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Habitat Selection, Reproductive Success, and Impaling Patterns of a Migratory Population of Loggerhead Shrikes

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Habitat Selection, Reproductive Success, and Impaling Patterns
of a Migratory Population of Loggerhead Shrikes.

(TITLE)

BY

Jeffrey D. Esely Jr.

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

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THIS PART OF THE GRADUATE DEGREE CITED ABOVE

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Abstract

I studied habitat selection and reproductive success of a migratory population of Loggerhead Shrikes (Lanius ludovicianus migrans) as well as the temporal and spatial patterns of impaling exhibited by this population during the nesting season. The selection of breeding habitat was investigated at different spatial scales. Thirty-eight (67%) of 57 nests were located in osage orange (Maclura pomifera) trees. Shrike territories (area ≤ 200 m from nest site) contained significantly more pasture, fenceline, and perch sites, but less corn, alfalfa, and forest than random sites. At larger spatial scales, more grassland was detected within 300 m of shrike nests than random locations. However, no differences were detected between shrike nests and random sites when larger radii (600, 900, 1500 m) were analyzed. Nest success (49%) and productivity (3.63 young/pair) were similar to North American averages, and habitat variables appeared to have little influence on nest success. However, nests located along roadways were significantly less successful (35%) than interior nests (70%).

I detected impaled prey on 88% of 24 breeding territories searched, with an average of 1.77 items found per search. Insects and reptiles were the most common taxa impaled comprising 56% of all items detected. Honey locusts (Gleditsia triacanthos) were the most frequently used impaling substrate holding 67% of all items. Abundance of impaled prey was highest during the nestling stage (2.24 ± 3.40 items/search), and shrikes impaled significantly closer to the nest during this stage (18.13 ± 11.02 m) than during either the incubation (31.13 ± 12.2 m) or fledgling (25.03 ± 8.08 m) stages. Finally, a significant positive correlation was observed between the abundance of impaled prey and reproductive output of successful nests.

These results suggest that energy demand was an important factor affecting impaling patterns, and supplemental food delivery to incubating females and nestlings was a primary function of impaling during the nesting period.

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**Habitat Selection and Reproductive Success of the Loggerhead Shrike: A
Hierarchical Approach.**

Introduction

Habitat selection involves choosing among alternative habitat types that could differentially affect survival and reproductive success (Hilden 1965; Bergin 1992). The selection of a particular habitat is affected by proximate cues such as habitat structure, and ultimate factors such as long-term food availability (Hilden 1965). The precise mechanisms controlling habitat selection are still poorly understood (Hilden 1965; Bergin 1992), and recently, attention has been directed towards the importance of considering multiple spatial scales in studies of habitat selection (Morris 1987; Orians and Wittenberger 1991; Bergin 1992).

Organisms are thought to make a series of step-wise selection decisions based on different sets of criteria at various spatial scales (Bergin 1992). Because habitat selection choices are affected by cues from multiple spatial scales, descriptions of habitat selection are scale-dependent. Thus, results at one scale cannot necessarily be extrapolated to other levels (Bergin 1992). This indicates that deliberate attention to performing analyses on multiple spatial scales is essential in studies of habitat selection (Orians and Wittenberger 1991).

This study incorporated a hierarchical approach in an attempt to isolate factors affecting breeding habitat selection and associated reproductive success of the Loggerhead Shrike (Lanius ludovicianus). Habitats containing short grasses

interspersed with small trees and shrubs are generally preferred because these areas provide suitable nest sites, hunting perches, and access to a diverse array of prey species. (Yosef 1996; Cade and Woods 1997). Landscapes possessing these characteristics include scrublands, deserts, savannas, and some agricultural areas. Widespread population declines of Loggerhead Shrikes over the past several decades have stimulated several studies investigating habitat selection of this species (Kridelbaugh 1983; Gawlik and Bildstein 1990; Tyler 1992; Prescott and Collister 1993). However, studies incorporating multiple spatial scales are limited (Brooks and Temple 1990; Novak 1995).

Although the Loggerhead Shrike is still a widespread breeding species in North America, its distribution and abundance have both declined since the 1940's (Morrison 1981; Yosef and Lohrer 1995; Cade and Woods 1997). Breeding populations have declined at a mean rate of about 3% per year since 1966 (Hands et al. 1989; Peterjohn and Sauer 1995), and the species has been included on the American Birds "Blue List" since its inception in 1972 (Tate 1986). The eastern migratory race (L. l. migrans) has declined rapidly at a rate of 5.8% per year since 1966 (Peterjohn and Sauer 1995), and was designated as a category 2 candidate for protection under the U.S. Endangered Species Act in 1985 (Cade and Woods 1997). Habitat loss on breeding and wintering ranges, human disturbance, road kills, pesticides, and range expansion of fire ants have all been suggested as possible contributing factors to these declines (Busbee 1977; Anderson and Duzan 1978; Kridelbaugh 1981; Luukonen 1987; Brooks and Temple 1990).

I investigated several variables potentially affecting breeding habitat selection and reproductive success of a migratory population of Loggerhead Shrikes in northwest Missouri. This area is predominantly an agricultural landscape characterized by large amounts of apparently suitable habitat and moderate shrike densities. Some consideration was given to habitat variables at the microhabitat level (nest tree and nest site), but stronger emphasis was directed toward macrohabitat scales.

The specific objectives of this study were to:

1. Locate 30-40 Loggerhead Shrike breeding pairs in northwest Missouri, and determine their reproductive success.
2. Measure breeding habitat variables potentially affecting habitat selection and associated reproductive success at several spatial scales.
3. Isolate those habitat variables and spatial scales with significant influence on breeding habitat selection and reproductive success of this population.

Methods

Study Area;

I studied shrikes on a 655 km² section of Nodaway County in the northwest corner of Missouri. This landscape is characterized by gently sloping to moderately steep hills drained by both the Nodaway and 102 River basins. Cold winters and long hot summers are typical with an average daily maximum summer temperature of 27° C and a mean annual precipitation of 89 cm (Zimmerman 1986). Historically within the tallgrass prairie region, this landscape is now predominantly agricultural containing primarily rowcrops, pastures, and hayfields (Zimmerman 1986).

Nesting Success;

I located breeding territories in March 1997. These territories were located by driving county roads in the study area and searching probable habitat with binoculars. Nest searching began 20 April. Most nests were located by following the flight paths of adults carrying nest material or food. Nests were monitored every 3-5 days until the nest fledged or failed, and mirrors attached to poles were used to check higher nests. A successful nest was one that fledged at least one young. If unsuccessful, the condition of the nest was recorded as intact, damaged, or destroyed. From these data, clutch initiation dates, and hatching dates were estimated through back calculation (assuming a 16 d incubation period), and the mean clutch initiation date was computed for all initial nest attempts.

Habitat Measurements;

I measured habitat characteristics after nesting had ceased. Habitat variables were examined at the microhabitat, territory, and macrohabitat levels. The following microhabitat descriptors were recorded: nest tree species, nest tree height, nest height, and distance of the nest from the central axis of the tree.

Land use maps were constructed for calculation of territory-scale habitat parameters. This level consisted of a 200 m radius circular plot (12.6 ha) centered on the nest, approximating the size of a shrike territory (Kridelbaugh 1982; Luukkonen 1987). Length measurements were made using a distance measuring wheel. Roadways, fencelines, utility wires, and isolated trees, were designated on the maps as well as cover type. I used the following land-use classifications for cover types: pasture, soybeans, corn, old crop field, hayfield, alfalfa, forest, roadway, and residential

lawn. Old crop fields were identified by the presence of perennial weeds and invading woody plants and were not grazed or mowed. From these maps, length of roadway, distance of the nest to the nearest roadway, length of fenceline, and length of utility wires were determined for each plot. Utility lines with multiple wires were measured as one length. The number of potential perch sites was calculated by adding the number of isolated trees and the total meters of timber edge divided by 10. Percent composition of each of the 9 cover types was calculated using an area grid. For the purpose of comparison, land-use maps were also constructed for 25 unoccupied sites of equal size randomly selected from within the entire study area (hereafter referred to as “unpaired random sites”), as well as 25 sites centered 1km (in a random direction) from an actual nest, and at an equal distance from the nearest roadway as the nest site (hereafter, “paired random sites”). Since the distance of nests to the nearest roadway was biased due to the nature of my nest searching method (i.e., from the roadside), this distance was not changed between pairs in order to eliminate further bias caused by variables associated with roadways (fencelines, utility lines). Unpaired random sites were also positioned at a distance from the nearest roadway equal to that of a randomly selected nest site. Comparing habitat variables around nest sites with unpaired random sites was expected to provide more conspicuous results on habitat selection (i.e., grass preferred over rowcrop), whereas testing against paired sites would detect more subtle differences (i.e., pasture selected over hayfield). This is due to the close proximity of the nests to paired sites which should result in increased habitat similarity, whereas nest and unpaired sites are likely to contain more dissimilar habitat characteristics.

