THE ONTOGENY OF CRICKET KILLING AND MOUSE KILLING IN LOGGERHEAD SHRIKES (*LANIUS LUDOVICIANUS* L.)

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The Loggerhead Shrike (*Lanius ludovicianus*) is a predatory passerine native to much of the United States. It feeds not only on insects, but also on small rodents and birds. The prey-attack behavior of young Loggerhead Shrikes has been studied by Smith (1973). After observing the mouse-killing behavior of hand-reared shrikes, she concluded that once they reached the age of 40 days, they were capable of killing mice in apparently the same manner as adult shrikes, even if they had no prior experience with live food. Miller (1931) concluded that the mouse-killing behavior of juvenile shrikes improved with age, but he described no ontogeny.

Some pet shrikes that I raised in 1972 appeared to have a complex ontogeny for mouse killing, and, unlike Smith's (1973) shrikes, were generally unable to kill a mouse on the first attempt, even if the birds were over 40 days old. To determine the nature of this ontogeny and a related one, I observed the killing of mice and crickets by young Loggerhead Shrikes. This paper is based on those observations.

MATERIALS AND METHODS

Twelve clutches of Loggerhead Shrikes from San Diego, California were removed from their nests at 10 days of age and hand raised. They were color-banded, and one bird from each clutch was randomly selected for the early group, which was tested for prey killing starting on the 25th day of age. A separate clutch of 5 shrikes formed the late group, which was tested for prey killing starting on the 50th day of age. The shrikes were hand reared until 38 days of age in 40 × 40 × 90-cm wire cages containing nest-sized cloth-lined bowls, one clutch per cage. So that they would be tame, the shrikes were handled about twice a day, and were reared in a room where there generally was human movement throughout the day. On the 38th day they were permanently transferred to a 2.4 × 2.4 × 5.4-m outdoor cage. The shrikes were weighed daily.

The shrikes' diet was primarily horsemeat and chopped whole rat and hamster, mixed with vitamins and minerals, with supplements of mealworms and thoroughly crushed crickets. They were hand fed as nestlings and fledglings, and at fledging age (about 20 days) were given constant access to meat and water, and to many-forked branches through which sharpened nails had been driven for impaling their food. After fledging, they were given 30 min to 2 hr a day to exercise in an outdoor flight cage.

Beginning on the 25th day of age for the early group, and on the 50th day for the late group, the cricket-killing and mouse-killing behavior of the shrikes were observed daily in a 1.8-m cage of ½-inch (1.27 cm) mesh wire aviary cloth. Trials were conducted prior to the daily renewal of the food supply. Each shrike was offered, in a random order, an adult house cricket (*Gryllus domesticus*) and a young 13 to 16-g grey house mouse (*Mus musculus*). The prey was placed in a 7.5-cm cube releasing box which was on an arm 50 cm over the center of a glass-fronted arena (fig. 1). The arena was an open-topped plywood trapezoid with 20-cm high walls, 75 cm long, 65 cm wide in the rear, and 75 cm wide in the front, a design allowing an unrestricted view. A strip of plastic tape on the inside of the top edge kept the crickets from crawling out. A branch containing sharpened nails for impaling ran the width of the cage 1 m above the arena. The shrike was given a 3-min acclimation period, following which the prey was released through a trap door by means of a clear nylon monofilament line leading from the releasing box to an observation blind 5 m away. Observations were recorded on a tape recorder, and time measurements were made to the nearest five seconds with a stop watch. The basic trial, 2 min long, was extended 2 min in mouse trials if the shrike had attacked the mouse, and then extended up to an additional 4 min as long as the shrike was holding the mouse with its feet or beak or had wounded it to such a degree that the mouse did not run from the shrike. The shrike was allowed to eat any cricket and a portion of any mouse it killed. For the early group, cricket-killing trials were ended on the 44th day of age, and mouse-killing trials were ended on the 48th day. Both types of trials were ended on the 59th day of age for the late group.

(The twelve birds in the early group were a control group for another study and received from 15 to 30 μl of corn oil orally per day.)

RESULTS

The mean body weight of the 17 shrikes was 4.0 g at 1 day of age, 10.7 g at 4 days, 17.2 g at 7 days, 33.4 g at 10 days, 36.7 g at 13 days, and 42.5 g at 16 days. Thereafter, their weights ranged in mid 40's.

