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Responses to Starvation in a Mantis, *Paratenodera angustipennis* (S.)

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Summary. Survival period, pattern of decrease in body weight and metabolic rate under starvation conditions were examined to clarify responses to starvation of a predatory insect, the mantis, *Paratenodera angustipennis* (S.). (i) The average survival period in starved condition was the shortest in the 1st instar larvae (5.4 days) and the longest in the adults (15.0 days for males, 26.7 days for females). (ii) The body weights of the 3rd and the 5th instar larvae decreased almost linearly during fasting period, whereas those of adults decreased greatly during the initial 5 days, and then exhibited little further decline until their death. (iii) The carbon dioxide production by the adult mantids in the dark condition at constant 26° C was measured by the improved Boysen-Jensen's method. There was a linear relationship between the body weight and the metabolic rate per individual on a double logarithmic scale, and the regression coefficient b was 0.806. (iv) The metabolic rate per individual was greatest at satiation, but the rate per unit weight was maximum on the 5th day after satiation when the food had been just digested completely, and both decreased with the progress of starvation. (v) Based on the above mentioned results, properties of *P. angustipennis* as a predator were discussed.

Introduction

Animals living in habitats with poor food resources are often exposed to starvation. It is expected that starvation is a more frequent occurrence in predatory animals than in phytophagous ones, due to uncertain food supply. Even phytophagous insects, occurring on small patches of food plants, may also be faced with starvation by intraspecific competition for food.

Although limitation of food is a major factor which limits the density of animal populations, ecological aspects of starvation have not been explored sufficiently (Ivlev, 1955). After Ivlev's studies (1955), several ecological studies about responses to starvation have been performed, mainly with spiders (Ito 1964; Miyashita 1969; Nakamura 1972a; Anderson 1974; Wise 1975). However there are few such studies which concern predatory insects. In the present study, survival period, pattern of decrease in body weight and metabolic rate under starvation conditions were examined, using a mantis, *Paratenodera angustipennis*.

P. angustipennis is an ambush-type predator. It is a common species of grassland in Japan except for Hokkaido. First instar larvae hatch early in June in Kyoto (Matsura 1979), and they become adults after six or seven larval instars (Matsura et al. 1975). Adult emergence is during the period from the end of August to the beginning of September, and they survive till the end of November.

Materials and Methods

Experiments on Survival Period and Pattern of Decrease in Body Weight

Studies were made on 1st, 2nd, 3rd, and 5th instar larvae, and adults. The 1st to the 3rd instar larvae were reared on live adults of *Drosophila melanogaster* and 4th and 5th instar larvae were reared on *Musca domestica*. The 1st instar larvae were given flies for three days from just after hatching, then they were deprived of food.

The 2nd, the 3rd and the 5th instar larvae were fed sufficient flies during 24 h just after moulting, then food was deprived. The larvae of mantids can capture flies immediately after moulting, therefore they might be satiated in the course of 24 h. Since newly hatched larvae have high mortality by factors other than starvation, they were given food for 3 days.

Newly emerged adult mantids were collected from Tanabecho in Kyoto Prefecture on 8 September 1979. Grasshoppers, *Oxya japonica*, were fed *ad libitum* to the extent of satiation during 24 h before fasting.

Mantid larvae were reared in a transparent plastic cylindrical container whose top surface was covered with gauze (9 cm in diameter and 4.5 cm in height for the 1st and the 2nd instar larvae; 12 cm × 6 cm for the 3rd instar larvae; 12 cm × 10 cm for the 5th instar larvae), and adults were reared in a cage (17 cm × 17 cm × 25 cm) covered with nylon gauze. Although they could move about freely in these containers, they were resting almost all the time on the gauze. In the fasting period, water to drink was sprayed onto the gauze several times in a day. The 3rd, and 5th instar larvae, and adults were weighed almost every day before watering.

All the experiments were carried out under uncontrolled room temperature (see Table 1) and uncontrolled humidity.

Experiments on the Metabolic Rate

Metabolic rates of the adults were measured at a fixed time each day during the fasting period. The measurements were made by using Ito's (1961 and 1964) titration technique which is an improved Boysen-Jensen method. The principle of the method is shown below.

At first, a test animal was put into a closed glass cylinder which contained nearly CO_2-free air. After a given interval of time, the CO_2 produced in the cylinder was absorbed by 0.05 N-KOH solution. Then, titration was made by 0.03 N-HCl. The difference of the volume of 0.03 N-HCl between the control cylinder and the test cylinder is equivalent to CO_2 produced by respiration of test animal.

