The Condor 95:127–131

EFFECT OF VEGETATION HEIGHT ON HUNTING BEHAVIOR AND DIET OF LOGGERHEAD SHRIKES[1]

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Abstract. Prey distribution, environmental conditions, and competition should affect animals' choice of patches, hunting method, and prey types. Loggerhead Shrikes are sit-and-wait predators and rarely hunt in flight. We observed the effect of sub-optimal substrate on their hunting capabilities. Hunting attempts and hunting success were not significantly different before and after the substrate in six territories was mown, although significant differences occurred in the number of prey caught by aerial chases and hovering and in the number collected from perches. In two territories that were not mown, no significant differences occurred. None of the shrikes adjusted the boundaries of their territories; all were apparently able to overcome the effects of high vegetation by altering their hunting behavior.

Key words: Foraging; hunting capability; high vegetation; Loggerhead Shrike; Lanius ludovicianus; *Florida.*

INTRODUCTION

Foraging organisms should maximize net energy gain (Schoener 1971, Charnov 1973, Pyke et al. 1977) contingent on prevailing prey distribution, environmental conditions, and competition. A foraging animal must choose among different habitat patches, hunting methods, and prey types (Charnov 1973, Mills 1979). Optimal diet theory assumes that animals are capable of evaluating prey and deciding whether to attack (Craig 1978, Mills 1979). Charnov (1973) suggests that prey distribution may be an important factor regulating the movements of predators among patches. The Loggerhead Shrike (*Lanius ludovicianus*) is an example of a ground-hunting predatory bird for which Charnov's model appears appropriate because it is a sit-and-wait predator which scans for prey from suitable perches scattered throughout individual or pair territories (Yosef and Grubb 1992). The prey-encounter rate for perch-hunting birds is a function of area hunted, prey density, prey type, and vegetational structure (Mills 1979). Here, we report the effects of sub-optimal, tall-grass substrate on the hunting performance of shrikes. We hypothesized that tall vegetation would severely limit the hunting capabilities of shrikes, and that shrikes would compensate by adopting alternative hunting tactics or by changing the composition of their diet. Shrikes are typically found in habitats such as pastures, that are marked by short vegetation. However, during 1990 and 1991, dog fennel (*Eupatorium capillifolium*) in shrike territories at our Florida study site reached heights of 1.5 to 2 m by the end of the rainy season (May–September). This meant that shrikes had to alter their hunting behavior. To investigate how apparently sub-optimal habitat might affect shrike foraging ecology, we collected data on the hunting behavior of shrikes in territories dominated by dog fennel before and after the territories were mown, a routine management practice on cattle ranches. Data recorded were hunting attempts per hour, hunting efficiency (captures/attempt), and composition of diet. We also checked to see if shrikes in dog fennel hunted more from the wing, either by actively chasing prey or by hovering, or defended larger territories containing more hunting perches to compensate for reduced huntable substrate per perch.

METHODS

During 1990 and 1991, we studied Loggerhead Shrikes at the MacArthur Agro-ecology Research Center (MAERC, 480000 E, 3004000 N, UTM; 11 m ASL), a 4,000-ha cattle ranch near Lake Placid, Florida that is a division of the Archbold Biological Station. We compiled activity-budgets of shrikes on six territories before and after the territories were mown. Territories were randomly chosen for sequence of observation. Each territory was observed for 12 two-hour periods between 06:00 and 18:00 hr. Unfortunately, ranch management practices prevented us from in-

[1] Received 27 May 1992. Accepted 26 October 1992.
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cluding unmown territories in an *a priori* experimental design. The two territories which were mown last, however, were successfully observed for 24 hours each as unmanipulated "controls" and their data were used to test for seasonality effects on hunting behavior and diet composition.

The six territories, located in improved bahia grass (*Paspalum notatum*) pasture, were 5.3–9.6 ha (mean 8.35 ± 0.66 ha). All records for time-activity budgets were collected from shrikes hunting from fence posts that were 135 ± 6 cm (mean ± SD, n = 100) tall. All study animals had previously been captured in a composite treadle-bal-chatri trap (Yosef and Lohrer 1992) and banded for individual identification with U.S. Fish and Wildlife Service aluminum bands and with color bands.

By using a balanced sampling design, we initially recorded 24 hours of hunting related activity in each of the six territories, all of which had vegetation ≥1 m in height for at least 5 m in all directions from all hunting perches. Prey items were identified to taxa when possible. After mowing (to ≤4 cm above ground), an additional 24 hours of time-budgets was collected for each of the six mown and two unmown territories.

