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NESTING BEHAVIOR OF *LYRODA SUBITA* (SAY) (HYMENOPTERA: SPHECIDAE)

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Abstract.—Observations made on 17 females of *Lyroda subita* (Say) nesting in upstate New York extend the range of variation in the behavioral components and nesting parameters of this species. Characteristic features include nesting in a variety of friable soils, beginning nests from pre-existing depressions, leaving entrances open during provisioning activities, practicing mandibular prey transport, usually in low flights, preying upon mostly immature gryllids which are incompletely paralyzed and stored in multicellular nests, and attaching the egg to the venter of the prey's thorax between the fore- and midlegs. Several of the cells were parasitized by satellite-flies of the genus *Senotainia* (Sarcophagidae: Miltogramminae). The components of *L. subita* behavior are discussed and compared with those of other (exotic) species in the genus.

The genus *Lyroda* contains only two species, *subita* (Say) and *triloba* (Say), in North America north of Mexico (Krombein, 1979). *Lyroda subita* occurs transcontinentally in southern Canada and the U.S., whereas *L. triloba* has been reported from Canada, D.C., Illinois, Indiana, Kansas, Louisiana and Texas (Krombein, 1979). Using larval characters, Evans (1964) placed the genus in the tribe Miscophini. A study of adult characters supports this placement (Bohart and Menke, 1976).

Nothing is known about the biology of *L. triloba*. Patton (1892) reported on the provisions and prey transport of *L. subita*. The Peckhams (1898, 1905) observed a female of *L. subita* nesting in Wisconsin and described prey transport, nest entry, cell depth, prey paralysis, and larval development. Williams (1914) mentioned the searching activity of *L. subita* females. Evans (1964) reported on nest-site selection, cell depth, prey transport, nest entry, provisions, number of prey per cell, egg placement, and parasitism. Our observations add to the knowledge of the nesting behavior of this species, particularly nest structure, dimensions, and cell contents.

Ethology

Nest-site selection.—Females of *L. subita* were observed nesting at three localities in Cayuga County, N.Y. during August and September 1969–71. Selection of a nesting site involved much searching activity on the surface and exploration below ground level. Active nests were located in the center and at the edge of a sand pit, border of a field, and slope of an erosion ditch. Wasps utilized for nesting sites deep cracks and crevices in the sand as well as both emergence and provisioning burrows of the cicada-killer *Sphecius speciosus* (Say), provisioning burrows of *Tachytes validus* Cresson (Sphecidae), and resting burrows of larval tiger beetles, *Cicindela* spp. In each case the insect had abandoned the site before *Lyroda* began using it.

Hunting behavior.—Females searched for prey on and in the ground, exploring holes, cracks, and crevices and foraging near the bases of vegetation. The distance of this activity from the nest varied with the success of the excursion; the wasp usually began nearby and gradually moved farther from the entrance. Prey capture was observed twice. In both cases the wasp pounced upon a cricket and inserted her sting in the throat for several seconds. She then reinserted the sting in the throat and, later, after repositioning herself, stung it near the base of a hindleg. The wasp then malaxated the cricket and/or rested on the sand and cleaned.

Prey transport, nest entry and exit.—Following prey paralysis, the female positioned the cricket ventral side upward or on its side (once dorsal side upward) and head forward, and grasped its antennae with her mandibles. She then proceeded forward to the nest either on the ground or in flight. The usual manner of transport involved a series of short, low flights, during which the legs assisted in holding the prey. Some provisioning females returned directly to their nests, almost in a straight line, and plunged inside without hesitating. These wasps left head first several s or min later and resumed hunting activities. One wasp spent one and one-half h provisioning a cell with five crickets, spending 6 to 55 ($\bar{x}$ = 18) min between successful hunting excursions.

Nest structure and dimensions.—The entrance to a nest of *L. subita* was either that of the original inhabitant, sometimes slightly modified, or simply an opening in the ground. The tumulus often had been eliminated entirely by weathering. The diameter of the entrance and proximal burrow usually divulged the first inhabitant. For example, burrows of renovated *T. validus* nests leading to burrows and cells of *L. subita* were 6–7 mm wide, those of the cicada-killer, 20–24 mm wide, except for one which narrowed to 6 mm at the entrance, and those of larval tiger-beetles, ca. 6 mm at the entrance, narrowing to 4 mm farther down. One nest had three species, *S. speciosus, T. validus* and *L. subita* nesting in succession, all utilizing a common entrance and proximal burrow.