The size of cylinder was 3.5 cm in diameter and 15 cm in length. The replacement of CO_2-free air in the test cylinder was made for 15 min. Then it was wrapped with aluminum foil and kept in a thermostatic chamber (26 ± 0.5° C) for $1^3/_4$ h.

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Table 1. Average survival periods in every developmental stage under starvation conditions and average room temperature during the experiments

Stage		Average survival period ±95% C.L. (days)	Range (days)	Sample size	Duration of experiments	Average temperature (°C)
1st instar		5.4±0.4	3–7	30	7 June–14 June	24.2
2nd instar		7.1±0.5	5–9	20	16 June–25 June	26.4
3rd instar		11.6±1.6	8–15	10	25 June–10 July	25.5
5th instar		15.1±2.2	10–21	10	10 July–31 July	27.6
Adult	male	15.0±2.9	11–21	7	12 September–3 October	25.5
	female	26.7±3.9	19–37	11	12 September–19 October	24.2

Results

Survival Period and Pattern of Decrease in Body Weight Under Starvation Conditions

Table 1 shows average survival periods under starvation conditions, their ranges and average room temperature during the experiments for larvae and adults. The survival periods increased as larvae grew older and that of adults was the longest. Since adult females survived 10 days longer than males, tolerance for starvation of the males was weaker than the females. Although four female mantids laid eggs during the experiments, there were no significant differences in the survival periods between females which laid eggs and those which did not (p of $t<0.001$).

Patterns of decreases in body weight of the 3rd, the 5th instar larvae and the adults are shown in Fig. 1. The females which had laid eggs were ommitted from the calculation. The vertical axis shows the ratio of the body weight during the fasting period to that at satiation. Data were plotted until half of the mantids had died. The initial weight loss was generally rapid compared to later weight loss, particularly in the adults. There was little decrease in the body weight in females after the 11th day from the start of fasting. It seems that the occasional increases of the body weight were due to drinking water.

The remarkable decreases in the body weight in the early time of fasting are probably the results of digestion and excretion of food substances within their digestive tracts. Time of retention of food within the digestive tract is estimated from these curves to be about 5 days in the adults.

In order to estimate the time of retention of food in the adults more precisely, another experiment was performed. Five adult females whose digestive tracts had been cleared were given *O. japonica ad libitum*, then they were put into a fasting condition. The amounts of faeces were weighed every day from the beginning of fasting. The data are shown in Fig. 2. The insects were kept under constant 26° C always. Figure 2 shows that the adult females digested almost all the food within their digestive tracts in 5 days after satiation. This value coincides with estimates from the curves shown in Fig. 1.

The ratio of the body weights measured one day before death to those at satiation for every stage of mantids are presented in Table 2. The 3rd and 5th instar larvae and the adult males died after decreasing their body weight to nearly 70% of those at satiation. However the adult females did not die until their body weight had been reduced by nearly half. This suggested that they had filled their tracts with more food than either the larvae or the male adults. For the purpose of evaluating the degree of true exhaustion of body weight, the ratio of the body weight at the time when food within the digestive tract had just been cleared to that one day before death was calculated. The loss of the body weight during the fasting period until death was 13.3% in the males and 19.3% in the females. The reason why the exhaustive rate was higher in the females than in the males is that the females had more energy stock in their

