

Laboratory studies on the praying mantis *Orthodera ministralis* (Mantodea: Mantidae)

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Abstract

Aspects of the biology of the mantid *Orthodera ministralis* (Fabricius) were studied in the laboratory. Oothecae contained an average of 34 eggs per case, with a mean length of 11.3 mm. Oothecal and nymphal development was temperature dependent, and 6 instars were found. Adult female mantids consumed up to 6 large blowflies (Calliphoridae) in 6 hours, with a mean of 2.5 flies per female, and up to 26 *Musca domestica* (L.) in 3 hours, with a mean of 17.5 flies per female. Cannibalism among 3rd and 4th instar nymphs was highly significantly ($p < 0.01$) reduced by the presence of *Drosophila melanogaster* (Meig.), and highly significantly increased ($p < 0.01$) at the higher mantid density. Cannibalism by 4th instar nymphs on 1st instar nymphs was very highly significantly ($p < 0.001$) reduced by the presence of *D. melanogaster* and a complex environment, and very highly significantly ($p < 0.001$) increased by a higher 1st instar density.

Keywords: Mantoidea; Mantidae; *Orthodera ministralis*; praying mantis; oothecae; cannibalism; predation; functional response; development; rearing.

INTRODUCTION

The most common species of praying mantis found in New Zealand (*Orthodera ministralis* (Fabricius)), was first recorded here in the 1870s, and it has been suggested that it was unintentionally introduced at the time of the commencement of gold diggings, when large amounts of hay were imported from Australia (Hutton 1896). Its present distribution has not been accurately described, although it appears to be abundant throughout the North Island and parts of the South Island (Sharell 1971). It is univoltine, overwintering in Palmerston North as eggs in a hardened ootheca, with young nymphs hatching out in spring, although adults and nymphs have recently been found in Auckland during late winter (Crosby 1984).

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These studies were initiated to fill in obvious gaps in the reproductive, feeding, and developmental biology of this insect, as previous workers had published few data on the oothecae, the number and size of nymphal instars, and growth rates of the nymphs.

In a review of cannibalism, Fox (1975) found 3 factors to be consistently important for its occurrence: the density of the species, the availability of alternative food, and the complexity of the environment, including possible refugia. Since mantids are voracious predators from the middle instars onwards, an examination of the importance of these factors to cannibalism was warranted.

MATERIALS AND METHODS

Rearing

Adult mantids were collected from all over Palmerston North in March and April 1978, through an advertisement in the local paper offering a reward of 5 cents per insect. They were kept in population cages made from modified cardboard bottle cartons. The boxes were cut in half across the bottle dividers, and gauze was placed over the open ends. Small trap doors were cut into the closed ends of each compartment, to enable controlled feeding of individual mantids. One hundred and twenty mantids were maintained in these cages, held at $25^{\circ} \pm 1^{\circ}\text{C}$, 35-40% R.H., and 16L:8D. They were fed a diet of 1 large blowfly each per day (the flies were generally *Calliphora* sp. initially, although *Musca domestica* was used when these became scarce). Females were mated in the laboratory (in case this had not occurred in the field), and only 4 cases of cannibalism upon males noted. Oviposition began immediately in some females, and in a few cases continued to do so until late June, far later than normal for Palmerston North (April-May).

Measurements of oothecae

Oothecae laid in the laboratory ($n = 136$) were measured with callipers accurate to 0.05 mm, weighed, and the number of operculae counted. After hatching, the oothecae were reweighed, and dissected ($n = 110$) to determine the number of eggs present. A field sample of oothecae was collected ($n = 32$) to check for differences between the laboratory and field populations. One egg case was dissected immediately after oviposition, and several of the individual eggs weighed. The dates of the first and final nymphs hatching were recorded.

Embryonic development

Freshly laid oothecae were collected daily and measured as described, before being lightly glued to newspaper discs (to maintain their upright position) and placed in 300 ml plastic tubs with perforated cellophane lids, kept at either $25^{\circ} \pm 1^{\circ}\text{C}$, 35-40% R.H., 16L:8D, or $30^{\circ} \pm 2^{\circ}\text{C}$, 18-24% R.H., 16L:8D.

