

**AN INVESTIGATION INTO THE HABITAT USE OF BARRED OWLS (*STRIX VARIA*)
IN RESPONSE TO URBANIZATION GRADIENTS**

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Abstract

Urbanization is a major threat to global biodiversity, with its effects being well-studied and multi-faceted. We captured Barred Owls (*Strix varia*) throughout the Virginia peninsula and tracked their habitat use with GPS loggers to understand how these owls are adapting to urbanization, especially in regards to highly variable roads. We were particularly interested to investigate if these highly variable roads were a limiting mechanism in diurnal owl habitat. Resource selection functions were fitted to diurnal and nocturnal schedules. The mean nocturnal home ranges were 48.76 ha, while mean diurnal home ranges were 23.95 ha. We found that owls avoid arterial roads during diurnal periods but avoid residential roads during nocturnal periods. Our findings highlight a need for wildlife biologists to further consider how all aspects of a studied landscape may differ, even among artificial structures.

Introduction

Over the past century, global biodiversity has been in decline at a rate that many ecologists argue would quantify as a sixth mass extinction in what is being deemed the “Anthropocene”, named after the fact this mass extinction event is caused by human action (Rull, 2022). While multifaceted, this loss in biodiversity is largely driven by changes in land use patterns that result in habitat loss for both plants and animals (Jaureguiberry et al., 2022). These changes in land use are often a result of expanding human settlements in a process that is known as urbanization. Urbanization’s impacts on global biodiversity have been well-studied, with effects including reducing populations (Fahrig, 2003) and increasing competition for resources (Pardini et al., 2018). Less talked about, is the ability for urbanization to facilitate the presence of

various species, such as the Barred Owl (*Strix varia*) (Bierregaard, 2018).

An increasing body of evidence suggests that Barred Owls, previously thought to prefer mature, mixed forests (Bierregaard, 2018; Haney, 1997) can thrive in urban environments. This idea may seem contradictory based on the “urban desert” idea of cities (Spotswood et al., 2021); however, many older suburban forests are old enough that they can share similar habitat structures to mature, rural forests that can thus facilitate their presence (Bierregaard, 2018). Additionally, a more diverse diet that encompasses rodents (Hindmarch & Elliott, 2015), birds, amphibians, and even occasionally fish (Bierregaard, 2018) allow Barred Owls to have predictable food sources across a variety of dynamic urban landscapes. Understanding how wildlife can adapt to urban systems will be crucial to combatting losses in biodiversity and promoting human-wildlife coexistence. Thus, due to their generalist lifestyle, wide spanning range, and ability to thrive in urban environments, makes Barred Owls a great model organism for understanding how wildlife can adapt to rapidly changing environments, and what challenges wildlife attempting adaptation to human disturbance may face. With 70% of global human populations expected to live within cities by 2050 (Eurostat, 2016), it is crucial that adaptation of wildlife to urbanization is studied so loss in biodiversity can be combated, and human-wildlife coexistence be promoted.

Despite an increasing body of knowledge of Barred Owl habitat use in urban systems, gaps in knowledge still exist. Roads are known to have some level of effect on owls in urbanized systems, whether it be directly through sources of mortality (i.e. car collisions, (Gagné et al., 2015), or indirectly through changed habitat use (Clement et al.,

2019; Clément et al., 2021). Barred Owls are unfortunately often struck by vehicles and seem to avoid available habitat near roads when that habitat is fragmented. While these discoveries do represent an advance in the knowledge of how roads impact habitat use, these studies largely simplify the true complexity of roads. The U.S. Census Bureau itself gives eight different classifications for what could colloquially be referred to as a “right of way for vehicles” that are based on the function and accessibility of the road (U.S. Census Bureau, 2025). Roads also exist in the context of their landscape. Not only will the existence of roads impact surrounding development of cities, underlying geography and geology will impact where the road gets constructed. This results in studies with conflicting results with Barred prefer (Irwin et al., 2018) and avoid using roads (Clément et al., 2021). The aforementioned studies both discuss the underlying geography of the area as an explanation as to why their studies found that Barred Owls either avoided or preferred using habitat near roads, but neither discuss the components of the road themselves. While these studies recognize that roads exist in the context of their landscape, they fail to recognize the variation that exists within the roads themselves. While it has been recognized that some road components, such as higher speed limits, can result in a higher number of vehicle collisions (Gagné et al., 2015), little has been investigated about how these variable roads may be influencing habitat selection.

