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AN ANALYSIS OF THE PREDATORY BEHAVIOR OF THE LOGGERHEAD SHRIKE

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ABSTRACT.—Fluctuations of some aspects of the predatory behavior of the Loggerhead Shrike were examined relative to cycles in prey availability and other physical and biological environmental factors during the nonbreeding period (September 1972–April 1973) near Davis, California. The attack rate of shrikes declined significantly after a minimum temperature threshold was reached, apparently because of the reduced availability of poikilothermic prey at low temperatures. Attack rate stabilized when prey density was high. Average prey size taken was constant with time and well below the maximum that shrikes are capable of capturing. The capture efficiency of shrikes was higher than that reported for other predators. Capture efficiency increased at very low prey density (availability), tending to balance the decreased attack rate. Handling time, though probably a significant variable in predation by shrikes, did not reduce time available for other activities during nonbreeding months. Handling time was highly correlated with length of prey squared.

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STUDIES of the mechanisms of feeding ecology generally assume that parameters of feeding biology are unchanging. Schoener (1974) recently pointed out that mathematical theory in ecology has ignored major kinds of biological variability. In some models, species are considered to have static niches, in that their utilizations (of available resources), consumption rates, and efficiencies (e.g. capture efficiency) are assumed to vary neither with the abundance of resources nor with time. These assumptions limit the reality and applicability of many ecological models and demand study. Furthermore, examination of the elements of the feeding response of a solitary predator, the purpose of this paper, may also help reveal selective pressures responsible for shaping a given animal into an efficient feeding machine in a particular environment.

The workings of a complex ecological process are best analyzed when the process is partitioned into its component parts and each component is then studied in detail (Holling 1959a). Using this approach Holling (1959b) devised the "disc" equation, which sets out the major components thought to regulate the number of prey captured by an individual predator (Holling 1963, 1966; Griffiths and Holling 1969). These are: time exposed to prey, capture efficiency, prey density, and handling time.

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Salt and Willard (1971) pointed out how relatively insensitive attack rate is to variation in prey density. Conversely, attack rate is most sensitive to the handling time and contact time between predator and prey. They reasoned that because only prey density is not within the control of the predator, the other three are probably influenced by variations in the conditions acting on the predator. Much of the variability of predator-prey systems is likely due to diurnal and seasonal changes in the environment and corresponding activities in the animals.

In the present study, the following questions were considered: (1) Does the attack rate vary in a predictable way because of fluctuations in the abundance of suitable prey or seasonal changes in energetic demand of the predator? (2) Is capture efficiency constant, and, if not, does it vary with changing prey density or with time of day or season of the year? (3) Does the average size of prey captured (which is used here as equivalent to caloric return) vary seasonally with the availability of different sized prey? And (4) Is handling time an important general parameter that regulates number of prey captured?

In most studies of predation, such things as handling time, attack rate, and capture efficiency have been measured in the laboratory, using simple organisms and unnatural prey density conditions. This study was initiated to observe directly the stated components of the predatory response in the field, allowing natural fluctuations in the environment and prey density to produce the experimental conditions.

The Loggerhead Shrike (*Lanius ludovicianus*) was chosen for observation because of its diurnal activity, its relative abundance in the area, and its conspicuous manner of hunting. The Loggerhead Shrike is a medium-sized passerine, adults weighing approximately 50 g. The systematics and natural history of the species have been described by Miller (1931) and Bent (1950).

Shrikes are territorial throughout the year, primarily insectivorous, and nonmigratory in central California. Shrikes are known to feed heavily on arthropods, although small mice, birds, reptiles, and amphibians are sometimes taken (Bent 1950).

Shrikes characteristically hunt from perches (approximately 4 m above the ground) that give an unobstructed view of the ground below. Outer branches of small trees and telephone wires are favored hunting perches. When prey is sighted, the bird dives from the perch in a rapid descent. After a capture the bird usually returns to a perch to devour the prey. The prey is conspicuous to an observer at this time. Prey size ranges from 5 mm (<0.001 g) insects to 25 g mice or snakes.

Shrikes are known for their habitat of impaling large prey items on twigs and fences; hence the name butcherbird. Impaling allows the tearing apart of large prey items and, to some extent, food storage. This habit is an important adjunct of the feeding strategy. However, because frequency of return to an impaled item was very rare, a detailed analysis of impaling is not presented. For detailed information concerning the impaling behavior, see Lorenz and Saint Paul (1968), Wemmer (1969), and Smith (1972).

METHODS

The study area.—The study area is located adjacent to agricultural cropland, 3.2 km northeast of Davis, Yolo County, California. The study area is 3.2 km long and runs east-west along County Road 29 on the Willow Slough Bypass. Within the study area 10 resident shrikes arranged themselves linearly along a telephone line and windbreak of small poplars (*Populus* sp.) and willows (*Salix* sp.) parallel to Road 29. During the fall and winter, shrike territories were essentially contiguous. Males occupied territories alternating with females along the telephone line and windbreak. In late February, adjacent territorial boundaries disappeared so that overlapping territories were established for each pair.

