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Weather Influence on Native and Alien Mantis Dynamics and Their Abundance in the Current Climate Change Conditions

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Abstract: Humans have traded and transported alien species for millennia, both with and without intention to spread them to new areas. Consistent knowledge of their ecology will allow decision makers to take suitable conservation actions, with the aim of avoiding threatening native species. Praying mantids (Mantodea) are predatory insects with a high impact on local invertebrates' fauna. An alien mantis species (*Hierodula tenuidentata*) could create a disequilibrium in both the local ecosystem and in autochthonous mantid species (*Mantis religiosa*) if it can adapt to the local ecological conditions. Through this study, we reveal that the number of *Hierodula tenuidentata* individuals from an Eastern European Natura 2000 site was 7.6 times higher than the number of *Mantis religiosa* suggesting a higher density of the allochthonous species in the study area. According to a GLM analysis, the population of *Mantis religiosa*, measured from August to the end of October, declines more rapidly and is negatively influenced by the number of days from the first day of the year, while the population of *Hierodula tenuidentata* is influenced by local weather factors. This is the first study which analyzes the influence of local weather factors (namely air temperature, precipitation, daily atmospheric pressure, daily wind direction and speed, daily cloud cover, sunshine duration and number of days from the first day of the year) on the abundance dynamic of mantises in order to understand their ecology in the current climate change influence.

Keywords: mantis religiosa; Hierodula tenuidentata; Eastern Europe; species conservation

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1. Introduction

The current effects of climate change are likely to substantially affect species interaction and distribution, population dynamics and biodiversity structure, making it challenging to predict the climatic influence on different species across taxa and trophic levels [1,2]. Insects, integral biotic components of nearly all ecosystems, will be affected by these changes in a variety of ways which are not yet completely assessed by scientists [3]. While some studies show that insect population is likely to increase with climate change [4], most recent research highlights insect decline as a result of climate change [5]. However, rising air temperature could create advantages for species that are well-adapted to warmer climates, sometimes to the detriment of native species.

Humans have traded and transported alien species for millennia with two notable step changes: the end of the Middle Ages and the beginning of the Industrial Revolution [6]. These habits have increased in recent times, with some species being transported intentionally, but most of them accidentally, within cargo containers, by ships or airplanes. By using human means of transportation, some species can reach areas where their expansion would have been impossible in a natural way. Increasing transport networks and demand for commodities have led to pathway risk assessments becoming the frontline in the prevention of biological invasions [6].

Knowledge about alien species ecology can lead to suitable conservation actions for threatened native species. In some cases, this expertise on alien species ecology in their native habitats may not be sufficient and further research is necessary to understand the competition between native and alien species and to assess control measures.

At the moment, there are more than 1300 insect species that are non-native to Europe [7]. Each year, more allochthonous species are discovered on the European continent. Praying mantids (Mantodea) are such a case, being prone to expand in recent conditions of climate change. This occurs not only in Europe (Palearctic realm) but also in the Nearctic, Oceania and Australasia [8]. In Europe, seven species are considered invasive [8,9]. Of these invasive species, only one species, namely *Hierodula tenuidentata* (Saussure, 1869), was detected in Romania, in 2018 [10].

Hierodula tenuidentata originated in Asia and reached the European territories more than 100 years ago in the Caucasus region [11]. However, until recently, there were no other records of this species in Europe, when it started to be observed in more countries in a short interval of time, especially in urban areas [10,12–19]. This fact suggests an ongoing expansion enforced by globalization. Although *Hierodula tenuidentata* have developed stable populations in many European countries, not much is known about its biology and how this species interferes with native fauna, especially with the widely distributed European mantid species *Mantis religiosa* (Linnaeus, 1758). Published papers are mostly focused on its distribution in Europe, and only a few discuss aspects regarding its ecology [10,16,19,20].

The aim of this study is to analyze the abundance and activity of *Hierodula tenuidentata* and *Mantis religiosa*. Another aim is to test the influence of several weather variables on these parameters in a seminatural and natural setting, near the Black Sea (Agigea Sand Dunes protected area) and from the Agigea Research Station in Romania, respectively.