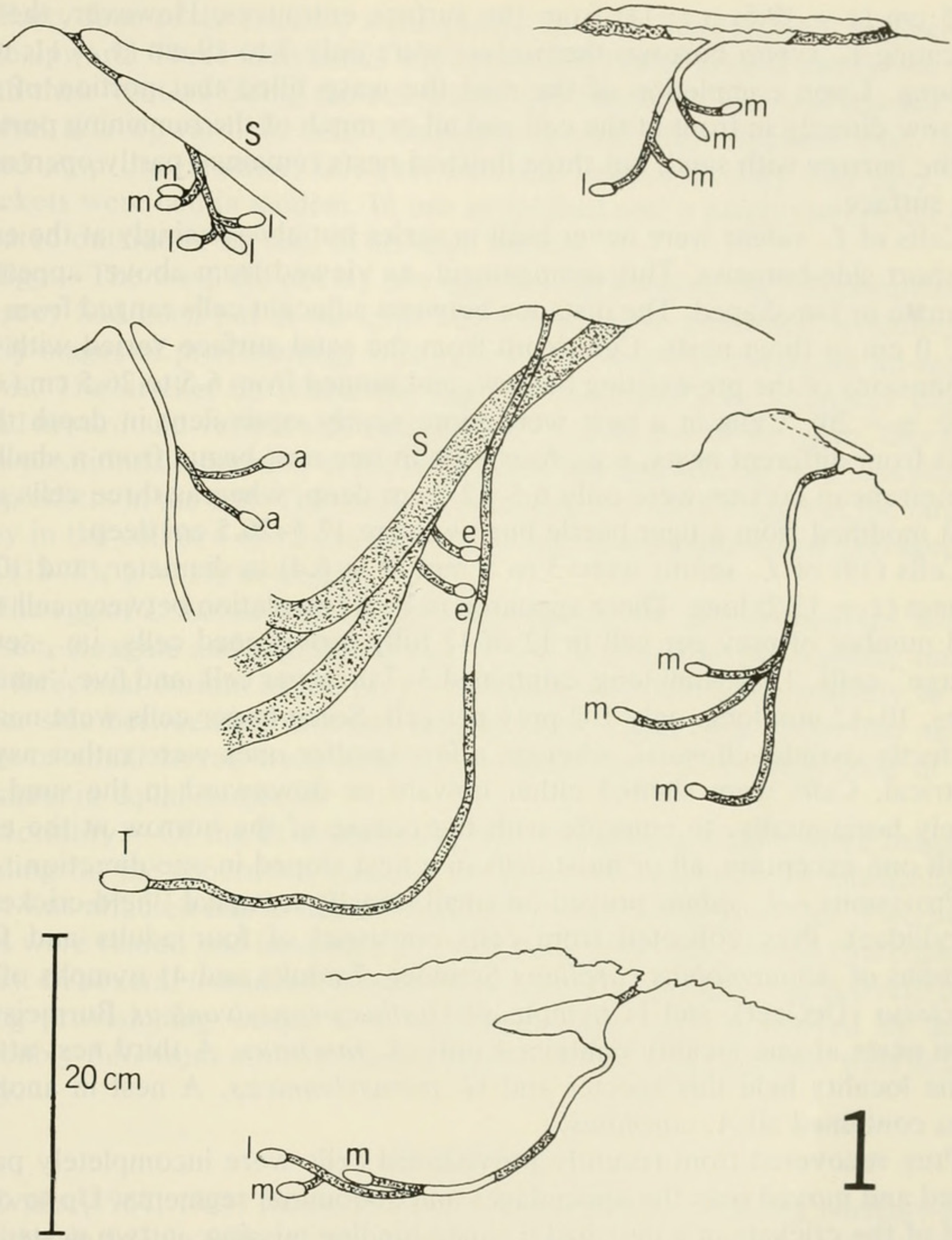

Fig. 1. Six nests of *Lyroda subita*, as viewed from the side, showing structure of burrow and placement of cells. Abbreviations: S = *Sphecius speciosus* burrow; T = *Tachytes validus* cell. *L. subita* cellular contents: e = egg; l = larva; m = maggot(s); a = ants. Stippling indicates burrow filled with sand. Scale at lower left refers to all six nests.

