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AMBUSH AND OVIPOSITION SITE SELECTION BY GIANT ASIAN MANTIS *Hierodula membranacea* Burmeister (MANTODEA: MANTIDAE) IN TROPICAL WET EVERGREEN FORESTS, WESTERN GHATS, INDIA

Peroth Balakrishnan*

Wildlife Research & Conservation Trust, c/o. Anupallavi, Chungathara P.O., Nilambur– 679 334, India Present address: Department of Zoology, NSS College Manjeri, Malappuram- 676 122, India.

Abstract

The ambush and oviposition site characteristics of Giant Asian Mantis *Hierodula membranacea* were studied in a tropical wet evergreen forest in Silent Valley National Park, in the Western Ghats during January 2002 to May 2005. Ambushing mantids were located on 12 plant species, at a mean height of 1.63 ± 0.12 m (0.7-4.2 m) above ground. Ambush sites were characterized by high shrub density that provides camouflaging backgrounds to lie in wait to ambush prey. *Lantana camara* was the most commonly used plant species for placing oothecae. Oothecae were placed at a mean height of 2.1 ± 0.15 m (0.9-3.5 m) above ground on delicate branches, and this could be an antipredator strategy as they provide less accessibility to arboreal predators like birds and reptiles. Preference of sites with floral resources indicates that flowers may be used as a cue for prey abundance, as they attract a continuous supply of pollinating insects. Thus preference of sites with dense vegetation, camouflaging backgrounds, abundant floral resources and delicate braches by Giant Asian Mantids may provide effective predator avoidance, increased foraging efficiency and reproductive success and thereby increase ecological fitness.

Key words: Ambush predator, habitat selection, ootheca, praying mantids, Silent Valley National Park

INTRODUCTION

Mantids (Insecta: Mantodea), popularly known as praying mantis, are one of the largest group of predatory arthropodes, consisting of more than 2,000 reported species globally (Ehrmann, 2002). The majority of praying mantids capture their prey from ambush sites, with individual mantids sometimes remaining in the same site for days or weeks (Prete et al., 1999). Most mantids are sexually dimorphic and produce large numbers of eggs typically deposited in protective egg sacs, known as oothecae. The ambush site selection and placement of oothecae are important because site selection critically affects reproduction and survival, which in turn influences

both population and community dynamics (Morris, 2003). Habitat selection theory suggests that in an ideal case, an animal should select habitats that maximize its life time fitness (Rosenzweig, 1981). In general, the process of habitat selection is influenced by a number of factors such as physical habitat structures, resource availability, predators, densities of conspecifics, inter-specific competitors, and microclimatic conditions (Mangel, 1990). Site selection in an ambushing predatory arthropod may be affected by the physical properties of the environment, and by ecological components such as food abundance, the type and strength of competitive interactions and predation risk (Janetos, 1986). Similarly, the densities

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^{*} E-mail: baluperoth@gmail.com

of conspecifics and natural enemies (egg predators, parasites) and developmental needs and nutrient availability of offspring also affect a female's oviposition site selection (Janz, 2002). Thus, studies on habitat selection have profound implications for population dynamics, community structure, and ecosystem function and are therefore important in understanding ecological systems.

A large number of studies examined the life history strategies and habitat selection of several species of praying mantids. For example, sexual cannibalism in Hierodula membranacea (Birkhead et al., 1988), foraging strategies in Paratenodera angustipennis (Inoue and Matsura, 1983), habitat selection in Ciulfina sp., (Hill et al., 2004) and Tenodera aridifolia sinensis (Wilder and Rypstra, 2005) and oviposition and hatching in Hierodula patellifera (Leong, 2009). Prete et al. (1999) provided a more complete review of the ecology of the praying mantids. However, relatively few studies examined the habitat selection in natural conditions (Hill et al., 2004). In the present communication, I report the ambush and oviposition site characteristics of Giant Asian Mantis Hierodula membranacea in the tropical evergreen forests of the Western Ghats.