Twenty-five aerial photographs of both occupied sites and unpaired random sites were used to determine cover type proportions at several larger (macrohabitat) spatial scales. These photographs, taken in 1996, were obtained from the Nodaway County Soil Service Agency. Cover types were measured within circles of the following radii; 300 m (28.3 ha), 600 m (113 ha), 900 m (254 ha), and 1500 m (707 ha). The largest of these scales was broad enough to contain the shrike's entire home range, as well as any areas used by maturing fledglings, which may be of additional importance in breeding habitat selection (Novak 1995). Cover type determinations were confirmed by ground truthing. For this analysis, cover types were broken into three categories; grassland, row crop, and timber. I collectively classified pastures, hayfields, alfalfa, roadside grass, Conservation Reserve Program (CRP) fields, and residential lawns as grassland due to similar structural characteristics, and their similar appearance on aerial photographs. From these maps, the proportion of each of the three cover types in each plot was estimated using a transparent area grid. Habitat proportions of nest sites and random sites were tested for significant differences at each spatial scale.

Data Analysis;

Overall nest success was calculated by multiplying the following probabilities; nest survival during incubation, survival during the hatching period, nest survival during the nestling period, and survival of individual eggs and nestlings (Mayfield 1961, 1975). I also determined mean clutch size, hatching success (% of nests where ≥ 1 egg hatches), mean number of eggs hatched per nest, fledging success (% of nests fledging ≥ 1 young), number of fledglings produced per nest, number of fledglings produced per

successful nest, % of nesting pairs to produce ≥ 1 fledgling, and number of fledglings produced per pair.

Paired t-tests were used to compare habitat variables between nest and paired random sites at the territory scale. Two-sample t-tests were used to compare habitat variables between nest and unpaired random sites. I used all 50 unoccupied sites to perform stepwise discriminant function analysis (SAS 1989) on the habitat variables in an effort to reveal independent variables with significant influence on breeding habitat selection at the territory level. For this analysis, variables were included in the discriminant model based on an entry / removal criterion of $F = 0.10$, with variables contributing most or least to the discriminatory power of the model (as measured by Wilk's lambda) being entered or removed, respectively (SAS 1989). Two sample t-tests were used for comparison of the three habitat cover types at the various macrohabitat spatial scales (300 m radius and above).

All nests were classified according to their proximity to roadways. Nests located along roadway fences were classified as "roadside". When a roadway fence was not present, then the nest was designated as "roadside" if positioned ≤ 15 m from the road (longest distance between a road and roadway fence). Nests not meeting these criteria were classified as "interior". Using the method suggested by Johnson (1979), probability of nest survival was compared between roadside and interior nests for both incubation and nestling periods. T-tests were used to compare habitat variables between successful and unsuccessful nests, and stepwise logistic regression analysis (SAS 1989) was also performed to isolate microhabitat and territory scale variables with significant influence on the probability of nest survival. As before, a

significance level of 0.10 was selected for entry into the model. Shrike nesting attempts were treated as individual sampling units and all data are presented as means \pm SD. I chose $P < 0.05$ as the minimum acceptable level of significance, although values falling between $P = 0.05$ and $P = 0.10$ were considered marginally significant.

Results

Microhabitat Selection;

Shrikes used 7 plant species for nest support (Figure 1). Thirty-eight (66%) nests were found in osage orange (Maclura pomifera), eight (14%) in mulberry (Morus sp.), four (7%) in multiflora rose (Rosa multiflora), two each (4%) in honey locust (Gleditsia triacanthos), eastern redcedar (Juniperus virginianus), and black cherry (Prunus serotina), and 1 (2%) in slippery elm (Ulmus rubra). The average nest height was $2.36 \pm 1.33\text{m}$, and mean nest tree height was $4.35 \pm 2.21\text{m}$. The mean distance of the nest from the nest tree's central axis was $0.53 \pm 0.80\text{m}$.

Territory Selection;

Comparison of nest and paired random sites revealed that occupied territories had significantly more pasture ($t=4.3$, $P<0.001$), more meters of fenceline ($t=3.3$, $P<0.01$), more perch sites ($t=2.9$, $P<0.01$), less corn ($t=-2.7$, $P<0.05$), and less alfalfa ($t=-1.9$, $P=0.08$) (Table 1). Comparison of nest and unpaired random sites had similar results with occupied sites again containing more pasture ($t=3.7$, $P<0.001$), more fenceline ($t=3.9$, $P<0.001$), more perch sites ($t=3.0$, $P<0.01$), and less corn ($t=-2.3$, $P<0.05$). However, in this analysis the amount of alfalfa did not differ significantly, but nest sites did have less forest ($t=-2.7$, $P<0.01$) (Table 2). Stepwise discriminant function analysis of the 14 variables (comparing nest sites with all 50 random sites)

identified 3 potential discriminators (length of fence, number of perch sites, area of forest) of occupied and unoccupied areas. At the macrohabitat level no significant difference in percent cover of the three landuse types was observed between nest sites and random except for the percent grassland within 300m of the nest ($t=2.53$, $P<0.05$). Nest sites had a significantly higher proportion of grassland ($60.5\pm18.26\%$) within 300m of the nest than random sites ($43.3\pm27.6\%$)(Table 3).

Productivity;

During the 1997 nesting period, 55 breeding pairs and 62 nesting attempts were observed (Table 4). The mean clutch initiation date of first nesting attempts was 25 April. Clutch size ranged from 3-7 eggs with a mean of 5.6 ± 1.24 . Hatching success (percentage of nests where ≥ 1 egg hatched) for all nests was 83%, whereas the mean number of eggs hatched per nest was 4.6 ± 2.29 . Apparent nest success (% of nests fledging ≥ 1 young) was 65%; the number of young fledged per nest was 3.16 ± 2.51 , with 4.9 ± 1.05 fledging per successful nest. The proportion of nesting pairs to fledge ≥ 1 young was 72%, and the number of fledglings produced per pair was 3.63 ± 2.54 .

Nine of 50 (18%) nests failed during incubation for a daily nest survival rate of 98.3%. Thus, the probability of nest survival during the 16 day incubation was 76%. The hatching period in shrikes is normally two days, but the date that the first egg began hatching was considered the final day of incubation for that nest. A total of 204 of 218 (94%) eggs present at hatching time produced nestlings within two days of the onset of hatching, giving a probability of survival during the hatching period of 94%. Of 32 nests observed during the nestling period, 12 failed producing a daily survival

rate during the nestling period of 98.4%, consequently, the probability of nest survival during the 19 day nestling period was then 74%. Loss of individual eggs did not occur but 13 individual nestlings were lost during 3014 nestling days of exposure. This produced a daily individual nestling survival rate of 99.6%, and an overall individual nestling survival probability during the nestling period of 93%. The probability that eggs present at the start of incubation would produce fledglings was then computed: $(0.76 \times 0.94 \times 0.74 \times 0.93) = 0.49$. Thus, 49% of eggs laid produced fledglings (Table 4).

Roadside nests were less productive than interior nests (Table 4). Nesting success for interior nests was 70.0%, whereas roadside nesting success was only 35.0%. Comparison of mortality rates between interior and roadside nests revealed that daily mortality rates during incubation were significantly higher ($z=3.0$, $P<0.05$) in roadside nests than interior nests. Daily mortality rates during the nestling period were not significantly different between roadside and interior nests ($z=0.52$, $P>0.10$).