The *L. subita* portion of the nest exhibited a basic pattern, which included a main burrow and branching side-burrows leading to rearing cells (Fig. 1). The number of completed cells per nest ranged from two to five, the wasp finishing ca. one per day. Cells were located at distances of from 12.5 to

29.5 cm ($\bar{x}$ = 19.5; n = 11) from the surface entrances. However, the bifurcating *L. subita* burrows themselves were only 3 to 19 cm ($\bar{x}$ = 11; n = 6) long. Upon completion of the nest the wasp filled that portion of the burrow directly in front of the cell and all or much of the remaining portion of the burrow with sand, but three finished nests remained partly open near the surface.

Cells of *L. subita* were never built in series but always singly at the ends of short side-burrows. This arrangement, as viewed from above, appeared palmate or fan-shaped. The distance between adjacent cells ranged from 2.5 to 7.0 cm in three nests. Cell depth from the sand surface varied with the dimensions of the pre-existing burrow, and ranged from 6.5 to 26.5 cm ($\bar{x}$ = 14.0; n = 20). Cells in a nest were more nearly equivalent in depth than cells from different nests; e.g., four cells in one nest begun from a shallow subterranean crevice were only 6.5–12.5 cm deep, whereas three cells in a nest modified from a tiger beetle burrow were 17.5–26.5 cm deep.

Cells (19) of *L. subita* were 5 to 8 mm ($\bar{x}$ = 6.4) in diameter, and 10 to 16 mm ($\bar{x}$ = 13.2) long. There appeared to be a correlation between cell size and number of prey per cell in 12 of 17 fully-provisioned cells, i.e., seven "large" cells, 13–16 mm long, contained 3–7 prey per cell, and five "small" ones, 10–12 mm long, only 1–2 prey per cell. Some larger cells were nearly perfectly ovoidal-elliptical, whereas a few smaller ones were rather asymmetrical. Cells were slanted either upward or downward in the sand, or rarely horizontally, to coincide with the course of the burrow at the end. With one exception, all or most cells in a nest sloped in one direction.

Provisions.—*L. subita* preyed on small, mostly nymphal "field-crickets" (Gryllidae). Prey collected from cells consisted of four adults and four nymphs of *Allonemobius carolinus* Scudder, 7 adults and 41 nymphs of *A. fasciatus* (DeGeer), and 11 nymphs of *Gryllus pennsylvanicus* Burmeister. Two nests at one locality contained only *A. fasciatus*. A third nest at the same locality held this species and *G. pennsylvanicus*. A nest in another area contained all *A. carolinus*.

Prey recovered from recently provisioned cells were incompletely paralyzed and moved only the appendages and abdominal segments. Up to one-half of the crickets in a nest had a single hindleg missing; in two nests, the missing leg on four crickets was the left, and in one nest with two prey, the right.

The number of prey stored in fully provisioned cells ranged from 1–7 ($\bar{x}$ = 3; n = 17). The weights of the individual crickets varied from 11–73 mg ($\bar{x}$ = 35; n = 48). Female wasps weighed, on the average, 21 mg (n = 4). The weight of all prey in a completed cell averaged 107 mg (39–173; n = 17). Cells with a greater biomass usually contained more crickets rather than fewer, larger prey.

Forty-four of 49 crickets were placed in cells head inward and ventral side upward. Three individuals were positioned head inward and on the side with their venters facing the cell walls, and two were put head inward and dorsal side upward. In cells containing several prey, crickets were often piled atop one another; however in some cells with only two prey, the crickets were laid in tandem. In one unfinished nest a paralyzed cricket was located outside of the cell in an open burrow.

Egg.—The wasp did not lay her egg on a cricket until the full complement of prey had been put in the cell. Three cells were unearthed, evidently in early stages of provisioning, with only one or a few crickets and no egg or larva. The cricket on which the egg had been laid was invariably placed head inward and ventral side upward (n = 12). In five of six cases, this prey was positioned innermost in the cell. Once, the egg-bearing prey was placed atop others in the cell. The cricket containing the wasp's egg was the largest prey in the cell in 4 of 12 examples. The egg-bearing individual averaged 36 mg (18–73; n = 13) in weight.

