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Parasitic Wasps and Arthropod Communities in Oothecal Microhabitats of Two Mantid Species, *Hierodula tenuidentata* and *Iris oratoria*

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ABSTRACT

This study examined the role of oothecae from two mantid species, *Hierodula tenuidentata* (Saussure, 1869) (Mantodea: Mantidae) and *Iris oratoria* (Linnaeus, 1785) (Mantodea: Eremiaphilidae), as microhabitats for parasitoid wasps and shelters for associated arthropods. A total of 32 oothecae were assessed, including 28 from *H. tenuidentata* and four from *I. oratoria*, collected from tree branches in Semnan and Khorasan Razavi Provinces in Iran, respectively. A total of 167 parasitoids removed from collected oothecae including three torymid species, *Podagrion splendens* (Spinola, 1811), *Podagrion gibbum* (Bernard, 1938), and *Podagrion bouceki* (Delvare, 2005), and one eulophid species, *Melittobia megachilis* (Packard, 1864), were recovered from *H. tenuidentata* oothecae. All of them belong to Hymenoptera. In contrast, only *P. splendens* emerged from *I. oratoria* oothecae. Additional arthropods included flies, mosquitos, ants and lacewings. All recorded parasitoid wasps and arthropods: *Meoneura* sp. (Carnidae), *Lycoriella* sp. (Sciaridae), *Pheidole* sp. as well as members of Cecidomyiidae, Psychodidae (Diptera), and Hemerobiidae (Neuroptera) represent the first documented associations with the oothecae of *H. tenuidentata* and *I. oratoria*. These finding highlight the potential complexity of various arthropods interactions within mantids oothecae as a suitable microhabitate.

Keywords: Mantid oothecae, parasitoid wasps, Diptera, Formicidae, northeastern Iran.

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INTRODUCTION

The order *Mantodea*, encompassing over 2,500 species, is distributed globally across a wide range of ecosystems, including forests, deserts, agricultural fields, gardens, and greenhouses (Otte, Spearman, & Stiewe, 2023). A defining feature of mantids is their highly efficient predatory behavior (Prete, Wells, Wells, & Hurd, 1999). Both nymphs and adults consume a wide range of prey, including aphids, flies, mosquitoes, ticks, grasshoppers, crickets, moths, and lepidopteran larvae (Prete et al., 1999). Larger species have even been observed preying on small vertebrates such as lizards and birds (Nyffeler, Maxwell, & Remsen, 2017). With advanced vision capable of detecting motion up to 60 feet away, mantids use raptorial forelegs to secure prey. This predatory capacity contributes significantly to the ecological regulation of prey populations (Prete et al., 1999; Moran & Hurd 1998). The Giant Asian mantis, *Hierodula tenuidentata* (Saussure, 1869), and the Mediterranean mantid, *Iris oratoria* (Linnaeus, 1785), are widely distributed across Asia and the Mediterranean Basin, respectively, with confirmed occurrences in northeastern, eastern, and southern Iran (Battiston, Picciau, Fontana, & Marshall, 2010; Mirzaee & Sadeghi, 2019). Like other mantid species, females deposit eggs in an ootheca, a protective case formed by secretions from accessory glands adjacent to each ovary. Upon air exposure, the secretion hardens into a resilient structure that shields the eggs from predators, physical damage, environmental stress, and desiccation (Courrent et al., 2008; Song et al., 2020).

Mantids attach their oothecae to diverse substrates, such as tree branches, herbaceous vegetation, soil surfaces, rocks, and undersides of stones (Mirzaee, Lotfalizadeh, & Sadeghi, 2022a). Balakrishnan (2012) noted that *Hierodula* species favor oviposition sites on taller plants, away from the main stem and within more open, less dense vegetation compared to typical ambush locations. Oviposition behavior may also be shaped by prey availability. Plants with prominent flowers attract pollinators, which serve as prey and may be selectively chosen to improve hatchlings' foraging prospects (O'Hanlon, Holwell, & Herberstein, 2014).

Several wasp species parasitize mantid oothecae. For example, *Podagrion* wasps are highly specialized and exclusively oviposit within mantid oothecae (Mirzaee et al., 2021b). In addition, mantid oothecae may act as temporary shelters for various insects and arthropods. These associations represent complex ecological interactions embedded within broader ecosystems (Grissell, 1995; Vanitha, 2018). However, interactions between mantid nymphs and co-inhabitants remain poorly characterized.

Hierodula tenuidentata and *I. oratoria* are common in northeastern Iran (Mirzaee et al., 2026). Identifying parasitoid wasps and arthropods associated with their oothecae may provide novel insights into the ecological dynamics of these predatory insects. Oothecae may also be unintentionally transported with commercial goods or medicinal plants, thereby introducing mantids and their parasitoids beyond their native ranges (Battiston et al., 2010, 2020). Consequently, numerous mantid species—primarily originating from Asia, including *H. tenuidentata* have been reported outside their natural distribution zones (Battiston, Leandri, Dipietro, & Andria, 2018).

