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Avian Behavior, Ecology, and Evolution

Use of space by urban Loggerhead Shrikes (*Lanius ludovicianus*) as a window into habitat suitability

Uso del espacio por alcaudones americanos (*Lanius ludovicianus*) urbanos como una ventana a la idoneidad del hábitat

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ABSTRACT. Wild animals in urban environments face new challenges that may change how they use space and, at the same time, how they use space provides clues to suitability of habitat: bird territories in desirable areas tend to be smaller and populations denser. Loggerhead Shrikes (*Lanius ludovicianus*), historically associated with shortgrass habitats such as pasture and shrub steppe, occur widely in urban areas of the southeastern United States. For a complete picture of shrike use of space in urban spaces, we present three measures for a population inhabiting urban areas of Horry County, South Carolina: population density, home range size, and nest spacing. We maintained an individually banded population of shrikes in a core 8.4 km² study area of occupied shrike habitat within a larger 19.8 km² monitored area. We estimated breeding season, non-breeding season, and year-round home range sizes by mapping perch locations of 38 banded shrikes throughout the year. We used records of 142 nests to calculate distance to nearest neighboring nest. Over a three-year period, the 8.4 km² core area supported 6.9 shrikes/km². The extended monitored area supported 2.9 shrikes/km². Year-round home range estimates averaged 2.5 ha, and breeding and non-breeding home range sizes did not differ. Median distance to nearest active nest for 85 focal nests was 354 meters (range 43–1751 m). Comparisons of these metrics with other published studies indicate that shrikes in this urban area are at higher densities, maintain smaller home range sizes, and nest more closely to their neighbors than their rural conspecifics, indicating that urban areas likely provide richer resources for Loggerhead Shrikes than rural areas.

RESUMEN. Los animales silvestres enfrentan nuevos desafíos en entornos urbanos que pueden cambiar la forma en que utilizan el espacio y, al mismo tiempo, evaluar cómo utilizan el espacio proporciona pistas sobre la idoneidad del hábitat: los territorios de las aves en áreas deseables tienden a ser más pequeños y las poblaciones más densas. *Lanius ludovicianus*, una especie históricamente asociada con hábitats de pastizales cortos como pasturas y estepas arbustivas, está presente en amplias áreas urbanas del sureste de Estados Unidos. Para obtener una imagen completa del uso del espacio por parte de *L. ludovicianus* en áreas urbanas, presentamos mediciones de tres variables para una población que habita en áreas urbanas del condado de Horry, Carolina del Sur: densidad de población, tamaño del área de acción y espaciado de nidos. Se anillaron los individuos de una población de *L. ludovicianus* en un área de estudio núcleo de 8,4 km² con hábitats ocupados por la especie dentro de un área monitoreada más extensa de 19,8 km². Se estimó el tamaño del área de acción durante las temporadas reproductiva, no-reproductiva, y durante todo el año mediante el mapeo a lo largo del año de la ubicación de las perchas de 38 individuos anillados. Se utilizaron registros de 142 nidos para calcular la distancia al nido activo más cercano. Durante un período de tres años, el área núcleo de 8,4 km² presentó una densidad de 6.9 individuos/km². El área monitoreada, de mayor extensión, presentó una densidad de 2,9 individuos/km². Las estimaciones del tamaño del área de acción durante todo el año promediaron 2,5 hectáreas, y los tamaños del área de acción durante la temporada reproductiva y no-reproductiva no difirieron. La distancia mediana al nido activo más cercano para 85 nidos focales fue de 354 metros (rango 43–1751 m). Comparaciones de los valores de estas variables con otros estudios publicados indican que los individuos en esta área urbana presentan densidades más altas, tamaños de área de acción más pequeños y anidan más cerca de sus vecinos que sus congéneres rurales, lo que indica que las áreas urbanas probablemente proporcionan más recursos para *L. ludovicianus* que las áreas rurales.

