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Use of space and foraging behavior of loggerhead shrikes in urban areas

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USE OF SPACE AND FORAGING BEHAVIOR OF LOGGERHEAD SHRIKES IN URBAN AREAS

By

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Abstract

Loggerhead shrikes, *Lanius ludovicianus*, are a declining grassland songbird native to North America. Land-use change has been associated with the decline of grassland bird species. However, the process of urbanization creates novel short-grass habitats reminiscent of shrikes' natural habitats. Loggerhead shrikes have been observed living in developed areas, particularly in Southeastern coastal states. Understanding the long-term impacts of urban-dwelling on loggerhead shrike populations is vital to identifying whether urban areas offer refuge or act as an ecological sink for shrike populations.

In chapter one, I quantified the use of space by shrikes in urban habitats within Horry County, South Carolina. I calculated home range sizes using minimum convex polygons and kernel density estimators. I used the detection histories of a banded population of shrikes to calculate the average population density of my study area. I also calculated internest spacing of shrike nests using a three-year dataset of nesting locations. I found that compared to their rural counterparts, shrikes in urban areas maintain smaller home ranges (1.6-6.1 ha), are more densely populated (2.9 shrikes per km^2) and maintain close internest spacing (median distance to neighboring nest: 354 m). These results indicate that loggerhead shrikes are actively taking advantage of the habitats provided by developed areas and that those habitats provide better resources than more agricultural sites.

In chapter two, I compare the foraging behavior of shrikes in urban and rural areas. I observed shrikes foraging within both land uses during 30-minute periods throughout both the breeding and non-breeding season. I recorded perch parameters (type and height), foraging style (aerial or terrestrial attempt), ambient temperature, prey type, as well as outcome of foraging attempt. I used a MANOVA to compare the forage behavior of urban and rural shrikes. Using a generalized linear mixed model, I investigated how aspects of foraging behavior impact foraging outcome. The foraging strategy of shrikes in urban areas was consistent with that of shrikes in rural areas. Shrikes in urban areas used anthropogenic perches more often than natural, though this may be a reflection of availability rather than choice. Shrikes in my study foraged at an average rate of 16 attempts per hour with an 80% capture efficiency. The top-ranked model predicting foraging outcome included four predictor variables: foraging style, perch type, perch height, and ambient temperature. Foraging success was greater from tall perches, natural perches, in warmer temperatures, and during terrestrial foraging attempts. Results from this study indicate that while the urban matrix alters habitat structure, urban shrikes are able to forage as successfully as their rural counterparts.

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Chapter 1: Use of Space by Loggerhead Shrikes as a Window into the Suitability of Urban Areas as Habitat

Abstract

The distribution of a species throughout an environment lends information on the suitability and resource availability of its habitat. Wildlife living in urban environments is presented with new challenges associated with development that may change how they use space. Loggerhead shrikes (*Lanius ludovicianus*) occur in urban areas of the Southeastern United States, despite the species' historical association with shortgrass habitats such as pasture and shrub steppe. To understand how shrikes use the urban matrix, I measured the population density, home range size, and nest spacing of a population of loggerhead shrikes inhabiting urban areas of Horry County, South Carolina. I used detection histories for a banded population of shrikes as well as sightings of unbanded shrikes to estimate the average density of shrikes across my study area. To estimate home range sizes I mapped perch locations of banded shrikes during breeding and non-breeding seasons. I used these coordinates to calculate minimum convex polygons (95% and 100%) and kernel density estimators (50%) as estimates of each bird's home range size. I used records of 142 loggerhead shrike nests and calculated distance to the nearest neighboring nest. I found that over a three-year period the study area supported an average of 2.9 shrikes per km^2. A core area of occupied habitat was able to support a denser population of

6.9 shrikes per km^2. I estimated home range size for 39 birds throughout the year, plus 24 birds during the breeding season only and 19 during non-breeding season only. Home ranges averaged 1.6 - 6.1 ha depending on the season and method used. Estimates using 50% kernel density estimators were slightly smaller than estimates using 95% minimum convex polygon; both of those were smaller than 100% minimum convex polygon estimates. Breeding and non-breeding home range sizes did not differ. However, breeding home range sizes were smaller than year-round home ranges when estimated using minimum convex polygons. Median distance to nearest active nest for 85 focal nests was 354 meters (range 43-1751). Comparisons of these metrics with other published studies indicate that shrikes in this urban area are more dense, maintain smaller home range sizes, and nest closer to each other than their rural conspecifics indicating that urban areas may provide suitable habitat for a population of loggerhead shrikes to survive.

Introduction

Understanding the use of space by individuals provides insight into the ecology of a population. Both home range and territory are concepts used to quantify the distribution of individuals in space. Home range encompasses the space an organism traverses while engaging in daily activity while territory includes all space that is defended, whether from conspecifics or other species. Home range size is an indicator of local resource availability. In the midst of abundant resources and unoccupied space, individuals can meet their needs in a smaller space, and individuals with smaller home range sizes are often healthier and produce more offspring (Yosef and Grubb 1992, Schradin et al. 2010, Spencer 2012, Pfeiffer and Meyburg 2015).

The conversion of wildlands into human-dominated environments poses unique challenges to wildlife. Urban areas are associated with biotic homogenization, high rates of pollution, changes in prey availability, habitat fragmentation, increase in impervious surface coverage, vegetative cover change, and increased presence of non-native biota (Goldstein et al. 1986, Collins et al. 2000, McIntyre 2000, McKinney 2002, 2006). As the world becomes increasingly urbanized, it is essential to understand the effects these changes have on native wildlife populations. The direct effects are highly dependent upon the interaction of a given species' life history with land use. While some species are intolerant of urbanization, others are able to take advantage of the resources presented by the urban matrix (McKinney and Lockwood 1999, Callaghan et al. 2019a, b).

The loggerhead shrike, *Lanius ludovicianus,* hereafter referred to as "shrikes," is one of two shrike species native to North America. Shrikes are sit-and-wait predators found in open landscapes with sparse, short vegetation (Pruitt 2000), whose foraging behavior resembles that of a bird of prey (Craig 1978, Bohall-Wood 1987). Along with many grassland birds, shrikes have experienced a dramatic population decline and their abundance decreased by 74% in North America during 1970–2014 (Rosenberg et al. 2016).

In much of their range shrikes use naturally occurring steppe habitats (Scott and Morrison 1990, Telfer 1992, Woods and Cade 1996, Collister and Wilson 2007, Stanley et al. 2012, Smallwood and Smallwood 2021), but shrikes in eastern North America depend almost entirely on shortgrass habitats that are maintained directly or indirectly by humans. Most eastern shrikes are found in and near pastures and other agriculture (Collister 1994, Yosef and Grubb 1994, Froehly et al. 2020, Donahue et al. 2021) but 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 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 2022; this study), Alabama, Georgia, and Texas (unpublished survey of the Eastern Loggerhead Shrike Working Group, 2019). The number of shrikes inhabiting urban areas is widely unknown and may account for a large proportion of the total population in some southeastern states. Only one study has investigated shrikes living in a predominantly urban environment (Boal et al. 2003), and all previous studies investigating the spatial ecology of shrikes were conducted on shrikes inhabiting rural areas.

Territory size has been shown to indicate habitat quality for shrikes specifically. 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 were 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 their home range size by an average of 138% (Yosef and Deyrup 1998). Home range size and population density have an inverse relationship in territorial species, and small home ranges allow for a more densely packed population (Yosef and Grubb 1994).

I studied the population density, home range size, and nest spacing of resident shrikes in an urban area of the coastal plain of South Carolina. My 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, and (5) compare these estimated densities, home range sizes, and nest spacings to published accounts from shrikes in rural areas in the same region.

Methods

Study Area

This study was conducted this study along a section of the Highway 501 corridor from Conway to Myrtle Beach in northeastern South Carolina. The study area (33.69°N-33.83°N, 79.05°W-78.90°W) consisted of four distinct sites with a combined area of 1983 hectares (Figure 1.1). The land along this highway corridor is highly developed, consisting of strip malls, housing developments, and industrial parks. A non-migratory population of shrikes has been monitored along this corridor since 2018. From 2018 to 2022, adult shrikes were captured using both drop-in and walk-in traps. Captured 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). Nestlings were banded at 12 days old, and plastic bands were melted closed using a battery-powered soldering iron.

Population Density

To estimate the shrike population density of the study area, observers surveyed known shrike territories on foot twice monthly. Searches lasted for an average of 15 minutes within the territory and observers determined color band combinations of resighted shrikes using binoculars, spotting scopes, and telephoto cameras. Portions of the study area with inappropriate habitat (e.g., wooded areas) were not surveyed regularly. In addition to territory searches, observers conducted road surveys of the study area while traveling in between known territories. All present shrikes were recorded. To track the occupancy and movement patterns of shrikes in the study area, observers created monthly maps for each site. These maps included banded shrikes encountered on biweekly surveys as well as any unbanded shrikes observed.

I calculated the shrike population by combining the number of banded adult shrikes present during a month with the number of unbanded shrikes reported on the respective monthly maps. I averaged the monthly populations from September 2019 to July 2022 and divided by the total study area to calculate my study area's shrike population density in shrikes present per square kilometer. A banded shrike was considered present from the time it was banded until the last time I observed it in a territory. While it was present, I considered gaps during which a shrike was not encountered for one or two consecutive months (but was later re-sighted) to be failures of detection rather than true absences. However, if a shrike was not encountered for three consecutive months, even if it was later resighted, it was considered absent from the study area's population during the gap in detections. An analysis of gaps in detections of banded shrikes in this study area determined that shrikes missing for three months were more likely to never return than shrikes undetected for two months, indicating that gaps of only two months were likely a result of failed detection rather than absence from the study area (C. Hill, unpublished data). To account for the patchiness of the population throughout the urban matrix, I calculated density for the entire study area (1983 ha) as well as the areas of known territories which were occupied. I also compared the population density during the breeding (March-August) and non-breeding seasons (September-February) using a Wilcoxon Rank-Sum test. All analyses were conducted in R version 4.2.1 using RStudio version 2022.7.2.576 (R Core Team 2022, RStudio Team 2022).