Shrikes primarily hunt a 15 m wide strip of ground beside the road bed (toward observers) and between the road and the telephone wires. The vegetation of this strip is mixed grasses and herbs dominated by oats (*Avena sativa*), with occasional plants of wild mustard (*Brassica campestris*). This roadside strip is burned annually in July, resulting in little accumulated litter. Directly below the wires is a small slough (1–2 m wide) that maintains some water throughout the year. The slough supports a vegetation of cattails (*Typha latifolia*), tules (*Scirpus* sp.), and salt grass (*Distichlis spicata*). Shrikes occasionally hunt into the borders of the agricultural fields on the opposite side of the wires and into the edges of the slough. The zone actively used by the shrikes under study is a band approximately 30 m wide and 3.2 km long, with the telephone wires and small trees running down the center of it. The total area is approximately 9.6 ha. The strip of vegetation in and bordering the slough remains green throughout the dry summer. Most prey (insect and mammalian) live in this strip. Weather data were collected at the University of California at Davis, some 8 km from the study site.

Observation methods.—The study deals only with the hunting behavior of adult shrikes during fall and winter. Observation was carried out by teams of volunteer observers. Because the validity of the data depends to a large extent on the acuity of these observers, something should be said of this method of accumulating large volumes of data. Observers were all university seniors and graduate students in zoology and all had prior field experience. Observers were given a period of training to ensure acceptable observation. Their instructions were simple and direct; all data were tabulated on preprinted data sheets. Observers worked in two-person teams so that data could be tabulated without losing sight of the birds. Field teams spent 2 h of observation per period. Observation periods were divided into 30 min intervals of continuous observation of single birds.

The data recorded were date, time, weather conditions, location within territory, general behavior, site location, number of attacks, number of captures, attack interval (time between attacks), handling time, size of prey, and, when possible, type of animal caught. The type of prey (cricket, grasshopper, larva, beetle) was often not discernible. Identifications of individual prey items are not included in the present analysis. Attack interval was measured, using the sweep-second hand of a wristwatch. Handling time was measured using a stopwatch and noted to the nearest 0.1 s. Handling time was defined as the time elapsed from first contact with prey until the prey was swallowed. Prey-size estimation demanded a certain amount of judgment on the part of the observer. The size could usually be seen even though the type of animal could not be discerned. Prey size for insects was estimated using a relative number scale—1 being the smallest and 7 the largest:

- | | |
|--------------------------------|----------------------|
| (1) 5 to 8 mm long, <2 mm wide | (5) 16 to 22 mm long |
| (2) 5 to 8 mm long, >2 mm wide | (6) 22 to 30 mm long |
| (3) 8 to 12 mm long | (7) 30 to 50 mm long |
| (4) 12 to 16 mm long | |

Data were summarized for each month and for each of five periods of the day. The five periods were each 2 h long during the winter when there were 10 daylight hours per day. During the fall and spring the first interval after sunup and the last 2 h of daylight remained as 2 h segments. The central three intervals were enlarged to accommodate the increased hours of daylight hunting time. For convenience, the intervals have been designated as 2 h intervals after first light: 0–2, 2–4, 4–6, 6–8, 8–10.

Laboratory methods.—Eight Loggerhead Shrikes were captured and maintained separately in the laboratory. Handling time was measured after 5 days of laboratory acclimation. Each bird was starved at least 14 h and then offered a prey item of known length and weight. The time required to manipulate the prey was measured by stopwatch. All prey given in this manner were insects between 9 and 40 mm long.

The daily existence metabolism of the Loggerhead Shrike in the wild was approximated for various seasons of the year, using a method developed by Kendeigh (1949, 1970) and others (Siebert 1949, Davis 1955, West and Hart 1966). This method is based on food consumption under changing temperature conditions in the laboratory. Daily mean temperatures can relate existence metabolism to calories burned per day.

