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Notes on the parasitoids found within the nests of *Delta dimidiatipenne* (Hymenoptera, Vespidae)

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Abstract

An examination of parasitoids that had completed their development but were trapped within *Delta dimidiatipenne* nests revealed 15 species of insect parasitoids, belonging to eight families under two orders. A new association of Miltogramminae (Diptera: Sarcophagidae) with this wasp is also reported.

Keywords

Diptera, Miltogramminae, parasitoids, potter wasps, Sarcophagidae

Introduction

Potter wasps (Eumeninae) are the largest vespid wasp subfamily in the world, comprising nearly 3800 species in more than 210 currently described genera (Pickett and Carpenter 2010; Auko et al 2014; Pannure et al. 2016; Tan et al. 2018). Nevertheless, the ecology and phylogentic relationships of this mega-diverse lineage is poorly studied (Carpenter and Marques 2001; Pickett and Carpenter 2010; Hermes et al. 2013; Bank et al. 2017). Adult Eumeninae feed on nectar while the larvae are predatory. Females build nests made of mud, deposit eggs, and hunt for prey, usually larvae of Lepidoptera, Curculionidae, and Chrysomelidae (Júnior et al. 2012), to provide food for their own larvae (Evans 1956; Krombein 1979; Carpenter and Marques 2001; Hunt et al. 2003). The females usually sting to paralyze the prey before carrying it to the nest and depositing it in the cell. The wasp larvae develop by feeding on the prey externally, thereby completing their development inside the cell, and they emerge as adults by breaking open the nest cell (Matthews and González 2004; Prezoto et al. 2007; Matthews and Matthews 2009). In some studies, potter wasps were reported to be effective generalist predators of some economically important Lepidoptera (Boesi et al. 2005; Buschini and Buss 2010; Abarca et al. 2012; Udayakumar et al. 2022).

Eumeninae's main natural enemies are birds, ants, bats, and parasitoids (West-Eberhard et al. 1995). Some parasitoids of potter wasps have adapted to infest the nest while it is under construction, whereas others infest it after the nest has been built and sealed, using their mandibles or ovipositors to puncture the nest cell wall (Berland and Bernard 1938; Krombein 1979; Gauld and Hanson 1995; West-Eberhard et al. 1995; Liu et al. 2014). Regardless of the infestation timing, parasitoids that specialize on potter wasp nests, after completing their development, normally have morphological adaptations to break open the nests (Martynova 2020). Nevertheless, occasionally parasitoids may fail to emerge from the nest cells (Buschini and Buss 2010).

Apart from these nest parasitoids, several studies have also reported the occurrence of parasitized prey and parasitoids of the prey insects trapped in the nests of solitary wasps. This may occur when the potter wasps collect and bring to the nest already parasitized prey (Bohart et al. 1982; Jennings and Houseweart 1984; Tscharntke et al. 1998; Buschini and Buss 2010; Auko et al. 2015; Segoli et al. 2020; Leduc et al. 2022). In contrast to the nest parasitoids, the parasitoids of the prey species are not likely to have adaptations to break out of the mud cells, as most commonly, they do not develop inside a potter wasp nest. In this context, we documented the parasitoids of the potter wasps and of their prey species that were trapped inside potter wasp nests in Israel's Negev and Judean Deserts.