Home range

I estimated the sizes 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, I recorded the location 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, CA). I recorded multiple locations per visit as the shrike foraged and changed locations. The goal was to record at least twenty perch locations per bird over multiple days. I was careful to watch the shrikes from a distance that did not cause a change in behavior.

I constructed 95% and 100% minimum convex polygons (MCP) as well as 50% kernel density estimators (KDE; Mohr, 1947; Seaman and Powell 1996). I chose to use the 50% KDE isopleth because larger isopleths tend to overestimate home range by incorporating unusable areas unique to urban habitats such as centers of rooftops and large highways. Presenting multiple metrics allows for easier comparisons between past and future studies as spatial ecology methodologies develop (Anich et al. 2009; Figure 1.2). For minimum convex polygons, I used the function *mcp.area* of package *adehabitatHR* to estimate the size of each shrike's home range (Calenge 2006). The function *kernelUD* was used to visualize KDEs while *kernel.area* was used 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). Only birds with 20 or more locations per season were included in analysis. If a bird relocated to a different territory within a season, it was excluded from analysis. A relocation to a different territory was classified as 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, see results). 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 within the study area for signs of nesting activity (e.g., courtship feeding, nest-building, or adults carrying food to nests). After a nest was found, observers recorded the coordinates of the nest with 1-2 m precision using aerial imagery from Google Earth and Google Maps (Google, Inc., Mountain View, CA). The stage of the nest was determined using behavioral observations and a camera on an extendable pole. Observers estimated chick age and inferred hatch date using images taken of the nest cup. Nests were visited at least twice a week until they failed or the chicks reached banding age.

To understand nest spacing in the urban matrix, I measured the distance between nests and their closest neighbor. As a territorial species, internest distance may be a determinant of the density of a population. Because breeding pairs of shrikes nest multiple times per breeding season, I randomly selected one focal nest per breeding pair each season to include in my nearest nest analysis. I measured the distance between the focal nests and the closest nest on another territory whose hatch date was within a breeding cycle, or 55 days (C. Hill, unpublished data) of the focal nests' hatch date.

Results

Population Density

From February 2018 to July 2022, researchers banded 144 adult shrikes and 399 juveniles within the study area. At any given time during the study, about 90% of the adult shrikes in the study area were banded. Between September 2019 and July 2022, the average adult population of the study area was 57 shrikes. Average breeding season population was 59 shrikes compared to 57 shrikes during the non-breeding season, however this difference was not statistically significant ($W = 166.5$, $p = 0.67$). On average, the entire study area supported 2.9 shrikes per km^2. Shrike density was greatest at the beginning of the breeding season and declined until the end of the breeding season while density throughout the non-breeding season increased (Figure 1.3). Within the larger study area, occupied shrike territories were consistently confined to a smaller (838 ha) core of suitable habitat. This occupied core supported a more dense population of 6.9 shrikes per km^2 (Table 1.1).

Home range sizes

I recorded 2084 perch locations of shrikes, 938 in the non-breeding season and 1146 in the breeding season. An average of 2 locations per visit (range 1-18) were taken for each bird. Forty-two birds had more than twenty locations (mean= 41 ± 15 locations) throughout the year, qualifying for home range analysis. Of those 42 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. One bird relocated during the non-breeding season and was excluded from calculations of non-breeding home range size. Three birds relocated territories between seasons and were excluded from the year-round analysis. Home ranges ranged from 1.6 to 6.1 ha depending on method of quantification and season (Table 1.2). Home range sizes using KDE did not differ significantly between breeding, non-breeding, and year-round (breeding and year-round: W= 336, p= 0.084; non-breeding and year-round: W= 381, p= 0.73). Breeding season home range sizes did not differ significantly from non-breeding home range sizes (W= 298, p= 0.089). Year-round territories were significantly larger than breeding territories (100% MCP: W= 240.5, p=0.002; 95% MCP: W= 218, p=0.0005), but not non-breeding territories.

Nearest Nest

Throughout three breeding seasons, 142 nests were monitored (2019: 40 nests; 2020: 50 nests; 2021: 52 nests). After choosing one random nest per breeding pair per year, I had 85 focal nests (2019: 21 nests, 2020: 31 nests, 2021:

33 nests). The median internest distance was 354 meters (range 43-1751 m; Figure 1.4).

Discussion

In this study, I quantified the of use of space by urban-nesting shrikes and found that they have small home ranges, high population density, and close nest spacing. While shrike populations are experiencing a range-wide decline, my results suggest that urban areas in coastal South Carolina may provide shrikes with novel habitats in which they can be successful. Moderate levels of development provide short-grass habitat which mimics natural grasslands. Urban areas may provide a greater abundance and variety of hunting perches than nearby rural areas (K. Maddox, unpublished data). Additionally, ornamental and landscaping plants offer abundant suitable nesting substrate commonly used by shrikes.

Home range size varies with resource availability and habitat quality (Buchmann et al. 2011, Diemer and Nocera 2014). Home ranges estimated in this study were smaller than all previous estimates regardless of method used (Table 1.3). This reduction in home range size in urban areas is consistent with the response of other taxa to urbanization (O'Donnell and delBarco-Trillo 2020). While fragmentation is likely a driver in shrike home range reduction, there were often unoccupied areas of comparable habitat directly adjacent to shrike home ranges that went unused. This indicates that the reduction in home range size may be a function of habitat quality as well as fragmentation. An analysis of habitat quality of occupied and unoccupied space would be necessary to fully understand the cause of the reduction in home range size of shrikes.

Seasonal changes in resource availability can also affect home range size (Chiang et al. 2012, Zurell et al. 2018). O'Brien and Ritchison (2011) found that shrikes maintained larger home range sizes during the non-breeding season in Kentucky than previously recorded during the breeding season and argued that winter territorial expansion may be due to a difference in prey availability outside of breeding season. Shrikes in coastal South Carolina experience milder winters than shrikes in Kentucky and do not expand their home ranges because they may not experience the same level of depletion in prey availability. The home range sizes derived from MCPs differed significantly between the breeding season and year-round home range. The year-round home ranges contain more locations for an individual and may be more reflective of the occasional wanderings of an individual shrike outside its most used area. The lack of difference in KDE derived home ranges may be because the home ranges produced by a 50% KDE represent a core area of use and do not reflect any occasional movements from the core area.

Home range is inversely related to population density (Morse 1976). Shrike home ranges in my study area were not only small but were often adjacent to other shrike territories. Maintaining small home ranges allows for a more densely packed population. While a dense urban population is not a sole indicator of high habitat quality, when taken into account with other measures of success, it can indicate successful habitat (Stracey and Robinson 2012). Within my study area, there are areas of unoccupied space which appear similar to occupied home ranges, indicating that competition for space is not the sole driver for smaller home range sizes.

Different shrike populations have experienced varying levels of decline which may result in different population densities throughout their range. In the Sandhills region of North Carolina, 140 km from my study area, systematic roadside surveys resulted in a density of 0.05 shrikes/km^2 (McNair 2015). This low density corresponds to a decline of 89% along the Atlantic Coast from 1970 to 2014. In the Intermountain West, shrikes have experienced a lower decline of 48% during this same period which may help to explain a greater shrike density (Rosenberg et al. 2016). Density within a wind resource area in California was 1.5 shrikes/km^2 (Smallwood and Smallwood 2021) and in a portion of the Chihuahuan Desert of New Mexico, density was 0.84 shrikes/km^2. (St. Louis et al. 2010). While estimates of population density may be strongly affected by study area size and regional population decline, my overall population density of 2.9 shrikes/km^2 was dramatically higher than any previous densities reported in non-urban populations (Table 1.4).

Few previous studies have quantifiably addressed the distribution of shrike nests in reference to their conspecifics, and metrics in those studies varied between mean internest distance and minimum nest distance. In Virginia, nests of adjacent territories were on average 546 m apart (n=5; Luukkonen 1987); the mean internest distance in this study was 428 m. In North Carolina, McNair (2015) found only one pair of shrike nesting territories (out of 45) within 1 km of each other; in this study, 78 out of 85 nests had another nest less than 1 km away. In Colorado, the closest two active nests were reported as 400m apart (n=77; Porter et al. 1975); in this study the closest internest distance was 43 m with 55 out of 85 nests being less than 400 m from their neighbor. Urban areas provide birds with more opportunities for nesting resulting from ornamental plantings as well as a greater density of pre-existing unused nests which may allow for these areas to support denser nesting populations (Chiang et al. 2012, Lövy and Riegert 2013).

Many species have been documented altering their behavior and constricting their home ranges as a response to urbanization (O'Donnell and delBarco-Trillo 2020). Urbanization is widely regarded as having a negative effect on wildlife, but grassland-mimicking urban habitats may have no effect on population densities of some species. In suburban Chicago, only one of seven grassland bird species surveyed was shown to have a negative association with level of development (Buxton and Benson 2016). The level of response to urbanization is widely dependent on species and habitat characteristics. In long-eared owls, home range sizes are smaller at a moderate level of development (Lövy and Riegert 2013), while lesser spotted eagles maintain smaller home ranges closer to human settlement (Mirski et al. 2020). Response may also vary within a species: shrikes in my study area readily utilize urban sites while shrikes in Arkansas actively avoid development (Brett DeGregorio, pers. comm.).

My results suggest that shrikes in the southeastern U.S. are actively taking advantage of the novel habitats being created by moderate levels of development. Within the undeveloped areas of Horry County, there is abundant agricultural habitat, yet these non-urbanized areas are sparsely populated by shrikes (pers. obs.). Despite the possible challenges associated with higher road density within urbanized areas and the resulting road mortality (Novak 1989, Flickinger 1995, Mumme et al. 2000), shrikes are able to persist and reproduce in this area.

Further studies of shrike population ecology, particularly breeding ecology, in urban environments are necessary to understand how this novel habitat might affect population dynamics of this rapidly declining species.

