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New host, old tactic: first record of the parasitism on allochthonous *Hierodula* oothecae by *Mantibaria seefelderiana* in Europe (Mantodea: Mantidae; Hymenoptera: Scelionidae)

Antonio FASANO[1,*], Alessio DE MARTINO[2]

[1] *Università degli studi di Salerno, Via Giovanni Paolo II, 132, 84084 Fisciano, Salerno province, Italy* – mantisdroxita@gmail.com; ORCID: https://orcid.org/0000-0003-3030-1982
[2] *Università degli studi di Modena e Reggio Emilia (Unimore), Via Università, 4, 41121 Modena province, Italy* – alessiodemartino2004@gmail.com
*Corresponding author

Abstract
This study reports the first record of parasitic activity by *Mantibaria seefelderiana* (De Stefani, 1891) (Hymenoptera: Scelionidae) in Italy targeting *Hierodula patellifera* (Audinet-Serville, 1839), an alien mantid species of Asian origin that has spread in several regions of the country. *M. seefelderiana*, known for its specialization as a mantis oothecal parasitoid, had not previously been associated with exotic hosts in the Italian territory. Observations were conducted between summer and autumn 2024 in urban and peri-urban environments in northern Italy. Adult specimens of *M. seefelderiana* were found on several adult females of *H. patellifera*, suggesting active host-seeking behavior. Furthermore, the parasitism process on the oothecae was directly observed and documented—photographically and through video recordings—for the first time, confirming *H. patellifera* as a possible suitable host. This finding represents a notable example of trophic interaction between a native parasitoid and an introduced mantid species, with potential implications for the population dynamics of invasive mantids and the adaptive flexibility of native natural enemies. This record expands current knowledge of the biology of *M. seefelderiana* and provides a foundation for future research into its possible role as a natural control agent against non-native Mantodea in Europe.

Keywords: alien mantids, *Hierodula*, *Mantibaria*, parasitoids, trophic interactions.

Introduction

Hierodula Burmeister, 1838 is a genus of mantids belonging to the family Mantidae, subfamily Mantinae and tribe Hierodulini, characterized by a more or less robust body, broad head, pronotum with moderately marked supracoxal dilatation, and well-developed flight organs in both sexes (Battiston et al. 2010). Currently, more than a hundred species are known (Otte & Spearman 2025), although the taxonomy and phylogeny of the Hierodulini are not yet well defined, and synonyms in this large group of mantids are frequently rediscussed and updated, especially between the genera *Hierodula*, *Rhombodera*, *Titanodula* and *Sphodromantis* (Battiston & Massa 2008; Vermeersch 2020; Vermeersch & Unnahachote 2020). The native range of distribution of this genus is very wide and ranges from the Caucasus regions to Oceania, passing through mainland Asia, the islands of Japan, south-east Asia and the Indonesian archipelago. Two species, both allochthonous, are currently present in Italy:

The Indochinese giant mantis or Harabiro mantis [(*Hierodula patellifera* (Audinet-Serville, 1839)], is a species native to the Far East and widespread in China, Taiwan, India, Nepal, Japan, Korea, Singapore, Vietnam, Thailand, Malaysia, the Philippines, Java, and Sumba (Patel & Singh 2016; Oshima 2021). In Europe, it appears to have first arrived in France (Moulin 2020), and was then reported in Italy, in the Veneto and Lombardy regions (Battiston et al. 2019, 2020), in Croatia (Martinovic et al. 2022). According to the data available in Battiston et al. (2020), a possible dynamic of distribution in Italy for this species has been proposed: adult individuals or oothecae, carried on wooden artifacts, exotic plants, or other goods from the East, starting from a single point, such as a wholesale market, a commercial warehouse, or a train station, subsequently reach retail outlets and citizens' homes located in residential areas. On the other hand, one is less inclined to speculate that the introduction of this species was caused by hobbyists who bred and subsequently released specimens or oothecae into the environment, although *Hiero-*

Fig. 1 – The first specimen of *Mantibaria seefelderiana* begins to position itself at the site of oviposition chosen by the female *Hierodula patellifera*. Photo: Alessio De Martino.

