



Reconstructing the invasion and the life-history data of alien species of Mantodea in France

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Abstract. – Data from France on the distribution of three alien species of Mantodea (*Hierodula tenuidentata/transcaucasica*, *Hierodula patellifera* and *Sphodromantis viridis*) are presented here; 160 exogenous Mantodea data were recorded. *Hierodula patellifera* was the first species to be recorded in France in 2013. Populations of the two *Hierodula* species overlap in two departments of southern France, Bouches-du-Rhône and Vaucluse. New data on behaviour are provided.

Résumé. – Reconstitution de l'invasion et des données sur le cycle de vie des espèces exotiques de Mantodea en France. Des données sur la répartition en France des trois espèces exotiques de Mantodea (*Hierodula tenuidentata/transcaucasica*, *Hierodula patellifera* et *Sphodromantis viridis*) sont présentées ; 160 données des Mantodea exogènes ont été enregistrées. *Hierodula patellifera* est la première espèce à avoir été signalée en 2013. Les populations des deux espèces de *Hierodula* se chevauchent dans deux départements du sud de la France, les Bouches-du-Rhône et le Vaucluse. De nouvelles données sur le comportement sont fournies.

Keywords. – Alien species, distribution, new records, behaviour.

The increases of global trade and human mobility over the last century have resulted in unprecedented numbers of invasions by non-native species all over the world. France has not been spared, with the arrival of three new species of Mantodea since 2013 (BATTISTON *et al.*, 2020a, b; MOULIN, 2020; MOULIN *et al.*, 2023; MOULIN & ROUARD, 2023): *Hierodula patellifera* (Audinet-Serville, 1838), *Sphodromantis viridis* (Forskål, 1775), and the complex *Hierodula tenuidentata/transcaucasica* (DE VIVO, 2024). Even after comparing genitalia, biogeography, and morphological criteria (BATTISTON *et al.*, 2018b; SCHWARZ *et al.*, 2018), the synonymy of *H. transcaucasica* Brunner von Wattenwyl, 1878, with *Hierodula tenuidentata* Saussure, 1869, is not accepted by all authors (LOMBARDO, 1993; EHRMANN, 2011; VAN DER HEYDEN, 2018a, 2018b, 2021; ROMANOWSKI *et al.*, 2019; SHCHERBAKOV & BATTISTON, 2020; LIU *et al.*, 2021; VAN DER HEYDEN & SCHWARZ, 2021; MOULIN & ROUARD, 2023; ZAFEIRIOU & AGAPAKIS, 2023). According to recent work (DE VIVO, 2024), a species complex is used to refer to *H. tenuidentata* and *H. transcaucasica*. These three species are spreading in mainland Europe at different speeds (EHRMANN, 2011;

MARABUTO *et al.*, 2014; BATTISTON *et al.*, 2017, 2018b, 2019, 2020a, b; CIANFERONI *et al.*, 2018, 2023; VAN DER HEYDEN, 2018a, b; SCHWARZ & EHRMANN, 2018; OLIVEIRA & FERREIRA, 2019; DI PIETRO & BATTISTON, 2021; KULIJER *et al.*, 2022; MARTINOVIĆ *et al.*, 2022; SEVGILI & YILMAZ, 2022; DI PIETRO *et al.*, 2023; LÁSZLÓ *et al.*, 2023; PETRI & TABARELLI DE FATIS, 2023; STANICZEK, 2023; VUJIC & IVKOVIĆ, 2023), and on islands (CANYELLES & ALOMAR, 2006; RUZZANTE & LEO, 2012; BATTISTON *et al.*, 2017, 2020a, b; SCHWARZ & EHRMANN, 2018; LANGOUROV *et al.*, 2022; FASANO & DE MARTINO, 2023), often favoured by the effects of climate change. In their native countries and elsewhere, the increase in temperature affects their distribution and phenology (PINTILIOAIE *et al.*, 2022; SHIN *et al.*, 2023).

Their presence in France is recorded through citizen science websites and smartphone applications (iNaturalist.org, faune-france.org, INPN Espèces...). Today, these means of disseminating knowledge are unrivalled for enriching taxonomy and biogeography with data (SUPRAYITNO *et al.*, 2017; SEVGILI & YILMAZ, 2022). We detail here the history of distribution in France of *H. patellifera*, *H. tenuidentata/transcaucasica* and *S. viridis*, and give some additional data on biology and ecological niche. We discuss the potential need to set up monitoring of these species in the coming years.