Comparison of habitat variables between successful and unsuccessful territories revealed that successful nests were positioned closer ($t=-1.94$, $P=0.056$) to the central axis of the nest tree (0.38 ± 0.72 m) than unsuccessful nests (0.79 ± 0.87 m). Successful nests were also located in taller trees and higher in the tree, however, these differences were not significant (Table 5). Stepwise logistic regression of the 17 habitat variables identified 2 potential discriminators (distance of nest from nest tree central axis and nest tree height) influencing nest success.

Discussion

Habitat Selection;

Studies of shrikes conducted within the range of the eastern red cedar (Juniperus virginianus) have typically shown that shrikes most commonly select this species for nest support (Graber et al. 1973; Siegel 1980; Kridelbaugh 1983; Temple and Brooks 1986; Luukkonen 1987). However, a variety of plant species are used. Porter et al. (1975) reported that nest site selection was based on the degree of cover a plant provided rather than the particular species. Shrikes on my study area most often selected osage orange (67%) for nest support; only 4% of nests were found in eastern red cedars. Osage orange was more common on my study area, and dense, thorny plants such as this provide good nest support and most likely discourage mammalian predators. These trees also provide suitable impaling substrates.

Contrary to expected, the results of the two methods of territory comparison (paired vs. unpaired) were very similar with each identifying 5 significant variables. Length of fenceline, number of perch sites, and area of pasture and corn around nest sites were significantly different from both paired and unpaired random sites. This similarity in results may be due to the homogeneous character of my study area. A less uniform landscape may have resulted in a greater difference between the two approaches. The discriminant function analysis also had similar results to these univariate tests by identifying length of fenceline, number of perch sites (both positively related to shrike presence), and area of forest (negatively related) as discriminators between nest and random sites.

These territory - scale habitat selection results are similar to those observed in other studies (Kridelbaugh 1973; Luukonen 1987; Brooks and Temple 1990). The selection of pasture-dominated open areas for nest sites is consistent with the shrike's "sit and wait" foraging mode (Yosef and Grubb 1994). Length of fenceline was likely an important discriminator between occupied and unoccupied sites because fences create numerous hunting perches. Similarly, the number of potential hunting perches was an important discriminator because they aid in the shrike's foraging method. An increased number of suitable perch sites results in a greater amount of usable foraging area for the shrike (Yosef and Grubb 1994). The area of forest was a significant negative discriminator between occupied and unoccupied sites because it was probably the least useful habitat type to the shrike on the study area.

Utility wires often provide valuable hunting perches for foraging shrikes and thus would be expected to be important in territory selection. Several authors have shown that shrikes favor utility wires as perch sites (Craig 1978; Bohall-Wood 1987; Gawlik 1988). While some studies have found that shrike territories contain a greater length of utility wires than unoccupied sites (Burton 1990; Novak 1995), I did not observe any correlation between shrike nest sites and utility lines. This may be partially explained by the fact that all of my unoccupied sites were of equal distance to roadways as the nest sites, and utility wires were generally located along roadways. Future experiments with unique designs are needed to eliminate biases caused by these highly correlated variables.

At the macrohabitat spatial scale, correlation of grassland with nest sites was only detected within 300 m of the nest (Table 3). In Minnesota, Brooks and Temple

(1990) observed occupied sites to contain significantly more pasture and grassland within 400 m of the nest than unoccupied sites. In New York, Novak (1995) found occupied sites to contain significantly more pasture within 750 m of the nest than unoccupied sites. The fact that I did not detect any correlation between shrike sites and amount of grassland at larger spatial scales may be the result of several factors. Brooks and Temple (1990) and Novak (1995) both compared occupied and unoccupied sites. Because a set of random landscape locations known not to be used by shrikes was not available, I compared used and available landscapes. Therefore, shrike territories could potentially have existed within the random sites. Comparison of used and unused landscapes may have resulted in significant differences at larger scales. Another possible explanation for these results may have been that my study area contained large enough amounts of suitable habitat throughout the site that responding to these larger scale habitat selection cues may not have significantly affected survival or fitness. In other words, it is plausible that almost any position within the study area would contain adequate amounts of suitable habitat at macrohabitat scales above a 300 m radius circle. If so, selection should operate such that focusing on smaller scale habitat selection cues would then have greater influence on survival and reproductive success. If the landscape contained lesser amounts of adequate habitat, then these large scale cues may then become more consequential. A third possible factor influencing these results may be the fact that I collectively classified several cover types as grassland, some of which may be unsuitable to shrikes. Some of these cover types may include hayfields, alfalfa, and CRP fields. Finally, shrike density may have played a role in these results. Densities were probably lowest in New York and highest in my study

area. At low density, shrikes probably select the center of the largest expanse of suitable habitat. This would tend to create a situation (as found by Novak[1995]) in which used and unused habitats differed at larger scales.

Productivity;

Reproductive output for Loggerhead Shrikes in northwest Missouri in 1997 was similar to that reported by other researchers in the United States (Table 6). Although it appears that nesting success observed in this study was slightly lower than the North American average (55-60%), it must be emphasized that the 49% nesting success observed here includes the effects of partial nest losses (e.g., partial depredation, brood reduction), which are generally not considered in nesting success calculations. Ignoring the effects of partial losses, the success rate was 53% for this study. Additionally, the lowered nesting success may also be due to the large number of roadside nests included in this study. These nests suffered a significantly higher failure rate than interior nests (Table 4). Other reproductive parameters appeared to agree closely with those of other North American populations (Table 6) in that Loggerhead Shrike reproductive output is relatively high. Even when nests located in unproductive areas (roadways) are considered, overall productivity is still high for a passerine species. While populations of Loggerhead Shrikes are decreasing, low nesting success does not appear to be a factor in this decline.

During my study, nest failures appeared to be highly affected by chance, although some habitat variables seemed to influence this probability. Successful nests were closer to the central axis of the nest tree than unsuccessful nests. Since the majority of shrikes in my study area nested in small, brushy, thorned trees, nests closer

to the center of the tree were offered more protection from predators and weather. Nest tree height may have been identified as a discriminator between successful and unsuccessful nests because taller trees may offer both more protection from weather and concealment from aerial nest predators.

The most important factor affecting nest success appeared to be the proximity of the nest to a roadway. Nests located along roads were significantly less productive than interior nests (Table 4). The majority of this difference occurred during the incubation period. During incubation 9 of 38 roadside nests failed whereas all 24 interior nests remained active throughout incubation. Other studies have also found reduced success and increased predation rates in roadside nests (Burton 1990; De Geus 1990). The low nesting success experienced along roadsides is most likely due to features of roadside habitat which make nests in these areas more vulnerable to predation. Yosef (1994) observed higher depredation of shrike nests located along fencelines than interior nests. Linear habitat features such as roadsides, fencelines, and forest edges often act as travelling lanes for predators (Crabtree et al. 1989) both because these areas provide cover, and because prey are often concentrated in these areas when the landscape is fragmented. An alternative explanation for the decreased nesting success experienced along roadsides is that shrikes nesting in these areas were of lower quality and had been excluded from better habitats by higher quality conspecifics (Yosef 1994). While other studies have not discovered evidence of this phenomenon occurring (Luukonen 1987; De Geus 1990; Yosef 1994), I detected that mean clutch size was significantly lower for roadside nests (Table 4). This suggests that shrikes nesting along roadsides were in fact, of lower quality or possibly younger.

Summary

In conclusion, Loggerhead Shrikes in my study area selected short grassy areas with suitable nest trees and ample perch sites. My study area contained large amounts of apparently suitable habitat and moderate shrike densities. While habitat preference was not detected at spatial scales larger than 28.3 ha, these larger scales may be important during habitat selection when landscapes contain limited amounts of suitable habitat, or when shrike densities are lower. While little association was observed between habitat variables and reproductive success, roadside nests were found to be unproductive nesting areas for shrikes.

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Table 1. Comparison of habitat variables within 200 m of Loggerhead Shrike nest sites and paired random (unoccupied) sites located 1 km from a shrike nest (N=25).

