Research Article

Notes on nesting behaviour and larval development of *Ammophila gracilis* Lepeletier de Saint Fargeau (Hymenoptera: Sphecidae)

Notas sobre el comportamiento de anidación y el desarrollo larvario de *Ammophila gracilis* Lepeletier de Saint Fargeau (Hymenoptera: Sphecidae)

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Abstract. Notes on nesting behaviour of *Ammophila gracilis* Lepeletier de Saint Fargeau, 1845 are provided, based on observations carried out in Rio de Janeiro state, southeastern Brazil, in an area covered with a typical vegetation type that grows in sandy soil of marine origin in coastalplains. Description of stereotyped motors patterns related to nesting behaviour are emphasized. Observations on larval development are also provided.

Key words: Ammophilinae, Ammophilini, biology, immature, solitary wasp.

Resumen. Se proporcionan notas sobre el comportamiento de anidación de *Anunophila gracilis* Lepeletier de Saint Fargeau, 1845, en base a observaciones realizadas en el estado de Río de Janeiro, sureste de Brasil, en un área cubierta con un tipo de vegetación que crece en suelos arenosos de origen marino en planicies costeras. Se enfatiza la descripción de los patrones de motores estereotipados relacionados con el comportamiento de anidamiento. También se proporcionan observaciones sobre el desarrollo larvario.

Palabras clave: Ammophilinae, Ammophilini, biología, inmaduro, avispa solitaria.

Introduction

The genus *Ammophila* Kirby, 1798 contains 240 species (Pulawski 2020) of groundnesting caterpillar-hunting wasps widespread around the world (Bohart and Menke 1976). Neotropical region is relatively poor in species of *Ammophila* (Amarante 2002) compared with others biogeographic regions. Only ten species have been cited in South America, the most common being *Ammophila gracilis* Lepeletier de Saint Fargeau, 1845, that occurs throughout the eastern region of the continent (Menke 2004). In Brazil, *A. gracilis* is a very conspicuous and widely distributed species, but even so, it is still little known (but see Gaimari and Martins 1996). In present paper, further biological notes on this species are provided.

Materials

Study area. The fieldwork was carried out at Restinga de Barra de Maricá (city of Maricá, Rio de Janeiro state), an area covered with restinga, a typical vegetation type that grows in

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sandy soil of marine origin in coastal-plain; this vegetation type is included in the Atlantic Forest biome. The studied area is partially protected inside the Área de Proteção Ambiental de Maricá (22°52′ to 22°54′S and 42°48′ to 42°54′W), since April 1984. Maricá region climate was classified as warm tropical, super humid, with sub drought periods (Nimer 1972). Pereira *et al.* (2001) provided the following meteorological dates collected in the neighbouring city of Niterói, from 1931 to 1968 (Departamento Nacional de Meteorologia): annual average temperature 23.2°C; the warmest month is February, with average of the maximum temperature of 32.2°C; the coldest month is July, with 69.2% occurring from November to April.

Results

Nesting habitat and annual occurrence pattern. *A. gracilis* is a common species in the studied area. Nesting females were observed in every month of the year. The nesting density was clearly greater in November and December, a hot and rainy period of the year. The nesting females were observed in sun-exposed areas, without low vegetation nearby and soil composed by compacted coarse sand, usually mixed with clay. Females nest solitarily.

Nest provision. Nests with one (n = 4) and with three caterpillars (n = 1) were found. Females laid their eggs on lateral portion of second or third abdominal segment of first item prey stored in the nest.

Structure of the nest. Nest is L-shaped, with a principal cylindrical tunnel perpendicular to the soil surface, 0.6 - 0.7 cm in diameter (n = 3) and 3.2 - 5.0 cm (n = 4) in deep, and a smaller tunnel that parts perpendicularly from the bottom of the principal cannel, with 1.8 - 2.0 cm in length (n = 2). Prey items are stored in the bottom of the smaller tunnel.

