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Michelle A. Krauser and Christopher E. Hill



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Cover Photograph: A territorial urban Loggerhead Shrike surveys highway traffic in Myrtle Beach, South Carolina. Photograph © Chris Hill.

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Loggerhead Shrike Occurrence Along Urban Gradients in South Carolina's Coastal Plain

Michelle A. Krauser¹ and Christopher E. Hill^{2*}

Abstract - The urban landscape is understudied compared to less developed ecosystems, despite providing suitable habitat for wildlife, including some species of grassland birds. Loggerhead Shrikes (*Lanius ludovicianus*) are predatory songbirds that frequent grasslands and have been observed using grassy areas in developed and more natural landscapes, yet remain largely unstudied in developed landscapes. We investigated the effects of development, measured as impervious surface percentage, on Loggerhead Shrike occurrence in urban areas in South Carolina, U.S.A, and also tracked canopy cover (%), highway density (m/ha), non-highway road density (m/ha), total road density (m/ha), and powerline density (m/ha). The first author searched 300 2.25-ha sites in Charleston, Florence, Georgetown, and Horry counties for shrikes along a gradient from low to high impervious surface. All predictor variables were measured within every 2.25-ha survey site and also for a 20.25-ha “neighborhood” surrounding and including each survey site. Impervious surface and canopy cover were also measured within a 1-km circular buffer around each survey site. We used generalized linear models to identify factors associated with Loggerhead Shrike occurrence. In total, we detected Loggerhead Shrikes at 31 sites. Shrikes occurred at 2.25 ha sites with a wide range of impervious surface, ranging from 6.9 to 84.6%, with an average of 37.6% (SD = 26.2). Habitat variables at larger spatial scales (20.25 ha and 1 km circle) did not explain occupancy, but Loggerhead Shrike occurrence had weak negative relationships with impervious surface and highway density at the 2.25-ha scale. Highway density ranged from 0 to 148.1 m/ha at occupied sites, with a median of 0 m/ha. Despite its classification as a grassland bird, this study shows that Loggerhead Shrikes can use developed areas, including high-intensity development.

Introduction

Although high-intensity human development only accounts for 3% of the United States' land cover (Bigelow and Borchers 2017), development is the third leading cause of habitat loss for terrestrial mammals and birds, behind agriculture and logging (Tilman et al. 2017). Public policy, rising incomes, and rural-urban migration contribute to expanding metropolitan areas (McCatty 2004, Nechyba and Walsh 2004) and suburban sprawl on the outskirts of cities (Pendall 1999). Worldwide, built infrastructure is expected to increase by 1,527,000 km² by 2030, with some development occurring in biological hotspots (Seto et al. 2011, Seto et al. 2012). Urbanization in the United States has outpaced population growth, with urban land cover increasing at twice the population growth rate from 1945 to 2012 (Bigelow and Borchers 2017). Therefore, studying the effects of human-driven land use change on ecological systems can help understand present-day ecosystems (Grimm et al. 2000, Vitousek et al. 1997) and more accurately predict consequences of future development.

The alteration of native ecosystems by urbanization causes observable changes in avian biodiversity (Aronson et al. 2014, Ibanez-Alamo et al. 2016). Intense development has been

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shown to decrease biodiversity (Blair 1996; Blair and Launer 1997; Germaine and Wakeling 2001; McKinney 2002, 2008; Sol et al. 2014), but moderate urbanization, such as suburban and exurban development, can sometimes increase species diversity (Blair 1996, Blair and Launer 1997, Germaine and Wakeling 2001, McKinney 2008) due to high productivity (Falk 1976) and increased habitat diversity at small spatial scales (Blair 1996, McKinney 2008). Individual species or guilds are likely to exhibit different responses to urbanization based on their life-history traits, and these responses may range from adaption and exploitation to local extinction. Generalist species are better suited for developed environments (Bonier et al. 2007, Cooper et al. 2022), cavity nesters are common in human-dominated ecosystems, and some foraging guilds such as seedeaters, omnivores, and ground foragers also tend to adapt well (Beissinger and Osborne 1982, Croci et al. 2008, Kark et al. 2007, Lancaster and Rees 1979, McKinney 2002).

