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Host nest recognition by the parasitoid wasp *Dasymutilla scaevola*¹

Reconocimiento del nido de su anfitriona por la avispa parasitoide *Dasymutilla scaevola*¹

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Abstract.

The solitary wasp *Dasymutilla scaevola* (Blake) parasitizes the free-living fossorial solitary wasp *Cerceris fumipennis* Say. A female *D. scaevola* must locate the host's nest in the course of walking over the soil surface. This raises the question of how they identify the sites of their hosts in the broad soil expanse of the habitat. Three experiments tested the hypothesis that the parasite recognizes the odor applied to the nest substrate (excavated soil) by the host. The results corroborate the hypothesis that this serves as an important cue for the parasite in her search.

Key Words. *Cerceris fumipennis*, Mutillidae, nest odor, nest parasite, Sphecidae

Resumen.

La avispa solitaria *Dasymutilla scaevola* (Blake) ataca a la cría en los nidos de otra avispa solitaria, *Cerceris fumipennis* Say. Al caminar sobre la superficie del suelo, la hembra de *D. scaevola* busca nidos de su anfitriona. De ahí surge la cuestión de cómo la avispa parasitoide llega a reconocer el sitio del nido bajo la amplia superficie arenal de su hábitat. Por medio de tres experimentos, probamos la hipótesis de que lo reconoce por el olor aplicado al suelo por la avispa anfitriona. Los resultados indican que el olor puede servir como una señal clave para la avispa parasitoide.

Palabras Clave. *Cerceris fumipennis*, Mutillidae, olor del nido, parasitoide del nido, Sphecidae

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Introduction

Wasps of the family Mutillidae (Hymenoptera) parasitize prepupae and pupae of solitary wasps and bees, as well as immature stages of some other insects enclosed in pupal cases (Brothers 1989, Williams et al. 2024). They are commonly referred to as velvet-ants on account of the dense coat of hairs covering the body, and are known for their very painful stings (Schmidt 2016). The wingless females of velvet ants can be found searching for host nests, while most males are winged and are commonly seen flying low over the ground in search of females. . Results from two *Dasymutilla* spp. in North-American arid regions indicate that both females and males are active virtually throughout the daylight hours, although sometimes with a break during the hottest midday period (Linsley et al. 1955, Manley & Spangler 1983).

Females enter host nests in search of prepupae or pupae. On locating one of these, they chew a hole in the cocoon or cell and lay an egg inside. The developing larva feeds on the host individual and then spins its own cocoon and pupates inside the nest.

The nesting biology of mutillids has been little studied. Even the hosts of the great majority of North America's nearly 500 species are unknown (Iwata 1976, Krombein et al. 1979). To date, fewer than 10 species have received detailed life-history study (Brothers 1989). What is known indicates that their prey arrays do not follow consistent taxonomic patterns, in contrast to some other solitary wasps (O'Neill 2001: Ch. 2, Ronchetti & Polidori 2020). Accordingly, knowledge of one species' host(s) is a poor predictor of those of congeners.

Dasymutilla scaevola (Blake) parasitizes soil-nesting philanthine solitary wasps, including *Cerceris fumipennis* Say (Sphecidae) (Hook & Evans 1991, O'Neill 2001: Table 2-4). Both species are found throughout most of the USA east of the Rocky Mountains (Krombein et al. 1979, Williams et al. 2024:131).

A *C. fumipennis* female excavates a single nest of 20 or more cells provisioned with a variety of buprestid beetles and capable of rearing an adult. The entrance hole usually has a mound of excavated soil, or tumulus, beside it (Evans & Rubink 1978, Hook & Evans 1991). *D. scaevola* females often engage in behaviors that can be interpreted as scent marking the tumulus and the area immediately around it; they rub the hindlegs against the underside of the abdomen, which they then press against the nest entrance, tumulus, and nearby features while walking (A.W. Hook, unpubl.).

Cerceris fumipennis females commonly nest in aggregations, where *D. scaevola* females would have access to multiple nests in close proximity of one another. Preliminary data suggest a high rate of parasitism by *D. scaevola*. In an examination of six *C. fumipennis* nests with up to 12 pupae,

A.W. Hook (unpubl.) found a median of 38% pupae/nest parasitized. Some *C. fumipennis* females remain with their nests during a prolonged post-reproductive guarding phase. They are often found sitting in or just below the burrow entrance, only leaving the nest once or twice a day, presumably to feed (A.W. Hook, unpubl.). Almost certainly, they are guarding against nest parasites while their brood developed. Although this and other digger wasps suffer from a diversity of natural enemies, such post-reproductive guarding is most likely effective only against mutillids, as these are the only nest parasites that can attack cocooned brood. Preliminary observations at the study site show that marked *D. scaevola* females are found visiting up to six *C. fumipennis* nests for up to 15 days and that there can be up to eight females at a time coming to a given nest (A.W. Hook, unpubl.).