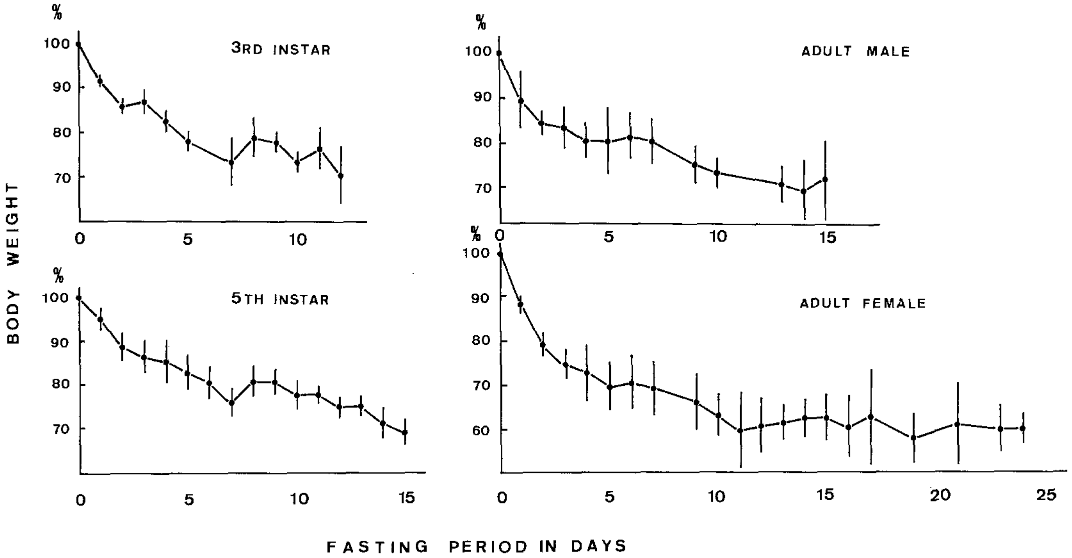

Fig. 1. Decreases in body weight of the 3rd instar, the 5th instar larvae and adults under starvation conditions. Body weight is shown by a ratio to that at satiation. Vertical bars represent the 95% confidence limits

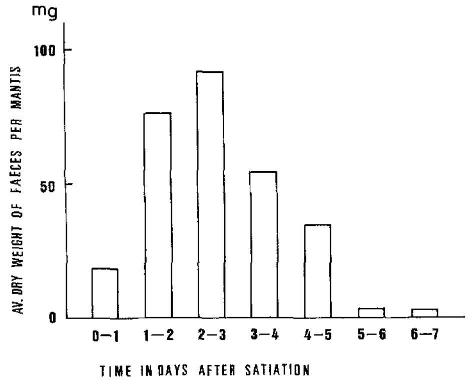

Fig. 2. Time of retention of food in the digestive tract of the adult female

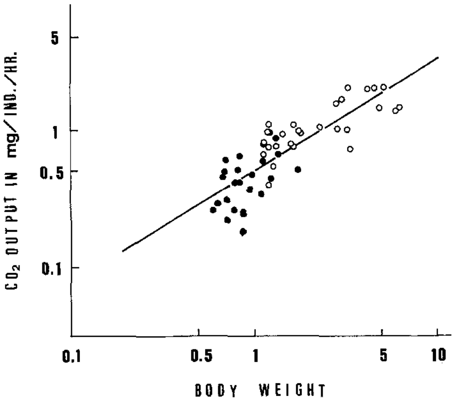

Fig. 3. Relationship between body weight and metabolic rate per individual. Males and females are expressed by solid circles and by open circles, respectively

Table 2. Ratios of body weights measured one day before death to those at satiation

Stage	$W_{d\text{-}1}/W_0 \times 100$ (%)	$W_{d\text{-}1}/W_5 \times 100$ (%)
3rd instar	72.1	–
5th instar	69.5	–
Adult male	71.6	86.7
female	56.0	80.7

W_0, body weight at satiation; $W_{d\text{-}1}$, body weight one day before death; W_5, body weight on the 5th day after satiation

fat bodies and ovaries. When dead mantids were dissected, their fat bodies or ovaries were contracted and the integuments consisted almost entirely of cuticle.

Metabolic Rate under Starvation Conditions

The relationship between the intensity (M) of metabolism per individual and the body weight (W) of animals generally has been shown by an equation:

$$M = aW^b \tag{1}$$

where a and b are constants. Thus, the relationship between log W and log M can be shown by a linear equation.

Linear relationships between the two were obtained in all cases of different fasting period, except for the 21st day after satiation, and there were no significant differences among them. Therefore, all data were plotted in Fig. 3. The regression line is:

$$\log M = 0.806 \, \mathrm{Log} W - 0.305. \quad (r = 0.830, \ P < 0.001) \tag{2}$$

From this equation, the relationship between M and W can be obtained:

$$M = 0.495 \, W^{0.806}. \tag{3}$$

According to Duncan and Klekowski (1975), published values for b vary considerably but most of them lie between 0.6 and 0.8. Mill (1972) indicated that the oxygen consumption in animals with tracheae or lungs are proportional to body weight ($b = 1$). Thus, the value $b = 0.806$ (S.E. $= 0.076$) in *P. angustipennis* seems to be reasonable.

Figure 4 shows some examples of changes in metabolic rate (mg CO_2/ind./h) of an individual male (*a*) and female (*b*) during starvation conditions. Metabolic rates of the females were almost the greatest at satiation and decreased with the progress of starvation. On the other hand, those in the males were generally less and decreases in the intensity of respiration during starvation were not as great as in the females.

