SEASONAL ASPECTS OF THE PREDATORY BEHAVIOR OF LOGGERHEAD SHRIKES

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ABSTRACT.—Aspects of the foraging behavior of Loggerhead Shrikes were analyzed in the nonbreeding and breeding seasons in southern California. The birds obtained more food during the breeding season by attacking more often, not by taking larger prey. Attack rate during the breeding season was twice that in the nonbreeding period, with no apparent difference in capture efficiency. No distinct relationship between attack distance and capture efficiency was noted. Time between attacks decreased during breeding in response to greater food demands. Pursuit, encounter, and handling times did not significantly change between seasons. A positive significant correlation between prey handling time and the square of prey length was found. Handling time did not severely reduce the amount of time that could be devoted to hunting during any season. However, total movements averaged considerably higher during breeding than attack rate alone, adding to the energy expenditures of a hunting shrike and possibly placing constraints on the amount of hunting time available.

An important part of the daily activity budget of an animal is that portion devoted to foraging. More food is needed during the breeding season, when the nutritional requirements of the nestlings must also be satisfied. Studies of the temporal patterns of foraging behavior thus lend insight into changing energy needs of a species.

This study reports on the foraging behavior of the Loggerhead Shrike (Lanius ludovicianus). Impaling (caching) behavior has been discussed by Watson (1910) and Applegate (1977), and methods for carrying prey were noted by Esterly (1917) and Caldwell (1967). Slack (1975) hypothesized that shrikes select small prey that would be easier to catch, instead of larger prey that would provide more food once captured. Food items taken by shrikes were listed by Judd (1898), Stephens (1906), and Wayne (1921). An important paper by Craig (1978) described the various components of shrike attack behavior, mostly during the nonbreeding season. Attack behavior of shrikes might be expected to differ between nonbreeding and breeding seasons owing to the need to obtain additional food during breeding. I report here on differences in the components of a shrike's attack between breeding and nonbreeding seasons.

STUDY AREA AND METHODS

My 6-ha study area was in the southeast end of the Whittier Narrows Nature Center, South El Monte, Los Angeles County, California (elevation 67 m). The center was bordered by a channeled river on the south and by major roads and freeways on the remaining sides. Vegetation on the site was relatively homogeneous, consisting mainly of a low (<1 m) growth of mustard (*Brassica campestris*) interspersed with grasses and herbs. Widely scattered elderberry (*Sambucus mexicana*) and walnut (*Juglans californica*) grew to 7 m. Transmission lines supported by three towers crossed the site. A chain-link fence and a dirt road ran parallel with the lines and bordered the south edge of the site adjacent to the river; the river was about 50 m from the towers.

From 24 December 1977 through 23 August 1978 I visited the study area for about 60 h on 31 days. During the pre-breeding season I collected data on seven adult shrikes occupying the area. Data were collected on one pair during the breeding and post-breeding seasons; this pair raised two broods of three young each during 1978.

I recorded perch height, height of perch support (e.g., tree, tower), pursuit distance (distance from bird to prey), pursuit time (time to fly toward prey), encounter time (time to subdue prey), handling (feeding) time, attack interval (time between attacks), and vegetation height surrounding prey. Prey size was estimated, and prey type was listed simply as beetle, butterfly, grasshopper, or small insect. Only data resulting from at least 30 min of continuous observations of a single bird were analyzed; several observation periods lasted two hours.

A stopwatch was used to measure encounter time. Other times were measured with the second hand of a wristwatch. Data were usually collected while I sat about 40 m from a hunting shrike.

Data were summarized for each of the following periods: pre-breeding (*PB*), 24 December 1977 to 11 March 1978; breeding (*B*), 18 March to 15 July 1978; and post-breeding (*PoB*), 7 August to 23 August 1978. The "nonbreeding" season refers to *PB* and *PoB*, collectively. Most observations were made from one and five hours after sunrise. Data were collected on only three dates following breeding (*PoB*), so few meaning-ful comparisons could be drawn between this period and *PB* and *B*.

Student's *t*-test was used to compare *PB* and *B* (and in a few instances, *B* and *PoB*); for percentages the arcsine transformation (Sokal and Rohlf 1969:607–608) was employed. Much of the terminology follows Craig (1974, 1978).