Nest excavation. Several nests in distinct phases of the nesting cycle were observed, but the complete excavation of a nest was observed only one time. Based principally on this complete observation, it is possible recognise three phases of excavation, as follows. (1) In first phase, female digs in several directions, randomly throwing the earth aside with the mandibles; she does not fly carrying the earth, and apparently does not use her legs to dig, only the mandibles. (2) In second phase, after a few minutes from excavation started, female begins to carry the earth in flight seized with the mandibles and apparently with the first leg pair; but the number of distinct trajectories of flights initially varies greatly, being gradually reduced. (3) In third phase, female travelled only one trajectory to discard the earth. Discarding site was about 35 cm from the nest entrance. The earth did not form a mound near the nest. The position in which the female entered at the nest is always opposed to the cell position, probably the definitive trajectory of earth discard is defined when the female defines the position of the nest's cell. Total time of the complete excavation was 40 minutes.

Temporary closure of the nest. The females always temporarily close the nest soon after completing the excavation and after stocking it with a prey item. First step of the temporarily close of the nest is to select carefully a stone with of suitable size to block the nest entrance. Females examine several little stones at nest surroundings, seizing it with the mandibles. Sometimes they grab stones with the mandibles and repeatedly raise and lower the head, as if evaluating its weight; commonly they promptly rejected small stones. After blocking the nest entrance with the stone, the females scuff sand over the nest, throwing it backward

under her body with very quickly movements of the first leg pair. The legs movement is so quickly that it is not possible to distinguish whether it is alternated or synchronic.

Inspection of the nest. After temporarily closing the nest, the females fly away in search for caterpillars. During this step of the nesting cycle, frequently the females return to the nesting site to check the nest and its surroundings. In two occasions females open the temporarily closed nests to check them and subsequently close the opening again. Both of these nests had not been provisioned and the females remained a long time away, possibly the females were in searching for prey items and were unsuccessful.

Definitive closure of the nests. The behaviour of definitively nest closing was observed four times in detail from the beginning to the end. The wasp firstly selects a stone, in the same way she makes when temporarily close the nest; sometimes the female uses the same stone before used to temporarily close the nest. However, the stone is put deeper inside the nest. Thus, the layer of sands and debris put in the principal tunnel is greater. After that, a layer of small stones is added, where two observed females used four stones, and another one placed 14. Thereafter, the female put sand over the nest, which was threw beneath her body with the first leg pair as previously described. Sometimes the female releases the soil with the mandibles, at the same time that threw sand backward to nest direction. One female, about 10 minutes after placed the stones, returned to working in the closing of the nest. She spent eight minutes putting sand and stones over the nest. Once she removed the soil from the nest, put one stone and started to put sand again. Sometimes the female compacted with a stone in the mandibles the sand over the nest entrance. The final phase of nest closing consists of putting objects, as small stones and fragments of wood over the nest entrance. This behaviour, which could be interpreted as camouflaging the nest, spent approximately two minutes. The objects used in this stage usually are selected at greater distance from the nest. The total time spend in the nest closing was 10 to 12 minutes. During the closing of the nest wasp frequently chasing away ants that pass nearby.

Prey paralysis. After the larvae have been paralysed, they are still able of expelling faeces and to do very shorts and fast movements with the body. Usually it is not necessary to sting the prey during the prey transport; only once has this behaviour been observed. To sting the caterpillar, the female bends the gaster and reaches the ventral portion of its prey, which remains grasped with the mandibles.

Prey transport. Usually the female transports the caterpillar exclusively walking on the ground, although she often flaps her wings as she walks, apparently to help propel her body forward. During the transport, the female grasps the prey near the thorax and holds her body with the first leg pair; the ventral portion of the caterpillar always faces upward. Just in one of the many times that prey transport was observed, the female travelled part of the way to the nests in flight, however, the prey observed on this occasion was exceptionally small and this unusual behaviour probably was related to this fact.