Grassland bird populations are declining faster than almost any other guild of North American birds (Rosenberg et al. 2019), and because some grassland specialist birds may occur in metropolitan areas and in grassy areas embedded in urban development (Boal et al. 2003, Buxton and Benson 2016), understanding how these species use human-altered landscapes may help predict future population trends. Urban areas provide various short-grass habitats, such as athletic fields, vacant lots, roadside verges, and medians. *Dolichonyx oryzivorus* Linnaeus (Bobolink), *Spiza americana* Gmelin (Dickcissel), *Sturnella magna* Linnaeus (Eastern Meadowlark), *Ammodramus savannarum* Gmelin (Grasshopper Sparrow), and *Centronyx henslowii* Audubon (Henslow's Sparrow) have been documented in isolated patches of habitat within the greater Chicago metropolitan area (Buxton and Benson 2016). Buxton and Benson (2015) suggested that grasslands in developed areas are not only suitable for some grassland birds but may decrease nest predation and brood parasitism compared to rural grasslands.

Lanius ludovicianus Linnaeus (Loggerhead Shrikes) are an example of a grassland bird that has been documented using shortgrass habitats in cities and suburbs in some portions of its range (e.g., Boal et al. 2003, McNair 2015). Shrikes prey on arthropods and small vertebrates, skewering their prey on barbed wire fences and thorny shrubs (Rosenberg et al. 2016). Historically, Loggerhead Shrikes were considered a rural and grassland species and have been observed using active pastures, shortgrass and tallgrass prairies, desert scrub, shrub-steppe, old fields, open pine forests, and agricultural fields (Froehly et al. 2019, Gawlik and Bildstein 1993, McNair 2015, Pruitt 2000). Loggerhead Shrikes require grassy habitats with unobstructed perches, open areas for foraging, and suitable nest sites such as trees or shrubs (Becker et al. 2009, Brooks 1988, Luukkonen 1987, Pruitt 2000).

Loggerhead Shrikes have experienced range-wide declines since the early 1900s (Graber et al. 1973, Hess 1910) and have been extirpated from large sections of their twentieth century breeding range (Cade and Woods 1997). From 1970 to 2014, the Loggerhead Shrike population decreased by 89% in the Atlantic Coast region and Partners in Flight has listed the Loggerhead Shrike as a common bird in steep decline and in 2016 predicted a further 50% reduction in population by 2031 (Rosenberg et al. 2016). The Breeding Bird Survey has indicated widespread population loss across physiographic strata, with an estimated annual decline of -4.7% in South Carolina from 1966 to 2017 (Sauer et al. 2018). The causes of shrike declines are unknown, but several ideas have been proposed, some of which are contradictory. Gawlik and Bildstein (1993) reported that Loggerhead Shrike declines are correlated with the loss of pastures in the southeastern United States. Conversely, studies have also indicated that suitable unoccupied habitat is plentiful in the upper Midwest (Brooks 1988) and Quebec, Canada (Jobin et al. 2005), suggesting that the loss of breed-

ing habitat is not the primary driver of population loss in these regions. It's possible that Loggerhead Shrike declines may be attributable to different causes in different regions, or that seemingly suitable unoccupied habitat may be unsuitable based on unidentified factors. Additional proposed causes of Loggerhead Shrike losses include pesticide use, juvenile mortality, and winter mortality (Burnside and Shepherd 1985, Brooks and Temple 1990, Lymn and Temple 1991).

The habitat characteristics necessary to support Loggerhead Shrike populations, including grassy foraging areas, unobstructed perches, and suitable nest sites, are found in some developed areas such as parks, cemeteries, and vacant lots. Loggerhead Shrikes have been observed at such urban sites in seven states, all of which host resident, non-migratory shrike populations: Florida (Grubb and Yosef 1994), Louisiana (Worm and Boves 2019), North Carolina (McNair 2015), South Carolina (this study), and Texas, Georgia and Alabama (C. Hill, Coastal Carolina University, Conway, SC, 2019, unpublished survey of Eastern Loggerhead Working Group). Because shrike populations in commercial and industrial areas may be denser than nearby rural populations (K. Maddox and C. Hill, Coastal Carolina University, Conway, SC, 2022 unpubl. data), urban shrikes may constitute a significant portion of the population in some areas and the distribution and population dynamics of these urban shrikes may in part determine the dynamics of regional populations as a whole.

Although Loggerhead Shrikes have been documented using highly developed sites such as industrial parks, cemeteries, and race tracks (McNair 2015), only one study has explicitly focused on shrikes nesting in cities and suburbs (Boal et al. 2003). While regional differences in climate or in the shrikes themselves may influence the use of urban sites, the presence of Loggerhead Shrikes in some urban areas and their absence in others also suggests shrikes may be attracted to specific characteristics within the urban landscape, which are currently unknown. Studies in less developed areas suggest road density, powerline density, presence of bare ground and lack forest cover may affect shrike occurrence (Froehly et al. 2019, Gawlik and Bildstein 1993, Johnson 2017, Pruitt 2000). Roadside verges in developed areas may be attractive to Loggerhead Shrikes because of the reduced canopy cover and increased availability of short grass, bare ground or pavement, and powerlines along many roads.