	Nest Sites	Paired Sites	t Statistic	P-value
Length of Fenceline¹	1114.9 ± 403.5	796.4 ± 412.2	3.29	0.003
Length of Roadway¹	429.2 ± 221.5	422.2 ± 203.7	0.23	0.82
Distance to Road¹	53.2 ± 73.4	52.8 ± 73.7	1.0	0.33
Length of Utility Wire¹	388.1 ± 325.4	356.4 ± 296.3	0.54	0.60
Pasture²	48.1 ± 28.8	15.2 ± 17.5	4.28	0.0003
Soybeans²	16.6 ± 19.1	18.7 ± 21.5	-0.36	0.72
Corn²	13.2 ± 16.0	34.2 ± 33.6	-2.70	0.01
Old Crop²	3.4 ± 12.0	2.2 ± 6.3	0.54	0.60
Hayfield²	8.3 ± 19.4	5.8 ± 19.2	0.44	0.66
Forest²	1.2 ± 2.5	3.1 ± 7.9	-1.30	0.21
Alfalfa²	1.9 ± 4.0	10.1 ± 3.2	-1.85	0.07
Roadway²	3.9 ± 2.0	4.2 ± 1.9	-0.86	0.40
Lawn²	0.9 ± 1.8	1.2 ± 2.6	-0.54	0.60
Number of Perch sites	77.3 ± 70.4	36.7 ± 26.2	2.88	0.008

¹ Mean length in meters

² Mean percent of total area

Table 2. Comparison of habitat variables within 200 m of occupied Loggerhead Shrike nest sites and unpaired random sites (N = 57, 25).

	Nest Sites	Random Sites	t Statistic	P-value
Length of Fenceline¹	1086.0 ± 388.0	789.5 ± 396.9	3.90	0.0002
Length of Roadway¹	427.3 ± 214.7	406.2 ± 180.8	0.54	0.58
Distance to Roadway¹	57.2 ± 94.3	52.8 ± 72.9	0.27	0.79
Length of Utility Wires¹	391.9 ± 325.6	338.2 ± 249.1	0.96	0.34
Pasture²	41.6 ± 29.7	22.3 ± 26.0	3.74	0.0003
Soybean²	17.3 ± 21.0	21.8 ± 25.9	-0.99	0.33
Corn²	17.5 ± 22.1	29.9 ± 32.2	-2.29	0.02
Old crop²	2.3 ± 9.5	1.7 ± 5.7	0.36	0.72
Hayfield²	9.1 ± 17.4	5.3 ± 15.3	1.21	0.23
Forest²	0.9 ± 2.1	3.6 ± 6.6	-2.74	0.008
Alfalfa²	3.7 ± 7.6	6.8 ± 16.3	-1.25	0.21
Roadway²	4.1 ± 2.3	4.1 ± 1.7	0.16	0.87
Lawn²	1.2 ± 2.5	0.7 ± 1.9	1.00	0.31
Number of Perch sites	66.2 ± 53.4	41.5 ± 31.3	2.95	0.004

¹ Mean length in meters

² Mean percent of total area

Table 3. Comparison of three cover types within 300, 600, 900, and 1500 m of Loggerhead Shrike nests and random sites (N = 24).

	Nest Site	Random Site	t-Statistic	P-value
Percent Grassland¹				
300 meters	60.5	43.3	2.53	0.01
600 meters	50.6	42.8	1.15	0.25
900 meters	43.8	38.2	1.00	0.32
1500 meters	41.4	35.8	1.29	0.20
Percent Row Crop				
300 meters	36.5	47.3	-1.41	0.16
600 meters	45.1	49.0	-0.53	0.60
900 meters	50.6	53.0	-0.41	0.68
1500 meters	52.5	56.1	-0.76	0.45
Percent Forest				
300 meters	3.1	7.9	-1.38	0.17
600 meters	4.4	8.2	-1.15	0.25
900 meters	5.6	8.7	-1.10	0.28
1500 meters	6.2	8.1	-1.23	0.22

¹ Pastures, hayfields, alfalfa, roadside grass, CRP, and residential lawns are collectively classified as grasslands.

Table 4. Comparison of the reproductive success of Loggerhead Shrikes nesting near (≤ 15 m) roadsides (“roadside nests”) with those nesting away (> 15 m) from roadsides (“interior nests”) in Northwest Missouri, 1997.

	Roadside Nests	Interior Nests	t Statistic	P-value	All Nests
Number of nests	38	24	----	----	62
Clutch size	5.21 ± 1.29^A	6.14 ± 0.48	-3.57	0.001	5.58 ± 1.24
Hatching success	76.3% ^B	100.0%	----	----	83.0%
Number eggs hatched per nest	3.90 ± 2.64	5.64 ± 1.05	-3.34	0.002	4.6 ± 2.29
Fledging success	55.3%	79.2%	----	----	65.0%
Number fledged per nest	2.53 ± 2.47	4.17 ± 2.28	-2.62	0.01	3.16 ± 2.51
Number fledged per successful nest	4.57 ± 1.21	5.26 ± 0.73	-2.21	0.03	4.9 ± 1.05
Percent of pairs fledging ≥ 1 young	66.0%	83.0%	----	----	72.0%
Number of young fledged per pair	2.82 ± 2.74	4.35 ± 2.14	-2.19	0.03	3.63 ± 2.54
Mayfield's (1975) nest success	35.0%	70.0%	----	----	49.0%

^A Mean \pm SD.

^B Mean percent.

Table 5. Comparison of habitat variables within 200m of successful and unsuccessful nests.

	Successful Nests (N = 36)	Unsuccessful Nests (N = 21)	T Statistic	P-value
Nest tree height ¹	4.6 ± 2.6	4.0 ± 1.3	1.05	0.30
Nest height ¹	2.5 ± 1.6	2.2 ± 0.6	0.97	0.34
Distance from central axis of tree ¹	0.4 ± 0.7	0.8 ± 0.9	-1.94	0.06
Length of fence ¹	1022.8 ± 378.1	1194.4 ± 389.6	-1.63	0.11
Length of road ¹	433.7 ± 206.6	416.4 ± 232.7	0.29	0.77
Length of power line ¹	355.7 ± 312.9	453.9 ± 345.1	-1.10	0.28
Distance to road ¹	62.1 ± 98.4	48.9 ± 88.7	0.50	0.61
Pasture ²	40.1 ± 29.7	44.2 ± 30.2	-0.51	0.61
Soybeans ²	17.5 ± 21.7	17.0 ± 20.4	0.08	0.93
Corn ²	16.5 ± 20.3	19.3 ± 25.5	-0.47	0.66
Old crop field ²	3.4 ± 11.8	0.2 ± 1.0	1.62	0.11
Hayfield ²	10.6 ± 19.2	6.6 ± 13.6	0.92	0.36
Forest ²	1.2 ± 2.3	0.5 ± 1.5	1.25	0.22
Alfalfa ²	3.0 ± 7.0	4.9 ± 8.5	-0.85	0.40
Roadway ²	4.4 ± 2.6	3.7 ± 1.7	1.26	0.21
Lawn ²	1.3 ± 2.6	1.0 ± 2.5	0.47	0.64
Perch sites	68.9 ± 60.5	61.4 ± 39.5	0.57	0.57

¹ Mean length in meters. ² Mean percent of total area.

Table 6. Nesting Success of Loggerhead Shrikes in North America.

Location	N ¹	Clutch size	No. hatched per nest	No. fledged per nest	No. fledged per successful nest	Nest Success	Source
Missouri	55	5.7	4.85	3.04	4.40	69.1 ³	Kridelbaugh 1982
Colorado	77	6.4	5.05	3.51	5.40	66.2 ³	Porter et al. 1975
Alabama	37	5.0	4.25	2.50	3.96	43.2 ³	Siegel 1980
Illinois	25	5.6	3.47	--	4.80	71.0 ²	Graber et al. 1973
Illinois	13	5.2	3.98	2.86	3.90	71.9 ²	Anderson and Duzan 1978
South Carolina	49	5.3	4.40	3.0	4.70	65.3 ³	Gawlik 1988
Minnesota	34	5.7	4.18	3.02	4.33	62.0 ²	Brooks 1988
Virginia	57	5.1	3.23	2.46	3.96	62.1 ²	Luukkonen 1987
Virginia	35	5.2	4.58	--	3.57	55.2 ²	Blumton 1989
Iowa	222	5.6	5.0	--	4.70	35.3 ²	De Geus 1990
Indiana	107	5.7	3.39	2.60	4.56	31.0 ²	Burton 1990
Mean	64	5.5	4.22	2.87	4.39	57.5	-----
Missouri	62	5.6	4.60	3.16	4.90	49.0 ² (53.0) ⁴	This Study