Additionally, recent evidence suggests that diurnal habitat for owls may be limited, especially in urban environments (Jirinec et al., 2024), however the mechanism driving this limitation is unclear. One possible mechanism that is driving this limit is daytime traffic densities, especially considering the noise generated by high

traffic volume and the sensitivity of owls towards noise. Several detrimental effects of artificial noise have been observed for several species of owls, such as reduced vocalizations and reduced hunting success (Sordello et al., 2026). It is possible that vehicular noise has effects throughout the Barred Owls diel cycle, including limiting diurnal habitat when an owl would be attempting to rest.

We hypothesized that the mechanism limiting Barred Owl diurnal habitat is the noise generated from nearby roads. We predict that owls avoid using habitat near high-intensity roads during the day and are less avoidant of low-intensity roads. During the night, we also predict that when traffic intensity is lower, the effect size of road avoidance will be smaller for both arterial (high traffic volume) and residential roads (low traffic volume). We will test this by investigating third-order habitat selection using population-level resource selection functions (RSFs). RSFs function at the third-order of habitat selection, which investigates how resources within a given home range are used, relative to the availability of those resources (Johnson, 1980).

Methods

Territory Identification, Capture, and Processing of Owls

Barred Owl territories were identified through variety of ways. We identified territories through a combination of previously known occupied sites (Biggerstaff et al. *unpublished data*), personal communication with landowners, eBird sightings, and intuitive guesses on where owls were likely occurring. Capture sites were located in a variety of public and private locations throughout the urban-rural gradient, representing a gradient from a wildlife refuge to the William and Mary campus. All sites were accessed with

permission from relevant landowners and/or managers. Site locations ranged in location from Chickahominy National Wildlife Refuge in the northernmost site to the Mariner's Museum and Park for our southernmost site (Figure 1)

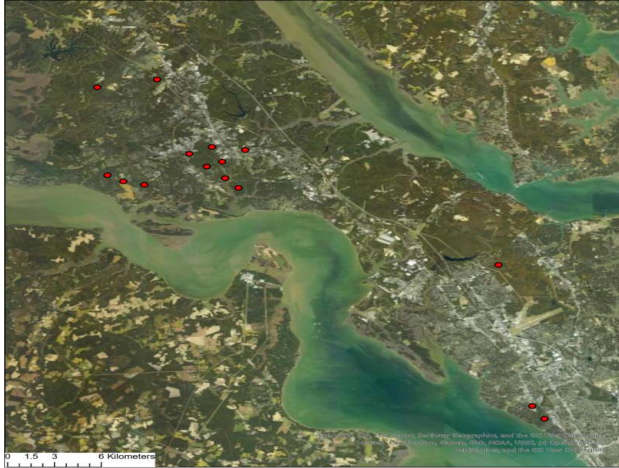


Figure 1: Map of Study Area. Red points are representative of approximate capture locations. Capture sites spanned throughout the Virginia peninsula.

Barred Owls were captured regularly throughout late April 2025 to the end of March 2026. All owls were captured using a combination of mist nets that were stacked vertically. Initially, we used two stacked 12x2.6m (127 mm mesh) nets (Avinet) with five shelves each but eventually upgraded to three stacked 12x2.6m (121mm mesh) Japanese nylon nets with three shelves. The Japanese nets were generally easier to work with as the reduced number of shelves generally had less entanglements, were less prone to “bounce outs” (owl hit the net, but was able to escape), and were easier to remove an owl from. Both setups were supported by an aluminum pole system that ranged 8 – 10m in height (Triple High Mist Net Pole System; Bat Conservation and Management, Carlisle, PA), dependent on existing vegetation at the capture location. To lure owls to net location, we played various conspecific, territorial vocalizations from a speaker array (JBL Xtreme 2

Bluetooth). These speakers were arranged so that one speaker was located underneath the net, and two others flanked each side of nets. Once the central speaker succeeded in luring an owl in, the flanking speakers would be alternated as the owl followed the vocalizations, until the owl eventually intercepted the net in the case of a successful capture event. During the breeding season (~mid-February to ~end of July), we would primarily target males for capture as females may be incubating and brooding in their nest. GPS data from a breeding female would thus more represent nest site selection rather than habitat selection across a home range. During the non-breeding season, females were captured in larger numbers as males were far less active and responsive to territorial challenges.

