

Notes on the biology of the wasp, *Chalybion spinolae* (Hymenoptera: Sphecidae), an obligatory predator of *Latrodectus* (Araneae: Theridiidae) spiders in South Africa

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Some aspects of the biology of the wasp *Chalybion spinolae* are documented. This includes behaviour relating to life cycles, nesting, mating, oviposition and prey interaction of this wasp. The physical appearance of the wasps and their prey are described and some measurements are given. The prey of *C. spinolae* are two species of spiders, *Latrodectus indistinctus* and *Latrodectus geometricus* (Araneae: Theridiidae). The observations spanned a period of 5 years, and involved approximately 200 wasp nests. This study serves to provide more observational information about the biology of the wasp and its predatory behaviour.

Keywords: *Chalybion*; *Latrodectus*; Sphecidae; Theridiidae; spider; wasp

Introduction

On a farm in the Western Cape Province, South Africa, the first author discovered a large number of paralysed button spiders *Latrodectus geometricus* (Koch, 1841) and *Latrodectus indistinctus* (Cambridge, 1904) (Theridiidae) in an old abandoned cowshed. This alerted him to the possible presence of predatory wasps. The southern African subregion has at least four families of wasps known to parasitize spiders. The Eurytomidae and Ichneumonidae parasitize spider egg sacs, whereas the Pompilidae are known as the spider-hunting wasps and members of Sphecidae are known as the mud-dauber wasps. Subsequent observations on the farm revealed the existence of three species of predatory wasps in the area. These wasps were identified to be in the Sphecidae family and were further identified as *Sceliphron spirifex* (Linnaeus, 1758), a mud-dauber wasp, *Chalybion tibiale* (Fabricius, 1781) and *Chalybion spinolae* (Lepelletier, 1845), both water-carrier wasps. However, *C. spinolae* was the only wasp provisioning its nest cells with spiders belonging exclusively to the spider genus *Latrodectus*. It was therefore the focus for this study. The species of wasp, *C. spinolae*, is known from South Africa, Ethiopia, Tanzania and Democratic Republic of Congo (WaspWeb 2012).

Gess et al. (1982) reported on some aspects of the behaviour of *C. (Hemichalybion) spinolae* in the Eastern Cape. Their study was based on the observations of only a small sample of *Latrodectus* nests. Their study revealed that species of *Chalybion* and *Sceliphron*, both of the Sphecidae, construct nests raised above

ground. *Chalybion* species excavate cells within vertical structures such as earth banks and modify pre-existing cavities, whereas *Sceliphron* species build free aerial mud cells (Gess et al. 1982). Both genera are exclusively spider hunters (Behart and Menle 1976; Coville 1987).

This paper presents observations on *C. spinolae*, over a 5-year period (1983–1987). It spans the period from the first observation of the wasp colony until the colony was killed by a fungus infection. It confirms many of the observations made by Gess et al. (1982) but also presents new information about the biology and behaviour of the wasp. The two prey spider species involved were the cosmopolitan *L. geometricus*, which occurs worldwide, and the endemic species *L. indistinctus*, which are known from southwest and north-west regions of the Western and Northern Cape Provinces of South Africa and the coastal areas of Namibia (Lotz 1994).

Material and methods

Study site

All the observations were made on the farm *Joostenbergkloof* (33°46' S, 18°46' E), 13 km from Durbanville en route to *Agter Paarl* (South Africa, Western Cape Province). The observations started in October 1983 and ended in May 1987. The study was terminated in May 1987 because the entire roof of the shed containing the wasp colony collapsed. This resulted in the nests being exposed to the elements, which allowed fungus to invade the nests and caused the death of the colony. The shed in which the observations were made had previously been used as a shelter for cattle. It had a corrugated iron roof and two sections with feeding troughs. The walls were constructed of hand-made soft clay bricks consisting of about 90% sand and 10% clay. The structure was built approximately 70–80 years before the study period.

