Regina, Regina, Saskatchewan, Canada.
- Noonan, M. J., M. A. Tucker, C. H. Fleming, T. S. Akre, S. C. Alberts, A. H. Ali, J. Altmann, P. C. Antunes, J. L. Belant, D. Beyer, N. Blaum, K. Böhning-Gaese, L. Cullen, R. C. de Paula, J. Dekker, J. Drescher-Lehman, N. Farwig, C. Fichtel, C. Fischer, A. T. Ford, J. R. Goheen, R. Janssen, F. Jeltsch, M. Kauffman, P. M. Kappeler, F. Koch, S. LaPoint, A. C. Markham, E. P. Medici,

- R. G. Morato, R. Nathan, L. G. R. Oliveira-Santos, K. A. Olson, B. D. Patterson, A. Paviolo, E. E. Ramalho, S. Rösner, D. G. Schabo, N. Selva, A. Sergiel, M. Xavier da Silva, O. Spiegel, P. Thompson, W. Ullmann, F. Zięba, T. Zwijacz-Kozica, W. F. Fagan, T. Mueller, and J. M. Calabrese. 2019. A comprehensive analysis of autocorrelation and bias in home range estimation. *Ecological Monographs* 89:e01344. <https://doi.org/10.1002/ecm.1344>
- Ofstad, E. G., I. Herfindal, E. J. Solberg, and B.-E. Sæther. 2016. Home ranges, habitat and body mass: simple correlates of home range size in ungulates. *Proceedings of the Royal Society B: Biological Sciences* 283:20161234. <https://doi.org/10.1098/rspb.2016.1234>
- Ontario Ministry of the Environment, Conservation and Parks. 2021. Eastern Whip-poor-will general habitat description (*Caprimulgus vociferous*). Government of Ontario, Ottawa, Ontario, Canada. <https://www.ontario.ca/page/eastern-whip-poor-will-general-habitat-description>
- Ontario Ministry of Natural Resources and Forestry, Provincial Mapping Unit. 2013. Ontario Wetlands. Ministry of Natural Resources and Forestry, Peterborough, Ontario
- Ottaviani, D., S. C. Cairns, M. Oliverio, and L. Boitani. 2006. Body mass as a predictive variable of home-range size among Italian mammals and birds. *Journal of Zoology* 269:317-330. <https://doi.org/10.1111/j.1469-7998.2006.00060.x>
- Parker, G. A., and W. J. Sutherland. 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Animal Behaviour* 34:1222-1242. [https://doi.org/10.1016/S0003-3472\(86\)80182-8](https://doi.org/10.1016/S0003-3472(86)80182-8)
- Peris, A., F. Closa, I. Marco, P. Acevedo, J. A. Barasona, and E. Casas-Díaz. 2020. Towards the comparison of home range estimators obtained from contrasting tracking regimes: the wild boar as a case study. *European Journal of Wildlife Research* 66:32. <https://doi.org/10.1007/s10344-020-1370-7>
- R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rand, G. J. 2014. Home range use, habitat selection, and stress physiology of Eastern Whip-poor-wills. Thesis. Trent University, Peterborough, Ontario, Canada.
- Rappole, J. H., and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62:335-337.
- Recalde, F. C., C. P. B. Breviglieri, M. F. Kersch-Becker, and G. Q. Romero. 2021. Contribution of emergent aquatic insects to the trophic variation of tropical birds and bats. *Food Webs* 29:e00209. <https://doi.org/10.1016/j.fooweb.2021.e00209>
- Rolando, A. 2002. On the ecology of home range in birds. *Revue d'Écologie (La Terre et la Vie)* 57:53-73. <https://doi.org/10.3406/rev.2002.2381>
- Schilke, P. R., M. Bartrons, J. M. Gorzo, M. J. Vander Zanden, C. Gratton, R. W. Howe, and A. M. Pidgeon. 2020. Modeling a cross-ecosystem subsidy: forest songbird response to emergent aquatic insects. *Landscape Ecology* 35:1587-1604. <https://doi.org/10.1007/s10980-020-01038-0>
