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## Non-breeding Behavior and Diet of Loggerhead Shrikes in an Intensive Agricultural Region

Emily R. Donahue<sup>1,\*</sup>, Kevin J. Krajcir<sup>1</sup>, Lee C. Bryant<sup>1</sup>, Rhett Raibley<sup>1</sup>,  
Jacob L. Wessels<sup>1</sup>, Joseph Youtz<sup>1</sup>, and Than J. Boves<sup>1</sup>

**Abstract** - As agricultural conversion has transformed the landscape across the central United States, populations of grassland-associated species, such as those of *Lanius ludovicianus* (Loggerhead Shrike), have declined. Understanding the ecology and behavior of grassland species in these highly anthropogenic, agricultural landscapes provides vital information for conservation efforts. However, few studies have assessed the ecology and behavior of this species in intensive agricultural areas, especially during the potentially critical non-breeding season. To help fill these knowledge gaps, we used direct behavioral and larder surveys to describe the non-breeding ecology and behavior of Loggerhead Shrikes in the agriculturally dominated Lower Mississippi Alluvial Valley of Arkansas. Over 3 winters, we observed behavior of Loggerhead Shrikes and found that they spent most of their time perched and scanning for prey (81%), mainly from utility wires (68% of used perches). On average, they made  $14.9 \pm 1.2$  foraging attempts/hr and focused their efforts mostly in right-of-way grasses and adjacent agricultural fields. Overall, individual foraging success rates averaged 58%, did not differ amongst microhabitats, and were comparable to rates reported for breeding Loggerhead Shrikes from other habitats at similar latitudes. Arthropods were the most frequently captured prey (76%; based on direct behavioral surveys), and anurans were the most commonly cached prey (43% of observed cached items). In total, our study highlights the importance of utility wires and rights-of-way for foraging and arthropods as food sources, throughout even the coldest months of the year at this latitude, and increases our understanding of the behavior and ecology of the Loggerhead Shrike in these contexts.

### Introduction

With ever-growing human populations driving the need for mass food production, conversion of native grasslands to intensive agricultural landscapes has become the global norm (Tilman et al. 2011). In North America, over 80% of native grasslands have already been converted to agricultural lands (With et al. 2008), which now cover 379 million ha in the United States alone (Fernandez-Cornejo et al. 2014). This ongoing landscape conversion is often considered an underlying cause of the severe declines of grassland bird populations across the United States over the past half century (Murphy 2003). In fact, grassland birds have experienced greater declines in population than any other avian group in North America (Rosenberg et al. 2019), and our ability to conserve these species through management decisions may rely on how they adapt to and use agricultural landscapes.

*Lanius ludovicianus* L. (Loggerhead Shrike, hereafter also Shrike) is one example of a grassland-associated species that has declined across its range. Breeding

<sup>1</sup>Department of Biological Sciences, Arkansas State University, Jonesboro, AR 72467. \*Corresponding author - emilyrdonahue@gmail.com.

Shrike populations inhabiting the eastern United States have faced average annual declines of 5%, which equates to a total loss of about 92% from 1966 to 2015 (Sauer et al. 2017), and land-use changes are likely implicated in this decline (Prescott and Collister 1993, Pruitt 2000, Yosef and Grubb 1992). In addition to the role that agricultural conversion has played, the associated demographic cause(s) of Shrike declines also remains (remain) unclear, but some studies suggest that low survival rates during the non-breeding season have been highly influential (Blumton 1989, Brooks and Temple 1990). Historically, Shrikes inhabited native grasslands and savannas during both the breeding and non-breeding seasons (Yosef 1996). However, with the clearing of forests and large-scale conversion of grasslands for agricultural purposes, Shrikes are now also found in many agricultural landscapes (Pruitt 2000). Despite their presence in these areas, we still lack basic information about behavior and ecology of Shrikes in the agricultural habitats that now dominate the central United States.

Time-activity budgets and foraging behavior of Shrikes are 2 aspects of non-breeding ecology that remain understudied. As sit-and-wait predators, Shrikes typically conserve energy by spending most of their time perched and scanning for prey items (Yosef and Grubb 1992). However, Shrikes can adjust their daily activity patterns to suit changing environmental conditions, such as with mowing regimes on cattle pastures (Yosef and Grubb 1993) and with fluctuating prey availability (Craig 1978) and energy demands (Morrison 1980) among seasons. One key habitat component that affects Shrikes' ability to optimize their energy consumption, by optimizing effective foraging area and minimizing home-range size, is the availability of suitable perches (Becker et al. 2009, Yosef and Grubb 1994). Other studies of perch use by Shrikes have found that the height of perches used may vary, either because of availability or foraging optimization, across habitats (Gawlik and Bildstein 1993, O'Brien and Ritchison 2011) and seasons (Morrison 1980). Our study aims to describe Shrike behavior, including perch use, during the non-breeding season in an intensive agricultural area to allow for comparison to pre-existing studies and to serve as a baseline for future studies across seasons and changing conditions.

Foraging behavior represents an important aspect of daily activities that can be altered to compensate for seasonal fluctuations in energy demands and prey availability. Craig (1978) found that the energy requirements of Shrikes, in some contexts, can increase substantially during the non-breeding season, with demands rising by over 40% during the coldest periods. Shrikes may have several strategies for maximizing caloric intake and compensating for the increased energy demands during periods of lower temperatures, shorter day length, and reduced resource availability. These strategies include increasing the proportion of vertebrate prey items in their diet, increasing overall foraging rates, and increasing foraging efficiency (Craig 1978). *Lanius borealis* Vieillot (Northern Shrike), which overwinters at more northern latitudes, has been found to double its intake of certain vole species during the non-breeding season (Atkinson and Cade 1993), and Loggerhead Shrikes may also increase their intake of vertebrate prey as

temperatures decrease (Graber et al. 1973, Kridelbaugh 1982, Tyler 1991). However, it is not yet known if and how these behaviors and compensation strategies occur in intensive agricultural landscapes.