2. Materials and Methods

2.1. Study Area

The study area covers the Marine Research Station "Prof. Dr. Ioan Borcea" in Agigea and the Natura 2000 site, Marine Dunes from Agigea (44°5′14″ N, 28°38′32″ E). The research stations have a protected area of 10.55 ha and 15.16 ha, respectively. They lie near the Black Sea coast and in the immediate vicinity of Constanța Harbor, respectively (Figure 1). The special protected area was designated to ensure conservation measures for sand dune habitats and contain characteristic plant, reptile and invertebrate species. The area is doubly recognized as both the Natura 2000 site and a natural reserve, and access to this area is limited. This "green island" is rich in biodiversity and surrounded by agricultural land, built-up and industrial areas. It represents a refuge, not only for many plants and invertebrate species but also for birds during their migration movements.

2.2. Study Design and Data Collection

Due to its importance for migratory birds, the study area hosts the first Romanian bird observatory and is active for most of the year. In this area, 500 m of mist nets for bird trapping are installed. Each evening, from the beginning of August 2021 to the end of October 2021 (92 days in total), we conducted two transects along the mist nets and counted the number of *Mantis religiosa* and *Hierodula tenuidentata* that were attached to the mist nets. These months were chosen to be able to mark the adult individuals that started to appear in August. The first transect was conducted daily at 21.00 PM EEST. The second transect was carried out later, at 23.00 PM EEST. We chose these hours based on preliminary data that showed that the day activity of mantids in mist nets yielded no results (with the exception of a few scattered observations over the three-month period). Every time the transect was taken, the observers noted the location of each individual. They marked each individual with a line code for subsequent recognition, according to the Figure 2. This combination of markings can count 99 individuals with one color. With 3 colors, we can record 297 individuals. During the survey, only adult individuals were marked. At this stage, they do not molt and will keep the line code until death. Each individual was photographed in order to have a comparative image for further observations of the same individual. The markers were tested to see their resistance with time. They showed to last for more than 30 days.

All the observations were recorded in a GIS database using ESRI ArcGIS Pro 2.9.2. The same software was used to produce a map of the study area.

2.3. Predictive Weather Variables

To analyze the influence of weather variables on the presence of *Mantis religiosa* and *Hierodula tenuidentata* individuals, we used weather data for 11 parameters (Table 1).

Table 1. Weather variables used for a general linear model (GLM) approach to determine their influence on the *Mantis religiosa* and *Hierodula tenuidentata* individuals.

Variable Name	Variable Abbreviation
Number of days from the first day of the year	Datenr
Mean daily air temperature (°C)	T_med
Maximum daily air temperature (°C)	T_max
Minimum daily air temperature (°C)	T_min
Precipitation amount per day (mm)	Pp
Mean daily pressure (hPa)	Pression
Mean daily wind direction (degrees)	Windg
Mean daily wind direction (factorial)	Windc
Mean daily wind speed	Winds
Mean daily cloud cover (eights)	Cloud cover
Daily sunshine duration (hours)	DSS