Arthropods Present within the Oothecae of These Two Species.

Given this expanding range and the need for a deeper understanding of their biological associations, the present study aimed to identify parasitoid wasps and other arthropods present within the oothecae of these two species.

MATERIAL METHODS

Oothecae Collection

Sampling of mantids oothecae was conducted twice in the sampling areas, on 15 and 20 March 2024. A total of 32 mantid oothecae were collected: 28 from *H. tenuidentata* and 4 from *I. oratoria*, across various tree species in northeastern Iran. The oothecae of these two mantid species were collected from branches and the main trunks of both fruit and non-fruit trees.

Sampling Locations

Specimens were collected from four sites in Semnan Province (Faculty of Agriculture, Allameh Majlesi Boulevard, Baft Ghadim, and Silu) and one site in Khorasan Razavi Province (Ebrahimabad region). Notably, all *H. tenuidentata* oothecae were obtained from Semnan Province, whereas all *I. oratoria* oothecae were collected from Khorasan Razavi Province (Fig. 1). Host trees included *Malus* sp., *Prunus* sp., *Pinus* sp., *Olea* sp., *Ficus* sp., *Pistacia* sp., *Punica* sp., *Morus* sp., and *Fraxinus* sp. (Table 1).

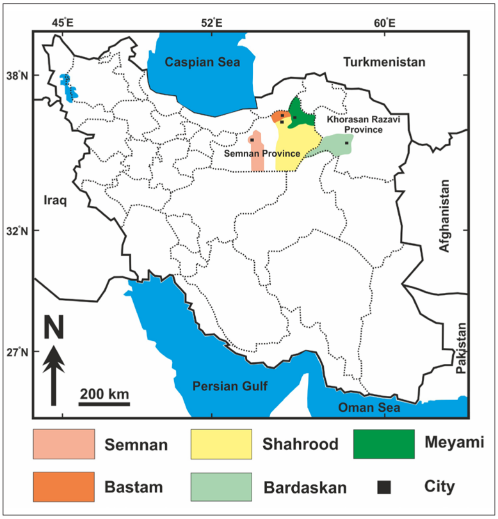

Figure 1. Sampling regions in Semnan and Khorasan Razavi Provinces, Iran.

All oothecae were carefully detached from their substrates and maintained under controlled laboratory conditions (25 ± 1 °C, 50% relative humidity, and a 14:10 h light: dark photoperiod). Each ootheca was photographed using a Canon digital camera before being individually placed into 15×15×15 cm plastic containers with mesh lids and monitored daily. The number of emerging mantid nymphs, parasitoid wasps, and other arthropods from each ootheca was recorded by collection site.

Table 1. Geographical position of sampling regions of *Hierodula tenuidentata* and *Iris oratoria* oothecae and host plants.

Sampling Regions	City	Geographical Position (Latitude, Longitude)	Elevation (m)	Host Plant	Ootheca Species	Ootheca Number
Faculty of Agriculture	Bastam (Semnan Province)	36° 30' 16" N, 55° 00' 18" E	1408	*Malus sp., Prunus sp., Pinus sp.,*	*H. tenuidentata*	6
Allameh Majlesi Boulevard	Shahrood (Semnan Province)	36° 23' 42" N, 54° 56' 58" E	1318	*Olea sp.*	*H. tenuidentata*	2
Baft Ghadim	Meyami (Semnan Province)	36° 24' 40" N, 55° 39' 30" E	1076	*Prunus sp.*	*H. tenuidentata*	3
Silu	Semnan (Semnan Province)	35° 33' 56" N; 53° 22' 31" E	1092	*Ficus sp., Pistacia sp., Punica sp, Morus sp., Fraxinus sp.*	*H. tenuidentata*	9
Ebrahimabad	Bardaskan (Khorasan Razavi Province)	35° 15' 24" N, 57° 54' 58 " E	956	*Pistacia sp*	*I. oratoria*	3

RESULTS

Geographical Documentation

Geographic characteristics of the sampling sites are presented in Table 1 and mapped in Fig. 1. Representative photographs of the collection areas are shown in Fig. 2 (a-e). Fig. 3a and 3b display adult specimens of *H. tenuidentata* and *I. oratoria*, while Fig. 3c-3f illustrates their oothecae attached to tree branches. Among the collected oothecae, 23 exhibited bright coloration (Fig. 3c, 3f), and several showed small perforations (Fig. 3d), suggesting either predator activity or the presence of arthropods. In contrast, 13 oothecae appeared darker and showed deep cracks and holes (Fig. 3e), consistent with structural aging and potentially failed emergence.