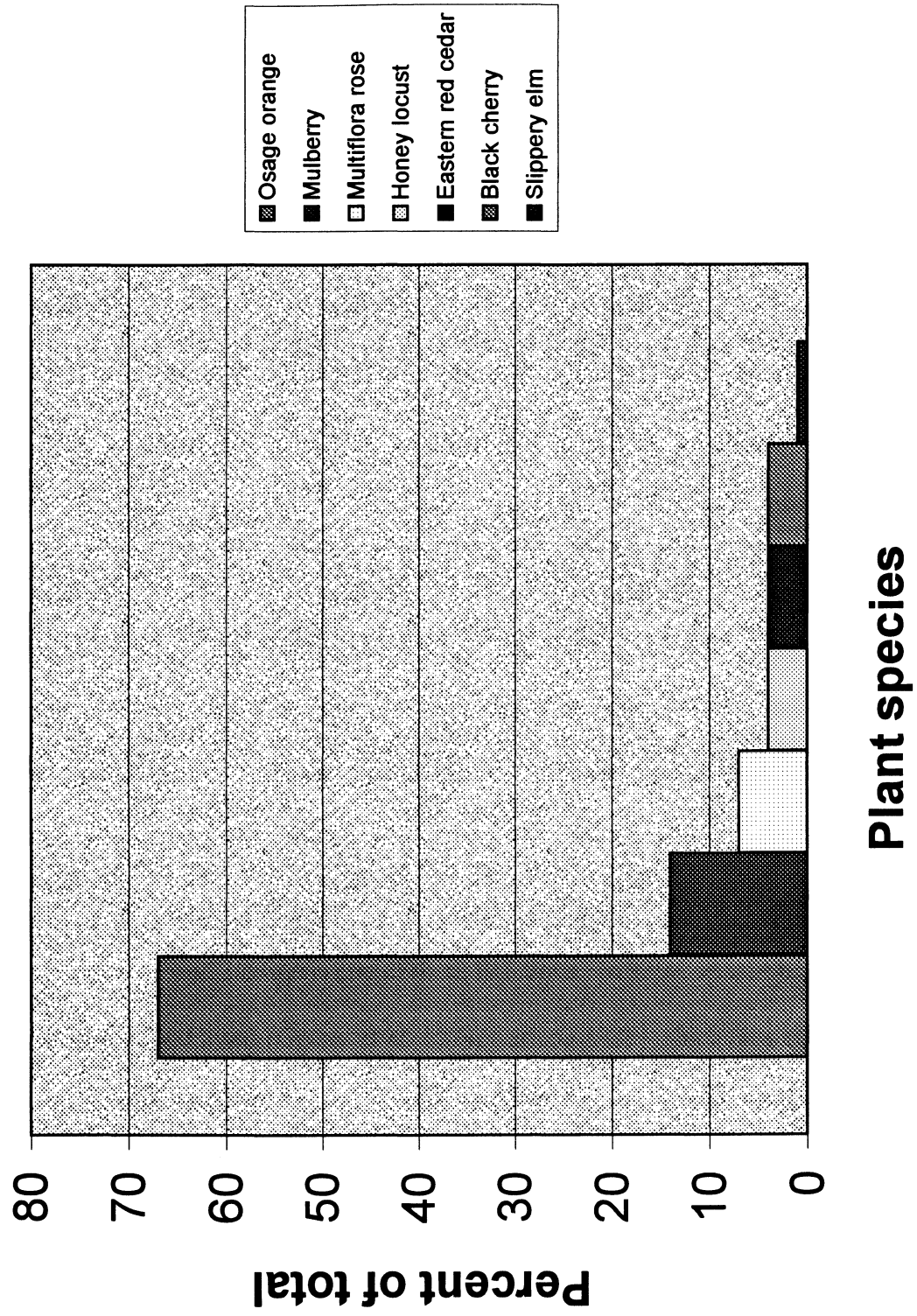
¹ Number of nests used to calculate nest success.

² Used Mayfield's (1961) method for calculating nest success.

³ Apparent success (number of successful nests / number of nests monitored).

⁴ Nest success excluding partial losses.

Figure 1. Species distribution of 57 plants used for nest support by Loggerhead Shrikes in Northwest Missouri, 1997.



Patterns of Impaling in a Migratory Population of Loggerhead Shrikes.

Introduction

Uncharacteristic for a passerine taxa, members of the genus Lanius display predatory behavior much like that of raptors. They employ their relatively large head and hooked bill to kill prey of various sizes. In contrast to the raptors, however, shrikes do not possess the strong talons necessary for tearing small pieces from larger prey items. This restriction limits the size of prey that may be consumed by most passerines (Smith 1972). It is believed that shrikes have overcome this potential limitation through the evolution of impaling behavior (Smith 1972). True shrikes (Laniinae) are characterized, in part, by their unique behavior of impaling various prey items on thorn trees, barbed wire fences, or other suitable substrates (Bent 1950). This adaptation acts as a substitute for talons and allows shrikes to exploit a broader range of prey sizes (Smith 1972).

It has been suggested that impaling behavior may now serve other functions (Sloane 1991). Food storage is one of these functions. In some situations, shrikes cache impaled food items (Graber et al. 1974; Carlson 1985) which may serve as a larder (Beven and England 1969). Hernandez (1995) observed that the rate of food caching by Red-backed Shrikes (Lanius collurio) increased as the number of nestlings increased. Carlson (1985) found that Red-backed Shrikes maintained a high delivery rate of food to young by exploiting the cache over periods when foraging success was low. Applegate (1977) predicted that impaling may serve as a division of labor

between sexes. Males may hunt and impale while females feed themselves and their young with the impaled food. Another postulated function of impaling is that of advertisement, both of territory ownership to conspecifics (Sloane 1991; Mizzel 1993) and of male quality to female shrikes (Yosef and Pinshow 1989). In Texas, Mizzel (1993) observed a significant increase in the cache size of resident Loggerhead Shrikes during the period prior to the arrival of migrant shrikes (L. l. migrans) for the winter. Yosef and Pinshow (1989) found cache size to affect mate selection by female Northern Shrikes (Lanius excubitor), and that reproductive success was higher in individuals with larger caches. More recently, Yosef and Pinshow (1995) found that mates of male Northern Shrikes with naturally large or augmented caches laid a second clutch soon after the first hatched and males cared for the first brood. In pairs with small initial caches, both parents cared for the young until fledged; females then laid the second clutch after fledging occurred.

Thus, the function of shrike impaling behavior appears to be flexible. Therefore, shrikes should adjust the patterns and use of impaling behavior according to the environmental constraints they encounter to maximize their fitness. Consequently, while several studies (see above) have examined the patterns and functional role of impaling, little work has been done on Loggerhead Shrikes, and no published studies have quantitatively described the impaling patterns of a migratory population. Migrant populations encounter environmental and time constraints unlike those operating on nonmigratory animals. Thus, a gap exists in our knowledge and understanding of this multifunctional behavior. The purpose of this study was to document the patterns of impaling exhibited in a migratory population of Loggerhead Shrikes, and to make

predictions as to the adaptive significance of this behavior to this subspecies (L. l. migrans) during the nesting period. The major objectives were to determine: (1) the taxonomic composition of impaled food items; (2) the abundance and location of impaled prey during the incubation, nestling, and fledgling stages of the breeding period; and (3) if a correlation existed between reproductive output and impaling patterns.

Study Area

I investigated the impaling patterns of Loggerhead Shrikes on a 655 km² section of Nodaway County in the northwest corner of Missouri. This landscape is characterized by gently sloping to moderately steep hills drained by both the Nodaway and 102 River basins. Cold winters and long hot summers are typical with an average daily maximum summer temperature of 27°C and a mean annual precipitation of 89 cm (Zimmerman 1986). Historically within the tallgrass prairie region, this landscape is now predominantly agricultural containing primarily rowcrops, pastures, and hayfields (Zimmerman 1986).

