Biology, ecology, and biogeography of the enigmatic desert praying mantis *Blepharopsis mendica* (Insecta: Mantodea)

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Abstract

Background. *Blepharopsis mendica* (Fabricius, 1775), is a large mantid species found from the Canary Islands across North Africa, the Middle East, and Pakistan. Research on this species has been limited, especially in Iran, despite the country's potential significance for studying its biology and distribution. Adults of this species are easily recognizable by their marble-white pattern and rhomboidal leaf-like pronotum. They are sit-and-wait predators that inhabit various open environments, including trees and shrubs.

Methods. Field observations were conducted across various regions of the Devil's flower mantis (*Blepharopsis mendica*) global distribution, with a focus on Morocco, Tunisia, and Iran. Distribution data for *B. mendica* were gathered from fieldwork, museum collections, online biodiversity databases, and publications, totaling 593 occurrence points. Ecological niche modeling was performed using environmental data, and various models were evaluated for suitability. Phylogeographic analyses involved DNA sequencing and construction of a

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haplotype network to examine genetic relationships between populations. Divergence time estimation and biogeographical range expansion models were applied to explore historical distribution shifts of the species across different regions. The study provided comprehensive insights into the biology, distribution, and genetic history of *B. mendica*.

Results. We provide information on the life cycle, ootheca, defense behavior, habitat, and biogeography of ~~the Devil's flower mantis,~~ *Blepharopsis mendica*. This mantid is an overwintering univoltine species with nymphs emerging in summer and becoming adults in spring. In the wild, females start oviposition in April and can lay their first ootheca within a week after mating. The species is distributed from the Canary Islands to Pakistan in the dry belt. Thus, its distribution is associated with xeric areas or savanna-like habitats. Phylogeographic analyses revealed three major genetic lineages, (i) in the Maghreb, (ii) from Egypt via Arabia to Iran (with internal substructures), and (iii) likely in Pakistan; the estimated onset of differentiation into these lineages is of Pleistocene age. Defense behavior involves flying away or extending wings broadly and lifting forelegs. Performing laboratory breeding, we documented life cycle and color changes from first instar to adulthood. Due to overwintering, the last larval instar needs considerably longer than the others. At 25 °C (± 2), average adult life span was 118 days (± 6 SD) for females (range: 100–124) and 46 days (± 5 SD) for males (range: 39–55), with a significant difference among sexes. On average, oothecae contained 32.3 eggs (± 10.1 SD) and the mean incubation period was 36.8 days (± 2.9 SD). We did not find evidence of parthenogenesis. In general, the biology of *B. mendica* shows a variety of adaptations to its often extreme and little predictable type of habitat.

Keywords: ~~Devil's flower mantis~~, life history, ootheca, mantid, adaptation, extreme habitats

Introduction

Praying mantids occupy an important ecological niche, playing vital roles as predators. These creatures are renowned for their distinctive appearance and predatory prowess, wielding their razor-sharp forelegs with precision to capture and subdue a wide array of prey, including other insects, small fauna, and even their own kind. In this intricate web of life, their presence underscores the delicate balance and the indispensable role of these fierce predators in maintaining the equilibrium of insect populations within many of the world's diverse ecosystems.

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The color changes of different stages of mantids also provide insights into their ecology and behavior. For example, coloration may play a role in camouflage, mate selection, or predator avoidance, and understanding these factors can help us to better understand the role that these species play in their ecosystems (Battiston & Fontana 2010).

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One rather spectacular mantid species is ~~the Devil's flower mantis~~ *Blepharopsis mendica* (Fabricius, 1775). This large species is found from the Canary Islands throughout North Africa and the Middle East to Pakistan (Battiston *et al*. 2010). Adults can be distinguished by their marble-white pattern all over their bodies and the rhomboidal leaf-like shape of their pronotum. This mantid, a sit-and-wait predator, inhabits open areas where it lives in trees as well as in green and dried shrubs. It exhibits exceptional camouflage with its cryptic shape, color, and behavior (Fig. 1), making it difficult to spot in its natural habitat (Battiston *et al*. 2010).

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Although *B. mendica* is a fascinating mantid, only two relatively old studies (i.e., Korsakoff 1934, 1935) dealt in more detail with the species' life cycle, biology, and other ecological aspects, while the more recent publications mostly address its distribution or are only presenting new faunistic records (Ehrmann, 2011; Caesar *et al*. 2015; Panhwar *et al*. 2020; Nasser *et al*. 2021). In particular, for Iran, there are practically no studies concerning the biology and distribution of *B. mendica*, and only records of this species from some parts of the country (Lorestan and Fars provinces) have been published so far (Mirzaee & Sadeghi 2019, 2021a). However, Iran with its strikingly diverse array of ecosystems and hence high diversity of (often endemic) insect species (cf. Zehzad *et al*. 2002) is a particularly important region for the study of *B. mendica*, primarily owing to its geographically extended arid and semi-arid landscapes, often characterized by scrub vegetation, the ecosystems where this species typically thrives.

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Here, we provide detailed information regarding the color change of *B. mendica* along its development under optimal laboratory conditions, its biology, life cycle, and behavior. Defensive behaviors of individuals in the wild are also documented and discussed. New data on the distribution of the species across Iran, where the species still is rather poorly studied, is presented together with additional information on its life history in the wild. These data in conclusion allow a more comprehensive understanding of the species' biology including its life history, ecology, evolution, distribution, and historical biogeography.

Materials and methods

Collecting and observation in the wild

Field observations have been done along the global distribution of this species to contextualize the data in a wider perspective. Wild specimens were observed and documented in three focal points of the global distribution of this species: western habitats in Morocco, central habitats in Tunisia, and eastern habitats in Iran. Individuals of *B. mendica* from nine regions in five different provinces of Iran (Lamerd, Fasa, Shiraz, Fars province; Jam, Soroo, Tombak, Busheher province; Khomeini Shahr, Isfahan province; Abadan, Khozestan province; Eshkanan, Hormozgan province) were collected by the first author during field surveys from 2019 to 2021. The presence of individuals and their defense behavior were observed and photographed within natural habitats. Three oothecae of this species were collected from branches of trees or bushes in Darab, Fars Province, and Jam, Bushehr Province, during June and July 2020 by the first author, but they were empty and already hatched at the time of collecting. Species and ootheca identification were carried out by the first author (Z.M.) following Battiston *et al*. (2010). All materials collected during this survey are preserved in the following collections: Zohreh Mirzaee private collection, Müncheberg, Germany (ZMPC); Zoological Museum of Shiraz University, Shiraz, Iran (ZM-CBSU); and Mantodea collection of Senckenberg German Entomological Institute, Müncheberg, Germany (SDEI).