Insect sampling.—Beginning in September 1972, insect populations were sampled, using a model 1-A D-vac (engine powered vacuum) insect sampler. An aluminum cylinder (radius of 39.9 cm and a height of 50 cm) was used to demarcate 0.5 m² quadrats. All ground and vegetation were completely vacuumed of insects within the cylinder. Eight 0.5 m² quadrats per sample were found to optimize sample precision (Oosting 1956, Menhenick 1963, W. Cothran, pers. comm.). In addition to collecting samples by the D-vac-quadrat method, standard sweep net samples and a D-vac swath sample were taken concurrently. Five samples of each type were taken each week in the early afternoon. Quadrats were chosen as objectively as possible and all samples were frozen. Later the samples were thawed and the insects separated from the vegetation and duff. All insects were separated individually according to family,

TABLE 1. Caloric content (kcal/individual) of various kinds and sizes of prey

	Class size ^a					
	2	3	4	5	6	7
Miscellaneous insects (Coleoptera, Hemiptera, Homoptera)	0.002	0.003	0.1	1.4	2.8	—
Butterflies						
Larvae	—	—	0.1	0.7	3.2	6.3
Adult	—	0.003	0.08	0.3	0.6	—
Spiders	0.001	0.01	0.04	1.7	3.5	—
Crickets	—	—	0.1	0.8	2.0	—
Grasshoppers	0.001	0.01	0.08	0.6	1.6	4.1
Mice			Average mouse—30.7			

^a See text

feeding habit (herbivore, carnivore, omnivore), and size class (1–7) and weighed. For details of the insect sampling program see Craig (1974).

Energetics of the prey.—Several kinds of data were gathered to determine the energetic value of each individual prey. The number of kcal/g (dry weight) of tissue has been calculated for many species using calorimetric techniques (Golley 1959, 1961; Slobodkin and Richman 1968; Brisbin 1970). No caloric data exist for several types of prey in the shrike's diet, but terrestrial arthropods, in general, are not extremely variable in caloric content per gram dry weight. All insect samples were weighed, desiccated, and reweighed to determine the percentage of dry weight per gram of live weight. The estimated number of calories per prey item is summarized in Table 1. Obviously, the size classes are arbitrary points along a continuum. Nevertheless, each was chosen because it represents a discrete size class that is commonly found. The kcal per individual were calculated by multiplying (kcal/g dry weight) × (average dry weight of animals in the particular taxon and size class).

Mouse density estimation.—Preliminary trapping showed that mice (*Mus musculus*) were found only on the edges of the narrow slough where vegetation remained green. Territories of the mice tended to be linearly arranged along the small band of green vegetation. Mouse populations were estimated five different times, using live-trap mark-recapture methods (see Southwood 1968, Giles 1969). A total of 4,200 trap-nights were completed. Population estimates were made by applying mark-recapture data to a variation of the basic Lincoln Index (Lincoln 1930) developed by Schnabel (1938).

RESULTS

The maximum kcal expenditure of shrikes is in mid-December; the minimum in September. The estimated caloric demand is more than 40% greater in December than in September (35 kcal/day vs. 20 kcal/day). There are approximately 13 h of daylight (time available for hunting) in September and less than 10 in December at this latitude. Thus, in December each shrike has greater energy demand but less time to find prey. If the shrike is to survive during this time it should either increase attack rate or increase energetic return per attack by increasing efficiency of capture or by concentrating on larger prey sizes.

Table 2 is a summary of insect availability during the period of the study. Obviously, these prey items are patchily distributed and do not occur uniformly in these proportions. Nonetheless, it is possible to determine relative differences in type and size of prey available from month to month. From September to December the density of large insects decreased until in November and December no size 6 or 7 insects were found at all. Size 6 crickets became available in January.

Table 3 summarizes the data for estimated mouse density at each of the sampling periods. Mouse populations remained fairly constant at about one mouse every 5 m

TABLE 2. Insect prey availability (individuals/m²), Willow Slough Bypass, Davis, California

	Size class ^a						
	1	2	3	4	5	6	7
<i>September</i>							
Miscellaneous insects		20	20				
Butterflies				0.3	0.6	0.6	
Larvae			0.3	0.8			
Spiders		1.5	1.2	0.3		0.3	
Crickets					0.1		
Grasshoppers							0.5
Total		20	20	1.4	0.7	0.9	0.5
<i>October</i>							
Miscellaneous insects	5	8	20				
Spiders		2.0	0.8	0.1		0.4	
Crickets					0.1		
Grasshoppers							0.1
Total	5	10	20	0.1	0.1	0.4	0.1
<i>November</i>							
Miscellaneous insects	20	40	30				
Spiders		1.0	0.2	0.1			
Crickets					0.2		
Total	20	40	30	0.1	0.2		
<i>December</i>							
Miscellaneous insects	10	20	1.2	15			
Spiders		5	2	0.1			
Crickets					0.3		
Total	10	25	3	15	0.3		
<i>January</i>							
Miscellaneous insects	15	80	3	5			
Butterfly larvae			1		1		
Spiders	1	20	8	11	2		
Crickets						0.8	
Total	16	100	12	16	3	0.8	
<i>February</i>							
Miscellaneous insects	15	30	7	0.25			
Butterflies					0.1		
Spiders		30	10	7	0.4		
Crickets						0.4	
Total	15	60	17	7	0.5	0.4	
<i>March</i>							
Miscellaneous insects	20	12	0.9	0.9			
Butterflies					0.1		
Spiders		4	5	0.3		0.2	
Total	20	16	6	1.2	0.1	0.2	

^a See text

along the slough except in early spring, when numbers appeared somewhat lower. The house mouse was the only species sufficiently numerous to be included.