Methods

I employed two methods to investigate the impaling patterns of Loggerhead Shrikes. First, focal observations of adult shrikes were conducted to develop a time-use budget, and to document the use of impaled items during the nesting cycle. Second, I conducted territory searches to determine taxonomic composition and abundance of impaled items (number of items / search), as well as other impaling patterns. I located breeding territories in March 1997 by driving county roads in the study area and searching probable habitat with binoculars. Nest searching began on 20 April. All

nests found were checked every 3-5 days to monitor their progress and determine their fate.

Focal Count Observations;

Focal count observations were employed to quantify behavioral patterns and to develop a time budget of adult shrikes during the nesting period. Focal counts were conducted periodically on breeding territories throughout the nesting period from 14 May to 5 June, 1997. Length of individual focal counts ranged from 5-45 minutes depending on the length of time the individual remained on the site. Focal counts were split into fifteen second intervals with the behavior of the focal individual being recorded at each interval. Behavior was categorized as perching/scanning, prey acquisition (diving, pouncing), impaling, flight, food delivery, or aggressive behavior with other birds. From these data, time use proportions were calculated for the six behavior types during the nesting period. All food deliveries to mates and nestlings were recorded and classified as either fresh killed or impaled.

Impaled Food Item Searches;

Searches for impaled food items were conducted on breeding territories beginning 10 May and continuing through 17 July. I repeated searches on territories every 5-9 days during the nesting period in an effort to complete at least one search per nesting stage (incubation, nestling, and fledgling) per territory. Each search lasted 20 minutes, began at the nest tree and then expanded out to approximately 75m from the nest. Each impaled item was identified, recorded, and classified as whole or partially eaten. Type of impaling substrate used, height of the item, and distance from the nest were also recorded. For items impaled in trees or shrubs, I recorded the position on

the plant as either interior or periphery with items located within 10 cm of the terminal end of a branch being designated as periphery. I grouped all impaled items by taxonomic class, and all searches were grouped according to the nesting stage and month from which they occurred. Finally, all territory searches were classified according to success or failure of the nest to produce ≥ 1 fledgling.

One hundred-one impaled food item searches were completed on 24 breeding territories. Shrike territories were treated as individual sampling units, and all data is presented as the mean \pm SD. Because some nests were found after incubation was completed, and other nests failed prior to fledging, some data are missing. Paired t-tests were used for comparison of impaling patterns between nesting stages. Two-sample t-tests were used to compare impaling patterns on successful and unsuccessful territories, and Pearson correlation coefficients were calculated to determine the relationship between impaling variables and reproductive output. I chose $P < 0.05$ as the minimum acceptable level of significance, although values falling between $P=0.05$ and $P=0.10$ were considered marginally significant.

Results

Focal Count Observations:

Thirty-six focal counts were performed on 14 breeding territories. Mean focal count duration was 15.9 minutes, and 510.75 total minutes of observation were conducted. Time-use breakdowns were perching-scanning (71.4%), food delivery (9.9%), prey acquisition (9.4%), flight (7.2%), aggressive behavior (1.4%), and impaling (0.7%) (Figure 1). I observed 54 food deliveries to incubating females and nestlings. In 39 (72%) of these, fresh killed prey (not impaled) was the food source,

while impaled food items were the source in 15 (28%). In 4 instances captured prey was impaled and then directly used for feedings. The total number of impaling events observed was 12. In 6 of these situations, the prey was fed on immediately after being impaled.

Impaled Food Item Searches

Impaled prey was detected on 21 (88%) of the breeding territories that were searched. A total of 146 impaled food items were observed with a mean of 1.70 ± 2.08 items found per territory, and 1.77 ± 3.31 items found per search. These 146 items consisted of the following taxa: insects (36%), reptiles (22%), mammals (16%), amphibians (15%), birds (9%), crustaceans (1%), and earthworms (<1%) (Figure 2). The majority of impaled reptiles were colubrid snakes, primarily garter snakes (*Thamnophis radix*) which comprised 50% of all snakes. Mammals impaled included meadow voles (*Microtus pennsylvanicus*)-33% of impaled mammals, deer mice (*Peromyscus maniculatus*)-29%, least shrews (*Cryptotis parva*)-17%, and white-footed mice (*Peromyscus leucopus*)-9%. Twelve percent of the impaled mammals could not be identified. Cricket frogs (*Acris crepitans*) were the only amphibians found impaled. Birds impaled included the Common Yellowthroat (*Geothlypis trichas*)-23%, Savannah Sparrow (*Passerculus sandwichensis*)-23%, House Wren (*Troglodytes aedon*)-8%, Brown-headed Cowbird (*Molothrus ater*)-8%, Eastern Bluebird (*Sialia sialis*)-8%, House Sparrow (*Passer domesticus*)-8%, and 23% could not be identified.

Honey locusts (*Gleditsia triacanthos*) were the most commonly observed impaling substrate containing 67% of all items. Other substrates used included osage orange (*Maclura pomifera*) 19%, barbed-wire fence (12%), and mulberry (*Morus* sp.)

2%. Mean height of impaled items observed was $1.49 \pm 0.62\text{m}$ ($N=146$). Sixty-seven percent of these items were found whole, and 33% were partially eaten.

Shrikes impaled prey a mean distance of $24.5 \pm 13.2\text{m}$ from the nest. Eight items were impaled directly on the nest tree. Prey were impaled significantly closer to the nest during the nestling stage than both the incubation ($t=3.42$, $P<0.05$), and fledgling ($t=2.42$, $P<0.05$) stages (Figure 3). There was no significant difference between successful and unsuccessful territories with respect to distance of impaled prey from the nest (22.01 ± 10.0 and 20.9 ± 14.0 respectively, $P>0.10$).

Eighty-seven percent of impaled items found during this study occurred on the periphery of the plant. The proportion of items impaled per territory on the periphery was somewhat higher ($t=1.77$, $P=0.10$) early in the nesting period than late with 91% of items occurring on the periphery prior to 10 May, and only 72% after 10 May.

Overall impaling abundance was highest during the nestling period (2.24 ± 3.40 items/search) (Figure 4). Abundance was also significantly higher ($t=2.85$, $P<0.01$) in May (2.21 ± 2.92 items/search) than June (0.55 ± 0.76 items/search). While impaled prey abundance did not vary significantly ($t=0.18$, $P>0.1$) between successful (1.69 ± 2.24 item/search) and unsuccessful (1.56 ± 1.27 items/search) territories, a significant positive correlation ($r=0.46$, $P<0.05$) was detected between the number of young fledged from successful nests and the abundance of impaled prey.

Discussion

The results of this study suggest that impaling in this migratory shrike population served both in prey dismemberment and in supplemental food delivery to

nestlings. Prey dismemberment was directly observed in 4 situations when captured prey were immediately impaled, dismembered, and fed to nestlings.

Due to the fact that this study did not begin until after breeding pairs had formed and breeding territories had been established, the potential role of impaling in territory advertisement and mate choice could not be directly addressed, although evidence from this study suggests that impaling has other important functions during the nesting season. Mizell (1993), who conducted her study after the breeding season, postulated that impaling served in territory ownership display. There only 19.7% of impaled items were partially eaten when initially found. I observed a significantly higher proportion (33%) of items partially eaten ($\chi^2=11.4$, $P<0.001$). Sloane (1991) also postulated territory ownership display as a function for impaling, citing examples in which shrikes impaled inedible objects. I did not observe this behavior. I did, however, detect a decrease in the proportion of items impaled on the periphery of the plant in the second half of the nesting period. This may indicate some function in advertisement occurring early in the season, with a shift toward other functions (e.g., food delivery) later.

My results suggest that this shrike population is using impaled food items as caches to aid in food delivery. Food energy demands are high during the nestling stage of the breeding period (Carlson 1985). Variations in food delivery rates to nestlings caused by low foraging success could be reduced by the utilization of these stored prey (Carlson 1985). The positive correlation between impaled prey abundance and number of fledglings produced per successful nest suggests that supplemental food delivery is a function. While this correlation could simply be the result of more proficient hunters or

more productive territories producing more young, additional results from this study suggest other factors. First, one of every five food deliveries observed was from cached prey. Also, the increase in abundance of impaled prey during the nestling period as well as the fact that items were impaled significantly closer to the nest tree during this stage are both strongly suggestive of the supplemental food delivery function. The pattern of impaling prey close to the nest when energy demands are high (nestling period) would allow the parent to maintain a stable food delivery rate at a lower energetic cost (Carlson 1985).