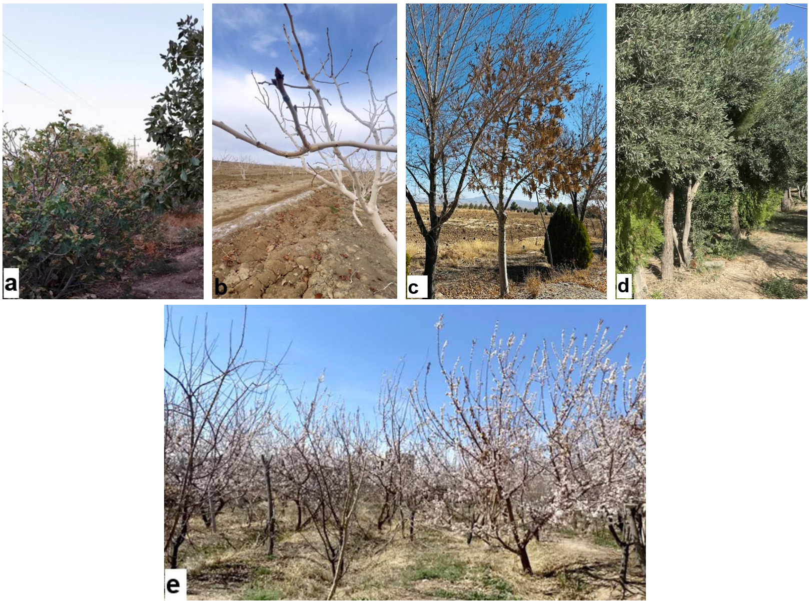

Figure 2. Sampling regions: a) Silu; b) Ebrahim abad; c) Faculty of Agriculture; d) Allameh Majlesi Boulevard; e) Baft Ghadim.

Arthropods Present within the Oothecae of These Two Species.

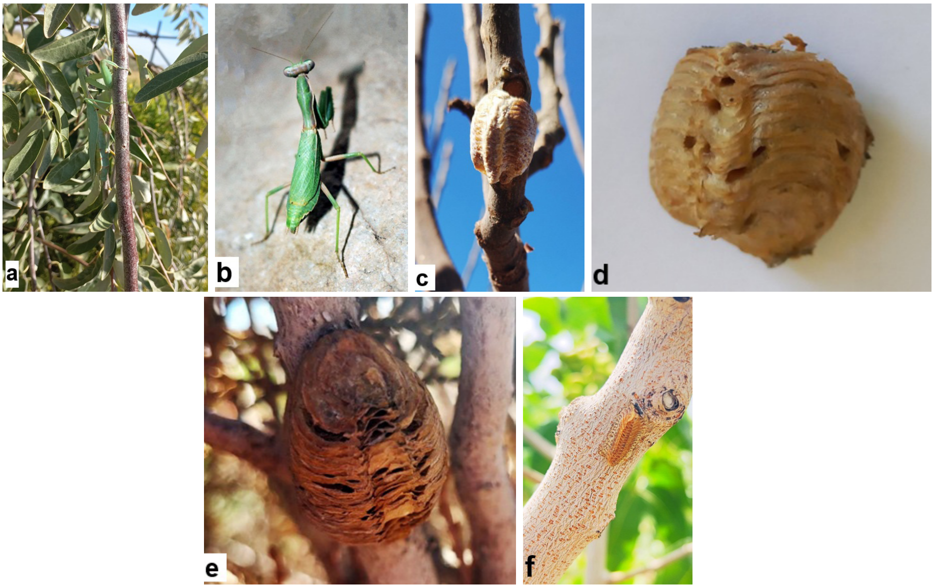

Figure 3. Mantids and their oothecae. a) *Hierodula tenuidentata*; b) *Iris oratoria*; c) bright and new oothecae of *Hierodula tenuidentata*; d) oothecae of *Hierodula tenuidentata* with small perforations; e) dark and old oothecae of *Hierodula tenuidentata* with deep holes and cracks; f) new oothecae of *Iris oratoria*.

Field observations indicated that 23 of the 32 collected oothecae (71.9%) from *H. tenuidentata* and *I. oratoria* successfully hatched, producing nymphs at varying densities and exhibiting a notable female bias (Table 2). the hatching rate for *H. tenuidentata* and *I. oratoria* were obtained 92% and 81%, respectively. The remaining nine oothecae (28.1%) did not hatch, likely due to reduced viability associated with aging. *H. tenuidentata* oothecae hatched 40-50 days post-collection in early May 2024, whereas *I. oratoria* oothecae required 50-60 days, hatching in late May.

Table 2- Number of parasitoid and arthropod emerged in association with mantid oothecae.