MATERIALS AND METHODS

We used the GPS records from the INPN biodiversity database (<https://openobs.mnhn.fr/>), from one of the world's most popular online wildlife databases (<https://www.inaturalist.org/>), from the LPO biodiversity database (<https://www.faune-france.org/>), from the website Observation.org (<https://observation.org/>), and from social networks as Instagram, Facebook.

The geographic scope of this work extends to France only. The distribution maps were made using QGIS software 3.8 Zanzibar. The administrative area is from <http://www.diva-gis.org>.

Observed specimens were identified using the key published in BATTISTON & MASSA (2008) on Caucasian Mantodea, in BATTISTON *et al.* (2010) on Mantids of the Euro-Mediterranean area, and in BATTISTON *et al.* (2019, 2020a) on Mantodea from Italia. From photos produced by citizens, it is often difficult to identify specimens down to species level, for reasons of inadequate quality of the images, distance from the subject, position, or stage of development of the specimen. Thus, for the genus *Hierodula* Burmeister, 1838, many specimens could not be identified beyond this level. However, on several occasions, particularly for oothecae, they were reared in order to identify the species that emerged.

The systematics of Mantodea used here follow the latest update (SCHWARZ & ROY, 2019) and names are available in the national taxonomic reference, TAXREF (TAXREF [eds], 2024).

RESULTS

Combined dataset on species occurrence. – In this study, we constructed a dataset comprising 158 records of alien Mantodea occurrences in France from 2013 to 2024 (table I): 73 of *H. patellifera* (fig. 5-8, 22), 35 of *H. tenuidentata/transcaucasica* (fig. 1-4, 23), 43 of *Hierodula* spp. and 7 of *S. viridis* (fig. 9-12, 21). The first species to appear in France was *H. patellifera*, near the port of Marseille, in 2013. The other two species arrived later, in 2016. From 2020, citizen naturalists began collecting data, and the number of observations increased; up to 20 times more specimens observed in three years for *H. tenuidentata/transcaucasica* (table I).

Table I. – Number of records from citizen science for the taxa occurrence in each period.

Taxon	2013-2015	2016-2019	2020	2021	2022	2023	2024	Total
<i>Hierodula patellifera</i>	2	6	10	21	5	15	14	73
<i>Hierodula tenuidentata/transcaucasica</i>	-	1	1	1	5	20	7	35
<i>Hierodula</i> spp.	-	1	1	5	6	26	4	43
<i>Sphodromantis viridis</i>	-	2	0	0	3	2	1	8
Total	2	10	12	27	19	63	26	159