Attack rate.—Between September 1972 and March 1973, 2,946 attacks were observed in 710 half hour observation intervals. The overall average attack rate was 4.15 attacks per half hour, or one attack every 7.2 min.

The average numbers of attacks observed during each time interval for each month were calculated. These averages (for months and for time intervals) were treated using a randomized block analysis of variance. The average numbers of attacks for each month were designated as the treatments and each 2 h division of

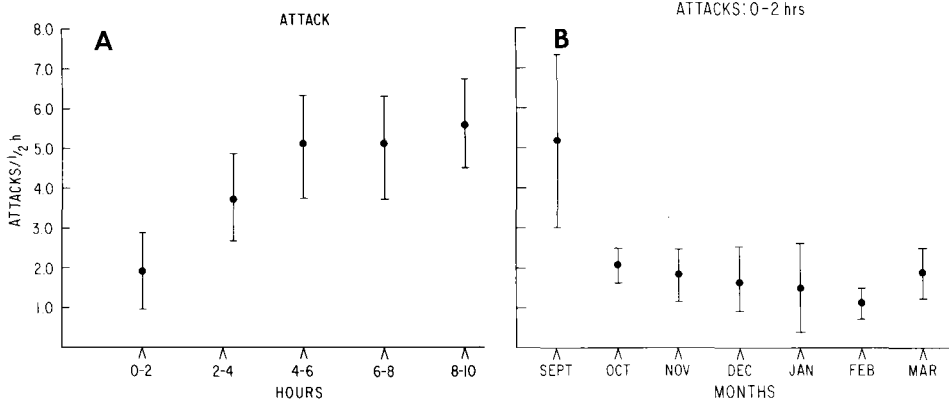


Fig. 1. A. The mean number of attacks per half hour during the five divisions of the day throughout fall and winter. B. The mean number of attacks per half hour during the first 2 h after dawn in each of the nonbreeding months. Bars represent the 95% confidence limits of the mean.

the day as the blocks. The *F* statistic was significant at the 0.05% level for both treatment and blocks, showing that the shrike varies its attack rate both seasonally and diurnally.

Figure 1A shows the overall diurnal trend in attack rate. The attack rate is low in the early morning and increases to an asymptote. The attack rate appears to be influenced by environmental conditions. Low prey availability in morning hours appears to be the cause of fewer attacks in the morning. The bulk of the months considered are winter months, characterized by cold, overcast mornings; insect activity is low in these early morning hours. In September, a very warm month in the study area region, the trend is entirely different; the 0-2 time interval is the one of highest hunting activity and the midday interval during maximum heat is the lowest (Fig. 1B). Diurnal variation in attack rate appears to be closely related to temperature, which in turn regulates availability of poikilothermic prey. Decrease in attack rate during midday in September may reflect heat stress on the shrikes themselves.

Factors that may affect the monthly trend in attack rate are complex. As ambient temperature declines in winter the shrikes' energy expenditure increases (Kendeigh 1970) and both the average size and density of insect prey decreases (Table 2). Furthermore, day length, the total time available for hunting, decreases. Attacks per half hour would be expected to be highest in December. This was not observed (Table 4).

The attack rate is higher in February and March than would be expected to satisfy the estimated caloric demand. In February, male and female shrikes begin to as-

TABLE 3. Mouse density estimates for study area

Date	Trap-nights	Estimated number of mice per linear meter
October 28-30, 1972	600	0.18
December 7-9, 1972	600	0.20
April 18-20, 1973	600	0.11
October 2-4, 1973	600	0.25
May 1-3, 1974 ^a		
May 7-10, 1974	1,800	0.12

^a May 1974 sampling estimates are combined (see Southwood 1968)

TABLE 4. Monthly attack rate of Loggerhead Shrikes

	Sep	Oct	Nov	Dec	Jan	Feb	Mar
Attack rate \bar{X}	2.5	4.1	3.6	3.7	6.5	5.2	6.0
SD	1.1	1.2	1.4	1.0	1.6	1.3	2.0
n ^a	68	116	134	71	108	132	81
Half hours/day	25.0	22.5	20.4	19.0	19.6	21.6	24.0
Mean temperature (C°)	21	17	10	3	7	11	12

^a No. of half hour observations

sociate in precourtship display. During courtship the female approaches the male, fluttering her wings and squawking. The male appears to be stimulated to attack prey by this behavior. He will attack soon after the female approaches; when successful, he feeds the female. The number of attacks by the male not linked to courtship closely fits the existence metabolism projections.