We focused on the wasp species *Delta dimidiatipenne* de Saussure, 1852 (Hymenoptera, Vespidae, Eumeninae), which has been recorded in Afghanistan, Algeria, Chad, Djibouti, Egypt, Eritrea, Ethiopia, India, Iran, Israel, Jordan, Mauritania, Morocco, Nepal, Niger, Oman, Pakistan, Qatar, Saudi Arabia, Spain, Somalia, South Africa, Sudan, Syria, Tajikistan, Turkey, Turkmenistan, the United Arab Emirates, Uganda, and Yemen, mainly in desert habitats (Rafi et al. 2017; Hamzavi et al. 2019; Segoli et al. 2020). These wasps construct nests, composed of multiple mud cells, on rock surfaces. Females lay a single egg per cell (usually) and provision it with several caterpillars. In Israel, the wasps can be found in drier areas, from the center to the south of the country, and they are active mostly between March and June (Alon and Kugler 1989). The wasp's most common prey species in the deserts of Israel are caterpillars of noctuid moths, especially *Heliothis nubigera* Herrich-Schäffer, 1851, which are often found on the desert shrub *Zygophyllum dumosum* Boiss. (Segoli et al. 2020; Leduc et al. 2022). Evidence for the occurrence of caterpillars parasitized by *Copidosoma primulum* (Mercet 1921) in *D. dimidiatipenne* nests has been documented in multiple sites in the Negev Desert, and in ca. 70–80% of the observed newly constructed nests (Segoli et al. 2020; Leduc et al. 2022). These authors also found that potter wasp larvae that develop with parasitized caterpillars had lower developmental success, probably because the parasitized prey is of lower quality. We recorded the content of *D. dimidiatipenne* nests from previous years and identified the dead parasitoids found within them.

Materials and methods

The current study was conducted in Israel's Negev and Judean Deserts during 2021–22. The climate is characterized by hot, dry summers, with an average maximum daily temperature of around 36 °C (Judean Desert) and 27 °C (Negev Desert) in July–August, and cold winters, with an average minimum daily temperature of around 18 °C (Judean Desert) and 9 °C (Negev Desert) in January–February. Annual precipitation is ca. 100 mm (data retrieved from the Israel Meteorological Service, https://ims.gov.il/en). A total of 11 field sites were selected, especially ones in proximity to temporary water holes that are used by potter wasps for drinking and nest construction. *Delta dimidiatipenne* normally build nests under rock ledges and in concealed rock surfaces, presumably to avoid direct insolation by the sun, which may result in overheating of the brood cell, and also to avoid the nest from being washed away by the heavy rains that occasionally occur during the nesting season. In each of the field sites, we sampled from five to 10 nests. However, it was difficult to estimate the exact number of nests that were sampled because the nests sometimes partially overlapped. In each nest, we sampled between three to 18 cells. This is again a rough estimation as some cells were partially disintegrated or contained secondary residences such as spiders, beetles or bees. We located nests from previous years, which can easily be recognized by the presence of emergence holes. Some nests had emergence holes in each cell, suggesting complete successful emergence, while other nests had some emergence holes and some intact cells, suggesting partial emergence success. In a few cases, we also found nests that were completely sealed without any emergence holes, suggesting that neither parasitoids nor potter wasps emerged successfully. Wherever feasible, we opened the cells by carefully dampening them with water and gently breaking the cell walls open using forceps and collecting all the parasitoids within. Apart from the focal study species, *D. dimidiatipenne*, we also collected and documented other vespid potter wasps in the study area by sweeping with nets near the water hole. We identified all the collected insects to the lowest taxonomic level possible, using keys published by Broad (2011) for Ichneumonidae and by van Achterberg (1990a) for Braconidae, and we confirmed the identities by consulting respective experts for each group and by comparing the specimens with the available reference collections at the Steinhardt Museum of Natural History, Tel Aviv, Israel. Geographic coordinates are given in WGS84. The specimens were then deposited in the Steinhardt Museum.

Results and discussion

Potter wasp species, other than *D. dimidiatipenne*, that were collected include the following: *Delta asina mixtum* (Giordani Soika, 1944), *Delta hottentotum elegans* (De Saussure, 1852), *Katamenes niger* (Brullé, 1839), *Katamenes dimidiativentris* (Giordani Soika, 1941), *Katamenes jenjouristei* (Kostylev, 1939), and *Ancistrocerus biphaleratus* (de Saussure, 1852). We identified *D. dimidiatipenne* nests based on their distinctive pot-shaped entrance with a size of approximately 1 cm in diameter. Moreover,

Table 1. List of parasitoids found within *Delta dimidiatipenne* nests.

