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NESTING BEHAVIOR OF *LARROPSIS CHILOPSIDIS* AND *L. VEGETA* (HYMENOPTERA: SPHECIDAE: LARRINAE)

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In their revision of the genus *Larropsis,* Bohart and Bohart (1966) reported prey records for only two of the 25 described species. *L. divisa* (Patton) had been observed preying on immature camel crickets, *Ceuthophilus* sp., by Williams (1913), who also presented notes on nesting behavior; and R. M. Bohart himself had taken *L. filicornis* Rohwer with an adult camel cricket of the genus *Ammobaenetes.* A detailed study of the nesting behavior of *Ancistromma distincta* (Smith), a member of a closely related genus (often ranked as a subgenus of *Larropsis*), was published by Evans (1958a). The present paper adds to the limited knowledge of *Larropsis* biology by reporting observations on the nesting behavior of *L. chilopsidis* (Cockerell and Fox) and *L. vegeta* (Fox). These two species are very similar structurally, live in sand dune habitats, and exhibit virtually identical nesting behavior.

METHODS

Behavioral data were collected by following individual females as they walked over the sand surface searching for burrows of their camel cricket prey. Observations were read into a Sony cassette tape recorder and were later copied into a field notebook. Burrows were excavated to determine nest dimensions and to locate cells and prey. Cell contents were kept in rearing tins with moist sand.

Voucher specimens of both species of *Larropsis* and their prey and parasites have been placed in the collection of Colorado State University.

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OBSERVATIONS ON *L. CHILOPSIDIS*

According to Bohart and Bohart (1966) this species is distributed from Chihuahua, Mexico, north to southern Colorado and east into Texas. Our observations were made during late June and early July 1975 in sand dunes bordering the Rio Grande valley, at the La Joya Waterfowl Preserve, 20 miles north of Sorocco, New Mexico. At this locality, females were commonly observed in the dunes during the morning and again during late afternoon; during the heat of midday they were rarely seen. Their activity consisted mainly of walking in sinuous patterns over the sand and investigating small depressions and burrow entrances in the sand surface. In contrast to some Larrinae, females did not flicker their wings while hunting. Often they dug with the front legs and occasionally they entered holes in the sand. Most females were followed by one or more satellite flies hovering 6-8 cm behind (Table 1). We captured several of these flies and found that two species were involved: *Senotainia rufiventris* (Coquillett) and *S.* (?) *flavicornis* (Townsend) (Sarcophagidae, Miltogramminae) (det. R. J. Gagné) (Table 1). *L. chilopsidis* females appeared to spend a great deal of time searching, as evidenced by the many hours we spent following them before one was observed to locate her prey. All *L. chilopsidis* observed preyed on *Ammobaenetes phrixocnemoides* (Caudell) (Gryllacrididae, Rhaphidophorinae), a sand treader camel cricket (4 records).

Table 1. Records of satellite flies observed following female *Larropsis* species.

Number of flies per ♀	Number of females *L. chilopsidis*	*L. vegeta*
0	11	7
1	15	1
2	1	0
3	0	0
4	1	0

Observation A.—The first interaction between female and prey was observed at 0920 on 27 June. The wasp was seen moving over the sand surface and digging briefly in various places. She flushed a sand treader camel cricket from just beneath the surface. The cricket jumped approximately 1.5 m but the wasp did not follow. We recovered the cricket and threw it at the wasp, which seized it and held on while the prey still jumped around. The wasp stung the prey several times, preventing further movement. After a short period the wasp grasped the antennae of the cricket and started to pull it. However, the cricket was twice the length of the wasp and doubtless weighed several times as much, and after a few seconds she stopped trying to move it and began to feed at the ventral side of the neck region. After 30 seconds she abandoned the prey and resumed her searching behavior. She did not return to the cricket, which after one hour was collected for identification.

Observation B. — Another wasp was observed at 0905 on 28 June, moving up a 20 degree slope in the dunes, straddling a paralyzed cricket and holding it by the antennae, beating her wings rapidly to gain additional traction up the slope. After moving 0.5 m, she left the prey briefly and walked up the slope investigating several holes before she resumed dragging the prey. A satellite fly hovered around the wasp and prey and at one point perched briefly on the cricket. After dragging the prey another 0.5 m the wasp once again left it and moved about the sand surface for about 2 minutes. She returned quickly and carried the prey into an open hole. No satellite flies followed her to the hole.

