

## Prey Carriage and Nest Tending Observations of *Liris argentatus* (Palisot de Beauvois, 1811) (Hymenoptera: Crabronidae) in Sioux City, Iowa, USA<sup>1</sup>

G. K. Lechner<sup>2</sup>

**Abstract:** The activities of the fossorial wasp, *Liris argentatus*, were observed over a two-week period at a retaining wall on a residential lot in Sioux City, Iowa. Evidence of prey carriage and nest tending were encountered.

**Key Words:** *Liris argentatus*, prey carriage, nest tending, *Gryllus*, Sioux City, Iowa, USA.

### Introduction

*Liris* is a large cosmopolitan genus of larrine wasps (Hymenoptera: Crabronidae) containing over 260 species most of which inhabit the tropics (Bohart and Menke, 1976). A large revisionary study was published by Krombein and Gringras (1984) covering the *Liris* of North America of which they recognized 24 species. In a long account of *Liris* biology, Krombein and Gringras base their discussion on *Liris argentatus* (Palisot de Beauvois, 1811) extensively detailing the observations of this species by many previous workers going back to 1894. In this paper, I report my observations of *L. argentatus*<sup>1</sup> apparent nesting behavior through the openings in a concrete block retaining wall located along the north lot line of my residential lot in Sioux City, Iowa, USA (Figure 1).

### Methods

My chance observations of *L. argentatus* were the result of my more systematic observations of The Great Black Wasp, *Spheg pensylvanicus* Linnaeus, 1763 (Hymenoptera: Sphecidae), which had been nesting as an aggregation in the soil behind the aforementioned retaining wall. I have observed *S. pensylvanicus* activities in this aggregation for fifteen years (unpublished). It was only in 2006 that *L. argentatus* was a newcomer to the retaining wall. Although I could not devote my full attention to this wasp, from 15 to 29 August 2006 I noted over 40 appearances of *L. argentatus* in the wall, with activities in the area between Blocks 5, 6, 7, 8, and 9 (my numbering system for wasps' entry ways into the wall).

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<sup>1</sup> Submitted on November 30, 2021. Accepted on December 2, 2021. Last revisions received on December 29, 2021. The correct specific epithet of this species of *Liris* is *argentatus*, not *argentata*.

<sup>2</sup> 3624 Virginia Street, Sioux City, Iowa 51104 USA. E-mail: [garylecherner22@gmail.com](mailto:garylcherner22@gmail.com) .

### Results and Discussion

Table 1 summarizes my observations, some which are of a most intriguing nature, especially in the realm of prey carriage and nest tending. A discussion follows the table.

Table 1. *Observations of Liris argentatus* North Lot Line Retaining Wall, 3624 Virginia Street, Sioux City, Iowa 15 - 29 August 2006.