Order	Family	Taxon/ Species	No. of individuals	Place of collection	Potential host
Diptera	Sarcophagidae	Miltogramminae	1	Nahal Peres (31°00'31.52"N, 35°28'39.95"E)	Wasp larva (Spofford et al. 1989; Pape 1996)
	Tachindae	Undetermined	1	Mamshit (31°02'31.47"N, 35°06'70.13"E)	Could be prey or wasp larva (Belshaw 1994)
Hymenoptera	Ichneumonidae	*Netelia fuscicornis* (Holmgren, 1860)	1	Ein Bokek (31°19'86.72"N, 35°35'03.57"E)	Prey (Townes 1965)
		Barylypa rufa (Holmgren, 1857)	1	Nahal Shoalim (30°95'29.57"N, 34°91'39.78"E)	Prey (Ahmed 1950)
		Ophion similis (Szépligeti, 1905)	1	Nahal Daroch (30°86'09.39"N, 34°85'96.41"E)	Prey (Gauld 1988)
	Braconidae	*Cotesia vanessae* (Reinhard, 1880)	17 individuals from three nests	Nahal Gov (30°90'38.30"N, 35°12'77.89"E) & Nahal Shoalim (30°95'29.57"N, 34°91'39.78"E) & Ein Zik (30°80'36.54"N, 34°85'10.00"E)	Prey (a gregarious parasitoid) (Hervet et al. 2014)
		Microplistis sp.	9	Nahal Gov (30°90'38.30"N, 35°12'77.89"E) & Nahal Afran (30°86'38.14"N, 34°92'71.31"E)	Prey (Takasu and Lewis 1995)
		Schoenlandella deserta (Telenga, 1955)	1	Nahal Mador (30°86'99.66"N, 34°96'40.56"E)	Prey (Huddleston and Walker 1988)
		Chelonus sp.	4	Mamshit (31°02'31.47"N, 35°06'70.13"E), Nahal Afran (30°86'38.14"N, 34°92'71.31"E)	Prey (Jourdie et al. 2008)
		Rogas sp.	1	Nahal Shoalim (30°95'29.57"N, 34°91'39.78"E)	Prey (Reardon 1973)
		Phanerotoma sp.	11	Ein Bokek (31°19'86.72"N, 35°35'03.57"E)	Prey (van Achterberg 1990b)
	Encyrtidae	*Copidosoma primulum* (Mercet, 1921)	Hundreds emerging out of 28 mummified caterpillars	In all the collection sites	Prey (Gregarious parasitoid) (Segoli et al. 2020)

Order	Family	Taxon/ Species	No. of individuals	Place of collection	Potential host
Hymenoptera	Torymidae	*Monodontomerus* sp.	3	Nahal Afran (30°86'38.14"N, 34°92'71.31"E)	Could be prey or wasp larva (Grissell 2000, 2007)
	Eulophidae	*Melittobia acasta* (Walker, 1839)	4	Nahal Zafit (30°97'21.47"N, 35°29'69.26"E)	Wasp larva (a gregarious parasitoid) (Gonzalez et al. 2004)
	Chrysididae	*Stilbum* sp.	1	Saraf (30°78'72.25"N, 35°02'99.82"E)	Wasp larva (Gess and Gess 2014)

D. dimidiatipenne adults are the largest (approximately 2.5 cm long) of all the above-mentioned potter wasp species, and they construct the largest nests, comprising ca. 20 cells. Also, whenever we collected fresh cells (e.g., as part of our other published studies), this species always emerged from them. We have also recorded 12 imagines of *D. dimidiatipenne* that were trapped within the cell. This reaffirms that we have sampled only the nests of *D. dimidiatipenne*.

Our collections from the nests resulted in a total of 15 parasitoid species, belonging to two orders and eight families of insects. Based on the literature, most of them are probably parasitoids of species that the potter wasps collect as prey, while some are nest parasitoids of the potter wasps themselves. The details are presented in Table 1.