Rearing and lab condition

From two adult individuals collected from xeric shrublands of Bushehr province (27° 50' 37.35" N, 52° 03' 51.92" E), one female laid one ootheca, which was kept in a glass jar (15 × 15 × 10 cm) at room temperature (25–27 °C). The relative air humidity (RH) was maintained at 40–45 % with water misted on a regular basis. A digital terrarium hygrometer (HTC2) (Dongguan City, China) was used to measure RH.

The hatched nymphs were kept in separate glass jars (6 × 6 × 4 cm) during the first and second instar, thereafter transferred to bigger jars (12 × 12 × 10 cm). The jars containing the nymphs were maintained at 33–35 °C. One stick was placed in each jar to assist molting. Ventilation was enabled by three holes (2 mm in diameter each) in the lid of the jars. During the first and second instar, nymphs were fed with fruit flies (*Drosophila melanogaster* Meigen, 1830), two to three individuals per nymph every three days. Later instars were fed with living mealworm larvae (*Tenebrio molitor* Linnaeus, 1758), small living grasshoppers (*Calliptamus* spec.), moths (mostly *Eupithecia* spec. and *Leucania* spec.) and house flies (*Musca domestica* Linnaeus, 1758) twice a week.

All jars were checked daily. We recorded all information regarding the dates of molting and number of molts. To prevent contamination or disturbance, we removed all unfinished or dead prey. The sex of each individual was noted after the last molt. The adults were used for further breeding, testing different conditions (i.e., mated, not mated).

Data analyses of breeding

We calculated the mean number of days (with their standard deviations) between molts and adulthood (based on nymphs reaching the adult phase), separately for males and females. To assess the difference in mean adult longevity between males and females, a two-sample t-test was conducted. The t-test is appropriate for comparing the means of two independent groups. Statistical analysis was performed using RStudio 3.6.3 (R Core Team, 2021) with the base R package. Oothecae resulting from the first generation bred in captivity were measured, and the numbers of egg chambers inside fertilized and unfertilized oothecae were counted. Based on descriptions provided by Brannoch *et al*. (2017), the length, width, and height of each ootheca were assessed. To count the number of eggs per ootheca, they were dissected along their length and examined under a LEICA M205 C binocular microscope. The ootheca parameters were measured as shown in Figures 2a and b. A digital camera, Canon EOS 700D, was used to take pictures.

Distribution data

Fieldwork, museum collections, online biodiversity databases, and publications were used to collect distributional data. In total, 63 records were obtained from various districts of Iran over a seven-year survey period of the first author (2015–2021); 272 records were obtained from museum collections, including those at the State Museum of Natural History Karlsruhe, Germany (SMNK), the Zoological Research Museum Alexander Koenig, Germany (ZFMK), (all museum specimens were identified by the mantid specialist R. Ehrmann,); 28 records were obtained from the Global Biodiversity Information Facility (GBIF; https://doi.org/10.15468/dl.y25v89), 140 from iNaturalist, including only specimens with pictures that allowed accurate species identification (confirmed by ZM); and 90 additional records from Naseer et al. (2021). In total, we obtained 593 occurrence points, which were used to generate a distribution map in QGIS v. 3.22 (https://qgis.org/en/site/). Google Earth v. 9.174.0.2 (https://earth.google.com/web/) was used to georeference specimens without coordinates based on the information present on the corresponding labels.

Ecological niche modeling

The occurrence records were reduced in number using spatial thinning, accomplished with the R package "spThin" (Aiello-Lammens et al. 2015), in order to create the ellipsoid niche model. To avoid issues associated with spatial autocorrelation, we maintained a minimum distance of 10 km, considering the spatial resolution of the variables (~9.2 km at the equator) (Kramer-Schadt et al. 2013). This resulted in a final count of 270 records, following the methodology outlined by Cobos et al. (2018), which were used to calibrate and establish the final models.

Environmental data at a spatial resolution of 2.5 arc-minutes (~4.6 km at the equator) were obtained for this study from WorldClim (version 1.4, http://www.worldclim.org; Hijmans et al. 2005). WorldClim is based on interpolations of weather station data, encompassing monthly precipitation, minimum and maximum temperatures, from the period 1950–2000. Out of the 19 available variables, four (mean temperature of wettest quarter, mean temperature of driest quarter, precipitation of warmest quarter, precipitation of coldest quarter) were excluded a priori due to known spatial inconsistencies between adjacent grid cells (Escobar et al. 2014; Campbell et al. 2015). Following the approach of Dey et al. (2021), we tested three different environmental sets to calculate the ellipsoid niche of *B. mendica*, aiming to avoid bias in characterizing the species niche centrality:

'Set 1' included all 15 variables.

'Set 2' included only temperature-related variables.

'Set 3' included only precipitation-related variables.

For each of these sets, we conducted a principal component analysis (PCA) using the 'kuenm_rpca' function in the 'kuenm' package (Cobos et al. 2019) within RStudio 3.6.3 (R Core Team, 2021). The first three components, which collectively explained more than 90% of the total variance in the dataset, were retained for model calibration (see Table 1).

The models were constructed using the 'ellipsenm' package (Cobos et al. 2020), calibrated using the 95% pairwise confidence region for the ellipsoid, and evaluated using the 'ellipsoid_calibration' function (Cobos et al. 2020). Two distinct methods were employed to create ellipsoid models:

'covmat,' which generates ellipsoids based on the centroid and a matrix of co-variances of the variables.

'mve1,' which produces an ellipsoid that minimizes the volume without losing the data contained within (i.e., minimum volume ellipsoid; Van Aelst & Rousseeuw 2009).

Model selection was based on statistical significance (partial ROC; Peterson et al. 2008), while the proportion of testing data known to be in suitable areas and the prediction of unsuitable areas relied on omission rates (E = 5%; Anderson et al. 2003) and prevalence (i.e., the proportion of space identified as suitable for the species; Cobos et al. 2020). The partial ROC metric was calculated using 500 bootstrap iterations, with 50% of testing data used in each iteration, and 5% testing data error due to uncertainty. Prevalence was calculated in both geographical and environmental spaces, considering only pixels with distinct combinations of all variable values (Cobos et al. 2020; Nuñez-Penichet et al. 2021).

The calibration area, which includes regions accessible to the species (Barve et al. 2011), featured a 50 km buffer from the occurrence records utilized in our models. The buffer size was determined based on observations of this species in its natural habitat, particularly males, which possess efficient wings and fly to locate females for mating.