There was tall grass (> 60 cm in height) surrounding the shed. In summer, it became dry and was trampled by grazing cattle. Adjacent to the grass area, there were large stubble-covered fields that were used for wheat production. There were also extensive vineyards nearby. There was a small dam, about 78 m from the shed, which was filled during winter rainfall, and retained a supply of water during the summer.

The locality provided a unique triad of circumstances, i.e. (1) the shed provided protection and a suitable substrate for nest construction, (2) there was an abundance of food supply for the developing larvae of *C. spinolae*, and (3) the dam was in close proximity, which provided a water supply for the female wasps to make the necessary mud pellets for plastering and nest closure activities.

Methods

Most of the results were based on non-invasive purely observational data. However, during the breeding season (October 1983 to February 1984) the cells that were provisioned and sealed were marked with bright yellow non-toxic poster paint. This marking with paint made it easy to see and count cells that had been opened by the emerging wasps. The marking was done on 14 November 1983.

All length measurements given were taken using a metal slide ruler (Mitutoyo, Kawasaki, Japan). The mass measurements were taken using a medical laboratory

balance of unknown make and within 12 hours of collection. All temperatures were recorded using a Bailey thermocouple thermometer. A stopwatch was used to time some of the aspects of the wasp's behaviour.

Results

General observations of the wasp colony showed that the flight season of *C. spinolae*, started in October and ended in May. The females had an average weight of 282 mg ($n = 4$) and the males weighed on average c.90 mg ($n = 2$).

Emergence of young females and mating

The emerging young female wasps used their mandibles to break away the soil around the rim of the mud plug of the nest cell. No soil particles were seen on the outside of the cell. Just before the females exited the cell, they made sweeping movements with their antennae outside the cell. This whole process of emergence took about 1 hour. The emerging young female wasps made a buzzing noise while still inside the cell. The males were observed walking around unopened cells, which suggested that they could probably detect these vibrations before the female broke through the mud plug. It was also suggested that the females had a unique and specific frequency, which the males recognized. Males were observed moving around, periodically flicking their wings, but always returning to the spot where the females were going to emerge. They would palpate the area around the opening being made by the female with one or both antennae, sometimes probing into the opening. On one or two occasions, the males made darting movements at the emerging heads of the females. At times, the males would fly away, only to return again after a short period. Therefore, the males were always in the vicinity of emerging females so they could attempt to copulate with the females as soon as they emerged.

Copulation usually took place just outside the cells. The smaller male grasped the larger female before her wings could expand as she emerged. The male would grasp the female from above and encircle his legs around her body, with her dorsum facing his ventral surface (Figure 1A). Copulation lasted about 20 seconds, with the female making a high-pitched sound. When copulation ended, both wasps fell to the ground, separated and flew off. Only two occasions of successful copulation were recorded. Most mating encounters were unsuccessful. It appeared that unless the male ambushed the female before the female became fully airborne, the chance of successful copulation was slight.

New nest cell construction

Female wasps often use old nest cells of others, which they rebuilt into new cells. They began by removing all the old spider remnants and other debris. They followed this by placing one mandible inside and one outside the rim of the opening. They then rotated around the opening, biting and gouging out a circular area leaving a rim sloping externally at an angle. The marks left by the mandibles were clearly seen. The opening was enlarged (to a diameter of about 9.5–12 mm) leaving a slight neck, which was a little narrower than the internal cavity. It was this slightly narrowed region that sometimes caused an obstruction when the wasp inserted a large spider into the cell.