Though Bombyliidae is one of the most commonly occurring parasitoids in potter wasp nests (Yeates and Greathead 1997), we did not collect any of them, but we witnessed pupal cases that were most likely of bombyliids (Fig. 1a) in some nests, suggesting that they were able to emerge out of the nest successfully. Apart from the below list, we found some interesting secondary inhabitants of the nests, *viz.*, a neuropteran larva, many different species of spiders and bees, earwigs, and a scorpion exuvium. We also observed fully developed adult potter wasps that had failed to break open the cell and died within (Fig. 1d).

Caterpillar parasitoids

Based on their known ecology, all the ichneumonids, braconids, and the encyrtid that were documented in this study, *i.e.*, 10 out of 15 recorded species, are parasitoids of the prey caterpillars brought by the potter wasps to the nests. In this sense, it is perhaps not surprising to find them trapped within potter wasp nests, as they are not likely to have adaptations that enable them to emerge successfully through the hardened mud cell walls. Moreover, the occurrence of most of these prey parasitoids seems to be rare. Such low occurrence could perhaps represent a generally low parasitism rate on the prey by these parasitoid species in the field. In addition, some predatory insects are known to

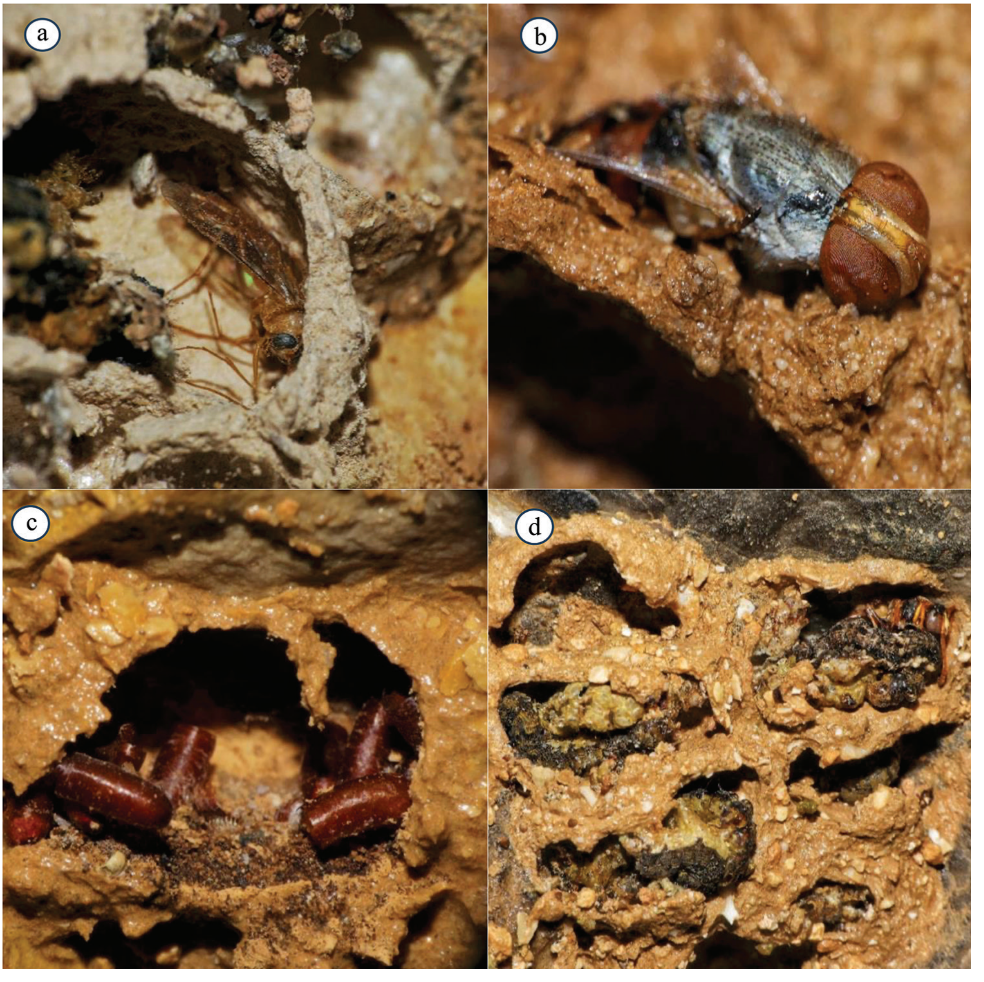

Figure 1. Interior of some opened nests showing trapped parasitoids and unemerged wasps **a** *Netelia fuscicornis* **b** Miltogramminae **c** emerged fly pupal cases **d** *Copidosoma primulum* infested caterpillars and an unemerged male of *Delta dimidiatipenne*.

discriminate against parasitized prey, which are often of lower quality (e.g., Aparicio et al. 2020; Leduc et al. 2022; Perier et al. 2022). The fact that some of these parasitoids were not consumed by the potter wasp larvae and were able to complete their development inside the cell could perhaps also support the interpretation that they are not a good food source for the developing potter wasp larvae.

An exception was the high occurrence of *Copidosoma primulum*, which was found in all 11 study sites and was the most abundant of all the parasitoids that we documented. This accords with previous studies conducted on these species (Segoli et al. 2020; Leduc et al. 2022), suggesting that *D. dimidiatipenne* frequently collects caterpillars that are already parasitized by this gregarious parasitoid, possibly due to the lower susceptability of the parasitized caterpillars to predation risk (Leduc et al. 2022).

In such cases, the parasitoid larvae feed on the caterpillar internally, depleting the food required for *D. dimidiatipenne* development, thereby reducing the probability that the wasp larvae can survive and successfully pupate (Segoli et al. 2020; Leduc et al. 2022).

