ECOLOGY, BEHAVIOR AND BIONOMICS

Comparative Study of the Nesting Behaviour of *Tachysphex inconspicuus* (Kirby) (Hymenoptera: Crabronidae) in Two Locations in Southeast Brazil

Sandor C. Buys

Depto. Entomologia, Museu Nacional, Univ. Federal do Rio de Janeiro, Quinta da Boa Vista, São Cristóvão, 20.940-040 Rio de Janeiro, RJ, sbuys@biologia.ufrj.br

Neotropical Entomology 36(3):327-330 (2007)

Estudo Comparativo do Comportamento de Nidificação de *Tachysphex inconspicuus* (Kirby) (Hymenoptera: Crabronidae) em Dois Locais do Sudeste do Brasil

RESUMO - O comportamento de nidificação da vespa solitária *Tachysphex inconspicuus* (Kirby) foi comparativamente estudado com base em observações feitas em dois locais ambientalmente distintos do Sudeste do Brasil: porções superiores de duas praias arenosas e uma estrada de terra em uma área florestada. Os padrões motores relacionados à construção dos ninhos foram similares em todas as vespas observadas, mas algumas características comportamentais, que foram diferentes entre as vespas observadas nos dois ambientes, parecem ser delimitadas por fatores ecológicos. *T. inconspicuus* pode ser diferenciada comportamentalmente de várias outras espécies do gênero pela seguinte combinação de características: fechar temporariamente o ninho durante seu aprovisionamento; não deixar a areia escavada formar um monte em frente da entrada do ninho, construir ninhos unicelulares, aprovisionar o ninho com baratas. Além disso, as fêmeas de *T. inscospicuus* usam suas pernas traseiras de uma forma peculiar para manipular as presas que as permite associar o uso das mandíbulas no transporte da presa com a possibilidade de escavar o fecho temporário e entrar no ninho sem largar a presa. *Chorisoneura lopesi* Albuquerque, *C. excelsa* Albuquerque & Silva e uma espécies não identificada de *Riatia* (Blattodea: Blatellidae) foram encontradas como presas e *Amobia floridensis* (Towsend) (Diptera: Sarcophagidae) como parasitóide de *T. insconspicuus*.

PALAVRAS-CHAVE: *Amobia*, biologia, etologia, parasitóide

ABSTRACT - The nesting behaviour of the solitary wasp *Tachysphex inconspicuus* (Kirby) was comparatively studied based on observations made in two environmentally distinct locations in southeast Brazil: upper portions of two sandy beaches and a dirt road in a forested area. Motor patterns related to nest construction were similar in all observed wasps, but some behavioural features, which were different among the observed wasps in the two environments, seem to be constrained by ecological factors. *T. inconspicuus* can be behaviourally differentiated from several other species of the genus by the following combination of features: they close the nest temporarily during its provision, do not let the excavated sand to form into a mound in front of the nest entrance, construct unicellular nests, and provision the nest with cockroaches. Moreover, females *T. inscospicuus* use their hind legs in a peculiar way to manipulate the prey, which allows them to associate the use of the mandibles in prey transport with the possibility of excavating the temporary plug and entering the nest without releasing the prey. *Chorisoneura lopesi* Albuquerque, *C. excelsa* Albuquerque & Silva, and unidentified species of *Riatia* (Blattodea: Blatellidae) were found as prey and *Amobia floridensis* (Towsend) (Diptera: Sarcophagidae) as parasitoid of *T. insconspicuus*.

KEY WORDS: *Amobia*, biology, ethology, parasitoid

Tachysphex Kohl is a large genus of solitary wasps that nest in excavated burrows in the ground and hunt on ortopteroid insects to provision their nests (Bohart & Menke 1976). There are several extensive studies on the behaviour of *Tachysphex* species, but most of them deal with acridid-hunting species belonging to the *pompiliformis*-group and *terminatus*-group (e.g. Kurczewski 1987a, 1987b, 1989). *Tachysphex inconspicuus* (Kirby) is a cockroach-hunting species belonging to the *brulli*-group (Pulawski 1988). Knowledge about the biology of this species is limited to the short notes published by Callan (1942, 1954, 1993). Callan observed females gregariously nesting in sandy sites and preying on cockroaches of the genera *Chorisoneura* Brunner and *Riatia* Walker (Blattodea: Blatellidae). In the

present paper the nesting behaviour of *T. insconspicuus* is comparatively studied, based on observations carried out in two environmentally distinct locations in southeast Brazil.

Voucher specimens of *T. inconspicuus* and its preys and parasitoids were deposited at the Museu Nacional - Universidade Federal do Rio de Janeiro (MNRJ), Rio de Janeiro, Brazil. Additional specimens of the wasp were deposited at the Museu de Zoologia - Universidade de São Paulo (MZUSP), São Paulo, Brazil.