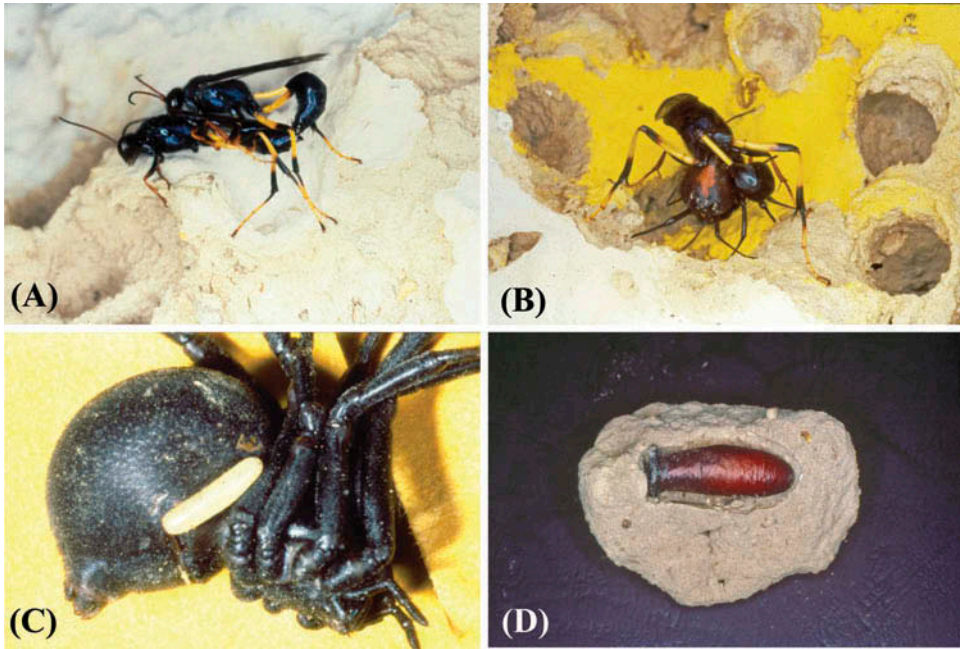


Figure 1. (A) *Chalybion spinolae* copulating; (B) *Chalybion spinolae* carrying a spider into a nest; (C) *Chalybion spinolae* larva feeding on *Latrodectus* prey; (D) pupal casing of *Chalybion spinolae*.

In these cases, it forced the wasp to work a bit harder to insert the spider. The cell was moulded and construction was completed using mud pellets.

It was suggested that the internal nest temperatures were lower than the external environment of the nest. However, the data were incomplete and further investigations into nest temperatures are needed.

Mud pellet formation

Mud pellets are used by the wasps for cell construction as described above, and to line the inside of the cells. After gathering the moistened clay in their mandibles, the females transported it to where it was needed. The making of a pellet took only 8–13 seconds. The average number of pellets made per single visit to the dam was 12 ($n = 14$). On return from the dam with the pellet, the wasp entered the cell and used the tarsal claw to grasp the open edge of the cell. The wasp often made a high-pitched buzzing noise while applying the mud lining. It was speculated that these sound waves may have helped to spread the clay evenly and fix it firmly to the inside of the cavity. The sound was audible from about 2.4 m away and appeared to be generated by gaster tergites and was transmitted to the entire body. The wings also seemed to vibrate, although the vibrations could not be felt when the wings were touched. The vibrations could be felt in the hind limbs. Touching the wings or the hind limbs did not appear to upset the wasp. However, when the gaster was touched, the wasp stopped abruptly, backed out of the cell and very often flew off, clearly upset by the contact.

Water collecting

The wasps used a thickly matted plant surface near the water's edge as an access point to the water. The plant material was sufficient to support the wasp and enabled them to access the water. It usually took 6–12 seconds for the wasp to navigate to water. The actual drinking time recorded was about 10–12 seconds. Total time it took for the wasp to leave and return to the shed was approximately 60–90 seconds, depending on the wind.

The spider prey of C. spinolae

The prey of *C. spinolae* was exclusively two species of Theridiid spiders, identified as *L. geometricus* and *L. indistinctus*. The same spider species were also collected from *C. spinolae* nests near Grahamstown by Gess et al. (1982). Other members of the wasp genus *Chalybion* have been recorded to have as many as 42 host species (Landes et al. 1987).