Both active and abandoned *C. fumipennis* nests at the study site are very attractive to *D. scaevola* females, which compete vigorously with each other for control of host nests (A.W. Hook, unpubl.). Given this high level of competition for nests, it is predicted that natural selection will favor the ability to recognize the location of host's nests below the soil surface. We hypothesize that the critical cues are not physical but more likely chemical deposits on the soil.

Two kinds of odor traces from the host female could plausibly be perceived by the searching parasite. First, in moving through the nest burrow the host female will almost unavoidably mark the soil with cuticular hydrocarbons. Second – although less likely in our view – the soil may be tagged by a glandular product from the host. Much research has been conducted on the morphology and function of exocrine glands in social wasps and bees (Downing 1991, Duffield et al. 1984); solitary wasps have not received such attention, but it is reasonable to suppose that they also have and utilize exocrine glands.

Without suggesting its exact source or chemical nature, we hypothesize that *D. scaevola* recognizes the scent of her host by way of odor added to nesting materials. The most likely such material that *D. scaevola* normally encounters in her searches is the mounds of soil (tumuli) that collect around nest entrances from the process of digging by the host. Such tumuli average about 6 cm in diameter and 1-3 cm in depth. In digging a nest *C. fumipennis* loosens the soil with the mandibles, then backs up the borrow, cradling the spoils under the venter and pushing them out of the entrance with the pygidium, a sclerite at end of abdomen. Such contact is almost certain to transfer cuticular hydrocarbons from the host to soil, including the tumulus. It is also possible that the host transfers labial secretions to the soil in the process of breaking up the soil with the mandibles. In an analogous study to ours, Kroiss et al. (2008) showed that nest-mound material from the solitary wasp *Philanthus triangulum* Fabr. provided chemical cues to a nest-parasitic wasp in locating *Philanthus* nests. Preliminary study suggests scent marking by *D. scaevola* on and around the

host's nest entrance, possibly as a signal to herself or conspecific females.

Our purpose here is to test the hypothesis that host odor from excavated nest material on the soil surface is attractive to female *D. scaevola* relative to control samples of soil. We also tested the parasite's response to tumulus soil of the sympatric *Cerceris rufopicta* F. Smith. This wasp is broadly sympatric with *C. fumipennis* and *D. scaevola*, although in at least part of their area of co-occurrence it tends to nest in somewhat different microhabitats (Kurczewski & Miller 1984). It is not known whether it is a host of *D. scaevola*.

Materials and Methods

We collected 25 *Dasymutilla scaevola* females in May 1992 at a nest aggregation of *Cerceris fumipennis* at Pedernales Falls State Park, Texas, USA. These females were used in Assays 1 and 2. At the same time we collected tumulus soil from 21 active *C. fumipennis* host nests at the aggregation into separate zip-lock bags and in the same locality a quantity of soil at a depth of up to 10 cm at least 50 cm away from any known nest. This latter served as control soil in the assays. In the laboratory shortly after collection, we mixed this latter soil and moistened so as to closely resemble tumulus soil. At the Brackenridge Field Laboratory in Austin, Texas, where all assays were conducted, we maintained the *D. scaevola* on a diet of sugar-water in small plastic cups with lids.

The test chamber was a lidded plastic petri dish 14 cm in diameter and 2.2 cm in depth with a midline marked on the floor (Fig. 1). The floor of the chamber was left bare to a distance of 2 cm on each side of the midline, leaving two test sectors each of about 54 cm². On one of these, we evenly spread one tablespoon (about 15 ml) of test soil and, on the other side, an equal amount of control soil. The position of the test sector, whether to the left or right of the midline as the observer sat, was decided by a coin toss. All assays were single-blind, such that the observer was unaware which was the test sector of the chamber. The ceiling of the chamber was sprayed with fluon to prevent any wasp from climbing away from the floor. The chamber was cleaned with isopropyl alcohol after each test.

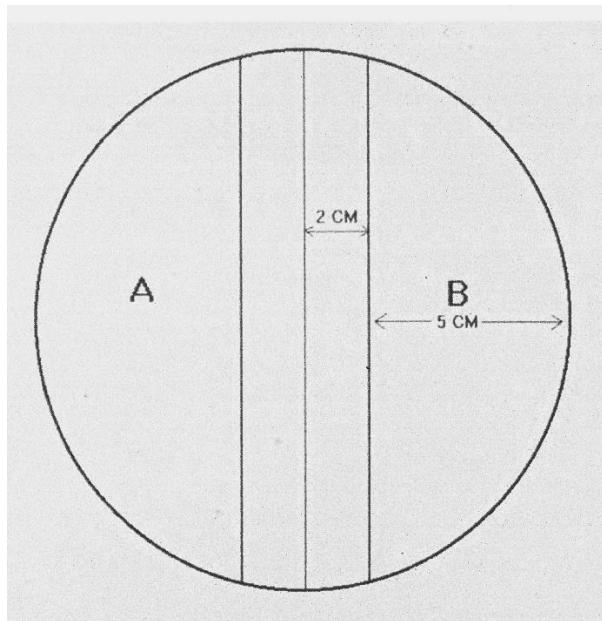


Figure 1. Floor plan of the test chamber. Sectors A and B were covered with sand from the field site, while the 4 cm. central band remained bare. The test wasp was released in the central band.