At 0942 the wasp was observed to reappear at the mouth of the burrow, digging at the sides of the hole. As she moved toward the surface she turned, and sand from the burrow gradually filled the burrow behind her. At 0943 she flew away, leaving the top 1 cm of the burrow unfilled. She made no attempt to use sand from the dune surface to fill the hole. The burrow was evidently that of a cricket, possibly the one she had captured. It was dug into a slope of about 20 degrees and was steep for the first 15 cm (about 30-35 degrees with the surface); the first 11 cm was filled with sand and the next 4 cm was open. Beyond this the burrow had been filled and was impossible to trace. The cell with the paralyzed cricket was located 28 cm below the sand surface and 40 cm from the burrow entrance. The prey was positioned on its back and bore the *Larropsis* egg as well as a small satellite fly larva (Fig. 1).

Observation C. — At 1735 on 28 June a wasp was seen entering a burrow. About 1.5 min later she emerged 15 cm from the burrow mouth and immediately dug herself back in. Both times she entered the ground she had to dig for 15-20 seconds in order to get through the loose surface sand. At 1915 the wasp had not emerged from the burrow. At 0830 on the following day we excavated the area around the filled burrow and found a female camel cricket 19 cm deep and 35 cm from the burrow mouth. An egg was present on the cricket, which had completely recovered from paralysis.