Latrodectus geometricus (the brown button spider) is a cosmopolitan species, common and widespread throughout southern Africa (Lotz 1994). The species is known to have a wide colour variation, ranging from pale white to grey, from brown to almost jet black (Cambridge 1902; Smithers 1944; Lotz 1994). In pale-coloured specimens, there were red geometric markings covering the dorsum of the abdomen with a characteristic bright orange–red hour-glass pattern on the ventral surface. The full spectrum of colour variation as quoted above was encountered during this study. Their webs are usually found on the outside of buildings, window ledges, under gutters, inside houses, under chairs, in post boxes and under loose bark still adhering to old trees. The nest cavity was constructed of strong silken webbing with a main and a secondary entrance. In front of the entrance there was a network of strong catching threads (Lamoral 1968).

Latrodectus indistinctus (the Cape black button spider) is known from the southwest and northwest regions of the Western and Northern Cape Provinces of South Africa and the coastal areas of Namibia (Smithers 1939; Lotz 1994). It is recognized by the black body and legs with only a red spot caudally on the dorsal side of the abdomen. In the study area the nests of *L. indistinctus* were usually found at the base of the stems near the ground of *Galenia africana* L. (Aizoaceae) (*kraalbos*). *Galenia africana* is a short to medium-sized, deeper rooting, non-succulent shrub. The nests were deep in the shrub and were often not visible. In addition, bits of dead plant material dropped onto the surface of the nest, which provided additional camouflage. Other shrubs where nests were found were *Eriocephalus* sp. (Asteraceae) (*kapokbos*), low-growing *Protea* spp. (Proteaceae) and certain *Restio* spp. (Restionaceae).

The webs and nests of *L. indistinctus* consisted of sac-like cavities that were made with strong silken threads and a tunnel running externally with catching threads at the entrance. There were non-sticky aerial threads anchored to grass stems or other plant material that seemed to act as an alarm system. There were sticky vertical ground threads that were anchored to objects on the ground. The catching snare threads were found as far away as 1 m from the nest entrance (Lamoral 1968).

Location of the spider

The female wasps seem to have an ability to locate the nests of the spiders upon which they prey. On a hunting trip, the wasps usually returned with a paralysed spider,

within 10–30 min. These spider weighed between 70 and 700 mg. The nests of spiders were well camouflaged.

Transporting the spider

The wasps carried the larger spiders upside down with the cephalothorax of the spider facing the front of the wasp. The ventral surface of the spider faced the ventral surface of the wasp (Figure 1B) and the wasp grasped the spider by its pedipalpi or one of the front legs using its mandibles. The wasp's first and second pair of legs were used to encircle the legs of the spider. Due to the paralysis induced by the wasp, the spider's legs were easily folded back acutely alongside the abdomen. This positioning of the legs of the spider helped the wasp to deposit large spiders into the nest cells. Had the legs remained extended, the insertion would have been extremely difficult. No observations were made on how small immature spiders were transported.

The wasps encountered difficulty in remaining airborne while transporting heavy prey. The weight of the spider forced the wasp down. As a result the transportation of the spider took place for short distances over the ground and small obstacles. If the wasps encountered a firm grass stem, they would climb to the top and become airborne again for a short distance. The wasps repeated the procedure over and over again until they had returned to the nest in the shed. Spiders were collected for weighing either by extracting them from the nest cells or by collection of spiders dropped by the wasps into the troughs below the nests. In one instance, a large female wasp weighing 385.2 mg carried a spider (*L. indistinctus*) with a weight of over 700 mg. The weights of the spiders caught by the wasps over the sample period were:

L. indistinctus (adults) an average 388.1 ± 10.01 mg ($n = 114$)

L. indistinctus (juveniles) an average of 94.2 ± 8.12 mg ($n = 28$)

L. geometrius (adults) an average of 210.7 ± 16.54 mg ($n = 13$) and

L. geometrius (juveniles) an average of 50.5 ± 13.24 mg ($n = 7$).

Once inside the shed, the wasp would climb up the vertical wall and locate her nest cell. Should she fail to locate the cell immediately, she would continue to search, dragging the spider around with her. Sometimes the female would become airborne again and make a more accurate landing closer to her own nest cell.