Final parameters were selected based on the best-evaluated models and used to create the final models through ten replicates with bootstrapped subsamples, each comprising 75% of the data. These replicates were generated by excluding one occurrence record at a time. The ecological niche and suitability levels of *B. mendica* in geographical space were visualized, with binarization using a suitability threshold to exclude the 5% of data with the most extreme values. Visualization of results was carried out using QGIS v.3.10 (QGIS Development Team, 2020).

Phylogeographic analyses

Mesocoxal muscle tissue from 15 preserved *B. mendica* specimens was stored in 96 % ethanol. Genomic DNA was extracted using the E.N.Z.A.® Tissue DNA Kit protocol designed for animal tissue. We specifically targeted the barcoding region of the cytochrome c oxidase I (COI) gene, with a length of 658 base pairs, for amplification and sequencing. The primer sequences used were LepF1 (5′ATTCAACCAATCATAAAGATATTGG-3′) and LepR1 (5′TAAACTTCTGGATGTCCAAAAAATCA-3′), as previously described by Hebert et al. (2004). Polymerase chain reaction (PCR) was conducted on a SENSQUEST Lab Cycler, with the following thermal conditions: initial denaturation at 95 °C for 5 minutes, followed by 38 cycles of denaturation at 95 °C for 30 seconds, annealing at 49 °C for 90 seconds, extension at 72 °C for 60 seconds, and a final extension at 68 °C for 30 minutes. Gel electrophoresis was used to confirm proper amplification and check for contaminations. The resulting PCR products were purified using Thermo Scientific Exonuclease I and the FastAP Thermosensitive

Alkaline Phosphatase Clean-up Kit. Sequencing was performed at Macrogen Europe, ensuring adequate overlap with adjacent regions for sequence accuracy. Geneious R10 (https://www.geneious.com) was employed for nucleotide editing and contig assembly. A multiple sequence alignment was carried out using Bioedit 7.2.5 (Hall, 1999) and was subsequently converted into Fasta and Nexus formats for various analysis programs. All sequences were deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank/) with the following accession numbers: OR588779-OR588792. To visualize genetic relationships between different geographic populations, a haplotype network was constructed using the TCS network algorithm (Clement *et al*. 2002) as implemented in PopART v. 1.7.2 (Leigh and Bryant 2015).

For Bayesian analysis, the Akaike Information Criterion (AIC) implemented in jModelTest v.2.1.10 was used to select the best-fitting DNA substitution models (Guindon and Gascuel 2003; Posada, 2008). The HKY model (Rodriguez *et al.* 1990) with a significant proportion of invariant sites (I = 0.7270) (HKY + I) was identified by jModelTest as the best model and run for 100,000,000 generations, sampling every 1000th generation. The first 10 % of generations were discarded as burn-in. We used the remaining trees with average branch lengths to create a 50 % majority-rule consensus tree with the sumt option of MrBayes. TRACER (Rambaut et al. 2018) was used to check that analyses reached an effective sample size (ESS) over 200 in order to ensure correct chain convergence. Posterior probabilities (pp) were obtained for each clade, where pp ≥ 0.95 indicated significant support for clades. The run with the best log-likelihood score was selected. Consensus trees were visualized and rooted with *Empusa pennicornis* Pallas, 1773 as an outgroup in FigTree 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/), and edited using Inkscape vector graphics editors (ver. 1.2). *Empusa pennicornis* was chosen as the outgroup because this genus belongs to the same family (Empusidae).

Divergence time estimation was conducted using BEAST 2 v. 2.7.5 (Bouckaert *et al.* 2019). We determined the substitution model by employing jModelTest version 2.1.10. The HKY model with estimated base frequencies and gamma distribution (with 4 categories) was chosen. Due to the unavailability of fossils for *Blepharopsis* or closely related genera, we calibrated the tree using standard gene substitution rates, a method also employed in prior studies (Papadopoulou *et al*. 2010; Wendt *et al.* 2022). Consequently, a clock rate of 0.0177 was applied based on Papadopoulou *et al*. (2010). To explore the potential impact of different models, we conducted two separate analyses utilizing Yule and Birth-Death tree priors. Each

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analysis consisted of four independent Markov Chain Monte Carlo (MCMC) runs, each running for 50 million generations and sampling trees every 5,000 generations. After discarding the initial 10 % of trees as burn-in, we assessed convergence using Tracer version 1.7.1 (Rambaut *et al*. 2018). The final trees were combined using Tree Annotator v.1.10.4 and further edited using FigTree v.1.4.4 (http://tree.bio.ed.ac.uk/).

To explore the historical shifts in the geographical distribution of *B. mendica*, we employed two models for biogeographical range expansion: The Dispersal-Extinction-Cladogenesis (S-DEC) model and the Dispersal-Vicariance (S-DIVA) model, both implemented in RASP 4.3 (Yu et alet al. 2020). The input data for this analysis consisted of an ultrametric tree generated using BEAST v. 2.7.5. To enhance the precision of our analysis, we removed the outgroup from the tree using a feature provided by the RASP software.

We delineated seven geographical regions based on our knowledge of the current distribution of the species: (A) southern and central Iran, (B) Pakistan, (C) Lebanon, (D) Tunisia, (E) Morocco, (F) Canary Islands, and (G) Oman.

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To account for uncertainties stemming from the tree's structure, we incorporated all trees sampled from BEAST analyses, excluding the initial 500 trees. In the S-DIVA analysis, we selected the "Allow Reconstruction" feature, which permitted a maximum of 100 reconstructions employing three random steps. Subsequently, we conducted up to 1,000 reconstructions to obtain the final tree. Each node in the analysis has attributed the potential for up to four distinct areas.

The results of the most suitable S-DIVA reconstructions were then summarized by utilizing the pruned maximum-clade-credibility tree derived from our Bayesian phylogenetic analysis. In the S-DEC analysis, we assumed equal probabilities of dispersal between areas, and all values in the dispersal constraint matrix were set to 1, considering four as the maximum number of areas.

Results

Field observations

Life cycle. Our research in the field indicates that *B. mendica* is an overwintering univoltine species. Thus, the nymphs emerge in summer (late July), as we have only found the first instar nymphs from late July to early August in their natural habitat, and they continue to grow throughout the season. Then, the larvae overwinter in the last instar (five records of living nymphs during winter from last week of October to first week of February) and become adults in spring (first sightings of adults; males first week of May; females second week of May). Regarding oviposition, females began to lay their oothecae in June, as they often mate within two weeks after reaching adulthood and typically lay their first ootheca within one week after mating. However, it is important to note that oviposition timing can vary depending on various factors such as temperature, humidity, and food availability. This trend has been observed however with small differences in the distribution of this species from western North Africa to the far Middle East.