Nymphal development

Newly hatched nymphs were anaesthetized with carbon dioxide and the head capsule width and body length measured under 2X magnification. The nymphs were then transferred to a rearing cage, consisting of cellophane-covered Dixie cups (size 104w) with perforated bottoms, mounted into the top of a cardboard box. Bottles of emerging *Drosophila melanogaster* were placed in the base of each cage, relying on the tendency of the adult flies to crawl up into the Dixie cups to feed the mantids. One cage containing 12 nymphs was placed at each temperature (as in embryonic development above), and the nymphs were measured weekly for 5 weeks. Only nymphs which survived to the end have been included in the analysis. Time and equipment constraints prevented following the same nymphs through to the adult, or the use of other temperature regimes. However, other nymphs that had been reared earlier at the lower temperature were followed through from 4th instar to the adult.

Predation rate

Female mantids were placed in experimental cages (16.5 × 14.0 × 13.0 cm) made from halved cardboard flagon cartons, with 4 cages per carton. Gauze was glued over the ends, and a large trap door was placed in the back of each chamber. Cages were lined with white paper. Two types of prey were used, a mixture of field collected *Calliphora* sp., and laboratory reared *Musca domestica*. One female mantid, which had been subjected to 42 hours of starvation, was placed in each cage, and randomly assigned a density of prey. The prey were anaesthetized with carbon dioxide and visually standardized for size and vigour before being added to the cages. The experiments using *Calliphora* sp. employed densities of 5, 7, 10, and 15 flies per female, with 8 replicates, and lasted for 6 hours. The number of flies eaten was recorded to the nearest half fly at the end.

The experiment using *Musca domestica* had densities of 10, 15, 20, 25 and 30 flies per female, and lasted for 3 hours, with 8 replicates. Half-hourly readings were made, and the data were analysed using the Rodgers (1972) random predation equation.

Cannibalism

Experiments were designed to test for the importance of 3 factors in cannibalism : food, conspecific density, and environmental complexity, using a 2 × 2 × 2 factorial design. The first experiment used 3rd and 4th instar nymphs, caged in 300 ml plastic tubs with gauze and cellophane lids, with a moist filter paper triangle kept between the lids to keep the humidity high. A design matrix was formulated, with 2 levels for each variable:

1. Presence or absence of alternative food (an excess of *D. melanogaster*);
2. High or low mantid density (3 or 9 mantids per cage);
3. A simple or complex environment (a green construction paper "tree" was used to add refugia to the otherwise simple tubs)

The paper trees consisted of a circular base designed to fit snugly in the plastic tub, and 2 vertical sections glued to the base. The vertical sections each had 4 horizontal flaps, and a 120° bend in the middle. The particular shape of the "trees" was arbitrary; however, the aim was to interrupt the line of sight within the tubs as much as possible.

The number of surviving nymphs in each of the 8 treatments was checked at the same time daily, and dead or eaten nymphs were replaced from a parallel supply held in the same conditions, with or without food. The experiment was maintained for 10 days, with 2 replicates.

The 2nd experiment was very similar to the 1st, except that a single 4th instar nymph was placed in each tub, and the high and low densities were filled by day-old 1st instar nymphs. First instar nymphs were counted daily and replaced when necessary, for 10 days, with 2 replicates performed. The Yates algorithm was used to calculate the significance of the effects of the factors and their interactions in both experiments, and analysis of variance techniques were used to assign significance levels of the effects (Bailey 1975).

RESULTS

Oothecae

Table 1 shows the results from the measured oothecae, which did not vary significantly ($p < 0.05$) from the field sample for any parameter. The mean values for the numbers of eggs and operculae suggest a value of 2 eggs per chamber, but the correlation coefficient was surprising low ($r^2 = 0.34$), indicating a great deal of variability in this relationship.

A few eggcases ($n = 5$) had 100% hatching success, and these oothecae had an average of 71% of the total oothecal mass due to the hatching nymphs. Five eggs

Table 1. Anatomical statistics of *O. ministralis* oothecae.