Shrikes normally show little outward appearance of active involvement in the specific task of hunting. Many complete half hour observation intervals were spent with no attacks. There is a definite seasonal and diurnal distribution of these "empty half hours" (Table 5). In September there were no half hour observations between 0-2 when shrikes did not attack. The proportion of half hour observation intervals with no attacks at this time period increases to a maximum in February when 60% of the observation intervals had no attacks. The opposite trend is seen for midday intervals.

Capture rate and efficiency.—Average capture rate per half hour was 2.42 during the nonbreeding months. Capture rate from September to March tracks the attack rate as does diurnal capture rate. Capture rate in January is significantly higher than that found in any other month (except December when capture rate was extremely variable). All other months show no significant difference. Like attack rate, capture rate in early morning is significantly lower than in midday and evening.

Salt (1967) states that the degree of success in hunting is lower than most people suppose, the average being about one capture for every ten attacks. He found terns to be somewhat more efficient—15% in spring and 39% in fall. Shrikes averaged an efficiency rate of about 65% (Fig. 2), which is an extremely high rate according to Salt. Randomized block analysis of variance revealed no statistical difference in efficiency between times of day, but did reveal a significant difference between months. During courtship in March, shrikes were significantly lower in efficiency than in other months; in December shrikes were significantly more efficient as revealed by Tukey's test for Multiple Comparisons (Guenther 1964).

Handling time.—Handling time includes the kill, the retrieval of the prey to the perch, and the manipulations needed to consume the prey. Most insects were killed,

TABLE 5. Proportion of half hour observation intervals with no attacks (the lower the proportion the greater the hunting activity in that time period)^a

Interval	Sept	Oct	Nov	Dec	Jan	Feb	Mar
0-2	0	0.28	0.37	0.40	0.53	0.60	0.39
3-4	0	0.22	0.16	0.44	0.18	0.13	0.18
4-6	0.18	0.13	0.06	0	0	0	0
6-8	0.20	0.33	0.08	0	0	0.08	0.17
8-10	0.38	0.33	0.14	0	0	0.11	0

^a Total number of half hour observation periods was 710, ranging between 11 and 39 for any interval in a given month. Total number of half hour observations per month is given in Table 4

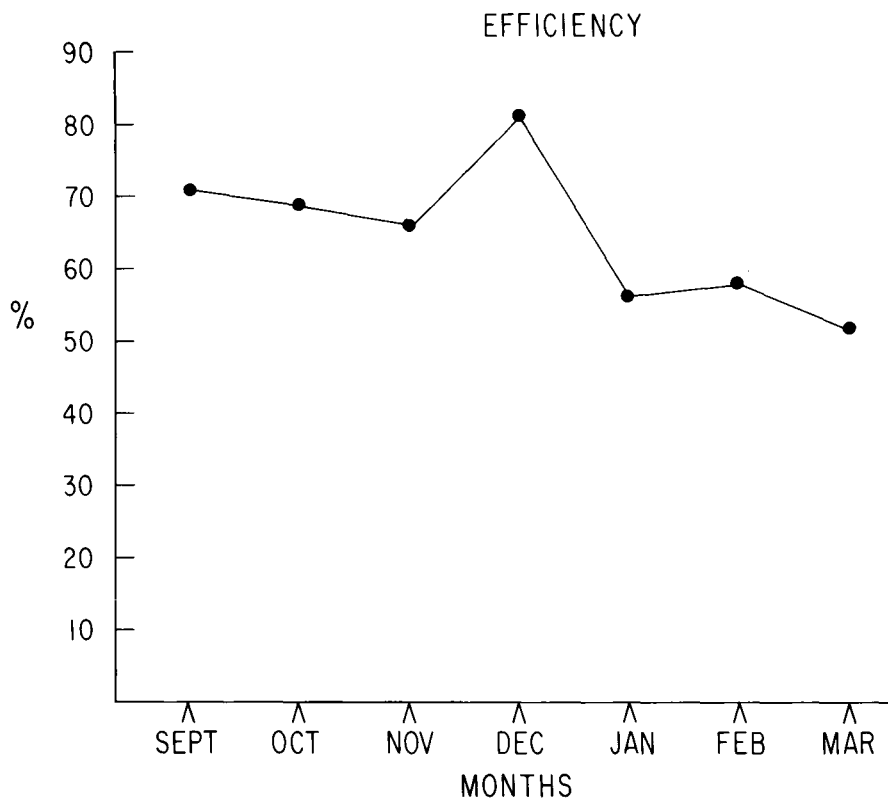


Fig. 2. Capture efficiency of Loggerhead Shrikes.

