

A first look at the biodiversity of praying mantids (Insecta: Mantodea) in Sabah, Borneo

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Abstract. Light-trapping was conducted in February and March 2003 near Kinabalu Park and in the Danum Valley Conservation Area in Sabah, Malaysia. During 18 sample nights a total of 106 praying mantids, comprising 28 species, were collected in three different habitat types: a heavily disturbed farmland site, a selectively logged forest and an undisturbed canopy site in a primary dipterocarp forest. Species richness, within-habitat diversity (expressed as Fisher's α) and estimated "true" species richness were highest on the farmland site, followed by the primary forest site and the secondary forest site. The between-habitat diversity indices Jaccard and NESS indicate the highest similarity of the species community between the farmland site and the primary forest site. Similar microclimatic conditions in the open farmland and the upper canopy might be responsible for this effect. The high biodiversity of generalist predators such as mantids on the farmland site could be explained by large abundances of potential prey species that profit from anthropogenic disturbances, such as orthopterans and moths. The value of light-trapping as an effective means to assess the biodiversity of praying mantids is discussed.

Keywords: biodiversity, Borneo, habitat disturbance, Mantodea

INTRODUCTION

Praying mantids (Mantodea Burmeister 1838) form an order of exclusively carnivorous insects. Living solitarily in the vegetation – or, more rarely, on the ground – they ambush insects, spiders and occasionally even small vertebrates (Prete *et al.* 1999). Mantids belong to the top predators of the arthropod community. Some species wear cryptic colours and resemble leaves, flowers, sticks or bark (examples are provided in Plates 1 & 2). Mantids are characterized by their highly specialised raptorial forelegs and a mobile head with powerful compound eyes that allow for binocular sight. An elongated prothorax is also typical. Phylogenetically, they are placed in the vicinity of termites and cockroaches, with which they form the superior taxon Dictyoptera (see also Prete *et al.* 1999). In spite of their close relationship to these long-established groups, mantids themselves do not appear in the fossil record in their modern form before the Cretaceous (Ehrmann 2002). There are approximately 2300 species known worldwide (Ehrmann

2002), the majority of which occur in the tropics and subtropics. African forests and savannahs contain the highest known species richness, followed by the rain forests of South East Asia.

In spite of their size and often spectacular appearance, surprisingly little is known about the ecology of praying mantids. However, numerous studies concerning their physiology, neurology and behaviour do exist – most of them focusing on visual performance, and defensive, courtship and feeding behaviour (e.g. Mittelstaedt 1957, Maldonado 1970, Rossel 1983, Liske *et al.* 1989). Mantids are also used as model organisms in studies on predator's behaviour and strategies (e.g. Inoue & Matsura 1983, Matsura & Nagai 1983, Iwasaki 1998). An overview of mantid ecology and behaviour is given in Prete *et al.* (1999). Comprehensive ecological studies usually concentrate on a single or few species, often from temperate regions (e.g. Rathet & Hurd 1983, Daniels *et al.* 1985). The information about South East Asian species is limited (e.g. Lieftinck 1953). There is almost no literature on mantids from Borneo: Shelford (1903) published descriptive notes on some mantids from Sarawak. So far, 102 species out of 47 genera have been recorded to occur in Borneo (Ehrmann 2002).

The objective of this study is to contribute to the knowledge of the biodiversity of praying mantids in Sabah. To our knowledge, this is attempted for the first time. Mantids are often caught incidentally in studies concerning other insect groups, but they rarely receive full attention in biodiversity studies. Moreover, further information about the impact of anthropogenic disturbance on tropical mantid communities is provided.

To collect specimens, we took advantage of the well-known fact that mantids are attracted to artificial light sources during the night (Ehrmann 2002). Males especially fly during the dusk and the night to find mating partners. In doing so, they avoid their most dangerous diurnal predators (birds and reptiles), but are exposed to bat predation. As other nocturnal insect orders, mantids have evolved auditory organs sensitive to bat echolocation calls, together with active escape behaviours (Yager *et al.* 1990). Females, on the other hand, tend to stay constantly in one area (Ehrmann 1985) and are generally more sedentary than the males. In several species females have reduced wings and are not able to fly over longer distances.