Key Words: *Home range size; Lanius ludovicianus; Loggerhead Shrike; nest spacing; population density; urbanization*

INTRODUCTION

Understanding the use of space by individuals provides insight into the ecology of populations. Home range sizes usually vary inversely with local resource availability; amidst abundant and predictable resources, individuals can meet their needs in a smaller space, and individuals with smaller home range sizes can be healthier and produce more offspring (Yosef and Grubb 1992, Schradin et al. 2010, Spencer 2012, Pfeiffer and Meyburg 2015). Spatial ecology in a novel environment may therefore provide clues into how a species is responding to that environment.

The conversion of wildlands into human-dominated environments poses unique challenges to, and sometimes opportunities for, wildlife. Urban areas are associated with biotic homogenization, high rates of pollution, changes in prey availability, habitat fragmentation, increases in impervious surface coverage, increased road mortality, vegetative cover change, and increased presence of non-native biota (Goldstein et al. 1986, Flickinger 1995, Collins et al. 2000, McIntyre 2000, Mumme et al. 2000, McKinney 2002, 2006). Responses to urbanization are highly dependent upon the interaction of a given species' life history with land use. Whereas some species are

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intolerant of urbanization, others are able to take advantage of resources presented by urban environments (McKinney and Lockwood 1999, Callaghan et al. 2019a, 2019b). Better understanding how animals use urban spaces may provide insights into how a given species is responding to those challenges and opportunities.

Loggerhead Shrikes (*Lanius ludovicianus*), hereafter shrikes, are one of two shrike species native to North America. Shrikes are sit-and-wait predators of invertebrates and small vertebrates (Craig 1978, Bohall-Wood 1987) in open landscapes with sparse, short vegetation (Pruitt 2000). Along with many grassland birds, shrikes have experienced a dramatic population decline: their abundance decreased by 74% in North America between 1970 and 2014 (Rosenberg et al. 2016). In much of their range, shrikes use naturally occurring open landscapes such as prairies (Collister and Wilson 2007), shrub steppe (Woods and Cade 1996), grasslands (Stanley et al. 2012, Smallwood and Smallwood 2021), and longleaf pine (*Pinus palustris*)-wiregrass (*Aristida stricta*) ecosystems (Engstrom et al. 1984). However, in eastern North America, most shrikes depend on shortgrass habitats that are maintained by humans either directly (as by mowing) or indirectly (by allowing cattle grazing). Most eastern shrikes are found in and near agricultural areas such as fallow fields and pastureland which mimic grassland types maintained elsewhere by arid climate or fires (Gawlik and Bildstein 1990, Telfer 1992, Collister 1994, Yosef and Grubb 1994, Froehly et al. 2020, Donahue et al. 2021). Shrikes also use developed and urban areas where mowing and other human activity create a mix of short grass and bare ground. Shrikes have been documented dwelling within developed or urban areas in eight states, of which seven are in the southeastern U.S. coastal plain: Florida (Grubb and Yosef 1994), Louisiana (Worm and Boves 2019), North Carolina (McNair 2015), South Carolina (Krauser and Hill 2023), Alabama, Georgia, and Texas (Eastern Loggerhead Shrike Working Group, 2019, *personal communication*). The number of shrikes inhabiting urban areas is poorly known, but urban shrikes could account for a large proportion of the total population in some southeastern states. Only three studies have investigated shrikes living in a predominantly urban environment (Boal et al. 2003, Hill et al. 2023, Krauser and Hill 2023), and none of these investigated use of space in detail.

Territory size can indicate habitat quality. As sit-and-wait predators, perches play an important role in the foraging behavior of shrikes. When the number of hunting perches in shrike home ranges was experimentally increased, the resulting home range sizes decreased by 76% (Yosef and Grubb 1994). Those shrikes that maintained smaller territories had greater fledging success and fledged more young (Yosef and Grubb 1994). When the insect prey base within a home range was decreased as a result of fertilizer application, shrikes increased home range size by an average of 138% (Yosef and Deyrup 1998). Perhaps due to lower prey availability in winter, shrikes in Kentucky expanded their home ranges substantially in the non-breeding season (O'Brien and Ritchison 2011).