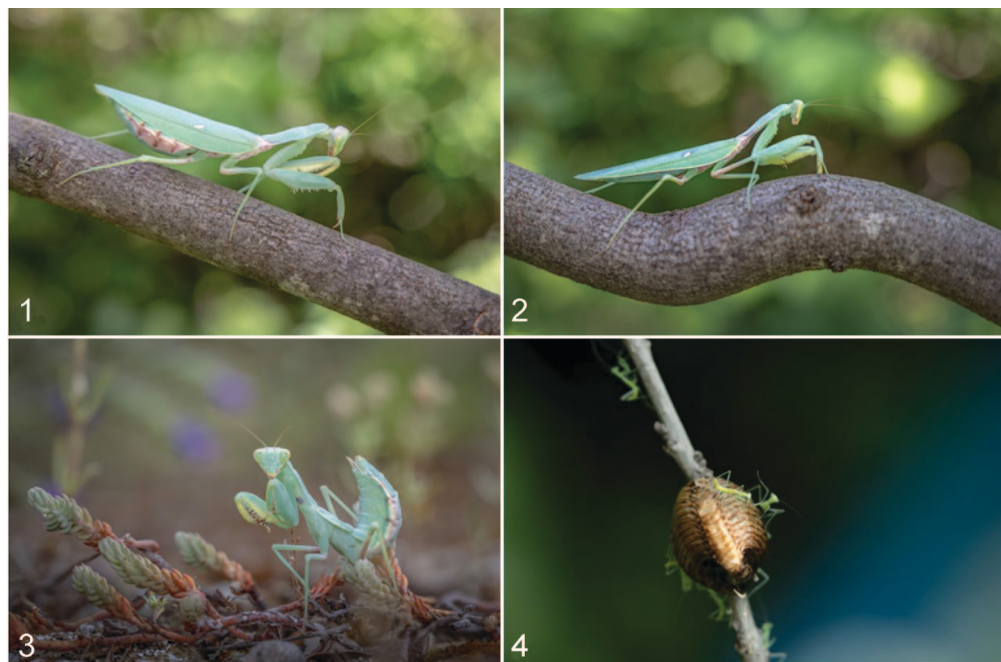


Fig. 1-4. – *Hierodula tenuidentata/transcaucasica*. – 1-2, Adult female, from Juvignac, France. – 3, Nymph female, from Juvignac, France (Photograph J. Rouard). – 4, Ootheca, from Lombardy, Italy (Photograph Paolo Zucca).

Activity period at the life stages. – Nymphs (whose identification to species is certain) and adults of Mantodea are combined in these results because there are not enough specimens observed.

The first records of *H. patellifera* in the year are around June-July (fig. 13). It is necessary to wait until the morphological criteria (calloused spots on the inner side of the anterior coxae) are clearly visible on the nymphs to ensure its identification. The number of records increases until October when the adults are more visible and easily identifiable. Some adult individuals were exceptionally observed in December. Oothecae can be seen hanging from the branches of trees and shrubs.

Hierodula tenuidentata/transcaucasica is observed between July and November, with a maximum number of records during September (fig. 14). As with *H. patellifera*, oothecae can be seen hanging from the branches of trees and shrubs.

Recordings of nymphs unidentified with the species can only provide information concerning the phenology of these Mantodea species. (fig. 16).



Fig. 5-8. – *Hierodula patellifera* (Serville). – 5, Adult female, from Mourières, France (Photograph V. Derreumaux). – 6, Adult male, from Fontvieille, France (Photograph Y. Nielsen). – 7, Nymph, from Arles, France (Photograph G. Paulus). – 8, Ootheca, Mourières, France (Photograph P. Moulin).



Fig. 9-12. – *Sphodromantis viridis* (Forskål). – 9, Adult female, from Cheraga, Algeria (Photograph B. Noguès). – 10, Adult male, from Sardinia (Photograph K. Weissleder). – 11, Ootheca from Palma, Balearic Islands (Photograph T. Bosch). – 12, Predation of an adult female *Mantis religiosa* (Linnaeus) by an adult female *S. viridis*, Almeria, Spain (Photograph J. J. Rueda).