Loggerhead Shrike habitat selection may occur at multiple spatial scales, but the literature provides contradictory conclusions. In rural South Carolina, Loggerhead Shrikes were most sensitive to pasture land at the 1-km scale (Froehly et al. 2019). In a separate study, shrike occupancy decreased as forest cover increased at the 2.5-km scale in the southeastern United States (Johnson 2017). Loggerhead Shrikes may select habitat based on landscape-scale features because nearby high-quality habitats may be important if a portion of their territory becomes unsuitable. This is supported by research showing that shrikes adjust the size of their territories based on resource availability (Yosef and Deyrup 1998, Yosef and Grubb 1994). In Missouri, Loggerhead Shrike occupancy was associated with the length of fence, the number of perch sites, and the area of pasture and corn at the 200-m scale but was not affected by any characteristics at scales >600 m (Esely and Bollinger 2001). It is possible that in areas where shrikes do not respond to characteristics at large spatial scales, there is enough suitable habitat that any location is adequate from a macrohabitat scale.

Methods used to define urbanization are inconsistent, and what constitutes "urban" is often assumed or subjective versus explicitly defined (McIntyre et al. 2000). Studies have defined development intensity by measuring impervious surface (Buxton and Benson 2016; McKinney 2002, 2008; Seto et al. 2011), classifying land use (Blair 1996, Blair and Launer 1997, Boal et al. 2003, McLaughlin et al. 2014, Nilon et al. 1995), and measuring

the distance from city centers (Medley et al. 1995). In the social sciences, urbanization is often measured using population density (McIntyre et al. 2000). Inconsistent methods limit comparisons among studies. In this study we used impervious surface percentage as an objective, quantitative measurement that is simple to calculate given the data layers available for public use in geographic information systems.

Our primary goal in this study was to measure shrike occupancy across the complete available gradient of impervious surface available in developed parts of South Carolina's coastal plain, although we also collected other publicly available habitat characteristics. We examined patterns at the scale of one shrike territory (about 2.15 ha in urban areas; K. Maddox and C. Hill, Coastal Carolina University, Conway, SC, 2022 unpubl. data), at a neighborhood scale (a polygon that could contain one territory and all neighboring territories) and at the landscape scale (1-km radius) to inform conservation decisions regarding Loggerhead Shrikes in developed environments. South Carolina's coastal plain contains resident urban shrike populations in multiple cities and suburbs, making it an ideal location to study the habitat characteristics associated with Loggerhead Shrike occurrence in the urban landscape.

Methods

Study area

We chose survey points in urban areas in developed areas of Charleston ($n = 92$ points), Florence (64), Georgetown (24), and Horry (120) counties (Fig. 1) using a stratified random selection process designed to insure equal coverage across all levels of % impervious surface (Fig. 2). Habitat measurements and point selection were completed using ArcMap version 10.7.1.11595. We used the "Create Fishnet" tool to place a 2.25-ha fishnet over developed areas of each county. To calculate impervious surface at the 2.25-ha scale, we used the National Land Cover Database (NLCD), which measures impervious surface and canopy cover at a 30-m resolution (Dewitz 2019, NLCD 2016). The 2.25-ha squares were stratified into ten equal-interval bins by % impervious surface. We generated a random number for each point, sorted the lists, and selected points starting with the smallest number. We examined aerial imagery to ensure each point satisfied all criteria, eliminating points with >75% canopy cover at the 2.25-ha scale as unsuitable for shrikes, and we discarded inaccessible points, such as golf courses, residential neighborhoods, and storage yards. The minimum distance between survey points was 450 m (about three times the diameter of an urban shrike territory) to ensure independence. Eight points were inaccessible when visited and were replaced with the next point on the list that satisfied all criteria. The 300 surveyed points represented the range of impervious surfaces (3.2–96.3%, Fig. 2) found in the study area.

Survey protocol

The survey protocol consisted of a single observer (the first author) actively searching the 2.25-ha survey site with binoculars for ten minutes. Sites were surveyed from December 8, 2020 to February 23, 2021. The same observer had conducted pilot surveys at 30 survey sites in August 2020 and determined that a 10-minute survey window was adequate to search all potential perches and foraging sites. In a previous Loggerhead Shrike study, 5–16 minutes was found to be sufficient time to scan foraging areas and perch sites of a typical territory in commercial and industrial areas (Krauser 2022). Because Loggerhead Shrike detections are typically visual, the observer for the current study moved within the survey