Activity was timed with a stopwatch and divided into the following categories: (1) lookout, (2) flying, usually to or from collecting prey, or chasing conspecifics or heterospecifics from the area, or changing lookout perches, or hovering, (3) handling prey, a category with two components, attack until consumption or landing with prey at cache site until completed impaling, (4) preening, and (5) resting. A shrike was considered to be on lookout when it showed signs of searching the substrate in its vicinity for prey.

Miller (1931) stated that 15 to 30 minutes was adequate to map a shrike's territory, but Kridelbaugh (1982) believed that at least two to three hours of observation were needed to accurately measure territory size. We observed each individual for 24 hours, over three-week periods, before and after mowing. Individual shrike locations were marked on aerial photographs (1 in. = 400 ft.) and digitized with Arcinfo software. Territory size was calculated as the minimum polygon bounded by defended points of the habitat.

Differences between time budgets before and after mowing, and aspects of behavior and diet were tested for significance with paired t-tests. Activities of the two birds on the same territory were not considered statistically independent, so the territory was used as the primary sampling unit. All percentage data were arc-sine transformed prior to application of t-tests. Results are presented as means ± SE.

RESULTS

Mowing territories affected Loggerhead Shrike behavior (Table 1). Comparing unmown with mown conditions, total flight time decreased (11.3 vs. 6.6%), while lookout (79.5 vs. 83.3%), preening (1.7 vs. 2.3%), and resting time (2.3 vs. 3.4%) increased. Prey handling time was unchanged (5.2 vs. 4.5%). A shift from aerial chase to ground hunting occurred, and significantly fewer Odonata were captured after mowing.

Paired t-test comparisons of the number of hunting attempts (11.3 vs. 11.0 attempts per hour) and hunting success (73 vs. 76%; 8.3 vs. 8.4 successful attempts per hour) of the 6 pairs of shrikes before and after mowing were not significant ($t = -1.11$, $P = 0.316$ and $t = -0.44$, $P = 0.678$, respectively). Significant differences occurred in the number of prey caught by aerial chases and hovering ($t = 12.24$, $P = 0.0001$) and in those collected on the ground from perches ($t = 7.74$, $P = 0.0006$). In unmown territories, fewer invertebrates were collected from the ground (282 vs. 937) and more captured in aerial chases (357 of 639 vs. 36 of 973), than in the mown condition. Further, in the unmown condition, more amphibians (125 vs. 78), and fewer reptiles (96 vs. 161) were captured.

Dragonflies (*Odonata* spp.) decreased in shrike diets after mowing, but all other prey items remained essentially unchanged. The overall diet composition of prey taken in high substrate was similar to that of low substrate; in high vegetation 82% of the prey were insects, 10% amphibians, and 8% reptiles, whereas in low vegetation the same taxa accounted for 80, 6, and 13% of the diet, respectively.

In the two "control" territories, which remained unmown, we found no significant differences in hunting behavior between time periods corresponding to the before-mowing and after-mowing intervals in the other six territories (Table 2). Neither did significant differences occur in the number or types of prey taken.

No significant change in territory size or configuration occurred in either the six territories (before, 8.35 ± 0.66 ha vs. after, 8.22 ± 0.64

TABLE 1. Percentages of various activities, hunting success, and mean number of prey items caught per pair during 24 hr of observations of each of six territorial pairs of Loggerhead Shrikes before and after the vegetation on their territories was reduced by mowing from >1 m to ≤4 cm. All data are presented as means ± SE and for each prey type, the percentage of all prey taken is shown in parentheses. For paired *t*-tests, percentages were arc-sine transformed and the territory was considered the primary sampling unit. Bonferroni's correction (P = 0.05/number of tests) was used to determine significance for each of the separate analyses of activity, hunting success, and diet selection; statistically significant values are underlined.