In conclusion, variations in impaling patterns exhibited by this shrike population appeared to be dependent on energy demands. While it is plausible that this behavior functions in advertisement early in the year when shrikes are establishing breeding territories and forming breeding pairs, the results of this study suggest that food delivery to nestlings may be the primary function of impaling during the nesting period.

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Figure 1. Time budget of adult Loggerhead Shrikes during the nesting season in Northwest Missouri, 1997.

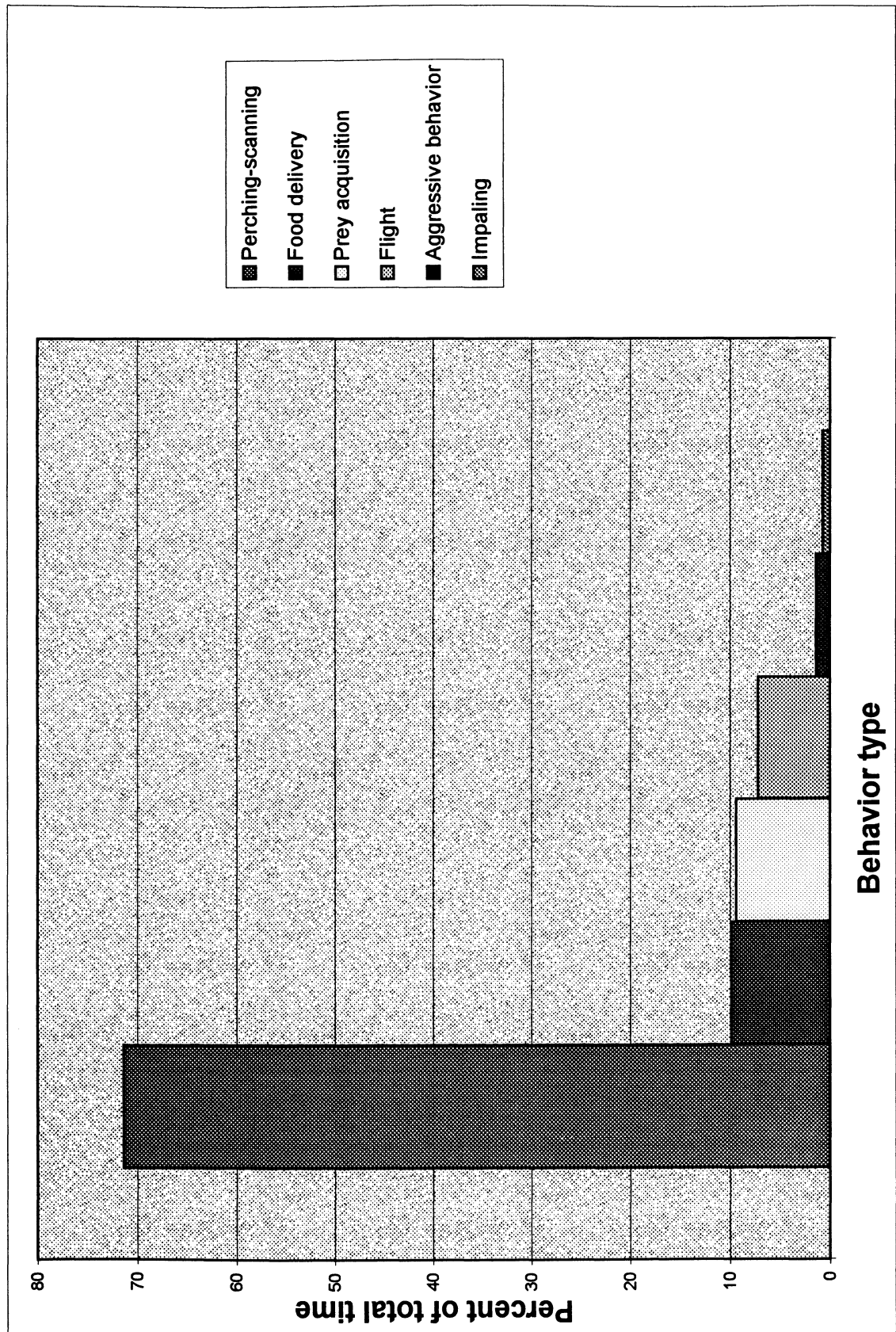


Figure 2. Composition of impaled items observed on Loggerhead Shrike breeding territories in Northwest Missouri, 1997 (N=146).