Diet composition may reflect some of the adjustments Shrikes make to their time budgets and foraging strategies to meet energy demands and/or changes in prey availability. Species in the family Laniidae are unique among songbirds in that they not only feed on a variety of invertebrate species, but also regularly prey upon small mammals, snakes, amphibians, and even other passerines (Tyler 1991, Yosef and Grubb 1993). In addition, shrikes cache prey items by impaling them on thorns, barbed wire, or other sharp substrates (Yosef 1996). In previous studies, investigators have used observational surveys (O'Brien and Ritchison 2011, Yosef and Grubb 1993), pellet analysis (Kridelbaugh 1982, Scott and Morrison 1995), larder analysis (Burton and Whitehead 1990), and stomach-content analysis (Graber et al. 1973) to understand shrike diet. However, these different methods could lead to varied inferences. In a comparison of 3 diet-analysis methods, Tryjanowski et al. (2003) recommended the combined use of nestling collar samples, pellet contents, and larder caches in future diet analyses of *Lanius colurio* L. (Red-backed Shrike) after finding that pellet contents overrepresented ground-dwelling coleopterans while larders overrepresented orthopterans and vertebrates. A similar comparison of Loggerhead Shrike behavioral and larder surveys, specifically, is needed to determine the value of each and the possible benefits of combining methods. Our study also sought to clarify if results from the 2 methods show a significant discrepancy during the non-breeding season in an agricultural area with relatively mild winters.

To improve our understanding of their behavior and ecology during the non-breeding season in an intensive agricultural landscape, we studied Shrikes in the Lower Mississippi Alluvial Valley (LMAV) of the central United States. Since the early 20<sup>th</sup> century, the LMAV has undergone extensive conversion from natural ecosystems to the intensive row-crop monocultures that dominate the land today (Twedt and Loesch 1999). Despite broad-scale agricultural conversion, Shrikes are present throughout this region year-round (Sullivan et al. 2009), making this an ideal location to study their ecology and behavior in an agricultural landscape during the non-breeding season.

Within this context, our specific objectives were to: (1) create a time-activity budget for Shrikes, (2) describe characteristics of used perches, (3) compare Shrike foraging behavior (i.e., attempts and success) across different ambient temperatures and agricultural microhabitats, (4) assess diet composition using both behavioral observations and larders, and (5) compare observational and larder surveys as methods for assessing Shrike diets. We made several predictions associated with these objectives, based on previous behavioral studies of Shrikes in other contexts. First, we predicted that Shrikes would conserve energy by spending most of their time perched and scanning for prey rather than actively chasing prey or defending territories. Second, we predicted that Shrikes would use anthropogenic

structures as perches more frequently than natural structures. Third, to compensate for increased energy demands as temperatures decline, we predicted that Shrikes would employ one or more of the following non-mutually exclusive strategies: increasing prey caloric intake by capturing more vertebrate prey items, increasing foraging rates, and increasing rates of capture efficiency (i.e., success). Fourth, we predicted that observational and larder surveys would provide different inferences about diet composition, with larders consisting of more vertebrate prey. In total, this study fills several knowledge gaps related to Shrike behavior and ecology that may be important to develop effective management and conservation strategies and to move eco-agricultural integration forward.

### Field-Site Description

We studied Loggerhead Shrikes in Craighead and Poinsett counties (35.44°N–36.00°N, 90.28°W–91.04°W) within the Lower Mississippi Alluvial Valley (LMAV) of northeastern Arkansas. Prior to European colonization, land cover in this region is thought to have consisted of bottomland hardwood forests and wetlands interspersed with upland prairie, including the Grand Prairie of east-central Arkansas (King et al. 2006, Stanturf et al. 1998), although the historical extent of grasslands in this region is still debated (Heitmeyer et al. 2000). Regardless, over 75% of the LMAV has since been urbanized or converted to agricultural lands (Dosskey et al. 2012, Twedt and Loesch 1999). Our study area, encompassing ~3800 km<sup>2</sup>, is now heavily dominated by row crops, and is divided by Crowleys Ridge, a narrow, forested ridge where no (or few) Shrikes are present (E.R. Donahue and T.J. Boves, unpubl. data). The low, level lands on either side of this north–south ridge, as described in the National Land Cover Database for 2011, consisted of ~74% row crops interspersed with some pasture (3%), urban areas (7%), and small, isolated forest stands (15%) (Homer et al. 2015). In 2017, the major crop types in this region were *Glycine max* (L.) Merr. (Soybean; 53%), *Oryza sativa* L. (Rice; 21%), *Gossypium* spp. (cotton; 10%), and *Zea mays* L. (Corn; 7%), and the remaining fields were planted with various winter cover crops (e.g., *Triticum aestivum* L. [Wheat] and *Medicago sativa* L. [Alfalfa]) (USDA-NASS 2018). Most cultivated fields are harvested and left with stubble from the previous summer's crop during the non-growing season instead of planting cover crops, and we observed few Shrikes with territories next to fields with these winter cover crops. All crops in this area are grown as monocultures using mechanized agricultural practices that result in large expanses of homogeneous vegetation, typically with tilled, burned, or otherwise disturbed soil following harvest (E.R. Donahue and T.J. Boves, pers. observ.). Utility wires, fence lines, and vegetation along roadsides and in irrigation ditches provide potential perches and semi-natural habitat for Shrikes (Fig. 1; Eiseley and Bollinger 2001). Climatically, our study area has relatively mild and wet winters (mean temperature = 3 °C, mean min–max = -4–9 °C; mean precipitation = 31 cm; National Centers for Environmental Information 2018), but can potentially include periods of much colder weather (Runkle et al. 2017).



## Methods

### Time–activity budget and perch use

From November through February 2016–2019, we located Shrikes by scanning utility lines and other potential perches while driving slowly along public roads. The consistent grid of roads and open, agricultural fields throughout the study system allowed for high visibility of observed Shrikes and their foraging attempts. As the sparsely available perches, including utility wires, agricultural equipment, and trees, in this area are strongly associated with roads and their bordering ditches, Shrikes are also typically found along these roadside habitats and rarely observed in areas restricted to other habitat types, such as field interiors (E.R. Donahue and T.J. Boves, pers. observ.). Thus, we are confident that we were able to observe nearly all Shrikes and their available habitats from roadsides and that our surveys capture the true variation of habitat types used within our study area.