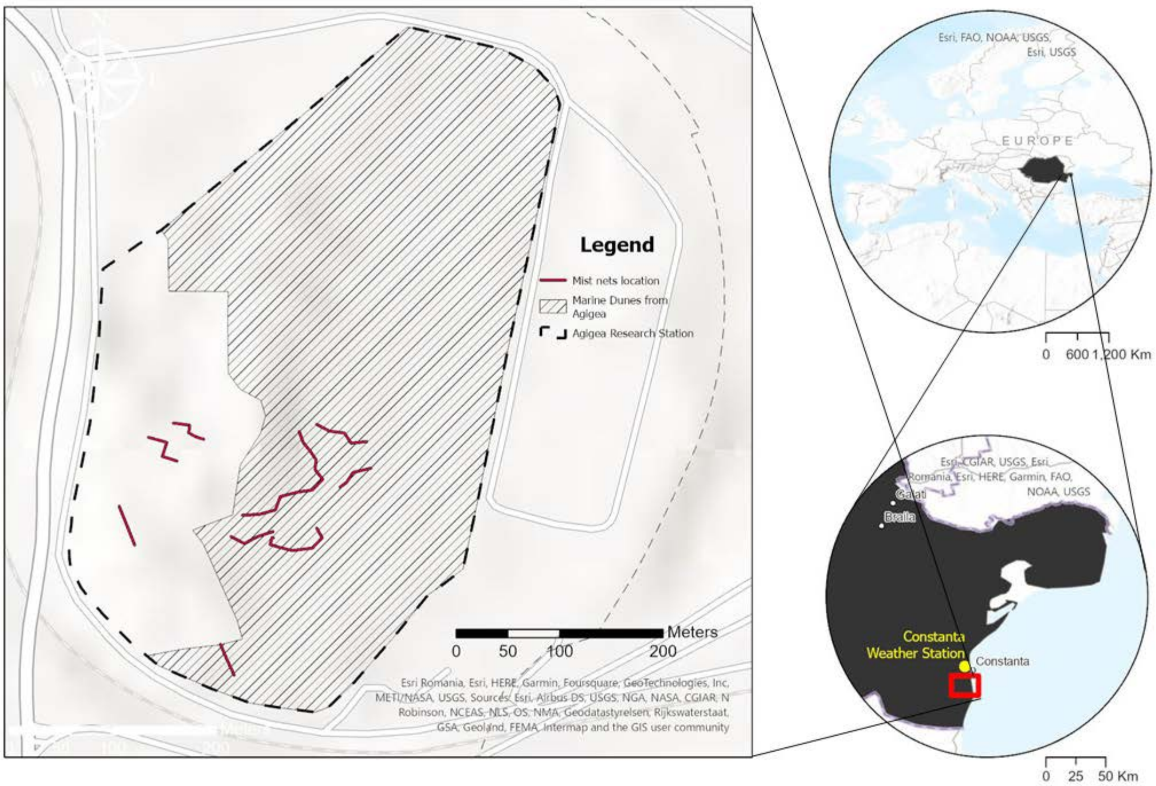

Figure 1. Study area location (with Romanian territory in black) and the distribution of mist nets survey in the study area located in the extreme south-eastern part of Romania.

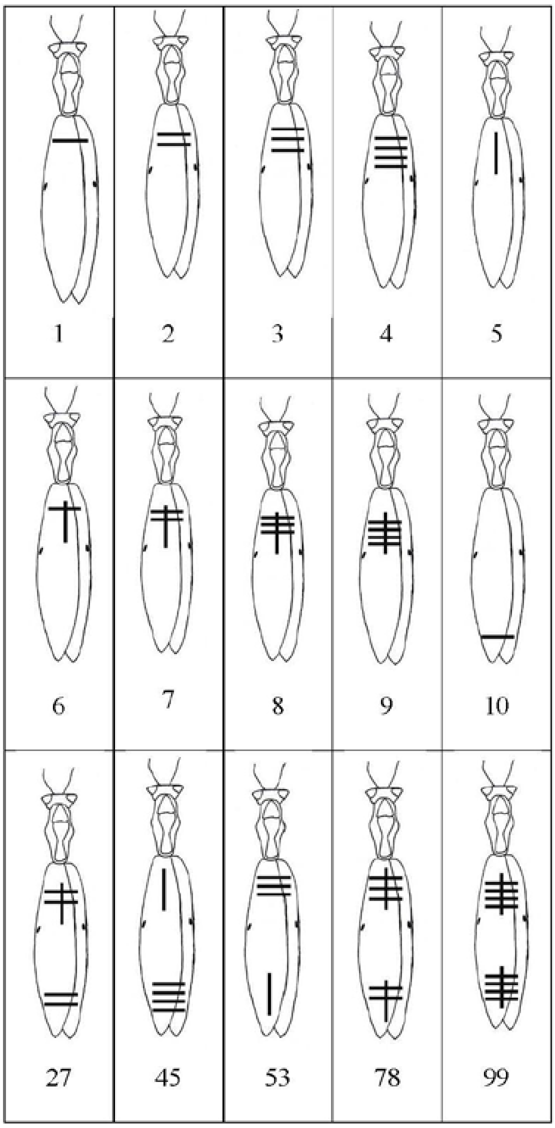

Figure 2. Marking system used for *Mantis religiosa* and *Hierodula tenuidentata* individuals.

In the general linear model (GLM) analysis, these weather variables are considered as predictors of the number of *Mantis religiosa* and *Hierodula tenuidentata* that were counted in the study area daily to check the competition between these two species.

The climate data were downloaded for the weather station of Constanța, with the nearest weather station situated in the vicinity of the study area, at less than 15 km towards the north. These weather data were taken from the NOAA Integrated Surface Database [21].