Because animals gravitate to areas with resources that allow them to succeed, population density can also be an indicator of habitat suitability. Because habitat for most species is patchily distributed, it is useful to think of population density at multiple scales. One can measure the density within patches of occupied habitat, which provides information about the biology of the species such as how territory defense may set an upper limit on local density. An ideal study design to measure avian population density at a local scale is to have individually marked birds and mapped territories because sampling techniques such as point counts and transects, where individuals are not identified, are less precise and can introduce substantial errors (O'Donnell et al. 2019). Alternatively, to estimate population size in a larger region, the favored class of methods include randomly or systematically chosen sample points across that entire region (Newell et al. 2013, Sauer et al. 2019), an approach that is superior for estimating regional population size but that provides less information about the life history of birds in occupied habitat.

We studied population density, home range size, and nest spacing of resident shrikes in an urban area of the coastal plain of South Carolina to test the hypothesis that urban spaces in this area provide habitat for the species. Our specific objectives were to (1) estimate the population density of shrikes in an urban environment, (2) map and quantify resident shrike home ranges, (3) determine whether shrikes maintain different home range sizes between breeding and non-breeding seasons, (4) quantify the spatial distribution of shrike nests as another measure of density, and (5) compare these estimated densities, home range sizes, and nest spacings to published accounts from shrikes in non-urban areas in the same region. Presenting multiple metrics allows for easier comparisons with past and future studies as spatial ecology methods develop (Anich et al. 2009), so we employed multiple methods to estimate home range size. Our main focus in this study is shrike density within occupied habitat, but for greater comparability with more extensive studies of shrikes elsewhere (e.g., McNair 2015, Smallwood and Smallwood 2021), we also measured density of a larger area that surrounds and contains the core marked population.

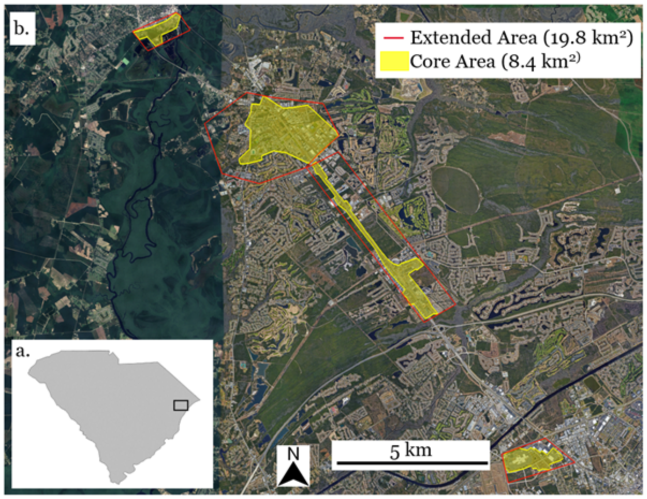
METHODS

Study area, study duration, banding, and monitoring

This study was conducted between 2019 and 2022 along the Highway 501 corridor from Conway to Myrtle Beach in northeastern South Carolina (approximately 33.84°N, 79.°W—33.71,78.92°W; Fig. 1). The area has a warm and humid climate and no measurable snow in most years. Annual daily maximum temperatures average 24 °C, daily minimums average 12 °C, and overall average annual temperature is 18 °C. The area receives an average of 140 cm of precipitation fairly evenly divided amongst months (South Carolina State Climatology Office 2024). Land along this highway corridor is mostly developed, consisting of strip malls, housing developments, and industrial parks, with residential neighborhoods, river floodplain, and pine and mixed woods also nearby. According to the National Land Cover Database, the most common land cover types in 50 km² of highway corridor that surrounds and contains our study area are (most abundant first) woody wetlands, developed/open space, developed/low intensity, developed/medium intensity, evergreen forest, and developed/high intensity, with the four developed categories making up 60% of the total area (United States Department of Agriculture 2023).

