

October 1987

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Recommended Citation

Kurczewski, Frank E. and Spofford, Margery G. 1987. "Further Observations on the Nesting Behavior of *Liris Argentatus* (Hymenoptera: Sphecidae)," *The Great Lakes Entomologist*, vol 20 (3)

Available at: <https://scholar.valpo.edu/tgle/vol20/iss3/3>

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**FURTHER OBSERVATIONS ON THE NESTING BEHAVIOR OF
LIRIS ARGENTATUS (HYMENOPTERA: SPHECIDAE)**Frank E. Kurczewski and Margery G. Spofford¹

ABSTRACT

A three-celled nest of *Liris argentatus* was excavated and examined in upstate New York. The nest was constructed from the terminus of an abandoned cicada-killer burrow and the cells contained 1-4 incompletely paralyzed *Gryllus pennsylvanicus* as prey. Two of the three cells were cleptoparasitized by the satellite fly *Senotainia trilineata*. The components of the ecology and behavior of *L. argentatus* we observed are compared with those from previous studies on this species.

Despite the fact that *Liris argentatus* (Beauvois) has been studied for nearly a century, there is much to learn about its nesting behavior. Although many prey species of Gryllidae are listed for *L. argentatus* (Ashmead 1894, Williams 1914, Rau and Rau 1918, Rau 1922, Krombein and Evans 1955, Krombein 1958, Kurczewski and Kurczewski 1971, Steiner 1976, O'Brien and Kurczewski 1982a), the list has not been exhausted. The number of prey per cell varies from only a single, rather large, late instar *Gryllus veletis* (Alexander and Bigelow) in each of 13 fully-provisioned cells (O'Brien and Kurczewski 1982a), to as many as six, small, immature crickets per cell (Ashmead 1894). Nest locations of *L. argentatus* are variable, with some wasps using pre-existing cavities and others constructing burrows from the sand surface (Bohart and Menke 1976, O'Brien and Kurczewski 1982a). Our observations on *L. argentatus* supplement the recent study by O'Brien and Kurczewski (1982a). Specifically, they were made later in the year than theirs, involve a different generation of wasps, and add new information to the behavior and ecology of this species.

On 9 August 1985, at the edge of a field bordering a man-made sand pit near Owasco Lake, just south of Auburn, Cayuga County, New York, we observed a female *L. argentatus* hunting for crickets in holes and depressions on a south-facing, moss-covered slope. This habitat was nearly identical to that described by O'Brien and Kurczewski (1982a). The next day, on a bare sandy road leading into the sand pit, we observed a slightly smaller *L. argentatus* transporting prey. The cricket was grasped by the bases of its antennae with the wasp's mandibles, ventral side up, and carried to the nest in low flights, 8-12 cm in length. During each of three subsequent provisioning trips this wasp lost her way and made several circles, 30-50 cm in diameter, in the vicinity of her entrance. After traversing 15-20 cm she would climb to the top of a low plant, pause while retaining her grasp of the prey, and look around, perhaps a form of navigation. During one such circle the provisioning wasp attracted a female of the satellite fly *Senotainia trilineata* (Wulp) (Sarcophagidae: Miltogramminae) which trailed in flight at a distance of 15 cm. When the provisioning wasp paused, the fly alit on the cricket's abdominal sternites and larviposited. As the female resumed transport to the nest, the fly

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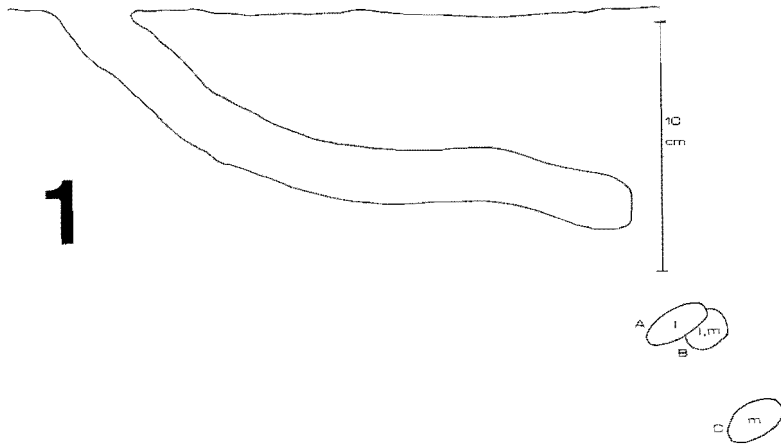


Fig. 1. Abandoned burrow of *Sphecicus speciosus*, lateral view, and cells of *Liris argentatus*; l = larva, m = maggots.

rode on the cricket's sternites for 4 cm, flew off, landed, and remained motionless on the sand. The wasp proceeded unimpeded into the nest entrance, seemingly unaware of the maggot(s) on the prey.