Tables and Figures

Table 1.1 Population density of urban loggerhead shrikes in the coastal plain of South Carolina between September 2019 and June 2022 (shrikes/km^2).

Study Area	2019	2020	2021	2022	Average
Entire Study Area (19.8 km^2)	3.2	3.2	2.8	2.6	2.9
Occupied Habitat (8.4 km^2)	7.6	7.6	6.6	6.1	6.9

Table 1.2 Average home range size of urban loggerhead shrikes 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[1]	2.9 ± 2.1[2]	1.6 ± 1.4
Non-Breeding (November-15 March)	19	2.5 ± 1.6	3.6 ± 2.4	2.0 ± 1.4
Year-Round	39	3.3 ± 2.0[1]	6.1 ± 6.7[2]	2.5 ± 2.7

[1],[2]: Year-round home ranges estimated by MCP were significantly larger than breeding territories; all other differences were not statistically significant.

Table 1.3 Estimated loggerhead shrike home range sizes in ten studies. All previous studies were conducted in non-urban populations.

Location	Area (ha)	Season	Method	Study
Missouri	4.6	Breeding	Not available	Kridelbaugh 1982*
New York	6.7	Breeding	Not available	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 available	Pruitt 2000
Virginia	17.5	Non-Breeding	95% MCP	Blumton 1989
California	34.0	Breeding	Not available	Scott and Morrison 1990
Kentucky	85.0	Non-Breeding	100% MCP	O'Brien and Ritchison 2011

*All previous estimates of home range, regardless of season or method, were larger than comparable estimates from this study (see Table 1.2). *As cited in Pruitt 2000.*

Table 1.4 Loggerhead shrike population density estimates. All but the current study are for non-urban populations.

Location	Density (shrikes/ km^2)	Method	Study	Study Area Size (km^2)
South Carolina	*6.9*	*Tracking marked individuals*	*This Study*	*8.4*
South Carolina	*2.9*	*Tracking marked individuals*	*This Study*	*19.8*
California[1]	1.5	Sampling plot surveys	Smallwood and Smallwood 2021	167.6
New Mexico[1]	0.84	10-minute point counts	St-Louis et al. 2010	45.4
North Carolina[1]	0.05	Roadside surveys	McNair 2015	1772

All previously reported population densities were estimated during the breeding season. [1]Density in shrikes/km^2 was extrapolated from nests/km^2 or pairs/km^2.

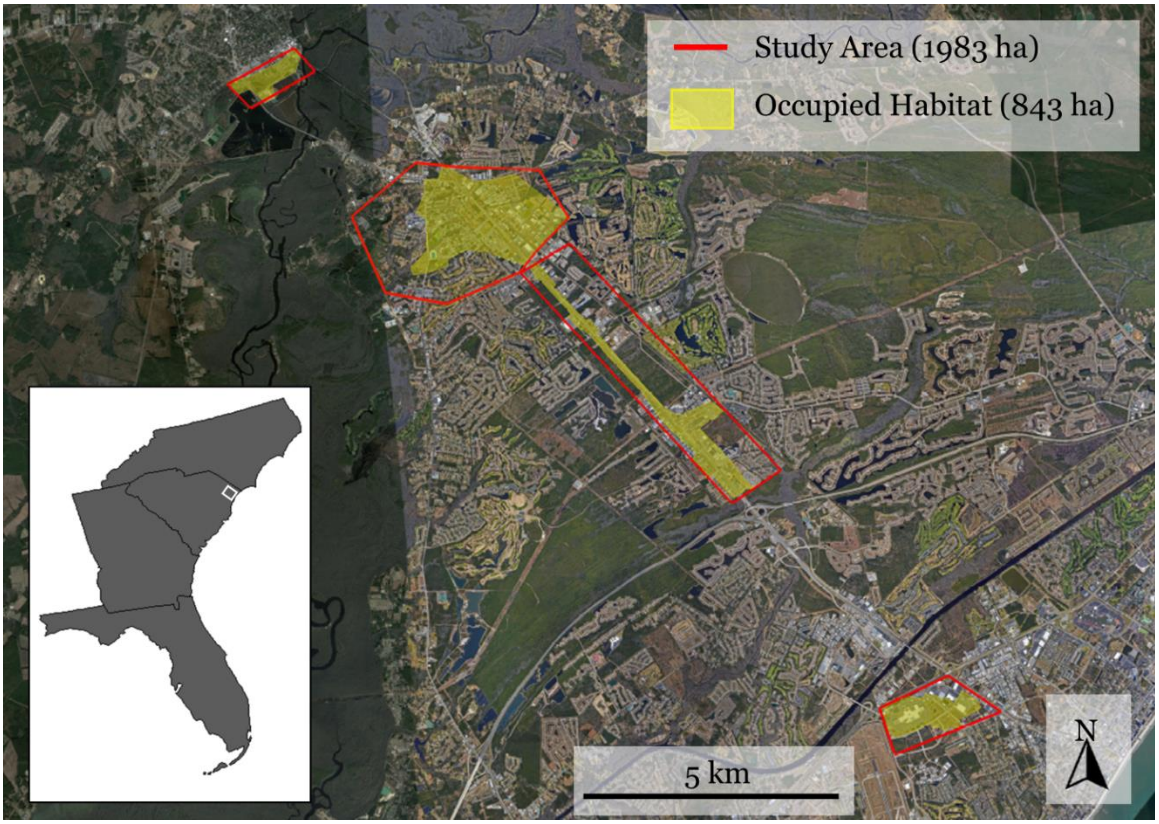

Figure 1.1 Map of the study area and occupied loggerhead shrike habitat within Horry County, South Carolina.

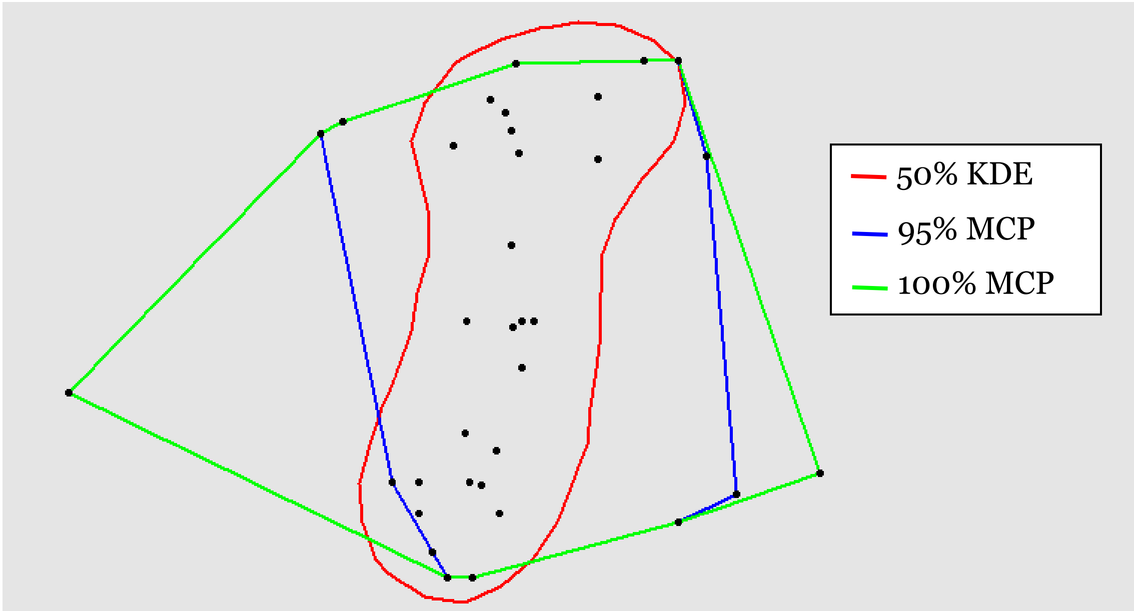

Figure 1.2 Example of home range estimations using a loggerhead shrike's year-round locations. The distribution of perch locations (black dots) within the kernel density estimator shows how forays from the core area used by a shrike can influence minimum convex polygons, especially the 100% MCP.

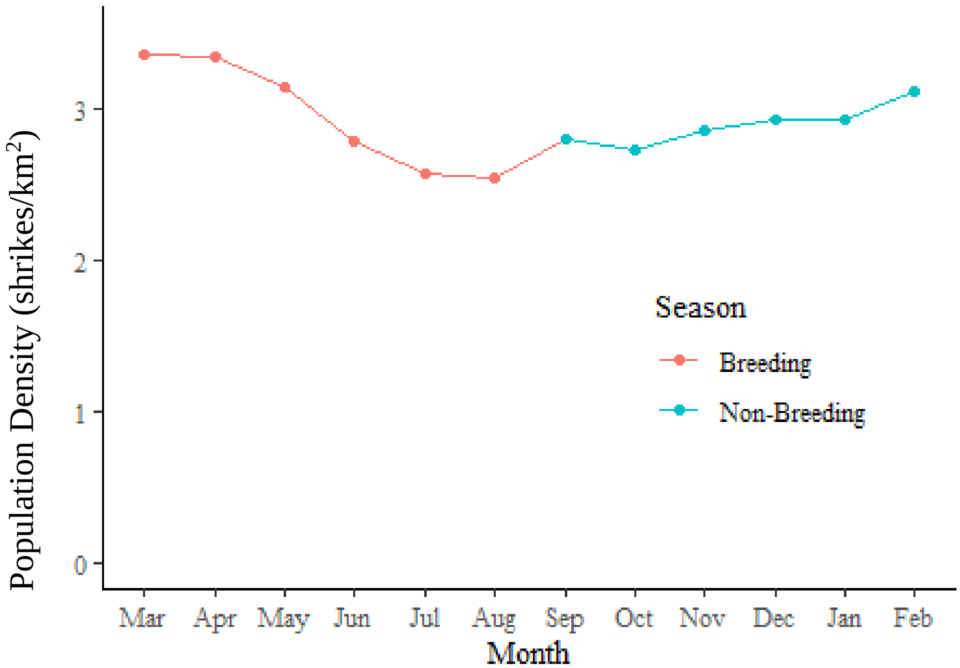

Figure 1.3 Population density trend of loggerhead shrikes in urban areas along South Carolina's coastal plain. Datapoints represent average monthly density from September 2019 to July 2022.