MATERIALS & METHODS

Light-trapping was carried out in February and March 2003 near Kinabalu Park and in the Danum Valley Conservation Area in Sabah, Malaysian Borneo. The light-trap consisted of a 125 W ultraviolet mercury vapour bulb powered by a portable petrol generator and surrounded by a white gauze cylinder 1.6 m in height and 0.8 m in diameter. Trapping was conducted between sunset and sunrise, i.e. 18:30 pm to 06:00 am. All specimens of mantids found on the gauze tower or within a 5 m radius in the surrounding vegetation were collected by hand. Vegetation was checked thoroughly approximately every 30 minutes. Specimens were stored in silica gel or 70% ethanol and, when possible, identified to at least genus level by a key published online by Oliveira (1996) and by Ehrmann's (2002) comprehensive catalogue of the mantids of the world. Unfortunately, actualised general identification keys to species level exist only for some groups, so most of the further sorting had to be carried out using the morphospecies concept (Beattie &

Oliver 1994). About half of the specimens were brought to Würzburg University for preparation and more precise identification, a task that is still ongoing – for three species even the genus affiliation is yet unclear. Voucher specimens were deposited in the collection of Sabah Parks headquarters.

Three sampling sites with different degrees of human habitat disturbance were chosen: (1) The first site (N06°01'33", E116°46'13") was situated in an extensively cultivated area ca. 7 km outside of the Kinabalu Park at Poring Hot Springs, at an altitude of 350 m a.s.l. The site was covered by banana plants, palms and grass and framed by bushes. This site is subsequently referred to as PorC. (2) The second site (DanS: N04°58'07", E117°50'17") lied along a logging road near the Danum Valley Field Centre in a secondary forest (selectively logged in 1988 and 1989), overlooking a small valley from an altitude of 340 m a.s.l. (3) The third site (DanP: N04°57'53", E117°47'47") was situated on a canopy platform 40 m high in the lowland dipterocarp primary forest of the Danum Valley Conservation Area, 220 m a.s.l. More information about the forest types in Danum Valley and the surrounding areas is provided by Marsh & Greer (1992). Seven consecutive sample nights were carried out at site PorC, six nights at site DanS, and five nights at site DanP.

In order to evaluate the efficiency of light-trapping, 10 transects of 100 m length each were searched systematically for mantids in the primary forest understorey of Danum Valley (using the established "West Grid" system). One daylight hour was spent per transect. Mantids discovered accidentally apart from these transects, or at light sources other than the light-trap described above, were also collected, but not included in any analysis.

To measure within-habitat diversity, the α -value of the log-series distribution (Fisher's α), and its standard deviation were calculated using the "Programs for Ecological Methodology 2nd ed." (Exeter Software 2002, v. 6.1) from Krebs (1999). To ascertain whether the data fitted the log-series distribution, the observed species frequencies were compiled in octaves and compared to expected values by chi-square tests using Statistica 6.0 (StatSoft 2001).

The "true" species richness within the three habitats was estimated with the non-parametric estimators Chao1, ACE (Chazdon *et al.* 1998) and Jack-knife1 (Colwell 1997) using the programme EstimateS v. 5 (Colwell 1997). Chao1 and ACE are abundance-based estimators, whereas Jack-knife1 is incidence-based. The ACE (Abundance-based Coverage Estimator) may be especially well suited for data sets with a large proportion of rare species (Chazdon *et al.* 1998).

For the measurement of between-habitat diversity the indices of Jaccard (see e.g. Southwood & Henderson 2000) and NESS (Grassle & Smith 1976) were calculated. The Jaccard index determines the relative similarity of the species inventory between two communities using presence-absence data only. It is therefore especially sensitive to rare species. In contrast, NESS values point out the normalized estimates of shared species if random samples of size m were drawn from two communities. The sensitivity of the NESS index can be adjusted by means of this parameter m . For $m = 1$ the NESS index is most sensitive to common species. With rising m , it grows more susceptible to rare species. Here, NESS values for $m = 10$ are presented (results

did not change essentially for different values of m). For both β -diversity calculations the programme Biodiv97 (see above) was used.