Regions	Mantid emergence from ootheca	Parasitoids	Parasitoid total number	Male number of parasitoids	Female number of parasitoids	Co-existing fauna in oothecae	arthropod number
Bastam	47	*P splendens,* *M. megachilis*	20 1	3 -	17 1	Fly (*Meoneura* sp.), Mosquite (*Lycoriella* sp., Cecidomyiidae, Psychodidae), Ant (*Crematogaster inermis*)	35
Shahrood	51	-	-	-	-	-	-
Meyami	66	*P. splendens,* *P. gibbum*	15 1	2 -	13 1	-	-
Semnan	1765	*P. bouceki*	118	37	81	Fly (*Meoneura* sp.), Lace wing (Hemerobiidae)	3
Bardaskan	51	*P. splendens*	12	3	9	Ant (*Pheidole* sp.)	3

Four parasitoid wasp species emerged from *H. tenuidentata* oothecae collected from all sites except Shahrood. These included *Podagrion splendens* (Spinola, 1811) (Hymenoptera: Toryminae), *Podagrion gibbum* (Bernard, 1938) (Hymenoptera: Toryminae), *Podagrion bouceki* (Delvare, 2005) (Hymenoptera: Toryminae), and *Melittobia megachilis* (Packard, 1864) (Hymenoptera: Eulophidae). In contrast, only *P. splendens* emerged from *I. oratoria* oothecae (Fig. 4 a-f).

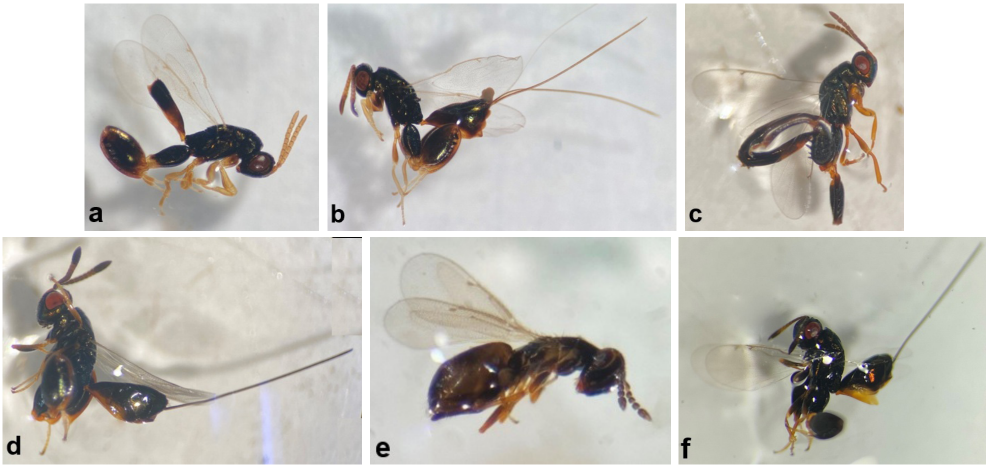

Figure 4. Parasitic wasps of mantis oothecae, *Hierodula tenuidentata* and *Iris oratoria*: a) *Podagrion bouceki*, male; b) *Podagrion bouceki*, female; c) *Podagrion splendens,* male; d) *Podagrion splendens,* female; e) *Melittobia megachilis*, female; f) *Podagrion gibbum,* female.

The Silu site in Semnan Province yielded the highest emergence numbers, with 1,765 mantid nymphs and 118 parasitoid wasps all identified as *P. bouceki* (Table 2). Taxonomic analysis showed that *Podagrion* species comprised nearly the entire parasitoid assemblage. *P. bouceki* was the most abundant, *P. splendens* appeared at intermediate frequency, and only a single specimen of *P. gibbum* was recorded (from the Meyami region). *M. megachilis* was the sole non-*Podagrion* species identified.

Taxonomic account

Order: Hymenoptera Linnaeus, 1758
Superfamily: Chalcidoidea Latreille, 1817
Family: Torymidae Walker, 1833
Genus: *Podagrion* Spinola, 1811

Podagrion bouceki (Delvare, 2005)

Material examined: 37♂♂, 81♀♀; Semnan Province, Semnan, Iran, 24.03.2024, 27.03.2024, and 03.04.2023; Coll. M. Ajamhassani.

Comments: In the present study, *P. bouceki* was recorded for the first time emerging from *H. tenuidentata* oothecae attached to fig trees in Semnan. This species is distributed across the Palearctic region, including Morocco, Portugal, Spain, France, Corsica, Greece, Oman, and Iran (Delvare, 2002). It has also been reported in Senegal, Gambia, Guinea, Burkina Faso, Ivory Coast, Benin, Cameroon, Somalia, and South Africa (Delvare, 2005). Previous rearing records include oothecae of *Empusa pennata* (Thunberg, 1815) and *Mantis religiosa* (Linnaeus, 1758).