- Seigle-Ferrand, J., K. Atmeh, J.-M. Gaillard, V. Ronget, N. Morellet, M. Garel, A. Loison, and G. Yannic. 2021. A systematic review of within-population variation in the size of home range across ungulates: What do we know after 50 years of telemetry studies? *Frontiers in Ecology and Evolution* 8:555429. <https://doi.org/10.3389/fevo.2020.555429>
- Sells, S. N., and M. S. Mitchell. 2020. The economics of territory selection. *Ecological Modelling* 438:109329. <https://doi.org/10.1016/j.ecolmodel.2020.109329>
- Sharps, K., I. Henderson, G. Conway, N. Armour-Chelu, and P. M. Dolman. 2015. Home-range size and habitat use of European Nightjars *Caprimulgus europaeus* nesting in a complex plantation-forest landscape. *Ibis* 157:260-272. <https://doi.org/10.1111/ibi.12251>
- Shipley, J. R., C. W. Twining, M. Mathieu-Resuge, T. P. Parmar, M. Kainz, D. Martin-Creuzburg, C. Weber, D. W. Winkler, C. H. Graham, and B. Matthews. 2022. Climate change shifts the timing of nutritional flux from aquatic insects. *Current Biology* 32:1342-1349.e3. <https://doi.org/10.1016/j.cub.2022.01.057>
- Skinner, A. A., S. N. Matthews, M. P. Ward, I. Souza-Cole, J. R. Wright, F. R. Thompson III, T. J. Benson, and C. M. Tonra. 2023. Eastern Whip-poor-wills have larger nonbreeding home ranges in areas with more agriculture and forest fragmentation. *Ornithological Applications* 125:duac050. <https://doi.org/10.1093/ornithapp/duac050>
- Souza-Cole, I., M. P. Ward, R. L. Mau, J. T. Foster, and T. J. Benson. 2022. Eastern Whip-poor-will abundance declines with urban land cover and increases with moth abundance in the American Midwest. *Ornithological Applications* 124:duac032. <https://doi.org/10.1093/ornithapp/duac032>
- Spiller, K. J., and R. Dettmers. 2019. Evidence for multiple drivers of aerial insectivore declines in North America. *Condor* 121:duz010. <https://doi.org/10.1093/condor/duz010>
- Spiller, K. J., and D. I. King. 2021. Breeding habitat associations of Eastern Whip-poor-wills in managed forests. *Journal of Wildlife Management* 85:1009-1016. <https://doi.org/10.1002/jwmg.22045>
- Spiller, K. J., D. I. King, and J. Bolsinger. 2022. Foraging and roosting habitat of Eastern Whip-poor-wills in the northeastern United States. *Journal of Field Ornithology* 93(1):6. <https://doi.org/10.5751/JFO-00057-930106>
- Stemle, L., B. B. Rothermel, and C. A. Searcy. 2022. GPS technology reveals larger home ranges for immature gopher tortoises. *Journal of Herpetology* 56:172-179. <https://doi.org/10.1670/20-128>
- Sweet, S. K., A. Asmus, M. E. Rich, J. Wingfield, L. Gough, and N. T. Boelman. 2015. NDVI as a predictor of canopy arthropod biomass in the Alaskan arctic tundra. *Ecological Applications* 25:779-790. <https://doi.org/10.1890/14-0632.1>
- Tonra, C. M., J. R. Wright, and S. N. Matthews. 2019. Remote estimation of overwintering home ranges in an elusive, migratory nocturnal bird. *Ecology and Evolution* 9:12586-12599. <https://doi.org/10.1002/ece3.5723>
- Tozer, D. C., J. C. Hoare, J. E. Inglis, J. Yaraskavitch, H. Kitching, and S. Dobbyn. 2014. Clearcut with seed trees in red pine forests

associated with increased occupancy by Eastern Whip-poor-wills. *Forest Ecology and Management* 330:1-7. <https://doi.org/10.1016/j.foreco.2014.06.038>

Traba, J., J. Gómez-Catasús, A. Barrero, D. B. la Rosa, J. Zurdo, I. Hervás, C. Pérez-Granados, E. L. G. de la Morena, A. Santamaría, and M. Reverter. 2022. Comparative assessment of satellite- and drone-based vegetation indices to predict arthropod biomass in shrub-steppes. *Ecological Applications* 32:e2707. <https://doi.org/10.1002/eap.2707>