At first, the shrikes in the early group rarely appeared to look at the cricket, but by about the 30th day of age, they often looked at the cricket, especially if it moved. A typical first successful cricket-killing trial for the early group consisted of the shrike approaching the cricket, bowing and fluttering the wings toward it, and then capturing it after one or more misses. All approaches were accompanied by a capture. The mean age in days, with standard error, at the first approach was

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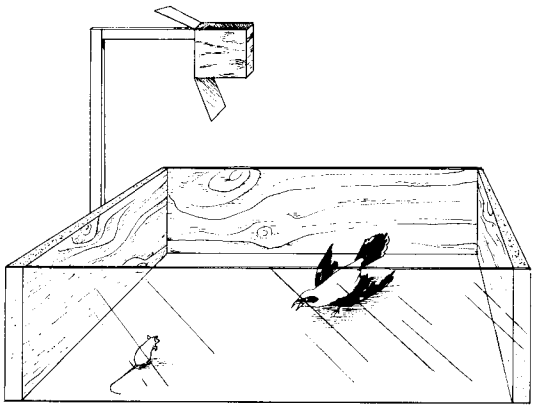

FIGURE 1. The testing situation. A cricket or mouse was released from the small box above into the glass-fronted arena below. The shrike was free to enter or leave the arena at all times.

37.0 ± 0.84 with a range of 33 to 44. The daily occurrence of the observed behavior patterns in the early group is shown in figure 2. It is important to remember that figure 2 is based on whether each behavior occurred during a particular trial, and not how often it occurred during that trial. I felt that although visual observation and note-taking were sufficiently accurate for determining whether a behavior occurred at least once during a trial, motion pictures would have been required for an accurate determination of the frequency of each behavior during a trial.

Figure 2 shows a gradual increase in the occurrence of all four behavior patterns; but while approaching-capturing continued to increase in frequency, the frequencies of missing, bowing, and fluttering soon decreased. At the same time, approaches and captures became more rapid, so that a typical later trial consisted of an immediate approach and immediate capture. "Approach time" was defined as the time between introduction of the prey and the landing of the shrike in the arena. The early group's median approach time for the first approach was 20 sec, for the second approach was 5 seconds and was 0 thereafter. For the late group, these figures were 10, 5, and 0 respectively. Because many of the approach times were very short, medians rather than means are presented so that trends would not be obscured by a few unusually long approach times. "Capture time" was defined as the time between the shrike's approach and its grasping of the cricket in its beak without letting it go in such a condition that it hopped away. Mean capture times are given in figure 3, which shows, for both groups, a rapid decrease during successive approaches.

The occurrence of behavior during the cricket-killing ontogeny was similar for both the early and late groups. On the first trial, all five of the birds in the late group approached the cricket and captured it after fluttering and bowing. Fluttering and bowing

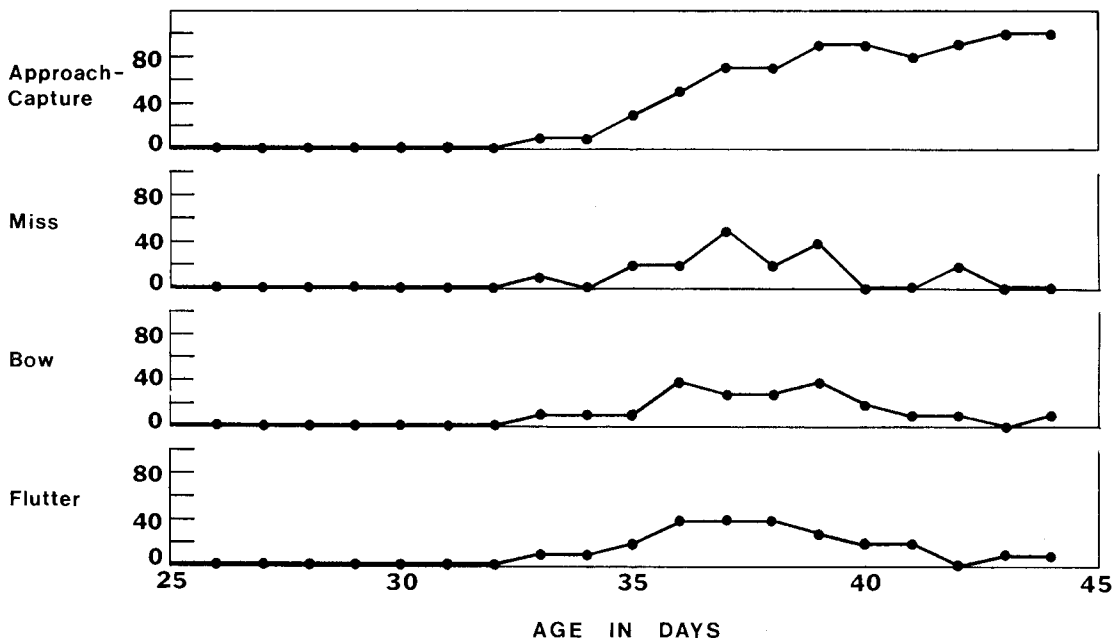

FIGURE 2. The occurrence of behavior during the ontogeny of cricket-killing in young Loggerhead Shrikes that were presented a cricket daily beginning on the 25th day of age. The vertical axis represents the percentage of shrikes performing the indicated behavior at least once at the indicated age.