Fig. 2 – The second parasitoid explores different sections of the ootheca, ultimately tracing a semi-circular path around its perimeter. Photo: Alessio De Martino.

dula patellifera seems to be quite common among insect breeders and is often found for sale on some websites.

The Asian giant mantis [(*Hierodula tenuidentata* (Saussure, 1869)], is a species with a truly extensive native range, including the Caucasus, central Asia and the Indian subcontinent (Ehrmann & Borer 2015; Schwarz et al. 2018; Mirzaee et al. 2022). In recent years there has been a rapid expansion of its distribution, coming both to occupy several territories north of its range, such as new areas of Ukraine and Russia (Pushkar & Kavurka 2016), but especially colonizing many new countries in Central and Southern Europe. This study was conducted with the aim of documenting the parasitic interaction between *Mantibaria seefelderiana* (De Stefani, 1891) and the exotic mantid species *Hierodula patellifera* in northern Italy. The interpretation of this association, however, is influenced by the long-standing taxonomic uncertainties surrounding the genus *Mantibaria*.

Since its original description, *M. seefelderiana* has never been subjected to a modern revision, and its distinction from other nominal Palearctic taxa remains unresolved. Early descriptions were based on limited material, and subsequent catalogues and taxonomic overviews have simply reiterated historical classifications without reassessment in the light of new data. This lack of consensus has been further compounded by the almost complete absence of molecular studies and the scarcity of detailed comparative morphological analyses. No phylogenetic framework currently exists for *Mantibaria*, and it is therefore unclear whether the nominal species recognized within the genus represent valid evolutionary lineages or are instead synonyms of a single, variable taxon. Consequently, the actual diversity and distribution of *Mantibaria* across the Palearctic remain uncertain and cannot be reliably interpreted without a comprehensive systematic revision. These unresolved taxonomic issues have direct implications for the interpretation of host–parasitoid associations. If all Palearctic populations of *Mantibaria* prove to be conspecific, records attributed to different species would need to be consolidated under a unified taxonomic framework, leading to a substantial revision of the known biogeographic and ecological patterns. Conversely, if cryptic species do exist, they may differ in host range or distribution, fundamentally changing our understanding of their interactions with both native and alien mantids. In this context, the case of *M. seefelderiana* in northern Italy cannot be fully understood without first addressing the broader systematic uncertainty affecting the genus as

Fig. 3 – The first parasitoid remains fixed in its initial spot for the entire reproductive process, whereas the second displays increased movement and adaptability in its behavior. Photo: Alessio De Martino.

a whole. Only an integrated approach combining morphological revision, molecular phylogenetics, and ecological data will be able to resolve these long-standing controversies and provide a reliable basis for interpreting the dynamics between *Mantibaria* and its mantid hosts, including the invasive *Hierodula patellifera*.

In recent decades, the accidental or intentional introduction of exotic species has profoundly altered the faunal composition of numerous ecosystems, contributing to the emergence of new and often unpredictable ecological dynamics (Mack et al. 2000). Among the alien insects recently reported in Europe, Asian praying mantids are gaining increasing relevance (Di Pietro et al. 2023), both due to their spread in urban and peri-urban environments and to the potential interactions they may establish with local fauna, including predators, competitors, and parasitoids. *Hierodula patellifera*, one of the most frequently introduced species (iNaturalist 2025), has found favorable conditions in several Italian regions, where it is now regularly reported. However, knowledge regarding its integration into local trophic networks remains limited.

In the regions where these mantids are native, they are effectively regulated by natural predators as well as a wide array of parasites and parasitoids, including nematomorph worms and various hymenopterans that have specialized in laying their eggs inside mantid oothecae, exploiting them as a nutritional resource. These natural control agents represent a fundamental component for maintaining ecological balance in their original habitats (Ehrmann 2002).