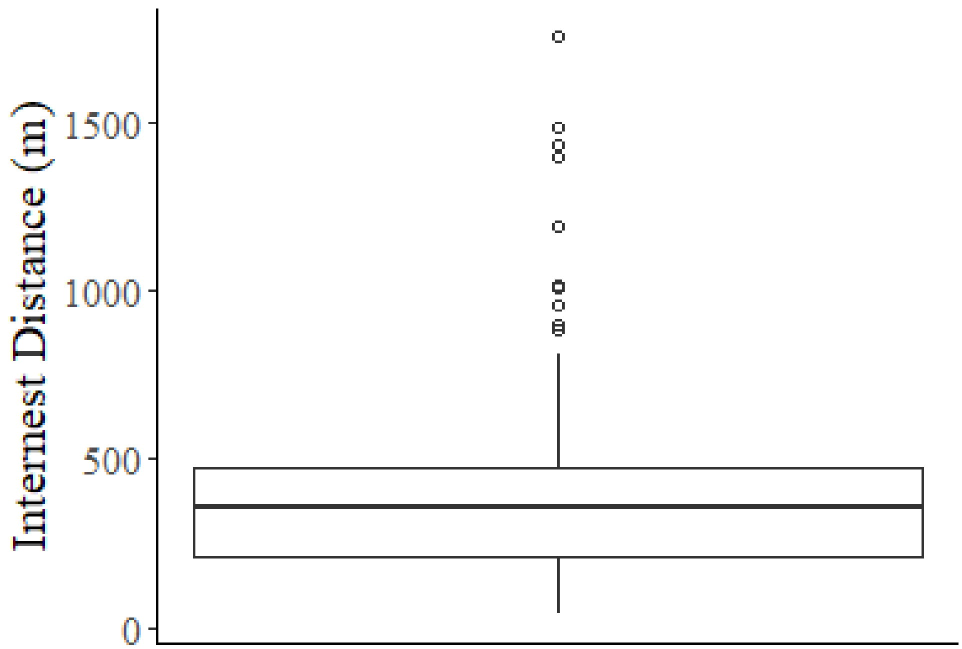

Figure 1.4 Boxplot of internest distances between neighboring active loggerhead shrike nests.

Chapter 2: Comparative Foraging Behavior between Loggerhead Shrikes in Rural and Urban Areas

Abstract

The process of development alters natural habitats and changes how organisms behave and acquire resources. Understanding how animals forage in urban areas is key to assessing the impact of urbanization on a species' life history and its ramifications on a population's long-term survival. Loggerhead shrikes (*Lanius ludovicianus*) are a predatory, grassland songbird which have been documented in urban areas in the Southeastern United States. In the present study, I compared the foraging behavior of shrikes in urban areas to their conspecifics in rural areas. I recorded shrike foraging behavior during 30-minute observation periods in Horry County, South Carolina from November 2020 to August 2021. I noted attempt outcome, prey, prey fate (eaten or cached), perch characteristics, foraging style (terrestrial or aerial pursuit), and ambient temperature. I used a MANOVA to compare the foraging behavior of shrikes foraging in urban areas and rural areas. I created a generalized linear mixed model to quantify how foraging behavior and perch characteristics impacted foraging outcome. I found no significant difference in the prey type, use of anthropogenic perches, caching rate of prey, perch height, or foraging style between shrikes in urban and rural areas. Shrikes in urban areas used more anthropogenic perches than natural, while shrikes in rural areas used both equally. Average foraging rate was 16 attempts per hour and did not differ between land uses or seasons. Capture

efficiency was consistent between land uses (80%), but shrikes during the breeding season were 10% more successful than during the non-breeding season (85% versus 75%). Foraging style, perch type, perch height, and temperature were included in the top-ranked model predicting foraging outcome. Shrikes were more successful from taller perches, natural perches, while foraging terrestrially, and at warmer temperatures. Habitat had no significant outcome on foraging success indicating that shrikes did not alter their foraging strategy as a result of urbanization.

Introduction

Foraging success is an indirect measurement of habitat suitability and is important to survival and reproduction. Optimal foraging theory predicts that animals make decisions while foraging which should minimize their expenditure of energy while optimizing their caloric reward (Pyke et al. 1977). Individual animals choose where to forage, what to forage on, and how to forage. Alterations to natural habitats resulting from urbanization, such as changes to community structure and land cover (McKinney 2002, Grimm et al. 2008), can affect how animals behave while foraging.

Urbanization alters the way animals, including birds, interact with their environment and how they acquire resources. Changes in anthropogenic food availability and arthropod diversity and distribution can affect the diet of birds in urban areas (McIntyre 2000, Robb et al. 2008, Planillo et al. 2021). These areas often alter habitat structure and provide novel perches (buildings, electrical wires, fences) and nesting sites (ornamental landscaping, eaves of buildings, rooftops; MacGregor-Fors and Schondube 2011, Reynolds et al. 2019). The land use changes resulting from development create habitats which are reminiscent of some natural foraging grounds and are therefore attractive to some species (Berry et al. 1998, Callaghan et al. 2019a, b).

Loggerhead shrikes (*Lanius ludovicianus;* hereafter referred to as "shrikes") are predatory songbirds whose foraging behavior mimics that of a bird of prey. They forage from conspicuous perches that offer a wide view of sparsely vegetated areas of short grass (Bent 1950, Kridelbaugh 1982 as cited in Yosef 1996). Although shrikes are able to forage in taller grasses, they spend less time flying and expend less energy when hunting in shorter grasses (Mills 1979, Yosef and Grubb 1993). The shrike's prey base is highly variable and includes arthropods, reptiles, amphibians, small birds and mammals (Bent 1950, Yosef 1996). Vertebrate prey, while less common than invertebrates in shrike diets, offer higher caloric returns (Craig 1978). However, the handling time required to catch and ingest vertebrates is greater and may negate the higher energetic payoff (Craig 1978). Vertebrate prey comprises more of shrike diets in some parts of their range where they readily forage on reptiles and amphibians (Arkansas: Donahue et al. 2021, New Mexico: Hathcock and Hill 2018). In other parts of their range, invertebrates are the dominant prey (South Carolina: Gawlik et al. 1991, Kentucky: O'Brien and Ritchison 2011, Florida: Yosef and Grubb 1993). In the western parts of shrike range, seasonal differences in diet have been observed (Craig 1978, Mills 1979), while diet in southern regions remains consistent across seasons (Howery 1991 as cited in Yosef 1996).

Because shrikes hunt from exposed perches, perch availability plays a large role in habitat preference (Bohall-Wood 1987, Yosef and Grubb 1994). Shrikes readily use anthropogenic perches, particularly electrical wires (Mills 1979, O'Brien and Ritchison 2011, Donahue et al. 2021). When presented with both natural and anthropogenic perches, shrikes use anthropogenic perches more often (Bohall-Wood 1987), perhaps because they are more likely to offer unobstructed viewlines. Compared to rural areas, urban areas may offer a more diverse array of tall, bare perches at varying heights from which shrikes can forage.

Early stage development resulting from urbanization creates open, short-grass habitats that may be particularly attractive to shrikes (Krauser 2022). Although shrikes have been documented using urban areas (Emlen 1974, Grubb and Yosef 1994, Boal et al. 2003, McNair 2015, Worm and Boves 2019) they are understudied in urban habitats and it is unknown how their foraging behavior is altered as a result of anthropogenic land use change. The objectives of this study were to (1) compare foraging behavior of shrikes in urban and rural areas, (2) compare foraging rate and capture efficiency across both land use (urban and rural) and season and (3) understand which aspects of foraging behavior contribute most to the outcome of an individual foraging attempt. These comparisons will allow for further insight into the challenges being faced by shrikes range-wide and their futures in human-dominated landscapes.

Methods

Study Site

The study was conducted in Horry County, South Carolina (33.91°N, 78.98°W), which is experiencing substantial human population growth and change (2021 population: 365,000; United States Census Bureau 2021) coinciding with change in land use. Most of the county is made up of rural areas with low levels of development and low population densities. However, the coastline of Horry County is highly developed, functionally creating an urban to rural gradient from east to west. From 2001 to 2019, Horry County experienced a 24% net increase in developed area and a 41% net increase in impervious surface area (Multi-Resolution Land Characteristics Consortium [U.S.] 2019).

Foraging Observations

Fieldwork was conducted during both the breeding season and non-breeding season. Non-breeding foraging observations were conducted from November 2020–February 2021 and foraging observations during the breeding season were conducted from June 2021–August 2021. I conducted observations only during daylight hours and never during rain or snow. Only adult shrikes were observed foraging, and each observation lasted 30 minutes (maximum) or until the shrike disappeared from view. Only observations lasting at least 20 minutes were included in analyses. Shrikes were observed using both Vortex Diamondback HD 10x42 binoculars and a Vortex Razor HD 22-48x65 spotting scope (Barneveld, WI). Temperature was recorded at the beginning of observation using The Weather Channel app for Android (TWC Product and Technology 2022, Atlanta, GA).