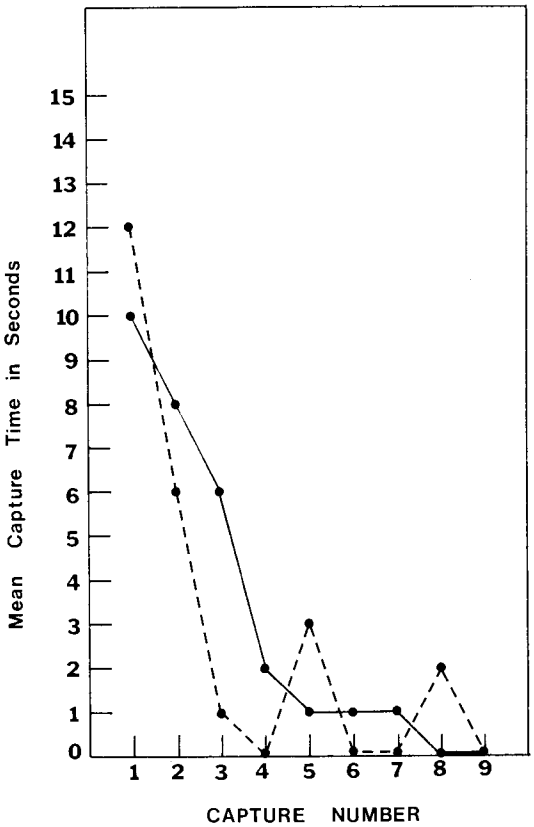

FIGURE 3. Successive mean cricket-capture times for young Loggerhead Shrikes that were presented a cricket daily. Capture time was the time between the shrike's landing in the arena and its grasping the cricket in its beak without letting it go in such a condition that it hopped away. The early group (solid line) began trials on the 25th day of age, and the late group (dashed line) began trials on the 50th day of age.

were not observed after the third trial. This appears only superficially to be a much more rapid ontogeny than shown by the early group because the initial approaches of the early group were scattered over several days, and all of the initial approaches for the late group were on the 50th day of age.

The mean ages of the shrikes at the first occurrence of each of the behavior patterns of the ontogeny of mouse-killing are listed in table 1. Note that the mean age of first kill was 53.4 days for the late group, which means that the mean trial of first kill was 3.4. None of the birds in the late group killed its mouse on the first trial, and one did not do so until the seventh trial. The daily occurrence of these behavior patterns, in relationship to the day of first kill are shown in figure 4. Because the ontogenies were not synchronous, graphing the occurrence by age obscures many trends. However, arbitrarily aligning the graph on the day of first kill produces an artifact. On the day of first kill, there is, of course, 100% killing success, and a high occurrence of behavior associated with successful killing. There then appears to be a sudden decrease in killing success and associated behavior, and a gradual regaining of killing proficiency. The graph is best interpreted by ignoring the peaks on the day of first kill. Again, it is important to remember that figure 4 presents only whether the behavior occurred on that day, and not how many times it occurred. During their first several trials, the shrikes in the early group often looked at the mouse only when it fell into the arena, but they soon began looking at it and tail-bobbing and fluttering on the perch. The late group, on the other hand, often tail-bobbed and fluttered during the first several trials. Other than this, the behavior of the two groups was similar, as indicated by figure 4. The approach times and kill times (the time between the approach and the death throes of the mouse) were also

TABLE 1. Comparison of the ages of first occurrence of the behavior observed during the ontogeny of mouse-killing in Loggerhead Shrikes that were presented a mouse daily.

	Age in days at initial trial					
	25			50		
Behavior	% of birds performing behavior	Mean age at first occurrence in days ± SE	Range	% of birds performing behavior	Mean age at first occurrence in days ± SE	Range
Tail bob	100	32.7 ± 0.60	29 to 34	100	50.0 ± 0.00	50
Flutter	100	32.5 ± 0.90	28 to 36	100	50.0 ± 0.00	50
Approach	90	40.3 ± 1.01	36 to 45	100	52.4 ± 0.72	50 to 54
Wing spread	90	40.3 ± 1.01	36 to 45	100	53.0 ± 0.94	50 to 55
Bow	90	40.7 ± 1.00	36 to 45	100	52.8 ± 0.76	50 to 55
Grab	60	40.3 ± 1.05	36 to 44	80	53.8 ± 0.86	52 to 57
Attack	80	40.5 ± 1.25	36 to 48	100	53.2 ± 0.96	51 to 57
Tail attack	80	40.5 ± 1.25	36 to 48	100	53.2 ± 0.96	51 to 57
Body attack	80	41.1 ± 1.26	36 to 48	80	53.2 ± 0.96	51 to 57
Head & neck attack	80	40.8 ± 1.32	36 to 48	100	53.4 ± 0.92	51 to 57
Kill	80	41.0 ± 1.30	36 to 48	100	53.4 ± 0.92	51 to 57