Parameter	mean (s.e.)	Sample size
length	11.32 (0.20) mm	136
width	5.77 (0.06) mm	136
height	5.96 (0.05) mm	136
mass	0.1864 (0.0050) g	110
number		
operculae	17.9 (0.4)	110
number eggs	34.3 (1.23)	110

Table 2. Anatomical dimensions of *O. ministralis* nymphs and adults (mm).

Stage	Head capsule width (s.e.)	Increase	Body length (s.e.)	Increase	Sample size
1st instar	1.65 (0)	—	6.20 (0)	—	10
2nd instar	2.03 (0.04)	1.23	9.97 (0.39)	1.60	8
3rd instar	2.58 (0.03)	1.27	13.14 (0.23)	1.32	9
4th instar	3.09 (0.04)	1.20	16.30 (0.53)	1.24	9
5th instar	3.62 (0.06)	1.40	20.46 (0.58)	1.26	12
6th instar	4.54 (0.06)	1.25	25.12 (0.36)	1.23	10
Adult male	4.82 (0.04)		30.46 (0.25)		13
Adult female	5.77 (0.04)		40.60 (0.36)		42

removed from the freshly laid ootheca had a mean mass of 0.00358 g, and 1 of the eggs hatched successfully at $25^{\circ} \pm 1^{\circ}\text{C}$.

The 11 oothecae kept at $30^{\circ} \pm 2^{\circ}\text{C}$ had the first nymph hatch after an average of 30.9 (s.e. = 1.08) days, with a mean spread of 0.91 days between 1st and final emergents. The 14 oothecae kept at $25^{\circ} \pm 1^{\circ}\text{C}$ had the 1st nymph hatch after an average of 43.4 (s.e. = 1.70) days, with a mean spread of 1.70 days between 1st and final emergents.

Nymphal development

Table 2 shows the head capsule widths and body lengths for the 6 nymphal instars, and the adults. The head capsules and body lengths follow a regular geometric progression, with one minor exception for each parameter. The average incremental growth with successive instars was 1.27 for the head capsules, and 1.33 for the body lengths. The growth rates of nymphs fed ad libidum on *D. melanogaster* were temperature dependent, with head capsule widths following the equations:

$$y = 0.264x + 1.48 \quad r^2 = 0.90 \quad (\text{at } 25^{\circ} \pm 1^{\circ}\text{C})$$

$$y = 0.394x + 1.53 \quad r^2 = 0.98 \quad (\text{at } 30^{\circ} \pm 2^{\circ}\text{C})$$

The body lengths increased according to the equations:

$$y = 1.76x + 5.84 \quad r^2 = 0.98 \quad (\text{at } 25^{\circ} \pm 1^{\circ}\text{C})$$

$$y = 2.77x + 6.14 \quad r^2 = 0.99 \quad (\text{at } 30^{\circ} \pm 2^{\circ}\text{C})$$

Wing buds appeared in the 4th instar, and development from hatching nymph to adult took a minimum of 11 weeks, at $25^{\circ} \pm 1^{\circ}\text{C}$.

Predation rate

The number of *Calliphora* sp. eaten in 6 hours was not related to the density of flies. On average 2.0 to 2.5 flies were consumed per female in all densities, with a range of 0 to 6.5 flies eaten per female. Mantid predation on *Musca domestica* in the first experiment had a mean of 17.5 flies eaten in 3 hours per female at the highest density, where the maximum of 26 flies was also recorded. The estimates for the attack rates for each time interval were relatively constant, while the handling time estimates increased from 1.1 to 7.6 minutes per fly, by the end of the experiment, according to the Rodgers (1972) random predation equation.

Cannibalism

The factors of the presence or absence of *D. melanogaster* and 4th instar mantid density, and the first order interaction between them, all had a highly significant effect ($p < 0.01$) on the level of cannibalism in the 1st experiment. The presence of *Drosophila* reduced cannibalism, while increasing the mantid density increased it. The interaction between food and density had a negative value, indicating that when alternative food and the high density were present together cannibalism was reduced, despite the opposition of the 2 factors. This suggests that alternative food is more important than conspecific density in this situation. The environmental complexity and the other interactions all had no effect on cannibalism.