Carrying-prey females in difficulties to found their nest were observed several times. One female in this situation walked in circles with her caterpillar for a few more than an hour and then was collected. It is interesting that the disorientation of finding the nest after hunting a prey items can be a cause of unsuccessful nesting and even egg mortality.

Adult feeding. The females were commonly observed feeding on *Borreria* sp. (Rubiaceae), a small herbaceous plant very abundant near the nesting sites.

Larval development. Five prey specimens bearing wasp's egg were maintained in laboratory. Two of these eggs did not hatch for undetected cause, the other eggs hatched

in the second day after the oviposition. Larvae remained partially inserted at prey's body up to almost the ending of the feeding phase. It is possible to observe by transparency internal wave movements of the larva, probably related to suction. The caterpillar could remain alive up to the second day of the larval development. In one of the observed cases, the caterpillar died before the wasp's egg hatches, even so the larva reached the maturity, suggesting that the prey did not to be necessarily alive to the larva of the wasp develop on it. As the wasp's larva grows the body of the prey gradually wilt from posterior portion to the anterior portion of the body. At the end of the third day of development only a small part of the anterior portion of the caterpillar's body remains. Then the larva abandons the prey's body interior and begins to consume it externally, remaining just the cephalic capsule at the developmental end. The feeding phase lasted three days, after this period the larva spent about two days spinning the silken cocoon.

Discussion

Care should be taken when studying *A. gracilis*, as its great morphological variability and wide geographic distribution provide evidence that it may actually be a complex of several distinct biological entities grouped under the same taxon. Therefore, comparison of biological parameters between different populations of *A. gracilis* can be useful to help clarify its complex taxonomy. The nesting behaviour of the population of *A. gracilis* studied by Gaimari and Martins (1996) differs from the population here studied at least in following noticeable aspects: (1) the nests are shorter and (2) provisioned with one or two caterpillars, (3) the females tend to nest gregariously and (4) are absent during the rainy season of October through January. These differences can be attributed to ecological characteristics, but can also be the result of genetically defined biological characteristics. In fact, the population studied by Gaimari and Martins (1996) occupied a different habitat, with apparently harder soil and the population suffered a strong pressure of parasitism. However, only the sum of comparative studies on morphology and behaviour carried out over the wide geographical range of *A. gracilis* can answer questions about the great variability attributed to this species.

Comparing *A. gracilis* with other species of the genus, for example, using the papers of Evans (1959), Powell (1964) and Weaving (1989a, b), we observed that it resembles several other species and has behavioural patterns considered to be more specialized in genus, such as discarding the earth from the nest in flight and providing the nest with more than one smaller prey, which can be transported in flight. It seems interesting to highlight the initial excavation behaviour of the nest, an aspect neglected in other papers. At this time, the female behaves like other ground-nesting species of Sphecidae, for example, *Penepodium luteipenne* (Fabricius, 1804) (Buys 2012). Then its behaviour gradually becomes specialized, and she flies to discard the excavated earth. It is certain that this initial phase can be interpreted not as excavation of the nest, but as part of the behaviour of choice of the nesting site. Anyway, it looks like an aspect that deserves attention in future studies.

Information on larval development of *Ammophila* or other sphecid wasps were very scarce. Grandi (1961) provided a classical sequence of illustration of a larva of the European *Ammophila heydeni* Dahlbom, 1845 consuming her caterpillar, the prey body of this species gradually wilt, similarly to the observed during the development of *A. gracilis*. The larval development of the related *Eremnophila binodis* (Fabricius, 1798), as observed by Buys (2009b), was somewhat different, in this species the egg was put more posteriorly on the prey body, and the wasp's larva abandon the prey body earlier and consume it externally. Different from the observed in *A. gracilis*, other sphecid need prey alive in the initial phase of the larval development (e.g., Buys 2006, 2009a,).

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