Tuck, S. L., H. R. P. Phillips, R. E. Hintzen, J. P. W. Scharlemann, A. Purvis, and L. N. Hudson. 2014. MODISTools - downloading and processing MODIS remotely sensed data in R. *Ecology and Evolution* 4:4658-4668. <https://doi.org/10.1002/ece3.1273>

Twining, C. W., J. T. Brenna, P. Lawrence, J. R. Shipley, T. N. Tollefson, and D. W. Winkler. 2016. Omega-3 long-chain polyunsaturated fatty acids support aerial insectivore performance more than food quantity. *Proceedings of the National Academy of Sciences of the United States of America* 113:10920-10925. <https://doi.org/10.1073/pnas.1603998113>

Vala, M. A., G. W. Mitchell, K. C. Hannah, J. E. Put, and S. Wilson. 2020. The effects of landscape composition and configuration on Eastern Whip-poor-will (*Caprimulgus vociferus*) and Common Nighthawk (*Chordeiles minor*) occupancy in an agroecosystem. *Avian Conservation and Ecology* 15(1):24. <https://doi.org/10.5751/ACE-01613-150124>

Walton, Z., G. Samelius, M. Odden, and T. Willebrand. 2017. Variation in home range size of red foxes *Vulpes vulpes* along a gradient of productivity and human landscape alteration. *PLoS ONE* 12:e0175291. <https://doi.org/10.1371/journal.pone.0175291>

Wiken, E., F. Jiménez Nava, and G. Griffith. 2011. North American Terrestrial Ecoregions—Level III. Commission for Environmental Cooperation, Montreal, Canada. <https://www.epa.gov/eco-research/ecoregions-north-america>

Wilcox, K. A., M. A. Wagner, and J. D. Reynolds. 2021. Salmon subsidies predict territory size and habitat selection of an avian insectivore. *PLoS ONE* 16:e0254314. <https://doi.org/10.1371/journal.pone.0254314>

Wilson, M. D. 2003. Distribution, abundance, and home range of the Whip-poor-will (*Caprimulgus vociferus*) in a managed forest landscape. Thesis. College of William and Mary, Williamsburg, Virginia, USA.

Wilson, M. D., and B. D. Watts. 2008. Landscape configuration effects on distribution and abundance of Whip-Poor-Wills. *Wilson Journal of Ornithology* 120:778-783. <https://doi.org/10.1676/06-108.1>

Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized

linear models. *Journal of the Royal Statistical Society Series B: Statistical Methodology* 73:3-36. <https://doi.org/10.1111/j.1467-9868.2010.00749.x>

Zabel, C. J., K. McKelvey, and J. P. Ward. 1995. Influence of primary prey on home-range size and habitat-use patterns of Northern Spotted Owls (*Strix occidentalis caurina*). *Canadian Journal of Zoology* 73:433-439. <https://doi.org/10.1139/z95-049>