We conducted surveys between dawn and dusk and avoided periods of rain. The earliest survey started at 8:45 and the latest at 15:52. Once a Shrike was located, we generated time–activity budgets (Martin and Bateson 2007) by recording the behavior of Shrikes for 30 continuous minutes, or until they were lost from view. In our analyses, we included all Shrikes observed for  $\geq 16$  continuous minutes. We placed each behavior into 1 of 8 categories: perching/scanning, active foraging/

Figure 1. A typical agricultural roadside area occupied by non-breeding Loggerhead Shrikes in the Lower Mississippi Alluvial Valley of northeastern Arkansas.



hunting, fighting/defending, vocalizing, eating, flying, cleaning/preening, and caching. Individuals nearly always appeared to be alert and actively scanning for prey when perched, except perhaps when preening or engaging in other maintenance activities, so we grouped perching and scanning into a single category. Active foraging/hunting included all attempts to capture prey (e.g., dropping to the ground from a perch, hopping around on the ground, hawking, hovering, or chasing). Flying included all flights unrelated to active foraging, primarily flying to different perches or repositioning after being flushed by a passing vehicle. Eating and caching activities also included the prey-handling time required to complete these tasks. We considered birds to engage in 1 behavior at a time and recorded the start and end time of that behavior (e.g., if a bird was preening, but also perched, we categorized it only as preening). When perched or caching, we also identified the perch type (e.g., tree, utility wire, or herbaceous plant) and used a measuring tape or clinometer to measure the height.

Although we could not always be certain that each observation period involved a unique individual, we took measures to avoid pseudoreplication. First, 35 of 101 individuals surveyed were banded with unique color combinations as part of a concurrent study. We captured individuals using a specialized Potter trap baited with a mouse, which was safely contained within a smaller, wire cage (Collister and Fisher 1995) and then marked them with federal bands (permit #23877) and unique combinations of 3 colored, wrap-around bands. Secondly, because annual and weekly resighting efforts suggest that Shrikes are site-faithful and maintain relatively small home ranges, as estimated by minimum convex polygons, during the non-breeding period in the region (E.R. Donahue, unpubl. data), we only conducted new surveys on individuals >1 km from previously sampled birds (banded or unbanded). We surveyed the study area over consecutive years and accounted for duplicated surveys of banded birds across years in our analyses (as random variables). We calculated the percentage of time spent on each activity for each individual and then averaged percentages across all individuals in our study sample. We report mean percentages  $\pm$  SE for our time–activity budget.

### **Foraging behavior and diet composition**

During behavioral surveys, we also recorded each foraging attempt and its outcome (success, failure, or unknown). We recorded the total number of attempts for each individual and calculated foraging rates per minute, which we then scaled up to an hourly rate (only including individuals observed for  $\geq 16$  continuous minutes and which had at least 1 known-outcome foraging attempt). We then calculated the average foraging success rate among all individuals with at least 1 known-outcome foraging attempt. For each observation period, we recorded temperature during the survey period from The Weather Channel mobile application (TWC Product and Technology LLC, Atlanta, GA). For each foraging attempt, we also recorded the microhabitat within which attacks were directed and identified captured prey items to the lowest taxonomic level possible. Based on the habitats available in our study area (Fig. 1), microhabitats were categorized as (1) right-of-way grasses (semi-natural strips of predominantly herbaceous vegetation

typically located under utility lines), (2) irrigation/run-off ditches (anthropogenic depressions usually filled with water and aquatic vegetation), (3) agricultural fields (with crop type identified when possible), and (4) roads (typically 2-lane and often gravel, but some paved).

Because individuals often foraged in multiple microhabitats, we constructed generalized linear mixed models to determine if foraging and success rates differed by microhabitat. First, we ran a Poisson model with foraging rate as the response variable, microhabitat type as the predictor variable, and individual identification as a random effect. Second, we ran a logistic regression model with success rate as the response variable, microhabitat type as the predictor variable, and individual identification as a random effect. We performed model selection using null-hypothesis testing ( $\alpha = 0.05$ ) and validated models by calculating the squared correlation coefficient and checking for a linear relationship between observed values and those predicted by the model. We then used the post-hoc Tukey test to compare differences between pairs of microhabitat types. We also assessed correlations between foraging rate, invertebrate capture rate, and success rate with temperature using a Kendall's tau test. To describe diet composition based on behavioral surveys, we averaged across all individuals and report mean percentages  $\pm$  SE.

After conducting behavioral surveys, we searched the vicinity for larders (i.e., prey caches) and also opportunistically found larders across the study area. We attempted to limit inclusion of caches to 1 per individual based on location and our best estimates of Shrike home ranges. Caches were not revisited. If we observed a Shrike both capture and impale prey, we counted this prey item for both the observational and larder surveys. At each larder, we identified the substrate (e.g., tree and barbed wire), identified plants used as substrates to the lowest taxonomic level possible, and photographed larder contents for identification. To describe diet composition based on larder surveys, we averaged across all individuals and report mean percentages  $\pm$  SE. We compared diet composition inferred from behavioral surveys to larder surveys using a chi-square test. All statistical tests were performed in Program R version 3.5.3 (R Core Team 2019) and we considered significance to exist at  $P \leq 0.05$ .

## Results

### Time–activity budget and perch use

We observed 101 Shrikes, including 20, 59, and 22 individuals in 2016–2017, 2017–2018, and 2018–2019, respectively. Of our 101 observational surveys, 82% were conducted for a full 30 minutes, and the average observation time was  $28.8 \pm 0.3$  min. Shrikes spent most of their time (80.8%) perched and scanning for prey and 5.6% of their time actively foraging (Table 1). Flying for purposes other than hunting represented 4.4% of their time and all other behaviors together represented  $<10\%$  of their time budget. Though infrequent, we did observe Shrikes acting aggressively toward conspecifics, as well as toward *Falco sparverius* L. (American Kestrel) and *Mimus polyglottos* (L.) (Northern Mockingbird). Shrikes switched perches, which included moving to a new perch or flying to a new location



on the same continuous perch, an average of  $12.6 \pm 0.8$  times/hr. When perched, Shrikes most often used anthropogenic structures, especially utility wires (68%), but trees and shrubs (20%) were also used as perches (Fig. 2). The mean height of used perches was  $7.33 \pm 0.07$  m (min–max = 0.01–20 m) for anthropogenic perches and  $3.92 \pm 0.25$  m (min–max = 0–25 m) for natural perches (Fig. 3).