The egg of *L. subita* was 2.0–2.5 mm long, 0.6–0.7 mm in diameter, white, elastic, elongate and slightly curved. It was attached by the cephalic end to the forecoxal corium of the prey, the caudal end extending laterally to the other side between the first and second pairs of legs (Fig. 2). In four nests, eggs or small larvae were attached to either the left or right sides of the crickets in equal numbers.

Mortality.—Of the 21 completed cells, 10 contained up to three maggots feeding on the innermost cricket. At least one cell in every multicellular nest was afflicted and in one nest, all three cells were destroyed. Two maggots were reared and identified as *Senotainia trilineata* (Wulp) (Sarcophagidae). In several instances, female *S. trilineata* were observed actively pursuing provisioning wasps. Two additional cells were destroyed by ants, probably *Solenopis molesta* (Say), and one nest contained cells with moldy prey.

Discussion

Evans (1964, 1973) found *L. subita* renovating pre-existing burrows and cavities in friable soils in Massachusetts and New York. The utilization of such depressions was reflected in the diverse architecture and dimensions of the several nests we excavated. *Lyroda formosa* (F. Smith) also nests in the ground in similar situations, utilizing deep burrows of large sand wasps and crevices for nesting sites (Iwata, 1938, 1964).

The Nearctic *L. subita* stores its nests with Gryllidae (see Patton, 1892; Peckham and Peckham, 1898; Evans, 1974), whereas some Asiatic and African species (*japonica* Iwata, *formosa, madecassa* Arnold) prey upon Tetrigidae (Iwata, 1938, 1963, 1964; Tsuneki and Iida, 1969). The fact that

Fig. 2. Egg of *Lyroda subita* attached to gryllid prey at right forecoxal corium and extending laterally between fore- and midlegs. Note missing left hindleg.

some of the *L. subita* nests we excavated contained only *Allonemobius fasciatus* or *A. carolinus* suggests either conditioning on the part of the female wasp during hunting or that individual wasps hunted in areas where each of these species was prevalent. Similar conclusions have been drawn regarding the hunting behavior of *Chlorion aerarium* Patton (Peckham and

Kurczewski, 1978) and *Liris argentata* (Palisot de Beauvois) (O'Brien and Kurczewski, unpublished data).

The transport of prey to the nest in *L. subita* is typically "larrine", i.e., on the ground or in flight depending on the size and weight of the prey, and grasping the prey's antennae with the mandibles. Similar details of prey transport for members of this genus have been recorded by Patton (1892), Iwata (1963, 1964), and Evans (1964). Tsuneki and Iida (1969), on the other hand, reported that females of *L. japonica* carried their prey with the middle legs.

The incomplete paralysis of the prey of *L. subita* coincides with that of most larrine wasps that utilize orthopterous prey (see especially Krombein and Kurczewski, 1963; Iwata, 1942, 1976; Evans, 1966, for summaries). Tsuneki and Iida (1969) reported only partial paralysis with eventual complete recovery of the prey in *L. japonica*.

Gryllid prey missing one or two hindlegs are common among the Sphecidae, e.g., *Chlorion aerarium* (Peckham and Kurczewski, 1978), *Liris nigra* V.d.L. (Steiner, 1968), so that finding a number of prey of *L. subita* missing one or more legs was not unusual. This appendage loss may reflect the manipulation of the prey during the stinging or attempted stinging process (see Steiner, 1968, Plate 22).

We found that the egg of *L. subita* may be laid on the first, last or intermediate prey taken into the nest. Tsuneki and Iida (1969) noted that the egg of *L. japonica* was laid invariably on the last provision taken into the nest. In *L. subita* (Evans, 1964), *L. formosa* (Iwata, 1964) and *L. japonica* (Tsuneki and Iida, 1969) the egg is laid in a rather typically larrine position between the first and second pairs of legs and is affixed to the forecoxal corium of one of the prey. In these species the egg is not laid until the full complement of prey had been placed in the cell despite Peckham and Peckham's (1898) account of progressive provisioning in *L. subita*.

The rather high incidence of miltogrammine parasitism we found in cells of *L. subita* substantiated work by Evans (1964), who noted many *L. subita* nests parasitized by miltogrammine flies, in two cases, *Metopia argyrocephala* Meigen.

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