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## Control of the Life Cycle in a Univoltine Antlion, *Myrmeleon bore* (Neuroptera)

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**Abstract** The larvae of *Myrmeleon bore* occur on dunes. Most of them reach the cocoon stage within one year after hatching. Developmental rate varies among individuals depending on prey consumption, but adult emergence is concentrated in mid-summer. We examined the basis of this periodicity by rearing the third (last) instar larvae with various feeding intervals either under uncontrolled temperature and natural daylength ("natural TD") or 25°C and LD 16 : 8 ("controlled TD"). All the larvae at controlled TD formed a cocoon, whereas some larvae at low food levels under natural TD did not form a cocoon and entered a second hibernation. Third instar larvae reared at short-days less than LD 13.5 : 10.5 were suppressed to form a cocoon. Larvae supplied with small amounts of prey formed smaller cocoons late in the season, but the duration of the cocoon stage was shorter due to the increased sand temperature and to a physiological factor related to pupal size. As a result, a longer duration of the third instar was followed by a shorter duration of the cocoon stage. We conclude that synchronous adult emergence in this antlion species is caused by the combination of such factors as feeding rate, photoperiod and temperature.

**Key words:** *Myrmeleon bore*; Neuroptera; antlion; life cycle.

### Introduction

Available food resources for predators fluctuate both temporally and spatially. Not only predators adopting active search tactics but also sit-and-wait predators often change their hunting site in order to increase their capture rate (*e.g.*, TOWNSEND & HILDREW 1980).

A pit-building antlion is a typical sit-and-wait predator. MATSURA (1987 a) found that *Myrmeleon bore* larvae, which mainly occur on seaside dunes, rarely relocate their pits even when they starve owing to reduction in prey capture rate. Therefore prey consumption by *M. bore* larvae in the field possibly varies among individuals. Low feeding rate during the larval stage can result in a small adult and a low developmental velocity (MATSURA *et. al.*, 1975).

Although it might be predicted from these observations that the period of adult emergence should be very long in *M. bore*, the emergence period is, in fact, rather short, from early July to mid-August (MATSURA, 1989). If adult emergence were more widely dispersed due to variation in the larval developmental rate, mating success would decrease because adult survival in *M. bore* is not very long (less than two months; MATSURA, unpublished observation). Antlions require a means of synchronizing adult emergence. Although there are a few excellent

papers concerning control of the life history in antlions (FURUNISHI & MASAKI, 1981, 1983), they did not deal with the synchronization of adult emergence. In this paper, we first clarify the life cycle of *M. bore* larvae, and then show that (1) prey consumption influences development rate, (2) nevertheless, adult emergence is synchronized and (3) there is a mechanism ensuring synchronous adult emergence.

## Materials and Methods

### 1. Field survey for *M. bore* larvae

To clarify the voltinism and the life history of *M. bore* larvae, we made two kinds of field survey. One, aimed at revealing seasonal changes in frequency of each larval instar, was carried out at a seaside dune in Tango-Kitsu, about 100 km northwest of Kyoto City. Here, we established a research site (10 m × 10 m) in a sandy area containing sparse patches of plants such as *Artemisia capillaris* THUNB. and *Oenothera Lamarckiana* SER. We picked up antlions from the bottom of pits, and counted larvae of each instar once a month from April to November in 1986 and 1987.

The other survey was made at a sandy area in an abandoned filtration plant at Fushimi-ku in Kyoto City (MATSURA, 1986). All pits of second and third instar larvae found in the research site (10 m × 15 m) were counted once a week from May to November in 1981. We marked larvae on the dorsal side of abdomen with two different colors of feltpens when they were first caught, and then released them. All the larvae caught on the same day were marked with the same combination of colors. These surveys were carried out on a fine and/or cloudy day when the sand was dry.

### 2. Laboratory experiments

First instar larvae of *M. bore* after hibernation were collected from the seaside dune at Tango-Kitsu on 25 April 1986. They were reared in the laboratory under natural temperature and daylength conditions. We fed etherized adult *Drosophila melanogaster* to the first instar larvae and chironomid larvae (mean live weight ± S.D.,  $22.1 \pm 3.9$  mg) to the second instar larvae *ad libitum*. We could estimate their hunger levels from the shape of pits, because satiated antlions did not build a pit.

Newly moulted third instar larvae were kept under constant temperature ( $25 \pm 1^\circ\text{C}$ ) and daylength (LD 16 : 8). We separated them into seven groups (Feeding level I to VII) and fed one chironomid larva to each antlion at a constant interval from 1 to 20 days (see Table 1). Each larva was reared in a cylindrical container (9 cm × 4.5 cm) half filled with sand.