Within the European context, and particularly in Italy, several ootheca-parasitizing parasitoids associated with native mantids are present, although their diversity and ecological impact remain poorly understood. Among the few known representatives, *Mantibaria seefelderiana* (De Stefani, 1891) is of particular interest. It is actually the only European representative of the genus *Mantibaria*, a scelionid hymenopteran (Scelionidae: Scelioninae) highly specialized in exploiting the oothecae of various mantid species, within which it lays its eggs. The larvae, upon development, feed on the host eggs, ultimately compromising the entire clutch (Maglić & Žikić 2021). Its distribution in Mediterranean areas and the observed trophic specialization suggest a close evolutionary adaptation to local Mantodea species, while also raising questions about its potential ability to recognize and parasitize non-native hosts.

The possibility that an autochthonous parasitoid such as *M. seefelderiana* could utilize *H. patellifera* oothecae as a trophic resource had never before been documented. Such an interaction, if confirmed, would suggest a rapid ecological adaptation of the parasitoid to a new potential

host, expanding the range of interactions between native fauna and exotic species. The implications of this dynamic are multifaceted: on one hand, it could represent a natural form of biological control against the alien species; on the other, it might influence the biology of the parasitoid itself, potentially inducing changes in its phenology, oviposition behavior, or host selectivity.

In the present contribution, we report for the first time the potential ability of *Mantibaria seefelderiana* to exploit the oothecae of *Hierodula patellifera* as a substrate for larval development. This observation opens a new perspective in the study of interactions between native and alien species, suggesting that, in a context of increasing synanthropy and anthropogenic pressure on ecosystems, even native parasitoids may rapidly expand their ecological preferences to include recently introduced hosts. This evidence contributes to a more comprehensive understanding of the emerging trophic dynamics in urban and natural systems, and represents a starting point for further investigations into the potential role of parasitoids in the biological control of exotic Mantodea naturalized in Italy.

Materials and methods

The research began with the active collection of adult females of *H. patellifera* during the summer of 2024 in the province of Padua (Veneto region). Eight specimens were located and collected through visual search in urban and peri-urban environments, particularly in green areas such as gardens, hedgerows, and tree-lined streets, where the species is known to be well established. Collected specimens were carefully transported to a controlled laboratory environment for captive rearing and observation.

Each mantis was housed individually in a plastic terrarium measuring 22 × 14 × 25 cm. The enclosures were equipped with three mesh-covered sides to ensure adequate ventilation, and the bottom was lined with absorbent paper to maintain proper humidity levels. Environmental parameters were monitored and regulated to mimic natural conditions and to promote normal reproductive behavior. The enclosures were inspected daily to monitor the health and behavior of the mantids, with particular attention given to oviposition events and potential signs of parasitism.

During routine observations, several female *H. patellifera* specimens were found to carry small hymenopteran individuals on their bodies. This unexpected finding led to a focused effort to document the potential parasitic interaction. Suspecting the involvement of scelionid parasitoids, a systematic photographic and video documentation of the oviposition process using a Samsung Galaxy S10e smartphone was set up. Recordings were carried out in real-time within the rearing containers, capturing both the deposition of mantid oothecae and the simultaneous behavior of the suspected parasitoids.

Following oviposition, the oothecae were not removed but kept in the same containers alongside the adult mantids to allow for natural incubation. Particular care was taken to maintain consistent temperature and humidity conditions throughout the incubation period, as these factors are

Fig. 4 – *Mantibaria seefelderiana*: ventral view. Photo: Mary Antonio Donatello Todaro & Alessio De Martino. Scale bar: 1000 µm.

known to influence both host and parasitoid development (Salt & James 1947). Conditions were monitored using standard digital thermohygrometers, and the enclosures were kept in a laboratory setting shielded from direct sunlight and with minimal disturbance.

To confirm the identity of the hymenopteran parasitoids, adult specimens were examined under optical microscopy using the standard equipment available in the biology laboratories of the University of Modena and Reggio Emilia (Unimore). Morphological identification was conducted with the aid of current dichotomous keys and relevant taxonomic literature. Specimens were compared to published descriptions and illustrations to ensure accurate classification. No molecular analyses were conducted thus far.