Oviposition and insertion of the spider

Once at the nest cell, the wasp stabilized the spider. The wasp then folded her gaster under her legs (either on the left or right side). Once a suitable area on the anterior part of the spider's abdomen was found, the wasp proceeded to oviposit. During oviposition, the wasp remained motionless and the only movement seen was propulsive contraction of the gaster until an egg was deposited. Oviposition took between 30 and 40 seconds to complete.

The egg was small, sausage-shaped and off-white in colour. The egg ranged in length from 3.40 to 3.92 mm (3.59 ± 0.05 mm) and in width from 0.78 to 1.00 mm (0.90 ± 0.20 mm) ($n = 13$). The average weight of an egg was 2.95 ± 0.15 mg ($n = 4$). The eggs took about 4 days to hatch into larvae.

The wasps always deposited the eggs in more or less the same position. It did not appear as if prey size was important in triggering oviposition. If the wasp had difficulty in positioning a spider before oviposition, she aborted the attempt. The wasp would then repeat the process upon the next newly captured spider. On one occasion two eggs were deposited, one on each side of the spider's abdomen. Oviposition always took place outside the nest cell.

When oviposition was successful, the wasp would insert the spider into the nest cell. If the prey was small, the wasp simply entered the nest cell with the spider. In the cases where the spiders were larger and the opening could not accommodate both spider and wasp, the wasp resorted to a technique of grasp and let go movements, pushing the spider slowly into the cell. Sometimes the abdomen of a large spider would be blocked by an obstruction. The wasp would then use her head to push against the abdomen of the spider (even producing a temporary dent in the skin) while using her powerful hind legs to provide the counter-thrust. Other times, when a spider became stuck, the wasp inserted her mandibles into the groove where the abdomen of the spider touched the rim of the opening and made a buzzing sound. The wasp continued to move around the circumference systematically, buzzing continuously until the spider was inserted. It was suggested that these vibrations caused by the buzzing aided the insertion.

After insertion of the spider, the wasp closed the cell. This process was recorded on two separate occasions. It took 12 (flying distance of 1.87 km) and 16 (2.49 km) trips to the dam, with total construction times of 68 min and 140 min, respectively.

***Chalybion spinolae* development**

Larval development

The small wasp larvae were legless and remained attached to the spider's abdomen where the eggs were deposited (Figure 1C). The larvae perforated the spider's skin and fed on the spider's tissues. It was observed that if the larva fell off the spider before it had attained a length of at least 1.5 mm, it did not survive. At this early stage (i.e. before 1.5 mm length), the larvae were only capable of corkscrew-like movements. It appeared that it was unable to reattach itself and feed. When the larvae were about 6.25 mm long the mandibles were clearly visible, and they were tightly clamped to the spider's abdomen. Continuous peristaltic movements in the larvae were observed during feeding. Within a week, after having attained a body length of 10 mm, the mandibles of larvae had become very effective cutting and devouring tools, leaving only minute amounts of spider tissue.

Pupa development

A *C. spinolae* larva (weight = 588.8 mg) was removed from the nest and pupal development was observed. Pupal development started when the larva began to encase itself in a cocoon of pale yellow threads. This stage took about 12 hours, after which it was totally enclosed in a whitish papery capsule. The pupa was still visible through the silk. After about another 8 hours the silken mesh became imbedded in a 'matrix' fluid closing all the mesh openings. At this stage the pupal case was a dull yellow. After another 12 hours, the case had darkened to a light

brown colour. When an additional 24 hours had elapsed, the pupal case had become a dark brown with the larva barely visible inside.