Material and Methods

The study was conducted in two locations: (1) sandy beaches in Vila do Abraão and (2) an unpaved road in the Reserva Biológica de Poço das Antas. Vila do Abraão is a small village in a 193 km^2 island near the continent, called Ilha Grande (Angra dos Reis, southern Rio de Janeiro State). The observations were made in two beaches: Praia Comprida and Praia Preta. The Tropical Floresta Atlântica covers most of the island and grows at the adjacencies of the beaches. Observations were made from November 2000 to March 2001, and June 2002. Poço das Antas is an area about 50,000 km^2 covered with lowland Tropical Floresta Atlântica in Casimiro de Abreu and Silva Jardim, northern Rio de Janeiro State). The observations took place on the main road that crosses the reserve. One- to three-day visits per month were made in the area in 2001.

Results

Habitat and aggregation. In Vila do Abraão, large assemblages of nesting wasps, sometimes with more than one hundred specimens were observed in open sites in the upper portion of beaches. The area occupied by a large assemblage was estimated at 2 m^2. Active females dig their nests as close as 20 cm from each other, in areas with very loose sand in the superficial stratum and more compacted sand below. Wasp aggregations remained cohesive during the observation periods although apparently similar environmental conditions were found in extensive surrounding areas.

In Poço das Antas, solitary females and small aggregations of approximately 5-10 nesting wasps were found in the unpaved road. The females dug their nests in small patches of loose sand scattered on the hard-packed road soil. The sand was not autochthonous; apparently, it was put in some sites to improve the road conditions for traffic.

Daily activity. The daily activity of the wasps as described below is based on two consecutive days of observations in Praia Comprida (June 20-21, 2002), when the nesting area could be observed uninterruptedly from approximately 7:00 am to 6:00 pm. At 8:00 am, the wasps were resting on the foliage of a tree exposed to the sun, approximately 2-2.5 m from the ground. The tree was adjacent to the nesting area, which was shaded at that moment. At 9:00 am, as the sun gradually covered the nesting area, the wasps started going there and occupying just the sunny patches. This behaviour is quite indicative that the wasps need the heat of the sun to warm up their bodies before they can engage in the nesting activity. In the nesting area, males and females hovered about 3 cm to 5 cm over the ground, in sinuous and apparently random trajectories. Buzzing sounds were not heard while wasps were in hovering flight or at anytime during the nesting cycle. At about 9:30 am, females digging nests started to appear in the nesting area whereas most wasps remained hovering until approximately noon or 1:00 pm. After that, the hovering flight activity gradually decreased, but females continued digging and provisioning their nests until 5:00 pm or 6:00 pm, when all nesting activity finally stopped.

In warmer summer days nest activity starts earlier. For example, in the Praia Preta (November 3, 2000), wasps were observed in hovering-flights over the nesting area at 6:50 am; at about 7:30 am, hovering wasps reached their maximum density.

Digging behaviour and nest structure. A female does not spend a lot of time walking on the ground, searching for the nesting site. It seems that her choice of nesting site occurs mostly while she is in hovering-flight. To dig the nest, the females crust the soil with the mandibles and throw it backwards and beneath the body with the forelegs. The thrown sand usually reaches about 1-2 cm beyond the wasp body. Sometimes, after digging a lump of sand from the burrow, the wasp walks backward in a straight line, as far as 5 cm from the nest, scattering the sand with the forelegs. Furthermore, she often interrupts burrow digging and scatters the sand in front of the nest entrance. Thus, the female does not let the excavated sand to form into a mound. Instead, there is usually a slight shallow depression in front of the nest. The nests are strongly oblique burrows with a final cell.

The nests found in Vila do Abraão were about 5 mm in diameter and 6 cm to 7 cm deep (n = 12). In Poço das Antas, the nests were about one to 2.5 cm deep (n = 8). Nest depth in the later site was the same as the thickness of loose-sand layer covering the compacted road soil. Females were apparently unable to crust the road soil because it was too compacted.

Temporary closure and accessory burrows. Soon after the nest is ready the female enters, turns 180° around and comes out headfirst, throwing sand backwards and over the nest entrance, thus temporarily closing the nest. Then, she scatters sand at the nest surroundings, makes an orientation flight and leaves in search for preys. Sometimes, she returns to the nest carrying no preys and hovers over the nesting site, probably to inspect it or to spatially orientate itself again.

The females found in Vila do Abraão usually dug one to four accessory burrows around the nest entrance. The accessory burrows were about 1 mm to 4 mm deep. These females spent up to seven minutes to close the nest, scatter the sand, and dig accessory burrows. Females in Poço das Antas did not make accessory burrows.