Ootheca. Three oothecae of *B. mendica* were collected from branches of trees or bushes during June and July 2020 (Figures 2d, e). They were already hatched when collected which could be recognized by the presence of white eclosion sack-like structures in the emergence area. The eggs in this species are arranged vertically in a row next to each other as was observed by dissecting the field-collected oothecae dorsally (Fig. 2c).

Defense behavior. The first author observed two different responses to disturbance in this species during field surveys. Either individual flew away when disruption happened, or they extended their wings broadly and lifted their forelegs (Fig. 3a, b). Additionally, one female made an odd menacing gesture (Fig. 3c).

Habitat and hosting plants. All individuals found in the field were encountered in more or less xeric areas, with scarce vegetation composed of both herbaceous vegetation and spiny bushes (Fig. 4). All specimens were found in Iran sitting on thorny bushes like *Prosopis* spec. (Fig. 5a), *Alhagi* spec. (Fig. 5b), and *Astragalus* spec. (Fig. 5c), as well as *Tamarix* spec. (Fig. 5d). Similar vegetation patterns were observed also in Morocco and Tunisia (Fig. 5e and f). Due to their coloring, *B. mendica* individuals are particularly suited for mimicking leaves, and prickly or dry plants, i.e., the typical flora of semi-deserts.

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Laboratory breeding

Development of immatures and their color changes. One ootheca was laid in the first week of June by a female collected from the xeric shrublands of Bushehr province (N 27° 50' 37.3"; E 52° 03' 51.9"). This ootheca was 18 mm long, 12 mm high, and 6 mm wide (Fig. 2c). It had a globular shape and, as mostly in this species, a very soft texture, completely covered with a layer of spongious material, white in color at the time of laying (Fig. 2a). After one day, the color turned into a creamy color. In total, 45 nymphs hatched from the ootheca's top rim after five weeks (34 days, in the second week of May).

Twenty-eight individuals (11 males, 17 females) of the 45 emerged nymphs completed their life cycle. Twelve did not reach the second instar and died possibly due to poor molting. Five died during the second and third instar. The time needed from hatching to adulthood on average was 18 weeks (130 days) (Table 2). While most nymphs became adults after six (all males) or seven molts (most females), four females required eight molts.

The first instar had a distinct color pattern on the thorax and legs, with mostly dark brown and some white and black stripes (Fig. 1c). The color changed from light brown to creamy or white from the second instar to subadult (Fig. 1d, e), and the adults' color ranged from bluish green to grass green (Fig. 1a, b). We also observed color changes in adult specimens under laboratory conditions. Thus, three adults first appeared ochre-brown or reddish, but after some days their thoraxes became reddish, their wings greenish, and some other body parts reddish brown (Fig. 1~~a,~~ b). The last larval instar had a longer lifespan than the others (Table 2). Overwintering of nymphs explains the long duration of the last instar since it seems that the last instar nymph will undergo a diapause process during winter (Table 2).

Adult longevity. The mean adult longevity of *B. mendica* at 25 °C ± 2 was 118 days (± 6 SD) for females (range: 100–124 days), and 46 days (± 5 SD) for males (range: 39–55 days). SD refers to standard deviation. The t-test recovered a statistically significant difference (P < 0.001) when comparing sexes (Suppl. Material Table S3). The average total life cycle was 216 days (± 9 SD) for females, and 132 days (± 7 SD) for males (P < 0.27) (Suppl. Material Table S4).

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Oviposition. To test for parthenogenesis, five of the 17 females who reached adulthood were not mated. Three of these produced three unfertilized oothecae, none of which hatched. The 12 remaining females were joined with the males in a separate terrarium for mating. Eight females successfully mated and produced a total of 11 oothecae, i.e., four laid one ootheca, two laid two, and one laid three. Only four of these oothecae hatched.

There were no observable physical differences or deformations between the unfertilized, unhatched, and hatched oothecae (Table 3). However, the number of eggs per ootheca varied depending on the type and size of the ootheca (Table 3). The average number of eggs per ootheca was higher in the hatched (mean: 43.7 ± 7.2 SD) and unhatched (mean: 31.8 ± 2.4 SD) oothecae compared to the unfertilized ones (mean: 18.0 ± 2.9 SD) (Table 3). ANOVA tests indicated significant differences among the three groups for all characteristics (i.e., weight, length, width, and number of eggs), except for height. There is also a significant difference in weight and length between the hatched and unfertilized ootheca, as both Tukey *p*-values are less than 0.05, but there is no significant difference in height or number of eggs. Comparing hatched and unhatched oothecae revealed significant differences in weight, length, and number of eggs; however, there was no significant difference in width or height (Table 4).

Distribution and Ecological Niche Modelling

Blepharopsis mendica is largely associated with dry grasslands~~, savanna-like habitats,~~ and xeric shrublands from the Canary Islands to Pakistan (Fig. 6). Almost identical vegetation pattern was observed in Morocco and in Tunisia where this species has been observed in the wild. In Iran, where the distribution was poorly known prior to this study, it is also widely distributed, only excluding the driest regions in the central and eastern parts of the country and the high mountain areas in the west. The new records from Iran are listed in Supp. Information S1. The geographic projections of the ecological niche of *B. mendica* showed widespread climatic suitability across North Africa and southwestern Asia; lower suitability was recovered for the Sahel zone and southern Africa (Fig. 7, Supp. Information Fig. S1). The best fitting method to construct the climatic ellipsoids was 'mve1', with environmental set 1, containing principal components of all 15 variables; mean AUC, *p*-value of partial ROC, and omission rates were significantly better than random expectations (P < 0.05; Table 1). The prevalence of mean ellipsoidal models in geographical (G-space) and environmental (E-space) space was relatively high (0.912; Table 1). The complete report of ellipsoid characteristics (e.g., centroid, covariance matrix, semi-axes length, etc.) is given in Supp. Information S3.

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Divergence dating, biogeography, and phylogenetic analyses

COI sequences of 15 specimens of *B. mendica* revealed 12 different haplotypes (Fig. 8). Bayesian tree and haplotype network analysis of *B. mendica* identified three distinct population groups: (i) Pakistan, (ii) Maghreb from Morocco to Tunisia, including the Canary Islands, and (iii) Middle Eastern populations from Lebanon, Oman, and Iran; the latter group is subdivided into a western subgroup (iiia) in Lebanon, Oman, and Khozestan (border Iran/Irak) and an eastern one (iiib) widespread in southern and central Iran (Fig. 9 and 10). Our biogeographic analysis using S-DIVA and S-DEC models revealed a divergence of the lineage in Pakistan from the ancestor of the other groups about 1.5 million years ago. Another vicariance event separated the Maghreb populations from the remaining ones about 1.3 Mya. Less than 1 Mya, a dispersion event led to the split between the Middle East (Lebanon, Oman, Khozestan) and

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most other Iranian populations (Fig. 9). Hence, historical events, including vicariance and dispersion, played pivotal roles in shaping the genetic pattern of *B. mendica* populations.