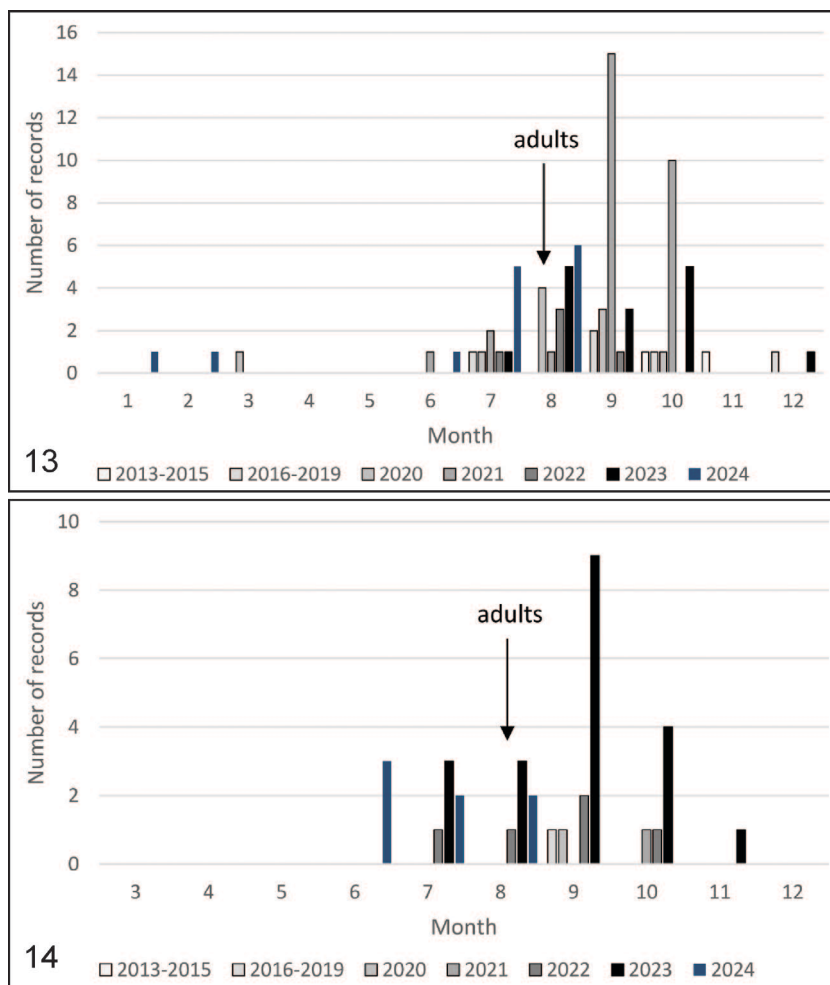


Fig. 13-14. - Observation period; indication of the first adults observed. - 13, *Hierodula patellifera* (Serville). - 14, *Hierodula tenuidentata/transcaucasica*.

Records of *S. viridis* are insufficient to describe the phenology (fig. 15). Few adults were observed between July and November.

Geographic distribution. - *Hierodula patellifera* is the first species to be recorded in France, around Marseille (fig. 17). Over the last eleven years, it has spread in four departments: Bouches-du-Rhône, Vaucluse, Gard, Corse-du-Sud. Data on the distribution of the *Hierodula* spp. taxa do not allow us to give a more detailed picture of the colonization of *H. patellifera*, because it is easily confused with *H. tenuidentata/transcaucasica* on poor-quality photos or nymphs.

Hierodula tenuidentata/transcaucasica is more scattered across the country (fig. 18). Given its current distribution in Italy and neighbouring countries to the east, it seems logical that the colonized departments are those located in the east of France. However, departments further west, such as Haute-Garonne, are home to this alien species. Currently, only *H. tenuidentata/transcaucasica* is present in Haute-Garonne. Therefore, unless there is evidence to the contrary, *Hierodula* nymphs are identified as *H. tenuidentata/transcaucasica* (fig. 19).