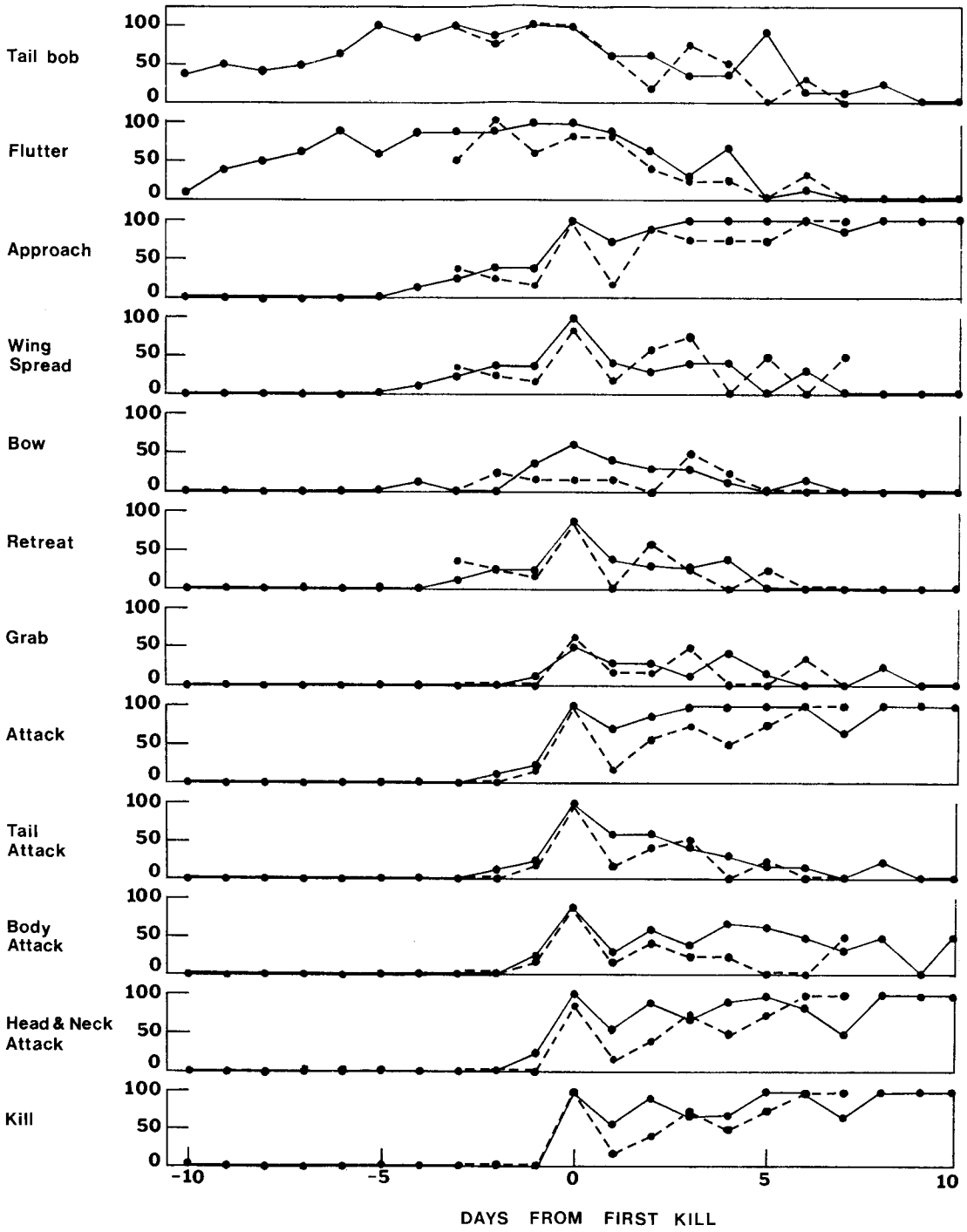

FIGURE 4. The occurrence of behavior during the ontogeny of mouse-killing in young Loggerhead Shrikes that were presented a mouse daily and killed at least one mouse. The vertical axis represents the percentage of shrikes performing the indicated behavior at least once on the indicated day. The ontogeny is presented synchronously by orienting it on the day of first kill rather than on the age of the shrikes. The early group (solid line) began trials on the 25th day of age, and the late group (dashed line) began trials on the 50th day of age.

similar, so the following results, unless otherwise noted, are for both the early and late groups.