Discussion

Life cycle and variability in nymphal development

The life cycle of mantids is divided into two phases: the developmental period from hatching to reaching adulthood and the reproductive period as adults, which is defined by adult longevity. Korsakoff (1934) recorded nine instars for females and eight instars for males of *B. mendica* from hatching to adulthood. In our study, nymphs only passed through fewer instars, i.e., six for males and seven (rarely eight) for females, which is similar to *Hierodula* species, which pass through six to nine instars to reach adulthood (Leong, 2009; Raut *et al*. 2014; Mirzaee *et al*. 2022a). The variability in the number of instars in mantids might be due to different factors, such as temperature, resource availability and quality, humidity, genetics, sex, and photoperiod (Esperk *et al.* 2007). Therefore, a higher temperature, humidity, and resource availability and quality in our study might decrease the number of molts in this species. The higher temperatures used to rare the nymphs of *B. mendica* in our study (33–35 °C), in comparison to Korsakoff's study (27 °C), could have accelerated the developmental rate of the specimens, resulting in fewer instars being needed to reach adulthood. Similarly, if the quality and availability of food were different between the two studies, this could have also influenced the developmental rate and the number of instars required for the mantids to reach adulthood. In Korsakoff's study specimens were fed by rose moth caterpillars but in our study, we used mealworms, flies, and grasshoppers. Additionally, differences in the genetic background and sex of the mantids used in the two studies could also have contributed to the differences in the number of instars e.g., the mantids used in this study were from Iran and the mantids Korsakoff used in his study were from North Africa.

As in our study, Maxwell (2014a) also observed a similar variation in the number of instars in *Stagmomantis limbata* bred in captivity, with 64 % of nymphs requiring six, and 36 % requiring seven instars. He considered this variation in the number of instars as a "bet-hedging" strategy used by females to produce variation in development among siblings (Maxwell, 2014b). It thus might be a survival strategy, for mantid species in general and for such species living in extreme and often largely unpredictable habitats like *B. mendica* in particular, because sisters hatching together will enter the reproductive phase at different points in time. This is increasing the

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chance that at least some females are reproductive in a suitable time window, hence safeguarding the survival of regional populations of the respective species.

Adaptations of the incubation time of oothecae, and nymphal overwintering

The incubation duration of oothecae in Mantodea often is species-specific, but can also be influenced by the environment. Therefore, it is important to consider the impact of environmental conditions when studying the developmental biology of any species (Greyvenstein *et al*. 2022). It seems that temperature, particularly daily maximum temperature, is the key factor for hatching in different mantid species such as *A. spallanzania* (Rossi, 1792) (Battiston & Galliani 2011). Various mantis species employ distinct strategies for overwintering and development, demonstrating their ability to adapt to diverse environmental conditions. These differences may be influenced by specific genetic factors, potentially resulting in different life cycles even when multiple species share the same habitat. Overwintering strategies in Mantodea can be different between different genera but little information regarding these strategies is available for this group of insects. Some Mantidae genera, for example, *Miomantis* Saussure, 1870, *Hierodula* Burmeister, 1838 and *Mantis* Linneus, 1758, go into a facultative diapause phase during the ootheca stage (Ramsay, 1984; Mirzaee *et al*. 2022a). However, some other species in different genera like *Ameles* Burmeister, 1838, *Empusa* Illiger, 1798, and *Severinia* Finot, 1902, have the strategy to overwinter as nymphs (Battiston & Galliani 2011; Shcherbakov & Govorov 2021). In our study, the last nymphal instar of *B. mendica* lasts longer than the previous ones (as shown in Table 2). This developmental pattern is also seen as an adaptation strategy to survive overwintering as a nymph.

In our study, the average incubation period for oothecae of *B. mendica* was 36.8 days (± 2.9 SD). This is similar to other members of the Mantidae family, such as *Hierodula tenuidentata* Saussure, 1869 (35.1 days), *Orthodera ministralis* (30.9 days), and *Hierodula ventralis* (25 days) (Suckling, 1984; Raut *et al*. 2014; Mirzaee *et al*. 2022). However, shorter (e.g., 16 days for *Ephestiasula pictipes*; Hymenopodidae) and much longer incubation periods (e.g., 142–209 days for *Stagmomantis limbata*; Mantidae) also exist (Robert, 1937; Vanitha *et al*. 2016). Therefore, the adaptation strategy for the incubation period can vary across different species. Even among species with similar incubation periods, the strategies used can be different. For instance, females of *Hierodula* *transcaucasica*~~species~~ lay their oothecae in late autumn, which then undergo~~es~~ a dormant process during winter, and egg development begins when

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temperatures become suitable; the same also applies to *Mantis religiosa* and *Sphodromantis viridis* (Kaltenbach 1963, Berg et al. 2011, Mirzaee *et al*. 2022a, Raut and Gaikwad 2016). On the other hand, females of *B. mendica* and *Empusa* spp. lay their ootheca in spring so that it is the nymphs that have an overwintering strategy.

Having a short incubation time for the ootheca seems to be an appropriate strategy in wet tropical areas without distinct seasonal variation. In contrast, temperate species require longer incubation periods or even dormancy, especially when the egg is in the overwintering stage. For species living in regions with an arid summer and a mild winter climate, an intermediate incubation time might be the most suitable adaptation. This is because egg maturation takes place during the hottest and driest time of the year when there is limited food supply. Then, the larvae hatch with the first autumn rains, and reproduction in the following year will end when the living conditions become unfavorable (Robert, 1937; Vanitha *et al*. 2016; Raut and Gaikwad 2016; Mirzaee *et al.* 2022a).

Color polymorphisms and variability as an adaptive defense mechanism

Coloration can be influenced by genetic factors and environmental conditions (Okay, 1953; James, 1944). The different colors of different instars and the color changes of *B. mendica* therefore might be interpreted as an adaptational defense according to the respective environmental conditions and the ability of the species to camouflage and thus avoid predators. A similar developmental strategy was also observed for *Mantis religiosa* often changing its color from brownish to green along its larval development (Battiston and Fontana 2010). Under artificial conditions, some adult brown *M. religiosa* females showed an incomplete but clearly visible variation toward green tones in some body parts, even when no green components were available in the cages. Even more, *B. mendica* is able to change its color in the adult stage without using the renovation processes of a molt. This latter phenomenon is also known for *Miomantis caffra* (Ramsay, 1990) and *M. religiosa* (Okay, 1953); the mechanisms behind are still unknown.