| Date      | Time      | Observations  |
|-----------|-----------|---|
| 15 August | 0945      | Wasp noted carrying prey on the wall nest to Block 6. She dropped prey and flew away.   |
|           | 1005      | Wasp flying near Block 6  |
|           | 1006      | Wasp noted on wall by Block 7 then entered aperture 7W. Traps jars set.   |
|           | 1012      | After six minutes, wasp exited from 7W into trap.   |
|           | 1130      | Wasp noted walking on wall next to 7W aperture. She dropped prey prior to capture.  |
|           | 1245      | Wasp noted walking with prey a few inches above ground level between Blocks 6 and 7. Captured both.   |
|           | 1300      | Wasp noted walking on the wall very near the base between Blocks 6 and 7.   |
|           | 1305      | Wasp noted walking on the ground below Block 5.   |
|           | 1310      | Wasp noted walking on the ground below Block 7 then climbing up to enter aperture 7W. Trap set.   |
|           | 1345      | After 35 minutes, wasp exited from aperture 7W into previously set trap. Wasp released.   |
|           | 1347      | Wasp noted entering aperture 7W. Traps set.   |
| 15 August | 1410      | Wasp noted walking on wall with prey above Block 5. She dropped down off the wall to ground and began climbing immediately. She repeated this up and down pattern five more times before finally entering aperture 5W. She did not stay there but exited and dropped down to the ground before climbing the wall again and entering 5W. She exited and then walked over to enter aperture 5E.   |
|           | 1445      | After 58 minutes, wasp exited from aperture 7W into trap.   |
|           | 1510      | Two wasps noted flying around wall exploring near Blocks 8 and 9.   |
|           | 16 August | 1230  |
| 20 August | 1020      | Wasp noted walking on wall above Block 6 apertures.   |
| 22 August | 1250      | Wasp with prey noted on wall and walking into 9W aperture. I prodded at the wasp, and she dropped her prey which fell to the ground. Wasp went down to retrieve it. She manipulated the nymph so that it was dorsum upward and then grabbed the base of the nymph's antennae with her mandibles. I could not discern if she was using any of her legs to support the prey. Wasp then started climbing the wall, and I disturbed her again. She dropped the prey and flew away. At his time, I also noted two apparently discarded nymphs on the ground below the 9W aperture. |
|           | 1600      | Wasp noted walking back and forth on the wall a few inches above ground level between Blocks 6 and 7.   |
|           | 1750      | The two nymphs previously noted on the ground below aperture 9W were gone. They may have fallen victim to ants which were besetting what appeared to be cricket parts lying on the ground.  |

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| 23<br>August | 1040          | Wasp with prey noted walking on the wall above Block 6. She climbed almost to the top of the wall then dropped to the ground where for about one minute she brushed her hind legs against her gaster. When she resumed prey carriage, she walked to the wall and began climbing. It appeared as if she were holding the nymph only with her hind legs since a considerable portion of the prey protruded out behind the end of her gaster. The wasp entered the 6W aperture but did not continue on into the interior of the block. Observations were discontinued at this point.   |
|              | several times | Random checks of the wall the remainder of the day found a few more wasps walking on the wall in the rambling manner as if they could not decide where the nest entrances were.   |
| 24<br>August | 1058          | Wasp with prey noted on the wall next to Block 8. She walked to the 8W aperture and left her nymph resting on the edge of the aperture while she went further inside. I prodded the nymph and noted that it was capable of walking a bit, but it made no attempts at continuous locomotion on its own nor did it jump or flee. In two or three minutes the wasp emerged and pounced on her prey whereupon they both fell to the ground below the 8W aperture. In a difficult-to-see maneuver, the wasp may have re-stung the nymph, but I could not discern this clearly. The wasp then walked to the wall with the prey, climbed and entered the 8W aperture carrying the prey with her this time. A trap jar was set. The wasp emerged in about two minutes, was captured in the trap, and then released.   |
|              | 1145          | Wasp was noted on the ground below the 7E aperture. She had a paralyzed nymph with her but was brushing her hind legs together back-and-forth. She then straddled the nymph and picked it up with her mandibles by the base of the antennae and began climbing the wall all the way to the top. At that point, the wasp with her prey dropped to the ground and walked eastward past Block 8 and went halfway toward the location of Block 9. She began climbing the wall again but only went a few inches and then turned and walked on the wall westward. She then dropped to the ground and then returned to climbing the wall about halfway between Blocks 8 and 9. At this point, the wasp resumed climbing the wall and ascended about three feet. I approached at this time for a closer look whereupon she dropped her nymph and flew away.   |
|              | 1205          | Wasp was noted on the ground about three feet in front of Block 7. She was carrying a nymph, and she was walking swiftly, periodically climbing up and dropping down from individual blades of grass as she progressed toward Block 8. Upon reaching the wall, she climbed and entered aperture 8W. In about one minute, she reappeared in the aperture but went back in and then out again. In the next approximately two minutes, I saw her repeat this enter and exit procedure three times. On her last exit, she dropped to the ground and walked westward toward Block 7. About halfway there, she encountered another <i>Liris</i> . A brief "wrestling match" ensued, the wasps separated, and one of them flew away. The remaining wasp searched for the nymph, and upon coming into contact, the nymph moved somewhat. At this point, the wasp appeared to sting the nymph twice although I could not discern the exact sting sites. The wasp then carried the nymph to the wall and climbed and entered aperture 7E. Unfortunately, I could not tell if this incident with the two <i>Liris</i> represented a successful theft of the prey or a successful defense against an interloper or neither. |