Appendix 1

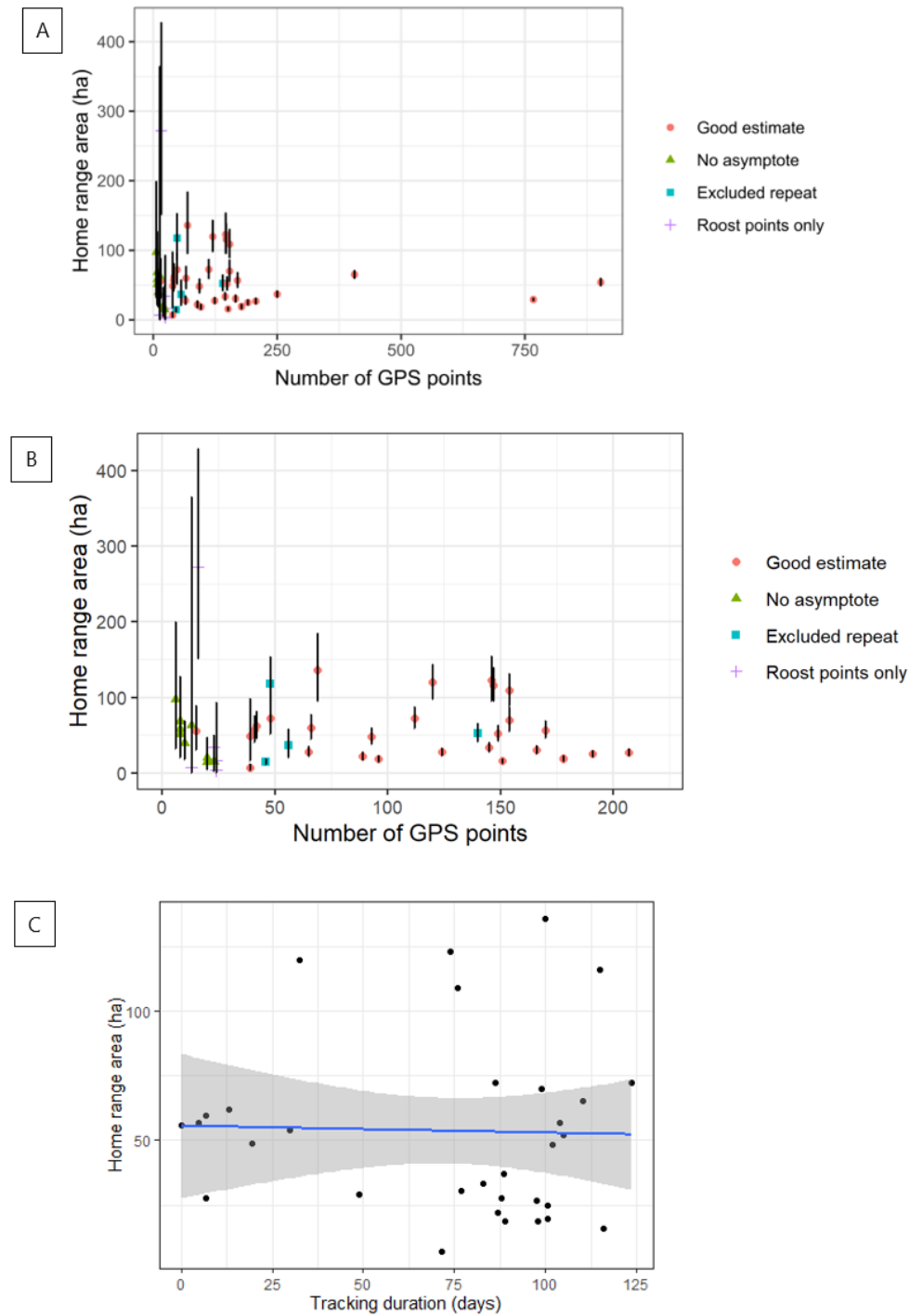


Figure S1. A and B show a comparison of mean home-range area estimates from tracking tags from this study ("good estimates") with estimates from test tracking tags with low sample sizes ("no asymptote" and "roost points only") that were not used in this study. "Excluded repeats" were the second home ranges estimated for repeat-tracked individuals, and not included in statistical analyses. A) all estimates; B) same data as in A, showing clearer view of estimates from tags with small sample sizes. C shows a lack of relationship between tracking duration and home range area.

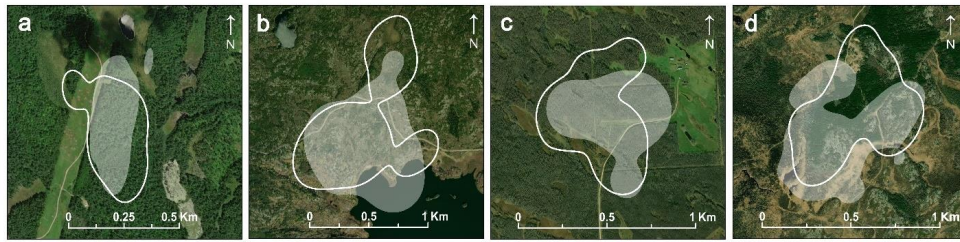


Figure S2. Repeat-tracking of four Eastern Whip-poor-wills (*Antrastomus vociferus*) over two breeding seasons estimated similar home-range size and location between tracking years one (white shaded) and two (solid white outline). Amount of overlap (and tracking years) were: a) 81% (2018 and 2019) for bird 123252703 in the Algonquin ecoregion, b) 68.5% (2018 and 2019) for bird 135268710 in the Northern Forest ecoregion, c) 75% (2018 and 2020) for bird ID 135268713 in the Plains ecoregion, and d) 65% (2019 and 2020) for bird 135268724 in the Northern Forest ecoregion.