Nest parasitoids

Out of the eight families that were collected, five families, *viz*., Sarcophagidae, Tachindae, Torymidae, Eulophidae, and Chrysididae, were most likely to be nest parasitoids, each represented by one species. These species and, more importantly, the potter wasp adults are all presumably well adapted to complete their development inside a potter wasp nest, and hence, it may be surprising that they were trapped within the nest. One possible explanation is that the occurrence of prey parasitized by *Copidosoma*, or other low-quality prey, led to the development of malnourished potter wasps, which were too small or not strong enough to break open the nest cell. This could potentially also be true for some of the other trapped nest parasitoids. Another possibility could be that the extreme desert conditions, such as exceptionally high temperatures or extremely dry conditions, occurring in this region, caused insect death inside the nests.

Miltogramminae (Diptera, Sarcophagidae) are primarily kleptoparasites of wasps and bees (Spofford et al. 1989; Pape 1996). The host range of Miltogramminae is wide, including many families of wasps (Crabronidae, Pompilidae, Sphecidae, and Vespidae) and bees belonging to the familes Andrenidae, Apidae, Colletidae, and Halictidae. Some Miltogramminae were reported to parasitize Orthopera and Diptera, and some invade termite and ant nests as well (Thompson and Love 1979; Verves 1979; Pape 1987; Spoford and Kurczewski 1990; O'Neill 2001; Pape 2006; Evans and O'Neill 2007; Polidori et al. 2009; Sinha 2012; Polidori 2017). The current study adds *D. dimidiatipenne* as a newly discovered host of Miltogramminae (Fig. 1b).

Usually, Miltogramminae are termed "satellite flies" as they wait on perching sites close to the entrance of a host's nest for a nest-returning host female and then follow it, in flight, at a fixed distance behind. Some Miltogramminae are termed "hole searchers" as they patrol the host's nesting site and enter the host's nest, and some are dubbed "stalkers" as they enter the host's nest after having detected the female host entering it (Newcomer 1930; Ristich 1956; Alcock 2000; Polidori et al. 2022). However, we cannot determine the behavior of the collected species as we did not directly observe them and were unable to identify them beyond subfamily level.

Future research based on host-parasitoid rearing can shed more light on factors causing different parasitoid species' emergence failure, their developmental nutritional requirements, and their ability to break open the nest successfully.

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