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| 24<br>August | 1240 | Wasp with prey was noted on the ground halfway between Blocks 7 and 8. She walked to Block 8, climbed, and entered aperture 8W. She exited briefly and then re-entered.   |
|              | 1300 | A paralyzed cricket, <i>Gryllus</i> , nymph was noted in the dirt in the 8W aperture. When prodded, the nymph moved a bit, but its locomotion was clearly impaired.   |
|              | 1302 | Wasp was noted flying in low with prey. She landed on the ground below Block 8 and then flew up an into aperture 9W.  |
|              | 1430 | Noted that a <i>Liris</i> had entered into a trap which had been set in the 9E aperture.  |
|              | 1440 | Noted a wasp with prey entering aperture 8E.  |
| 26<br>August | 1015 | Wasp with prey was noted walking on the wall between Blocks 5 and 6 going eastward. She walked past Block 6 while staying six inches or so above ground level. At Block 7, she started climbing and got about 18 inches above Block 7. She then dropped to the ground to the west of Block 7. She began climbing upward again and reached a height about four feet above Block 7. At this point, she dropped to the ground again and walked back to the wall three feet east of Block 7. She began climbing the wall for about sixteen inches then turned westward on the wall above Block 7 and then climbed upward and climbed four feet and then turned back east. At this point, I moved much closer and noted that she appeared to be gripping her prey only with her hind legs. As she walked eastward, she reached a point about four feet above Block 8. She then dropped to the ground about a foot from the wall and wandered around in this area a bit before setting the prey down. She regripped the nymph by the base of its antennae and again wandered around while going in a generally westward direction. At the level of Block 7, she began climbing the wall to the 7E aperture. Because of the loose dirt in this aperture, the wasp had difficulty, more or less “spinning her wheels”, as she tried to climb further into the opening. She retreated to the edge of the aperture and skirted this entrance then dropped to the ground again. At this point, she climbed again and upon reaching the bottom edge of the 7E aperture she paused and rested briefly. Here she left the nymph hanging at the bottom edge of the aperture while she climbed further into the opening out of sight. In a moment, the wasp came back out and retrieved the nymph, and then they both fell to the ground. At this time the wasp appeared to be resting the nymph ventrally just behind the head. I approached very close then, but the wasp then flew away. The entire above-described episode ended at 1035 hrs. |
|              | 1050 | For about the past ten minutes, a wasp was noted making its walk on the wall before finally entering the 9E aperture, then coming back out and dropping to the ground. She then climbed and dropped again and then climbed and entered the 9W aperture and then exited. At this point, the wasp released her nymph which retained enough neurological function to remain sitting on the vertical surface of the wall just outside the 9W aperture while the wasp walked up the wall eastward.   |
| 27<br>August | 1200 | For fifteen minutes, I watched one wasp walking on the wall with prey entering and exiting aperture 7W.   |
| 29<br>August | 1240 | Wasp was noted on the ground about two feet west of Block 7. She carried prey and crawled-hopped from one blade of grass to another before finally climbing and entering the 7E aperture.   |
|              | 1320 | Wasp was noted to fly in and land on the wall two feet west of Block 5. She then walked on the wall anywhere from six inches to twenty-four inches above ground level.  |

In sixteen encounters, *L. argentatus* was noted with prey, all cricket, *Gryllus*, nymphs about one-half inch (~1.3 cm) long. I would suggest that there is a strong indication that nest tending was occurring because I saw wasps carrying prey into the wall openings (apertures) on August 15, 23, 24 and 29 (herein abbreviated 8-15, 8-23, 8-24, and 8-29). Note from Table 1 that the wasp entering the 8W aperture on 24 August at 10:58 hours was seen exiting unencumbered from the same aperture two minutes later.