For both groups, the initial approach times were high, but they gradually decreased (figure 5). The first approaches were often accompanied by inefficient biting, by grabbing the mouse with the feet, and by spreading the wings and fluttering. Grabbing the mouse with the feet and holding it often re-

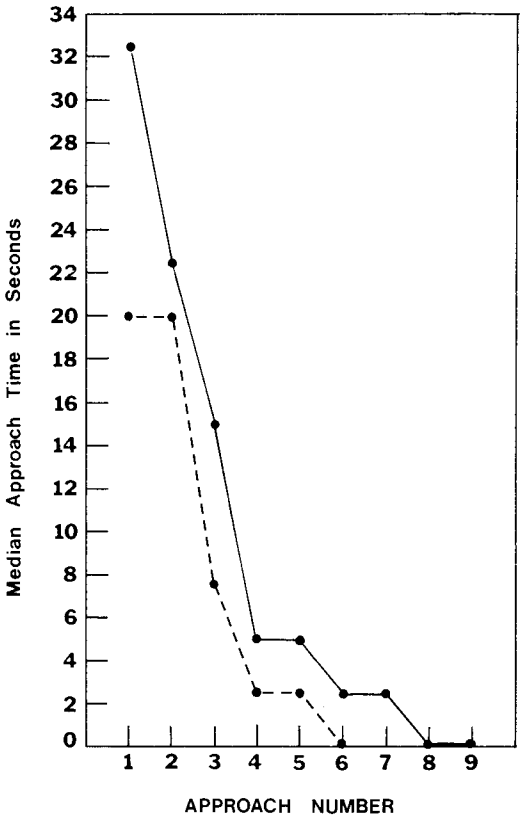

FIGURE 5. Successive median approach times for young Loggerhead Shrikes that were presented a mouse daily. Approach time was the time between the introduction of prey and the shrike's landing in the arena. The early group (solid line) began trials on the 25th day of age, and the late group (dashed line) began trials on the 50th day of age.

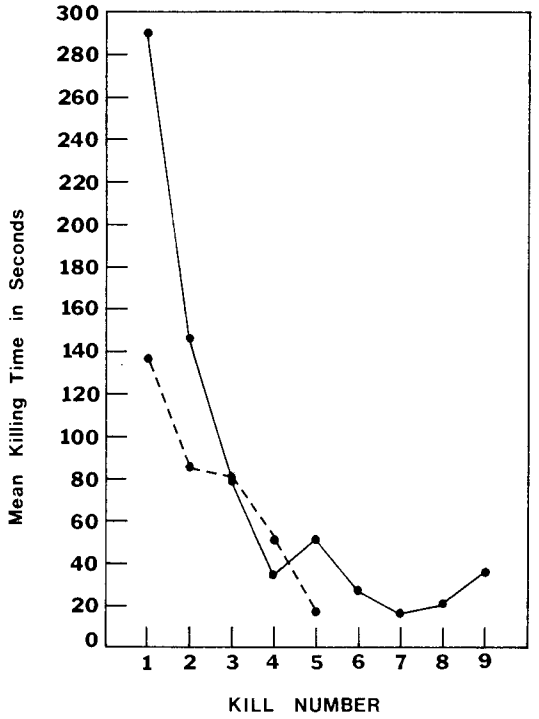

FIGURE 6. Successive mean killing times for young Loggerhead Shrikes that were presented a mouse daily and killed at least three mice. Killing time was the time between the shrike's landing in the arena and the initial death throes of the mouse. The early group (solid line) began trials on the 25th day of age, and the late group (dashed line) began trials on the 50th day of age.

sulted in the shrike and mouse tumbling over each other in the arena, but the shrike generally spread its wings and tail, and the tumbling ceased. After one such grabbing and tumbling encounter, one of the shrike's feet was bleeding. Fluttering the wings generally occurred while the shrike's body and head were roughly parallel to the ground and the tail was slightly raised. Bowing generally occurred while the shrike's head was lower than the body, and the tail was pointed upward. Wing-spreading is a behavior pattern in which the wings are extended far from the body and the tail is usually fanned. This behavior ranges from stationary half-extended wings, through flashing half-extended wings, to the wings being extended so far that their tips are in front of the shrike's beak and may touch the ground. While in the latter position, the shrike may jerk its entire body toward the mouse while keeping its feet stationary.

Although four birds in the early group and three in the late group killed the mouse on their first approach, early kill times were high, (fig. 6). The mean time of first kill for the late group was less than half of that for the early group, but by the third kill there was little difference between the two groups.

The method of killing was generally biting and chewing on the head and neck, but occasionally it appeared that sharp pecks were effective. Because the attacks were often rapid, discrimination between chewing, biting, and pecking was difficult. Therefore, only the portion of the mouse attacked was recorded. As efficient attacking increased in frequency there was a decline in bowing, wing spreading, retreating, and tail pulling. A typical later trial consisted of an immedate approach and a quick kill by attacking the neck. Two of the shrikes in the early group never killed a mouse, but all of the shrikes in the late group killed at least one mouse.