Figura 1. Plano de la cámara de pruebas. Los sectores A y B se cubrieron con arena del lugar de trabajo, mientras que la franja central de 4 cm permaneció sin cobertura. La avispa en la prueba fue liberada en la franja central.

In each run of an assay a novel randomly-chosen *D. scaevola* female was placed in the center of the test chamber in an overturned vial and left for several minutes to habituate, at the end of which we set her free by removing the vial. From the moment that she walked off the bare center strip onto one or the other soil sector, the observer recorded the time spent in contact with soil on each sector. In a preliminary run of the first assay, the wasp was enclosed in the vial for 5 min and then her movements recorded for 20 min. Each of these periods appeared unnecessarily long for consistent results, so that they were reduced to 1 and 10 min, respectively, in our assays.

During May-June 1992 we conducted four assays of *D. scaevola*'s responses to soil from 1) *C. fumipennis* tumuli, 2) simulated *C. fumipennis* tumuli, 3) simulated *D. scaevola*-affected *C. fumipennis* tumuli, and 4) *C. rufipicta* tumuli. We began with the first of these; if the mutillid showed no statistically significant association with the host's tumuli relative to the control, the other assays would have been moot. In the first and second assays it was assumed that the soil was not affected by previous contact with *D. scaevola*.

The second tested for the presence of cues left on the soil in the form of cuticular hydrocarbons or glandular secretions from the host female without the complicating presence of host brood. Seven host females were each placed in a small lidded cup about 2/3 filled with surface soil from the study site. For 5 min we made the females dig their way up through the soil by turning the cup over several times. Soil treated by each female served in either four or six tests.

The third tested for responses to her own presumed prior scent marking of tumuli. The preparation of test soil was as in assay 2, except that it was treated by *D. scaevola* herself ahead of the assay.

And the fourth tested whether *D. scaevola* responded to *C. rufopicta* tumuli as it did to those of *C. fumipennis*, following the same procedure as in the first assay.

We compared fractions of time spent in the two sectors with the Wilcoxon signed-ranks test, with each trial of a test regarded as a replicate.

Results and Discussion

The results of the four assays are summarized in Table 1. *Dasymutilla scaevola* females recognized the odor of the host *Cerceris fumipennis*. They spent on average substantially more time in contact with both natural (1) and simulated (2) *C. fumipennis* tumulus soil. In contrast, they showed hardly any relative affinity for simulated tumulus soil treated with their own scent (3). And they spent on average more time in contact with natural *C. rufopicta* tumulus soil than with control soil from, but not to a statistically significant level (4).

Table 1. Summary of results. The positive result is mean \pm SE among trials of the percentage of active time spent on the treatment half of the test chamber. Z is the test statistic (Wilcoxon Signed-Ranks Test Calculator 2024). Further explanation in the text.

Cuadro 1. Resumen de los resultados. Un resultado positivo (positive result) es la media \pm error estándar del porcentaje de tiempo activo pasado en el lado de tratamiento de la cámara de prueba. Z es la estadística de la prueba (Wilcoxon Signed-Ranks Test Calculator 2024). Explicación adicional en el texto.

Assay	No. of trials	Positive result	Z	p
1	20	57.3 \pm 3.21	-2.33	0.019
2	34	64.5 \pm 2.84	-3.94	0.000
3	19	54.0 \pm 4.22	-0.89	0.376
4	17	58.6 \pm 4.98	-1.59	0.113

The results of tests 1 and 2 corroborate the hypothesis that *Dasymutilla scaevola* females recognize the nesting substrate of their hosts, *C. fumipennis*, through odor cues in excavated soil. These are presumably cuticular hydrocarbons and/or labial- or mandibular-gland secretions transferred in the course of nest excavation, accumulated around the nest entrance in the tumulus. Both field-collected tumuli, and facsimiles generated in the laboratory were recognized.

The result of the third assay, in which *D. scaevola* females showed no significant discrimination between soil presumably treated with their own scent and with control soil, is baffling. It seems unlikely that our treatment did not add the wasp's scent to soil or that this was not perceived.

The negative result of the fourth assay may indicate that *C. rufopicta* serves only as an occasional or non-preferred host of *D. scaevola*, at least in the study area.

Taken together, our results are consistent with the expectation that nest-parasitic *D. scaevola* females associate more with soil from nests of the host *C. fumipennis* than with control soil. Further analyses of test and control soils could lead to identification of the chemicals attractive to *D. scaevola* as they search for hosts.

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