	Period PB	Period B	Difference
Attempts/min ^c	0.11 ± 0.048 (10)	0.22 ± 0.077 (15)	***
Captures/min ^c	0.07 ± 0.042 (10)	0.14 ± 0.052 (15)	**
Encounter time/attack (s)	2.7 ± 1.56 (62)	3.3 ± 4.33 (299)	*
Pursuit time/attacks (s)	1.6 ± 0.69 (66)	1.7 ± 1.00 (301)	n.s.
Mean perch height (m)	4.2 ± 3.09 (67)	7.1 ± 3.33 (302)	***
Mean perch substrate height (m)	7.8 ± 9.67 (67)	25.9 ± 8.67 (302)	***
Mean ground attack distance (m)	5.5 ± 3.86 (62)	7.2 ± 5.42 (239)	**
Prey size (mm)	26.4 ± 10.60 (29)	$26.2 \pm 13.86(160)$	n.s.
Attack interval (min)			
After miss	5.5 ± 4.67 (17)	3.8 ± 3.27 (97)	n.s.
After capture	8.8 ± 9.01 (28)	4.4 ± 4.22 (181)	*
Attack location			
Percent ground	95 (58)	79 (239)	
Percent air	5 (3)	21 (62)	

TABLE 1. Comparison of various attack parameters of the Loggerhead Shrike during the pre-breeding (Period PB) and breeding (Period B) seasons.^a

* Values = mean \pm SD (sample size). ^b n.s., not significant; * P < 0.05; ** P < 0.01; *** P < 0.001. ^c Sample size = no. of days of observation.

RESULTS AND DISCUSSION

PREY LOCATION AND SIZE

Shrikes took both insects in flight and prey on the ground. Ground attacks were more common in both *PB* and *B*, while air attacks became more frequent during B (Table 1). Flying prey were usually small flies and bees, which increased in abundance during spring. Larger flying prey, such as butterflies, were taken on or near the ground.

Overall prev size was nearly identical between PB and B (Table 1). Craig (1974:67-69) found that prey were larger during the breeding than the nonbreeding seasons (from his class 5, 16-24 mm, to class 6, 24-35 mm). This increase corresponded to an increase in the proportion of larger prey in the territory of the shrike; my study did not include prey sampling. The size of prey taken during my study would also be assigned to Craig's (1974) class 6. Great Tits (Parus major; Royama 1966) and Red-winged Blackbirds (Agelaius phoeniceus; Wilson 1978) take larger prey during the breeding season. In contrast, Craig's (1974) and my results show that shrikes do not capture larger prey as a means of meeting food demands during breeding.

Attack distance (analyzed for ground attacks only) was greater during B (Table 1). The higher perches selected by shrikes during B may have allowed a wider view of surrounding vegetation. This may have been in response to the greater height and density of vegetation (e.g., grass) during B relative to PB.

ATTACK RATE AND CAPTURE EFFICIENCY

Shrikes doubled their attack rate during B (Table 1). Most hunting during B was by the male, who supplied most of the food for the female during incubation and for the female and young after hatching.

Capture rate (captures per minute) was also doubled during B (Table 1), so the increase in attack rate necessary for a male to feed himself in addition to the female and young did not interfere with his capture ability. After the young hatched, the female hunted occasionally (alternating with brooding).

Based on a study in central California during the nonbreeding seasons, Craig (1978) reported an average attack rate of about 0.14 attacks per minute. I found a lower prebreeding (PB) attack rate of 0.11 attacks per minute. Differences in prey availability and size, and weather conditions could account for this difference.

Craig (1978) obtained a nonbreeding capture rate of 0.08 captures per minute; and I found a similar value of 0.07 captures per minute. Further, the average rate of prebreeding efficiency (64%) in my study was close to the 65% rate given by Craig (1978). The efficiency during the breeding season in this study was likewise 65%.

I also calculated attack and efficiency rates in 3-m concentric zones around the perch (Table 2). About 90% of the attacks and captures were within 9 m of the perch for PB, and about 14 m for B. Efficiency rate by zone showed no distinct trend for either

TABLE 2.	Comparison of attack and capture	efficiencies with distance	from the perch for	r Loggerhead Shrikes
during the	pre-breeding (Period PB) and bree	eding (Period B) seasons.		