Results

Material examined

Hierodula patellifera (Audinet-Serville, 1839):
ITALY: 8 ♀; Veneto, Padua province, Montegrotto Terme; 45°19’51.1”N 11°47’45,5”E; 45°19’40.01”N 11°47’25.8”E 11 m a.s.l.; 14 Sept. 2024; found on tree vegetation at the edge of a road; Alessio De Martino leg.

Mantibaria seefelderiana (De Stefani, 1891):
ITALY: 3 ♀; Veneto, Padua province, Montegrotto Terme; 45°19’40.01”N 11°47’25.8”E; 11 m a.s.l.; 14 Sept. 2024; Alessio De Martino leg.

During field sampling conducted in September 2024 in Montegrotto Terme, in the province of Padua (Northeastern Italy), researchers collected a total of eight adult female specimens of *Hierodula patellifera*. Among these individuals, two, representing 25% of the total sample, carry adult parasitoids identified as belonging to the Hymenopteran family Scelionidae. Each infested female hosts exactly two adult parasitoids. These parasitoids consistently anchor themselves on the thoracic region of the mantid, specifically at the base of the wings, between the mesothorax and metathorax. This location appears highly strategic, as it allows the parasitoids to remain firmly attached while remaining relatively undisturbed by the host’s movements or grooming behavior. Throughout their observed activity, the adult parasitoids do not detach from the host, even after the reproductive event concludes, instead maintaining their position until natural death, a behavior previously described in cases of scelionid parasitism in *Mantis religiosa* Linnaeus, 1758 (Chopard 1922).

A particularly detailed case of parasitic behavior was documented in the early morning hours during the deposition of an ootheca by one of the infested *H. patellifera* females. The event begins at approximately 7:15 AM, with both parasitoids positioned laterally on the host’s abdomen, one on the right and one on the left. The parasitoid on the right immediately shows significant motor activity, moving along the abdominal surface of the mantid until it reaches the margin of the ovipositor. It then assumes a stable position, orienting its abdomen toward the forming ootheca and its head toward the mantid’s body. This alignment seems optimal for precise and effective parasitic egg deposition. Meanwhile, the parasitoid on the left remains immobile for roughly 30 minutes. During this time, the female mantid begins to produce the initial foamy layers that constitute the ootheca’s structure. Shortly after oviposition begins, the right-side parasitoid extends its abdomen and everts its ovipositor in a pronounced fashion, initiating the insertion of parasitic eggs into the forming spongy matrix. The motion is both deliberate and deep, as the parasitoid immerses much of its abdomen into the foam (Fig. 1), securing the eggs in a well-protected location within the soft, freshly secreted material. Approximately 30 minutes later, the left-side parasitoid begins to move, although its movements are less coordinated and more erratic. It approaches the host’s cerci, triggering a defensive reaction: the mantid attempts to shake off the intruder using her hind legs. Despite this, the parasitoid continues undeterred, relocating from its original position toward the ovipositor and finally onto the developing ootheca, where it begins to lay eggs. Unlike the first parasitoid, which remains localized, the second shows a more itinerant pattern of activity. After initiating oviposition on the most recently secreted layers of foam, the parasitoid moves across various areas of the ootheca, eventually performing a semi-circular route along the edge of the structure (Fig. 2). This roaming behavior may serve to distribute parasitic eggs across a broader surface, potentially enhancing reproductive success by reducing intra-specific competition or predation risk. As the mantid continues her oviposition, the second parasitoid becomes momentarily encumbered by the frothy secretion, which limits its mobility and temporarily blinds it by covering its compound eyes. However, the parasitoid demonstrates effective self-grooming behaviors: it manages to clean at least one eye and regains visual capacity. Following this brief impediment, it secures a hold on one of the mantid’s cerci, climbs back up to the abdominal tip, and completes the cleaning process by removing residual foam. The parasitoid then rejoins the first individual at the base of the ovipositor, where both resume oviposition activities side-by-side. For the next one and a half hours, both parasitoids remain in proximity, showing minimal locomotion and consistent oviposition into the ootheca. The first parasitoid maintains its original position throughout the entire reproductive sequence, while the second continues to exhibit greater mobility and behavioral flexibility (Fig. 3). By 10:15 AM, as the mantid nears the end of her ootheca deposition, the first parasitoid ceases activity and shifts slightly upward on the ovipositor, inserting its abdomen