Podagrion gibbum (Bernard, 1938)

Material examined: 1♀; , Semnan Province, Meyami, Iran, 11.05.2024, Coll. M. Ajamhassani.

Comments: In Iran, a single female specimen of *P. gibbum* was recovered for the first time from a *H. tenuidentata* ootheca attached to a plum tree in the Meyami region. This species has previously been reported from Spain, France, and Greece and is likely distributed across the northern Mediterranean Basin. It has been reared from *I. oratoria*, *M. religiosa*, *Ameles decolor* (Charpentier, 1825), and *Ameles spallanzania* (Rossi, 1792) (Bernard, 1938; Grissell, 1995; Delvare, 2005). The type series was originally described from an *E. pennata* egg case; however, no additional records have been reported from this host since, despite extensive sampling throughout the Mediterranean region (Delvare, 2005).

Podagrion splendens (Spinola, 1811)

Material examined: 3♂♂, 17♀♀; Semnan Province, Bastam, Iran, 28.04.2024 and 14.05.2024, Coll. M. Ajamhassani; 2♂♂, 13♀♀; Semnan Province, Meyami, Iran, 11.05. 2024; Coll. M. Ajamhassani 3♂♂, 9♀♀; K. Razavi Province, Iran, 11.05.2024, 02.06.2024, and 4 June 2024; Coll. M. Ajamhassani.

Comments: In the current study, *P. splendens* was recorded for the first time from *Hierodula tenuidentata* oothecae attached to apple and plum trees in Bastam and to plum trees in Meyami. Additionally, specimens were recovered from *Iris oratoria* oothecae found on pistachio trees in Bardaskan. This species has been documented in Russia and Ukraine (Nikolskaya, 1952; Zerova & Seryogina, 1999), as well as Morocco, Spain, southern France, Italy, and Greece (Delvare, 2005). It has previously been reared from oothecae of *Empusa egena* (Charpentier, 1841) and *M. religiosa.*

Family: Eulophidae Westwood, 1829
Genus: *Melittobia* Westwood, 1848

Species in this genus are gregarious ectoparasitoids or hyperparasitoids of Hymenoptera, though they may also parasitize other insects, particularly those found near wasp nests (Assem & Maeta, 1978; LaSalle, 1994).

Melittobia megachilis (Packard, 1864)

Material examined:1 ♀; collected in Iran, Semnan Province, Bastam; collection date: 25 May 2024; collector: Maryam Ajamhassani

Comments: The rearing of *M. megachilis* (Hymenoptera: Eulophidae) is reported here for the first time in Iran. This also represents the first record of any *Melittobia* species emerging from the oothecae of mantids (Insecta: Mantodea). Previously, *M. megachilis* had only been recorded from the United States (Peck, 1963; Burks, 1979). Its occurrence in Iran marks the first known record of this species within the Palaearctic region. Known hosts of *M. megachilis* include three species from the family Apidae and three from Sphecidae (Peck, 1963; Burks, 1979; LaSalle, 1994), all within the superfamily Apoidea (Insecta: Hymenoptera), as well as *Monodontomerus* sp. (Torymidae: Chalcidoidea) (Peck, 1963; Burks, 1979).

In addition to mantids and parasitoid wasps, various other insects emerged from oothecae, including flies, ants, and a neuropteran species. These specimens were recovered from oothecae collected in Bastam, Semnan, and Bardaskan. No insects other than mantid nymphs emerged from oothecae collected in Shahrood, while only mantids and parasitoid wasps emerged from Meyami samples.

The identified insects included *Meoneura* sp. (Diptera: Carnidae), *Lycoriella* sp. (Diptera: Sciaridae), *Pheidole* sp. (Hymenoptera: Formicidae), and *Crematogaster inermis* (Hymenoptera: Formicidae: Crematogastrini). Due to limited specimen numbers, some taxa could only be identified to the family level, precluding detailed morphological or genitalia-based assessments. These included Cecidomyiidae (Micromyinae), Psychodidae (Diptera), and Hemerobiidae (Neuroptera) (Fig. 5 a-h; Table 2). The highest insect abundance was observed in oothecae collected from the Faculty of Agriculture in Bastam, where ants comprised 22 of the 35 specimens; the remaining individuals were various dipteran species.