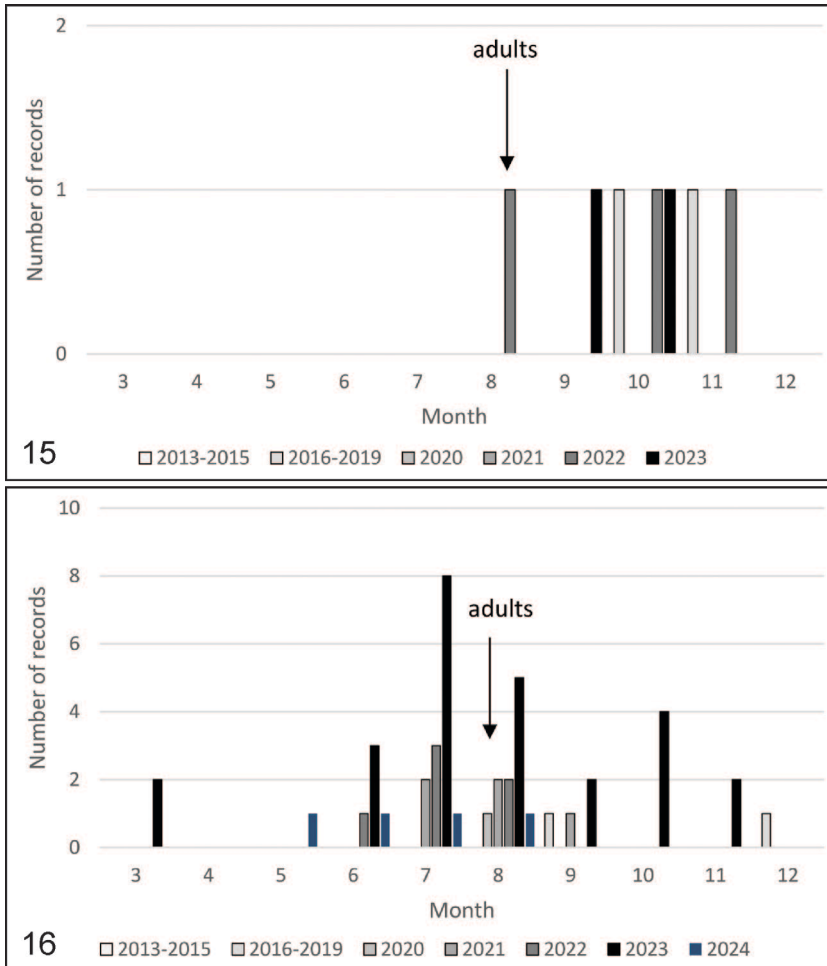


Fig. 15-16. – Observation period; indication of the first adults observed. – 15, *Sphodromantis viridis* (Forskål). – 16, *Hierodula* spp.

Sphodromantis viridis probably arrived in France via Spain and the Mediterranean Sea (fig. 20). This species has arrived in France on both sides of the Pyrenees, avoiding the mountains either naturally or by human transport. Data from Ile-de-France appear to be outliers, as current observations are made around the Pyrenees and in the Mediterranean basin. On the edges of the Pyrenees and on the island of Corsica, *S. viridis* and the two species of *Hierodula* could already be in sympatry.

Information about the predation. – On 2023, September 22nd, near Almeria in Spain, the predation of an adult female *Mantis religiosa* (Linnaeus, 1758) by an adult female *S. viridis* was observed (fig. 12). The strength of the forelegs of *S. viridis* did not allow the female *M. religiosa* to escape the grip. It seems to consume forelegs and head first, to protect itself from potential defence by the female *M. religiosa*.

Identification of the species. – Here, we provide illustrations to help to distinguish the three alien species from the native one, *M. religiosa* (fig. 21-24), to avoid the main confusion. As for the other native species, there can be no mistake in recognizing them.

DISCUSSION

Hierodula tenuidentata/transcaucasica appears to be arrived rapidly in Western Europe from the eastern regions of Europe, via human transport (SHCHERBAKOV &