into the subgenital plate and leaving only its head and thorax visible. About ten minutes later, the second parasitoid follows suit, fully embedding itself into the same anatomical structure, to the point of becoming nearly invisible. The ootheca deposition concludes at 10:38 AM, at which point the only visible parts of the parasitoids are the upper regions of their heads. Notably, both parasitoids remain attached to the host after oviposition ends. They do not leave the body but instead remain embedded, entering a terminal behavioral state as they await natural death. This persistent association between parasite and host reflects a high degree of behavioral specialization and supports previous hypotheses about the life cycle of scelionids associated with mantids (Masner 1976). The duration and intensity of the parasitic activity are noteworthy, as is the absence of aggressive defensive reactions from the host. Although the mantid attempts to dislodge the second parasitoid, she largely tolerates their presence and completes her own reproductive process without abandoning or significantly altering her behavior. The event provides a valuable opportunity to observe the behavioral ecology of scelionid parasitoids in real-time, and suggests a co-evolutionary interaction that allows the parasitoid to exploit the host's reproductive behavior for its own ends. Moreover, differences in the two parasitoids' behavior may suggest varying reproductive strategies or levels of maturity: one displays stability and early oviposition, while the other exhibits more erratic, distributed egg-laying. These differences could be linked to physiological variation or hierarchical coordination between conspecifics, though further research is needed to determine the exact causes. This event, while singular, provides compelling insights into host-parasite interactions, behavioral adaptation, and the ecological role of scelionids in mantid life history. The results also confirm that scelionids exploit the exact moment of ootheca formation, a critical and vulnerable phase in the mantid's reproductive cycle, to insert their eggs within a freshly secreted structure that offers both protection and developmental resources.

General description of the *Mantibaria seefelderiana* specimens collected*:* To provide a clear reference for the specific specimens examined in this study, ensuring that their diagnostic traits are explicitly recorded, we consider it useful to add the following short re-description of the species.

Body flattened, dorsally dark brown, with the mesosoma nearly black. Head laterally rounded, slightly granulate on the frontal surface, brownish in color. Antennae brownish, composed of 11 segments, with flagellomeres tightly connected. Ocelli large. Mandibles short, dark brown with black apices, bearing three apical teeth. Maxillary and labial palps greatly reduced. Legs highly specialized for parasitism, short, uniformly brownish, with prominent claws on the metatarsus. Femora and tibiae are flattened. Both forewings and hindwings are hyaline, transparent, densely covered with short setae, and completely lacking venation. Wings are self-amputated as an adaptation to their parasitic behavior on the mantid host. The metasoma is shorter than the thorax and dark brown ventrally (Fig. 4).

Discussion

The discovery of adult specimens belonging to the genus *Mantibaria* in urban and peri-urban contexts, on adult individuals of *Hierodula patellifera*, represents a highly significant record, especially when placed within the current state of knowledge regarding the distribution and ecological interactions of these parasitic Hymenoptera. Although the finding cannot provide definitive evidence of a direct trophic relationship between the two taxa—due to the absence of fertile oothecae from which to verify possible emergence of the parasitoids—it nevertheless opens interesting hypotheses and research prospects in the fields of urban ecology, evolutionary biology, and the biogeography of specialized parasitoids.

Although parasitoids have historically been rarely considered in studies of biological invasions, recent research highlights that they can follow similar pathways as their hosts during geographic expansion processes. In particular, passive transport through international commercial flows may facilitate the accidental co-introduction not only of well-known organisms like mantids but also of their parasites and commensals (Oliveira & Schoeninnger 2017). The increasing documentation of Dryinidae and other parasitic Hymenoptera outside their native ranges supports the idea that these often inconspicuous insects can colonize new environments following their hosts or exploiting new urban ecological niches.