During observations I recorded the outcome of each foraging attempt. A foraging attempt is a directed flight to the ground or toward potential flying prey, followed by a return to an elevated perch. Since shrikes will occasionally hunt on the wing, I recorded if the foraging attempt was to the ground (terrestrial) or an aerial pursuit. I calculated the hourly foraging rate using length of observation and number of hunting attempts. High-powered optical equipment allowed me to observe a shrike directly target and capture a prey item, indicating a successful attempt. In the case that I was unable to maintain a line of sight on the shrike while it was foraging on the ground, success of a foraging attempt was determined by the presence of a prey item in the beak or if the shrike was seen swallowing or feaking. Feaking is a behavior in raptorial birds when an individual wipes its beak on an object, most commonly a perch, after ingesting prey. If I was unable to maintain a line of sight on a foraging attempt, the lack of a prey item when returning to a perch indicated an unsuccessful attempt. If the outcome of an attempt was unable to be determined, it was recorded as unknown. Capture efficiency was calculated as captures per total attempts. For successful attempts, prey identity was determined to be invertebrate or vertebrate. I recorded the prey fate (whether the prey was consumed, cached, or fed to another shrike). Perch characteristics were also recorded: height (to the nearest meter) and type (anthropogenic or natural). I used the National Land Cover Database (NLCD) to classify the area directly surrounding the location where the shrike was foraging. I classified developed areas as urban and areas of planted crop, cultivated crop, herbaceous cover, or shrubland as rural (Multi-Resolution Land Characteristics Consortium [U.S.] 2019).

Data Analysis

All statistical analyses were conducted in R version 4.2.1 using RStudio version 2022.7.2.576 (R Core Team 2022, RStudio Team 2022). In order to compare and describe the foraging behavior of shrikes in urban versus rural areas, I combined data across seasons. To give equal weight to each shrike, I compared the averages of an individual shrike's foraging attempts. For each bird, I calculated the average perch height used, proportion of perches which were anthropogenic, proportion of perches which were electrical wires, proportion of attempts which were aerial, and proportion of prey which was cached. I used a multivariate analysis of variance (MANOVA) to compare the foraging behavior of shrikes in urban and rural areas. With land use as the independent variable, I included five dependent variables (1) average perch height, (2) average proportion of perches which were anthropogenic, (3) average proportion of perches which were electrical wires, (4) average proportion of foraging attempts which were aerial, and (5) average proportion of prey which was cached. I compared caching rate between urban and rural areas only during the non-breeding season because nesting stage of observed adults during the breeding season was unknown and likely would influence the fate of prey items. To compare perch usage within urban birds and rural birds, I conducted two Wilcoxon Rank-Sum tests on proportion of natural versus anthropogenic perches. All statistical tests were two-tailed.

I performed an additive two-way ANOVA to investigate the effects of season on attack frequency and capture success of individual. I then used the Tukey post-hoc test to compare significant differences between groups.

To understand which aspects of foraging behavior best predicted foraging success, I created a generalized linear mixed model with outcome (successful vs. unsuccessful) as a binary response variable. I considered six fixed effects: land use, season, perch type, perch height, foraging style, and temperature for inclusion in the model. Bird identity was treated as a random effect to account for individual differences. I used the vif() function in the "car" package to test for multicollinearity between my variables (Fox and Weisberg 2019). After testing for multicollinearity, the global model incorporated land use, perch type, perch height, foraging style, temperature, and bird identity. I used the glmer() function in package "lme4" to build the global model (Bates et al. 2015) and used the dredge() function of the "MuMIn" package to perform model selection (Bartoń 2022). I ranked the models based on AIC_c, ΔAIC_c, and Akaike weights. Then I performed fivefold cross-validation and computed the area under the curve (AUC) using package 'pROC' (Robin et al. 2011) for the top ten ranked models. For the top-ranked model, I computed the odds ratios of all included predictor variables.

Results

I observed 76 shrikes (37 urban, 39 rural) make 527 foraging attempts over the course of 34 hours of foraging observations. Observations lasted 27 minutes on average (range= 20-30 minutes). Less than 5% of attempts had unknown outcomes (25 attempts) and those were removed from analysis. Two shrikes did not forage during the observation period and were only included for foraging rate analysis.

Invertebrates comprised 99% of prey items; only 5 successful hunting attempts were on vertebrate prey: two frogs, one rodent, one bird (*Passer domesticus*, House Sparrow), and one lizard. All vertebrates were caught in urban areas. Hunting on the wing only contributed to a small proportion of foraging attempts and only 23 of 74 birds hunted aerially. The rate of aerial attempts did not differ with land use (urban: 8%, rural: 16%; $F_{1,72}$= 0.1125, p=

0.22; Table 2.1, Figure 2.1). Land use had no impact on caching rate and only four shrikes cached prey. In urban areas, prey was cached 1% of the time versus 3% in rural areas ($F_{1,36}$= 0.515, p= 0.48; Figure 2.2). Within urban and rural areas, shrikes used anthropogenic perches equally ($F_{1,72}$= 2.68, p= 0.11; Figure 2.3). Urban shrikes used anthropogenic perches more often than natural perches while rural shrikes used anthropogenic perches as often as natural perches (urban: 73% versus 27%, W=1018, p= 0.00001; rural: 58% versus 42%, W= 896, p= 0.066). Anthropogenic perches used in rural areas were limited to fences, posts, signs and wires while a more diverse range of perches (batting cages, buildings, guardrails, gravestones, posts, signs, and wires) were used in urban areas. Electrical wires were the most common anthropogenic perch used by shrikes in both areas (median values: urban: 5%, rural: 50%; $F_{1,72}$= 1.94, p=0.17; Figure 2.4). Average perch height did not differ significantly between land uses: 4.0m ± 1.9 in urban areas versus 4.8m ± 1.8 in rural ($F_{1,72}$= 3.50, p= 0.066; Figure 2.5).

Foraging rates did not differ between urban and rural habitats (median values: urban 18 attempts/hour, rural 14 attempts/hour; $F_{1,73}$= 1.595, p= 0.074) or seasons (median values: breeding: 14 attempts/hour, non-breeding: 17 attempts/hour; $F_{1,73}$= 2.953, p= 0.09). Capture efficiency did not differ between land use (median values: urban success rate: 79%, rural: 81%; $F_{1,71}$= 0.137, p= 0.674), however season had a significant effect (median values: breeding: 85%, non-breeding: 74%; $F_{1,71}$= 5.589, p=0.021).

Two candidate models predicting foraging attempt outcome had ΔAICc values <2. The most likely model of foraging success included predictor variables of foraging style, perch height, perch type, and temperature (Table 2.2). None of the predictor variables included in the top model had odds ratios with confidence intervals that included one, indicating that all variables had a significant relationship to outcome (Table 2.3). The odds of a terrestrial foraging attempt being successful is 2.3 times greater than an aerial attempt. The odds of a successful foraging attempt from a natural perch were 2.3 times greater than from man-made perches. The odds of success increased by 7% for every 1°C increase in ambient temperate and 18% for every 1-meter increase in perch height (Table 2.3). Success of terrestrial foraging attempts increased as perch height and temperature increase. Aerial foraging attempts showed the opposite trends (Figure 2.6, Figure 2.7). The success of a foraging attempt from either man-made or natural perches increased with both increased temperature and perch height (Figure 2.8, Figure 2.9)

Discussion

Loggerhead shrikes in urbanized habitats exhibited comparable foraging behaviors to their conspecifics in rural areas. Capture efficiency, foraging rate, foraging style, caching rate, perch use and perch height did not differ between land uses. The increased use of anthropogenic perches by shrikes in urban areas may be a response to the difference in availability of man-made perches rather than an indication of preference. With development comes human erected structures such as electrical towers and boxes, road signs, guardrails, and fences, yet urban and rural shrike perch height and usage did not differ. Despite a difference in structural complexity, shrikes in urban areas are not altering their foraging strategy in response and rather maintain the foraging behavior observed in non-urbanized habitats.

Shrikes in this study foraged at a rate of 16 attempts per hour and approximately 80% of all hunting attempts were successful. These results are most comparable to shrikes in Florida (breeding season; Howery 1991 as cited in Yosef 1996), where capture efficiency was 85%. Previous foraging studies have reported a relationship between latitude and capture efficiency. Hunting success is greatest in the southern extent of shrike range. In mid-latitudes, success was 66% (Kentucky, non-breeding season; O'Brien and Ritchison 2011) and 58% (Arkansas, non-breeding season; Donahue et al. 2021). In the northern extent of their range, success was estimated to be 28% in (Alberta, breeding season; Collister 1994). While this trend in capture efficiency may be explained by latitude, season may also be impacting efficiency.

Capture efficiency was significantly greater during the breeding season when demand for food is higher to support reproduction. Rather than increasing foraging rate, capture efficiency increased. This shift in foraging outcome during the breeding season to account for higher energetic requirements has been observed in other bird species including grey herons and pied babblers (Golabek et al. 2012, Matsunaga 2000). The diet composition findings are consistent with other observational studies of shrikes in the eastern part of their range with invertebrates accounting for the majority of prey items. Four of the five vertebrate prey captures occurred during the breeding season, suggesting that there may be a relationship between vertebrate captures and season. Shrikes during the breeding season may show a preference towards vertebrate prey when demand is high with an active nest of chicks. This strategy is opposite of shrikes in California which maintained their reliance on smaller invertebrate prey while increasing foraging rate (Morrison 1980). The low representation of vertebrate prey in this study helps to explain the low caching rate observed (3% of successful hunting attempts), as caching behavior of shrikes exists in part to handle and store larger prey (Yosef and Pinshow 2005 but see Yosef et al. 1996). In other parts of their range, vertebrate prey constitutes more of the diet, but vertebrates are still outnumbered by invertebrates (Kridelbaugh 1982 as cited in Yosef 1996). However, the low occurrences of vertebrate prey in this study are not able to provide enough power to fully support the relationship between vertebrate preference and season or compare my results with those of Morrison (1980). A study of prey diversity and abundance would be necessary to understand whether diet of shrikes in our region is a result of choice or a mere reflection of prey availability.

Perch type and perch height were both included in the top-ranked model. This supports the findings of other studies that viable perches, particularly wires, are vital to a productive territory for sit-and-wait avian predators (Yosef and Grubb 1994, Lynn et al. 2006). Despite the tendency for shrikes to use anthropogenic perches and shorter perches, success from natural perches and taller perches was greater. The preference towards shorter perches is consistent with a population of shrikes in Texas which had a wide range of natural perches available (Chavez-Ramirez et al. 1994). Perching lower to the ground allows shrikes to see prey more clearly, especially in areas of shorter vegetation like maintained grasses in urban landscapes (Mills 1979, Yosef and Grubb 1993).