	Before-mowing	After-mowing	Paired *t*-value	*P*
Lookout	79.5 ± 1.5	83.3 ± 1.2	−5.99	0.002
Total flight	11.3 ± 0.6	6.6 ± 0.2	7.51	0.0007
Change	6.7 ± 0.6	3.5 ± 0.2	5.85	
Chase	4.6 ± 0.3	3.2 ± 0.1	6.34	
Handling prey	5.2 ± 0.5	4.5 ± 0.3	1.57	0.18
Preening	1.7 ± 0.7	2.3 ± 0.6	−2.79	0.04
Rest	2.3 ± 0.7	3.4 ± 0.7	−3.31	0.02
Hunting (per hour)				
Attempts	11.3 ± 0.2	11.0 ± 0.1	1.01	0.36
Successful	8.3 ± 0.1	8.4 ± 0.3	−0.45	0.67
Aerial chase	2.5 ± 0.2	0.3 ± 0.1	11.75	0.0001
Ground	5.8 ± 0.2	8.2 ± 0.3	−7.49	0.0007
	Before-mowing	After-mowing	Paired *t*-value	*P*
Diet				
Insecta				
Odonata	24.0 ± 1.6 (12.1)	6.0 ± 1.7 (3.2)	−31.12	0.0001
Hemiptera	45.8 ± 2.3 (23.0)	39.0 ± 3.2 (20.6)	0.02	0.73
Coleoptera	44.3 ± 3.3 (22.3)	50.3 ± 3.5 (26.6)	−0.98	0.37
Lepidoptera	14.5 ± 1.3 (7.3)	10.3 ± 1.4 (5.4)	0.17	0.87
Orthoptera	33.5 ± 3.8 (16.8)	47.8 ± 2.9 (25.3)	−1.46	0.21
Amphibians				
Hyla cinerea	15.0 ± 0.6 (7.6)	2.2 ± 1.0 (1.2)	1.35	0.23
H. squirella	3.3 ± 1.0 (1.7)	10.5 ± 1.0 (5.6)	−1.41	0.22
Gastrophyne carolinensis	1.7 ± 1.1 (0.9)	0.2 ± 0.2 (0.1)	−0.22	0.84
Rana spenocephala	0.7 ± 0.3 (0.4)	0.2 ± 0.2 (0.1)	−0.38	0.73
Reptiles				
Anolis carolinensis	5.7 ± 0.5 (2.8)	3.2 ± 0.8 (1.7)	−0.09	0.93
Scincella lateralis	8.3 ± 1.1 (4.1)	5.5 ± 1.0 (2.9)	−0.05	0.97
Eumeces inexpectatus	2.0 ± 0.7 (1.0)	13.7 ± 2.0 (7.3)	−1.09	0.33

ha; t = 0.89, 5 df, P = 0.414), or the two control territories (before 7.0 ± 1.9 ha vs. after 7.2 ± 2.0 ha; t = −3, 1 df, P = 0.205).

DISCUSSION

By spending more time hunting from a hover or in aerial chases, shrikes appeared to incur greater hunting costs when the territories were unmown (Table 1). Many birds can hover, but only a few routinely employ this energetically costly behavior (Bernstein et al. 1973) while looking for food (Weis-Fogh 1973, Balgooyen 1976, Grubb 1977). However, hovering apparently can be more advantageous than hunting from perches when the rate of capture can be increased by hunting areas of greater prey availability and from heights that increase detectability (Mills 1979). In this study, all attacks from hovers appeared to be on prey located initially from perches, but which had moved from the location where first detected. This was particularly true for lizards. Almost all (95%) lizards were captured from a hover when the vegetation was high, but only 18% after the vegetation had been mown. This disparity suggests that the shrikes had difficulty in pin-pointing the exact location of mobile prey in high vegetation prior to initiating the final attack, or that lizards could see predators more.

TABLE 2. Percentages of various activities, hunting success, and mean number of prey items caught per pair during 24 hr of observations of each of two pairs of Loggerhead Shrikes before and after the vegetation on the territories of six other pairs was reduced by mowing from >1 m to ≤4 cm. All data are presented as means ± SE and for each prey type, the percentage of all prey taken is shown in parentheses. For paired t-tests, percentages were arc-sine transformed and the territory was considered the primary sampling unit. Bonferroni's correction (P = 0.05/number of tests) was used to determine significance for each of the separate analyses of activity, hunting success, and diet selection; statistically significant values are underlined.