RESULTS

A total of 106 individuals, representing 28 mantid species, were collected during the course of 18 sample nights. This is equivalent to almost a third of the 102 species reported to occur in Borneo (Ehrmann 2002). Three of these species have never been reported from Borneo before, and two of them seem to be altogether undescribed taxa and are subject of subsequent work. One additional specimen so far could not be identified at all. On average between five and eight individuals were caught per night, depending on the sampling site (see Table 1). The highest number of species was found in the cultivated area, totalling 16 – in contrast to 14 collected in the primary forest and 11 in the secondary forest.

Table 1. Numbers of collected species and individuals, sample nights, mean catches per night and values of the within-habitat diversity index Fisher's $\alpha \pm$ SD. Observed species richness and within-habitat diversity is highest in the cultivated area, followed by the primary forest. For sampling site designations see Materials & Methods.

Sampling site	Collected species	Individuals	Sample nights	Mean catch per night	Fisher's $\alpha \pm$ SD
PorC	16	40	7	5.7	9.9 \pm 6.6
DanS	11	28	6	4.7	6.7 \pm 5.0
DanP	14	38	5	7.6	8.0 \pm 4.2
Total	28	106	18	5.9	–

Within-habitat diversity expressed as Fisher's α (\pm standard deviation) was highest in the cultivated area (9.9 \pm 6.6), followed by the primary forest site (8.0 \pm 4.2) and the secondary forest site (6.7 \pm 5.0) as shown in Table 1. All three samples fitted the log-series distribution with $P > 0.95$.

Table 2 specifies all the specimens collected by light-trapping. Along the transects six specimens of probably four species were discovered. None of them could be identified, as all of them were nymphs. Mantids caught accidentally are listed in Table 3. Although they are not included in the biodiversity analysis, they might provide useful information about the distribution of the species.

Table 2. List of specimens collected at Poring Hot Springs and Danum Valley using an UV light-trap. Classification follows the traditional systematics of Beier, revised by Ehrmann and Roy (Ehrmann 2002). Asterisks indicate species previously unreported for Borneo (*) or entirely undescribed species (**). For sampling site designations see Materials & Methods.

Species	PorC	DanS	DanP
Amorphoscelidae			
<i>Amorphoscelis</i> spec. 1			3
<i>Amorphoscelis</i> spec. 2			1
Hymenopodidae			
<i>Acromantis</i> spec.	5	1	4
<i>Citharomantis</i> spec. (probably <i>C. falcata</i>)*		1	
<i>Creobroter</i> spec.	2	6	1
<i>Hestiasula</i> spec. 1		2	
<i>Pachymantis bicingulata</i>	1		
<i>Psychomantis borneensis</i>	1		
<i>Rhomantis moultoni</i>			1
Unidentified species (probably <i>Ephestiasula</i> spec. nov.)**			4
Liturgusidae			
<i>Humbertiella ocularis</i>	1		
<i>Theopompa</i> spec. 1		1	
<i>Theopompa</i> spec. 2			3
Tarachodidae			
<i>Leptomantella</i> spec. 1	4	1	10
<i>Leptomantella</i> spec. 2	4	1	
Iridopterygidae			
<i>Tropidomantis tenera</i>	11		1
<i>Xanthomantis flava</i>		7	2
Mantidae			
<i>Ceratocrania macra</i>	1		
<i>Deroplatys truncata</i>	1		
<i>Euchomenella matilei</i>	3		3
<i>Euchomenella heteroptera</i>	1		
<i>Gimantis insularis</i>			2
<i>Hierodula</i> spec. 1	2		2
<i>Hierodula</i> spec. 3	1	6	1
<i>Phyllothelys</i> spec.	1		
<i>Rhombodera</i> spec.		1	
Unidentified species	1		
Unidentified species (probably <i>Mythomantis</i> spec. nov.)**		1	

Table 3. Species caught accidentally in Poring Hot Springs and Danum Valley, but not included in the biodiversity analysis.