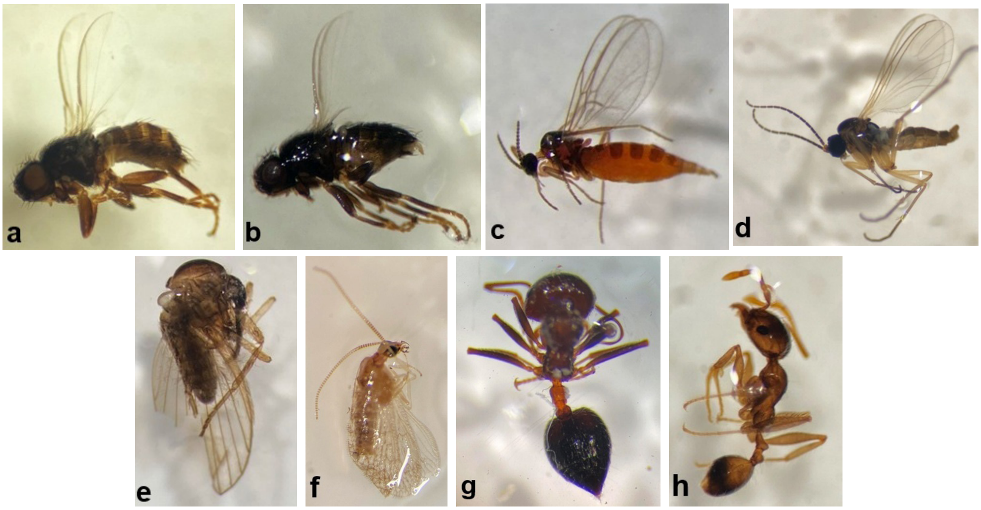

Figure 5. Arthropods communities in oothecal microhabitats of *Hierodula tenuidentata* and *Iris oratoria*: a, *Meoneura* sp. male; b, *Meoneura* sp. female; c, *Lycoriella* sp. female; d, species of the family Cecidomyiidae, e, species of the family Psychodidae; f, species of the family Hemerobiidae; g, *Crematogaster inermis;* h, *Pheidole* sp.

Table 3 summarizes the number of oothecae collected from Semnan and Bastam, organized by host tree species. Data from Tables 2 and 3 reveal that: (1) The highest number of mantid nymphs (n = 1765) emerged from oothecae collected in Silu, Semnan.

Arthropods Present within the Oothecae of These Two Species.

(2) All parasitoid wasps recorded in Semnan (n = 118) emerged from two oothecae located on fig trees.

(3) The two oothecae found on apple trees in Bastam yielded the highest arthropod density (n = 33) among all tree types surveyed.

All co-existing fauna reported in this study are newly recorded in association with the oothecae of *H. tenuidentata* and *I. oratoria*, thereby establishing both mantid species as new host records.

Table 4 show the recorded Flies associated with mantids oothecae from the world.

Table 3. Mantid emergence from ootheca, parasitoids number and arthropod number in association with host plants of Silu and Faculty of Agriculture regions.

Regions	Host Plant	Ootheca number	Mantid emergence from ootheca	Parasitoids number emergence from ootheca	Co-existing fauna number in oothecae
Silu (Semnan)	*Ficus* sp.	2	540	118	3
	Pistacia sp.	2	277	-	-
	Punica sp.	2	374	-	-
	Morus sp.	2	481	-	-
	Fraxinus sp.	1	93	-	-
Faculty of Agriculture (Bastam)	*Malus* sp.	2	25	20	33
	Prunus sp.	2	17	1	2
	Pinus sp.	2	5	-	-

Table 4. Recorded Flies associated with mantids oothecae from the world.

Fly Species	Fly Family	Mantid Species	Country	References
Gaurex sp.	Chloropidae	*Archimantis latistyla* (Serville) (Mantodea: Mantidae)	South Wales	Coombs (1994)
Lasiambia mantivora Nartshuk.	Chloropidae	*Mantis religiosa* (Linnaeus, 1758) (Mantodea: Mantidae)	Spain	Nartshuk & Sánchez (2010)
Polyodaspis picardi Séguy, 1946	Chloropidae	*Mantis* sp. (Mantodea: Mantidae)	South France	(Séguy, 1946, 1951, 1957)
Pseudogaurax mantivorus Séguy, 1941	Chloropidae	*Mantis* sp. (Mantodea: Mantidae)	Madagascar	(Séguy, 1946, 1951, 1957)
Pseudogaurax longinervis Sabrosky	Chloropidae	*Mantis* sp. (Mantodea: Mantidae)	-	Sabrosky (1945)
Pseudogaurax elachipteroides Sabrosky, 1945	Chloropidae	*Sphodromantis* sp. Stal, 1877 (Mantodea: Mantidae)	Africa	Sabrosky (1945)
Kurumemyia ongamea Kanmiya, 1983	Chloropidae	*Tenodera angustipennis* (Saussure, 1869) (Mantodea: Mantidae)	Japan	Kanmiya (1983)
Pseudogaurax signatus (Loew, 1876)	Chloropidae	*Unknown mantid ootheca*	North America	Loew (1876)
Pseudogaurax anchora (Loew, 1866)	Chloropidae	*Unknown mantid ootheca*	North America	Loew (1866)
Lioscinella tonnoiri Malloch, 1931	Chloropidae	*Unknown mantid ootheca*	Australia	Malloch (1931)
Polyodaspis picardi Séguy, 1946	Chloropidae	*Unknown mantid ootheca*	Southern France	Séguy (1946)
Meoneura sp.	Carnidae	*Hierodula tenuidentata* Saussure, 1869 (Mantodea: Mantidae)	Iran	this paper
Lycoriella sp.	Sciaridae	*Hierodula tenuidentata* Saussure, 1869 (Mantodea: Mantidae)	Iran	this paper
Unknown species	Cecidomyiidae (Micromyinae)	*Hierodula tenuidentata* Saussure, 1869 (Mantodea: Mantidae)	Iran	this paper
Unknown species	Psychodidae	*Hierodula tenuidentata Saussure, 1869* (Mantodea: Mantidae)	Iran	this paper