Temperature has ramifications on prey availability and foraging energy expenditure (Caraco et al. 1990, Diggs et al. 2011) and shrikes must adapt their foraging behavior accordingly. Aerial attempts tended to be less successful in hotter temperatures. Foraging aerially is more energetically taxing than sit-and-wait hunting and should be avoided at extreme temperatures. While my data suggests a relationship, I only observed 54 aerial foraging attempts and more occurrences would be necessary to fully understand this trend.

Shrikes in urban areas take advantage of the novel habitats created by development with no apparent cost to their capture efficiency or success. While urbanized areas alter the habitats of shrike foraging grounds, these changes have no apparent impact on the foraging outcome in urban areas. Although I found no relationship between urbanization and foraging success of individuals, it may be affecting other aspects of their life histories. Urbanization is associated with pollution (McKinney 2002), greater road densities, which could result in higher incidences of road mortality (Flickinger 1995, Mumme et al. 2000, Donahue et al. 2021) and changes in nest predator abundances (Jokimäki et al. 2005). Future studies of survival, breeding biology, and persistence of shrikes in urban areas are warranted to fully understand the impacts of urbanization on loggerhead shrike biology.

Tables and Figures

Table 2.1 Results of MANOVA comparing Loggerhead shrike foraging characteristics in urban and rural areas in the Coastal Plain of South Carolina. Values represent median values (with sample size) of individual birds' foraging behavior.

	Urban	Rural	p-value
Foraging Rate* (attempts/hour)	17.84 (1.9, N= 37)	13.65 (1.5, N= 39)	0.074
Capture Efficiency (proportion successful)	0.79 (0.03, N= 36)	0.81 (0.03, N= 38)	0.674
Perch Height (m)	3.95 (0.31, N= 36)	4.76 (0.30, N= 38)	0.066
Perch Type (proportion anthropogenic)	0.73 (0.06, N= 36)	0.58 (0.06, N= 38)	0.11
Perch Type (proportion electrical wire)	0.36 (0.07, N= 36)	0.49 (0.06, N= 36)	0.17
Foraging Style (proportion aerial)	0.08 (.03, N= 36)	0.16 (.06, N= 38)	0.22
Caching Rate† (proportion cached)	0.01 (0.01, N= 19)	0.03 (0.02, N= 19)	0.48

*Sample size for foraging rate included two shrikes who made zero foraging attempts during observation period.

†Caching rate sample sizes were smaller because only non-breeding season was considered. Nesting stage during the breeding season was unknown and would impact prey fate.

Table 2.2 Top ten generalized linear mixed models, ranked by AICc values, describing how foraging behavior predicts outcome of individual foraging attempts (N = 502 foraging attempts).

Model	AICc	ΔAICc	Akaike Weight	AUC (95% confidence interval)
Outcome ~ foraging style + perch height + perch type + temperature + (1|Bird)	524.195	-	0.535	0.702 (0.600-0.803)
Outcome ~ foraging style + land use + perch height + perch type + temperature + (1|Bird)	525.962	1.767	0.221	0.703 (0.601-0.804)
Outcome ~ perch height + perch type + temperature + (1|Bird)	526.872	2.678	0.14	0.693 (0.588-0.797)
Outcome ~ land use + perch height + perch type + temperature + (1|Bird)	528.436	4.241	0.064	0.691 (0.585-0.797)
Outcome ~ foraging style + perch type + temperature + (1|Bird)	532.61	8.415	0.008	0.649 (0.539-0.759)
Outcome ~ foraging style + perch height + temperature + (1|Bird)	532.976	8.781	0.007	0.643 (0.531-0.756)
Outcome ~ perch height + temperature + (1|Bird)	533.089	8.895	0.006	0.648 (0.528-0.769)
Outcome ~ perch type + temperature + (1|Bird)	533.506	9.312	0.005	0.639 (0.524-0.755)
Outcome ~ foraging style + land use + perch type + temperature + (1|Bird)	534.644	10.45	0.003	0.658 (0.551-0.764)
Outcome ~ foraging style + land use + temperature + (1|Bird)	534.77	10.576	0.003	0.618 (0.502-0.733)

Fixed effects: *foraging type* aerial or terrestrial foraging, *land use* urban or rural, *perch height* height of perch used (m), *perch type* man-made or natural perch, *temperature* ambient temperature (°C). Random effect: *(1|Bird):* bird identity.

Table 2.3 Odds ratio for top-ranked model predicting foraging outcome with 95% confidence intervals.

	Odds Ratio	Lower Confidence Interval	Upper Confidence Interval
Foraging Style (Terrestrial)	2.27	1.11	4.66
Perch Height (m)	1.18	1.07	1.31
Perch Type (Natural)	2.30	1.38	3.86
Temperature (°C)	1.07	1.04	1.11

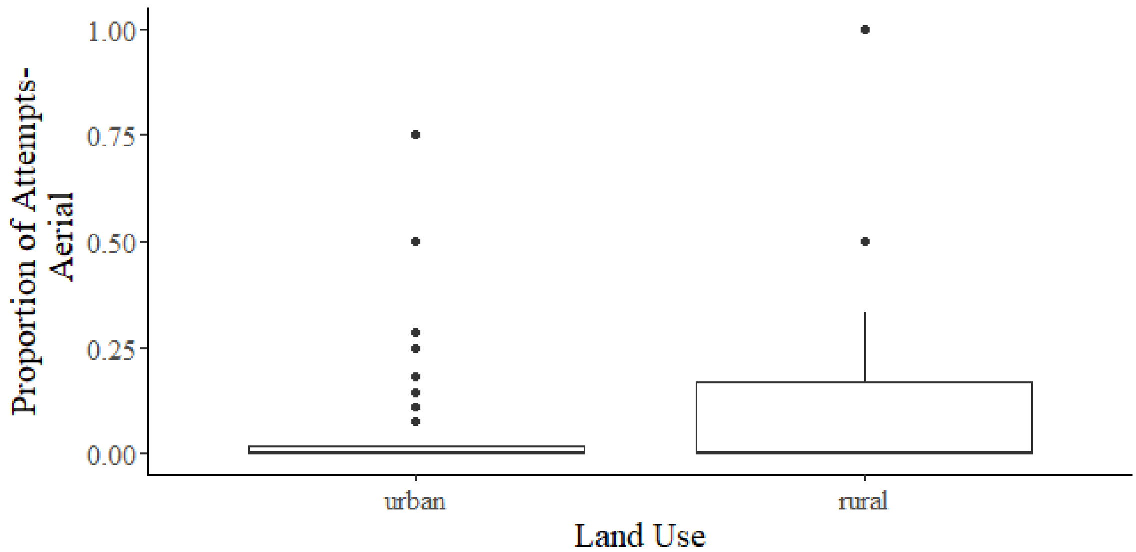

Figure 2.1 Boxplot of average proportion of foraging attempts which were aerial by loggerhead shrikes in coastal South Carolina in urban and rural areas. Data represents individual birds' foraging behavior. 51 of 74 shrikes never hunted aerially.

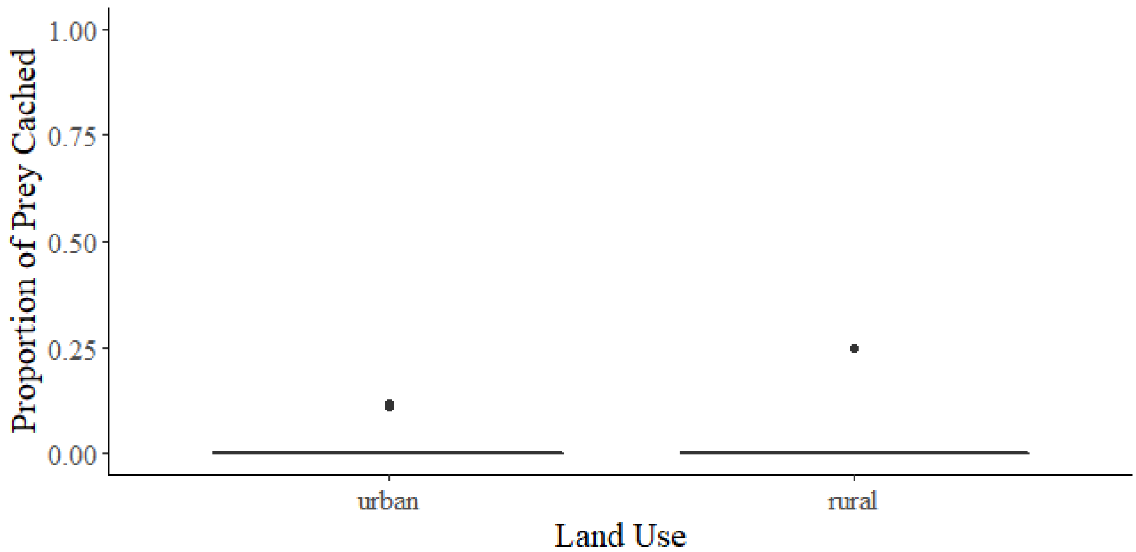

Figure 2.2 Boxplot of average proportion of prey which was cached by loggerhead shrikes in coastal South Carolina in urban and rural areas. Data represents individual shrike foraging behavior. Only 4 of 74 birds cached prey.