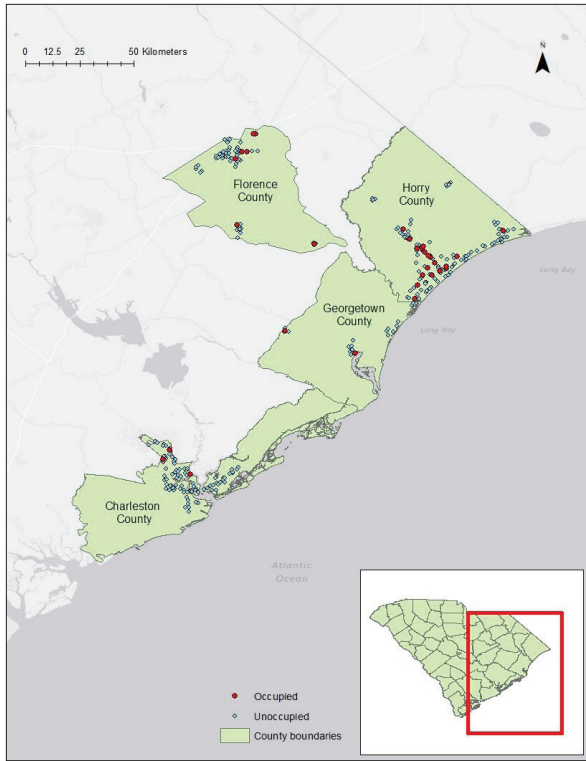


Figure 1. The locations of 300 survey points along urban gradients in Charleston, Florence, Georgetown, and Horry counties in coastal South Carolina, with occupied sites in red and unoccupied sites in blue.

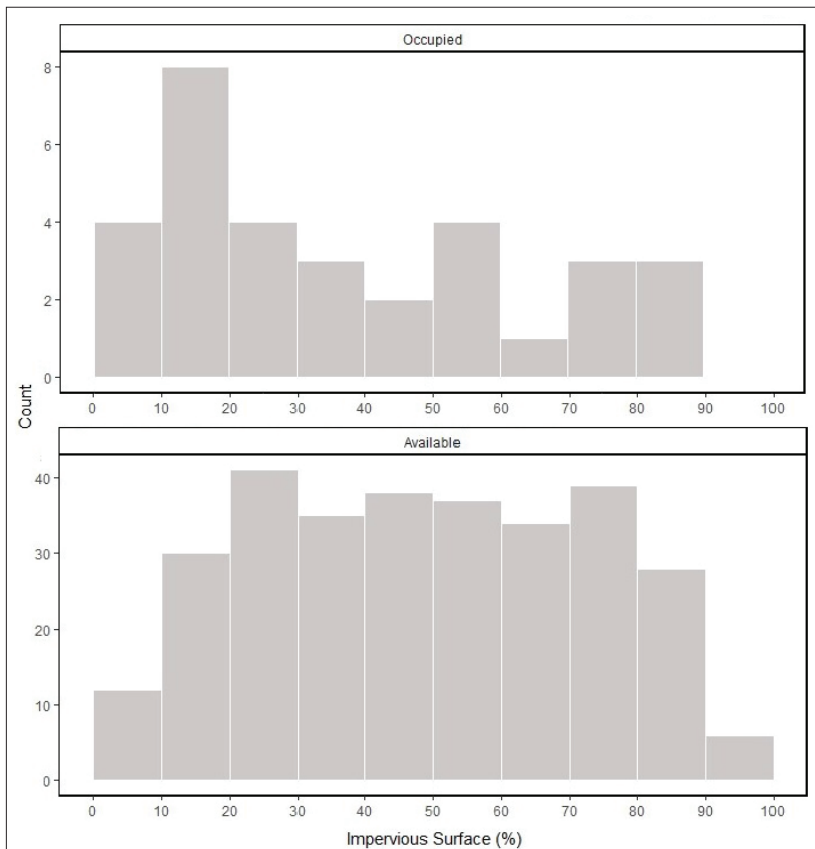


Figure 2. Impervious surface (%) at the 2.25-ha scale for 31 occupied sites compared to the availability of impervious surface at all 300 survey sites in coastal South Carolina urban areas. Impervious surface was measured using the National Land Cover Database (2016). Loggerhead shrikes were detected at sites with impervious surface levels that ranged from 6.9 to 84.6% and preferred lower impervious surface levels compared to what was available in the study area.

site to obtain views of all potential perches and foraging sites. From December 8, 2020 to February 23, 2021, the observer conducted one survey at each survey site. Because Loggerhead Shrikes are year-round residents in this area, winter surveys are also good predictors of breeding habitat (C. Hill, Coastal Carolina University, Conway, South Carolina, 2022 unpubl. data). The observer recorded the number of Loggerhead Shrikes seen inside and outside of each survey site. No surveys were attempted on days when the wind speed was greater than 29 kph or during periods of prolonged or heavy rain. We refer to survey sites at which a shrike was detected as “occupied,” and to sites where shrikes were not detected as “unoccupied.” Loggerhead Shrike detectability was estimated at 0.58 in a concurrent study in Horry County (Krauser 2022). Based on this detection rate, we chose to survey each site once rather than survey each site multiple times. We recognized that the single survey design would leave some occupied sites undetected (false negatives) but would allow surveys at more sites and increase overall detections.