2.4. Data Analysis

A GLM approach was used to determine the influence of weather variables and the presence and abundance of a possible competitor species on each of the two Mantis species in south-eastern Romania. For the analysis, we used the total number of each studied species (*Mantis religiosa* and *Hierodula tenuidentata*) recorded per day (n = 33 days) and the variables are presented in Table 1. Using this response variable (the number of *Mantis religiosa* and *Hierodula tenuidentata* recorded each day, respectively), the model employed a Poisson error structure and log link function. In the first step, we performed full models that included all climatic variables and the possible competitor species. We excluded the least significant variables in a stepwise procedure, using Akaike's Information Criterion (AIC) to select the best model. This model evaluation was carried out using the all–possible subsets method with the "MASS" package in the statistical software, R v.4.1. To evaluate the model adequacy, the residual versus fitted values and explanatory variables were plotted. No distinct patterns were observed. Moreover, the model multicollinearity effects were tested using the Variance Inflation Factors (VIF) function from the "cat" package. For our selected model, we get a VIF lower than 4, indicating that the variables are not correlated. To analyze the differences between the first and the second visits of the mist-nets, we used a *T*-test. The analysis was conducted in the statistical software, R v.4.1 [22].

3. Results

During our survey, we recorded 16 individuals of *Mantis religiosa* and 122 individuals of *Hierodula tenuidentata*. The maximum number of *Mantis religiosa* in one day was three, recorded on the 28th and 31st of August. This averages to 0.6 individuals per 100 m of mist nets (Figure 3). The maximum number of *Hierodula tenuidentata* recorded in one day was 15 on the 12th of September, averaging to three individuals per 100 m of mist nets.

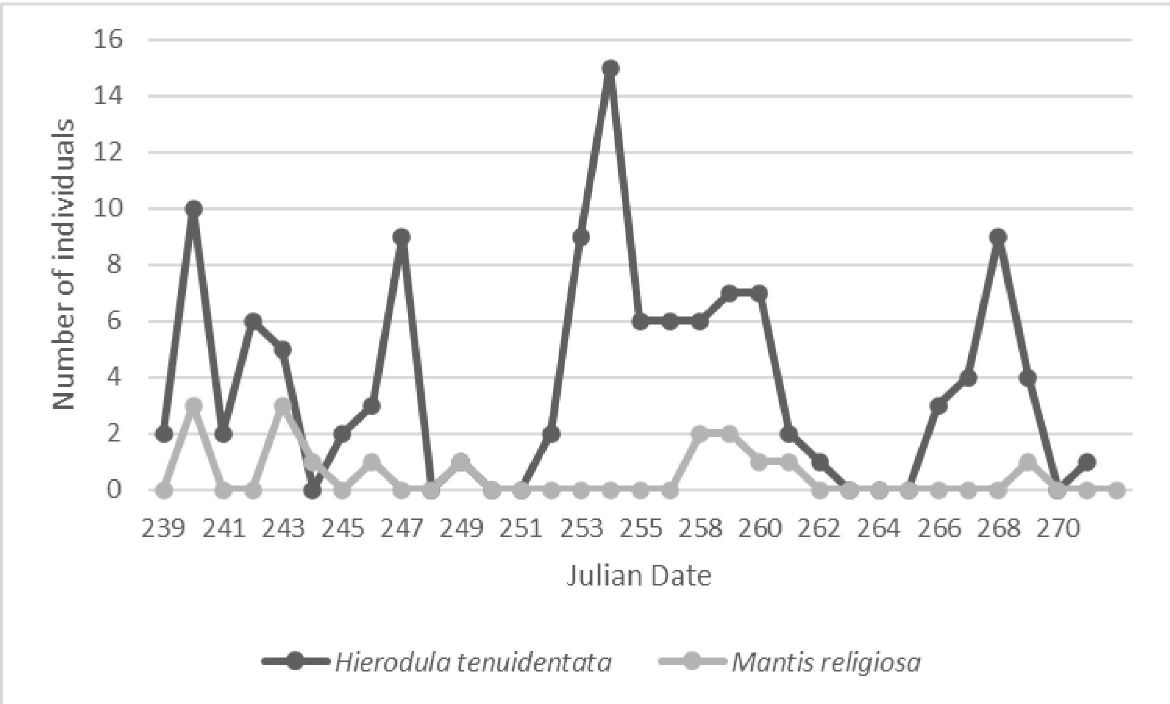

Figure 3. *Hierodula tenuidentata and Mantis religiosa* abundance per day (number of days from the first day of the year) during the study survey period, starting with the date of the first recorded individuals.

