Factors Affecting Egg Deposition of the European Mantis

Joanna KAJZER-BONK

Short communication

In this paper, we studied the egg-case (oothecae) deposition of the European mantis, *Mantis religiosa* (Linnaeus 1758), a predatory insect. We hypothesized that the height of ootheca deposition on a plant reflects the insolation requirements of the species, and would increase when plant cover is denser. We found that the taller the plants nearby, the greater the height of egg deposition. Oothecae were also oviposited higher in denser vegetation. The observed behavior may ensure the proper insolation of developing offspring. To our knowledge, this is the first description of an egg laying strategy of this species under natural conditions. This finding allows for a better understanding of habitat selection and the overall ecology of the European mantis. It may be also useful in identifying the mechanisms of the range extension of this species and is a potential tool to effectively conserve xerothermic ootheca-laying animals. Further studies are required to assess the flexibility of this behavior under different environmental conditions.

Key words: ootheca, oviposition strategy, parental care, praying mantis.

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Parental care, defined as any parental trait enhancing offspring fitness (SMISETH *et al.* 2012), is described for some arthropods (Blattodea, Coleoptera, Dermaptera, Embioptera, Hemiptera, Hymenoptera, Orthoptera) (WONG *et al.* 2013), but remains understudied in this group (TRUMBO 2012). One of the forms of parental care is attending and defending eggs or juveniles (TALLAMY 1999; KUDO 2001). In some exceptional cases, like in burying beetles, strategies similar to those observed within birds and mammals have been documented in which the feeding of juveniles, and even begging, is observed (SMISETH *et al.* 2010). Another important factor affecting offspring fitness is the building of nests, burrows (TRUMBO 2012), or clustering the eggs in complex cases called oothecae, which protect the eggs against desiccation, parasitoids, and predators. This strategy is convergent among different groups of insects (GOLDBERG *et al.* 2015). Cryptic, seed-like ootheca, are difficult for predators to find. On the other hand, once identified, oothecae are easily plundered.

It is also possible to enhance breeding success by selecting an optimal oviposition site. The non-random distribution of mantid oviposition sites may be driven by preferred plant stems (goldenrod, asters) and attraction to the pheromones released by other females, as in *Tenodera sinensis* (HURD 1999). Non-herbivorous invertebrates usually produce eggs and despite typically having no preference for a particular plant substrate (but see LAMBRET *et al.* 2018), they may deposit eggs at non-random sites according to predation (SEGEV *et al.* 2017; WALZER & SCHAUSBERGER 2011) and parasitism risk (REINHARDT & GERIGHAUSEN 2001). Selecting a safe, well-hidden site for egg deposition may be a strategy against biotic and abiotic dangers, which is especially important when eggs are non-cryptic (SPENCER *et al.* 2002). However, this behavior may lead to overcrowding, and thus, high levels of brood competition, exposing females to a higher risk of predation and decreasing the population size. Hence, in some cases, the optimal strategy for females is choosing egg-laying-sites that enhance female survival, rather than that of juveniles (SCHEIRS *et al.* 2000). As the demands of adults and eggs/offspring may be discrepant, it has been suggested that the selection of

an oviposition site may not always be treated as a form of parental care (SMISETH *et al.* 2012).

The only representative of the Mantodea order living within the temperate region of Central Europe is the European mantis *Mantis religiosa* (Linnaeus 1758) which prefers sunny and dry meadows (LIANA 2007). Females of this species produce oothecae attached to substrate, producing dozens to several hundreds of eggs (FAGAN & HURD 1994). Optimal microclimatic conditions for proper egg development include high insolation level. It is unknown however, whether females of this species make any choices throughout ootheca laying, e.g. if a particular plant species or oviposition height is selected. Since temperature may affect offspring size in some taxons (SCRIBER & SONKE 2011), females may try to hide or expose ootheca to the Sun to ensure optimal abiotic conditions. The strategy of hiding ootheca from parasites may fail due to phoresy and parasitic wasps that "hitchhike" to the place of egg laying (FATOUROS & HUIGENS 2012), but it may be important to avoid the predation risk to oothecae (RIES & FAGAN 2003).

In this study we assessed whether the European mantis preferred open-vegetation, being well insolated, or dense, shaded sites. We tested the hypotheses that the European mantis: 1) lays eggs according to the characteristics of the surrounding plant structure, i.e. oviposit ootheca higher-up on the stems of vegetation within tall and dense plant cover; 2) has a preference for micro-habitats with a high level of vegetation cover and density.