Shrikes in this area are non-migratory. To study population dynamics, we had previously established a study population in four subareas, totaling 8.4 km², where shrikes were regularly detected,

Fig. 1. A. Map showing study location in Horry County within the coastal plain in the northeastern portion of South Carolina, USA. B. Map of the core study area (shaded) and extended areas monitored for Loggerhead Shrikes (*Lanius ludovicianus*; outline) within Horry County, South Carolina.



hereafter, the core area (Fig. 1). In this core area during 2018 and 2019, we trapped and color banded all adult shrikes, using drop-in traps with live mice (protected in an inner wire mesh cage) as lures. Captured adult shrikes were banded with a United States Geological Survey numbered stainless steel band and a unique combination of three plastic wrap-around color bands (Haggie Engraving, Crumpton, Maryland, USA) melted closed using a battery-powered soldering iron. From 2019 on we monitored the core area year-round, visiting each territory on foot twice monthly and reading color band combinations with spotting scopes or cameras with telephoto lenses. We trapped any unbanded shrikes as soon as possible after they first appeared. For 31 unbanded birds that arrived in the core from late 2019 through 2020, median time from first detection to capture and banding was 8 days (new arrivals were readily recognized when they appeared among known banded shrikes in the core). During the period in which data were gathered for this study, an average of 93% of birds were color banded in the core and the few remaining unbanded birds were known as individuals from location and behavior (as in the trap-shy unbanded male paired to banded female eabm at the Water Tower territory). Because tracking movements and emigration of banded shrikes was a major goal of the population study, we also monitored a larger area surrounding the core areas, totaling an additional 11.4 km² and making our total monitored area, hereafter the extended area, 19.8 km² (Fig. 1). Monitoring of the roads, woods, fields, and neighborhoods making up the extended area outside the core was less intensive than in the core, but we regularly drove roads, scanning open areas that might be attractive to shrikes, including fields in which we had never seen territorial shrikes. We also followed up on shrike reports in the extended area that came to us through an active local birding community or that were reported to eBird (Cornell Laboratory of Ornithology, http://www.ebird.org). If a shrike was found in the extended area and remained a month or more, it was usually detected multiple times because of shrike's use of conspicuous perches, giving us confidence that we detected nearly all shrikes in the extended area, though transient birds likely moved through undetected. Shrikes do not use river bottomlands, swamps, or unbroken woods; therefore, we did not monitor those areas. The six most common land cover types in the monitored areas were identical to those listed above for the broader Highway 501 corridor, but because we excluded swamps and dense woods from monitoring efforts, the proportions were different. In particular, the four developed land cover types made up 78% of the extended area and 98% of the core. In the core area, shrike territories were most often in less developed, grassy parts of commercial or industrial parks, or in quite intensive developments, like Walmart parking lots, as long as there was a grassy verge nearby. They nested most often in trees or shrubs lining or within parking lots associated with stores, businesses, or a large mall, but also in a cemetery, on college campuses, and on a disc golf course.

Population density

We calculated density for both our core area and for the extended area. All sightings of banded shrikes were recorded in a database, and we also created monthly maps of the core showing all shrike territories. These maps included all the banded and unbanded shrikes we observed. We calculated the shrike population size by combining the number of banded adult shrikes present during each month (from the resightings database) with the number of unbanded shrikes recorded on the respective monthly maps. The population of shrikes varied over time, and we recorded the extremes, but for simplicity we calculated density for the average population size from September 2019–July 2022. All analyses were conducted in R version 4.2.1 using RStudio version 2022.7.2.576 (R Core Team 2022). All averages are presented with standard deviation unless otherwise noted. Home range sizes are presented in hectares and population density is presented in shrikes per square kilometer throughout.