The results from the 2nd experiment, involving cannibalism by a 4th instar nymph on 1st instar nymphs indicated very highly significant effects ($p < 0.001$) for all 3 factors (environmental complexity—in the form of a paper “tree”; alternative food—*D. melanogaster*; and 1st instar mantid density—3 or 9 per cage), as well as all interactions, except that between environmental complexity and food, which was not significant. The results indicated that presence of alternative food and greater environmental complexity reduced cannibalism, while the higher density and simpler environment increased it. Both the environmental complexity/alternative food and the nymph density/alternative food interactions had high negative values for the effects, and indicated a net reduction in cannibalism. In the second case, where the 2 factors were opposed, the presence of alternative food had a more powerful influence than density.

DISCUSSION

The oothecae are on average considerably smaller than reported elsewhere (11.3 mm, c.f. 20 mm in Sharell (1971), who may have only measured large oothecae). Each contained an average of 34 eggs per case, which was not closely correlated to the number of chambers in the ootheca (Table 1). Oothecae in other mantids contain 10-400 eggs (Key 1970), which puts *O. ministralis* at the low end of this range. The rate of embryonic development was temperature dependent.

Six nymphal instars occurred in *O. ministralis*, although this may be variable depending on the availability of food to the developing nymphs, as in *Paratenodera augustipennis* (Matsura et al. 1975). Nymphal development was clearly temperature dependent within the range investigated. The head capsules and body lengths increased according to Dyar's (= Brooks') rule (Crosby 1973) between successive instars (Table 2).

The absence of a functional response exhibited with *Calliphora* sp. was probably due to the large size of these flies, which would have tended to readily satiate the mantids. In the case of *M. domestica*, the handling time was found to increase as more flies were eaten, and it can be considered to be a major factor in determining the number of flies consumed over time. As laboratory experiments are likely to overestimate field predation rates, due to the favourable circumstance of high prey density, it is not practical to extrapolate from these results to the field. Mantids in the field are likely to feed irregularly due to factors such as the influence of weather on prey behaviour, and an uneven prey distribution.

It was noted on several occasions that female mantids would capture a fly and commence eating it, and capture a 2nd fly before finishing the 1st. According to Springett (pers. comm.) this type of behaviour, where a predator capitalizes on prey abundance by entrapping more than 1 prey at a time, is unusual, particularly among arthropods. It is clear from these experiments that mantids subjected to starvation followed by periods of plenty can consume large numbers of nuisance species (e.g., up to 26 houseflies in 3 hours).

Higher mantid density resulted in a highly significant ($p < 0.01$) increase in cannibalism in both experiments, which can be attributed to the greater probability of

encounters at the higher density, paralleling the functional response seen with flies. The presence of alternative food produced a highly significant decrease in cannibalism in both experiments. Satiated mantids are less likely to attack a prey that is as large or larger than themselves, according to Holling (1966), who showed that the mantids reactive distance (i.e., the distance across which an attack would occur) increased with hunger. The reactive fields of the mantids in the treatments without alternative food could be expected to increase, resulting in a higher probability of attack between mantids. The influence of the paper "trees" was different in each experiment. They had no influence on the rate of cannibalism in the 1st experiment, where the large size of the 3rd and 4th instars reduced the ability of the "trees" to provide refugia. This contrasted with cannibalism by 4th instars on 1st instars in the 2nd experiment, where the prey were small compared with the "trees", and could be hidden by them, with a net reduction in cannibalism. The large number of significant interactions in the 2nd experiment underlines the complexity of cannibalistic systems. It is conceivable that nymphal cannibalism could occur in the field, where an early hatching nymph could encounter a hatching ootheca, or other nymphs. Cannibalism is unlikely to be an important mortality factor in the field, due to the typically low density of this species.

The constraints imposed by a univoltine life cycle mean that an *O. ministralis* population is able to respond to changes in prey density between, but not within, seasons. This factor, combined with a polyphagous diet means that this species is unlikely to have an economically important role in pest control, although it would be necessary to have more information about the prey of nymphs in the field to establish this.

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