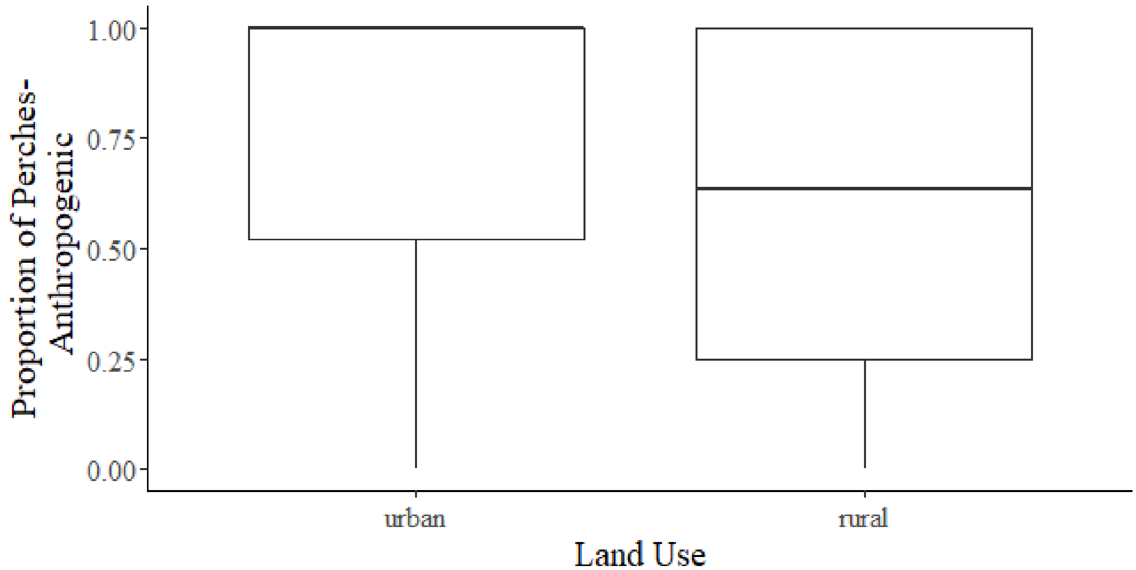

Figure 2.3 Boxplot of average proportion of perches which were anthropogenic used by 74 loggerhead shrikes in coastal South Carolina in urban and rural areas.

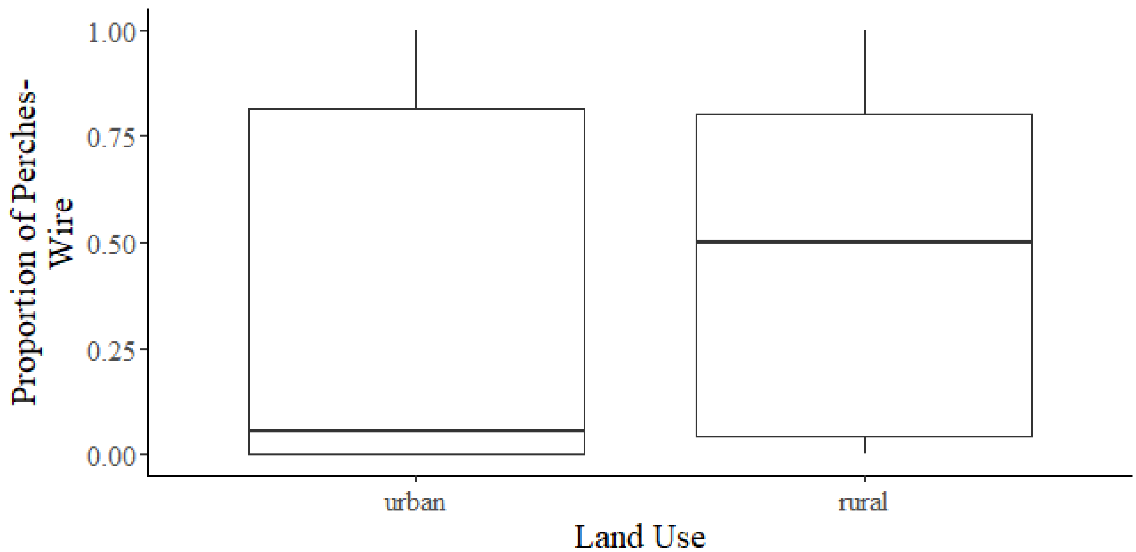

Figure 2.4 Boxplot of average proportion of perches which were wires used by 74 loggerhead shrikes in coastal South Carolina in urban and rural areas.

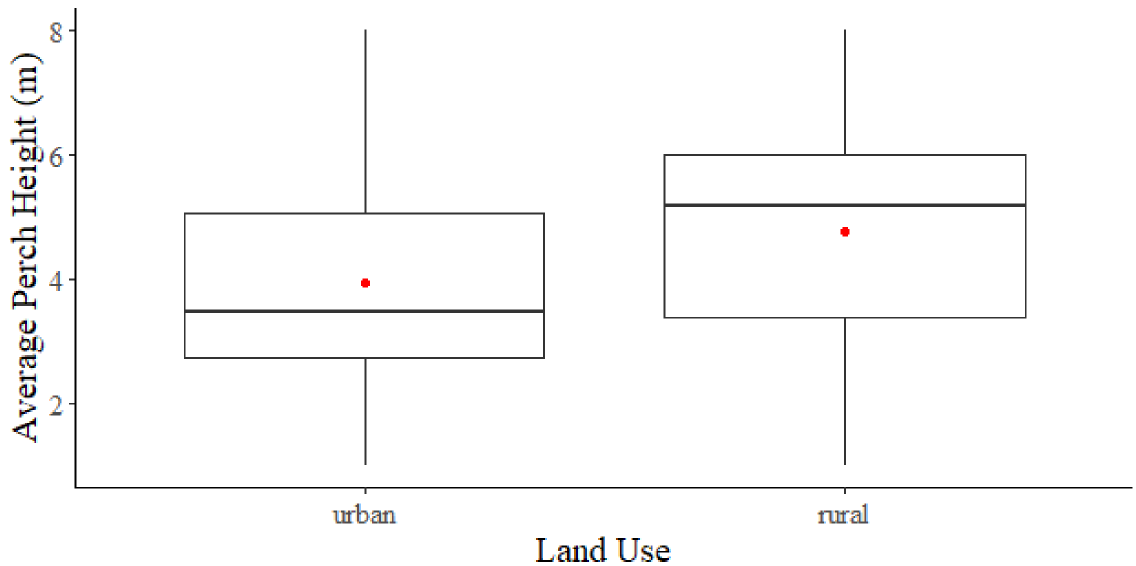

Figure 2.5 Boxplot of average perch height used by 74 loggerhead shrikes in coastal South Carolina in urban versus rural areas. The red dot represents the mean.

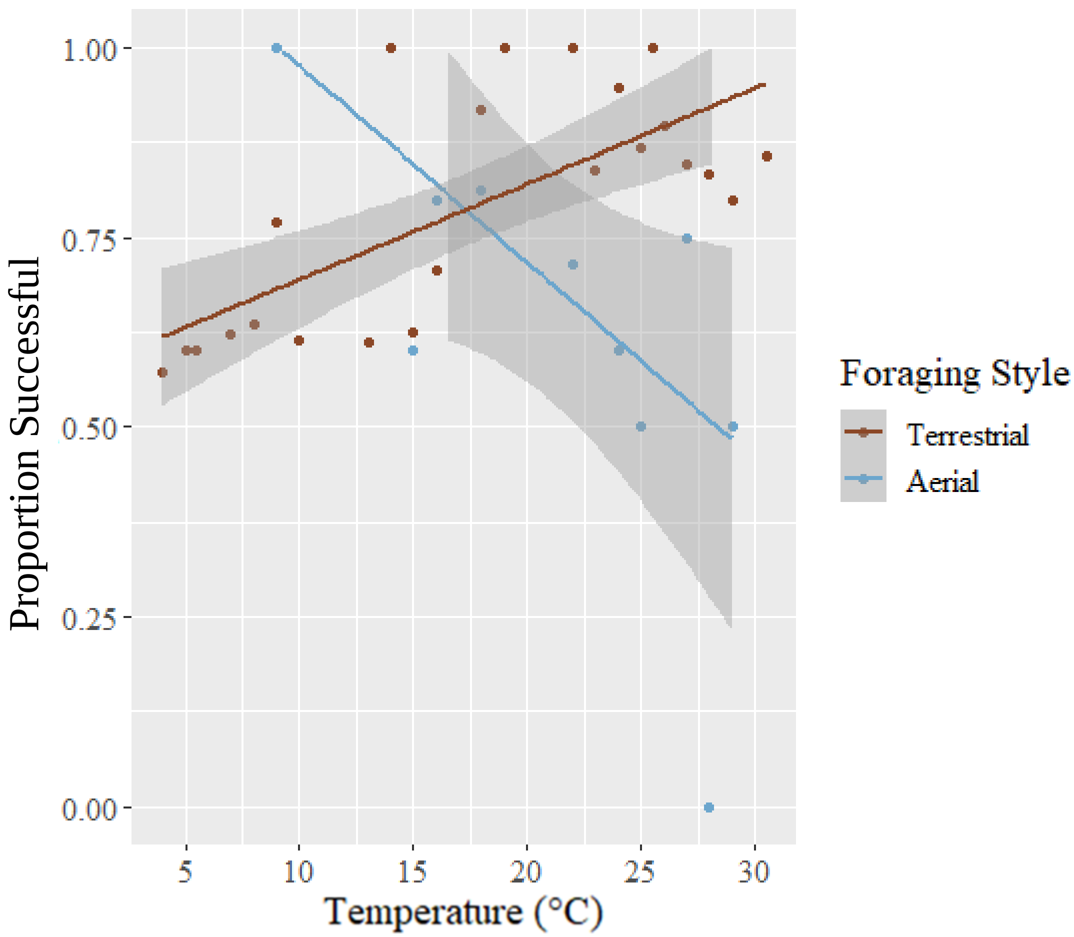

Figure 2.6 Linear regression of the proportion of attempts which were successful across temperatures and foraging styles. Terrestrial foraging attempts were more successful at greater temperatures. Success of aerial attempts tended to decrease with increased temperature. The shaded area represents the 95% confidence interval for the fitted values.