There also appears to be a habit for *L. argentatus* to set her prey down and continue with other tasks (e.g., brushing her gaster with her hind legs [8-24], checking inside a nest after setting the prey on the edge of the aperture [8-24]). In five instances, I saw what appeared to be prey abandonment (8-15, 8-22, 8-24 and 8-26), but I suspect that in three of these cases, I was the cause of it since the wasp flew away when I approached for a closer look. There may have been other times when the prey was abandoned anyway; I found two untended nymphs on the ground below the 9W aperture (8-22).

Regarding the mechanics of prey carriage, Bohart and Menke (1976) stated that the wasp uses her mandibles to grasp the cricket's antennae, a technique also attested to by O'Brien and Kurczewski (1982) and Kurczewski and Spofford (1987). These latter two papers further stated that the prey is carried venter upward. In my observations of *L. argentatus*, I also saw prey carriage with the wasps straddling the nymphs and grasping the bases of the antennae (8-22, 8-24 and 8-26). However, an exception to this was a wasp observed to retrieve her dropped nymph after it fell to the ground; and unless my eyes deceived me, she manipulated it into a dorsum upward position before she resumed carriage (8-22). This behavior is contrary to previously cited authors and is also at variance with Krombein and Gingras (1984) who stated that straddled venter upward is the "...normal method of prey carriage used by all wasps that transport their prey on the ground for then the legs of the prey would not catch on objects on the substrate and impede forward progress." I was not able to see if *L. argentatus* was using any of her legs to support the prey when using the mandibular method of transport.

The Steel Blue Cricket Hunter, *Chlorion aerarium* Patton, 1879, another sphecid wasp that provisions with *Gryllus* at my residential site, has been seen to manipulate a paralyzed cricket to a dorsum upward position before straddling it head-to-head and then continuing to transport along the ground (Lechner 2007).

In Evans' paper on the evolution of prey-carrying mechanisms in wasps (1962), it is stated that the most important factor to be considered in reference to prey carriage is the manner in which the prey is grasped by the wasp. Evans described the primitive condition as the one in which the wasp holds the prey with its mandibles while at a more advanced level the prey is held well back beneath the body by the legs. This leads to another interesting observation. I saw *L. argentatus* employing two different methods of prey carriage. Not only were they

using the mandibular method as previously mentioned, but they were also found holding their prey seemingly with the hind legs only since a good portion of the nymph's body protruded out behind the wasps' gaster. I noted this latter method only when the wasp was climbing the vertical face of the wall (8-23 and 8-26). The incident on 26 August is especially noteworthy since the wasp used both types of prey carriage on the same nymph!

The weak paralyzing powers of *Liris* venom have been commented upon frequently (Bohart and Menke 1976, Steiner 1976, O'Brien and Kurczewski 1982, Krombein and Gringas 1984, Kurczewski and Spofford 1987). I have found this to be the case at my study site also. *Gryllus* nymphs had the ability to move but did not do so voluntarily. When prodded, they could be induced to walk very slightly (8-24). One nymph was capable of sitting in a normal posture on the vertical surface of the wall outside the 9W aperture when left there by the wasp (8-26).

Steiner (1976) conducted extensive sting pattern studies on three species of *Liris* (*L. argentata*, *L. nigra*, and *L. aequalis*) under laboratory conditions. I noted what appeared to be stinging behavior by three *L. argentatus* although in these cases the action would constitute re-stinging since the nymphs were already paralyzed. I could not, of course, verify Steiner's sting patterns. Such degree of detail would require close-up slow motion camera footage. A possible re-stinging of a retrieved nymph (8-24) was difficult to see. That same day, a wasp appeared to re-sting her nymph twice. In a re-stinging noted on 26 August, it appeared that the wasp targeted the area just posterior to the nymph's head ventrally.