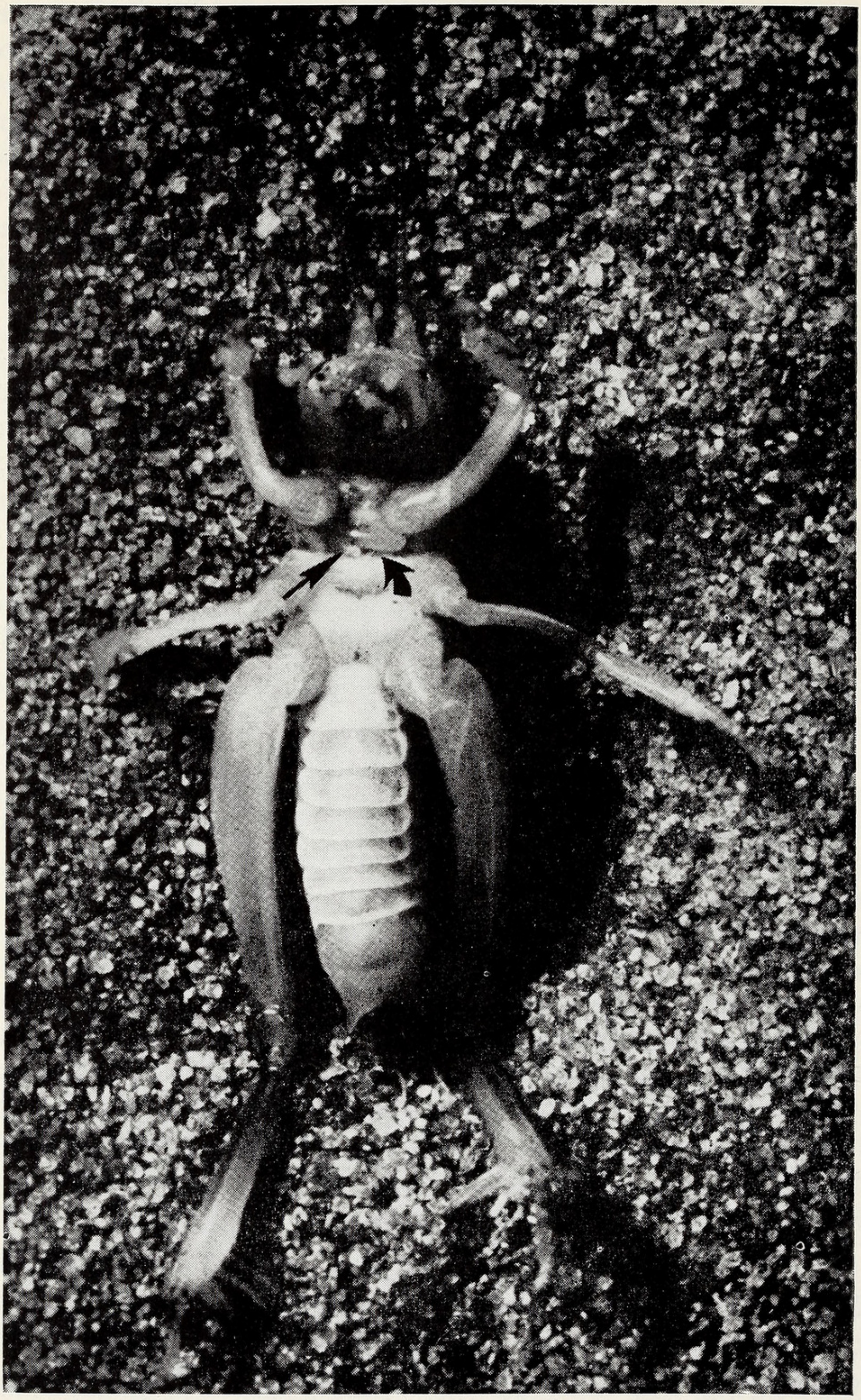

Fig. 1. Paralyzed *Ammobaenetes phrixocnemoides* bearing the egg of *Larropsis chilopsidis* (broad arrow points to the egg, slender arrow to the maggot of *Senotainia* sp. directly behind it).

Observation D. — At 0900 on 30 June a *Larropsis chilopsidis* female, followed by a satellite fly, was observed digging for about 30 seconds before entering a burrow. The fly perched on a small twig, about 3 cm from the burrow mouth, as the wasp entered. The fly then flew to the burrow mouth but soon returned to her perch; she continued to show interest in the hole and several times moved between it and various perches. This alternated with bouts of flying in 0.5 m circles around the burrow. At one point the perched fly oriented to a passing harvester ant, *Pogonomyrmex* sp., which was about the same size and color as female *L. chilopsidis.* At 0912 the fly was still present but seemed to show less interest in the burrow, and by 0930 it had left the area.

At 1000 the wasp had not emerged from the burrow so the mouth was covered with an insect net. Upon returning to the area at 1400 we found the dead wasp in the net, evidently a victim of the intense afternoon heat. The nest, which was located on level ground about 0.5 m from a large shrub, was excavated that afternoon, but the filled burrow was impossible to trace. Cell and prey were located 31 cm from the burrow entrance. The female camel cricket prey, which had an egg attached, was apparently just recovering from paralysis, as it was able to walk slowly.

Egg and Larva. — The egg of *L. chilopsidis* is 2.0-2.2 mm long and about 0.4 mm wide (N=3). It is laid transversely between the front and middle coxae of the prey, with one end pressed against one of the front coxal cavities (Fig. 1). This is exactly the same egg position described for *Ancistromma distincta* (Evans, 1958a). In two observations (C and D) the prey seemed to recover from paralysis about 6-8 hours after being stung. The egg from observation C hatched in 44 hours, which is comparable to the 2 days reported for *A. distincta* by Evans. The larva, however, died soon after hatching. The egg from interaction B failed to hatch. As mentioned above, a satellite fly had been observed landing on the prey in this instance. In the cell a single fly larva was observed immediately behind the wasp egg; it was 1 mm in length and positioned at one end of the egg, between it and the right middle coxa of the prey (Fig. 1). By 6.5 hrs after the egg was laid it had been completely consumed by the fly larva. Sixteen hours later the larva had entered the body of the cricket, which was dead. By the morning of 4 July (6 days after the egg had been laid) the maggot pupated, leaving only the legs, head, and end of the cricket abdomen unconsumed. The puparium was brick red in color and measured 2 × 5 mm.

OBSERVATIONS ON *L. VEGETA*

Females of this species are about the same size as those of *L. chilopsidis* (approximately 15 mm) but are much darker in color, almost black. Bohart and Bohart (1966) reported the species from the central Great Plains in Wyoming, Colorado, western Nebraska, northern Arizona, and the base of the Texas panhandle. Our observations were made near Hasty, in southeastern Colorado, in early July 1975.