Materials and Methods

Field records were conducted in October of 2010 within three sites in the Małopolska Upland (South-Central Poland: Ruda 1 (N 50.471259° E 21.234178°), Ruda 2 (N 50.471333° E 21.232046°) and Stawiany (N 50.603697° E 20.702622°). We (another observer and myself) searched carefully for oothecae, walking with a velocity of 5 km per hour in 3 m-wide transects within the boundaries of the studied sites. Once an ootheca was found, the plant taxon of oviposition was recorded as accurately as possible. Each ootheca was measured using calipers with a 0.01 mm accuracy, and if evidence was present, predation acts were recorded. Then, parameters associated with the micro-habitat were estimated: (1) height of ootheca above the ground (cm), (2) mean vegetation height (cm) in the 5 m distance was measured using the standard method described by BETZHOLTZ *et al.* (2007) and (3) vegetation density in a 0.5 m radius area using the three categories as follows: high (no soil visible and/or plants lower than 10 cm absent), medium (soil visible and/or plants lower than 10 cm covering 1-50% of the area), or low (soil visible and/or plants lower than 10 cm covering more than 50% of the area). A radius of 0.5 m

allowed for a look at the entire estimated area at the same angle without covering up by vegetation. Next, in randomly selected reference points, the analogous micro-habitat measurements were collected to determine if the European mantis shows further habitat selection. The number of reference points was equivalent to those with oothecae present at a given study site.

Statistical analyses

Analyses were performed using the 'lme4' package in the R software (BATES *et al.* 2020). A generalized linear mixed model (GLMM) with gaussian error variance was used for the analysis of factors influencing ootheca oviposition height. Mixed modeling was used in regard to the nested scheme of our study: 'study site' was set as a random factor in all models. The dependent variable was $\log_{10}$-transformed to reach normal data distribution. Mean plant height and density were the fixed effect. There was no correlation between plant height and density (Spearman correlation coefficient, $r_s = 0.325$, $p = 0.07$). In these analyses, interaction between plant height and density was of particular interest and therefore, also set as a fixed factor. We proceeded to backward selection, excluding the interaction terms of fixed factors from the final models if non-significant. Next, we analyzed factors influencing ootheca occupancy, using a GLMM with binomial error variance. Presence (1) or absence (0) in sites was the dependent variable. In this procedure, independent variables were the same as in the ootheca oviposition height analysis.

Results

In total, at the three studied sites, we found 33 oothecae with a mean length of 32.96 mm (SE=0.755) and mean width 25.92 mm (SE=0.210). The mean height of oviposition was 7.00 cm (SE=1.009). Members of the Poaceae family were the plants on which oothecae were most frequently laid (N = 24). Oothecae were also observed on *Rumex* sp. (N = 2), *Senecio* sp. (N = 2), *Solidago* sp. (N = 3), and on a plant that was not identifiable because it was dry, but had a strong, goldenrod-resembling stem (N = 1). Three oothecae were attached simultaneously to two different plants species: Poaceae and *Vicia* sp., Poaceae and *Achillea millefolium* as well as Poaceae and *Equisetum* sp. Four of the 33 total oothecae were destroyed by predators. The number of predated oothecae was too low to be included in the analyses.

Mean plant height and plant density significantly affected the height of ootheca oviposition (Table 1, Fig. 1). In contrast, we did not detect any effect of micro-habitat parameters (height and density of plants) on the presence of oothecae (Table 1).
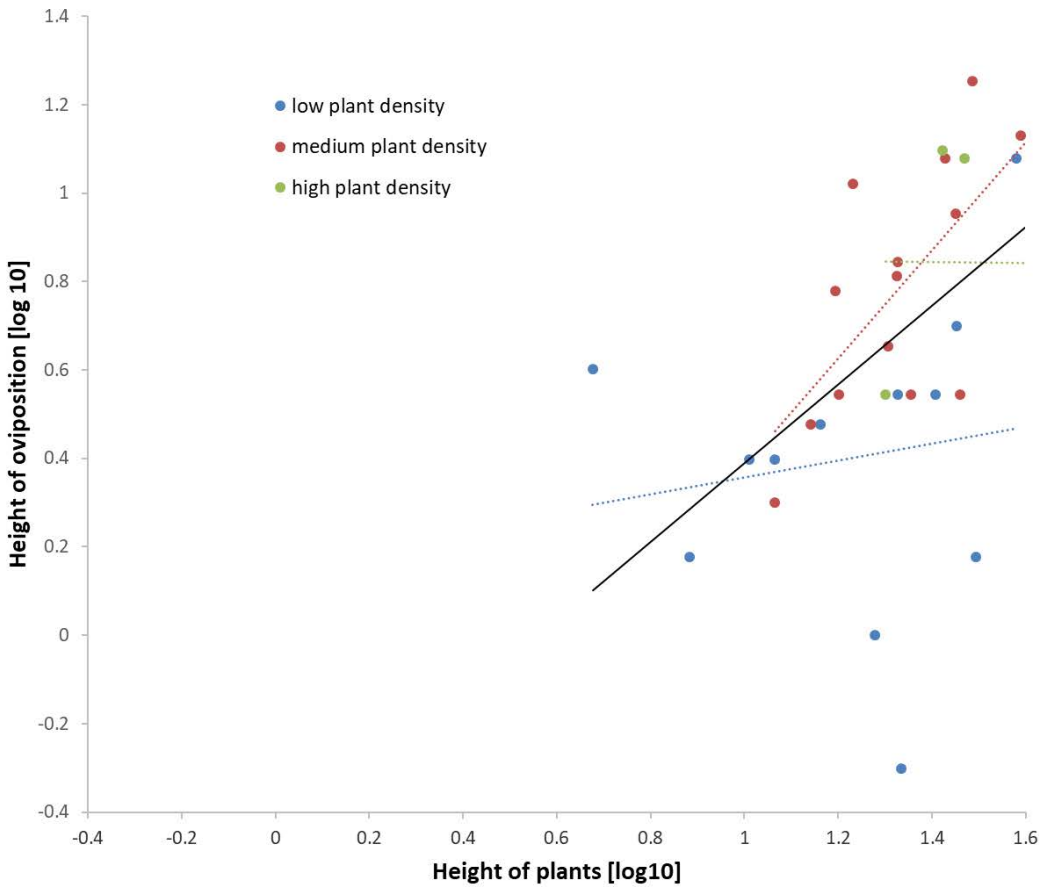
Fig. 1. The effects of mean plant height (the fitted line is black) and plant density (the fitted lines are blue, red and green for low, medium and high density categories, respectively) on the height of oviposition in the praying mantis, *Mantis religiosa* (L.).