In the most frequently observed behavior pattern, *L. argentatus* acted as if she could not find the aperture to her nest. Many times, they were seen walking back and forth on the wall, climbing upwards, often releasing their grip and descending to the ground (such maneuvers did not appear to be flight but rather a free fall), climbing up the wall again, sometimes entering and exiting apertures respectively. These journeys reminded me of aimless wandering as if the wasps were confused. Kurczewski and Spofford (1987) made note of *L. argentatus* making small circles in the vicinity of her nest entrance and climbing low vegetation as if to orient, but they reported nothing to the extent of the meanderings that I saw. As an example, I watched one wasp for twenty minutes on her march around the wall (8-26). Her path is approximately delineated on the north lot line retaining wall (Figure 1).

Finally, do *L. argentatus* steal nymphs from each other? I refer to the incident of 24 August (12:05 hours) when one wasp with prey encountered another wasp without prey. There was a brief struggle after which one of the wasps took flight. The remaining wasp retrieved the nymph and carried it into the 7E aperture. A successful theft or a heroic defense? Which wasp was which, I could not tell.

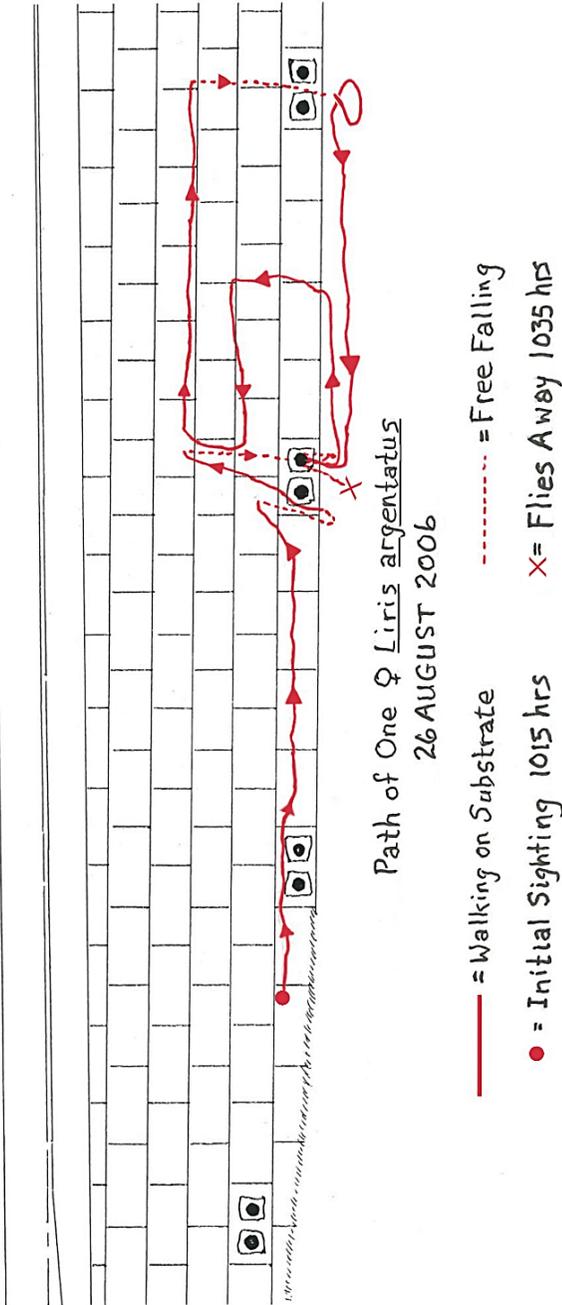


Figure 1. Perambulations and other behaviors of a *L. argentatus* female observed for 20 minutes on 26 August 2006. Scale of concrete blocks: 8" (or 20.3 cm) x 16" (or 40.6 cm).

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