Table 1. Non-breeding time–activity budget for Loggerhead Shrikes ( $n = 101$  individuals) based on 30-minute behavioral surveys conducted during the non-breeding season in the Lower Mississippi Alluvial Valley of northeastern Arkansas, 2017–2019.

Activity	Average % of time (min $\pm$ SE)	Min–max (%)
Perching/scanning	$80.8 \pm 1.4$	37.5–98.6
Hunting	$5.6 \pm 0.5$	0.0–37.9
Flying	$4.4 \pm 0.7$	0.0–44.5
Eating	$2.9 \pm 0.7$	0.0–40.3
Caching	$2.0 \pm 0.5$	0.0–19.9
Cleaning	$1.7 \pm 0.5$	0.0–33.4
Vocalizing	$1.1 \pm 0.6$	0.0–39.4
Defending	$0.5 \pm 0.2$	0.0–10.4

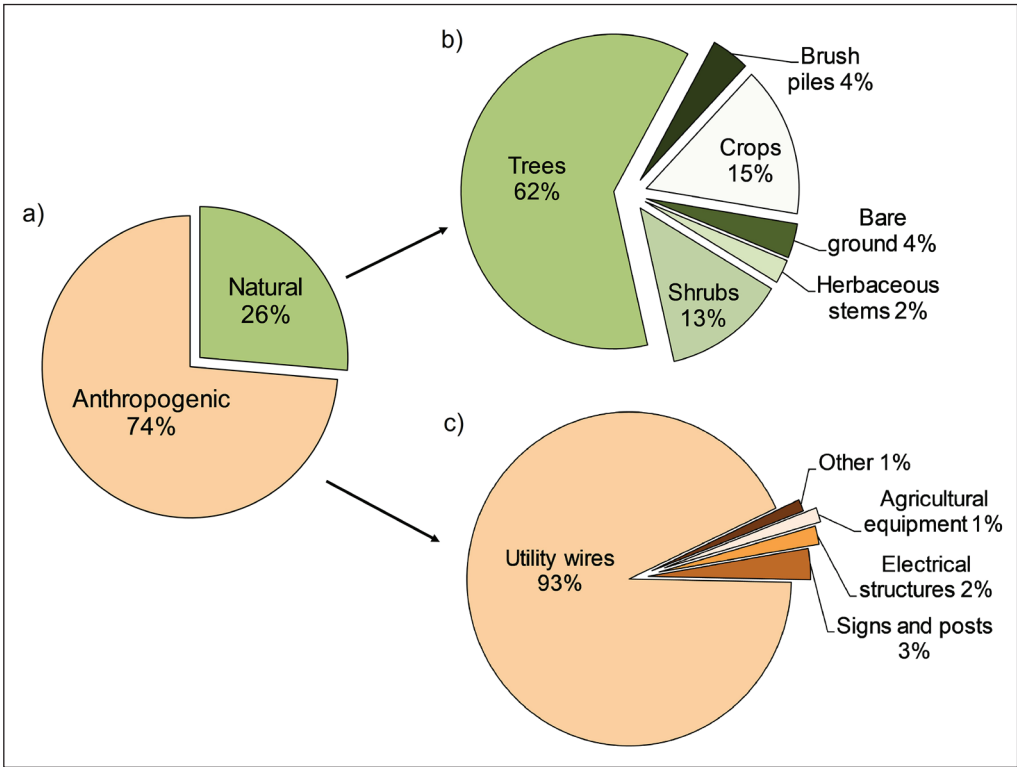


Figure 2. Average percentage of time spent perching by Loggerhead Shrikes ( $n = 101$  individuals) during the non-breeding season in the Lower Mississippi Alluvial Valley of northeastern Arkansas, 2017–2019 by: (a) anthropogenic vs. natural perches, (b) each type of natural perch (b), and (c) each type of anthropogenic perch.

### Foraging behavior

We observed 101 Shrikes make 706 foraging attempts and recorded the temperature (mean = 9 °C, min–max = -3.3–19.4 °C) during each attempt. Of these, 325 (46%) were successful, 280 (40%) were unsuccessful, and 101 (14%) were of unknown outcome. Shrikes made an average of  $14.9 \pm 1.2$  foraging attempts/hr ( $n = 101$ , min–max = 0–68), with an average success rate of  $57.6 \pm 3.1\%$  ( $n = 95$ , min–max = 0–100%). Foraging success was positively correlated with temperature ( $\tau_b = 0.21$ ,  $P = 0.02$ ; Fig. 4a), but neither foraging rate ( $\tau_b = 0.12$ ,  $P = 0.19$ ; Fig. 4b) nor invertebrate capture rate ( $\tau_b = 0.13$ ,  $P = 0.31$ ; Fig. 4c) was correlated with temperature. For foraging rate, the addition of microhabitat type as a predictor variable improved the null model and explained variation in foraging rate ( $\chi^2_{3,5} = 517.9$ ,  $P < 0.001$ ,  $r^2 = 0.54$ ), with rates differing significantly by microhabitat (all  $P \leq 0.001$ ). Foraging rate was greatest in right-of-way grasses (mean =  $5.6 \pm 0.4$  attempts/hr, min–max = 0–36 attempts/hr), followed by adjacent agricultural fields (mean =  $3.8 \pm 0.2$  attempts/hr, min–max = 0–16 attempts/hr) (Fig. 5). For foraging success rate, the addition of microhabitat type as a predictor variable did not improve the null model and did not explain variation in success rates ( $\chi^2_{3,5} = 4.0$ ,  $P = 0.27$ ).