DISCUSSION

Under the experimental conditions of my study, the ontogeny of cricket killing in Log-

gerhead Shrikes requires about three days, at one encounter per day, to reach a stage of proficiency such that capture is almost immediate. Because all approaches were accompanied by a capture, it appears that once the shrike approaches the cricket, the cricket's capture is almost assured; this would hardly be the case in the wild, however, because any insect that a shrike might encounter in the wild would not be conveniently restricted by an escape-proof enclosure.

Smith (1973) described fluttering and bowing in young wild shrikes, and her field observations document an increase in the invertebrate-killing proficiency of juvenile Loggerhead Shrikes as they mature in the wild. She reported observing a 19-day old shrike capture a small arthropod, and stated that 25- to 26-day old shrikes are more successful than younger shrikes in capturing arthropods, and that 30-day old shrikes regularly catch larger insects. Both the early and late groups in the present study likewise showed an improvement in their cricket-killing abilities. The approach times, capture times, and occurrences of behavior during the cricket-killing trials were similar in both groups, suggesting that a basic ontogeny had to be completed, regardless of whether the shrikes came into contact with crickets beginning on the 25th or the 50th day of age.

Smith's shrikes ate independently sooner than those that Miller (1931) observed and that I observed. Miller concluded that captive shrikes kill live insect food at the age of 30 days, but Smith's shrikes ate mealworms independently at 18 days of age. Other shrikes that I have raised would not pick up live or dead mealworms or crickets, or even pieces of meat, until they were about 25 days old. They evidently recognized the food objects, having been fed them previously, because they begged toward the food; but they would not pick it up, even though they were quite capable of doing so, as shown by their picking up twigs at an earlier age. When handed the food they generally ate it quickly, indicating that they were hungry.

The ontogeny of mouse-killing behavior in wild shrikes would be difficult to observe. Smith (1973) reported that she never saw a young wild shrike even chase a small mammal, and neither have I. This means that neither Smith's nor my observations can be verified as approximately normal by subsequent field work. The weight gain of the shrikes in this study was similar to that of a shrike nestling weighed periodically at its nest by Miller (1931), and the cricket-killing ontogeny was rapid and consisted of behavior that Smith observed in shrikes in the wild.

Most of the behavior patterns I observed during the mouse-killing trials have been described by Smith (1973). When she presented a stuffed mouse to caged shrikes, they wagged their tails, spread their wings, bowed, and fluttered their wings, as the shrikes in this study did when presented a mouse. Miller (1931) also observed wing-spreading in caged shrikes given a mouse to kill. Cade (1962) stated that the closely related Northern Shrike (*Lanius excubitor*) sometimes flushes birds out of bushes by spreading its wings. Young Loggerhead Shrikes that spread their wings when confronting a mouse may have better balance, and spread wings may stimulate the mouse to flee, thereby exposing the back of its neck to attack. However, ascertaining and interpreting correlations between wing-spreading and environmental changes that immediately follow wing-spreading have been difficult. For example, Hailman (1960) stressed that wing-flashing in Mockingbirds (*Mimus polyglottos*) flushes insects; and Selander and Hunter (1960) stressed that it is primarily communicative among conspecifics, that is, it results in behavioral changes in other Mockingbirds.

The shrikes in my study generally killed a mouse by biting and chewing the back of its neck; Smith (1973) stressed pecking at the back of the neck as the killing motion. Miller (1931) stated that Loggerhead Shrikes attack the back of the head or neck with rapid biting motions, and that the killing mechanism is a quick cut or snip. The Northern Shrike also kills with a series of bites which sever the cervical vertebrae (Cade 1967). An indication of the strength of the bite of Loggerhead Shrikes is their ability to neatly clip off the heads of Canaries (*Serinus canarius*) that attempt to escape through the bars of their outdoor cages when approached by a shrike, a predation reported as frequent by Bent (1950).

The age at which mouse killing develops in captive shrikes is approximately the age at which impaling develops. It has been assumed (Miller 1931, Cade 1967, Smith 1972) that as the ability to kill larger prey evolved in shrikes, the ability to secure that prey while ripping off swallowable chunks also had to evolve; otherwise, large prey could not be eaten. Hawks and owls hold large prey with their feet, but shrikes, with their passerine feet, appear ill-equipped to do so. In shrikes, impaling has evolved. I have given dead mice to shrikes that were proficient im-

palers, but that were in cages with no impaling devices. Their ineptitude at eating a mouse while holding it with their feet is demonstrated by their often falling as they jerked at the mouse with their beaks. Wemmer (1969) raised young shrikes in cages with various impaling devices, and found that most of the birds with appropriate (vertical) impaling devices became efficient impalers at about 35 days of age. Smith (1972) gave a model that shows impaling beginning to occur at about 30 days of age, and then reaching peak, presumably adult, frequency at about 40 days of age. The mean age at first kill for the birds in my early group was 41.0 days, with the first kill occurring on the 36th day of age. Smith's (1973) two groups on a similar regime killed their first mouse on the 35th and 37th day of age. Therefore, the development of the ability to kill prey that can be eaten only after impaling is accompanied by the development of the ability to impale that prey.