The internal surface of the pupal case had a smooth highly polished appearance (Figure 1D). The thickness of the pupal wall was about 0.08 mm. The cephalic end of the pupal case was also perforated by hundreds of microscopic holes similar to the micropyles of insect eggs.

The emerging adult wasp used its mandibles to bite out a circular tunnel through the mud plug of the cell, allowing it to escape. This opening was somewhat smaller than the original size of the mud plug and varied in size depending on whether the wasp was a male or female (the larger sex) and also on the wasp's nutritional state. The loosened mud, the remnants of the pupal case and spider were left behind in the cell.

Observations from 24 November to 27 December in 1984 showed that at least 190 individuals emerged during this 32-day period. However, one wasp emerged from a pupal case after about 325 days.

Observations of operation of the hind legs of the wasp

The powerful hind legs of these wasps were truly remarkable pieces of mechanical engineering, providing an unbelievable range of movements. The claws provided a phenomenal grip on the soil particles allowing the wasp's body to be held in awkward positions while the rest of the body and legs were occupied by other activities. For example, at the same time as the right leg may undergo a rotary movement with flexion at the femoral-coxal joint, the femoral-tibial joint may be acutely flexed and the left leg may be totally extended at all the joints. The range of movements possible is reminiscent of the individual eye movements of a chameleon. Most of the wasps' activities take place in a sheer vertical plane. From this, it was easy to comprehend the necessity of this diverse and vast range of movements, as well as the mechanisms initiating and executing them.

Natural enemies of C. spinolae

The wasp females were attacked by predators only twice. On one occasion, it appeared that the wasp was attacked by a bird, which resulted in an injury to the gaster. In the other incident, the wasp was caught in the orb-web of a spider (Araneidae: *Argiope* sp.). These observations suggested that these wasp females seldom succumbed to predators.

Conclusion

Much still remains unknown about many of the Sphecidae species and their prey. This is the third paper that shows the species preying mainly on *Latrodectus* spp.

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References

- Behart RM, Menle AS. 1976. Sphecid wasps of the world: a generic revision. Berkley (CA): University of California Press.
- Cambridge OP. 1902. Description on some new species, and characters of three new genera, of Araneidae from South Africa. *Ann S Afr Mus.* 3:143–165.
- Coville RE. 1987. Spider-hunting sphecid wasps. In: Nentwig W, editor. *Ecophysiology of spiders*. Berlin Heidelberg (Germany): Springer-Verlag.
- Gess FW, Gess SK, Weaving AJS. 1982. Some aspects of the ethology of *Chalybion (Hemichalybion) spinolae* (Lepelletier) (Hymenoptera: Sphecidae: Sphecinae) in the Eastern Cape Province of South Africa. *Ann Cape Prov Mus.* 14:139–149.
- Lamoral BH. 1968. On the nest structure of *Latrodectus* in South Africa, and some observations on the body colouration of *L. geometricus* (Araneae: Theridiidae). *Ann Natal Mus.* 20:1–14.
- Landes DA, Obin MS, Cady AB, Hunt JH. 1987. Seasonal and latitudinal variation in spider prey of the mud dauber *Chalybion californicum* (Hymenoptera, Sphecidae). *J Arachnol.* 15:249–256.
- Lotz L. 1994. Revision of the genus *Latrodectus* (Araneae: Theridiidae) in Africa. *Navors nas Mus Bloemfontein.* 10:1–60.
- Smithers RHN. 1939. Notes on the distribution of the “Knopiespinnekop” (*Latrodectus indistinctus*). *S Afr Med J.* 13:33–34.
- Smithers RHN. 1944. Contributions to our knowledge of the genus *Latrodectus* (Araneae) in South Africa. *Ann S Afr Mus.* 36:263–313.
- Waspweb. [Cited 2012 Aug 1] Available from: www.waspweb.com.