We again collected the first instar larvae in the same habitat in April of 1988, and reared them till the second moult under the similar conditions to those in 1986. Newly moulted third instar larvae were transferred to a hut and were kept

near the netted windows, which were left open. A chironomid larva was given to each third instar larva at the same intervals as those in 1986.

To examine the photoperiodic response in development of *M. bore* larvae, first instar larvae after hibernation were collected from the dune at Tango-Kitsu on April 21, 1989. On the next day, they were placed in 6 light-proof wooden cabinets with a 6 W fluorescent tube wired to a time switch. We put 20 first instar larvae in each cabinet, where each larva was kept separately in a small tube (2.5 cm × 4 cm) half filled with sand. Six different photoperiods were used, *i.e.*, LD 12 : 12, 13 : 11, 13.5 : 10.5, 14 : 10, 15 : 9, 16 : 8. First instar larvae were fed *ad*

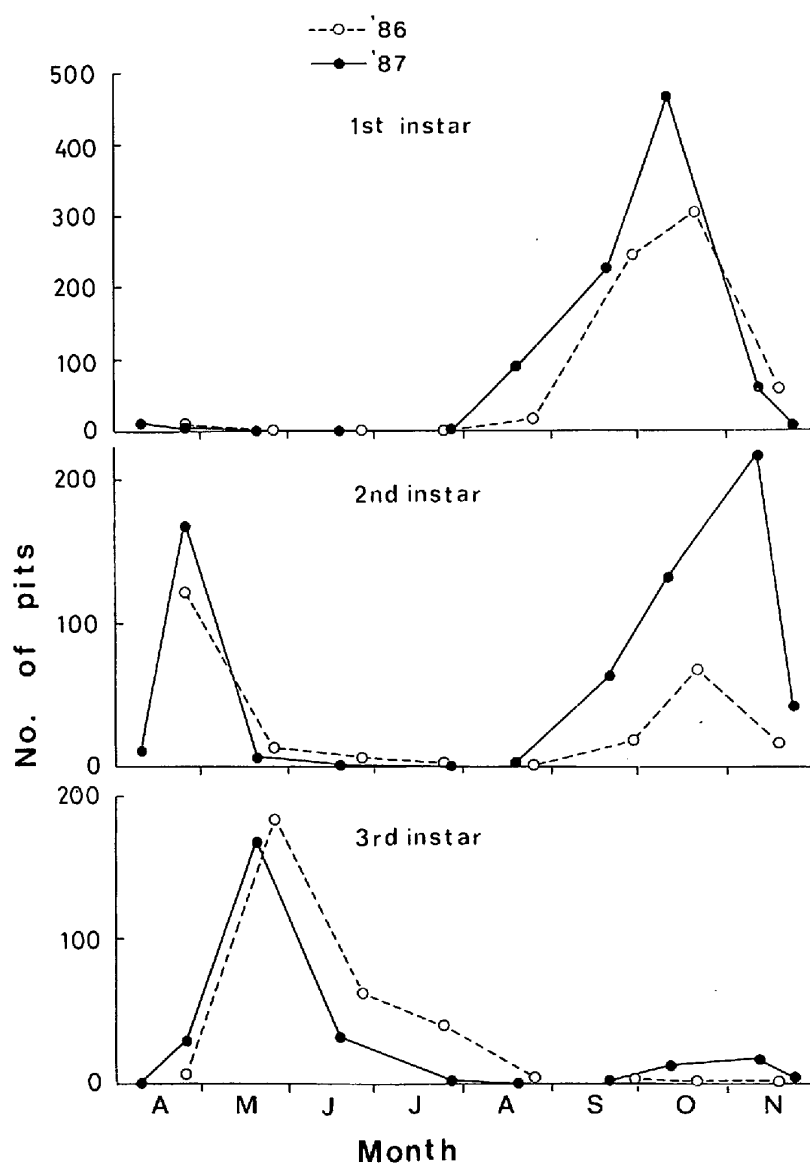


Fig. 1. Seasonal changes in number of pits observed at the seaside dune in Tango-Kitsu.

*libitum* adults of *D. melanogaster*, and second and third instar larvae were fed one chironomid every day.

## Results

### 1. Life history of *M. bore* larvae

There was a common tendency for the seasonal changes in the number of pits constructed by each instar larva in 1986 and 1987 (Fig. 1). The peaks of the first instar larvae in October were probably caused by hatching of eggs. Although a small proportion of the first instar larvae grew to the third instar before the first hibernation, *M. bore* larvae at Tango-Kitsu generally seemed to overwinter as first or second instars. Most larvae that had overwintered reached the third-instar before early summer. Since few larvae were found at the research site in mid-summer, most larvae probably pupated at this season. Therefore, we conclude that this species is basically univoltine.