Once a Barred Owl was captured, we placed a hood over the head of the owl to relax the bird while we processed it. After hooding, we would use an ultraviolet light to identify molt patterns with ultraviolet light following Weidensaul et al. (2011). This allowed us to estimate the age of the owl. If a given owl was confirmed to be in its second year, it would be assumed to be a range resident, and we would continue processing the owl for GPS tracking. For owls that were old enough for tagging, we weighed them, measured their wing and tail, and affixed a numbered USGS aluminum lock-on band generally on the right leg. We outfitted each individual with a GPS/accelerometer logger (VHF-450, Lotek Wireless) (n=23). Loggers were affixed via a backpack-style harness consisting of an adjustable elastic fabric that would be custom fit to each individual (Bierregaard, 2014; Jirinec et al., 2024). To ensure independence, we would only tag one

owl of each pair, with exception of one pair wherein the tag for the initially captured male was lost, and the female was then tagged at a later date.

GPS-tags were programmed to take regular GPS fixes in 4-hour intervals, resulting in fixes occurring at 0:00, 04:00, 08:00, 12:00, 16:00, and 20:00 (GMT) or 19:00, 23:00, 03:00, 07:00, and 11:00 in local time (EST). As we were interested in habitat selection at times of high and low vehicle traffic periods and investigating if they influence nocturnal and diurnal habitat patterns, we later assigned any fixes that occurred at 23:00 and 3:00 to a low traffic period that roughly correlated to nocturnal habitat use, and all other fixes to the high traffic period that roughly correlated with diurnal habitat use. While this did result in a disproportionate sample size, we felt that we still had a sufficient number of fixes per owl, per period, that were sufficient for resource selection function analysis (RSFs).

Sex Identification

We determined the sex of owls through several different ways. Male and female Barred Owls have slightly different vocalizations, with females having relatively higher pitched calls that end with noticeable vibrato (Odom & Mennill, 2010). For most capture events, we could reliably sex owls by ear. If an owl was captured without vocalizing, or at least two owls of different sex were actively vocalizing before capture, we would sex the owls through morphology. When capture occurred during the breeding season, breeding females have large visible brood patch not present in males. If we were not confident that the captured owl was breeding, or the capture occurred outside of the breeding season, we would check morphometrics (body weight, wing and tail chords). Males tend to be noticeably smaller than females (Pyle, 1997), with sizes falling

outside of an overlapping range (Acker, 2020).

Owl GPS Data Processing

We used the *ctmm* R package to process and analyze the location data (Calabrese et al., 2016) in R version 4.5.2 (R Core Team, 2025). Tags were calibrated by leaving a stationary tag running for nine days using a representative schedule for a hypothetical owl to achieve a User Equivalent Range Error (UERE). Fixes were standardized across all tags (Fleming et al., 2020), resulting in an average GPS fix error of 10.4 m (95% CI 9.18-11.65). Overt outliers were removed by filtering out fixes that had egregiously large DOP (Dilution of Precision) values (≥ 20 DOP). This removed fixes that were likely unrepresentative of where an owl actually was in space. This error then informed an assortment of continuous-time movement models that were fitted to for each owl's diurnal and nocturnal datasets. Models were ranked according to lowest AICc values (Calabrese et al., 2016). The top-ranked model was then used to calculate a weighted autocorrelated kernel density estimator (AKDE), which helped to control for autocorrelation by assigning weights to each raster cell within the AKDE, based on the level of autocorrelation that occurred within the area (Fleming & Calabrese, 2017). Following this framework, we generated two home ranges for each owl, a diurnal home range and a nocturnal home range, at the 95% contour. A population level mean home range size was then estimated using *ctmm*'s *meta()* function for both types of home ranges (Fleming et al., 2022). This approach used a χ^2 -based meta-analysis over the traditional sample-means approach to estimate a population home range, with the former being generally better at handling uncertainties and small sample sizes.