returned to the perch, and swallowed whole with no special manipulations. Large insects (>40 mm) and mice required extra time to kill. Many mice were so large they could be carried only with great difficulty. Shrikes in the wild were observed to take up to 90 min to capture, subdue, and manipulate mice before they were impaled and abandoned, at least temporarily. A mouse was always observed to take more than 40 min of handling prior to any significant feeding (mean = 65 min). The mean caloric return from mice per minute of handling time then is about 0.5 kcal/min whereas for the average size (5) insect taken it is between about 5 kcal/min and 14 kcal/min. The handling time cost per kcal of return then is greater for mice than it is for insects. Handling time is time not available for searching; therefore, as prey density and consumption increase, the total time remaining for searching decreases (Holling 1965). Average handling time was 9.2 s and average capture rate was 2.42 per half hour in the nonbreeding months. This means that the time lost from hunting due to handling of captured prey was about 22 s out of every half hour or about 1.2% of the total available time, if the shrike relies on insects alone. If the shrike takes mice, up to 10% of its time can be lost, time that could be allotted to territory defense and other activities. Average time lost due to unsuccessful attacks is negligible (less than 3 s per half hour).

Diurnal and seasonal differences in handling time could not be detected. An interesting relationship between handling time and length of prey, first revealed by Salt and Willard (1971), was corroborated. Their observations on handling time of fish by

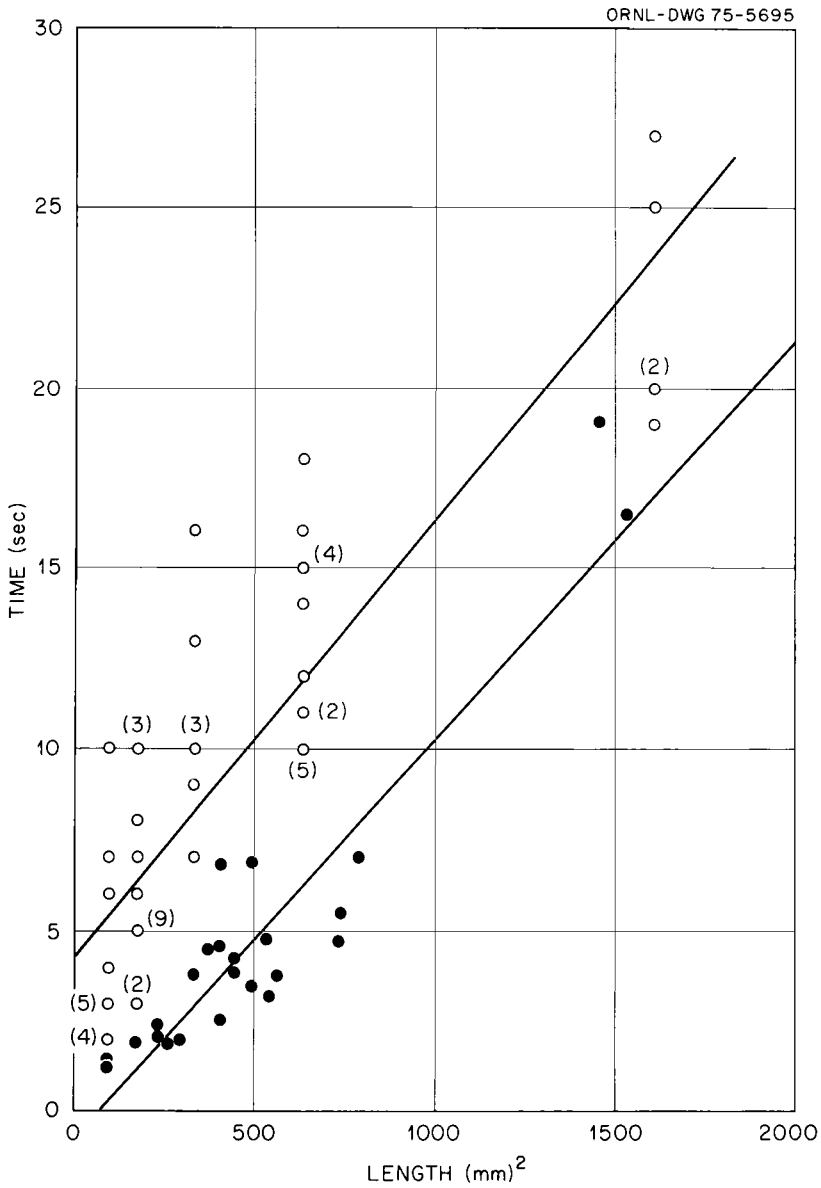


Fig. 3. Regression of handling time on prey length squared. The open dots refer to field observations where prey size was estimated. The solid dots refer to laboratory trials where prey were individually measured. For the upper line (field observations) the regression equation is $HT = 4.23 + 0.012L^2$, $r = 0.875$. For the lower line (laboratory) the regression equation is $HT = -0.65 + 0.011L^2$, $r = 0.930$. The numbers adjacent to several of the open dots refer to the number of observations at that point.

terns showed a quadratic increase in handling time with an increase in the size of fish caught. A sample of handling time versus estimated length of prey data was extracted at random from field observations ($N = 60$). Figure 3 is a plot of handling time versus length squared (length is the average for each size class: 1-7). Length squared gave a better correlation with handling time in the field ($r = 0.875$) than did simple

TABLE 6. Mean size of prey captured by shrikes under field conditions. Values refer to size classes.