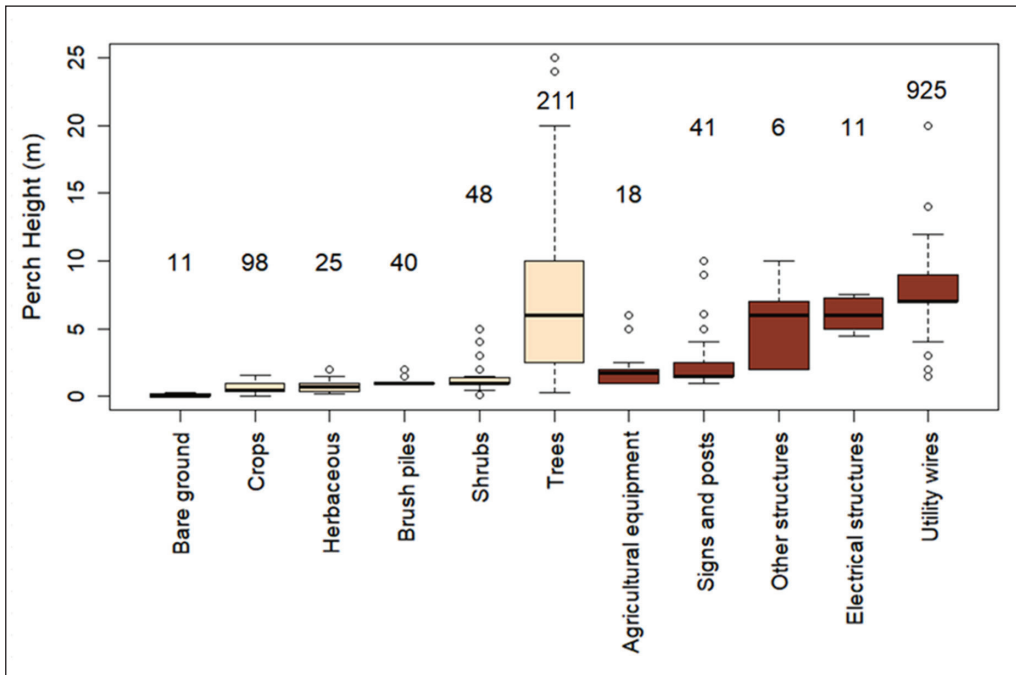
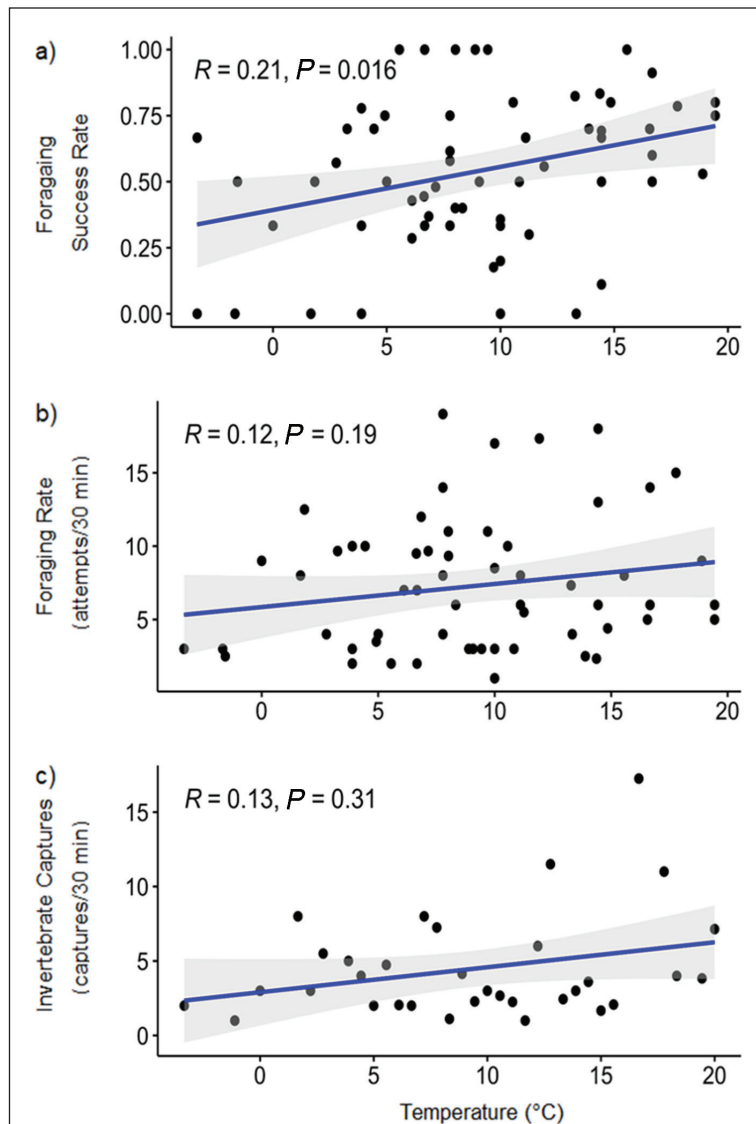


Figure 3. Heights (m above ground) of natural (represented by the first 6 categories) and anthropogenic (represented by the last 5 categories) perches used by Loggerhead Shrikes during the non-breeding season in the Lower Mississippi Alluvial Valley of northeastern Arkansas, 2017–2019. Sample sizes (above bars) reflect total number of observations for each perch type.

**Diet composition—behavioral observations**

During observational surveys, we identified 337 prey items captured by Shrikes. For successful attacks, we were able to identify prey for 325 of 345 attempts. We were unable to identify the prey for 268 of 280 unsuccessful attempts and for all 101 of the unknown outcome attempts. Shrike diet consisted mainly of arthropods (76%; Fig. 6a). Because arthropods other than orthopterans and coleopterans were too small to identify, we grouped them into a single category for behavioral surveys. Vertebrates made up 23% of observed foraging attempts; anurans were the most captured vertebrate prey (16%), and passerines and small mammals were the least frequently captured (7%) (Fig. 6a).

Figure 4. Average individual foraging success rates (a;  $n = 98$ ), foraging attempt rates (b;  $n = 98$ ) and invertebrate capture rates (c;  $n = 76$ ) of Loggerhead Shrikes in relation to air temperature during the non-breeding season in the Lower Mississippi Alluvial Valley of northeastern Arkansas, 2017–2019.