	Attacks		Captures			Beer
Distance from perch (m)	No.	Cumulative percent	No.	Cumulative percent	Percent of total attacks	Percent of attacks successful*
			Period PE	}		
0-3	24	39.3	11	32.4	39.3	45.8
46	22	75.4	14	73.5	36.1	63.6
7 - 9	9	90.2	6	91.2	14.8	66.6
10-12	1	91.8	1	94.1	1.6	100.0
13-15	4	98.4	2	100.0	6.6	50.0
16-18	1	100.0	0	100.0	1.6	0.0
			Period B			
0-3	65	27.2	43	28.3	27.2	66.2
4-6	85	62.8	54	63.8	35.6	63.5
7-9	27	74.1	13	72.4	11.3	48.1
10-12	27	85.4	19	84.9	11.3	70.4
13-15	21	94.1	15	94.7	8.8	71.4
16-18	6	96.7	5	98.0	2.5	83.3
19-21	6	99.2	2	99.3	2.5	33.3
22 - 24	0	99.2	0	99.3	0.0	_
25 - 27	0	99.2	0	99.3	0.0	
28-30	1	99.6	1	100.0	0.4	100.0
31-33	1	100.0	0	100.0	0.4	0.0

* When prey were captured.

period (i.e., not related to distance out to about 18 m). In B, for example, the greatest capture efficiency was between 16 and 18 m.

ATTACK INTERVAL

I divided the "attack interval" into the "time after miss" and "time after capture" (Table 1). The greater, though nonsignificant, interval after a capture was in part due to handling time of captured prey. Of importance was the relatively short attack interval after a capture during B. This was likely due to the increased food needs during breeding. I found, as did Miller (1931:210), that shrikes may pause for up to 30 min between attacks.

PREY CAPTURE

Prey capture includes flight time to prey (pursuit), time to subdue prey (encounter), retrieval (usually same as pursuit time as shrikes often return to same perch), and handling time (time needed to consume prey). Craig (1978) included the kill (which I defined as encounter) and retrieval in calculations of handling time. I believe, however, that handling time should not be based in part on the distance to the prey. Perhaps handling time should henceforth be based on encounter and actual feeding times.

Pursuit time was nearly identical for PB

and B; encounter time was higher during B but by less than 1 s (Table 1). Average handling time in B was 9.4 s (handling time was not recorded during PB). Based on 11 attacks, handling time during PoB was 8.7 \pm 9.8 s. Pursuit, encounter, and handling times thus remained fairly constant between seasons, and were not altered in response to varying prey demands.

An interrelationship between handling time and length of prey has been shown for Forster's Terns (*Sterna forsteri*; Salt and Willard 1971) and for shrikes (Craig 1978). I found a significant correlation (r = 0.666, n = 87, P < 0.01) between handling time and the square of prey length. I was able to measure handling time accurately for one non-arthropod prey—a 76-mm lizard required 60 s to consume.

Craig (1974) concluded that during periods of peak prey demand (breeding season), handling time could significantly reduce the time available for prey capture. Handling time (calculated as in Craig 1974, 1978) averaged about 14 s per capture. With an average capture rate of 0.14 per minute, the time lost from hunting while handling prey was about 59 s per 30 min or about 3.3% of the total available time; this would raise to 5.4% if based on maximum capture rate observed. I watched shrikes preening and resting for much of the late morning and early afternoon during all seasons. While I

TABLE 3. Movements of hunting Loggerhead Shrikes during the breeding (Period B) and post-breeding (Period PoB) seasons.^a

	Period B	Period PoB
Total moves/min	$0.36 \pm 0.118 (10)$	0.16 ± 0.056 (3)
Perch changes/min	0.12 ± 0.056 (10)	0.05 ± 0.051 (3)

^a Values = mean \pm SD (sample size = no. of days of observation). Differences between seasons in total moves per minute were significantly different (P < 0.05); those for perch changes per minute were not.

did not keep detailed records, "non-hunting" periods encompassed at least 15% of the daylight hours. Craig (1978) also noted many periods when no hunting took place ("empty half hours"). Thus, I do not believe that handling time severely reduced the amount of time that could be devoted to hunting.

Distance to prey (pursuit), when considered as a separate component of handling time, could be an important part of a shrike's energy expenditure during certain periods. The distance a shrike must fly to capture prey probably does not significantly reduce remaining hunting time during the nonbreeding season. When young are in the nest, however, reducing flight time would decrease energy expenditures and increase the time remaining for hunting. In my study, prior to breeding, shrikes used several perches within their territories for hunting. During the breeding period, perches were usually within 15 m of the nest. These shifts in perch sites were observed for three nesting pairs of shrikes. Hunting near the nest would increase the ability of the male to protect the female and young and at the same time, keep most attacks within 30 m of the nest. Contrary to these results, Craig (1974:71) found that shrikes usually hunted from perches more than 40 m from the nest. The types of perches available to a shrike (e.g., height, structure), along with other aspects of a particular territory (e.g., shrike density, prey availability, ground cover), probably function in perch selection. Analysis of vegetation and prey density at various distances from hunting perches should be included in future studies to help clarify this point.