Table 1

Factors affecting the height of ootheca oviposition and ootheca presence of the praying mantis *Mantis religiosa* (L.). Generalized linear mixed model procedure, significant results are bolded

Fixed effects	Effect on oviposition height					Effect on ootheca presence				
	Estimate	SE	95% CI	Chi^2	p	Estimate	SE	95% CI	Chi^2	p
Plant height	0.679	0.250	0.490	7.377	0.007	-0.008	0.0143	0.028	0.319	0.572
Plant density	0.200	0.090	0.176	4.901	0.027	0.032	0.3704	0.726	0.008	0.931

Discussion

The ootheca were laid mainly on members of Poaceae. The study by CHRISTENSEN and BROWN (2018) also suggests possible *Tenodera sinensis* female preferences for oviposition substrate. However, neither their study nor ours compared the selected plant taxons to their availability. It is probable that grasses were also the most abundant i.e. available plants. Hence, the observations may not reflect a clear preference for any plant taxon(s) and such assumption demands further studies.

To date, there was no evidence whether European mantis females make any choices regarding the selection of a site for oviposition under natural conditions. The decision determining whether eggs should be laid was affected by the height of the plants present and by their density. However, the height and density of plants of selected micro-habitats and of random reference points did not differ significantly. This result confirms conclusions produced by LINN and GRIEBELER (2016), who reported a preference of *Mantis religiosa* for egg deposition on heat-storing solid substrates in grazed and mown meadows, but did not investigate the preference in unmanaged habi-

tats. The results of our study are also consistent with those of BALAKRISHNAN (2012) who revealed that the oviposition sites of mantis *Hierodula* spp. were situated on taller plants, further from the main stem of the plant, closer to the path and in less dense shrubs compared to ambush sites, which suggests am insolation requirement for the offspring. It seems that the crucial factor driving the decision of females when choosing an optimal site for oviposition is insolation to ensure the proper development of offspring. Our results are in accordance with former studies.

We did not assess food availability in this study although this factor may also drive oviposition site selection. Plants with showy flowers attract pollinators (prey) and are attractive to adult mantids (CHRISTENSEN & BROWN 2018), and may be preferred by females in order to increase the foraging efficiency of nymphs. On the other hand, mantids are generalist predators (HURD 1999), which supports our results as oothecae were laid mostly on grasses without blooming flowers. Moreover, nymphs of different developmental stages forage at different plant heights, with the youngest instars on the lowest heights (WATANABE *et al.* 2013).

One cannot deny that a low level of predatory risk and parasitism affects the selection of the habitat and density of oothecae (FAGAN & FOLARIN 2001). Our study scheme did not allow to assess the predation risk along a plant height gradient. However, the selection of taller and more delicate stems may be an antipredatory behavior (BALAKRISHNAN 2012). To assess whether predatory risk is a relevant factor affecting oviposition site, further studies are required. Among these, manipulating the height of oothecae in the field could be revealing. Also, an assessment of the breeding success and the survival of nymphs within different types of habitats as well as using a wider spatial scale would be beneficial (for example comparing southern and northern European populations which may potentially reveal different oviposition strategies). Further studies are also needed to determine whether a trade-off exists between the need for insolation and the need to hide from danger in the case of potential predatory/parasitism risk. It would also be interesting to determine whether there are individual differences in strategies (i.e. caution vs. risky) and if females reveal flexible behavior as environmental changes occur.

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Author Contributions

Research concept and design, collection and/or assembly of data, data analysis and interpretation, writing the article, critical revision of the article, final approval of article – J.K-B.

Conflict of Interest

Author declares no conflict of interest.

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