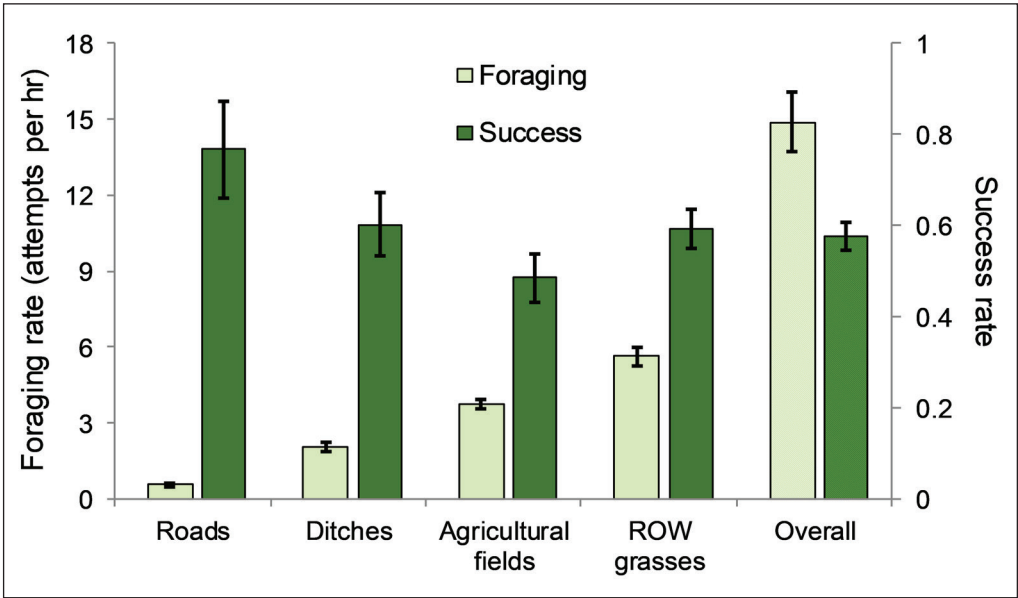
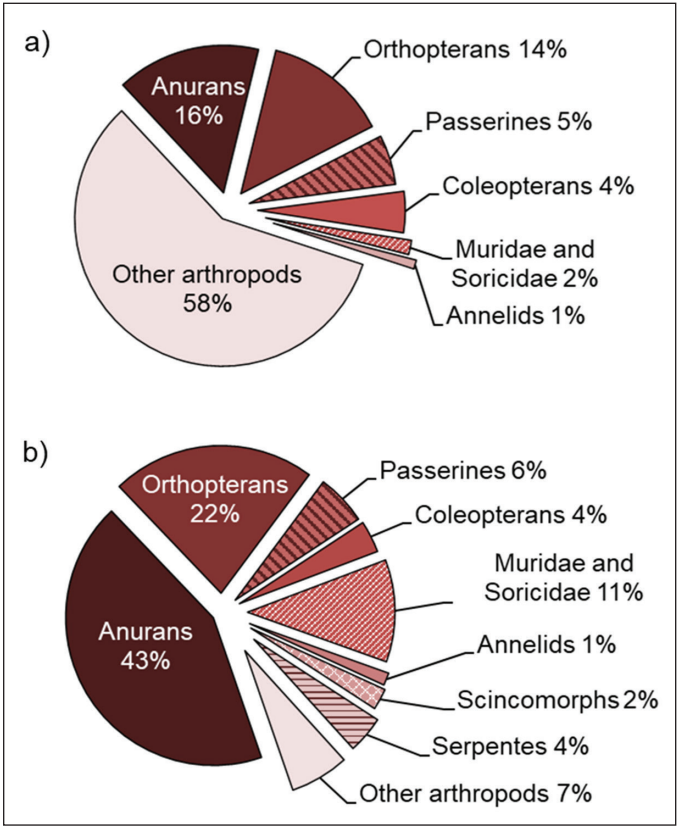


Figure 5. Foraging and success rates of Loggerhead Shrikes ( $n = 95$ ) by microhabitat type during the non-breeding season in the Lower Mississippi Alluvial Valley of northeastern Arkansas, 2017–2019. ROW = right-of-way.

Figure 6. Loggerhead Shrike diet composition based on (a) observational foraging surveys (averages of 87 observed individuals and 337 total foraging attempts) and (b) larder surveys (averages of 57 individuals and 122 total cached prey items) during the non-breeding seasons in the Lower Mississippi Alluvial Valley of northeastern Arkansas, 2017–2019. Reported observations limited to prey items that could be accurately identified.



### Diet composition—larders

Shrikes impaled a broad array of prey species on a variety of natural and anthropogenic substrates (Fig. 7). Anurans were the most common item observed in larders (43%), followed by orthopterans (22%) and small mammals (11%) (Fig.



Figure 7. Examples of prey items in Loggerhead Shrike larder caches found during the non-breeding seasons in the Lower Mississippi Alluvial Valley of northeastern Arkansas, 2017–2019. Prey identified from left to right, top to bottom are: *Chinavia hilaris* (Say) (Green Stink Bug), *Lumbricus* sp. (earthworm), and Orthoptera sp. (grasshopper), middle row: *Thamnophis proximus* (Say) (Western Ribbon Snake), *Dryophytes cinereus* (Green Treefrog), and Cricetidae sp. (small mammal), and bottom row: *Lithobates sphenoccephalus* (Southern Leopard Frog), *Acris blanchardi* (Blanchard's Cricket Frog), and *Scincella lateralis* (Say) (Little Brown Skink).



6b). Prey items were mostly impaled on branches of saplings and small trees (especially *Celtis* spp. [hackberries]) along agricultural ditches. Of 122 cached prey items (associated with 57 individual Shrikes), 83% were impaled on natural structures (60% tree branches and 23% herbaceous plants and crop stubble) and 17% on anthropogenic structures (14% on barbed wire and 3% on utility wire structures). Comparing impaled prey to prey captured during behavioral surveys, larders had a greater proportion of vertebrate prey ( $\chi^2_1 = 117.4$ ,  $P < 0.001$ ).