This conclusion was also confirmed from the results of mark-and-recapture ex-

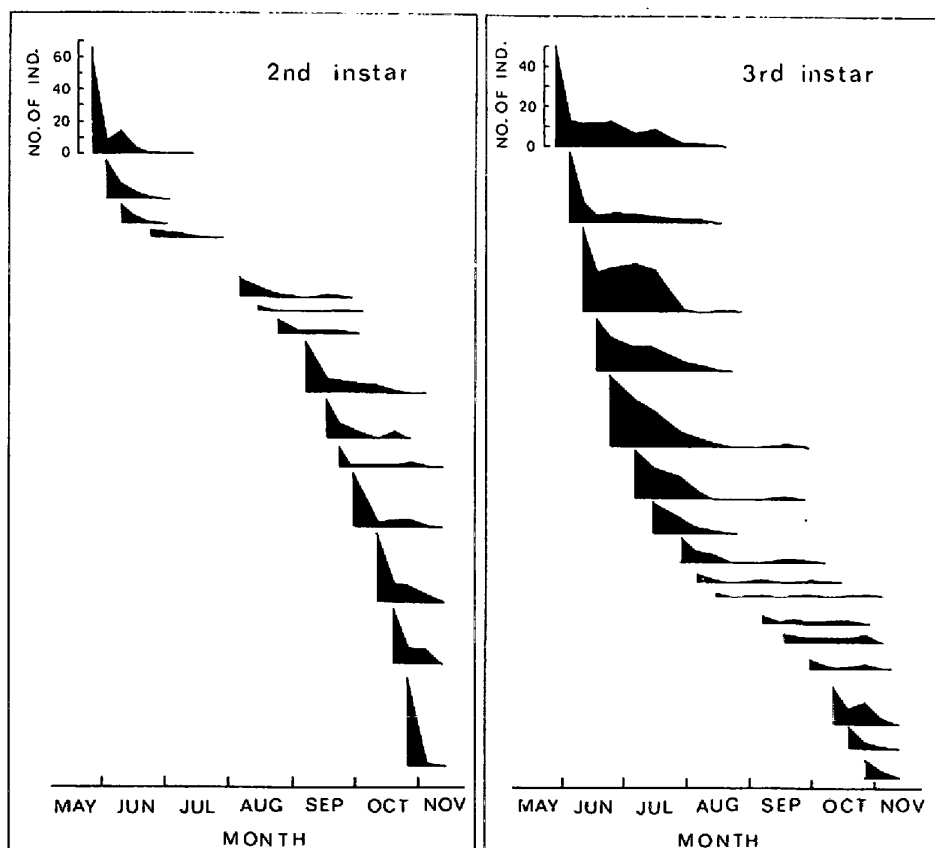


Fig. 2. Decrease in number of marked antlions in the sandy area of an abandoned filtration plant. The left end of each polygon indicates the day of marking.

periments (Fig. 2). One hundred and nine second instar larvae had been marked during the period in May and June and they were never found after mid-July because of moulting. The total number of third instar larvae marked before mid-August was 247, of which only 5 were recaptured on September 17. Most third instar larvae perhaps formed a cocoon in the sand before midsummer.

## 2. Influence of prey consumption on growth and development in *M. bore* larvae

Figure 3 shows a relationship between the amount of prey given per day and the period from the second ecdysis to cocoon formation (we call this period the "duration of the third instar" for convenience hereafter). Third instar larvae after hibernation were excluded from the calculation. There was a slight difference in the duration of the third instar between the larvae kept under controlled temperature and daylength (LD 16 : 8) conditions (controlled TD) and those under uncontrolled temperature and natural daylength (natural TD), but they showed similar tendencies. The duration of the third instar decreased with increase in daily prey consumption, and the rate of this reduction was greater at the lower feeding level. As a result, the third instar duration was more than two times as long at the lowest