Nest provision. Nests were provisioned with two to four preys, as a rule, blattelid cockroaches (Blattodea: Blatellidae). In Vila do Abraão, the females preyed on adults or nymphs of *Chorisoneura lopesi* Albuquerque (Blattodea: Blatellidae), but a nymphal *Riatia* sp. was found in one of the nests, and one female carrying a non-identified nymph Gryllidae

(Ensifera) was collected. In Poço das Antas, the females were observed preying upon *Chorisoneura excelsa* Albuquerque & Silva (Blattodea: Blatellidae).

Prey carriage. Females carry the prey predominantly in flight, grasping prey antennae with the mandibles and apparently holding prey body with their legs. After landing on nest surroundings she walks toward the entrance dragging the prey, which remains under her body. The wasp does not release the prey antennae until she enters the nest. When the female arrives at the nest entrance, she uses one hind leg to keep the prey above the ground. The prey remains in a characteristic position, with one side of the body more or less transversal to the ground. This position allows the female to excavate the temporary closure and throw the sand backward, while still holding the prey. The loose sand closing the nest is quickly removed and the wasp with the prey plunges into the burrow. The roach remains inside the nest ventral side up.

Oviposition and final nest closure. Oviposition occurs inside the nest, on the last hunted prey. The egg is white and cylindrical, with rounded extremities. It is laid on the prey's central portion of the ventral thorax. After provisioning the nest, the female permanently closes it as if she was closing it temporarily, but she does not dig accessory burrows. She only scatters the sand, unmaking the depression usually existent in front of the nest entrance.

Natural enemies. The wasps found in Vila do Abraão were strongly parasitized by *Amobia floridensis* (Townsend) (Diptera: Sarcophagidae). These flies persistently pursue females carrying preys in flight. Usually, the pursued wasp avoids approaching her nest and flies in different directions, apparently to mislead the flies. Sometimes the female rests on the vegetation or on the ground, but the parasitoids hover over her until she flies again. The female often discards the prey due to the parasitoid's persistence. A parasitoid fly was observed entering an accessory burrow, suggesting an effective mimicry of the nest. In Vila do Abraão, in an early morning, a masked water-tyranid, *Fluvicola negeta* L. (Aves: Tyranidae), was observed walking on the ground and easily capturing several wasps in hovering flight activity. Natural enemies were not found Poço das Antas.

Discussion

Comparative behavioural studies of a same species living in different habitats are valuable for understanding if environmental conditions affect behavioural patterns or if there is behavioural plasticity, which could be attributed to ecological factors or to genetic differences among populations. Thus, the motor patterns associated with nest construction observed in *T. inconspicuus* must be highly independent of the environment because they are similar among wasps from both locations. On the other hand, three wasp behavioural features are remarkably different in each of the two environments and seem to be related to ecological factors: (1) degree of aggregation of the nesting females; (2) depth of the constructed nest; and (3) construction of accessory burrows.

One could say that solitary wasps gregariously nest if there are stimuli that make the females construct nests near each other, with mutual tolerance. The aggregative stimuli are not understood in *T. inconspicuus*, but the wasp nesting assemblages clearly seem to be behaviourally determined due their persistence and cohesion in despite of the similarity of the surrounding environment. The close association of the nesting females found in Poço das Antas with scattered small patches of sand is the simplest explanation for the smaller assemblages of wasps in that place and possibly also for the solitary nesting. In the same way, the shallower nests found in Poço das Antas were sharply constrained by the thickness of the sand patches. Apparently, the wasps found in Poço das Antas were opportunistically exploring the scarce sandy substratum from that place. In contrast, the abundant sandy substratum in Vila do Abraão seems to propitiate the establishment of large assemblages of nesting wasps.

Accessory burrows have been interpreted as a way of protecting the nest against parasitoids (Evans 1966). Remarkably, the wasps found in Vila do Abraão were suffering a severe pressure by parasitoid flies and constructed accessory burrows, whereas the wasps observed in Poço das Antas did not build accessory burrows and parasitoids were not found. Besides the possibility for this situation to have occurred by chance, two other explanatory hypotheses raise from this observation: (1) the presence of parasitoids is the stimulus for the females to construct accessory burrows, or (2) the construction of accessory burrows has been positively selected in this area due to parasitoidism pressure.

Behavioural patterns have been used as auxiliary to recognise groups and sub-groups of species in the genus *Tachysphex* (e.g. Elliot & Kurczewski 1985, Kurczewski 1987a, b). Kurczewski (1987a) lists the following remarkable behavioural features in species of *pompiliformis*-group that were not observed in *T. inconspicuus*: (1) made no temporary closure of the nest during its provision; (2) preyed on Acrididae or, sometimes, on Tettigoniidae and Phasmidae; and (3) let the sand excavated from the burrow to form into a mound in front of nest entrance. Species in the *terminatus*-group differ from *T. inconspicuus* in (1) constructing multicellular nests and (2) in provisioning the nests with nymphs of Acrididae (Elliot & Kurczewski 1985).