Habitat measurements

Including the percent impervious surface used to select points, we measured six predictor variables: impervious surface (%), canopy cover (%), highway density (m/ha), other road (non-highway) density (m/ha), total road (highway + other road) density (m/ha), and powerline density (m/ha) at multiple spatial scales (Table 1). We added a 20.25-ha square polygon and a 1-km buffer (circle with 1-km radius) to each 2.25-ha square, with the 2.25-ha square at the center.

We used the “Zonal Statistics” tool to calculate impervious surface and canopy cover at each scale. Using data obtained from the South Carolina Department of Natural Resources’ Statewide Highways and Statewide Other Roads dataset and the “Intersect” tool, we measured road densities at the 2.25-ha and 20.25-ha scales. We used the “Clip” tool to calculate powerline densities at the 2.25-ha and 20.25-ha scales using the Electric Power Transmission Lines dataset from the Homeland Infrastructure Foundation Level Database. To measure the accuracy of the NLCD’s impervious surface estimates, we consulted the most current available aerial images for 30 randomly selected survey points and digitized impervious surface from those images. We then calculated the difference between the NLCD’s estimates of impervious surface and the estimates obtained from the more current measurements of the 30 randomly selected sites.

Table 1. Predictor variables hypothesized to influence Loggerhead shrike occurrence in coastal South Carolina urban areas and the scales at which they were measured.

| Predictor variable | Spatial scales measured | | |
|---------------------------|-------------------------|----------|------|
| | 2.25 ha | 20.25 ha | 1 km |
| Impervious surface (%) | x | x | x |
| Canopy cover (%) | x | x | x |
| Highway density (m/ha) | x | x | |
| Other road density (m/ha) | x | x | |
| Total road density (m/ha) | x | x | |
| Powerline density (m/ha) | x | x | |

Data analysis

We completed all analyses in R version 4.1.1 (R Core Team 2021). We used a binomial generalized linear models approach to investigate the relationships between the predictor variables and Loggerhead Shrike occurrence. Including an excessive number of variables in logistic regression can decrease the power to detect true associations and produce false associations (Ranganathan et al. 2017). Peduzzi et al. (1996) suggested that data

should contain a minimum of ten events per variable included in a logistic regression model. We therefore reduced the number of predictor variables to three because the dataset contained 31 detections.

To reduce the number of predictor variables, we examined notched boxplots of each predictor variable against the outcome, wherein the “notch” represented the 95% confidence interval of the median. Lack of overlap between notches suggests a significant difference between medians (Chambers et al. 1983). Two predictor variables at the 2.25-ha scale, impervious surface and highway density, and one variable at the 20.25-ha scale, total road density, had non-overlapping notches and were included in the logistic regression model. Powerline density, canopy cover, total road density, and other road density at the 2.25-ha scale, and canopy cover and impervious surface at the 1-km scale, were excluded from the model based on overlapping notches. All variables at the 20.25-ha scale except total road density were excluded based on overlapping notches. We calculated the variance inflation factor (VIF) using the `vif()` function in the “car” package (Fox and Weisburg 2019) to test for multicollinearity among predictor variables, ensuring that all variables had VIFs <5 (James et al. 2013). Then, we built all possible models to test for linear and quadratic relationships using the `glmulti()` function in the “glmulti” package (Calcagno 2020) and ranked them based on AIC_c , ΔAIC_c , Akaike weights. Next, we used the `ggplot()` function in the “ggplot2” package (Wickham 2016) to plot the logit of the outcome against each of the remaining predictor variables to ensure a linear relationship between the independent variables and the log odds of the outcome. We also conducted a Box-Tidwell test on impervious surface using the `boxTidwell()` function in the “car” package (Fox and Weisburg 2019) to further test for linearity. The Box-Tidwell test determines if the log odds of the outcome is a linear function of the predictor variable. To assess the model’s ability to predict class in an unseen dataset, we conducted a stratified 5-fold cross-validation using the “caret” package (Kuhn 2021). We used the “MLeval” package (John 2020) to calculate the area under the receiving operator characteristic (AUROC) and the area under the precision-recall curve (AUPRC). The ROC curve plots the true positive rate against the false positive rate at various thresholds. AUROC is often used to measure the performance of a binary classification system, but AUROC may not always reflect the true performance of a classifier for a highly imbalanced dataset. Total misclassification of the minority event may still result in a high AUROC score (Saito and Rehmsmeier 2015). Thus, AUPRC may provide a more accurate representation of model performance for imbalanced data sets (Davis and Goadrich 2006, Saito and Rehmsmeier 2015) depending on the purpose of the model.