A comparison of the mouse-killing ontogeny of my early and late groups suggests that, while maturation is important in increasing the proficiency of mouse-killing in Loggerhead Shrikes, experience is also of importance. The initial median approach time for the late group was about two-thirds that of the early group, and the initial mean kill time for the late group was less than half that for the early group. However, the birds in both groups exhibited a steady improvement in their proficency of mouse-killing, which suggests that a definite ontogeny must be experienced before adult proficiency is gained.

Smith (1973) concluded (p. 138) that "Experience of any kind is unnecessary; the entire behavior, which involves directing pecks at the back of the neck of large prey, is displayed by any shrike 40 days old or older." This conclusion was based on a series of tests involving the presentation of mice to a total of 45 shrikes ranging in age from 38 to 90 days. She reported that in all cases the shrikes immediately attacked the mice with bites to the back of the neck, and all the mice were dead within 15 min.

The 50-day-old shrikes in the present study did not react in this manner. Although every shrike in this group captured its cricket on the first trial, none of them killed its mouse on the first trial, and the mean number of presentations before the first kill was 3.4. The concurrent cricket-killing success indicates that the mouse-killing failure was not because of the strange situation. And immature mouse-killing behavior, such as attacking the tail, was common. Also, the reaction was generally not immediate (fig. 5).

These differences between Smith's (1973) results and mine may be due to differences in experimental design. When using live mice, she measured whether they were killed within either 10 min or 15 min by a group of one to five shrikes in a 0.2m^3-cage. My shrikes were observed in greater detail, and time measurements were made to the nearest 5 sec. The birds were individually presented a mouse for a basic period of 2 min in a 5.8m^3-cage in which the shrike, perched about a meter above the arena, had to fly to the mouse. This design may be more likely to give an accurate indication of what shrikes do in the wild.

Smith gave no maximum size for her mice, but stated that their body length was at least 5 cm. I used mice with a body length of 6.5 to 7.5 cm; these mice would weigh about twice as much as Smith's smallest mice. The ontogeny for killing small mice may be considerably simpler than for larger mice. Cade (1962) said that a Northern Shrike can kill a small mouse quickly, but may take several minutes and many bites to kill a large one.

Smith did not say how many of her 45 shrikes in the 38-to-90 day-old category were in groups of more than one when presented mice, and how many were tested singly. However, an overall picture can be reconstructed by comparing the total number of birds taken from the nest (given in the methods) with the number used in these and other experiments (given throughout the paper). It appears that 25 were tested in groups of 5, 12 in groups of 4, 2 in a group of 2, and 6 singly. Therefore, only 13.3% of these 45 birds were tested in a situation resembling that in which wild shrikes hunt, for they do not hunt in flocks. In addition, Smith found that the model-attacking behavior of the shrikes tested in groups was often directed at the "head" significantly more often than those tested singly, so it is likely that their attacking of live mice is also affected by being tested in groups. This need not be a strong effect to influence the results. A group of 5 shrikes that kills a mouse need contain only one shrike capable of killing a mouse, so any facilitation need only be strong enough to allow the most precocious shrike to kill a mouse in 10 or 15 min.

Smith (1973) also did not give the history of 28 of these birds, but said only that 14 were given their first mouse at 70 days of age, and 14 at 84 days of age. Again, an overall picture can be reconstructed by comparing the initial

number of shrikes with those used in these and other experiments. The 14 birds given mice at 70 days of age had all been presented 12 simple wooden models, half of which were moving, one model a day for 2 min each day, during the approximately 2 weeks prior to their being tested with live mice. The birds had probably also been presented a stuffed mouse for 4 min prior to their being tested with live mice but this is not clear. The 14 shrikes given their first mouse at 84 days of age were presented two cycles of the 12 models and stuffed mouse prior to their being tested with live mice. All 6 birds tested singly with live mice came from this group that had from 13 to 26 experiences with models or a stuffed mouse. Smith therefore had no data for mouse-killing behavior in naive shrikes in a one-mouse-one-bird situation, yet she concluded that experience of any kind is unnecessary, that the entire behavior of mouse killing is displayed by any shrike 40 days old or older.

Another possible source of difference is that Smith worked with a northern United States population of shrikes, and I worked with a southern one; there may be an ecological difference between the two. However, it would probably have to be a large difference to have resulted in the evolution of instinctive mouse killing in one and learned mouse killing in the other. At present there is no evidence that such an ecologcal difference exists.