Habitat Components and Resource Selection Functions (RSF)

To perform Resource Selection Function (RSF) analyses, we selected habitat components that could be analyzed at a landscape scale. As we were interested in how differences in the types of roads (and the traffic that they facilitate) may influence habitat selection, we wanted to have one covariate that looked at distance to local roads and another covariate that looked at distance to arterial roads. We also wanted to include biologically relevant variables that are known to positively influence Barred Owl habitat use. Water proximity has been shown to be important for Barred Owls, as streams and riparian areas can provide access to aquatic prey such as crustaceans and amphibians (Livezey, 2007). In urbanized areas, these aquatic resources have been shown to help facilitate owl habitat use near roads (Clément et al., 2021), making water proximity an especially important variable in this analysis. Road and water resource vector files were obtained from TIGER/Line Geodatabase (U.S Census Bureau, 2024). Arterial roads were obtained by classifying S1200 and S1400 road classes together while residential roads were obtained by classifying S1100 roads by itself (U.S. Census Bureau, 2024). Additionally, we had several storm retention ponds that were capable of supporting amphibians near several of our owls' home ranges. To include these, we used a publicly available landcover dataset (1 m resolution), extracted all water features, and combined them with the previous layers so that small retention ponds would be included (Virginia Department of Environmental Quality, 2025). All layers were re-sampled to the 10-m cell size so that they would match the error of our tags (10.4m).

The *ctmm* package allows for integrated RSFs that help to control for autocorrelation

and missing data that may occur within certain parts of an animal's home range (Alston et al., 2023), using the AKDEs that generated aforementioned home ranges. We specifically used the `rsf.select()` function, which used model selection on multiple habitat covariates and allowed for better conditioning of covariance matrices when calculating a population RSF model. RSF models were fit twice to each owl using standardized rasters, once for each day and night period. These models were integrated using a Riemann integrator (Alston et al. 2023) as opposed to the default Monte Carlo due to computational and time constraints. Due to data availability, only 15 of the 23 tracked owls' data were analyzed for the RSF analysis, as the full sampling schedule had not finished for seven of the owls at time of writing, and one owl had raster alignment issues within their home range that could not be resolved at this point.

Results

Of the 15 owls (10 females, 5 males) included in our RSF analysis, a total of 4,445 successful fixes were taken with a mean of 298.25 ± 57.36 SD locations per bird. Mean fixes per bird for the nocturnal schedule were 103.38 ± 21.05 while diurnal schedules were 194.86 ± 36.91 . Nocturnal home ranges were larger on average (47.86 ha, 95% CI: 36.72-60.81 ha) than diurnal home ranges (23.95 ha, 95% CI: 17.38-32.18 ha) (Figure 2). RSF model outputs differ by schedule as well. For the nocturnal population RSF model, distances to residential roads were significant (95% CI did not overlap zero) and positively associated owl habitat selection, but not significant for the diurnal schedule. Distance to arterial roads were significantly and positively associated with selection for the diurnal schedules, but not for nocturnal schedules. For both schedules, distance to water was significant and negatively

associated with selection (Table 1).

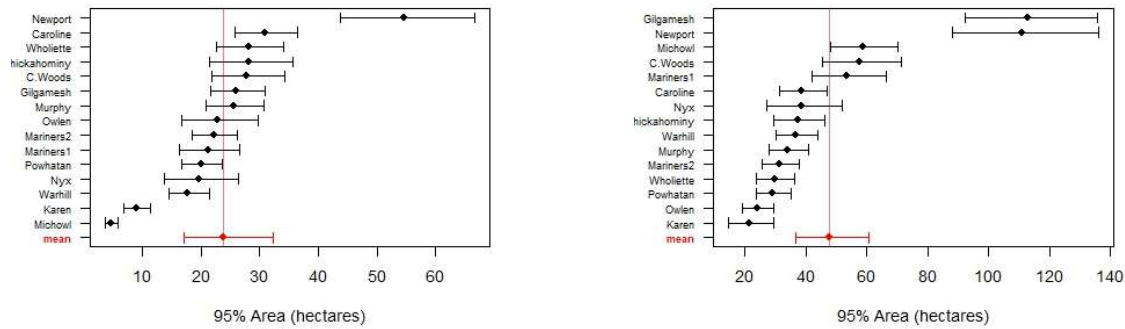


Figure 2 Comparison of Diurnal and Nocturnal Home Ranges. Meta-analysis tree plot of diurnal (left) and nocturnal (right) home ranges. Home ranges are organized with largest home ranges at the top (n=15)