Home range

We estimated size of home ranges from November 2020–July 2021. This timeframe encompassed both non-breeding (1 November–15 March) and breeding (16 March–25 July) seasons. After identifying an individual using its unique color band combination, we recorded locations of perches it used with 5 m or better precision by finding the perches on aerial imagery from Google Earth and Google Maps (Google, Inc., Mountain View, California, USA). Most perches were located to much finer than 5 m precision because individual signs, telephone poles, trees, and other perches in open areas were readily identifiable on aerial imagery. We recorded locations from each bird on multiple different days, and we recorded multiple locations per visit as the shrike foraged and changed locations. We did not approach close enough to flush shrikes when recording locations. Our criterion to include a bird in home range analyses was 20 locations within the time frame being analyzed.

We constructed 95% and 100% minimum convex polygons (MCP) as well as 50% kernel density estimators (KDE; Mohr 1947, Seaman et al. 1999). We chose to use the 50% KDE isopleth because larger isopleths tend to overestimate home range by incorporating unusable areas unique to urban areas, such as centers of rooftops and large highways. For minimum convex polygons, we used the function mcp.area of package adehabitatHR to estimate the size of each shrike's home range (Calenge 2006). We used kernelUD to visualize KDEs and kernel. area to calculate the area encompassed by the kernel density estimators. The h_{ref} smoothing parameter for the kernel density estimator was used to prevent overestimation of home range size (Seaman et al. 1999). If a bird relocated to a different territory within a season, it was excluded from analyses. A relocation to a different territory was indicated by a move > 0.5 km from previous sightings with no resightings between the two territories (this distance is approximately equal to twice the diameter of average home range size). Wilcoxon Rank-Sum tests were used to compare home ranges between breeding and non-breeding season.

Nest spacing

During the 2019, 2020, and 2021 breeding seasons, observers monitored the banded population of shrikes in the core area for signs of nesting activity (e.g., courtship feeding, nest-building, or adults carrying food to nests). Nests were most often found by observing a parent that disappeared into a tree or shrub, but sometimes nests were found by an intensive search of potential nest trees in a territory. We estimated that we found 95% of nesting attempts that resulted in at least one egg laid (C. Hill, *unpublished data*). After a nest was found, observers recorded coordinates of the nest with 1–2 m precision using aerial imagery from Google Earth and Google Maps (Google, Inc., Mountain View, California, USA). Nest stage was determined using behavioral observations and a camera on an extendable pole. Observers estimated chick age and inferred hatch date using images taken of nest contents. Nests were visited at least twice a week until they failed or nestlings reached 12 days of age.

We measured nest spacing as the distance between nests and their closest active neighboring nest. Because breeding pairs of shrikes at the latitude of South Carolina nest multiple times per breeding season (Gawlik and Bildstein 1990), we randomly selected one focal nest per breeding pair per year to include in nearest nest analysis. We measured the distance between focal nests and the closest contemporary nest on another territory, with contemporary defined as nests whose hatch date was within 55 days of the focal nests' hatch date, because 55 days is the approximate duration of one successful nesting attempt (Yosef 2020).

RESULTS

Population density

Between September 2019 and July 2022, adult population of the core averaged 57 shrikes (range: 42–78) and the extended area contained those same shrikes plus an average of 1.3 (range: 0–2) additional territorial shrikes. Shrike density in the core averaged 6.9 shrikes per km² and in the extended area 2.9 shrikes per km², with minor variation among years (Table 1).