MATERIALS AND METHODS

Study species: The genus Hierodula (Burmeister 1838) is one of the most speciose groups of praying mantids with about 105 species recognized (Ehrmann, 2002). Of the more than 163 species of mantids reported from India, 12 belong to the genus Hierodula (Mukherjee et al., 1995; Vyjayandi and Narendran, 2003). Hierodula membranacea. commonly known as Giant Asian Mantis (Image 1) is distributed throughout south-east Asia in India, China, Indonesia, Java and Sri Lanka (Mukherjee et al., 1995). The body length of the species average 81.6 mm (\pm 1.25 mm, n = 3) and both body and forewings are green in colour. H. membranacea has been subject

of several studies including sexual cannibalism (Prete *et al.*, 1999; Birkhead *et al.*, 1988). They are also very common in pet trade in UK and many European countries (e.g., ebay.co.uk, 2012; MantisPlace.com, 2012), however, the level of exploitation from the natural habitats for trade is unknown.

Study area: This study was conducted at the Silent Valley National Park (11° 00' and 11° 15' N and 76° 15' and 76° 35' E) and surrounding reserve forests in Kerala, India, between January 2002 and May 2005. The terrain is undulating and hilly, with elevation ranging from 600 m to over 2300 m. The mean annual rainfall recorded in the study area was above 5000 mm, half of which occurred during the south west monsoon period (May-September). Average monthly maximum and minimum temperatures during the study period were 25.8 °C and 19.8 °C respectively. The forests of Silent Valley National Park are typical wet-evergreen with montane sholas and grasslands at higher elevations. All the observations were made in the west coast tropical evergreen forests lying between 900 to 1200 m a.s.l. The study sites were dominated by large evergreen trees such as Cullenia exarillata, Canarium strictum, Calophyllum elatum, Eleocarpus serratus, Myristica dactyloides, Mesua ferrea, Jumbosa munronii, J. leata, Syzygium spp. Palaquium ellipticum, Persea macrantha and Poeciloneuron sp. Understorey species include Antidesma men asu, Chloranthus brachystachys, Clerodendrum viscosum, Lasianthus ciliatus, Maesa indica, Lantana camara, Strobilanthes spp. and Symplocos cochinchinensis (Balakrishnan, 2007).

Field methods: The ambush and oviposition sites were located by walking throughout the forest, both on and off trails, and during the course of other field studies (January to May in 2003 through 2005). The mantids and oothecae were located by scanning the vegetation using 7x50 binoculars. The sightings were generally restricted to about 3 m on either side of the



Figure 1. Hierodula membranacea laying eggs in the ootheca placed on Lantana camara

trails and up to a height of about 8 m due to the poor visibility in the dense vegetation. Different structural features were quantified at the ambush and oviposition sites and include: the height above ground, height of the tree or shrub on which the animal or ootheca was found, distance to the main stem, distance to the edge and presence of flowers within 0.5 m of the site. The relative heights of the ambush or oviposition sites were calculated by dividing the height of the site above ground by the height of the plant (Veldtman et al., 2007). Thus, if the ambush or oviposition site is near to the plant crown, the calculated relative height should be near to one. The plants used as ambush or oviposition site were identified to species level. Additionally, all the shrubs within 5 m radius circular plots (0.008 ha) centering the ambush or oviposition sites were counted as a measure of the vegetation complexity. Three adult female mantids were captured from the oviposition sites by hand and marked by gluing green

plastic tape on prothorax, which did not seem to inhibit movement and other behavioural activities. The positions of individually marked mantids relative to the oviposition sites were mapped on alternative days. A comparison of the structural features of the oviposition and ambush sites were done with Mann – Whitney U -tests.

RESULTS

A total of 36 H. membranacea were found in ambush poses on 12 species of plants in Silent Valley National Park. Maximum ambush sites were in Lantana camara (13) followed by Chloranthus brachystachys, Lasianthus ciliatus, Leea indica, Strobilanthes foliosus, Ziziphus rugosa, Chumanianthus sp. (three each) and one each in Lasianthus jackianus, Sarcococca coriacea, Symplocos cochinchinensis, Thottea siliquosa and an unidentified shrub (Table I). The ambush locations ranged from 0.7 m to 4.2 m above ground (mean = 1.63±0.12 m).