Characteristics of ootheca and parasitization

Various factors, including male presence, temperature, humidity, food availability, and genetics, affect the size, color, and structure of oothecae (Robert, 1937; Breland and Dobson 1947; Hurd *et al*. 1995). Mantid oothecae are consumed by certain beetles (*Orphinus* spp. *Attagenus* spec. *Phradonoma* spec.; Dermestidae) and parasitized by wasps (*Podagrion* spp.; Torymidae) (Kershaw, 1910; Hawkeswood, 2003; Bolu and Ozaslan 2015, Mirzaee *et al*.

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2021b, 2022b). These factors have a significant impact on not only the appearance of oothecae but also their survival rates and hatching, and therefore the population dynamics of mantids in their natural habitats. Korsakoff (1934) discovered that the chalcidoid wasp *Podagrion* spec. parasitized the oothecae of *B. mendica* that he collected from North Africa, with more parasitoids than *B. mendica* nymphs emerging. In our study, none of the oothecae were parasitized due to laboratory conditions, but further research is necessary to identify the species of beetles or wasps preying or parasitizing on *B. mendica* oothecae in the wild.

Distribution and ecological biogeography

Our climate suitability model recovered suitable areas that well reflect the known distribution of *B. mendica* (Figs. 7 and 8), ranging from the Maghreb in the west to the Middle East as far east as Pakistan and the driest parts of western India. Hence, high climatic suitability was exclusively recovered in hot and dry regions (Supp. Information Figure. S1). A recent study conducted by Nasser *et al.* (2021) analyzing *B. mendica* in Egypt equally found that temperature-related variables but also low altitude were the factors most significantly contributing to the climatic niche model. In their study in contrast to our work, however, precipitation-related variables had a relatively small influence.

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uniform in term of precipitation.

In contrast to our climate models, however, major climatically suitable areas, particularly in northern Libya (Supp. Information Figure. S1), represent a geographic gap within the known distribution extending to both sides. As this part of Libya is generally hot and dry, and the prevailing vegetation features may favor the occurrence of *B. mendica* (Ageena, 2013), we argue whether this distribution gap is real or not because it just might be due to sampling deficits. A similar gap of knowledge regarding the species' distribution applies to Saudi Arabia, where high climatic suitability levels were also recovered. Therefore, further fieldwork is needed in these two regions to clarify this aspect.

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However, a real geographic split into two major groups is also possible, one Maghreb group, largely distributed in north-western Africa, and one group around the Arabian Peninsula, ranging from Egypt via Israel, Iraq, and Iran to Yemen, but avoiding the driest inner parts of the peninsula. The formation of these two distinct geographic groups in *B. mendica* might be the result of a combination of historical and extant environmental factors shaping the distribution and genetic makeup of the species over time. Thus, these two groups originating from one common ancestral population might have been separated by a physical barrier, such as temporally existing stretches of extreme desert in northern Libya, preventing gene flow

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among these groups. Over time, genetic differences might have accumulated through genetic drift or natural selection, leading to the formation of two distinct gene pools. Environmental factors, such as differences in climate and vegetation (Mulligan *et al*. 2017), also might have played a role in shaping the distribution of *B. mendica*. For example, the drier parts of the Arabian Peninsula may not provide suitable habitats for the species, whereas the more humid areas around its coastlines as well as the southern Maghreb region may provide more favorable conditions.

Suitable climatic conditions were also recovered in parts of southern Africa. Thus far, however, the true absence of *B. mendica* in this region might be due to the interspersed, geographically rather large regions whose climatic conditions permanently have been completely unsuitable (i.e., tropical forests of central and eastern Africa; Supp. Information Figure. S1), in combination with the limited dispersal capability of *B. mendica*.

Despite some known occurrences in the Sahel zone, our model recovered only marginally suitable climatic conditions for this region. However, a Google Maps search revealed that one of the recorded locations is a truck parking lot in Sudan. It consequently is likely that the observed *B. mendica* specimen was accidentally transported there by truck, as studies have indicated that, similar to other insects, praying mantids, including their egg cases (i.e. oothecae), are frequently introduced to new areas through transportation, including railways and other commercial routes (Battiston *et al*. 2020). The two further specimens collected in southern parts of Chad and Niger are suspicious and need future confirmation. Consequently, three possibilities exist for these Sahel zone records: (1) They are wrong or represent displaced individuals; (2) the species is very rare in this zone offering it only marginal living conditions; (3) the species is frequent in the Sahel zone and the conditions are suitable, but the region is completely understudied for this species. Further studies in the Sahel region are therefore necessary to resolve this open question.

The only major region where *B. mendica* was frequently observed in areas not indicated as suitable by our model is the mountainous parts of northern Iran. We believe that this is due to the complex climatic structuring of this area with very heterogeneous microclimatic conditions (Heshmati, 2007). The hot and dry conditions needed by *B. mendica* are mostly restricted to relatively small pockets in the landscape, such as deep valleys, so the species is occurring rather locally. As the climate in most parts of these landscapes is unsuitable for *B. mendica* at the grit level, our model likely was unable to detect these small-scale pocket-like occurrences. This

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model confirms the general conservation assessment of this species (Battiston, 2016) which hypothesized the existence of diminutive and fragmented local populations within the extensive distribution range of *B. mendica*.

Divergence dating and phylogeographic analyses

Our study also provides insights into the evolutionary and biogeographic history of *B. mendica*. The distinct genetic lineages identified in Pakistan, north-western Africa (Morocco, Tunisia, Canary Islands), the Middle East (Lebanon, Oman, Iran-Iraq border, most likely Egypt), and Iran (south and central regions) reflect the species' ability to adapt to and to survive in different geographical with different environmental conditions (Figs 9 and 10).

The separation of *B. mendica* from other Empusid mantids might have occurred around 2.5 mya suggesting that this species has evolved independently from other Empusid mantids all along the Pleistocene. The subsequent divergence of the Pakistan~~i~~ lineage from the remaining populations around 1.5 mya may have been influenced by geographic barriers or environmental changes, maybe going along with the general aridification alongside the mid-Pleistocene Transition (1.2–0.8 mya), hence causing vicariance (Thunell, 1979; Bertoldi *et al*. 1989, Berends *et al*. 2021).