The Italian context, where *H. patellifera* has now become naturalized in several anthropized environments, is particularly suitable for observing such dynamics. The simultaneous presence of *Mantibaria* and *H. patellifera* in the same urban habitat—characterized by spontaneous vegetation and limited prey availability—cannot be considered a mere coincidence but rather a preliminary indication of a possible biological interaction between the two taxa. Although experimental confirmation is lacking, the hypothesis of a parasitoid-host relationship remains plausible and deserves further investigation.

The behavior defined as "hunter the hunters", meaning the tendency of certain parasitoids to colonize apex predators such as mantids, has recently been highlighted by several studies emphasizing its adaptive value. Such behaviors, in addition to representing a sophisticated form of parasitism, may have complex ecological implications, acting as indirect regulators of predator populations and contributing to the stability of trophic nerks (Kamila & Sureshan 2024). The observation of *Mantibaria* near mantids could thus fit within this theoretical framework, sug-

gesting an poorly studied role of these Hymenoptera in the ecology of urban entomological communities.

Furthermore, as reported by numerous authors, mantids are not immune to parasitism despite their high trophic position. Several insect groups, including some rare families of Hymenoptera, have been identified as potential parasitoids or predators of mantids. In this sense, *Mantibaria* fits perfectly within the overview provided by Ehrmann (2002), which includes a variety of trophic interactions involving mantids, although these are often poorly documented or overlooked. Therefore, the association observed in Italy may represent one of those cases that have so far escaped scientific attention.

The global presence of the genus *Mantibaria* has been documented in various tropical and subtropical regions, but the literature agrees that both taxonomy and distribution of the included species remain only partially known. Many authors emphasize that undescribed species may exist and that the current state of knowledge suffers from a severe lack of data from many geographic areas, particularly urban and anthropized contexts, where these insects can easily escape collection and classification efforts (Veenakumari et al. 2012). This makes every new observation particularly valuable, especially when it occurs in an area like southern Europe, where reports of Scelionidae associated with mantids (including native species) are quite rare (Caleca & Tortorici 2020).

In this specific case, the absence of emergence from the collected oothecae cannot be interpreted as a refutation of a possible trophic relationship. As previously noted, it is highly likely that the oothecae were infertile or unsuitable for parasitoid development, due to environmental conditions or lack of phenological synchronization. However, the finding of adult *Mantibaria* during the seasonal peak of activity of adult mantids, and in habitats frequented by them, suggests a non-random ecological overlap.

It cannot be excluded, furthermore, that *Mantibaria* uses mantids not only as hosts for reproduction but also as transportation means, in a form of phoresy already hypothesized for other Scelionidae or parasites such as mites (Kamila & Sureshan 2024). If confirmed, this behavior could explain the colonization of urban areas distant from origin sites, even in the absence of stable host populations. Phoresy would thus represent an important ecological strategy, functional to passive dispersal in heterogeneous and fragmented environments.

In light of these considerations, our finding can be interpreted as an important starting point for future research. In particular, it will be essential to conduct systematic monitoring, plan laboratory rearing of fertile *Hierodula* oothecae, and apply molecular tools for accurate identification of any emerging parasitoids. Longitudinal studies could also clarify the temporal dynamics of the interaction and evaluate the stability of *Mantibaria* populations in Italian urban contexts, as well as assess whether these parasitoids may have a significant impact on controlling populations of alien mantids, which currently seem to lack native predators or parasites limiting their spread.

Understanding the ecological role of *Mantibaria*, also in an evolutionary context, could ultimately help clarify the mechanisms by which parasitoids manage to colonize new habitats and their effects on the balance of urban trophic networks. In an era of rapid ecological changes and continuous biological introductions, observations like this are crucial to building a more complete picture of the hidden biodiversity animating our urban environments.

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Conflict of interest disclosure, Ethics approval statement

None conflicts to our knowledge, no special approval required

Contribution of authors

Antonio Fasano was responsible for drafting the manuscript and coordinating the experiments conducted in captivity; Alessio De Martino handled the field collection of specimens, their rearing, and the actual execution of most of the video recordings.