The behaviour of prey deposition into the nest varies among species of *Tachysphex*. Some species release the prey at the nest entrance while removing nest closure, then enter the nest, partially exit headfirst, grasp the prey and pull it into the nest (e.g. Kurczewski & Elliot 1978). Other species, which do not make temporary closure, enter the nest without releasing the prey (e.g. Kurczewski 1987a). The construction of temporary closures has been attributed to protection against parasitoid flies that respond to the image of the open nest, however, on the other hand this behaviour increases the prey exposure time to parasitoid flies that respond to the image of the prey-carrying wasps because of the time spent in opening the closure (Evans 1966, Evans & West-Eberhard 1970). *T. inconspicuus* is different from some other species of the genus in constructing a temporary closure, but does not release the prey to enter the nest. This behaviour speeds

up wasp deposit of the prey into the nest and prevents the prey to lay exposed outside the nest. Consequently, the time of prey exposure to flies which respond to the image of prey-carrying wasps decreases. Therefore, *T. inconspicuus* behaviour must have been evolutionarily constrained by both aforementioned categories of parasitoid flies. Evans (1962) discussed the evolution of the prey-transport behavioural mechanisms in wasps and found that the use of mandibles is the phylogenetically more basal mechanism and that, in a number of lineages, independently elaborated mechanisms of prey transport have evolved, in which the wasps use the legs or the sting. Evans pointed out that the most subtle consequence of the evolution of these elaborated mechanisms is to let the mandibles and forelegs free to open the temporary nests closure. Interestingly, *T. insconspicuus* associates the use of the mandibles in prey-transport with the possibility of excavating the temporary closure and entering the nest without releasing the prey. The construction of the nest in loose sand contributes with this behaviour, because it allows the female to dispense the use of the mandible to crust the closure.

Acknowledgments

I am in debt with Sérvio Túlio Amarante for identifying the wasp; Sônia Maria Lopes and Edivar Oliveira for identifying the cockroaches; Cátia Mello-Patiu for identifying the parasitoid flies; and Francisco Mallet-Rodrigues for furnishing information on the bird. I also thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the post-doctorate grant (process 151153/2005-1).

References

Bohart, R.M. & A.S. Menke. 1976. Sphecid wasps of the world – a generic revision. Berkeley, University of California Press, 665p.

Callan, E.M. 1942. A note on *Timulla* (*Timulla*) *eriphyla* Mickel, a parasite of *Tachysphex blaticidus* F.X. Williams, from Trinidad. Proc. R. Entomol. Soc. Lond. Ser. A Gen. Entomol.17: 18.

Callan, E.M. 1954. Observations on Vespoidea and Sphecoidea from the Paria Peninsula and Patos Island, Venezuela. Bol. Entomol. Venez. 9: 13-27.

Callan, E.M. 1993. Biological notes on some *Tachytes* and *Tachysphex* species (Hym., Sphecidae) in Trinidad. Entomol. Mon. Mag.129: 41-43.

Elliot, N.B. & F.E. Kurczewski. 1985. Nesting and predatory behaviour of some *Tachysphex* from western United States (Hymenoptera: Sphecidae). Great Basin Nat. 45: 293-298.

Evans, H.E. 1962. The evolution of prey-carrying mechanism on wasps. Evolution 16: 468-483.

Evans, H.E. 1966. The accessory burrows of digger wasps. Science 152: 465-471.

Evans, H.E. & M.J. West-Eberhard. 1970. The wasps. Ann Arbor, The University of Michigan Press, 265p.

Kurczewski, F.F. 1987a. A review of nesting behaviour in the *Tachysphex pompiliformis* group, with observations on five species (Hymenoptera: Sphecidae). J. Kans. Entomol. Soc. 60: 118-126.

Kurczewski, F.F. 1987b. Nesting behaviour of *Tachysphex laevifrons* and *T. crassiformis*, with notes on *T. krombeini* (Hymenoptera: Sphecidae). Proc. Entomol. Soc. Wash. 89: 715-730.

Kurczewski, F.F. 1989. Nesting behaviour of *Tachysphex acutus*, with a discussion of the multicellular nest excavation in the genus (Hymenoptera: Sphecidae). J. Kans. Entomol. Soc. 62: 44-58.

Kurczewski, F.E & N.B. Elliot. 1978. Nesting behavior of *Tachysphex pechumani* Krombein (Hymenoptera: Sphecidae) J. Kans. Entomol. Soc. 51:765-780.

Pulawski, W.J. 1988. Revision of North American *Tachysphex* wasp including Central American and Caribbean species (Hymenoptera: Sphecidae). Mem. Calif. Acad. Sci.10: 1-211.

Received 3/II/06. Accepted 29/IX/06.