Oothecae of the species have a foamy white coat with green colour at the base, which hardens and turns to brown in the following days. Hierodula membranacea selected five plant species as oviposition sites. Of the 23 oothecae recorded, 11 (47.82%) were on Lantana camara. The other species used for ootheca placement were Ziziphus rugosa, Olea dioica, Lasianthus ciliatus and Maesa indica (Table II). The oothecae were placed 2.1 m (±S.E. = 0.15 m; range = 0.9-3.5 m) above ground on delicate branches (mean diameter = 0.58 ± 0.13 cm) and at a relative height of $0.74 \text{ (}\pm\text{S.E.} = 0.02; \text{ range} = 0.5-0.93\text{)}$. The plants used as oviposition sites were taller than the plants used as ambush sites (Mann-Whitney U-test: U = 195.5, n1 = 36, n2 = 23, P < 0.01). Ambush sites were located in the top layer of the trees or shrubs (Mann-Whitney U-test: U = 241.5, n1 = 36, n2 = 23, P < 0.01) and closer to the main stem compared with the oviposition sites (Mann-Whitney U-test: U = 203.5, n1 = 36, n2 = 23, P < 0.01). Ambush sites of Hierodula membranacea were characterized by high shrub density (50.31±19.28 stems/0.008 ha) than that of the oviposition sites (32.17±16.09 stems/0.008 ha; Mann-Whitney U-test: U = 180.5, n1 = 36, n2 = 23, P < 0.01). The oviposition sites were closer to the patch edges (0.98±0.14 m) compared with the ambush locations (2.86 \pm 0.28 m; Mann–Whitney U-test: U = 128.5, n1 = 36, n2 = 23, P < 0.01). About 61% of the oviposition sites had floral resources within 0.5 m, while only 36% of the ambush sites were surrounded by flowers. Two marked individuals remained in the oviposition sites till the end of the observation period (12 days), but the third individual disappeared on the sixth day.

DISCUSSION AND CONCLUSIONS

The results of this study show *H. membranacea* selected sites with high vegetation density that provides camouflage to lie in wait to ambush prey, as in the case of most species of Mantodea (Prete *et al.* 1999). Selection of habitats

with high structural complexity (e.g. dense vegetation, presence of cavities and crevices, etc.) is common among invertebrates and especially praying mantids (Prete *et al.*, 1999; McNett and Rypstra, 2000). Preference for such structurally complex habitats may help them to obtain prey easily and minimize the predation risk. Such adaptive strategies are particularly important as predatory arthropods are generally food limited in the wild (Prete *et al.*, 1999).

The influence of food resources on the habitat selection is not assessed in this study. At the ambush sites, two foraging events by Hierodula membranacea were recorded. In both occasions the prey were large spiders. Although no systematic sampling was done to measure the food availability at the ambush and oviposition sites of Hierodula membranacea, studies in similar patches with high densities of shrubs (e.g., Lantana camara, Strobilanth es spp.) demonstrated higher abundance of arthropods (Balakrishnan, 2007). Preference of sites with floral resources indicates that flowers may be used as a cue in prey abundance, as they attract a continuous supply of pollinating insects (Morse, 1986). Moreover, female mantids that are located on the flowering plants are more likely to produce large oothecae than those without this advantage as found in the case of Chinese mantids, Tenodera sinensis (Prete et al. 1999). Furthermore, the resource abundance may directly influence the growth and survivorship of the mantid nymphs emerging from such sites.

The only predation event observed was by the Garden Lizard, Calotes versicolor, which consumed an adult Hierodula membranacea from the ambush site. Two species of birds, Brown-cheeked Fulvetta Alcippe poioicephala and Red-whiskered Bulbul Pycnonotus jocosus were found pecking the oothecae of Hierodula membranacea. Crimson-backed Sunbird Nectarinia minima, at Silent Valley used pieces of the oothecae for decorating their nests.

Table I. Ambush site characteristics (mean \pm SE) of Giant Asian Mantis *Hierodula membranacea* at Silent Valley National Park, Kerala, India.