Although not definitely concluding that mouse-killing in Loggerhead Shrikes is innate, Smith (1973) offered three reasons that it probably is innate: young shrikes attacked and killed mice in a precise stereotyped way; the response did not degenerate with time, even when models were used and there was therefore no reward; and the rewarding situation of allowing a shrike to kill and eat a mouse did not significantly affect the subsequent attack of models. The concept of innateness should be treated with caution, however, for as Schneirla (1966) pointed out, all claims for innateness in behavior are strictly hypothetical. Also, it is often the case that previous findings of innateness are brought into question by subsequent research (for example, see Denenberg et al. 1968). The refinement of experimental design and technique often discloses complexities in an ontogeny that had once been considered simple or nonexistent. Unfortunately, the labelling of a behavior pattern as innate can, as Lehrman (1953) stressed, lead investigations away from the fundamental analysis of developmental problems.

I have made no attempt to argue that certain portions of the shrike's mouse-killing behavior are learned, for this would be falling into what Schneirla (1966) called the blind alley of the innate-versus-acquired dichotomy. I have merely documented that complexity exists in the ontogeny of a behavior that has previously been described as occurring in a stereotyped manner without prior experience. It is probable that a further refinement of experimental design and technique, such as the extensive use of high-speed motion pictures, would show further complexities that went completely unnoticed in the present study.

SUMMARY

The cricket-killing and mouse-killing behavior of two groups of hand-reared Loggerhead Shrikes were observed as the shrikes were each presented a cricket and a mouse daily. One group, the early group, began trials on the 25th day of age, and the other group, the late group, began trials on the 50th day of age.

The cricket-killing ontogeny, similar for both groups, required about three days after the initial approach to reach high proficiency. The mean age at the first capture was 37.0 days for the early group and 50.0 days for the late group. The ontogeny began with the shrike slowly approaching the cricket, bowing and fluttering toward it, and then generally missing it once or twice before finally capturing it. The ontogeny ended with an almost immediate approach and capture.

The mouse-killing ontogeny, also similar for both groups, was more prolonged, taking about five to seven days after the initial approach to reach a proficiency such that a mouse would probably have been unable to escape the shrike in the wild. During the early stages of the ontogeny, tail-bobbing, fluttering, wing-spreading, and bowing were common, as well as such unproductive or dangerous behavior as retreating from the mouse, grabbing the mouse with the feet, and attacking the tail. These behavior patterns became fewer as approach and kill times decreased, until the entire behavior generally consisted only of attacking the head and neck. The mean age at first kill was 41.0 days for the early group. The late group required an average of 3.4 encounters with a mouse before killing one.

The similar trends for both groups in occurrence of behavior, in approach times, and in capture and kill times, suggest that experience is an important factor in the development of mouse killing behavior, and that a definite

ontogeny must occur before adult proficiency is gained.

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LITERATURE CITED

BENT, A. C. 1950. Life histories of North American wagtails, shrikes, vireos, and their allies. U.S. Natl. Mus. Bull. 197.

CADE, T. J. 1962. Wing movements, hunting and displays of the Northern Shrike. Wilson Bull. 74:386–408.

CADE, T. J. 1967. Ecological and behavioral aspects of predation by the Northern Shrike. Living Bird 6:43–86.

DENENBERG, V. H., R. E. PASCHKE, AND M. X. ZARROW. 1968. Killing of mice by rats prevented by early interaction between the two species. Psychonomic Sci. 11:39.

HAILMAN, J. P. 1960. A field study of the Mockingbird's wing-flashing behavior and its association with foraging. Wilson Bull. 72:346–357.

LEHRMAN, D. S. 1953. A critique of Konrad Lorenz's theory of instinctive behavior. Q. Rev. Biol. 28:337–363.

MILLER, A. H. 1931. Systematic revision and natural history of the American Shrikes (*Lanius*). Univ. California Publ. Zool. 38:11–243.

SCHNEIRLA, T. C. 1966. Behavioral development and comparative psychology. Q. Rev. Biol. 41: 283–302.

SELANDER, R. K., AND D. K. HUNTER. 1960. On the functions of wing-flashing in Mockingbirds. Wilson Bull. 72:341–345.

SMITH, S. M. 1972. The ontogeny of impaling behavior in the Loggerhead Shrike, *Lanius ludovicianus* L. Behaviour 42:232–247.

SMITH, S. M. 1973. A study of prey-attack behavior in young Loggerhead Shrikes, *Lanius ludovicianus* L. Behaviour 44:113–141.

WEMMER, C. 1969. Impaling behavior of the Loggerhead Shrike, *Lanius ludovicianus* Linnaeus. Z. f. Tierpsychol. 26:208–224.

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