The separation of the Maghreb lineage a little later, i.e., around 1.3 mya, likely also resulted from vicariance that again could have been triggered by the mid-Pleistocene Transition's aridification (Berends *et al*. 2021), maybe making the territory of today-Libya hostile for the species due to extreme dryness, indicating that climate-driven geographical isolation might have played an important role in the differentiation of *B. mendica*. Less than one mya and hence at the end of the mid-Pleistocene Transition, a dispersal event out of Iran (detected by our RASP analysis) was responsible for the colonization of the Arabian Peninsula or the Middle East with subsequent vicariance and differentiation among these three regions. The arid Pleistocene conditions in the Maghreb region prevailing during most of the last 0.5 my might also be responsible for vicariance between its eastern and western regions for *B. mendica* assumed 360.000 years ago, an often-observed fact in this region, but mostly with considerably higher vicariance age (Husemann *et al*. 2014). The colonization of the Canary Islands is a rather recent event dated by our molecular clock to 80,000 years before the present, and hence immediately before the true onset of the Würm glaciation (Ampferer, 1925).

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For empusid phylogeny see Wieland (
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Conclusion

This study adds information on the little-known desert mantid species *B. mendica*, including its life cycle, ootheca (egg case), defense behavior, and preferred habitat. Additionally, our climate suitability model provided important insights into the species' distribution, corroborating existing records while also pointing out areas where sampling has been limited and regions that still remain unexplored. However, to fully understand the distribution patterns with its underlying phylogeographical structures and the factors shaping the ecological niche of *B. mendica* across different geographical regions, further research, fieldwork, and validations are essential. These efforts will contribute to a more comprehensive understanding of the species distribution and its relationship with environmental factors.

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Conflicts of Interest: The authors declare no conflict of interest.

References

Adair, E.W. (1924) On parthenogenesis in *Miomantis savigny* Saussure. *Bulletin de la Société Entomologique d'Égypte*, 8, 104–148.

Ageena, I. (2013) Trends and patterns in the climate of Libya (1945-2010). Doctoral dissertation, University of Liverpool.

Ampferer, O. (1925) U¨ ber Wachstumsunterschiede zwischen Fern- und Nahgletschern. *Die Eiszeit,* 2, 41–49.

Battiston, R. Amerini, R. Di Pietro, W. Guariento, L.A. Bolognin, L. and Moretto, E. (2020) A new alien mantis in Italy: is the Indochina mantis *Hierodula patellifera* chasing the train for Europe? *Biodiversity Data Journal*, 88, e50779. https://doi.org/10.3897/BDJ.8.e50779.

Battiston, R. and Galliani, C. (2011) On the life-cycle of *Ameles spallanzania* (Rossi, 1792) (Insecta, Mantodea). *Natural History Sciences*, 152(1), 25–35. https://doi.org/10.4081/nhs.2011.25.

Battiston, R. Picciau, L. Fontana, P. and Marshall, J. (2010) *The Mantids of the Euro-Mediterranean Area*. World Biodiversity Association, Verona. pp. 240.

Battiston, R. Fontana, P. (2010) Color change and habitat preferences in *Mantis religiosa*. *Bulletin of Insectology*, 63(1), 85–89.

Bolu, H. Ozaslan, C. (2015) *Mantis religiosa* L. (Mantodea: Mantidae) a new host for *Podagrion pachymerum* Walker (Hymenoptera: Torymidae) in Turkey. *Agriculture & Forestry*, 61,183–187. https://doi.org/10.17707/agricultforest.61.2.16.

Brannoch, S.K. Wieland, F. Rivera, J. Klass, K, Bethoux, O. and Svenson, G.J. (2017) Manual of praying mantis morphology, nomenclature and practices (Insecta, Mantodea). *ZooKeys*, 696, 1–100. https://doi.org/10.3897/zookeys.696.12542.

Berends, C.J. Köhler, P. Lourens, L.J. van de Wal, R.S.W. (2021) On the cause of the mid-Pleistocene transition. *Reviews of Geophysics*, 59, e2020RG000727. https://doi. org/10.1029/2020RG000727

Breland, O. and Dobson, J. (1947) Specificity of mantid ootheca (Orthoptera: Mantodea). *Annals of the Entomological Society of America*, 40, 557–575. https://doi.org/10.1093/aesa/40.4.557.

Bertoldi, R. Rio, D. and Thunell, R. (1989) Pliocene-Pleistocene vegetational and climatic evolution of the south-central Mediterranean. Palaeogeography, Palaeoclimatology, *Palaeoecology*, 72, 263–275.

Caesar, M. Roy, R. Legendre, F. Grandcolas, P. and Pellens, R. (2015). Catalogue of Dictyoptera from Syria and neighbouring countries (Lebanon, Turkey, Iraq, and Jordan). *Zootaxa*, 3948(1), 71–92. https://doi.org/10.11646/zootaxa.3948.1.5.

Cukier, M. Guerrero, G.A. and Maggese, M.C. (1979) Parthenogenesis in *Coptopteryx viridis*, Giglio Tos (1915) (Dictyoptera, Mantidae). *The Biological Bulletin*, 157, 445–452. https://doi.org/10.2307/1541029.

Ehrmann, R. (2011) Mantodea from Turkey and Cyprus (Dictyoptera: Mantodea). *Articulata*, 26(1), 1–42.

Esperk, T. Tammaru, and T. Nylin, R. (2007) Intraspecific variability in number of larval instars in insects. *Journal of Economic Entomology*, 100, 627–645. https://doi.org/10.1093/jee/100.3.627.

Greyvenstein, B. Du Plessis, H. Moulin, N. and Van den Berg, J. (2020) Distribution of *Galepsus* spp. in Southern Africa and life history of *Galepsus lenticularis* (Mantodea: Tarachodidae). *Insects*, 11(2), 119. https://doi.org/10.3390/insects11020119.

Greyvenstein, B. Du Plessis, H. and Van den Berg, J. (2022) Notes on the lifecycle and distribution of *Sphodromantis gastrica* (Stâl, 1858) (Mantodea: Mantidae) in South Africa. *African Entomology*, 30(1). http://dx.doi.org/10.17159/2254-8854/2022/a13967.

Hawkeswood, T.J. (20039 Notes on the biology and food items of three Australian Dermestidae (Coleoptera). *Calodema*, 1, 1–4.

Heshmati, G.A. (2007) Vegetation characteristics of four ecological zones of Iran. International *Journal of plant production*, 1(2), 25–224. https://doi.org/10.22069/IJPP.2012.538.

Hurd, L.E. Eisenberg, R.M. Moran, M.D. Rooney, T.P. Gangloff, W.J. and Case, V.M. (1995) Time, temperature, and food as determinants of population persistence in the temperate mantid *Tenodera sinensis* (Mantodea: Mantidae). *Environmental Entomology*, 24, 348–353. https://doi.org/10.1093/ee/24.2.348.