Monthly							
	Sep	Oct	Nov	Dec	Jan	Feb	Mar
\bar{X}	4.9	5.1	4.7	4.5	4.7	5.0	5.1
SD	0.5	0.4	0.7	0.8	0.4	0.8	0.9
n ^a	98	271	262	160	345	329	191
Daily							
2-h intervals after first light							
	0-2	2-4	4-6	6-8	8-10		
\bar{X}		4.8	4.9	5.0	4.6	5.1	
SD		0.6	0.8	0.6	0.3	1.0	
n ^a		224	295	280	400	457	

^a Number of prey recorded

linear regression. The relation between handling time (HT) and length (L) can be calculated using the formula: $HT = 4.23 + 0.012L^2$. Handling time was also measured in the laboratory on captive shrikes. Again, length of prey squared gave the better correlation ($r = 0.93$, Fig. 3). The equation derived from laboratory trials is $HT = -0.65 + 0.011L^2$. The slopes of these two equations are not significantly different. The Y intercept in the laboratory equation is lower because the bird did not have to fly back up to a telephone wire or perch before consuming the prey but only to hop to a perch 30 cm or so above the floor of the cage. The normal flight time back to the perch was approximately 5 s (the difference in Y intercept). The relationship between length of prey and handling time appears to hold for both wild and captive shrikes.

It would of course be preferable to partition HT into the components of pursuit, subduing, returning to perch, and eating (manipulation of caught prey item). Unfortunately, under field conditions this was impossible. Nevertheless, it appears that pursuit and return time are fairly constant, and for the great majority of dietary items (small insects) subduing time is constant and negligible. Therefore, in actuality the variation in handling time is due to eating (and manipulation).

Prey size.—The strategy of a predator should be to gain the greatest possible energetic return per unit energy expended. An efficient way to do this would be to concentrate attacks on the largest available prey that it can handle. Salt and Willard (1971) documented large seasonal changes in the average size of fish taken by terns. The change in average prey size was attributed to seasonal changes in the size distribution of the prey population, apparently because terns concentrated on the largest size (age) class they could handle. When that age class grew too large for them to capture they turned to a lower age and size class. Similarly, Root (1967) attributed seasonal changes in prey size and foraging success to a change in the character of the prey population.

No significant difference was found in the size of prey taken by shrikes, either seasonally or at different hours of the day. The overall mean size of prey was size class 5 (Table 6).

DISCUSSION

Loggerhead Shrikes employ an effective and conservative search method to gain their energetic requirements. They are able to scan a significant amount of prey-filled environment from a perch, and therefore expend little energy in search. Shrikes

apparently can be stimulated to attack at any time of the day. Their hunting posture allows them to perform several biological functions at once. They can survey their territory for predators and interlopers, display for others of their species indicating an occupied territory, and they can hunt. Schoener (1969, 1971) presented two types of animal feeding strategies, relating the total net energy yield to the total time spent feeding during some long time period. The shrike fits his Type I strategy nicely; the expense in time and energy for feeding includes only that of pursuit, handling, and eating of prey, and not that of search.

The attack rate of the shrike increases during winter from very low in the morning to an asymptote by mid-afternoon (Fig. 1A). This is not a characteristic inherent within the shrike because the trend is opposite in warm months (Fig. 1B, Table 4). The inference from these opposing trends in hunting activity is that the attack rate is related to a seasonal variable. When prey are motionless in the foliage, they tend not to be detected by shrikes. Therefore, shrikes not only depend on the abundance of potential prey, but also on their movement. They depend on poikilothermic prey whose activity in turn is regulated by temperature. In the winter months, mornings were not warm enough for many prey to be mobile, and therefore few of them were available to the shrikes. Morning temperatures in the hot months were warm enough for insects to be active. Table 5 shows that the extended periods of no hunting activity occur in the morning during winter and in the afternoon in summer. The time that predators and prey are in contact is directly proportional to the attack rate (Holling 1966). Therefore, temperature is the main determinant of the amount of time that prey are exposed to shrikes during daylight.

It is obvious from Table 2 that the array of available prey varies in both kind and size throughout the year, yet the size of prey taken remains constant.