Results

The difference between the NLCD’s impervious surface estimates and remeasurement from current aerial images was 8.9%.

We detected Loggerhead Shrikes at 31 of 300 survey sites (Fig. 1). Of all possible models, five candidate models had Akaike weights >0 (Table 2). The top-ranked model included highways at the 2.25-ha scale and impervious surface at the 2.25-ha scale. A 10% increase in impervious surface decreased the odds of shrike occurrence by 17%, and a 10-unit (m/ha) increase in highway density decreased the odds of occurrence by 11%. The AUROC and AUPRC of the top-ranked model was 0.70 and 0.21, respectively. The second-ranked model ($\Delta AIC_c = 2.04$) included highway density at the 2.25-ha scale, impervious surface at the 2.25-ha scale, and total road density at the 20.25-ha scale.

Loggerhead Shrikes were distributed across a wide range of impervious surface levels but had a slight preference for areas with lower impervious surface (Fig. 2). Occupied sites had an average impervious surface of 37.6% (range = 6.9–84.6%, SD = 26.2) compared to 49.9% (range = 3.2–96.3%, SD = 23.4) at unoccupied sites and 48.6% (range = 3.2–96.3%, SD = 23.9) across all sites (Table 3). The median highway density at occupied sites was 0 m/ha (range = 0–148.1 m/ha) (Fig. 3), 58.4 m/ha at unoccupied sites (range = 0–266.0 m/ha), and 50.2 m/ha across all sites (range = 0–266.0 m/ha) (Table 3).

Table 2. Summary of the top five candidate models fit to identify the predictor variables associated with Loggerhead shrike occurrence in coastal South Carolina urban areas with AIC_c, ΔAIC_c, and Akaike weights. The summary includes all candidate models with Akaike weights >0. Impervious surface was measured in %, and highway density and total road density were measured in m/ha.

| Predictor variables | AIC _c | ΔAIC _c | Akaike weights |
|--|------------------|-------------------|----------------|
| impervious surface (2.25 ha) + highway density (2.25 ha) | 188.32 | 0 | 0.60 |
| impervious surface (2.25 ha) + highway density (2.25 ha) + total road density (20.25 ha) | 190.36 | 2.04 | 0.22 |
| highway density (2.25 ha) | 191.79 | 3.47 | 0.11 |
| highway density (2.25 ha) + total road density (20.25 ha) | 193.57 | 5.25 | 0.04 |
| impervious surface (2.25 ha) | 195.88 | 7.56 | 0.01 |