Husemann, M. Schmitt, T. Zachos, F.E. Ulrich, W. and Habel, J.C. (2014) Palaearctic biogeography revisited: Evidence for the existence of a North African refugium for western Palaearctic biota. *Journal of Biogeography*, 41, 81-94. https://doi.org/10.1111/jbi.12180.

James, H.G. (1944) Color changes in *Mantis religiosa* L. *The Canadian Entomologist*, 76(6), 113-116.

Kershaw, J.C. (1910) The formation of the ootheca of a Chinese mantis, *Hierodula saussuri*. *Psyche*, 17, 136–141. https://doi.org/10.1155/1910/78374.

Korsakoff, M.N. (1934) Contribution à l'étude du *Blepharopsis mendica* Fab. *Revue d'Écologie (La Terre et La Vie)*, 4(5), 272–276.

Korsakoff, M.N. (1935) Contribution à l'étude du Blepharopsis Fabr. (suite). *Revue d'Ecologie, Terre et Vie, Société nationale de protection de la nature*, 120-124.

Leong, T.M. (2009) Oviposition and hatching in the praying mantis, *Hierodula patellifera* (Serville) in Singapore (Mantodea: Mantidae: Paramantinae). *Nature in Singapore*, 2, 55–61.

Maxwell, M. (2014a) Developmental patterns in *Stagmomantis limbata* (Mantodea: Mantidae): Variation in instar number, growth, and body size. *Journal of Orthoptera Research*, 23, 49–58. https://doi.org/10.1665/034.023.0104.

Maxwell, M. (2014b) A synoptic review of the genus *Stagmomantis* (Mantodea: Mantidae). *Zootaxa*, 3765, 501–525. https://doi.org/10.11646/zootaxa.3765.6.1.

Mirzaee, Z. and Sadeghi, S. (2019) On a summer collection of mantids (Insecta: Mantodea) from Lorestan province with nine new records. *Iranian Journal of Animal Biosystematics*, 15(2), 175–187. https://doi.org/10.22067/ijab.v15i2.79314.

Mirzaee, Z. and Sadeghi, S. (2021) A survey on mantids fauna (Insecta: Mantodea) from Fars Province. *1st Fars Biodiversity Conference*, 1, 25.

Mirzaee, Z. Lotfalizadeh, and H. Sadeghi, S. (2021b) Chalcidoid parasitoids (Hymenoptera: Torymidae and Eupelmidae) of mantids (Mantodea) oothecae in Iran. *Phytoparasitica*, 50, 487–499. https://doi.org/10.1007/s12600-021-00965-1.

Mirzaee, Z. Sadeghi, S. and Battiston, R. (2022) Biology and Life Cycle of the Praying Mantid *Hierodula tenuidentata* Saussure, 1869 (Insecta: Mantodea). *Iranian Journal of Science and Technology, Transaction A: Science*, 46, 1163–1169 https://doi.org/10.1007/s40995-022-01325-2.

Mirzaee, Z. Sadeghi, S. Háva, J. Battiston, R. and Ruzzier, E. (2022b) New observations of Coleoptera associated with Mantodea ootheca and an overview of the previous records. *Bulletin of Insectology*, 75(2), 223–230.

Mulligan, M. Keulertz, M. and McKee, M. (2017) Environmental Factors in the MENA Region: A SWOT Analysis. CIDOB.

Nasser, M. Okely, M. Nasif, O. Alharbi, S. GadAllah, S. Al-Obaid, S. Enan, R. Bala, M. and Al-Ashaal, S. (2021) Spatio-temporal analysis of Egyptian flower mantis *Blepharopsis mendica* (order: Mantodea), with notes of its future status under climate change. *Saudi Journal of Biological Sciences*, 28(4), 2049–2055. https://doi.org/10.1016/j.sjbs.2021.01.027.

Okay, S. (1953) Formation of green pigment and color changes in Orthoptera. *Bulletin of Entomological Research*, 44(2), 299–315. https://doi.org/10.1017/S0007485300023099.

Panhwar, W.A. Tasleem, S. Asif, M. Alam, M. Anwar, F. Nisa, Z.U. *et al*. (2020) Praying mantis (Mantodea: Dictyoptera) of Pakistan: A review-based study. *Bulletin of Environment, Pharmacology and Life Sciences*, 9, 180–183.

Ramsay, G.W. (1990) Mantodea (Insecta), with a review of aspects of functional morphology and biology. *Fauna of New Zealand*, 19. https://doi.org/10.7931/J2/FNZ.19.

Raut, G.A. Bhawane, G.P. and Gaikwad, S.M. (2014) Laboratory studies on the life history of *Hierodula ventralis* Giglio-Tos, 1912 (Mantodea: Mantidae). *Journal of Entomology and Zoology Studies*, 6, 147–152.

Raut, G.A. and Gaikwad, S.M. (2016) Observations on the Life cycle, mating and cannibalism of *Mantis religiosa religiosa* Linnaeus, 1758 (Insecta: Mantodea: Mantidae). *Journal of Entomology and Zoology Studies*, 4(6), 478–482.

Robert, R.A. (1937) Biology of the Bordered mantid, *Stagmomantis limbata* Hahn (Orthoptera, Mantidae). *Annals of the Entomological Society of America*, 30, 97–109.

Shcherbakov, E. and Govorov, V. (2021) Riders on the storm? A short note on the biology of *Severinia turcomaniae* (Saussure, 1872) (Mantodea: Toxoderidae). *Annales de la Société entomologique de France (N.S.)*, 57,4, 372–378, https://doi.org/10.1080/00379271.2021.1950050.

Suckling, D.M. (1984) Laboratory studies on the praying mantis *Orthodera ministralis* (Mantodea: Mantidae). *New Zealand Entomologist*, 8(1), 96–101. https://doi.org/10.1080/00779962.1984.9722478.

Thunell, R.C. (1979) Climatic evolution of the Mediterranean Sea during the last 5.0 million years. *Sedimentary Geology*, 23(1-4), 67–79.

Vanitha, K. Bhat, P.S. Raviprasad, T.N. and Srikumar, K.K. (2016) Biology and behaviour of *Ephestiasula pictipes* (Wood Mason) (Hymenopodidae: Mantodea) under captive breeding. *International Journal of Pest Management*, 62, 308–318.

Walker, L.A. and Howell, I.G. (2016) Sexual cannibalism in a facultative parthenogen: The springbok mantis (*Miomantis caffra*). *Behavioral Ecology*, 27, 851–856.

Zehzad, B. Kiabi, H. and Madjnoonian, H. (2002) The natural areas and landscape of Iran: an overview. *Zoology in the Middle East,* 26,1, 7–10. https://doi.org/10.1080/09397140.2002.10637915.