The nest entrance being used by the female *L. argentatus* was that of an abandoned *Sphecicus speciosus* (Drury) (Sphecidae) burrow, 2.35 cm in diameter, which was also being used by the sphecid *Philanthus politus* Say and the pompilid *Anoplius marginatus* (Say). On 10 August, amidst the repeated nesting activities of the three species of wasps, two females of *Phrosinella aurifacies* Downes (Sarcophagidae: Miltogramminae) were seen to enter the *Sphecicus* entrance and one of the flies larviposited. The *P. politus* and *A. marginatus* nests were not excavated so we cannot ascertain the larvipositional frequency of *P. aurifacies* on their cells (prey), but no *L. argentatus* cell contained a *P. aurifacies* maggot.

The abandoned cicada-killer burrow was 25 cm long and terminated at a depth of 9 cm beneath the sand surface (Fig. 1). Three cells of *L. argentatus* were unearthed just beyond the terminus of the *Sphecicus* burrow at depths of 13, 14, and 18 cm. Cell A was located 4 cm almost directly beneath the terminus of the cicada-killer burrow and separated laterally from cell B by 2 cm; cells B and C were separated by 4 cm. The cells varied in shape and size: A, 1.1 cm wide and high, and 2.6 cm long; B, 1.3 cm wide, 1.5 cm high, and 1.7 cm long; C, 1.5 cm wide and high, and 2.4 cm long.

All prey were placed in the cells head inward and ventral side up or on the side. They were only lightly paralyzed and moved their antennae, mouthparts, and legs considerably; some actually walked or jumped out of the cells when unearthed. Cell A contained a single nymph of *Gryllus pennsylvanicus* Burmeister, weighing 152 mg, with a small wasp larva feeding at the left forecoxal corium and placed transversely across the cricket's thoracic sternum between the bases of the first and second pairs of legs. Cell B held two smaller nymphs of *G. pennsylvanicus* with one bearing an even smaller wasp larva in the same position as above and the other, three maggots. The wasp larva disappeared within 24 h. Cell C contained three small nymphs and one immature female of *G. pennsylvanicus*, and four maggots. No egg or wasp larva was found in this cell which appeared to be the oldest of the three. The smallest cricket in the cell weighed only 48 mg. All seven maggots formed puparia and three females and two males of *Senotainia*

trilineata emerged on 27 and 28 August 1985. The two other flies were determined as a female and male of *S. trilineata* from their pupal remains.

On 15 August this wasp was observed transporting a paralyzed cricket, as before, into another cicada-killer entrance, only the nest was active. (The female *S. speciosus* took in a paralyzed cicada shortly after the provisioning female *L. argentatus* entered). The nest was excavated on 19 August. The *S. speciosus* burrow was traced for 135 cm to a depth of 35 cm. It led to six fully-provisioned cicada-killer cells, but no *L. argentatus* cells were unearthed during the excavation.

DISCUSSION

The location of *L. argentatus* nests varies between study sites. Williams (1914) noted females nesting in the cracks of a sidewalk. Rau (1922) observed a wasp flying into a hole in a clay bank. All of the nests in O'Brien and Kurczewski's (1982a) study were started from the sand surface. In our study of *L. argentatus*, females nested from abandoned and active cicada-killer burrows.

The depths of *L. argentatus* cells reflect the variation in nest locations. Rau and Rau (1918) found a single cell of this species at a depth of 6.5 cm and another in a clay bank only 3.2 cm deep. Rau (1922) recorded a third cell of this species at a depth of 15 cm. O'Brien and Kurczewski (1982a) reported *L. argentatus* cells from four nests at rather uniform depths of from 9.0 to 14.5 cm. The maximum and minimum cell depths recorded in their study were from a 10-celled nest. Three cells from the nest in the present study were unearthed at depths of 13–18 cm. The terminus of the associated cicada-killer burrow was only 9 cm deep, indicating *L. argentatus* had constructed side burrows leading to its cells.

The species of prey of *L. argentatus* reflect the time of year and the varied habitats in which the wasps nest. For example, Krombein (1958) took a female with a nymph of *Orocharis saltator* Uhler in North Carolina in August, and Kurczewski and Kurczewski (1971) took two wasps with a male *Gryllus rubens* (Scudder) in Florida in March and an overwintering nymph of *Miogryllus verticallis* (Serville) in Kansas in May, respectively. In New York, *L. argentatus* preyed upon *Gryllus veletis* in May and *G. pennsylvanicus* in August (O'Brien and Kurczewski 1982a, present study).