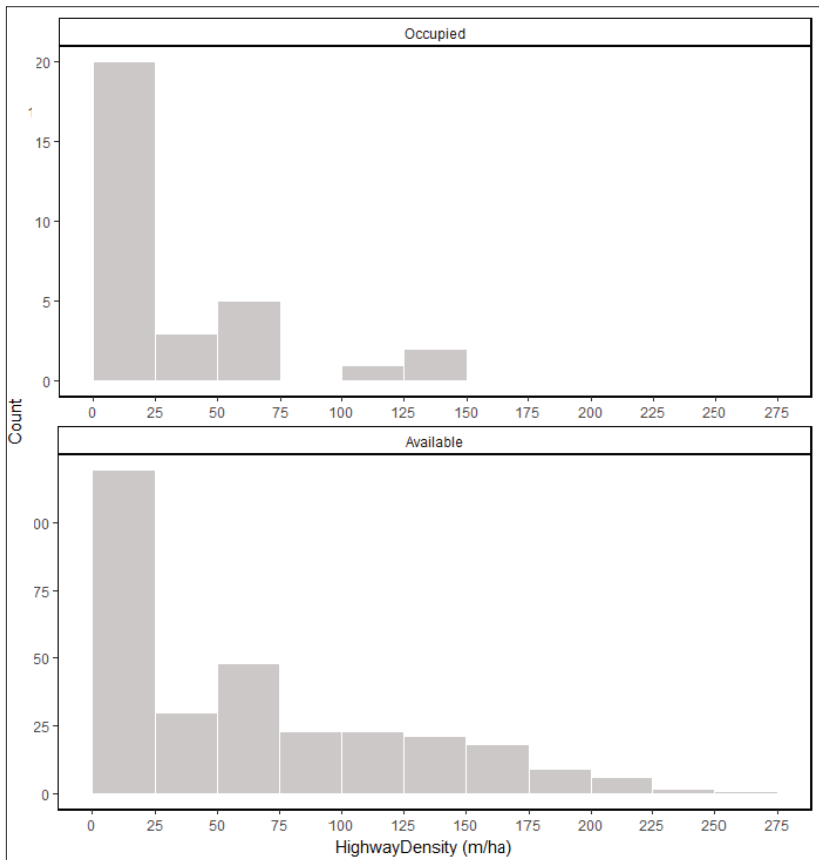


Figure 3. Highway density (m/ha) at the 2.25-ha scale for 31 occupied sites compared to the availability of highway density at all 300 survey sites in coastal South Carolina urban areas. Highway density was measured using the South Carolina Department of Natural Resources’ Statewide Highways and Statewide Other Roads dataset. Loggerhead shrikes exhibited some avoidance of highways, with half of occupied sites having a highway density of 0 m/ha, but did not avoid them entirely.

Table 3. Average values for each predictor variable for occupied, unoccupied, and all survey sites. Values are based on 300 surveys conducted along urban gradients in Charleston, Florence, Georgetown, and Horry counties, South Carolina, from December 2020 to February 2021. Standard deviations are in parentheses.

| Predictor Variable | Scale | Occupied | Unoccupied | All |
|------------------------------|----------|-------------|-------------|-------------|
| Impervious surface (%) | 2.25 ha | 37.6 (26.2) | 49.9 (23.4) | 48.6 (23.9) |
| Impervious surface scale (%) | 20.25 ha | 35.6 (15.5) | 40.0 (16.1) | 39.6 (16.1) |
| Impervious surface (%) | 1 km | 21.8 (13.8) | 23.6 (12.8) | 23.4 (12.9) |
| Canopy cover (%) | 2.25 ha | 3.2 (9.2) | 4.4 (8.4) | 4.3 (8.5) |
| Canopy cover (%) | 20.25 ha | 11.1 (9.3) | 13.8 (10.7) | 13.5 (10.6) |
| Canopy cover (%) | 1 km | 27.1 (13.1) | 29.5 (14.0) | 29.2 (13.9) |
| Highway density (m/ha) | 2.25 ha | 28.4 (42.2) | 65.3 (63.8) | 61.5 (62.8) |
| Highway density (m/ha) | 20.25 ha | 39.4 (43.5) | 54.5 (37.0) | 53.0 (37.9) |
| Other road density (m/ha) | 2.25 ha | 47.0 (61.8) | 32.0 (47.1) | 33.5 (48.9) |
| Other road density (m/ha) | 20.25 ha | 33.2 (32.1) | 32.0 (28.3) | 32.1 (28.7) |
| Total road density (m/ha) | 2.25 ha | 75.4 (61.3) | 97.3 (69.8) | 95.0 (69.2) |
| Total road density (m/ha) | 20.25 ha | 72.6 (42.1) | 86.5 (41.2) | 85.1 (41.5) |
| Powerline density (m/ha) | 2.25 ha | 9.3 (25.0) | 7.4 (30.7) | 7.6 (30.1) |
| Powerline density (m/ha) | 20.25 ha | 7.3 (13.2) | 7.4 (15.6) | 7.4 (15.3) |

Although we had not designated “county” as predictor variable in the study and did not include county in formal analyses, it became apparent after the fact that Loggerhead Shrikes were distributed unequally across counties (Fig. 1). Horry County had the greatest proportion of occupied sites at 15.8%, followed by Florence County at 10.9%, Georgetown County at 8.3%, and Charleston County at 3.3%.

Discussion

We found Loggerhead Shrikes occupying sites across the entire range of urban development in the South Carolina coastal plain, from 6.9%–84.6% impervious surface. Although models detected some concentration of occupied sites in areas of lower impervious surface and lower highway density, the relationship was weak, as indicated by the area under the receiver operator curve (0.71, near the lower edge of “acceptable” predictor values in a clinical setting; Mandrekar 2010). Since 10% of surveyed sites were occupied, the AUPRC provides an additional measure of the power to predict shrike occupancy. Compared to the baseline of 0.10 and a perfect prediction value of 1.0, the calculated AUPRC of 0.21 again indicates that the aspects of urbanization we measured only weakly predicted shrike occurrence. Based on their occurrence at sites with >80% impervious surface, it appears that shrikes can sustain themselves on small patches of mowed grass in urban surroundings in this region and do not require large rural grasslands.