Species	Poring Hot Springs	Danum Valley
Hymenopodiae		
<i>Hestiasula</i> spec. 2		*
<i>Pachymantis bicingulata</i>		*
Liturgusidae		
<i>Theopompa</i> spec. 1	*	
Iridopterygidae		
<i>Hapalopeza</i> spec.	*	
Mantidae		
<i>Deroplatys desiccata</i>	*	
<i>Deroplatys truncata</i>		*
<i>Hierodula</i> spec. 2	*	

Estimations of the true species richness, shown in Table 4, convey a similar picture as the observed species richness. The cultivated area near Poring Hot Springs contains the highest estimated number of species (25 to 29), while the primary and secondary forest habitats in Danum Valley are estimated to contain 17 to 20 and 17 to 24 species, respectively. Jack-knifing ranks the three habitats in the same way as the observed species richness and Fisher's α . The abundance-based estimators Chao1 and ACE, on the other hand, rank the primary forest as the least diverse habitat.

Table 4. Estimated species richness as calculated by the estimators Chao1, ACE and Jack-knife1. All estimators rank the cultivated area as the site with the richest species inventory.

Sampling site	Chao1	ACE	Jack-knife1
PorC	29	29	25
DanS	22	24	17
DanP	17	19	20

According to the Jaccard index the mantid communities of all habitats are moderately similar to each other, as shown in Table 5. Cultivated area and secondary forest have 23% of their species in common, secondary forest and primary forest 25%, and primary forest and cultivated area share 30% of their species. When taking abundance data into account the similarity between primary forest and cultivated area grows more substantial: the NESS index value ($m = 10$) amounts to 0.71 for these two habitats while all other habitat combinations have values of only around 0.5.

Table 5. Between-habitat diversity expressed as Jaccard and NESS index values. The similarity of the species inventory is highest between the primary forest and the farmland site.

Sampling sites (pairwise)	Jaccard index	NESS ($m = 10$)
PorC — DanS	0.23	0.48
DanS — DanP	0.25	0.49
DanP — PorC	0.30	0.71

DISCUSSION

Surprisingly, species richness, within-habitat diversity (Fisher's α) and estimated "true" species number were highest on the farmland site, followed by the primary forest site and the secondary forest site. In contrast to the results of this study, similar studies on other insect taxa have shown a general decline of species richness with increasing human habitat disturbance (e.g. Lawton *et al.* 1998, Floren *et al.* 2001, Beck *et al.* 2002). Several biotic and abiotic factors may account for this effect. Abiotic factors include direct mechanisms like alterations of microclimatic conditions or habitat structure, while biotic or indirect factors include changes in the food web like the loss of important food species or fluctuations in the population size of predators that in turn control the population sizes of their prey. This pattern cannot be applied universally, though, as no group studied so far has been found to serve as a good indicator taxon for changes in the species richness of other groups (Lawton *et al.* 1998). While a decline of mantid species richness from the undisturbed primary forest canopy to the moderately disturbed secondary forest understorey could be observed, the highly disturbed farmland habitat seemed to provide unexpected good living conditions for many praying mantids. Why could this be the case?

In general, a few species are always able to profit from the altered conditions in disturbed habitats (because of a decline of their predators or competing species, for example), rising to high abundances (e.g. Floren *et al.* 2001, Beck *et al.* 2006). As mantids are generalist predators that feed on a wide variety of taxa (e.g. Iwasaki 1998, Schwarz 2003 and pers. observation), they are not dependent on the fate of distinct prey species. Moths, orthopterans and dipterans – all constituting suitable prey for a mantid – exist in high numbers on farmland sites (pers. observation during the light-trapping, see also Beck *et al.* 2002, 2006). In addition, bushes along the field margins and wild growth provide sufficient habitat structure. The highly productive farmland habitat might thus provide perfect conditions for high abundance and diversity of Mantodea. However, members of the mantid families Amorphoscelidae and Liturgusidae were almost completely absent at the farmland site (see Table 3), probably because these flat bark-mimics require tree trunks as habitat. They were also largely missing in the secondary forest site, but five species could be discovered in the primary forest.