There is often an inverse relationship between the number of prey per cell and the size(s) of the cricket(s) in *L. argentatus*. O'Brien and Kurczewski (1982a) reported a single, large *G. veletis* in each of 13 cells. Rau and Rau (1918) noted four adult male *G. pennsylvanicus* in a single cell and two *G. pennsylvanicus* nymphs and one *Allonemobius fasciatus* (De Geer) in another cell. The present study reveals from one large to four small nymphs of *G. pennsylvanicus* per cell. We found no correlation between cell size and prey mass nor between cell depth and age of wasp progeny in *L. argentatus*. O'Brien and Kurczewski (1982a), likewise, noted no correlation between cell length and prey weight (size) in this species, but found that shallower cells held older larvae in one 10-celled nest.

Several authors have commented on the incomplete paralysis of the prey of *L. argentatus*. We found the prey crickets to be extremely lively, exhibiting considerable movement of the appendages, and, in some cases, walking or jumping from the cells when unearthed. The reason for the light paralysis of prey in *L. argentatus* is unknown, but very incomplete paralysis is well-documented for other larrine wasps such as *Tachytes mergus* Fox and *T. intermedius* (Viereck) (Krombein and Kurczewski 1963, Kurczewski and Kurczewski 1984). Steiner (1976), too, found only temporary paralysis with partial recovery of motory reflexes in three species of *Liris*. He believed that, because such wasps are rather primitive sphecids (Bohart and Menke 1976), their venom has only a limited effect both in time and space. He (1976, 1984) noted further that the mole cricket prey of another primitive larrine, genus *Larra*, recovers even more completely from the effects of the wasp's venom. The mole crickets behave normally, as if they had not been stung. Steiner (1976, 1984) related this complete recovery to the "weak venom

properties'' of the wasp and (or) the considerable size difference between the wasp and its enormous prey.

The 13 cells of *L. argentatus* excavated by O'Brien and Kurczewski (1982a) were devoid of cleptoparasites, yet two of the three cells we unearthed in the present study each contained several miltogrammine maggots (*Senotainia trilineata*). The fact that O'Brien and Kurczewski's (1982a) study was done in May when such flies are virtually absent, and our study was made in August when satellite flies are abundant, suggests adult overwintering in sphecids and pompilid wasps is a means to avoid such cleptoparasitism (O'Brien and Kurczewski 1982b, Alm and Kurczewski 1984).

In *L. argentatus* and an unrelated sphecids, *Podalonia luctuosa* (Cresson), which preys upon cutworms (O'Brien and Kurczewski 1982b), the spring-nesting (overwintering) generations appear to be larger in size than the mid to late summer-nesting generations in upstate New York. However, the spring-nesting generations of these species may be more obvious to the observer because there are practically no other wasps nesting at this time of year. M. F. O'Brien (pers. comm.) believes there may be two different (isolated) gene pools of ''*L. argentatus*'' comprising spring and summer sibling species that are synchronized with two sibling species of host crickets, *Gryllus veletis* and *G. pennsylvanicus*, whose adults are also allochronic (Alexander and Bigelow 1960, Alexander 1968). One larval *L. argentatus* that spun its cocoon in New York on 15 August 1985, died during late summer before pupating and did not provide us with the evidence to support O'Brien's hypothesis. Two sphecids that do not overwinter in the adult stage, *Ammophila harti* (Fernald) and *Oxybelus bipunctatus* Olivier, also have large spring and small late summer generations, based upon actual numbers of nesting females observed (Hager and Kurczewski 1986, pers. observ., respectively). Many individuals of each of these species have been reared to ascertain that a certain proportion of the spring population goes into the makeup of later generations of the same year. However, we do not know what proportion of the spring populations converts directly to spring generations of the subsequent year(s). In *Senotainia trilineata* and *S. vigilans* Allen, two sarcophagid flies cleptoparasitic on sphecids wasps, some larvae convert to adults in just a few weeks while others emerge as adults after undergoing diapause for 1-3 years (Spofford et al. 1986, pers. observ.). After reviewing and evaluating all of this information and examining the enormous amount of collecting data presented by Krombein and Gingras (1984), we believe that *L. argentatus* is at least bivoltine in New York State.

ACKNOWLEDGMENTS

We thank R. D. Alexander and M. F. O'Brien, Division of Insects, Museum of Zoology, The University of Michigan, for identifying *Gryllus pennsylvanicus* and for reviewing the manuscript; and A. S. Menke, BBII, ARS, USDA, for confirming the identity of *Liris argentatus*.

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