Home range sizes

We recorded 2084 perch locations of shrikes, 938 in the non-breeding season and 1146 in the breeding season. For 38 birds we obtained more than 20 locations (mean ± SD: 41 ± 14). We obtained the locations for each bird during 8-39 observation days; we recorded 2.1 ± 1.7 locations per territory visit. Of those 38 birds, 24 had sufficient observations (mean 30 ± 11) during the breeding season to calculate breeding season home range and 19 had sufficient observations (mean 29 ± 5) during the non-breeding season. Eleven birds had sufficient observations during both breeding and non-breeding seasons. Three birds moved to new territories between seasons and were included for within-season territory measurements but excluded from the year-round analysis. Average home ranges ranged from 1.6–6.1 ha depending on method of quantification and season (Table 2). We found no significant difference between breeding and non-breeding home range sizes using either MCP or KDE. Year-round home ranges were significantly larger than breeding home ranges when calculated with MCP (p = 0.0005). We judged the KDE estimator to be the best reflection of actual shrike home range because it was more successful at avoiding unusable space by taking into account use of areas rather than drawing straight lines from one used perch to another. However, we also present MCP to facilitate comparisons with studies using that method.

Table 1. Population density of urban Loggerhead Shrikes (*Lanius ludovicianus*) in the coastal plain of South Carolina during four years (shrikes/km²).

Study area	2019	2020	2021	2022	Average
Extended area (19.8 km²)	3.2	3.2	2.8	2.6	2.9
Core area (8.4 km²)	7.6	7.6	6.6	6.1	6.9

Table 2. Average home range size of urban Loggerhead Shrikes (*Lanius ludovicianus*) in the coastal plain of South Carolina using 95% and 100% minimum convex polygons and 50% kernel density estimators. Home ranges presented in hectares ± SD.

Season	N	95% MCP	100% MCP	50% KDE
Breeding (16 March–July)	24	1.9 ± 1.5[†]	2.9 ± 2.1[†]	1.6 ± 1.4
Non-breeding (November–15 March)	19	2.5 ± 1.6	3.6 ± 2.4	2.0 ± 1.4
Year-round	38	3.3 ± 2.0[†]	6.1 ± 6.7[†]	2.5 ± 2.7

[†] Year-round home ranges estimated by minimum convex polygons (MCP) were significantly larger than breeding territories (100% MCP: W = 240.5, p = 0.002; 95% MCP: W = 218, p = 0.0005); all other seasonal comparisons were not statistically significant.

Nearest nest

For 85 focal nests (2019: 21 nests, 2020: 31 nests, 2021: 33 nests), the median distance to the closest contemporary nest was 354 meters (range 43–1751 m; Fig. 2).

DISCUSSION

In contrast with shrikes in other regions, where shrikes avoid developed areas, shrikes in our study area readily used urban landscapes, where they maintained small home ranges, high population density, and close nest spacing. Many species have been documented altering their behavior and constricting their home ranges as a response to urbanization (O'Donnell and delBarco-Trillo 2020). Below, we compare use of space in the studied shrike population to those of other shrike populations in more rural or wild landscapes. We then speculate on why these urban shrikes maintained such stable and small territories, and what characteristics of the urban landscape in the study area made

Fig. 2. Boxplot of internest distances between neighboring active Loggerhead Shrike (*Lanius ludovicianus*) nests.