DISCUSSION

Although previous studies have reported *Podagrion* spp. as oothecal parasitoids of mantids (Thorette, 1992; Farooqi, 1986; Herting, 1971; Grissell, 1995; Delvare, 2005; Bernard, 1938), this study presents the first documented record of all four species parasitizing *H. tenuidentata* and *I. oratoria*. The highest parasitoid emergence was observed from two oothecae collected in the Semnan region (Silu), which were exclusively *P. bouceki*, indicating a markedly higher parasitism rate by this species compared to others. In contrast, no parasitoids were recovered from oothecae collected in the Shahrood region.

As shown in Table 1, in the two regions Silu and the Faculty of Agriculture, the number of collected oothecae was 9 and 6, respectively, which was higher than in the other areas (2-3 oothecae). Additionally, the oothecae were found on various tree species in these two regions, whereas in Meyami, Shahrood, and Ebrahimabad they were found on only single tree host (Table 1). Furthermore, Tables 2 and 3 show that the number of parasitoids and co-existing fauna associated with the oothecae in Silu and the Faculty of Agriculture—particularly in Silu—was higher than in the other regions. This difference among regions can be explained by the fact that the trees in both Silu and Faculty of Agriculture are not treated with pesticides. Instead, other control methods and biological control approaches are used to protect both fruit and non-fruit trees. In contrast, the olive trees in the green space of Shahrood, the plum orchards in Meyami, and the pistachio orchards in Ebrahimabad are sprayed with pesticides several times each year. As a result, pest populations—and consequently predators and parasitoids—are significantly reduced in these areas. In Silu, there is a rich fauna of insects of various body sizes, which provides more suitable conditions for mantid feeding and oviposition compared with other areas. In Silu, in addition to mantids, we observed a high diversity of Coccinellidae and Araneae groups throughout the cropping season, confirming the presence of abundant prey in the area (data unpublished).

These spatial differences in parasitism are consistent with previous findings by Mirzaee, Lotfalizadeh & Sadeghi (2021a), who reported parasitism rates ranging from 38% (*I. oratoria* parasitized by *Iridophagoides petiolatus*) to 92% (*Holaptilon* sp. parasitized by *Palachia pulchra*).

Environmental variables such as temperature, humidity, host plant species, and anthropogenic chemical exposure are known to influence insect-parasitoid dynamics (Wetherington et al., 2017; Chidawanyika et al., 2019). In this study, host plant identity strongly influenced parasitism patterns. In Silu, all parasitoids emerged from two oothecae attached to fig trees, which also exhibited higher nymph emergence rates compared to oothecae on mulberry, pomegranate, pistachio, and ash. Similarly, in Bastam, apple trees supported significantly higher parasitoid abundance (n = 20 from two oothecae) than plum (n = 1) or pine (none).

It should also be noted that fig trees in Silu and apple trees in Bastam are planted densely, the dense canopy creates a cool, humid and shaded environment. It seems that this condition with absence of pesticides effect on the high population of parasitoids. While, trees distance was 2-3 m in other areas. These plant-specific patterns of parasitoid emergence contribute to a broader understanding of trophic interactions and may have implications for integrated pest management, given mantids' established role as biological control agents (Moran & Hurd, 1998; El-Gepaly, 2020).