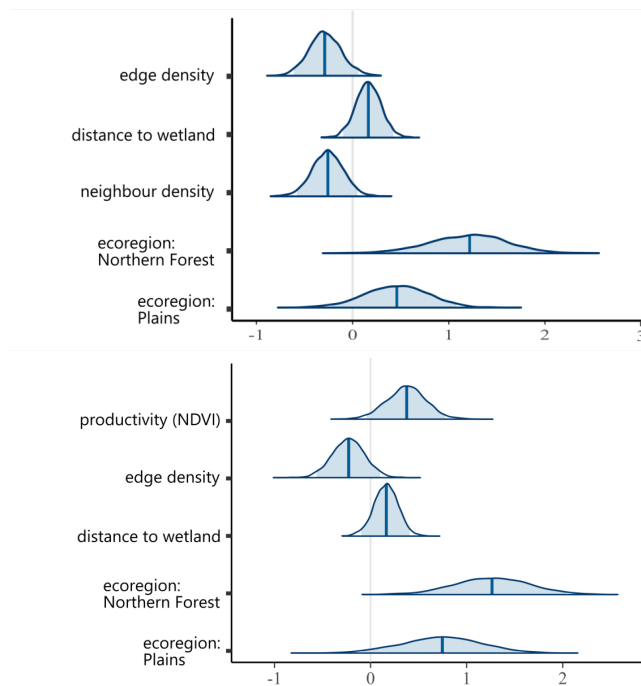


Figure S3. Results of models excluding a) NDVI or b) neighbour density.