Seasonal fluctuation in attack rate (Table 4) is more complex than a straightforward temperature or prey availability relationship. The attack rate is low in September when prey density is high and day length is long. It returns to a low level in December when the prey density is low. The attack rate is high in January when prey density is higher and it remains high in February and March, apparently due to courtship. The existence metabolism is higher in December; therefore, a higher attack rate than is observed would be expected because of the decreased hunting time available due to shortened daylight hours. Apparently the insect availability is low—below a threshold level that would allow a minimum number of contacts between shrikes and their prey. Shrikes during this time appeared to be stressed. Two individuals collected in December were both well below mean weight (39.8 g and 45.5 g). An increase in the number of crickets in January (Table 2) raises the prey availability above this threshold, and shrikes attack more frequently to replace weight loss.

The capture efficiency is much higher than that found in any other studies on predatory behavior (Salt 1967). It is significantly higher in December when prey density is low. The capture efficiency is not low in September when prey density is high. Apparently the density of prey affects attack rate and capture efficiency only when it is below a certain threshold. Both attack rate and capture efficiency are stable at increasing prey densities above that threshold.

The time that shrikes spend handling prey does not significantly reduce the amount of time that can be devoted to searching for prey in the nonbreeding months. It should be pointed out that handling time does become significant during periods of peak food demand (e.g. when adult shrikes are feeding nestlings, Craig 1974).

The importance of handling time may be related to the ratio of size of predators to size of prey. Predators that attack prey nearly their own size must spend a greater proportion of their searching time handling prey. Lions that attack large ungulates spend most of their time pursuing and handling prey and in digestive pause. Shrikes feed primarily on insects approximately one-hundredth their own weight. Handling time is less than 2% of their total search time. When shrikes take mice one-third to one-half their own weight, handling time increases to 10% of the total search time.

Birds do not masticate their food, therefore they must either swallow each item whole or tear it apart. Shrikes use both strategies; terns and most other nonraptorial birds use only the former. Shrikes swallow whole prey items less than approximately 40 mm long. Prey larger than this are impaled and torn apart. Apparently, the difficulty of manipulating prey in order to swallow them whole increases quadratically with the length of the prey item, likely due to difficulty in breathing while swallowing. Each item must be turned in the beak until an end (usually the head) is reached and then worked down the gullet with an up and down movement of the mandible. The longer the prey item, the more difficulty the bird has working it down. Handling time may be universally estimated for avian predators feeding on prey organisms that are swallowed whole by using the index of length of prey squared.

Other factors have been shown to affect handling time. Holling (1959b) showed handling time for insect predators decreased with increasing temperature. This would be expected for all poikilothermic predators. No such temperature relationship was observed in shrikes. Several authors (Ashmole and Tovar 1968, Orians 1969, Recher and Recher 1969) have noted that capture rate, capture efficiency, prey size, or handling time improve with age of avian predators. These studies show that there is a learning component in the predatory behavior of birds. All observations in this study were of adult birds. Overall efficiency and capture success is likely lower during the summer months when young shrikes are plentiful. Buckley and Buckley (1974) have shown that predation by adult terns is more efficient than predation by juveniles. From this they have concluded that models of predation must be complicated to the extent of accounting for age differences.

Prey whose size was at the upper range of the shrike's capacity to capture were not an important part of the diet. If shrikes are to utilize these large prey items exclusively, their hunting territory would have to be much larger, because such animals are more widely dispersed. For instance, within the perceptual field of a shrike there would likely be no more than 10 resident mice at any time. The frequency of finding one of these is not great enough to support a shrike. If a shrike could discover and capture them at a rate high enough to meet its energetic demand (1.5 + per day), the mouse population within its territory would likely be quickly decimated unless mouse generation time decreased and fecundity increased to unreasonable levels.

Could a bird the size of a shrike survive solely on mice? It would have to increase its perceptual field by hunting from a higher perch or by flying in search. In turn, its territory and the related energy demands would increase. Given the increased metabolism per gram of a small bird (shrike) over that of a larger bird (raptor or tern) that makes its living by hovering and soaring in search of prey, could the small bird fly over enough territory to ensure a likelihood of supplying its energetic needs? If a few physiological and behavioral parameters (e.g. weight, bill size, solitary life style, Type I predator) are defined, then possibly the rest of the parameters of an optimal feeding strategy, such as size of perceptual field, optimal prey size, territory size,

minimum prey density, time spent searching, handling time, attack rate, etc., would fall within calculable ranges.

The ultimate utility of this study is to contribute to the development of acceptable criteria for producing predictive, general models of predation by a searching type of avian predator. Models of predation and of optimal feeding strategies can be useful tools in elucidating selective pressures and the vague concepts of resource utilization within ecological systems (Schoener 1969, 1971). Before such models can be applied the inherent generalizations and assumptions must be examined and tested. The next step will be to apply the data gathered in this study to construct a model of the optimal feeding strategy of the Loggerhead Shrike.

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