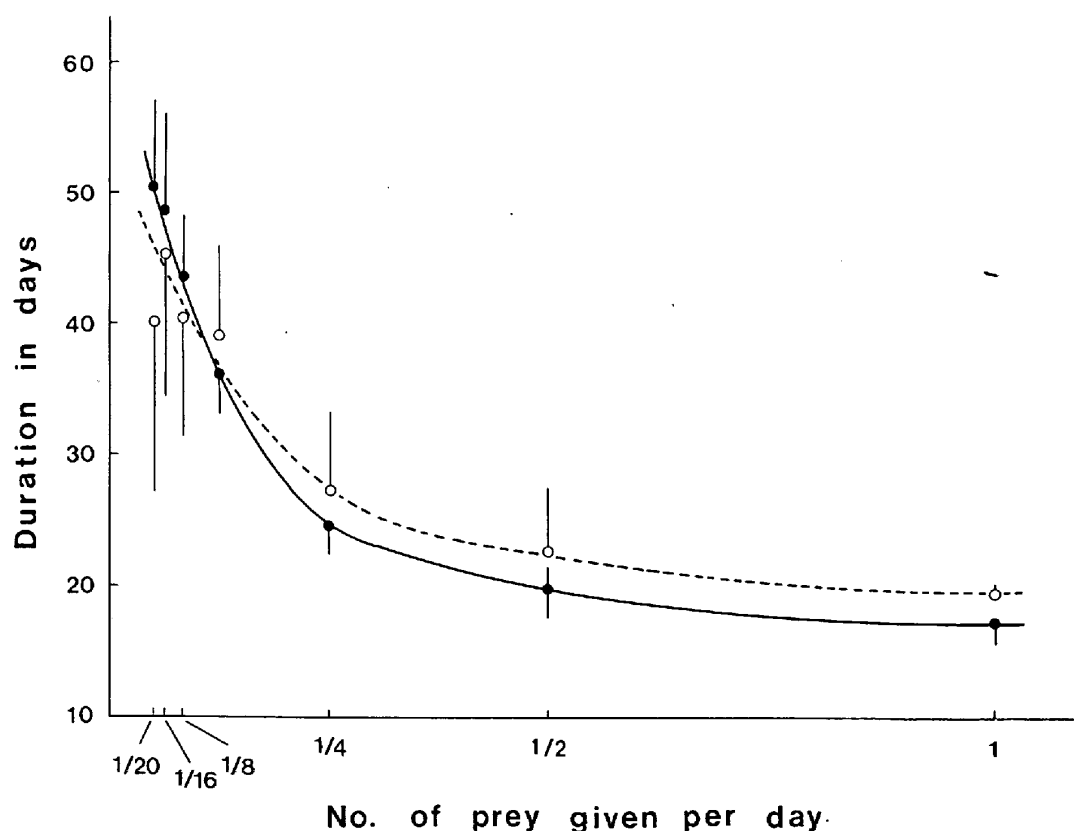


Fig. 3. Relationship between number of prey given per day and duration of the third instar. Solid circles show the duration at 25°C and LD 16 : 8 and open circles at natural TD.

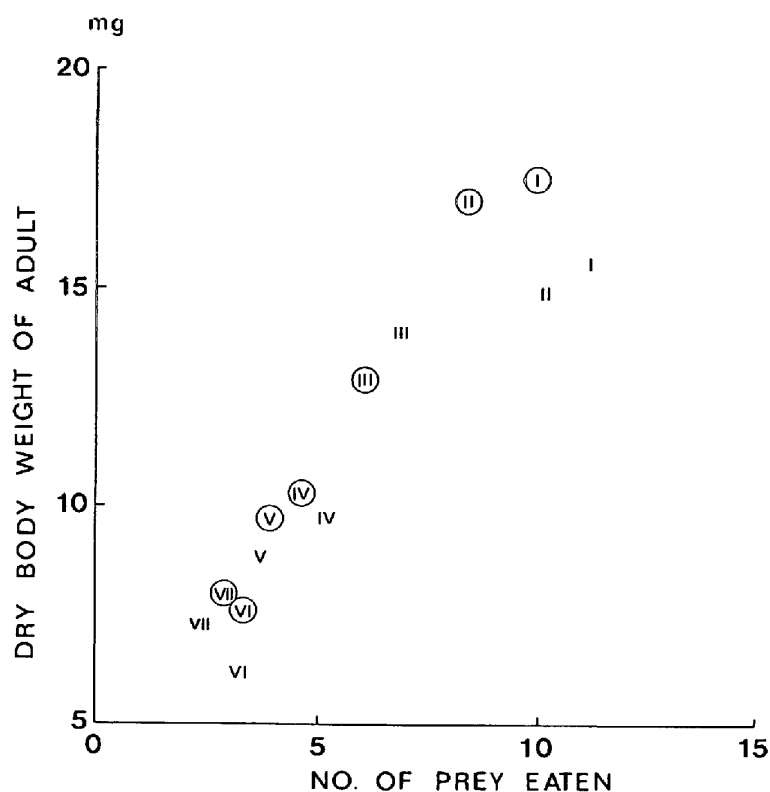


Fig. 4. Relationship between total number of prey eaten during the third instar and adult body size in *M. bore*. Roman numerals enclosed by a circle show the data at 25°C and LD 16 : 8, and those without a circle at natural TD.

feeding rate as that at the highest.