The behavior of this species appears almost identical to that of *L. chilopsidis*. Although one female *L. vegeta* was followed by a satellite fly (not identified), the majority were not (Table 1). Only one interaction between wasp and prey was observed. At 1000 on 5 July, a female was observed digging on the surface of a dune. She located a burrow and entered. We excavated the burrow about 5 minutes later; as it had not been filled it was easy to trace to the cell. The burrow formed an angle of about 10 degrees with the flat sand surface. It was straight for 34 cm, where the wasp and paralyzed prey were found about 15 cm below the surface. The prey was an immature female sand treader camel cricket, *Daihiniella* sp. The wasp had not yet laid an egg on her prey.

DISCUSSION

Both *Larropsis chilopsidis* and *L. vegeta* females obtain their prey by searching the sand surface for sand treader camel cricket burrows. Apparently they use olfactory cues to locate active burrows. Support for this hypothesis comes from an observation made after removing a cricket prey and egg of *L. chilopsidis* from the cell. A searching female walked into the hole we had dug out and showed much interest in the empty cell, digging in the area for several seconds.

Very little is known about the biology of sand treader camel crickets. There are several genera in the group (Tinkham, 1942), all characterized by a "sand basket" of spurs on the upper distal end of the posterior tibiae. An *Ammobaenetes phrixocnemoides* kept in the laboratory was observed to remove sand from its burrow by moving backwards, pushing sand behind it with the aid of the sand baskets. These insects are nocturnal and dig a simple, oblique burrow in which they pass the day (Tinkham, 1942). A searching female *Larropsis* is therefore more likely to find her prey deep in the burrow.

Our observations suggest that both species normally find and sting their prey underground, where the cricket has little opportunity to escape. In observation A (*L. chilopsidis*) the wasp had evidently encountered a cricket near the sand surface, where it was able to escape by leaping away from the wasp. Even though searching *Larropsis* females are usually followed by satellite flies, they normally successfully avoid these parasites by capturing their prey underground. *Senotainia* species will not enter burrows and will larviposit only on exposed prey outside the burrow (Evans and West Eberhard, 1970, p. 61). This was revealed when a satellite fly was observed to follow a *L. chilopsidis* female as she entered a camel cricket burrow. Although the fly appeared to show much interest in the burrow mouth she did not enter but perched nearby for about 20 minutes (observation D). A satellite fly was successful in larvipositing on the prey in the single observation (B) where the female had stung the prey outside the burrow. In this case the cricket had presumably escaped from the wasp and had been chased, subdued, and eventually dragged back to its burrow.

Both of the species studied do not dig their own nests but utilize burrows of their prey, thus conserving the energy required to dig a nest. Use of pre-existing cavities for nesting is common in the subfamily (Larrinae) to which *Larropsis* belongs, having been reported in such genera as *Liris* (Steiner, 1962), *Lyroda* (Evans, 1964), *Ancistromma* (Evans, 1958a), and *Larra* (Williams, 1913, 1928; Smith, 1935). *Ancistromma distincta* females do some digging, but usually take advantage of natural cavities in the rocky soil of their nesting habitat. Species of *Larra* evidently locate their mole cricket prey in their burrows using olfactory cues, then attack the prey and lay their egg in the host's burrow, much in the manner of *Larropsis* species. However, the position in which the egg is laid is quite different in the two genera, *Larra* spp. laying the egg just back of the base of a hind leg, *Larropsis* spp. between the front and middle legs. These different egg positions are undoubtedly adaptive and are related to the fact that mole crickets dig with their front legs, sand treader camel crickets with their hind legs. Mole crickets attacked by *Larra* recoved quickly from paralysis and resume normal activities until killed by the developing wasp larva; thus it is to the advantage of the wasp larva that it be coiled posteriorly and not in a position to interfere with digging by the host. Sand treader camel crickets attacked by *Larropsis* spp. also recover from paralysis within a few hours and appear to be able to resume normal activities. One cricket, which we dug up some 15 hours after it was stung (observation C, *L. chilopsidis*), leaped from the excavated cell, and it was only when we captured the insect and found the wasp's egg that we were able to be sure it was the prey. However, we have no actual evidence that the crickets are able to dig their way out of the cells into which they are packed by the wasps.

These traits (temporary paralysis and use of the host's burrow as a nest) are often regarded as primitive, since they resemble the condition in structurally generalized wasps such as Scolioidea (Evans, 1958a,b). However, they might equally well be derived traits, suited to the ecology of their prey, and likely to reduce the success of satellite flies.

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