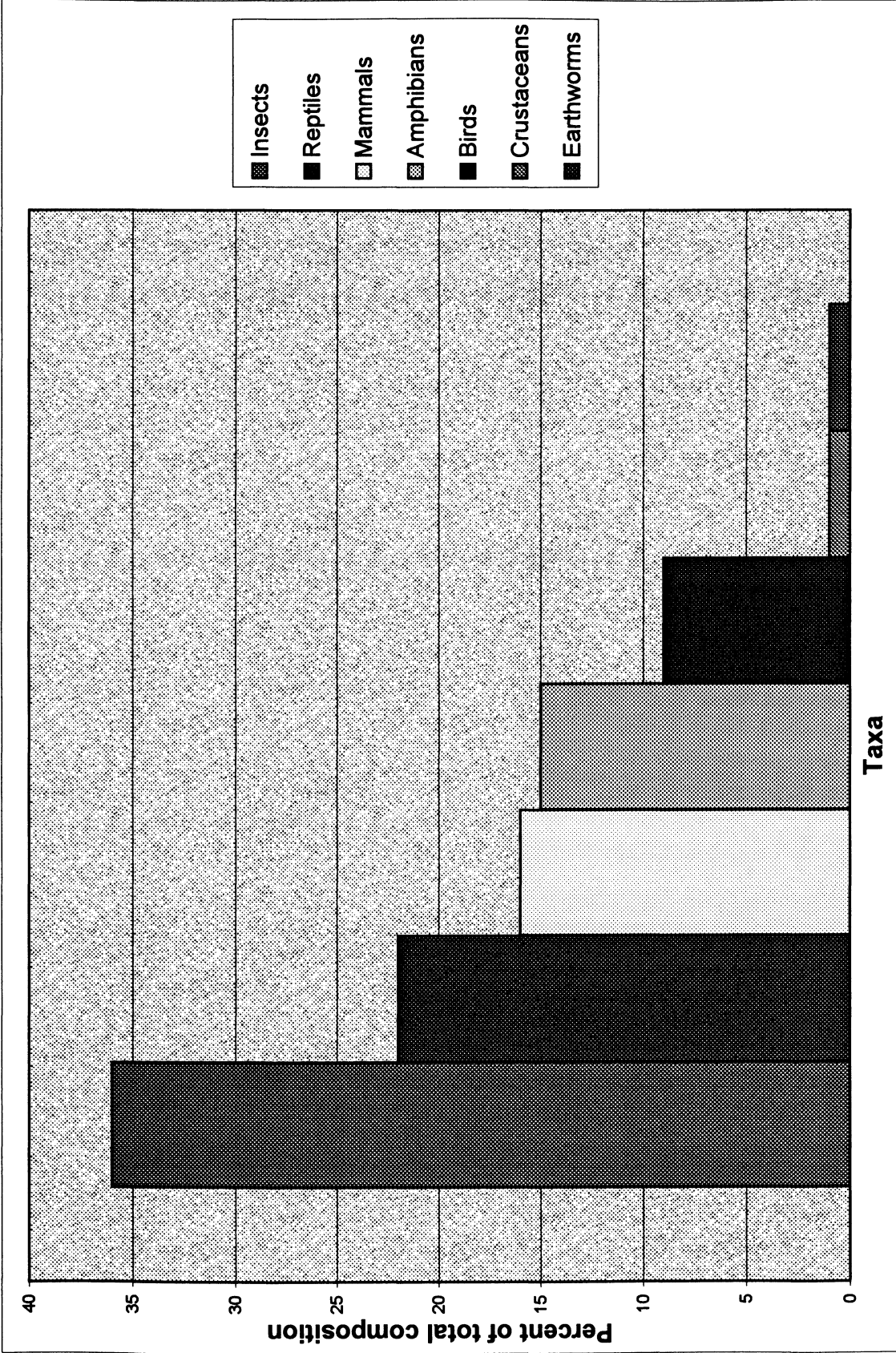
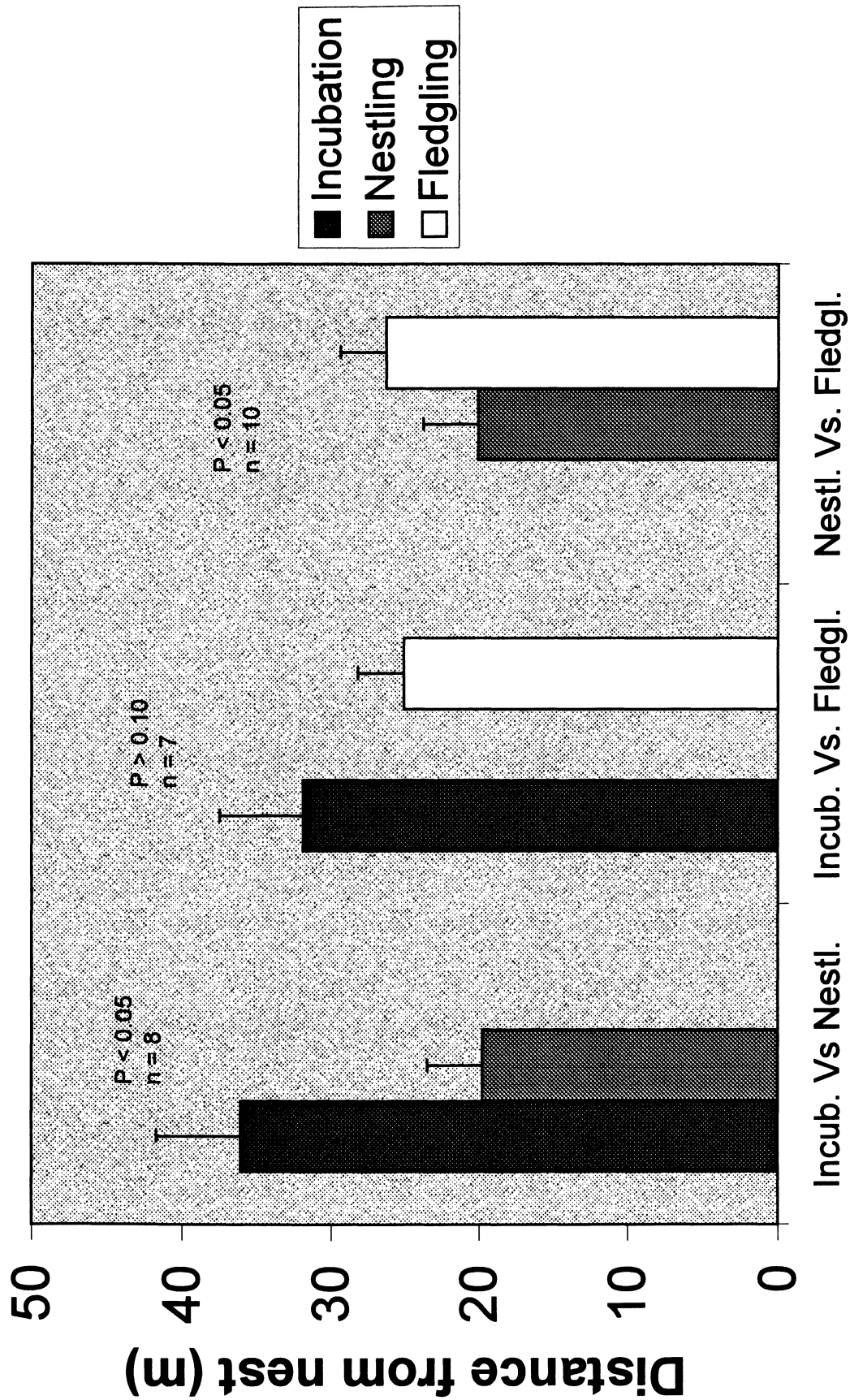


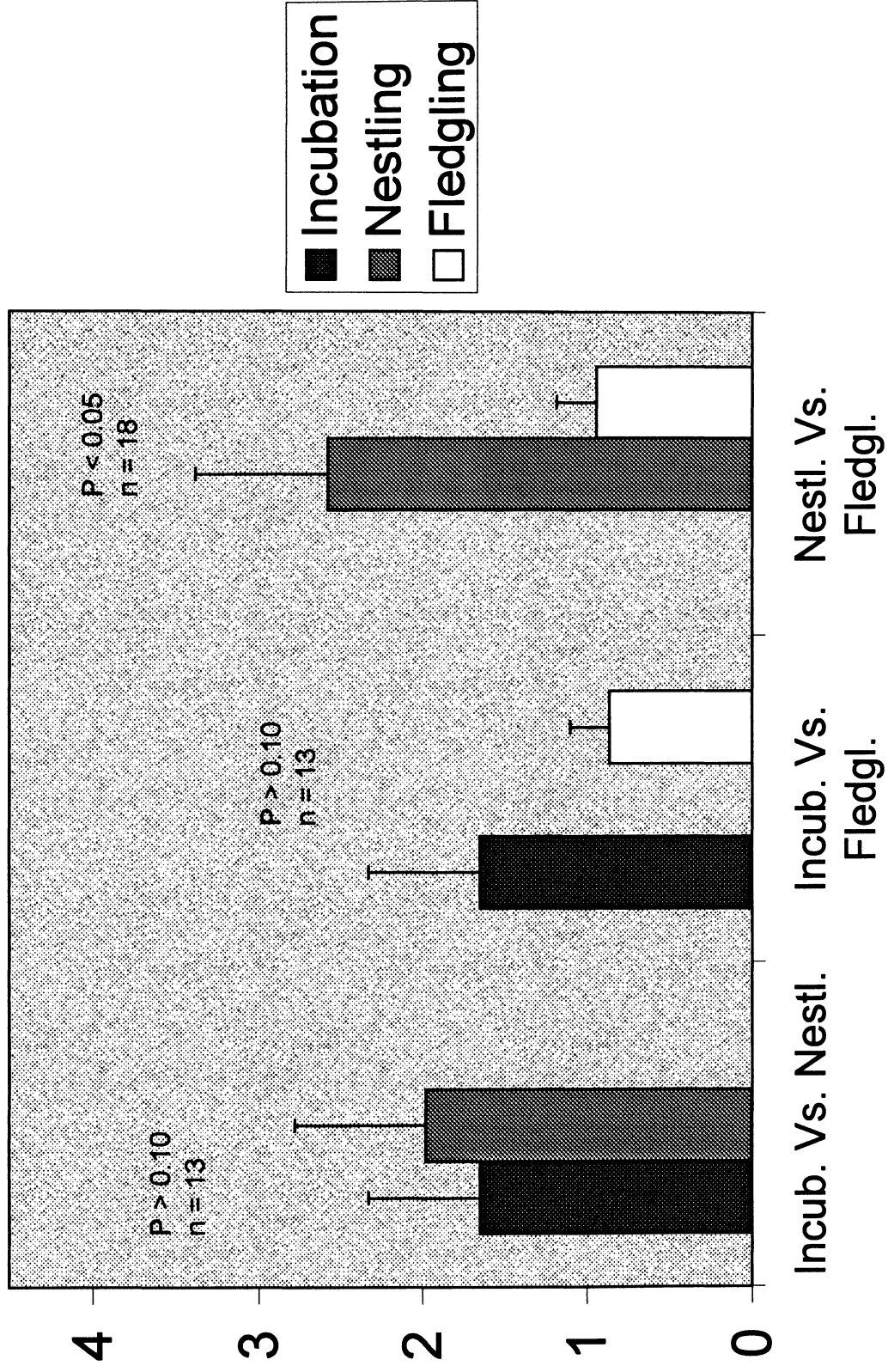
Figure 3. Comparisons (using paired t-tests) of mean distances of impaled items from the nest between the incubation, nestling, and fledgling stages. Means and sample sizes vary between pairwise comparisons due to missing data.



Nesting Stage

Figure 4. Comparisons (using paired t-tests) of abundances of impaled food items on Loggerhead Shrike territories between the incubation, nestling, and fledgling stages. Due to missing data, means and sample sizes vary between pairwise comparisons.

Number of Impaled Items



Nesting Period