Alternatively, the farmland area might experience a constant influx of mantids from less disturbed habitats in the vicinity. However, the colonization ability of mantids is considered to be limited, as females are usually poor flyers (Ehrmann 2002). With the nearest primary forest 7 km away, it seems therefore probable that the species found in PorC indeed form an established community.

The similarity of the species composition between cultivated area and primary forest site might be due to microclimatic similarities. Both habitats – the farmland site lacking large trees and the primary forest site being located in the open upper canopy layer (40 m height) – exhibit a higher exposure to the sun than the shady margin of the secondary forest. These conditions favour the thermophilic Mantodea. Unfortunately, no comparative measurements of solar irradiation or temperature were undertaken. Also, data from a primary forest understorey site would have been desirable to examine vertical stratification effects and for better comparability with the secondary forest site, which was located on the ground. It is nonetheless conceivable that microclimatic conditions affect the distribution of mantids more strongly than effects of disturbance, at least in this case.

The question why mantids are attracted to light remains to be further explored. Since many fully winged mantids fly over longer distances at night, especially males searching for mates, it can be supposed that they use similar orientation patterns as other nocturnal insects do (e.g. position of the moon). Consequently, they might be irritated by an artificial light source in the same way as, for instance, moths are (see e.g. Muirhead-Thompson 1991). However, many individuals could be observed hunting near the light or even on the gauze screen without any obvious orientation problems (as opposed to many moths). Maybe mantids are initially attracted by the light itself, but then stay mainly because of the concentration of prey around the light (as do spiders, bats and occasionally mice). It is interesting to note that 98% of the collected specimens were indeed males. As noted above, this can be attributed to the fact that the females of many species are less mobile and in some cases not even able to fly. In other studies, females of species that are fully winged in both sexes were also attracted, though more rare (e.g. Edmunds 1986).

Light-trapping, a frequently employed method in biodiversity research (e.g. Southwood & Henderson 2000), proved an effective means to collect praying mantids. Searching the vegetation along transects was substantially more time-consuming and is more difficult to standardize. Of course light-trap data measure activity and responsiveness to light rather than representing the true population structure. Some mantid species might not be attracted as strongly to light as others (Schwarz 2003), and – even more important – some species might not be attracted to light at all. However, this problem of selective sampling applies to all sampling methods (Southwood & Henderson 2000), and light sampling provided by far more species with much less effort than transect sampling. Further research is certainly needed to assess which species or larger taxonomic groups might be generally missed by light-trapping. Weather factors like temperature, relative humidity, rainfall and moonlight might also influence the activity of mantids, as it is known for moths (e.g. Holloway *et al.* 2001). However, while there is no knowledge of the attraction radius of light sources on mantids, for Lepidoptera the radii of attraction are surprisingly small (e.g. Muirhead-Thompson 1991) – even for hawkmoths (Sphingidae), which are certainly by far faster and more active flyers than mantids, effective attraction radii normally do not exceed 30 m (Beck & Linsenmair 2006). Therefore, situating a light source within a ‘homogenous’ habitat should be sufficient to attract mainly species from that habitat. Differences in the number of individuals, which might still result from different openness at the sampling site, can be normalized by appropriate (e.g. sample size independent) diversity measures like Fisher’s α and NESS in order to provide valid evaluations of mantid biodiversity in many situations. It would be desirable to repeat sampling, so effects of seasonality and annual differences could be taken into account. Particularly outside of the humid tropics seasonality might influence biodiversity estimates considerably.

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REFERENCES

Beattie, A.J. & Oliver, I. (1994). Taxonomic minimalism. *Trends in Ecology and Evolution* 9: 488-490.

Beck, J. & Linsenmair, K.E. (2006). Feasibility of light-trapping in community research of moths: attraction radius of light, completeness of samples, nightly flight times and seasonality of Southeast-Asian hawkmoths (Lepidoptera: Sphingidae). *Journal of Research on the Lepidoptera* 39: 18-36.

Beck, J., Schulze, C.H., Linsenmair, K.E. & Fiedler, K. (2002). From forest to farmland: diversity of geometrid moth along two habitat gradients on Borneo. *Journal of Tropical Ecology* 18: 33-51.