Larvae reared at the shorter feeding interval ate more prey during the third instar and became larger adults (Fig. 4). There was no significant difference in the regression coefficient of adult body weight on the number of prey eaten between the controlled TD and natural TD groups ( $P > 0.05$ ,  $t$ -test).

A difference in larval development between the controlled TD and natural TD groups was observed in the cocoon formation rate, the ratio of the number of larvae forming a cocoon to the number of larvae used (Table 1). All the larvae from feeding level I to VII at the controlled TD formed a cocoon, whereas some larvae fed at longer intervals at the natural TD did not form a cocoon and hibernated at the third instar. Nearly half of the larvae at feeding level VII under natural TD did not form a cocoon until next June after hibernation. The last cocoon formation at feeding level VII in natural TD was observed on 21 July 1988. The average number ( $\pm$ S.D.) of prey eaten up to this date was  $2.4 \pm 0.5$  for the larvae that formed a cocoon before hibernation and  $2.0 \pm 0.0$  for those that did not do so and the difference was not significant ( $P > 0.2$ ,  $t$ -test).

Table 1. Cocoon formation rate in antlion larvae reared under different conditions.

Feeding interval (days)	Controlled TD			Natural TD		
	No. examined	No. of cocoons	% cocoon formation	No. examined	No. of cocoons	% cocoon formation
every day	12	12	100	10	10	100
2	12	12	100	9	9	100
4	11	11	100	9	9	100
8	12	12	100	9	9	100
12	12	12	100	10	9	90
16	10	10	100	10	9	90
20	12	12	100	9	5	56

### 3. Factors governing synchronous adult emergence

Another marked difference between under the controlled TD and natural TD groups was found in the seasonal change of cocoon formation and adult emergence (Fig. 5). Some larvae kept at controlled TD formed a cocoon in August, but none kept at the natural TD formed a cocoon from August onwards.

Synchronization of adult emergence was more marked at the natural TD (Fig. 5, bottom right). Adults emerged from mid-July to mid-September at controlled

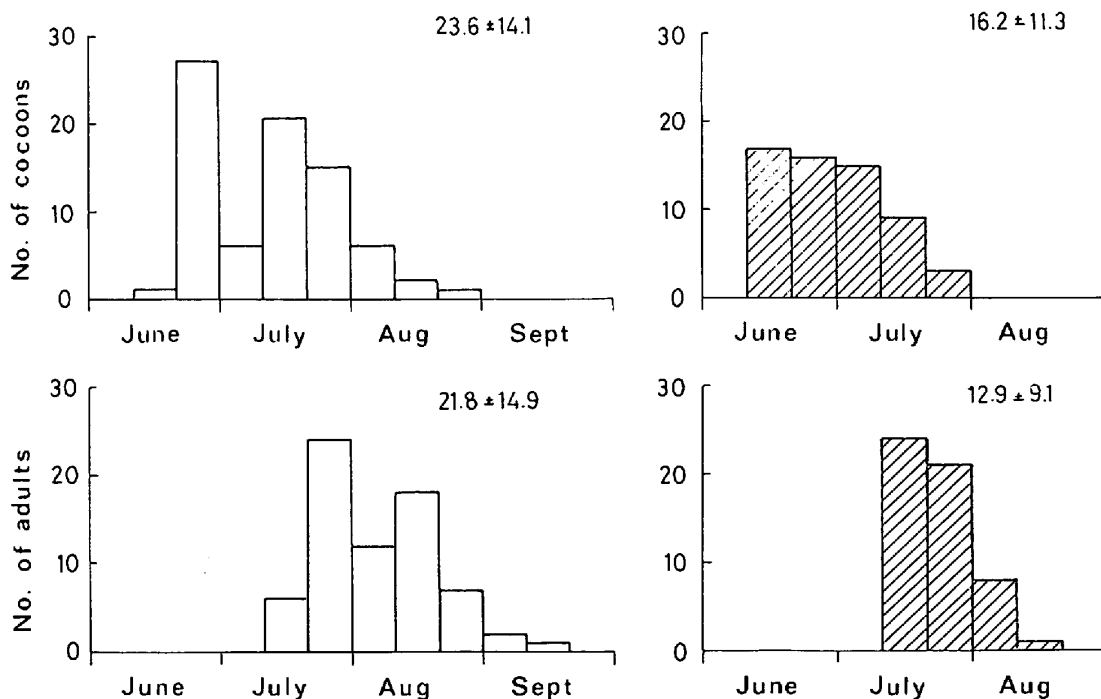


Fig. 5. Seasonal changes in number of individuals forming the cocoon (upper) and in number of emerging adults (lower). Open columns show the results obtained at controlled TD and striped columns at natural TD.