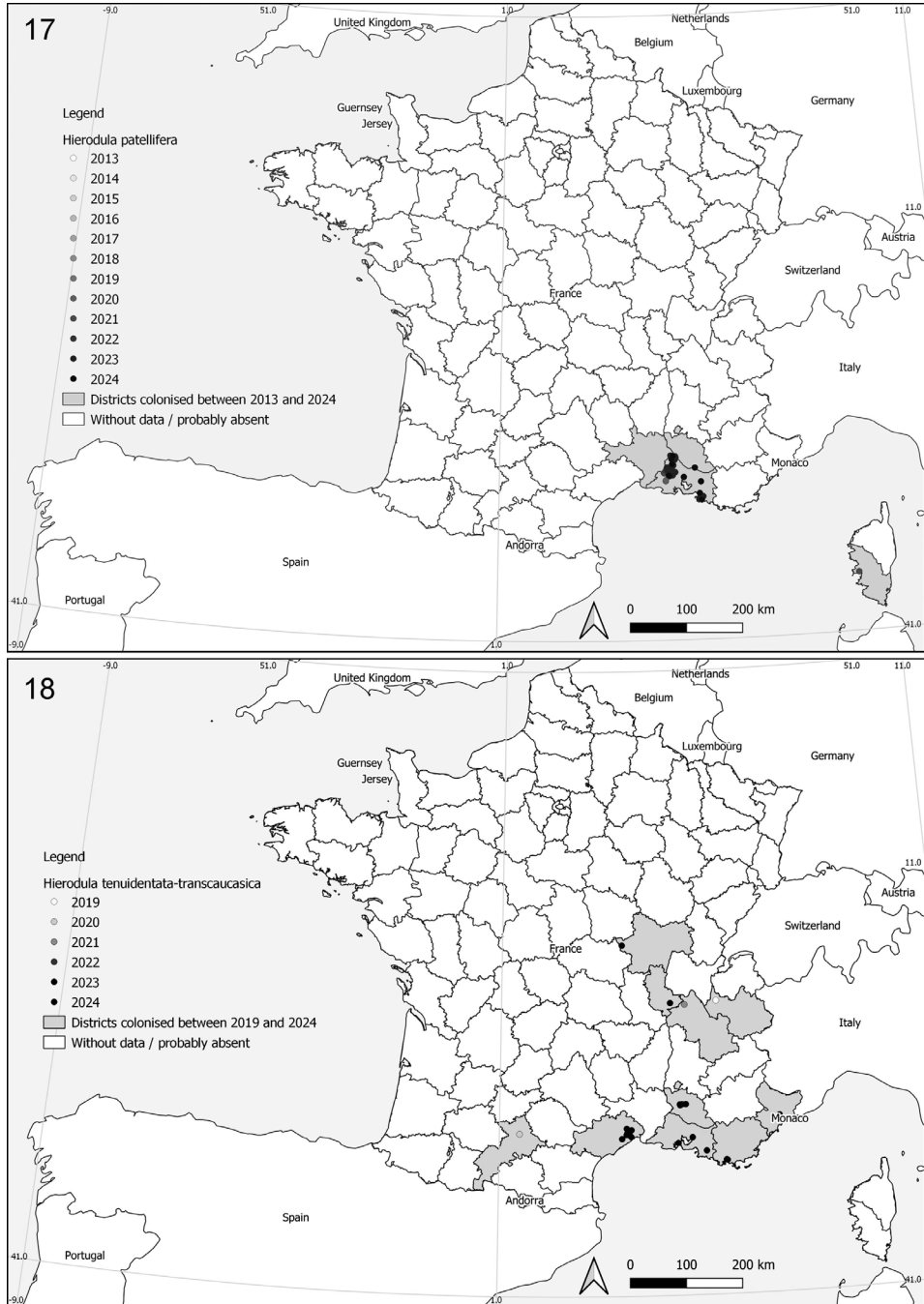


Fig. 17-18. - Distribution maps of *Hierodula* spp. in France. - 17, *H. patellifera* (Serville). - 18, *H. tenuidentata/transcaucasica*.

BATTISTON, 2020). Now widespread in northern Italy (BATTISTON *et al.*, 2018b; PETRI & TABARELLI DE FATIS, 2023; PINTILIOAIE *et al.*, 2023), human transportation has enabled females to cross the Alps, a biogeographical barrier that a Mantodea female cannot cross on her own, as fast as it occurred. Because of their size, weight, and the shape of