Beck, J., Kitching, I.J. & Linsenmair, K.E. (2006). Effects of habitat disturbance can be subtle yet significant: biodiversity of hawkmoth-assemblages (Lepidoptera: Sphingidae) in Southeast-Asia. *Biodiversity and Conservation* 15: 465-486.

Chazdon, R.L., Colwell, R.K., Denslow, J.S. & Guariguata, M.R. (1998). Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. (In) Dallmeier, F. & Comiskey, J.A. (eds.), *Forest biodiversity research, monitoring and modeling: conceptual background and Old World case studies*. Parthenon Publishing, Paris. Pp. 285-309.

Colwell, R.K. (1997). EstimateS: statistical estimation of species richness and shared species from samples (v. 5). User's guide and application. <http://viceroy.eeb.uconn.edu/estimates>.

Daniels, R.J.R., Hedge, M. & Vinutha, C. (1985). Observations on the biology of the praying mantis *Creobater urbana* Fabr. (Orthoptera: Mantidae). *J. Bombay Natural History Society* 86: 329-332.

Edmunds, M. (1986). The phenology and diversity of praying mantids in Ghana. *Journal of Tropical Ecology* 2: 39-50.

- Ehrmann, R. (1985). Standorttreue von *Mantis religiosa* (L.) (Mantodea: Mantidae). *Entomologische Zeitschrift* 96(5): 63-64.
- Ehrmann, R. (2002). Mantodea – Gottesanbeterinnen der Welt [Mantodea – Praying mantids of the world]. Natur und Tier – Verlag GmbH, Münster.
- Floren, A., Freking, A., Biehl, M. & Linsenmair, K.E. (2001). Anthropogenic disturbance changes the structure of arboreal tropical ant communities. *Ecography* 24(5): 547-554.
- Grassle, J.F. & Smith, W. (1976). A similarity measure sensitive to the contribution of rare species and its use in investigation of variation in marine benthic communities. *Oecologia* 25: 13-22.
- Holloway, J.D., Intachat, J. & Staines, H. (2001). Effects of weather and phenology on the abundance and diversity of geometrid moths in a natural Malaysian tropical rain forest. *Journal of Tropical Ecology* 17(3): 411-429.
- Inoue, T. & Matura, T. (1983). Foraging strategy of a mantid, *Paratenodera angustipennis* S.: mechanisms of switching tactics between ambush and active search. *Oecologia* 56: 264-271.
- Iwasaki, T. (1998). Prey menus of two praying mantises, *Tenodera aridifolia* (Stoll) and *Tenodera angustipennis* Saussure (Mantodea: Mantidae). *Entomological Science* 1(4): 529-532.
- Krebs, C.J. (1999). *Ecological methodology*. Addison-Wesley Educational Publishers, Inc., New York.
- Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S. & Watts, A.D. (1998). Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* 391: 72-76.
- Lieftinck, M.A. (1953). Biological and ecological observations on a bark haunting mantid in Java (Orthopt., Mantodea). *Trans. Ninth Int. Congr. Ent* 2: 125-134.
- Liske, E., Köchy, K. & Wolff, H.G. (1989). The thoracic nervous system of the Chinese praying mantis, *Tenodera aridifolia sinensis*: distribution of the nerves and the musculature they supply. *Zoolog. Jahrb. Anat.* 118: 191-199.
- Maldonado, H. (1970). The deimatic reaction in the praying mantis *Stagmatoptera biocellata*. *Zeitschrift für vergleichende Physiologie* 68: 60-71.
- Marsh, C.W. & Greer, A.G. (1992). Forest land-use in Sabah, Malaysia: an introduction to Danum Valley. *Phil. Trans. R. Soc. Lond. B* 335: 331-339.
- Matura, T. & Nagai, S. (1983). Estimation of prey consumption of a mantid, *Paratenodera angustipennis* (S.) in a natural habitat. *Res. Popul. Ecol.* 25: 298-308.