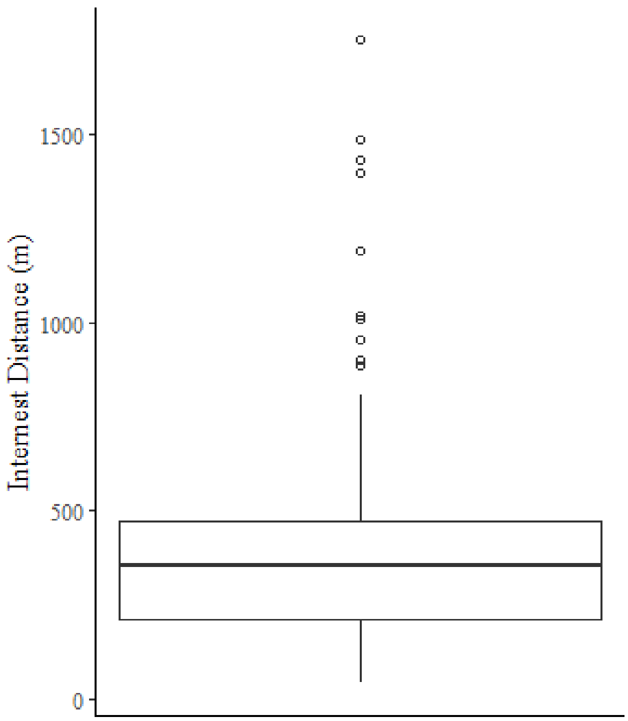


Table 3. Estimated Loggerhead Shrike (*Lanius ludovicianus*) home range sizes in ten studies, all on non-urban populations. All previous estimates of home range, regardless of season or method, were larger than comparable estimates from this study (see Table 2).

Location	Area (ha)	Season	Method	Study
Missouri	4.6	Breeding	Not given	(Kridelbaugh 1982)†
New York	6.7	Breeding	Not given	(Novak 1989)†
California	7.7	Breeding	100% MCP	(Lynn et al. 2006)
Alberta	8.5	Breeding	95% MCP	(Collister and Wilson 2007)
Florida	9.6	Non-breeding	100% MCP	(Yosef and Grubb 1994)
Arkansas	13.4	Non-breeding	100% MCP	(Donahue 2020)
Montana	8-25	Breeding	Not given	(Pruitt 2000)
Virginia	17.5	Non-breeding	95% MCP	(Blumton 1989)
California	34	Breeding	Not given	(Scott and Morrison 1990)†
Kentucky	85.0	Non-breeding	100% MCP	(O'Brien and Ritchison 2011)

†As given in Yosef 2020.

it so attractive to shrikes. Urbanization is widely regarded as having a negative effect on wildlife, but living in grassland-mimicking urban areas may have no effect on population densities of some grassland specialist bird species (e.g., Buxton and Benson 2016). We consider what effect urban living in shrikes might have on shrike population trends.

Home range size varies with resource availability and habitat quality (Buchmann et al. 2011, Diemer and Nocera 2014). Shrike home ranges estimated in this study were smaller than all previous estimates regardless of method used (Table 3). This reduction in home range size is consistent with studies of other vertebrates in urban landscapes: reptiles, other bird species, and mammals show home range size reductions in response to urbanization (O'Donnell and delBarco-Trillo 2020). Arthropod prey availability may explain why shrikes occupy urban areas in this region of coastal South Carolina but not other areas within their range. In particular, urban living in shrikes is undocumented in cooler climates. Arthropod abundance can drive bird community responses to urbanization (Planillo et al. 2021), and diet in this region of South Carolina is comprised almost entirely of invertebrate prey year-round (99% of successful hunting attempts; K. Maddox, *unpublished data*). This reliance on invertebrate prey may allow shrikes to capitalize on landscapes created by urbanization that might be less attractive if their diet was as reliant on vertebrate prey as shrikes in other regions (Hathcock and Hill 2019, Donahue et al. 2021). Seasonal changes in resource availability can also affect home range size (Chiang et al. 2012), and O'Brien and Ritchison (2011) found that shrikes maintained larger home range sizes during the non-breeding season in Kentucky than during the breeding season and suggested that winter territorial expansion may be due to lessened prey availability in winter. Shrikes in coastal South Carolina experience milder winters than shrikes in Kentucky and did not expand their winter home ranges, likely because they do not experience the same level of winter depletion in prey availability. Shrikes foraging within the study area had no seasonal difference in diet composition, indicating that sufficient invertebrate prey are available throughout the winter (Maddox 2022).

Although some populations of shrikes have non-contiguous, even widely separated, territories (McNair 2015), shrike home ranges in our study area were not only small but were nearly all adjacent to other shrike territories. Maintaining small home ranges thus allowed for a more densely packed population, although there were still unoccupied areas adjacent to many occupied territories in our study area, suggesting that small territories were due more to abundant resources than to boundaries restricted by territorial neighbors.