	Before-mowing	After-mowing	Paired t-value	P
Lookout	76.6 ± 1.9	78.0 ± 1.8	−29.0	0.02
Total flight	9.3 ± 0.8	8.9 ± 0.6	1.8	0.32
Change	5.2 ± 0.7	5.5 ± 0.3	−0.5	
Chase	4.1 ± 0.2	3.4 ± 0.3	4.3	
Handling prey	5.6 ± 0.4	5.4 ± 0.5	2.0	0.28
Preening	3.5 ± 0.4	3.5 ± 0.7	0.0	1.0
Rest	5.2 ± 1.1	4.4 ± 1.1	0.0	1.0
Hunting (per hour)				
Attempts	10.7 ± 0.4	9.8 ± 1.1	0.6	0.66
Successful	8.6 ± 0.4	9.3 ± 0.1	−1.86	0.32
Aerial chase	2.0 ± 0.8	2.7 ± 0.4	−1.44	0.39
Ground	5.9 ± 0.6	6.6 ± 0.4	−3.5	0.18
	Before-mowing	After-mowing	Paired t-value	P
Diet				
Insecta				
Odonata	24.5 ± 5.5 (10.5)	25.0 ± 1.0 (10.6)	0.33	0.80
Hemiptera	52.5 ± 0.5 (22.6)	45.5 ± 2.5 (19.3)	34.33	0.02
Coleoptera	50.0 ± 2.0 (21.5)	58.0 ± 7.0 (24.5)	−0.55	0.68
Lepidoptera	16.5 ± 0.5 (7.1)	12.5 ± 0.5 (5.3)	7.00	0.09
Orthoptera	37.5 ± 1.5 (16.1)	46.5 ± 2.5 (19.7)	−2.30	0.26
Amphibians				
Hyla cinerea	16.5 ± 0.5 (7.1)	13.5 ± 1.5 (5.7)	2.50	0.24
H. squirella	11.0 ± 3.0 (4.7)	10.5 ± 0.5 (4.5)	0.45	0.73
Reptiles				
Anolis carolinensis	4.5 ± 0.5 (1.9)	6.5 ± 0.5 (2.8)	−7.00	0.09
Scincella lateralis	7.5 ± 2.5 (3.2)	5.5 ± 1.5 (2.3)	1.71	0.34
Eumeces inexpectatus	12.0 ± 1.0 (5.2)	12.5 ± 3.5 (5.3)	−0.29	0.82

Loggerhead Shrikes on the ranch previously have been shown to capture an average of 7.4 prey per hour in open pastures and when flying down to the ground to catch prey out to a maximum of about 6.5 m from fence line perches (Yosef and Grubb 1992). The results of this study were similar; individuals in high (unmown) and low (mown) vegetation captured 8.3 and 8.4 prey per hour, respectively. These results do not support the hypothesis that rate of prey capture is severely limited in habitats with tall grasses or shrubs. Increase in hovering, aerial chases, and frequent perch changes resulted in an almost doubling of the amount of time spent in flight (Table 1). Preening, rest, and handling of prey were not significantly different between the two periods, a result in line with the similarity in prey captures. No changes in territory size or configuration occurred after mowing, and none of the shrikes left its territory. Thus, the shrikes were able to adjust to this annual modification of their habitat solely by altering their hunting behavior.

Mills (1979) thought that ground-hunting birds should hunt in tall grass only if higher prey density or greater prey size compensated for the lower visibility there. In the present study, the range of species captured did not vary with vegetation height and mowing did not affect the composition of the shrikes' diet. The limitations of our study (i.e., lack of true controls and absence of data on prey populations), hinder our ability to compare our results with those of Mills.

Red-backed Shrikes (*Lanius collurio*) derive greater energetic benefit in pastures, in which Brandl et al. (1986) reasoned that shrikes selected pastures because low vegetation allowed better access to prey and not because prey densities were higher. Bohall-Wood (1987) advanced a similar argument for the use of pastures by Loggerhead Shrikes in Florida. Our results support these views. Although shrikes probably caught as much food in the high vegetation, their metabolic expenditure was higher (i.e., they flew more). Thus, their net energy gain was probably lower than in short vegetation. Shrikes captured significantly more dragonflies when the vegetation was high, requiring longer aerial pursuits. After the vegetation had been mown, the number of dragonflies chased by shrikes decreased almost 75%.

Time spent in aerial pursuits affected personal-maintenance activities. Shrikes appeared to preen and rest more when the substrate was low than when it was high. The results substantiate the conclusions of others (e.g., Brandl et al. 1986, Bohall-Wood 1987) that grassland habitats permit energetically efficient hunting in shrikes and therefore are important to shrike management plans.

ACKNOWLEDGMENTS

We thank Dalit Yosef for her help in collecting data, and Fred Lohrer, A. S. Gaunt, T. A. Bookhout and two anonymous reviewers for improving an earlier draft of this ms. Work was supported by a Frank M. Chapman Award from the American Museum of Natural History, a Cruickshank Award from the Florida Ornithological Society, and a grant-in-aid of research by the Sigma Xi. This is contribution 10 of the MacArthur Agro-ecology Research Center of the Archbold Biological Station.

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