During the survey, we observed more individuals of *Mantis religiosa* in the first visit than the last one (T = −2.48994, p = 0.018). During the first transect, we recorded a total of twelve individuals, while only four individuals were recorded during the second transact. For *Hierodula tenuidentata,* we also observed more individuals during the earlier visit than the later one (T = −3.785431, p = 0.0006). During the first transect, we counted a total of 92 individuals, while for the second one, 30 individuals were recorded.

The number of marked individuals being re-observed during the survey is relatively low. During our study, we recorded nine individuals of *Hierodula tenuidentata* which were observed twice in the same day at both transects (at 21.00 PM EEST and at 23.00 PM EEST). Considering only individuals observed a second time in different observation days, we recorded ten individuals. The longest period between two observations of the same individual was twelve days. We also observed three individuals after eleven days, one after ten days, one after seven days, two after three days and two after one day. We also had two cases of individuals that were observed three times in three different days. In these two cases, the individuals were observed in three consecutive days.

Considering *Mantis religiosa*, we only had one case of an individual observed two times in the same day, at 21.00 PM EEST and at 23.00 PM EEST.

We did not record any predation between these two species during the surveys, but we observed them hunting different species of insects many times. During the transects, the recorded individuals did not look disturbed by the observers. However, in laboratory conditions, we observed one male of *Mantis religiosa* predating on a mid-stage nymph of *Hierodula tenuidentata*, both collected on the same date in the studied area.

To better understand the weather influence on either *Mantis religiosa* or *Hierodula tenuidentata* activity, we conducted a GLM analysis. The best GLM model for *Mantis religiosa* includes three out of twelve variables. For *Hierodula tenuidentata*, it includes seven out of twelve variables (Table 2).

Table 2. General linear model (GLM, R v.4.1.) of weather factors influencing the presence on *Mantis religiosa* and *Hierodula tenuidentata* on the mist nets for trapping birds. Significant *p*-values ($p < 0.05$) are in bold.

Variable	Estimate	SE	Z Value	*p*
		Mantis religiosa GLM analysis		
Intercept	3.434	9.427×10^{3}	0.000	0.9184
Wind N	−0.9735	1.333×10^{4}	0.000	0.9985
Wind NE	16.22	9.427×10^{3}	0.002	0.9988
Wind NW	−0.8045	1.046×10^{4}	0.000	0.9980
Wind S	19.20	9.427×10^{3}	0.002	0.9987
Wind SW	18.30	9.427×10^{3}	0.002	0.9983
Wind W	17.37	9.427×10^{3}	0.002	0.9988
DSS	−0.1202	0.1426	−0.843	0.399
Datenr	$\mathbf{-8.292 \times 10^{-2}}$	$\mathbf{3.977 \times 10^{-2}}$	**−2.085**	**0.037**
		Hierodula tenuidentata GLM analysis		
Intercept	$\mathbf{1.561 \times 10^{2}}$	**46.85**	**3.332**	**0.000862**
NRMR	8.687×10^{-2}	1.422×10^{-1}	0.611	0.541293
T_max	-1.758×10^{-1}	9.626×10^{-2}	−1.826	0.067788
Atmospheric pressure	$\mathbf{-1.537 \times 10^{-1}}$	$\mathbf{4.435 \times 10^{-2}}$	**−3.465**	**0.000529**
Wind N	1.876	1.298	1.445	0.148507
Wind NE	2.088	1.102	1.895	0.058106
Wind NW	−16.73	2.785×10^{3}	−0.006	0.995207
Wind S	**3.138**	**1.085**	**2.891**	**0.003836**
Wind SW	**2.301**	**1.077**	**2.137**	**0.032582**
Wind W	**2.653**	**1.071**	**2.477**	**0.013265**
Winds	$\mathbf{-1.301 \times 10^{-1}}$	$\mathbf{4.037 \times 10^{-2}}$	**−3.222**	**0.001273**
DSS	$\mathbf{2.935 \times 10^{-1}}$	$\mathbf{7.550 \times 10^{-2}}$	**3.888**	**0.000101**
Datenr	6.716×10^{-3}	1.874×10^{-2}	0.358	0.720095

According to the GLM analysis, the *Mantis religiosa* occurrence is negatively influenced by the number of days from the first day of the year (Z = −2.085, *p* = 0.037, Table 2). Due to the small number of individuals observed, we could not disentangle any relevant weather influence on *Mantis religiosa*.