The population density estimate we provide for the core area is higher than has been published for any other population. Although we did not randomly sample a large area for shrike presence and our study design was thus not suitable for estimating population density over all of urbanized Horry County, we provide a second density estimate across the extended monitored area, the largest area where we could be confident that we mapped all territorial shrikes, for comparison with other studies that surveyed for all detectable shrikes across an area with widespread suitable land cover types (Table 4). The density in this extended area is also greater than other published densities. The geographically closest primarily rural population for which a population density can be measured is that of McNair (2015), who doggedly censused shrikes in 1772 km² across four counties in North and South Carolina to locate 44–45 breeding territories per year, which he considered a complete count; the density in the current study is more than 50 times higher than that in McNair's (2015) study. Nest spacing also confirms the comparatively high density in this study. In North Carolina, McNair (2015) found only one pair of shrike nesting territories (out of 45 total territories) within one km of each other whereas, in our study, 78

Table 4. Loggerhead Shrike (*Lanius ludovicianus*) population density estimates. All previously reported densities densities are for non-urban populations estimated during the breeding season.

Location	Density (shrikes/km²)	Method	Study	Study area size (km²)
South Carolina	*6.9*	*Tracking marked individuals*	*This study*	*8.4*
South Carolina	*2.9*	*Tracking marked individuals*	*This study*	*19.8*
California†	1.5	Sampling plot surveys	(Smallwood and Smallwood 2021)	167.6
New Mexico†	0.84	10-minute point counts	(St-Louis et al. 2010)	45.4
North Carolina†	0.05	Roadside and foot surveys	(McNair 2015)	1772

†Density in shrikes/km² was extrapolated from nests/km² or pairs/km².

out of 85 nests had another active nest less than one km away. In Colorado, the closest two active nests of 77 total nests were reported as 400 m apart (Porter et al. 1975); in our study the closest internest distance was 43 m. In Virginia, nests of adjacent territories were an average of 546 m apart (N = 5; Luukkonen 1987); the mean internest distance in this study was 428 m.

Though shrike populations are experiencing a range-wide decline, these results suggest that urban areas may provide shrikes with novel habitats rich in resources. Four key resources for shrikes are open areas with short grass, bare ground, perches to hunt from, and appropriate trees or woody shrubs in which to nest (Pruitt 2000). Moderate levels of development provide extensive areas of mowed grass interspersed with pavement, provide a greater abundance and variety of hunting perches than nearby rural areas (K. Maddox, *unpublished data*) and often contain ornamental and landscaping shrubs, particularly live oaks *Quercus virginianus* commonly used as nest sites by shrikes. The use of space documented in this study suggests that shrikes in the southeastern United States are actively using novel landscapes created by moderate to heavy levels of development. Within the rural areas of Horry County (the county in which our urban population lives), there are abundant open agricultural areas, yet shrikes in these non-urbanized areas are sparsely distributed (K. Maddox, *personal observation*). In contrast, the most urbanized areas of Horry County support a dense population of shrikes despite possible challenges associated with urban dwelling. Krauser and Hill (2023) noted that even within the South Carolina coastal plain, shrike prevalence in urban habitats may vary from county to county, with prevalence particularly high in Horry County. The current study provides no new insights as to why.

It is still unclear how living in human-altered landscapes impacts population dynamics of this rapidly declining species, and landscapes can be attractive without being productive. Further studies of shrike population ecology, including breeding success and adult and juvenile survival in urban environments are necessary to understand long-term implications of city living on Loggerhead Shrikes.

Author Contributions:

K.A.M. initiated the study. Both K.A.M. and C.E.H. collected data and observations. K.A.M. conducted the analyses and wrote the paper with significant input and revisions provided by C.E.H.

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Data Availability:

The raw data and code supporting the findings of this study are available on Open Science Framework at https://doi.org/10.17605/OSF.IO/WGE9A.

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