Prior to this study, no species of the genus *Melittobia* had been recorded from the oothecae of mantid species (UCD Community, 2023). Members of this genus are typically gregarious ectoparasitoids or hyperparasitoids that target the larval or pupal stages of solitary bees and wasps when suitable hosts are available (Dahms, 1984; Freeman & Ittyeipe, 1993). It is therefore plausible that the structural resemblance between mantid oothecae and solitary wasp nests may lead *M. megachilis* to encounter and parasitize *Podagrion* species via hyperparasitism. The absence of male *M. megachilis* in the current study—and more broadly, the rarity of males across the genus—has been consistently noted in previous literature (Assem & Maeta, 1978; Dahms, 1984; Gonzalez, Teran, & Matthews, 2004). Typically, males emerge several days before females and engage in lethal combat, often eliminating competing male pupae before they emerge. In many cases, a single male survives and subsequently mates with all emerging females (Gonzalez et al., 2004).

In addition to parasitoids, a range of other insect taxa, predominantly ants and flies, emerged from the collected oothecae, supporting the characterization of these oothecae as microhabitats for diverse co-existing fauna assemblages. Of particular ecological relevance are the potential antagonistic interactions among co-inhabitants, which may influence mantid recruitment and survival. These observations are consistent with earlier reports documenting a broad spectrum of arthropods, including flies, ants, spiders, pseudoscorpions, thrips, beetles, and parasitoid wasps, associated with mantid oothecae (Cassar, 2016; El-Gepaly, 2020; Mirzaee, et al., 2022a; Plonski, Radac, & Cassar, 2021).

Notably, 22 individuals of the predatory ant *C. inermis* were recovered from apple tree oothecae in Bastam. This observation aligns with established evidence of ant-arthropod interactions, particularly the chemical cue-mediated predation behavior exhibited by *Crematogaster* species toward various hymenopterans (Schatz, Anstett, Out, & Hossaert-Mckey, 2003). Sharaf (2005) also demonstrated that several ant genera actively prey on arthropod eggs. The association between *C. inermis* and mantid oothecae observed here supports earlier findings by Mirzaee et al., (2022a) in *H. tenuidentata*, suggesting that ant presence may considerably influence both mantid and parasitoid emergence dynamics. Additionally, *Pheidole* sp. was recorded from *I. oratoria* oothecae. This genus, which accounts for approximately 8% of all described ant species, exhibits high ecological dominance and is particularly diverse in tropical ecosystems (Wang, Li, Zhng, & Chen, 2018).

A single brown lacewing (Neuroptera: Hemerobiidae) was also recovered from an *H. tenuidentata* ootheca in Semnan. Given that both larval and adult stages of Hemerobiidae are known predators of soft-bodied insects such as aphids and adelgids, their presence may indicate potential trophic interactions within the oothecal microhabitat. This finding complements previous observations by Mirzaee et al.

(2021a), who reported *Semidalis* sp. (Coniopterygidae: Conwentziini) inhabiting *H. tenuidentata* oothecae, further confirming the ecological complexity of these structures.

Diptera, known for their extensive ecological versatility, were also frequently observed. As one of the most taxonomically and functionally diverse insect orders, Diptera display considerable morphological variation and inhabit a wide range of ecological niches (Pape, 2009; Marshall, 2012). Their larvae exhibit a broad spectrum of feeding strategies, including herbivory, saprophagy, predation, and scavenging (Courtney, Pape, Skevington, & Sinclair, 2017). In this study, oothecae of *H. tenuidentata* yielded dipteran specimens from four families with distinct ecological roles: Carnidae, Sciaridae, Cecidomyiidae, and Psychodidae. Carnid larvae are typically saprophytic and associated with bird nests and droppings (Brake, 2010). Sciarid larvae feed primarily on decaying plant material and fungal tissues (Shin et al., 2013; Vergara-Pineda, Toledo-Hernández, Rodríguez, & Jones, 2025). Cecidomyiid larvae exhibit both predatory and gall-inducing behavior depending on species (Skuhrava & Skuhravy, 1992a, 1992b). Psychodid larvae inhabit microbe-rich, decomposing substrates and feed on organic matter and microorganisms in the soil (Brazil, Carneiro, Filho, Alves, & Falcão, 1997).

The present findings underscore the ecological relevance of mantid oothecae as microhabitats supporting a range of dipteran species, many of which may engage in scavenging or predation. The inclusion of Table 4, referencing earlier studies, reinforces the notion that mantid oothecae represent structurally and ecologically significant niches for Diptera.

Investigating species interactions within these confined habitats provides valuable insights into broader ecological processes. This study demonstrated that oothecae of *H. tenuidentata* and *I. oratoria* serve not only as protective structures for mantid offspring but also as microhabitats that harbor co-existing fauna, some of which may exhibit antagonistic or predatory behavior. Although the dataset was constrained by limitations in ootheca availability and sampling logistics, the patterns observed highlight the potential complexity of community-level interactions within these microhabitats. Continued research into ootheca-associated assemblages may deepen understanding of mantid population ecology and yield broader insights into co-existing fauna community dynamics in ephemeral, structurally unique environments.

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Arthropods Present within the Oothecae of These Two Species.

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