According to the GLM analysis, the occurrence of *Hierodula tenuidentata* is positively influenced by the wind direction from south (Z = 2.891, *p* = 0.0038, Table 2), south-west (Z = 2.137, *p* = 0.032, Table 2) and west (Z = 2.477, *p* = 0.013, Table 2) and by daily sunshine duration (Z = 3.888, p = 0.0001, Table 2). It is negatively influenced by daily mean pressure (Z = −3.465, p = 0.0005, Table 2) and mean daily wind speed (Z = −3.222, p = 0.001, Table 2).

4. Discussion

During our survey, the number of *Hierodula tenuidentata* individuals was 7.6 times higher than the number of *Mantis religiosa*, suggesting a higher density of the allochthonous species in the study area, in accordance with its invasive character and high ecologic plasticity. However, the asymmetry between these numbers can be explained, at least partially, by the species ecology. The apparently lack of competition between these two species was also a result of the GLM analysis, which is explained in the present study. Our data from the GLM analysis show that this allochthonous species can survive longer as adults in this type of climate compared to the adults of *Mantis religiosa*, which become less frequent at the end of the summer and beginning of autumn. The native species *Mantis religiosa* is more likely to prefer herbaceous and shrub vegetation [10,15], while *Hierodula tenuidentata* tend to be an arboreal species [10,13,15], making them more likely to end up in the mist nets. The higher number of *Hierodula tenuidentata* and the lower number of *Mantis religiosa* are confirmed by our daily observations in the study area during the entomological survey. During previous years, when *Hierodula tenuidentata* were discovered, its number was much lower. Putting all this together, it is possible that the population of *Mantis religiosa* from the studied area has a higher density compared to the one from our survey. Yet, there is no doubt that the adults and ootheca of *Hierodula tenuidentata* outnumber the native population of European mantis in the studied area (personal observations).

The GLM model confirms that the more rapid decline in *Mantis religiosa* activity is negatively influenced by the number of days from the first day of the year.

Our data show that *Hierodula tenuidentata* is negatively influenced by the daily mean pressure and daily wind speed. A high atmospheric pressure is commonly associated with no wind conditions, while a sudden drop in atmospheric pressure is usually followed by unstable weather and stronger winds, which are known to pose a threat to invertebrates. When the atmospheric pressure is high, the mantises are more likely to be inactive in terms of mobility. The lack of mobility is likely due to the lack of wind and higher atmospheric density, making it less suitable for insect movement. When the atmospheric pressure drops, the wind becomes stronger and can be used by mantises for spatial dispersion. If it becomes too strong, it can affect the insect activity by causing low movement. This phenomenon is also documented in beetles [23]. The increasing activity and mobility in insects under lower pressure was also observed in Hemiptera [24] and Orthoptera [25]. It is also known that some species within the Hierodula genus (eg. *Hierodula patellifera*) use airborne pheromones to attract partners [26]. It is very likely that *Hierodula tenuidentata* exhibit the same behavior, so that moderate wind speeds play a role in increasing the daily species mobility. However, in some Coleoptera and Lepidoptera species that use airborne pheromones, lower response and activity are observed under decreasing atmospheric pressure [27,28]. Further studies are needed on *Hierodula tenuidentata* in order to understand if they use airborne pheromones and how weather factors influence this activity.

The positive correlation between the wind direction from south, south-west and west and the increased number of active specimens can probably be explained by the location of the study area. Suitable habitats for this species exist nearby in these directions, from where the adults could be moving by flight. These wind directions also characterize the night breeze winds, which are capable of driving the individuals into the study region from the inner land towards the shoreline. The proximity of the harbor, the Black Sea and the Danube–Black Sea Canal in north-west, north, north-east and east are characterized by less suitable habitats for the species and can represent an obstacle for the movement of *Hierodula tenuidentata* towards our study area. These correlations cannot be explained by the dominant wind directions as a daily driving factor because the absolute frequency of wind direction is different (Figure 4).