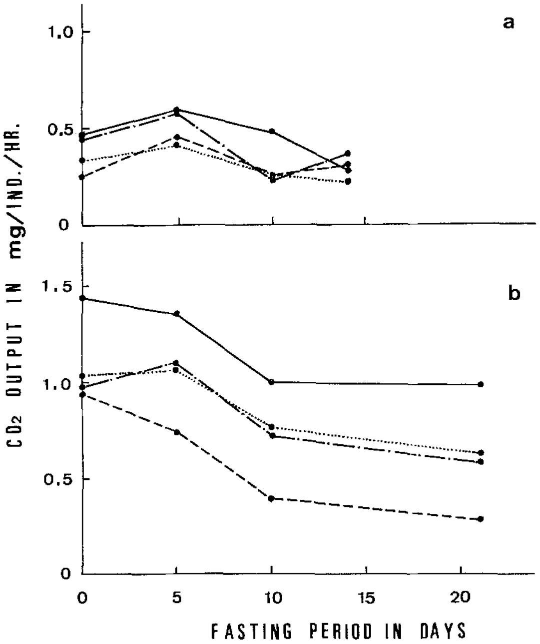

Fig. 4. Changes in metabolic rate of an individual male (**a**) and female (**b**) under starvation conditions

Metabolic rates (mg CO_2/g/h) per unit weight of the adult mantids during starvation conditions and sample sizes are indicated in Table 3. The author wished to know the true body weight of the adult mantis except for contents of digestive tract as the physiological basis, but it was not measured directly. So it was replaced with the body weight on the 5th day after satiation when the food within the digestive tract had been completely digested. Therefore the metabolic rates at satiation in Table 3 are somewhat underestimated, comparing with true metabolic rates. Based on Table 3, changes in the metabolic rates of the mantids during starvation are shown in Fig. 5. There were small differences between the metabolic rates of males and those of females, and those at satiation were rather lower com-

Table 3. Metabolic rates ($mgCO_2/g/h$) of adult mantids under starvation conditions and their sample sizes (numerals in parentheses)

Sex	Fasting period in days				
	0	5	10	14	21
Male	0.45 (7)	0.61 (7)	0.49 (6)	0.49 (5)	–
Female	0.51 (7)	0.60 (8)	0.53 (8)	0.46 (5)	0.37 (7)

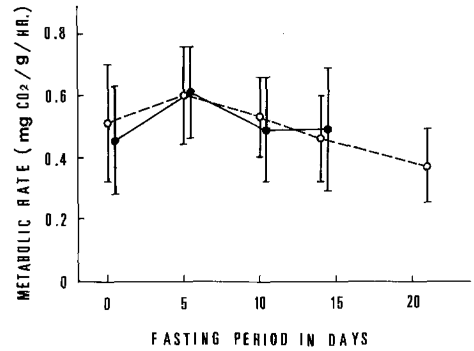

Fig. 5. Changes in metabolic rate ($mgCO_2/g/h$) per unit weight of the mantids under starvation conditions. Males and females are expressed by solid circles and by open circles, respectively. Vertical bars represent the 95% confidence limits

pared with the metabolic rate of spiders (Miyashita 1969, Nakamura 1972a). The metabolic rates reached the maximum on the 5th day after satiation and then decreased gradually during starvation.

Discussion

In *P. angustipennis* the younger the larva, the weaker was tolerance to starvation (Table 1), because younger larvae have higher metabolic rates per unit biomass due to the greater ratio of surface area to biomass in smaller animals and they require more energy. The shortage of prey probably causes the failure of moulting Turnbull (1962) and Mukerji and LeRoux (1969) observed with spiders (*Linyphia triangularis*) and predacious bugs (*Podisus maculiventris*), respectively. Larvae of the mantids capture few prey before moulting but capture much prey after it (Matsura, unpublished). Since they expend a great deal of energy during moulting, it might be dangerous for them to be exposed to starvation right after moulting. For these reasons, it is reasonable to consider that shortage of prey is an important factor of death for younger larvae of *P. angustipennis* in the field.

Metabolic rates of various kinds of arthropods and their body weights from published data are cited in Table 4. With the aid of Duncan and Klekowski's table (1975), they were converted into values at 20° C, supposed RQ=0.82. From Table 4, it was shown that the metabolic rate of *P. angustipennis* is nearly equivalent to that of spiders, *L. pseudoannulata* or *L. T-insignita*. However *P. angustipennis* has a higher metabolic rate than the spiders for its size, because smaller animals generally have higher metabolic rates than bigger ones as mentioned above.