TD, whereas most adults at natural TD emerged from mid-July to early August. To elucidate the mechanism synchronizing adult emergence at natural TD, we examined the relationship between the durations of the third instar and of cocoon stage (Fig. 6). Although there was a negative correlation between them under both controlled TD and natural TD, the regression coefficient in controlled TD was clearly smaller than that in natural TD ( $P < 0.01$ ,  $t$ -test). Since cocoons of *M. bore* normally occur at a few centimeters below the sand surface, day length should be excluded from the factors responsible for synchronous adult emergence. Therefore we analyzed the influence of another environmental factor, temperature, upon the duration of the cocoon. Average room temperature gradually in-

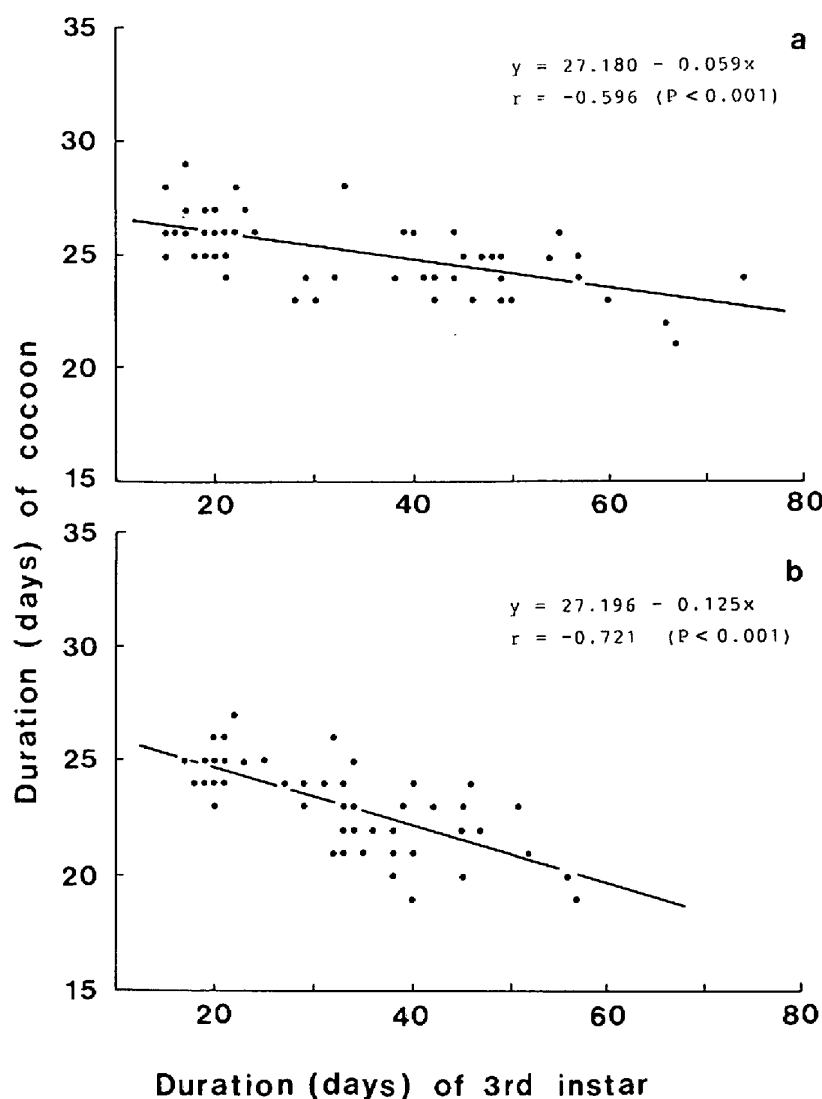


Fig. 6. Relationship between the duration of cocoon stage and that of the third instar in *M. bore*. a, controlled TD; b, natural TD.