## Discussion

### Time–activity budget and perch use

As we predicted, Shrikes in our study spent most of their time using a sit-and-wait hunting strategy by perching on utility wires and scanning for prey, and little time actively engaging in other behaviors. This is a pattern similarly observed during the breeding season and in a quite different landscape in Florida (Yosef and Grubb 1993). This dominant foraging style is likely preferred by Shrikes in general, as it is associated with reduced energy costs when compared with more active hunting methods that involve hovering and aerial chases (Jaksić and Carothers 1985, Vlachos et al. 2003). Although we did observe other foraging methods, such as active chasing and fly-catching, they were rare.

When not perched, Shrikes divided much of their time amongst active hunting, perch switching, and prey handling (a total of 15% of time). Flying usually only occurred in short bursts to either attack prey on the ground or move to a new perch. The frequency with which Shrikes make perch changes likely varies seasonally with fluctuations in food demands or prey availability and may result in considerable energy expenditure. While a population of breeding Shrikes in California only made about 7 changes per hour (Morrison 1980), our non-breeding Shrikes made an average of 13 changes per hour, perhaps reflecting a reduction in prey availability. Our Shrikes, especially on higher-use roads, also wasted energy on perch changes when disturbed by passing vehicles. Because of their tendency to take and cache large prey, prey handling can also be an energetically expensive and time-consuming activity. Shrikes in both our study and in Florida (during the breeding season; Yosef and Grubb 1993) spent about 5% of their time handling prey, which was divided about evenly between eating and caching in our study.

Our results clearly indicate that, as predicted, Shrikes used anthropogenic structures as perches more frequently than natural substrates. Based on our 30-min continuous behavioral surveys, this result provides evidence that anecdotal observations of Shrikes using utility wires (e.g., on eBird) are not simply the result of easier detectability of Shrikes on wires, as could have been the case if we simply recorded a single location used by each Shrike. These data further highlight the importance of utility wires as habitat features for Shrikes in this region, as has been suggested in other studies as well (Crouch et al. 2019, O'Brien and Ritchison 2011). Although we did not test for habitat selection in this study (i.e., did not assess availability of habitat features), anecdotal observations suggest certain perch

characteristics may in fact be preferred, such as perch height. In much of our study area, a natural choice experiment occurred as utility wires were often available at 2 (or more) heights at any given location (Fig. 1). We found that Shrikes typically used the lowest available wire, suggesting that this lower height was preferred. Furthermore, when using woody perches, which typically offered a more continuous range of available heights, we found that Shrikes typically chose to perch at heights similar to the average of chosen utility wire perches (~6–7 m above ground; Fig. 3). Therefore, although coincidental, utility wires may be constructed near the optimal height for scanning and foraging during the non-breeding season, and across average vegetation heights, in this region.

### **Foraging behavior and microhabitats**

Despite the extreme dominance of row-crop monoculture habitat in our study area, small-scale “grasslands”, in the form of linear right-of-way grasses adjacent agricultural ditches, were available and most frequently used for foraging by Shrikes (although again, we did not assess habitat selection in this study). Collister and Wilson (2007) also found that rights-of-way provide important foraging habitats for Shrikes in other landscapes and seasons. Other studies have found Shrikes to prefer such short (Kridelbaugh 1982, O’Brien and Ritchison 2011) and/or heterogeneous (Michaels and Cully 1998) vegetation often associated with rights-of-way. One difficulty to interpreting these microhabitat data is the fact that utility wires and right-of-way grasses were almost perfectly correlated, so it is currently unclear if the wires or the grasses (or both synergistically) drove the pattern of habitat use that we observed. For example, Shrikes did occasionally forage in and along the edges of agricultural fields, but it is unclear if they would use this microhabitat more frequently if field interiors had more perches available.

Unlike the variation found in Shrikes’ use of different microhabitats, foraging success rates did not vary significantly across microhabitat types. However, this lack of significance among microhabitat types may be a result of low statistical power, as few foraging attempts occurred in some microhabitats (e.g., roads). Thus, the raw differences in our values may still indicate biological importance. For example, raw foraging success was greatest in roads, which is biologically logical as the absence of cover would seem to make locating and capturing prey in those microhabitats easier. Conversely, raw foraging success was lowest in agricultural fields, where taller crop stubble may obscure prey. Other studies support this inference; for example, a foraging study during the breeding season in a railroad/right-of-way complex in southeastern Alberta found that Shrikes had highest success rates in right-of-way areas and significantly lower success in crop fields (Collister and Wilson 2007).

### **Energy optimization strategies**

Contrary to our prediction, we found little support for any of the 3 potential energy-optimization strategies related to foraging and temperature during the non-breeding season. First, Shrikes did not increase the rate at which they captured vertebrate prey as temperature decreased. Instead, they maintained a largely

arthropod-based diet throughout the non-breeding season, supplemented primarily, and unexpectedly, with ectothermic anurans (e.g., *Acris blanchardi* Harper [Blanchard's Cricket Frog], *Lithobates sphenoccephalus* (Cope) [Southern Leopard Frog], and *Drophytes cinereus* (Schneider) [Green Treefrog]). Unseasonably warm days may trigger arousal in hibernating ectotherms, making for sluggish and easily captured prey (Klaus and Loughheed 2013). Additionally, we observed neither increasing foraging rates nor efficiency (i.e., success rates) as temperatures declined. In fact, temperature was positively related to foraging success (Fig. 4a).

The lack of evidence for any of the tested optimization strategies could indicate that Shrikes are struggling to meet their energetic demands during this critical period in agricultural landscapes, potentially leading to increased non-breeding mortality (or carry-over effects to later life stages; Akresh et al. 2019, Harrison et al. 2011). Throughout the non-breeding season in temperate climates, average winter temperatures and weather events, like snowfall, can be correlated with increased stress levels, metabolic rates, and foraging rates in songbirds (Rogers et al. 1993, Swanson and Olmstead 1999). Extreme conditions, such as extended periods of below-average temperatures can even lead to increased mortality rates (Gardner et al. 2017). All recorded winter mortality events for a subset of Northern Shrikes in Virginia occurred during periods of below-average temperatures (Blumton 1989). During our 3-year study, however, the average temperature recorded during our behavioral surveys (9 °C) was higher than the 30-year average for the region across the same 4-month period (5.6 °C; Arguez et al. 2010), and we did not observe poor condition or unexpectedly high mortality rates in Shrikes during this time. Perhaps more likely, these observations, in addition to the absence of optimization strategies, may indicate that the climatic conditions during our study did not become extreme enough (for long enough) to require Shrikes to behave/compensate in such manners. Although more studies are needed during both the non-breeding season in general and in colder climates, our results suggest that Shrikes do not switch to vertebrate prey with fluctuating temperatures in mild climates.