Anderson (1974) indicated that an inverse relationship between metabolic rate and survival period under starvation conditions is found in the spiders, *L. lenta* and *F. hibernalis*. The mean metabolic rate of *L. lenta* was 64 µl $O_2/g/h$ and they survived 208 days on the average, whereas that of *F. hibernalis* was 30 µl $O_2/g/h$ and they survived 276 days. Miyashita (1968) also reported that nymphs of *L. T-insignita* collected before overwintering survived 45.7 days on the average under starvation conditions. Though it is difficult to discuss generally the difference of tolerance to starvation between mantids and spiders owing to different length of their lifespans, it would seem that *P. angustipennis* is not well adapted to starvation compared with the spiders.

Inoue and Matsura (1975) investigated the foraging strategy of *P. angustipennis* and found that (i) though satiated mantids are stationary, they become more active with rise of hunger level, (ii) when adult mantids are released to the experimental

Table 4. Metabolic rates of various kind of arthropods and their body weights from published data (see text for the convension method)

Oder Species	Stage	Live weight (mg)	Metabolic rate ($mg CO_2/g/h$)	Authors
Araneida				
Lycosa pseudoannulata	adult female	100	0.23	Ito, 1964
L. T-insignita	female final instar larva	10–60	0.38	Miyashita, 1969
L. lenta	adult female	955	0.10	Anderson, 1974
Flistata hibernalis	adult female	530	0.05	Anderson, 1974
Pardosa laura	adult female	5–28	0.60	Nakamura, 1972
Scorpionida				
Centruroides hentzi	adult female	212	0.06	Anderson, 1970
Orthoptera				
Schistocerca gregaria	adult male	2,060	0.57	Hamilton, 1964
Lepidoptera				
Bombyx mori	5th instar larva	1,000	1.36	Hiratsuka, 1917[a]
Leucania separata	6th instar larva	?	1.16	Shibazaki and Ito, 1969
Coleoptera				
Tribolium castaneum	adult	2	1.36	Duncan and Klekowski, 1975
Mantodea				
Paratenodera angustipennis	adult male	630–1,730	0.30	this paper
Paratenodera angustipennis	adult female	1,000–6,250	0.29	this paper

[a] After Ito and Murai (1977)

space in which patches with prey and those with no prey are set, the females stay longer in the patches with prey, whereas in the patches with no prey they begin to move about if their hunger level exceeded a certain threshold. That is, *P. angustipennis* switch their foraging strategy from waiting to searching according to the hunger level.

As shown in Fig. 5, the metabolic rate per unit weight of adult *P. angustipennis* was not maximum at satiation but rather lower than that on the 5th day after satiation. This suggests that though the mantis is inactive and keeps ambushing prey when food remains within its digestive tract, it becomes more active and starts to move about for another hunting site when its digestive tract becomes empty. Thus, the results of experiments on the foraging strategy of *P. angustipennis* conducted by Inoue and Matsura (1975) can be supported from the point of view of metabolism.

In adult mantids it took about five days to digest food completely (Fig. 2). Conversely speaking, some food remained within their digestive tracts for about five days, therefore the period after five days from satiation was true starvation period for them. Decreasing metabolic rate when exposed to starvation is found in many animals such as spiders (Ito 1964, Miyashita 1969, Nakamura 1972a, Anderson 1974), crabs (Roberts 1957, Vernberg 1959), zooplankton (Omori 1970, Ikeda 1974) and fishes (Yamagishi 1967). Tactics that decrease metabolic rate when exposed to starvation seem to be especially adaptive for ambush predators. Because even when they have been ambushing at a site to which few prey come up, they can expect an encounter with prey if they prolong their survival time by reducing the metabolic rate. On the other hand, in the case of predators of searching type, if they reduce the activities when exposed to starvation, their encounters with prey will become rarer. They must always move actively except during satiated periods. Therefore we can infer that ambush predators can survive longer than those of searching type when exposed to starvation.

According to Anderson (1974), reducing rate of energy expenditure under starvation conditions in *F. hibernalis* which builds a web was 40%. On the other hand, smaller values (12–13%) of reducing rate in *P. angustipennis* suggest that they are more active ambush predators. That is, they are not "passive predators" which remain quietly at the ambushing site by means of decreasing the metabolic rate, but have instead adopted a foraging strategy which causes them to abandon the site if prey availability is insufficient.

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