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SCIENTIFIC NOTE

Mantid expansion into North American salt marshes

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Abstract

Mantids are influential generalist predators in terrestrial systems. Therefore, large mantid species like the European mantid, *Mantis religiosa* (Linnaeus, 1758), are often used by humans and purposefully introduced as a form of biocontrol, greatly expanding their geographic ranges. However, mantids are rarely recorded in marine systems. In this study, we present an observation of European mantids living in a salt marsh and actively moulting in the vegetation in Elkhorn Slough, in Monterey Bay, California, United States of America. Not only are these European mantids a nonnative species, but every observed individual was a flightless juvenile, meaning they hatched nearby. Although mantids are not usually associated with intertidal ecosystems, there are multiple potential reasons that mantids would be drawn to salt marshes, including food, potential for camouflage, and lower predation pressure. The addition of a generalist predator could produce a complex mix of positive and negative impacts on the marsh itself and, given the importance of marsh systems, these possible effects warrant further study.

Résumé

Les mantes sont des prédateurs généralistes importants dans les écosystèmes terrestres. Pour cette raison certaines espèces de grande taille, comme l'espèce européenne *Mantis religiosa* (Linnaeus, 1758), ont été volontairement introduites par l'Homme à des fins de biocontrôle, augmentant ainsi fortement leur aire de distribution. Les mantes sont en revanche rarement signalées d'écosystèmes marins. Dans cette étude, nous rapportons l'observation de mantes européennes vivant dans un marais salé de la Baie de Monterey (site d'Elkhorn Slough), en Californie, aux États-Unis, et y muant dans la végétation. Non seulement ces mantes européennes représentent une espèce introduite, mais les individus observés étaient tous juvéniles, suggérant une éclosion locale. Bien que les mantes ne soient habituellement pas associées aux écosystèmes intertidaux, il existe de nombreuses raisons pour lesquelles elles pourraient se réfugier dans les marais salés, dont les sources de nourriture, des possibilités de camouflage et une pression de prédation moindre. L'introduction d'un tel prédateur généraliste pourrait se traduire par des impacts positifs comme négatifs sur le marais lui-même, ce qui, étant donné l'importance de ces systèmes, mérite de futures investigations.

Mantids are influential predators. They are generalist carnivores that consume a variety of arthropods, including conspecifics *via* cannibalism, and even birds (Harris and Moran 2000; Chong 2002; Nyffeler *et al.* 2017). Because of this, humans purposefully introduce mantids as a form of biocontrol for unwanted arthropod pests, for example, by releasing ootheca, or egg masses. As these ootheca are widely commercially available, biocontrol generates a large vector for nonnative insects to invade new regions (Cannings 2007). The European mantid, *Mantis religiosa*

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Figure 1. A juvenile, and thus flightless, European mantid, *Mantis religiosa*, climbs up a stalk of pickleweed, *Salicornia pacifica*.

Linnaeus, 1758 (Mantodea: Mantidae), has long been used for this biocontrol purpose because it is a large mantid species. European mantids on the North American east coast are recorded as far back as the 1890s (McLeod 1962). Database and photographic records exist for *M. religiosa* starting as early as 2002 in various counties in California, United States of America, but *M. religiosa* likely arrived and was spreading in California during the late 1900s (Global Biodiversity Information Facility 2022). Since then, the range of the European mantid has expanded, and it now occurs throughout the west coast of the United States of America (Global Biodiversity Information Facility 2022; CalPhotos, https://calphotos.berkeley.edu/, unlike in the distribution map in Battiston *et al.* 2010).

Although the European mantid is an abundant predator that lives in many terrestrial systems, it is not often associated with marine ecosystems. Few published records exist of mantids of any species in salt-marsh ecosystems globally (Gangstad 1992; Dreyer and Niering 1995; Kristín *et al.* 2011).

Here, we present an observation of European mantids in California salt marshes (Fig. 1) and, to our knowledge, the first observation of mantids moulting in an intertidal habitat.

On 2 August 2019, we observed 26 individuals of *Mantis religiosa* along a 180-metre transect between 09h:45 and 11h:55, local time, at the northeastern edge of Yampah Hill in Elkhorn Slough at the border of the salt marsh and upland. Elkhorn Slough is located in Monterey Bay, in central California, and is one of the largest tracts of salt marsh in California, second only to San Francisco Bay. Two individual mantids were observed actively moulting, and both green morphs were attached to pickleweed, *Salicornia pacifica* Standley (Chenopodiaceae) (Fig. 2). All mantids were in the salt marsh and atop four species of plants: pickleweed (*S. pacifica*) (20 mantids; 76.9%), alkali heath, *Frankenia salina*, (Molina) I.M. Johnston (Frankeniaceae) (three mantids; 11.5%),

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Figure 2. A green morph European mantid, *Mantis religiosa*, moulting while attached to pickleweed, *Salicornia pacifica*. This is the mantid's final moult before becoming an adult.

desert saltgrass, *Distichlis spicate* (Linnaeus) Greene (Poaceae) (two mantids; 7.7%), and salt-marsh dodder, *Cuscuta pacifica*, Costea and M.R. Wright (Convolvulaceae), parasitising pickleweed (one mantid; 3.8%; Supplementary material). Mantids were measured using the programme ImageJ (https://imagej.net) and calibrated with a ruler in the photos. Mantid length ranged from 2.38 to 5.00 cm, with an average length of 3.84 cm (n = 23; Supplementary material). Colour morphs ranged: we observed 13 green (50%), five brown (20%), four light brown (15%), and four pale (15%) mantids.