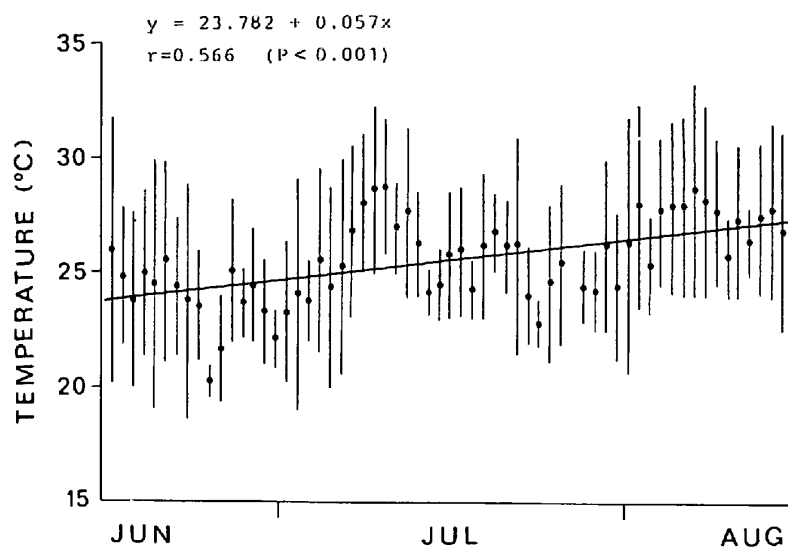


Fig. 7. Seasonal change in the daily mean room temperature during the period from 15 June to 15 August. Vertical bar shows range.

creased with the progress of season during the period from 15 June when the first cocoon was formed to 15 August when the last adult emerged (Fig. 7). Accordingly, the later the date of cocoon formation, the shorter the duration of cocoon stage (Fig. 8).

The duration of the cocoon stage was not fixed, even at constant temperature

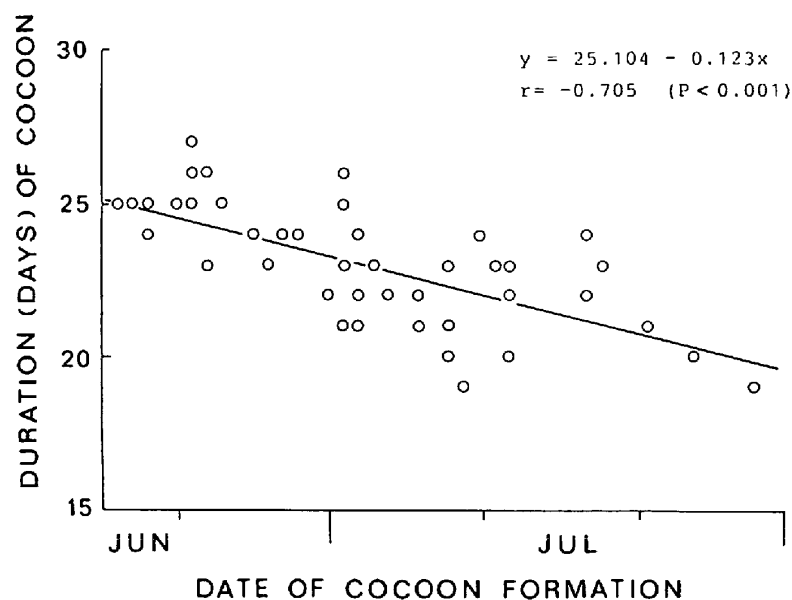


Fig. 8. Relationship between the date of cocoon formation and the duration of cocoon stage in *M. bore* at natural TD.