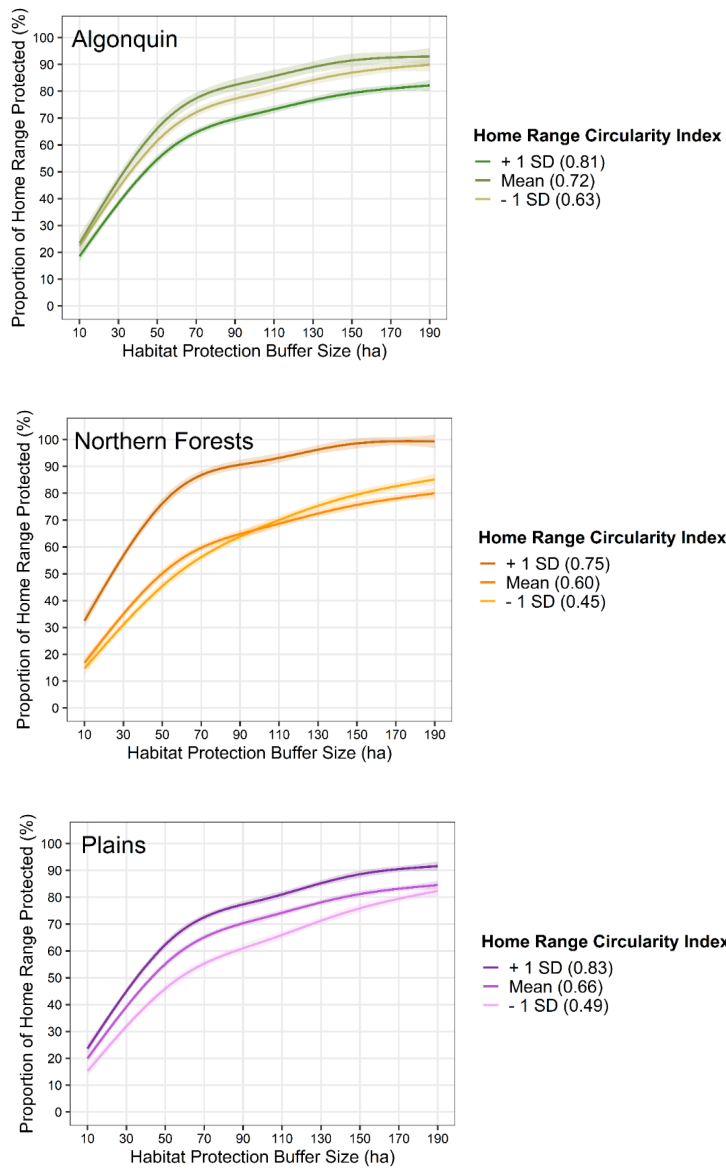


Figure S4. The moderating effect of circularity on required protection buffer size differed between ecoregions, because of variation in the relationship between home-range size and circularity. Moderator levels are at -1standard deviation (SD), Mean and +1SD home-range circularity index). A non-standard x-axis scale was chosen to ease comparison between commonly-used metrics for habitat protection areas for this species (e.g. 9 or 30 ha) and the average home-range size in this study (approximately 50 ha).

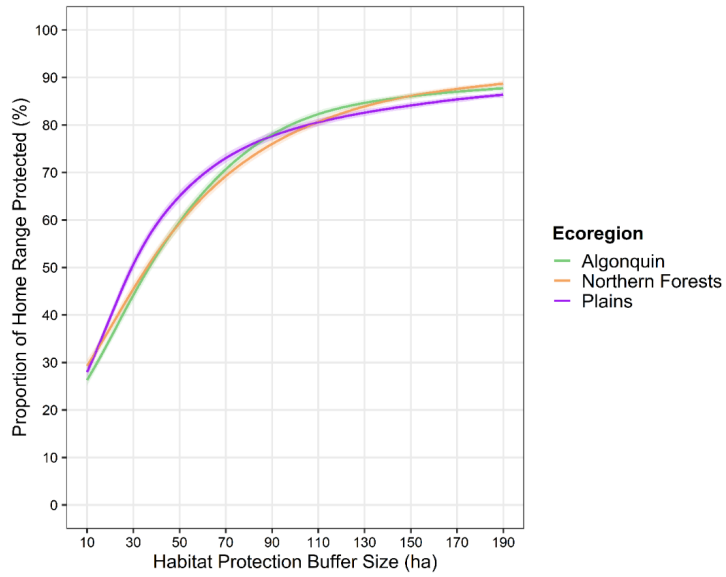


Figure S5. Results of a generalized additive model (GAM) predicting the proportion of home range protection (y-axis) achieved at a given habitat protection buffer size (x-axis) for the average Whip-poor-will home range in different ecoregions. A non-standard x-axis scale was chosen to ease comparison between commonly-used metrics for habitat protection areas (e.g. 9 or 30 ha) and the average home-range size in this study (approximately 50 ha).

Table S1. Datasets used to create a comprehensive wetland layer covering all study sites

Province	Dataset name	Data modification	Data originator	Data date range	Spatial resolution/scale	No. possible home ranges covered
Manitoba	Manitoba Wetland Inventory: Southern Peatlands 2013	excluded open water polygons	Manitoba Habitat Heritage Corporation (in partnership with Manitoba Sustainable Development, Manitoba Agriculture, and Ducks Unlimited Canada)	2013	Minimum mapping unit = 1 ha	9/16
Manitoba	1:20 000 scale Topographic Base Map series: Water Bodies	selected wetland features (marsh; swamp; quarry/pit (water); dugout (farm))	Manitoba Department of Conservation	1989-2002	1:20 000	7/16
Ontario	Ontario Wetlands (version 7)	removed 1 erroneous polygon ('unverified' in original dataset)	Ontario Ministry of Natural Resources and Forestry - Provincial Mapping Unit	1978-2013	Varies (1:10000 - 1:250000), depending on original source	15/15
Ontario	Forest Resources Inventory	Added (by union with Ontario Wetlands) OMS and TMS polygons that were not in the Ontario Wetlands dataset	Ontario Ministry of Natural Resources	2008 (NLF), 2007 (HR 2176 in Algonquin)	Positional accuracy generally within 10 m. Minimum polygon size for non-productive/non-forested areas = 1 ha	8/15