Since Loggerhead Shrikes are unreported in urban environments in many portions of their range (C. Hill, Coastal Carolina University, Conway, South Carolina 2019, unpub-

lished survey of Eastern Loggerhead Shrike Working Group), it may be of value to speculate on why shrikes have historically occupied cities in this region (Wayne 1910, Bent 1950) and continue to do so. Other species have also exhibited variable responses to urbanization: for example, Grasshopper Sparrow density in Illinois was unaffected by impervious surface intensity (Buxton and Benson 2016), while in Nebraska and Iowa, Grasshopper Sparrows declined as development intensity increased (McLaughlin et al. 2014). This suggests that the suitability of developed environments is location-specific. Possible correlates for the observed distribution of urban Loggerhead Shrikes may be warm climates, heavy reliance on invertebrate prey, or perhaps higher local abundance, and we cannot rule out genetic differences in habitat preference.

Loggerhead Shrikes were most sensitive to habitat characteristics at the 2.25-ha scale, unlike some studies that have suggested Loggerhead Shrikes respond to habitat characteristics at larger scales, including pasture at the 1-km scale (Froehly et al. 2019) and forest cover at the 2.5-km scale (Johnson 2017). In contrast, Esely and Bollinger (2001) reported that shrikes respond most strongly to habitat features ≤ 200 m from their nest site and suggested that in areas with abundant suitable habitat, shrikes are less sensitive to habitat at large spatial scales. Because research suggests that shrikes respond to different spatial scales based on resource availability, habitat suitability, and geographic location, conservation actions may be most effective when they consider both fine- and broad-scale land-use measurements.

Although “county” was not a planned variable in our study, we did note after surveys had been completed that Horry County had by far the highest percentage of occupied sites of the four counties in the study area, so we speculate here on reasons for that that may inspire or focus future study. Although a data layer that classifies open grass patches at small spatial scales was not available, visual inspection of satellite images suggested that Horry County had a higher density of open grass patches and larger such patches than Charleston, Florence, or Georgetown counties. These grass patches were largely roadside verges and storefront lawns. It is possible that shrikes prefer developed and transitioning habitats with many patches of open grass because such an arrangement could support a large number of shrikes, facilitating conspecific attraction. Conspecific attraction reduces the costs of finding a mate and has been observed in other species of territorial songbirds, such as *Troglodytes aedon* Vieillot (House Wren) and *Vireo atricapilla* Woodhouse (Black-Capped Vireo) (Muller et al. 1997, Ward and Schlossberg 2004). The human population of Horry County has increased by 23.3% from 2010 to 2020 (United States Census Bureau 2020), with many areas undergoing a transition from forested and rural habitats to commercial, industrial, and residential development. Shrikes may be attracted to this “early successional” phase of cities and suburbs where there is an abundance of cleared but undeveloped land. More focused research on the size and density of occupied grass patches might identify the specific landscape configurations that attract shrikes to cities and suburbs.

If cities and suburbs provide high-quality habitat for Loggerhead Shrikes, we believe marginal habitat in the urban landscape could be repurposed for shrikes at relatively low cost. For example, roadside verges, vacant lots, medians, and storefront lawns could be managed for Loggerhead Shrikes by adding unobstructed perches (Yosef and Grubb 1994) and a few trees suitable for nesting, particularly young *Quercus virginiana* Miller (Live Oak), which are both a widely used landscaping tree in this region and favored for shrike nesting (Bent 1950, C. Hill, Coastal Carolina University, Conway, South Carolina, 2018–2020 unpubl. data). These additions could possibly help support the species as grasslands disappear. However, population processes for Loggerhead Shrikes in the current urban

environment are not yet understood, and so the possibility that urban populations are a sink or ecological trap need to be explored. Although the average highway density of occupied sites (28.4 m/ha) was less than the highway density at unoccupied sites (65.3 m/ha), shrikes did not avoid highways altogether and more than half of occupied sites (52%) were located within 100 m of a highway. Vehicle collisions involving Loggerhead Shrikes in rural grasslands have been documented (Flickinger 1995, Gawlik and Bildstein 1990, Luukkonen 1987), and in Missouri shrike nests ≤ 15 m from a road produced fewer fledglings than interior nests (Esely and Bollinger 2001). In a songbird with similar body size and overlapping range, *Aphelocoma coerulescens* Bosc (Florida Scrub-Jay), roadside populations experience higher mortality rates than non-roadside populations, especially among road-naïve immigrants (Mumme et al. 2000) and a roadside population acted as a sink. Studies of both survivorship and reproduction in urban populations of Loggerhead Shrikes would clarify whether encouraging further colonization of urban spaces would be a net benefit or drag on regional populations over all.

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