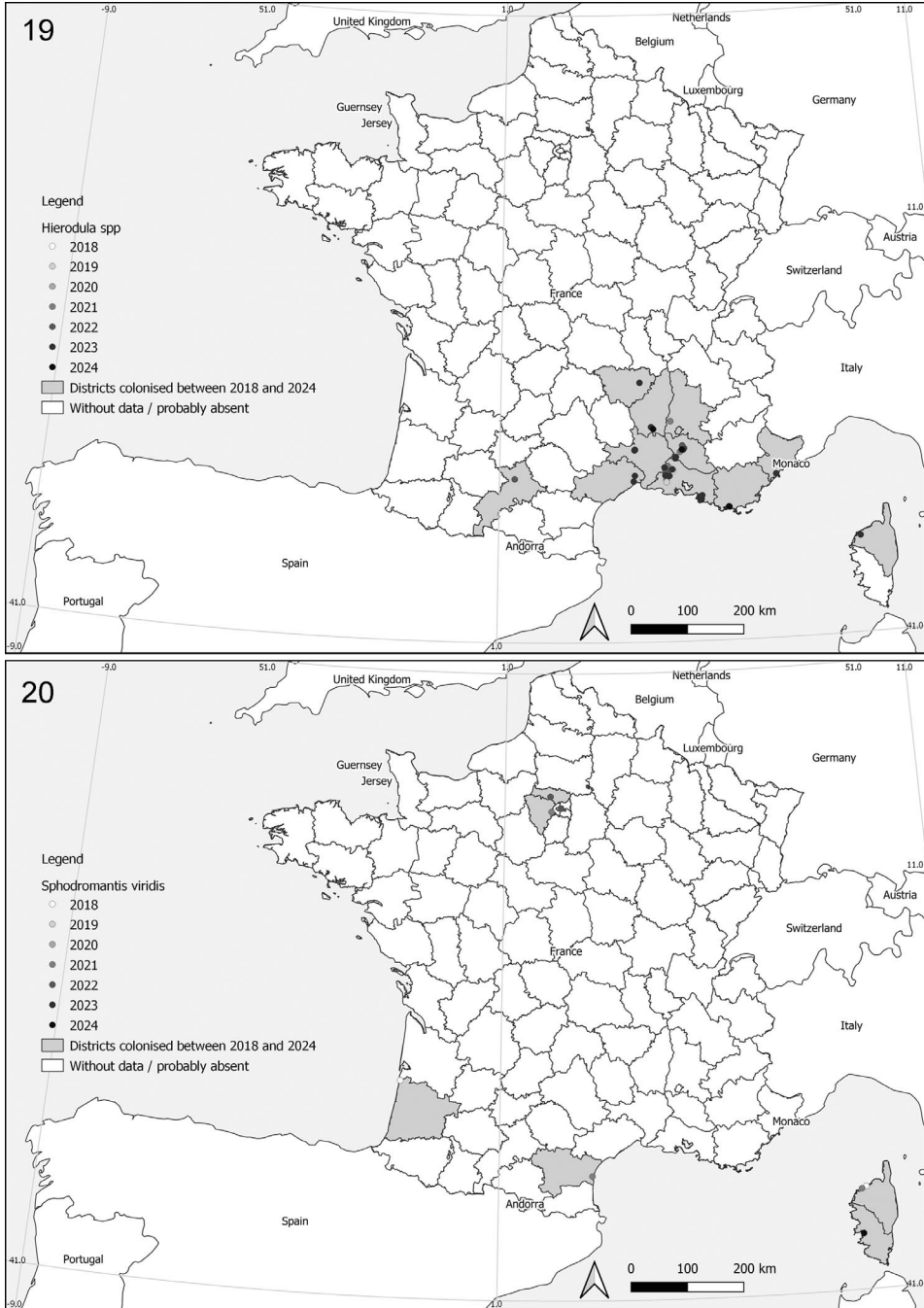


Fig. 19-20. – Distribution maps of Mantodea in France. – 19, *Hierodula* spp. – 20, *Sphodromantis viridis* (Forskål).

their wings, they cannot disperse over long distances. The inability of fertilized females to move has been extensively studied using the example of *Mantis religiosa*, a species with a morphology similar to that of mantids of the genera *Hierodula* and *Sphodromantis* Stål, 1871 (BERG *et al.*, 2011)... and yet they have crossed mountain passes. In Italy, numerous oothecae have been observed in anthropized environments



Fig. 21-24. Specific morphological criteria for foreleg coxae. - **21**, adult male *Sphodromantis viridis* (Forskål) (Photograph K. Weissleder). - **22**, adult male *Hierodula patellifera* (Serville) (Photograph S. Guiraudou). - **23**, nymph female *Hierodula tenuidentata/transcaucasica* (Photograph J. Rouard). - **24**, adult pair *Mantis religiosa* Linnaeus) (Photograph N. Moulin).

(gardens, urban areas, cultivated countryside, etc.) and along natural lines such as wooded strips. Deposited on shrubs, trees or in brambles (BATTISTON *et al.*, 2018b), the oothecae of *Hierodula tenuidentata/transcaucasica* show that the species is well established in a natural environment where it will compete with smaller, native species such as *Mantis religiosa*, *Empusa pennata* (Thunberg, 1815), *Ameles* spp., *Iris oratoria* (Linnaeus, 1758)... Moreover, various insects, including a parasitoid Hymenoptera, revolves around the oothecae of *H. tenuidentata/transcaucasica* (MIRZAEI *et al.*, 2021). It would be interesting to know whether such parasitoid, already present in the area, will continue to parasitize these foreign species. But beyond human introductions, the distribution of *H. tenuidentata/transcaucasica* appears to be largely influenced by climate change, rising temperatures and changes in precipitation (PINTILIOAIE *et al.*, 2023).