Table 1 Diurnal and Nocturnal Population RSF outputs. Asterisk denotes significance of covariate. Negative association with distance indicates attraction towards a resource while positive association indicates aversion. Above table represents population RSF model outputs for the diurnal and below table represents population RFS model output for the nocturnal pattern.

	Low 95%	Estimate	High 95%
Residential Road Proximity	-9.83e-03	1.18e-03	7.45e-03
Arterial Road Proximity*	1.92e-03	1.55e-03	2.93e-02
Water Proximity*	-9.76e-03	-8.15e-03	-6.55e-02
	Low 95%	Estimate	High 95%
Residential Road Proximity*	5.96e-04	6.46e-03	1.23e-02
Arterial Road Proximity	-1.78e-03	1.23e-03	4.24e-04
Water Proximity*	-9.81e-03	-7.05e-03	-4.28e-04

Discussion

We found evidence of support for our hypothesis that owls discriminate between different functional types of roads, albeit with marginal effects. Owls avoid habitat

near arterial roads during high traffic conditions to some degree, suggesting that, when an owl is roosting during the day, they will try to avoid habitat near busy roads. The noise generated from these roads limit what would otherwise be desirable habitat. Owls

are animals that are highly sensitive to noise (Sordello et al., 2026), and high noise during the day may cause them to avoid certain tracts of habitat, even when not actively trying to hunt for prey. For nocturnal habitat selection, when traffic volumes are lower, owls do not maintain this aversion to arterial roads and will use the habitat according to availability. Interestingly, during low traffic periods owls select against residential roads, even though traffic on residential roads will almost always be much lower than an arterial road, at any given time. This result may instead reflect an aversion to edge habitat, rather than the roads themselves, which is supported with similar research (Clément et al., 2021; Jirinec et al., 2024). It is possible that some interaction exists between selection of roads of various types and the degree of urbanization that exists within a home range, but this was not tested for in our models. I will explore these options in my final analysis.

These results, while preliminary, are clearly limited. Unfortunately, several issues occurred whilst fitting models to owls that forced us to drop important habitat variables such as forest proximity and distance to forest edge. Using the Riemann integrator for the *ctmm*'s package *rsf* function requires habitat rasters to have the same resolution (Alston et al., 2023; Calabrese et al., 2016). Despite our best efforts, we could not get the package to recognize that forest-related rasters were aligned and instead we had to compromise by only looking at the road-related rasters and the water proximity raster. The Montecarlo integrator would have avoided raster alignment issues, but this integrator would take much longer to

run (over 24 hours, per individual-level model) and would often have errors with RAM limitations, despite a function that is supposed to be built into the package to deal with RAM issues. Ideally, we also would have included a forest height raster and a understory canopy density raster, which have been shown to be of importance (Clement et al., 2019; Jirinec et al., 2024; Livezey, 2007) the Lidar data required to produce these layers for our study area was outdated (~13 years for some owl home ranges) and would have not been wise to use. Our raster layers that use distance to arterial and local roads are a proxy that stands in for traffic volume/density. While the state of Virginia does provide state-wide annual average daily traffic data for many roads (Virginia Department of Transportation, 2025), it is not spatially seamless for third-order habitat selection analysis, as many roads within our owls' home ranges were missing these data. Using this would also require using a moving window, which the proper size to use at the third-order habitat selection level, would be unclear.

Future directions for this project will attempt to include raster layers into population models so that models better reflect available habitat throughout an owl's home range. While running these models, the Virginia Lidar database was updated with 2024 Lidar (Virginia Department of Emergency Management, 2024) data for much of our study area, allowing us to include forest height and canopy understory density in the future studies. While marginal, our research does indicate that road types (and thus the levels of traffic that

they may facilitate) are discriminated against by Barred Owls. Not all roads are seen as equal for owls, and how owls select habitat near these roads changes throughout their diel cycle.

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