When compared with other studies, our observed average hourly foraging rate (15 attempts/hr) was greater than those rates found in Florida during the breeding season (in open pastures; ~11 attempts/hr; Yosef and Grubb 1993) and was closer to that of breeding Shrikes in California (in *Brassica rapa* L. (Mustard) fields; ~13 attempts/hr; Morrison 1980). Our estimates of foraging success also resembled documented breeding estimates, falling in line with a latitudinal gradient observed in other habitats. Our observed success rate (58 ± 3%) was closest to that of a California population at a similar latitude (~65%; Lynn et al. 2006), and was greater than estimates from the northern portion of the range (~28% in Alberta; Collister and Wilson 2007) and lower than observed farther south (~75% in Florida; Yosef and Grubb 1993). There may be an overall positive association between foraging rate and latitude and negative association between success rate and latitude, with Shrikes at the highest latitudes spending the most time actively foraging but making the fewest successful catches. This relationship may mean non-breeding populations at the northern-most edge of the range have a harder time balancing

energy demands and a greater need for optimization strategies than the Shrikes in our study.

### Diet composition

Previous Shrike studies have focused exclusively on either larder surveys (e.g., Burton and Whitehead 1990) or foraging observations (e.g., Yosef and Grubb 1993) on their own to describe prey composition, but, as predicted, our comparison of these 2 survey types clearly shows that they can produce drastically different inferences about Shrike diet, and together provide the most comprehensive perspective. However, these survey types both have potential limitations. For example, shrikes have the tendency to impale excess prey items in their larders that are never actually consumed (Beven and England 1969, Yosef and Pinshow 2005), and small captured prey items can be difficult to identify by observation alone. Therefore, it may also be worthwhile to augment and compare these surveys with additional techniques, such as collecting regurgitated pellets (Atkinson and Cade 1993) and using emerging molecular methods (e.g., fecal meta-barcoding; Pompanon et al. 2012, Trevelline et al. 2018).

Despite some uncertainty associated with these methods, it appears that Shrikes in our study relied primarily on arthropod prey, supplemented mainly with anurans. When compared with other studies of Shrike foraging behavior and diet, we can identify both differences and similarities. Though we did not see a reliance on more vertebrate prey as temperatures dropped, we observed higher average vertebrate consumption rates than at least 1 other non-breeding diet study conducted outside of an intensive agricultural habitat (in Kentucky; O'Brien and Ritchison 2011). Additionally, Shrikes in our study area relied heavily on anurans, which were only rarely reported as prey during a non-breeding season study in grasslands interspersed with cropland in Oklahoma (Tyler 1991). As our study area had greater coverage of row crops edged with drainage ditches, where anuran populations are likely dense, we produced similar anuran capture rates to those reported for breeding pairs on a Florida cattle ranch, which was also interspersed with ditches (Yosef and Grubb 1993). The reliance on ectothermic prey by Shrikes in our area may not remain a viable strategy if temperatures fall too low for an extended period.

It should be noted that although the agricultural landscape across this study area currently provides habitat (and food resources) for numerous Shrikes during the non-breeding season, it is possible that negative consequences for Shrike fitness may exist. First, foraging on, and near, roads could result in increased direct mortality via vehicular collisions, which are documented for both shrikes (Blumton 1989, Cadman 1986, Luukkonen 1987) and raptors (Boves and Belthoff 2012, Hager 2009). Second, roadside utility wires lack any concealment, so these perches may leave Shrikes more vulnerable to predation by raptors, which are also attracted to these features (Prather and Messmer 2010, Worm et al. 2013). The impact of raptor predation and vehicular collisions on Shrike populations is unclear, but both have been suggested as sources of winter mortality (Blumton 1989). During our study, we did observe a *Circus*

*cyaneus* (L.) (Northern Harrier) depredate a Shrike and recover a Shrike carcass that was likely killed by a vehicular collision. Finally, as tertiary/quaternary consumers, Shrikes may be susceptible to the bioaccumulation and biomagnification of toxins as they forage along agricultural ditches, where pesticide-laden runoff likely accumulates. Pesticides cause indirect effects on prey abundance and reproductive success for both the Loggerhead Shrike (Yosef and Deyrup 1998) and the Red-backed Shrike (Golawski and Meissner 2008). However, studies exploring the direct effects of pesticides on Shrikes show conflicting results (Anderson and Duzan 1978, Blumton et al. 1990, Herkert 2004). Future studies are needed to clarify the impacts of these anthropogenic factors on Shrikes in these habitats.

### Conclusion

Despite the recognition that Loggerhead Shrikes are found during the non-breeding season in agricultural landscapes dominated by row-crop monocultures, such as the LMAV, very little is known about the behavior and ecology of these declining birds in these contexts. In this study, we provide data on Shrike time use, foraging behavior, habitat use, and diet in these increasingly important contexts. We found that Shrikes limit energy expenditure by spending much of their time perched on unconcealed and relatively low utility wires and forage across a variety of available microhabitats in these landscapes, and particularly used right-of-way grasses. Shrikes also exhibited relatively high foraging efficiency, especially along roads. Their diet was diverse but dominated by arthropods and mainly supplemented with anurans, even during the coldest periods of the year. In total, the combination of utility wires, roads, ditches, and rights-of-way, along with a diverse prey base (especially arthropods and anurans) enable the persistence of Shrikes in this landscape. However, the possible negative effects associated with these landscapes, such as vehicular collisions and pesticide bioaccumulation, remain unquantified. We also found that the methods used for estimating diet composition, including direct behavioral observations and larder surveys, offered 2 different, but likely important, perspectives. This study furthers our understanding of Loggerhead Shrike non-breeding ecology and behavior within intensive agricultural habitats and provides guidance for future hypothesis-driven research necessary to move forward in both Shrike conservation and broader ecological-agriculture integration.

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