This study represents one of the few published observations of mantids of any species in salt marshes and the only published work that demonstrates that mantids use intertidal marshes when moulting. Another interesting dimension of the observation is the life stage of the mantids: every individual was juvenile. Because juvenile mantids cannot fly, these individuals must have hatched close to where they were observed. This indicates that salt marshes could also potentially serve as a nursery ground for European mantids.

A number of potential drivers could have caused juvenile European mantids to expand into salt marshes. Generally, the European mantid is a successful invasive species that is frequently introduced into new areas for biological control (Davis 1918). The species therefore may be saturating other nearby habitats and may have expanded into salt marshes. European mantids, as generalists, may also have such high plasticity that they are able to expand into and colonise salt marshes, with populations likely able to thrive there, where habitat specialists would not persist.

Vegetation structure, differences in predation pressure, potential for camouflage, and access to food may drive European mantids to use salt marshes. In its native habitats, *M. religiosa* is found in scrubland and steppes, in dry meadows, and in low matorral. Its hunting habits lead it to colonise the herbaceous stratum, including bare ground, and it is generally found on low, but not high, bushes or plants. The low level and open structure of salt-marsh vegetation matches the

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insect's habitat preferences and provides dense masses of stems in which to hide (Fig. 2). Similarly to cicadas (Puissant and Defaut 2005), mantid species spread over distinct layers of vegetation. Lush, green pickleweed also may provide an ideal camouflage substrate for green morphs during California summers, when drought dries and browns the region's upland environments. Di Cesnola's (1904) study showed that when European mantids were put in environments that did not match their colour – did not provide camouflage – mantid mortality rates dramatically increased due to predation. Although *M. religiosa* juveniles would not be directly attracted to the colour of pickleweed for increased chances of survival, expansion into marshes could make it harder for predators to detect them. During moulting, when mantids are highly vulnerable, the marshes could provide a space to safely moult during dry California summers. Because salt marshes are some of the most productive ecosystems on Earth (Valiela and Teal 1979), food could also be an important driver for the generalist predator's expansion into marshes.

Given that European mantids are successful generalist predators and that salt marshes provide a potentially safe and productive environment with ample food, what has kept mantids from expanding into salt marshes more widely? One reason may be that osmoregulation is uncommon among Mantodea, and marine systems therefore present an additional form of stress. However, some Orthoptera species are adapted to salt marshes, including *Epacromius tergestinus* (Megerle von Mühlfeld, 1825) (Orthoptera: Acrididae) (Defaut and Morichon 2015), and to stony beach habitats, including *Pseudomogoplistes vicentae* (Gorochov, 1996) (Orthoptera: Mogoplistidae) (Pelozuelo 2021). Additionally, the grasshopper *E. tergestinus* seems to feed in lower tidal marshes, moves up to mainland or down to its feeding areas according to the tide (Defaut and Morichon 2015), and is even able to be drowned for several hours and then to revive and be active without damage (Defaut and Morichon 2015). More broadly, it may also be possible that invasive species are generally more plastic than previously thought and therefore are more likely to temporally osmoregulate when saline-stressed (as observed in, for example, spiders; Pétillon *et al.* 2011). Saline stress tolerance partly aligns with habitat preference in ground-living wolf spiders. Tidal regime may also be a factor, and mantid individuals were observed only in the high marsh near the upland border, where only king tides inundate the area. During the observation period for this study, no mantids were observed in the low marsh where tides would flood the area and overtop the vegetation daily and would have particular impact on juvenile individuals, which cannot fly. The question of whether eggs in ootheca can survive flooding is certainly worth further study.

Overall, little is known about mantids in salt marshes. Most previously published studies mention mantids' presence in those environments only as exceptions and do not examine their potential impacts. Future studies could examine how survival at different life stages is impacted if mantid individuals live in salt marshes or terrestrial environments. Another important question to examine is how the addition of a generalist predator alters a salt marsh food web. Previous studies examining the impact of invasive arthropod generalist predators showed introduced species can have complex and unpredictable effects, such as outcompeting and replacing native predators (Snyder and Evans 2006). Fagan and Hurd's (1994) and Fagan *et al.*'s (2002) experiments using introduced European mantids found they lowered arthropod biomass by 45% and reduced the density of native wolf spiders, but that the overall impact on other species in the system was a mixture of positive and negative effects. Mantids are such influential arthropod predators that they can also generate trophic cascades in old field ecosystems (Moran *et al.* 1996): it is possible they do the same in salt marshes, changing the abundances, distributions, and behaviours of other arthropods and marsh plants in marshes. For example, by consuming marsh herbivores such as grasshoppers, mantids could indirectly promote pickleweed biomass, and by promoting foundational marsh plants, mantids could also contribute to marsh restoration goals despite being invasive. Understanding how invasive predators impact valuable salt marsh ecosystems, which are already under threat from many other forces, would be an important future line of study.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.4039/tce.2024.10.

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