Plant species	No. of sites (%)	Ambush height (m)	Plant height (m)	Relative height	Distance from main stem (m)	Distance to edge (m)	Shrub cover (%)
Lantana camara	13 (36.11)	1.62±0.11	1.89±0.11	0.86±0.03	0.20±0.03	3.06±0.52	61.07±3.96
Chloranthus brachystachys	3 (8.33)	1.03±0.18	1.13±0.20	0.92±0.04	0.02±0.02	3.33±1.20	61.00±2.52
Lasianthus ciliates	3 (8.33)	1.50±0.12	1.90±0.06	0.79±0.04	0.10±0.03	2.33±0.60	35.67±6.01
Leea indica	3 (8.33)	1.27±0.15	1.63±0.09	0.78±0.08	0.23±0.03	1.17±0.44	36.67±5.81
Strobilanthes foliosus	3 (8.33)	1.67±0.18	1.77±0.25	0.94±0.03	0.11±0.07	4.67±1.01	67.00±11.85
Ziziphus rugosa	3 (8.33)	2.57±0.20	3.33±0.17	0.77±0.03	0.37±0.09	1.33±0.33	27.00±2.65
Chumanianthus sp.	3 (8.33)	0.93±0.12	1.07±0.07	0.87±0.09	0.12±0.02	2.67±0.67	64.00±9.85
Sarcococca coriacea	1 (2.78)	3.20	4.00	0.80	0.15	3.00	14.00
Symplocos cochinchinensis	1 (2.78)	4.20	6.00	0.70	0.60	1.50	31.00
Thottea siliquosa	1 (2.78)	0.80	1.00	0.80	0.40	3.00	32.00
Laseanthus jackianus	1 (2.78)	1.10	1.80	0.61	0.20	4.00	34.00
Unidentified shrub	1 (2.78)	1.30	2.00	0.65	0.20	5.00	32.00

Table II. Oviposition site characteristics (mean \pm SE) of Giant Asian Mantis *Hierodula membranacea* at Silent Valley National Park, Kerala, India.

Plant species	No. of sites (%)	Oviposition height (m)	Plant height (m)	Relative height	Distance from main stem (m)	Distance to edge (m)	Shrub cover (%)
Lantana camara	11(47.83)	1.65±0.11	2.41±0.16	0.69±0.03	0.33±0.06	0.76±0.18	43.73±4.75
Ziziphus rugosa	5 (21.74)	2.88±0.19	3.84±0.39	0.77±0.05	0.42±0.09	1.24±0.25	18.80±1.83
Lasianthus ciliatus	3 (13.04)	1.43±0.15	1.63±0.19	0.88±0.03	0.13±0.06	0.73±0.39	27.67±3.38
Olea dioica	3 (13.04)	3.10±0.21	4.23±0.43	0.75±0.10	0.53±0.01	1.67±0.44	18.00±2.31
Maesa indica	1 (4.35)	2.20	3.00	0.73	0.45	0.70	28.00

At least two species of ants and many wasps present at the ambush and oviposition sites may be probable predators and parasites of the eggs of *Hierodula membranacea*. The placement of oothecae at the tip of the delicate branches could be an anti-predator strategy as they provide less accessibility to arboreal predators like birds (e.g., flycatchers, babblers, tits, etc) and reptiles (e.g., *Calotes* spp., *Dendrelaphis* spp). On the other hand, placement of oothecae in the habitat edges may increase the predation rates as seen in other species of mantids (*Stagmomantis limbata*, Ries and Fagan, 2003). All the sightings of *Hierodula*

membranacea were of single individuals and interactions with the conspecifics or mating behaviors were not recorded. However, more detailed studies are required to understand the role of such ecological interactions in the habitat selection of mantids.

Although the hatching of eggs and survival of the nymphs were not tracked in this study, presence of the marked adults at the oviposition sites indicates the presence of parental care behaviour in this species. Several other species of praying mantids are

also known to guard their egg sacs and nymphs (Prete et al., 1999; Tallamy, 1999).

In conclusion, the data presented herewith provide some insights into the ambush and oviposition habitat characteristics of a common insect predator. Yet, further research still needs to be done, with a combination of field and experimental studies to understand the cues used in the optimal site selection and how the selection influence individual fitness and population dynamics.

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