Mittelstaedt, H. (1957). Prey capture in mantids (*Parastagmatoptera unipunctata*). *Rec. Invert. Physiol. Univ. Oregon*: 51-71.

Muirhead-Thompson, R.C. (1991). *Trap responses of flying insects*. Academic Press, London.

Oliveira, D. (1996). Key to praying mantids.
<http://www.earthlife.net/insects/mant-key.html>.

Prete, F.R., Wells, H., Wells, P.H. & Hurd, L.E. (1999). *The praying mantids*. The Johns Hopkins University Press, Baltimore and London.

Rathet, I.H. & Hurd, L.E. (1983). Ecological relationships of three co-occurring mantids, *Tenodera sinensis* (Saussure), *T. angustipennis* (Saussure), and *Mantis religiosa* (Linnaeus). *The American Midland Naturalist* 110(2): 240-248.

Rossel, S. (1983). Binocular stereopsis in an insect (Mantodea). *Nature* 302: 821-822.

Schwarz, C.J. (2003). Diets and habitat preferences of neotropical praying mantids (Dictyoptera: Mantodea, Burm. 1838). Diploma thesis at the University of Würzburg, Germany (unpublished).

Shelford, R. (1903). Bionomical notes on some Bornean Mantidae. *The Zoologist* 7: 293-304.

Southwood, T.R. & Henderson, P.A. (2000). *Ecological methods*. Blackwell Science Publishers, Oxford. 575 pp.

Yager, D.D., May, M.L. & Fenton, M.B. (1990). Ultrasound-triggered, flight-gated evasive manoeuvres in the praying mantis, *Parasphendale agrionina* (Gerst.) I. Free flight. *J. Exp. Biol.* 152: 17-39.

PLATE 1



Hierodula spec. 3 - male



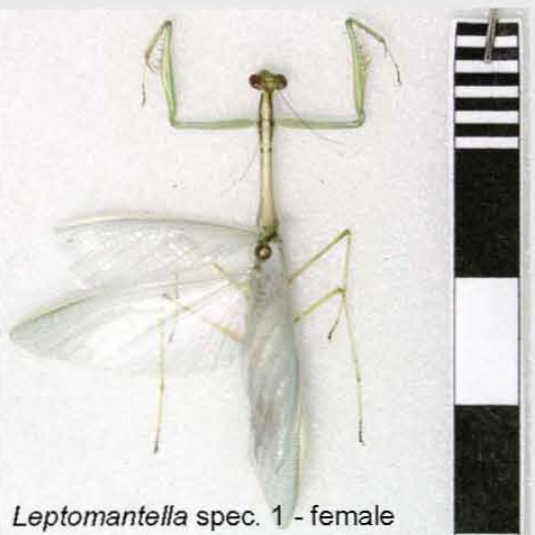
Euchomenella matilei



Acromantis spec. - male



Creobroter spec. - male



Leptomantella spec. 1 - female



Tropidomantis tenera - female

Plate 1. Examples of praying mantids frequently encountered in Sabah, Borneo.

PLATE 2

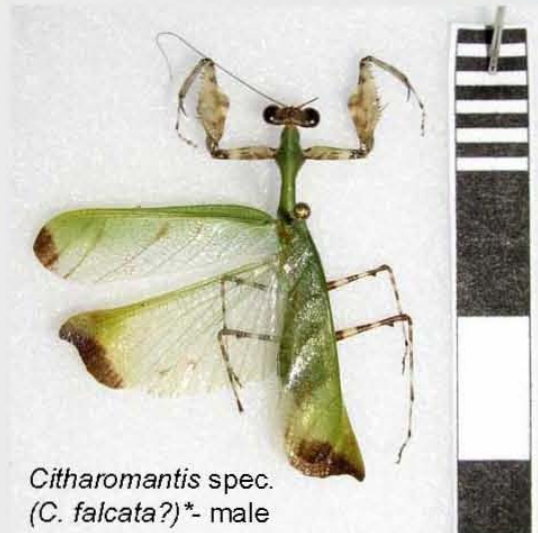


Plate 2. Examples of especially conspicuous pr previously unreported mantids collected in Sabah, Borneo. Asterisks as in Table 2.