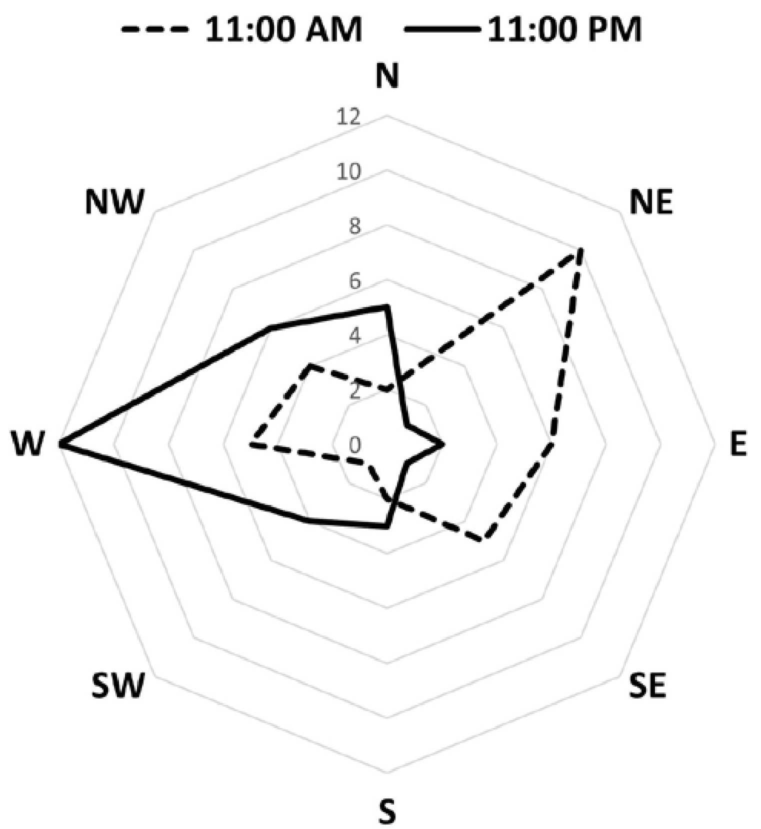

Figure 4. Absolute frequency of wind direction for 11 AM and 11 PM during the Mantises surveys at Constanța Weather Station.

The positive correlation with daily sunshine duration could be explained by the species preference for more stable weather, which is associated mostly with warm weather during the summer [10]. *Hierodula tenuidentata* were first recorded in the study area in 2019, and during the last four winters, the mean winter air temperature was 2 °C higher than the multiannual mean of 1981–2020 interval, according to the ERA-5 database [29]. The limitation to species survival during the winter will be tested in a future study, in order to identify if the present warming winter temperatures favor species survival during winter, which was supposed to be very harsh in recent decades.

The influence of weather on species dynamic and the lower rate of recapture (individuals which were seen second or third time during the survey) show that mantises have great mobility, probably traveling long distances during their activity as adults. Although its current distribution on the Black Sea coast is still sparse [10], it tends to colonize new territories even in wild areas such as shorelines. The species is now present on the entire Crimean coast, with the help of human aided dispersion at some point [12]. The hypothesis for the great mobility of mantids is also supported by the finding in September 2022 of several *Hierodula tenuidentata* adults in the most southern part of the Sacalin Peninsula from the Danube Delta. This piece of land, surrounded by water and far away from any harbor, is one of the wildest places in Europe. The closest locality is Sfântu Gheorghe, situated about 17 km away. from which *Hierodula tenuidentata* has been spreading south in recent last years, being present there since 2019 [10]. It is interesting to note that the specimens were observed to move only after dusk. Not a single individual was found moving during the day. This behavior can probably be explained by the activity of the species as a responsive to airborne pheromones. Similar results have been observed in *Hierodula patellifera*, in which the calling behavior of the virgin females reaches its maximum after dusk [26].

We cannot say for certain, at least for now, that *Hierodula tenuidentata* is affecting the local species. However, we recorded a higher number of *Hierodula tenuidentata* than the native species, which is adapted to the harsher winter season of this region. In addition, *Hierodula tenuidentata* is a predator species, meaning that it could create a decline in the local insect community. We need further studies to check if warming winter temperatures are one of the main variables that allow their survival. We also need to study the detailed competition with native fauna.

However, the presence of this species has seen a steep increase in the region. It has been observed in different places in the south-east and west of Romania. According to our observations, it has been highly dynamic, moving in the area. It seems suitable to rapidly colonize new territories, and individuals are already being observed for the first time in the Moldova region, in the south of the Vrancea county (Nănești commune) (Dora Constantinovici personal observation). With present climate change and knowledge of their ecology, it is very difficult to control the spread of the species. Further studies on species ecology will bring us closer to narrowing down the limiting factors and will provide us with the tools to implement suitable conservation measures to protect the local fauna and flora.

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