ACTIVITY

While hunting, shrikes often changed perches several times between attacks. Miller (1931:210) noted that "if food is not secured from a certain post within a minute or two, the bird moves on to another part of its territory." I calculated perch changes per minute and total movements per minute (i.e., perch changes, attacks) for B and PoB(Table 3). Although based on only three dates, perch changes and total movements during PoB were made about one-half as often as during B. The decrease following breeding probably resulted from decreased demand on adults for food after young were fledged. However, the roles of prey abundance and availability in determining movements need study. For example, as prey become more plentiful, less time and effort may be needed to find them.

Total movements per minute averaged about 38% higher than attack rate alone during breeding. Perch change and other interattack movements thus probably added considerably to the energy expenditures of a shrike. Each movement of a shrike (and other predators) should be considered in future analyses of energy expenditures.

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RECENT PUBLICATIONS

The Island Waterfowl .--- Milton W. Weller. 1980. Iowa State University Press, Ames. 121 p. \$10.95. This book is the first to examine comprehensively the many distinct forms of ducks and geese that have evolved on oceanic islands. Drawing on his extensive field work and the literature, Weller first describes the distribution and characteristics of each of these birds. He then considers the factors that influenced colonization by their ancestors, adaptations to island living, and the changes in the reproductive behavior of the solitary island ducks. This leads to a discussion of speciation in these birds and the development of their avifaunas. The book closes with a consideration of the status and conservation of these endemic waterfowl. A well-written, solid piece of work, this book offers much to those who study island biology and evolution as well as those who specialize in anatids.

The Hawaiian Goose/An Experiment in Conservation.—Janet Kear and A. J. Berger. 1980. Buteo Books. Vermillion, SD. 154 p. \$30.00. Captive breeding programs since 1949, first in Hawaii and later at the Wildfowl Trust in England, appear to have rescued the Nene from extinction. This book is chiefly devoted to the history of those efforts and what has been learned from them. Opening chapters comprehensively describe the habitat and the biology of the bird. In conclusion, the authors thoughtfully evaluate the success of this propagation program. The book is illustrated with photographs, diagrams, maps, and with drawings by Peter Scott and others. Appendixes, references, index. This case history will be of interest to those who are concerned with endangered species of birds and the methods for their salvation.

Character variation and evolution of sibling species in the the Empidonax difficilis-flavescens complex (Aves: Tyrannidae).—Ned K. Johnson. 1980. University of California Publications in Zoology 112. 164 p. Paper cover. \$9.50. "The numerous groups of closelysimilar species of New World flycatchers . . . offer considerable potential for insight into the fundamental evolutionary relationships between morphologic stability and isolating mechanisms. In the present report I offer relevant data from two polytypic species of tyrannids..., the Western Flycatcher and its allopatric close relative the Yellowish Flycatcher." Geographic variation in characters of size, color, and vocalization is elaborately analyzed in addressing questions about the distribution, evolution, and taxonomy of the group. In the course of resolving a particular taxonomic problem, this monograph makes an important contribution to the understanding of other groups of sibling species. Photographs, maps, diagrams, sound spectrograms, appendixes, references.

Vertebrate Ecology in the Northern Neotropics.— John F. Eisenberg, ed. 1979. Smithsonian Institution Press, Washington, D.C. 271 p. Paper cover. \$8.95. This volume is a collection of reports by investigators who have been associated with Smithsonian Institution projects in Panama and Venezuela. Most of the papers concern mammals. Betsy Trent Thomas provides an annotated list of "The birds of a ranch in the Venezuela llanos." Eugene S. Morton presents "A comparative survey of avian social systems in northern Venezuelan habitats." Ornithologists who work in the neotropics will find these two papers useful. Each has its own list of references.

Fool Hen/The Spruce Grouse on the Yellow Dog Plains .--- William L. Robinson, 1980, University of Wisconsin Press, Madison. 221 p. \$18.50. Of the North American species of grouse, the Spruce Grouse has been the least known, which is surprising in view of its utter approachability and wide range. Robinson (with the aid of his students) has now given us an intimate portrait of the bird, based on years of study in the Upper Peninsula of Michigan. After introducing the species, he describes the basic aspects of its life history and ecology. An unusual appendix tells where and how to see a Spruce Grouse. Writing in a clear, non-technical, and occasionally colorful manner, the author explains his findings and enlivens them with personal incidents and thoughts. His book is sufficiently informative for wildlife ecologists and game biologists, yet understandable and enjoyable for birders. Photographs, charts, references, index.