Hierodula patellifera is known to have been introduced to France by sea, in the port of Marseille (MOULIN, 2020), via human trade. It was probably introduced to Italy (Veneto, Lombardy) via the Adriatic Sea in the same way (BATTISTON *et al.*, 2019), and to Tuscany via the Mediterranean Sea (CIANFERONI *et al.*, 2023). Since then, in France, this species of Mantodea does not appear to be spreading across the country and remains confined to two departments around the Bouches-du-Rhône. The populations of France and Italy do not appear to be linked, with no continuity in their distribution (BATTISTON *et al.*, 2020a).

Sphodromantis viridis is a xerothermophilous species that has widely invaded the southern regions of Spain, as well as Portugal and adjacent islands. Warming temperatures in Europe because of climate change has enabled it to establish in the south of France, at both ends of the Pyrenees mountain range, as well as in Corsica Island. The genera *Sphodromantis* and *Hierodula* occupy similar arbusticolous to arboricolous niches in the Afrotropical and Oriental realms, respectively (SCHWARZ & EHRMANN, 2018). It would be interesting to see what happens when these two species meet in the south of France and share identical habitats. The meeting of *S. viridis* with *H. tenuidentata* has already been recorded in a same locality in Greece, where the effects of their interaction have not yet been recorded (BATTISTON *et al.*, 2020). In Italy, the two *Hierodula* species thrive in the same localities in Tuscany, but there are not yet observations of interspecific competition (CIANFERONI *et al.*, 2023). Finally, the aberrant data compiled in the Île-de-France region confirm that breeding new pets inevitably leads to the introduction of exotic species into the wild (BATTISTON *et al.*, 2022). These introductions can have major negative effects on biodiversity.

The three alien species are known to be voracious predator, as shown by the observation in Spain between *S. viridis* and *M. religiosa*. *Hierodula tenuidentata/transcaucasica* has also been observed fishing (BATTISTON *et al.*, 2018a) and *H. patellifera* catching little birds (KOLNEGARI *et al.*, 2022). These predatory insects consume many invertebrates and adapt quickly to their environment (BATTISTON *et al.*, 2018b; FASANO & DE MARTINO, 2023). The degree to which it is competitive on prey is not yet known but it is known that intraguild predation relationships are often determined by relative body size (FAGAN & ODELL, 1996), with larger predators typically preying on other smaller species (TURNER & POLIS, 1979). Also, they share some of the same habitats of native species, some of which may be endemic to islands in the Mediterranean Sea or of the coast of Africa (BATTISTON *et al.*, 2017; FASANO & DE MARTINO, 2023). However, in the adult stage, these alien species do not seem to share niches similar to those of native species (although predation between *S. viridis* and *M. religiosa* was

observed in a shrub). The alien species are mainly found in the arbusticulous and arboricolous niches at adult stage (WATANABE & YANO, 2009; MOULIN, 2020; SEVGILI & YILMAZ, 2022; MOULIN & ROUARD, 2023). At the nymph stage, alien species share the niche of herbaceous stratum with all the species native to France. It is known that preferred plant species used by mantids could change with development stage [i.e. *Tenodera aridifolia* (Stoll, 1813) (WATANABE *et al.*, 2013)]. It is during this stage of life that interspecific competition can have the greatest impact on these native Mantodea populations. They reproduce very efficiently, and it is recognized that, in certain closely related species, there may be reproductive interference. The males of one species are attracted by the pheromones of the females of another species (LÁSZLÓ *et al.*, 2023). These males would then be at risk of interspecific predation (FEA *et al.*, 2013). They can withstand the winter with the oothecae (PINTILIOAIE *et al.*, 2021). Then, they could have a major impact on native species. The issue of how predatory invasive species will affect the biodiversity in their newly settled habitats is very important (MATSUMOTO *et al.*, 2016; PYŠEK *et al.*, 2020; SAJI *et al.*, 2022; FASANO & DE MARTINO, 2023). Understanding the impact of a predatory alien species requires data (WILDER, 2005; ROY *et al.*, 2012; GALL *et al.*, 2017; PINTILIOAIE *et al.*, 2023). So, for these Mantodea, their diet should be studied i.e. using metabarcoding of gastric contents and observations in the wild. Their colonization of new territories depends mostly on us and our trade, as the females, even if they are winged, are unable to fly long distances.

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