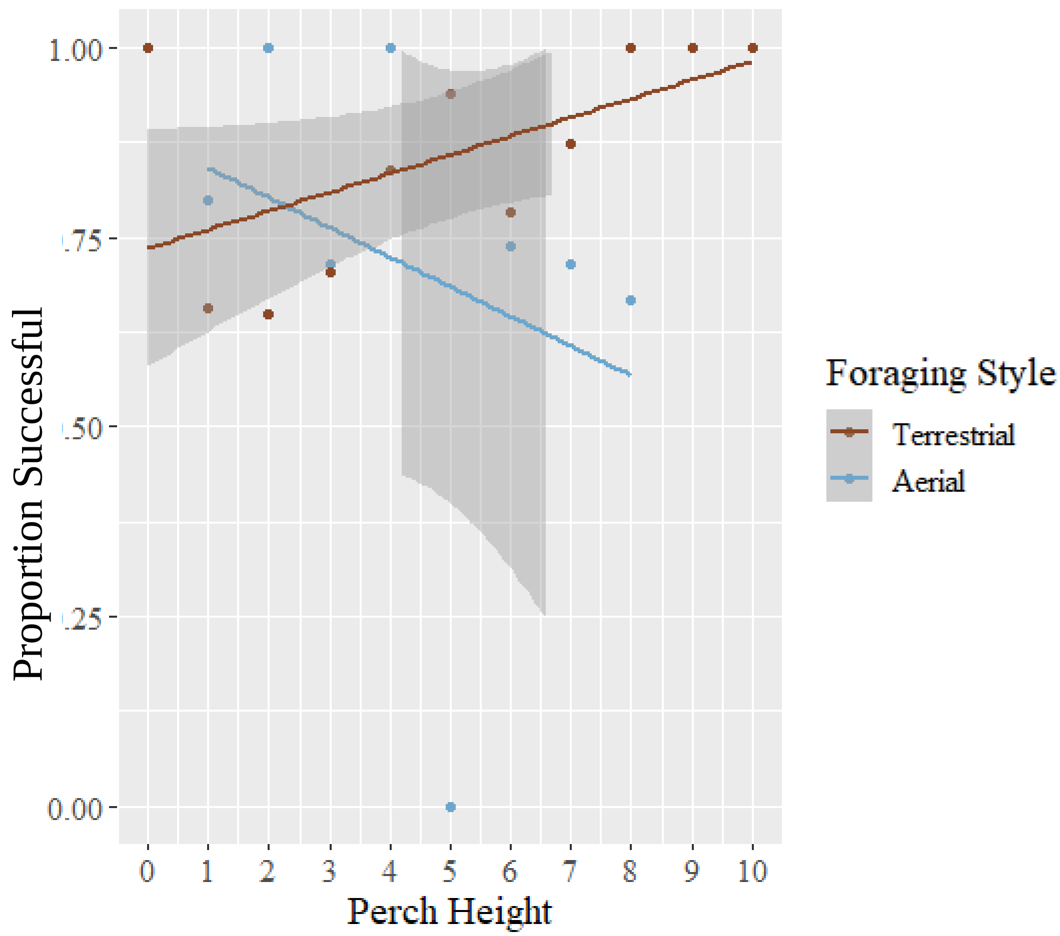

Figure 2.7 Linear regression of the proportion of attempts which were successful across perch height and foraging styles. Terrestrial foraging attempts were more successful as perch height increases while aerial attempts tended to be less successful with increasing height. The shaded area represents the 95% confidence interval for the fitted values.

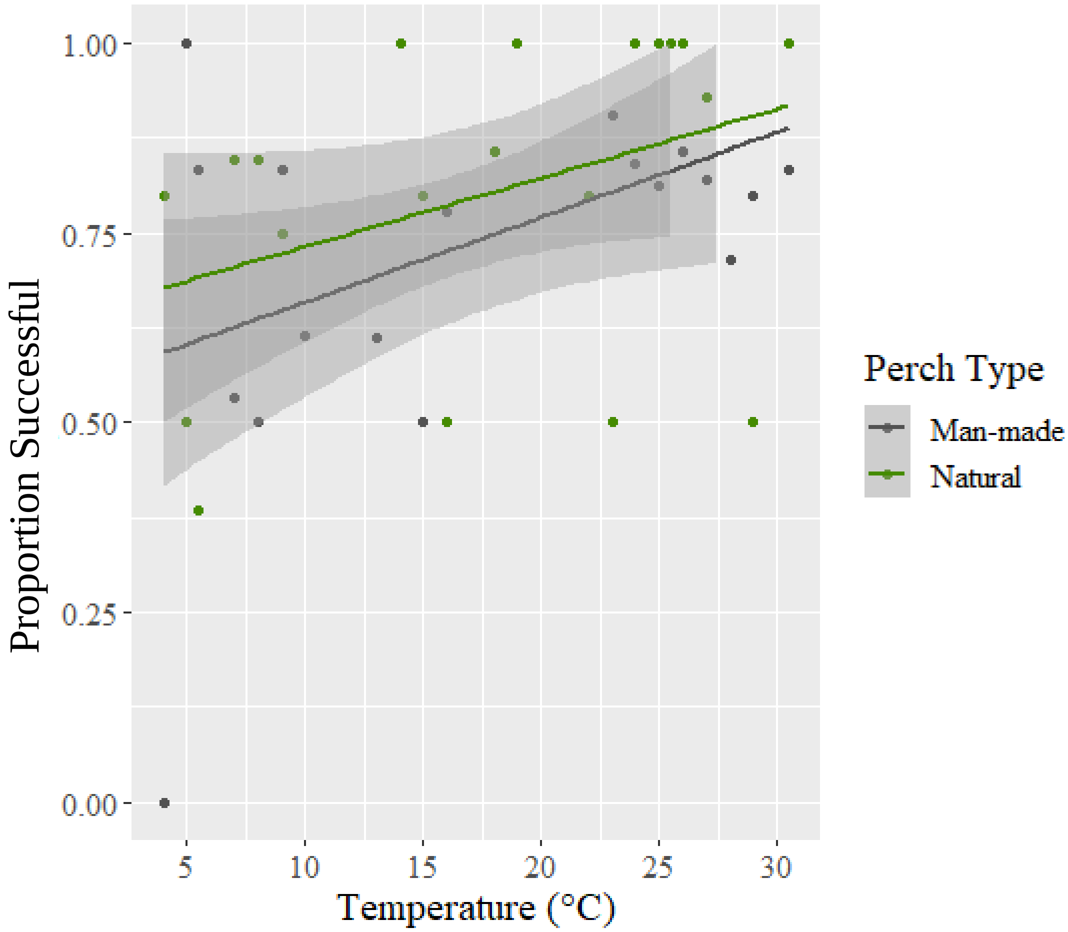

Figure 2.8 Linear regression of the proportion of attempts which were successful across temperatures and perch types. Regardless of perch type, success tended to increase in warmer temperatures. The shaded area represents the 95% confidence interval for the fitted values.

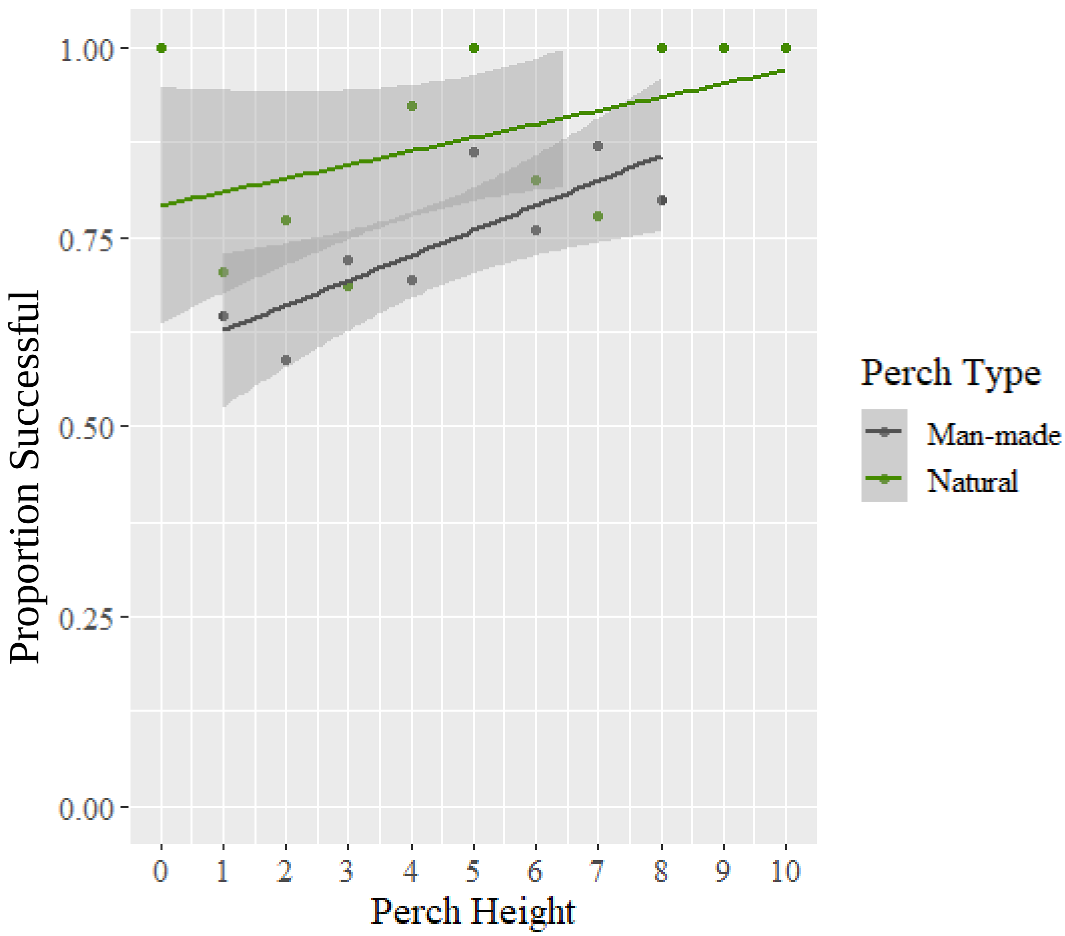

Figure 2.9 Linear regression of the proportion of attempts which were successful across perch height and perch types. Regardless of perch type, success tended to increase at greater heights. The shaded area represents the 95% confidence interval for the fitted values.

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