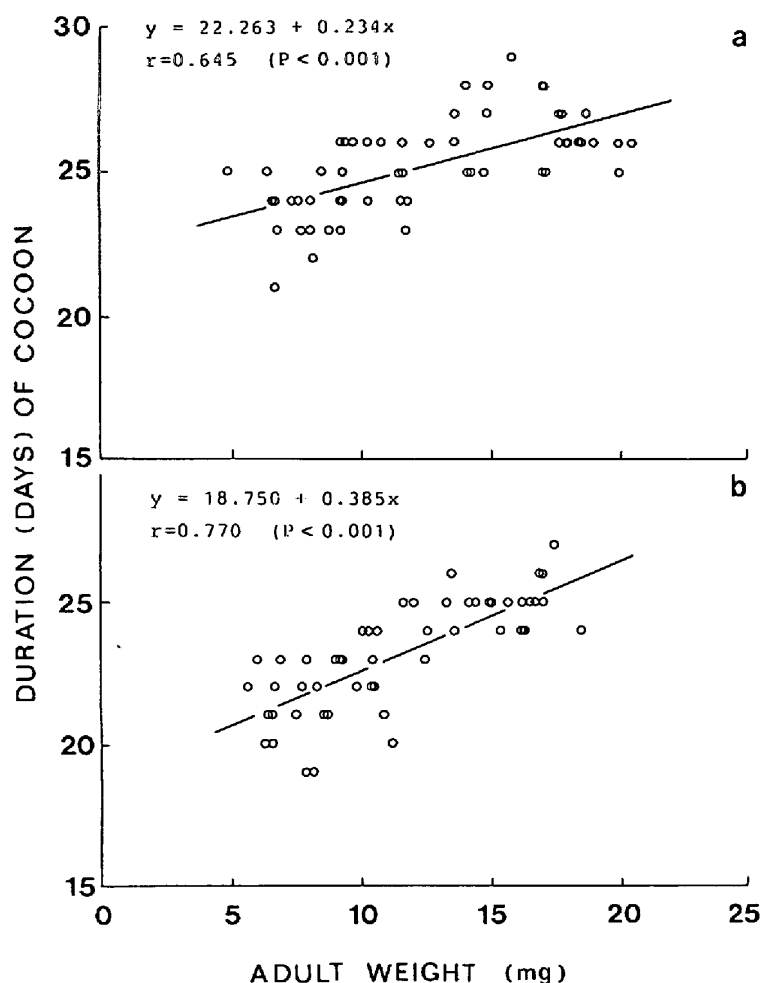


Fig. 9. Relationship between dry body weight of adult and the cocoon duration in *M. bore* reared at controlled TD (a) and natural TD (b).

(see Fig. 6 a). It became slightly shorter as the duration of the third instar increased. The antlions with longer duration of the third instar in Fig. 6 were possibly small sized ones due to the small amount of prey consumption (see Figs. 3 and 4). To examine the influence of body size on development rate, we computed the relationship between the duration of the cocoon stage and adult body weight (Fig. 9). Significant positive correlations were found both in controlled TD (Fig. 9 a) and in natural TD (Fig. 9 b).

#### 4. Photoperiodic response in the development of *M. bore*

Average durations of the second instar, third instar and cocoon stages at each daylength are presented in Table 2. There was no significant effect of daylength on the duration of second instar larvae ( $F = 0.710$ ,  $P > 0.25$ ). Although the difference in the duration of the cocoon stage among different daylength groups was signifi-

Table 2. Effect of photoperiod on the durations of larval and cocoon stages in *M. bore* at 25°C.

Stage	Photoperiod	No. examined	Durations (days) mean $\pm$ S.D.	Range (days)
Second instar	LD 12 : 12	15	15.5 $\pm$ 0.92	14–17
	LD 13 : 11	14	14.9 $\pm$ 1.49	13–17
	LD 13.5 : 10.5	15	15.3 $\pm$ 1.10	13–17
	LD 14 : 10	15	15.1 $\pm$ 1.85	13–20
	LD 15 : 9	14	15.3 $\pm$ 1.27	13–17
	LD 16 : 8	15	15.8 $\pm$ 1.52	14–20
Third instar	LD 12 : 12	14	32.9 $\pm$ 19.96	15–76
	LD 13 : 11	14	26.2 $\pm$ 13.49	16–67
	LD 13.5 : 10.5	15	29.9 $\pm$ 10.40	17–48
	LD 14 : 10	15	20.7 $\pm$ 4.34	16–32
	LD 15 : 9	14	18.9 $\pm$ 1.83	17–22
	LD 16 : 8	15	17.5 $\pm$ 2.72	13–23
Cocoon	LD 12 : 12	14	26.0 $\pm$ 0.96	25–28
	LD 13 : 11	13	25.8 $\pm$ 1.57	23–28
	LD 13.5 : 10.5	14	25.9 $\pm$ 1.14	25–29
	LD 14 : 10	14	24.8 $\pm$ 1.25	23–27
	LD 15 : 9	13	25.5 $\pm$ 0.97	24–27
	LD 16 : 8	15	25.2 $\pm$ 0.86	23–27

Table 3. Statistical test for the difference between mean durations of the third instar at various photoperiods.

Photoperiod	LD 13 : 11	LD 13.5 : 10.5	LD 14 : 10	LD 15 : 9	LD 16 : 8
LD 12 : 12	NS	NS	*	*	**
LD 13 : 11		NS	NS	*	*
LD 13.5 : 10.5			**	***	***
LD 14 : 10				NS	*
LD 15 : 9					NS

NS, non-significant; \*,  $0.01 < P < 0.05$ ; \*\*,  $0.001 < P < 0.01$ ; \*\*\*,  $P < 0.001$ .

cant ( $F=2.447$ ,  $0.01 < P < 0.05$ ), it was small. A clear effect of photoperiod was exerted on the third instar larvae ( $F=4.859$ ,  $P < 0.001$ ). They significantly delayed cocoon formation at daylengths less than 13.5 hours (see Tables 2 and 3).

### Discussion

The fact that *M. bore* in natural habitats has mostly a univoltine life cycle suggests that food supply for the larvae is rich. Their development would otherwise be retarded by food shortage (Fig. 3). MATSURA (1986) estimated the feeding rate of the third instar larvae of *M. bore* at the same site as the field survey by mark-and-recapture was conducted in this study, and reported that they captured daily

about one prey of a mean body length of 4.4 mm. That *M. bore* has the shortest life cycle among Japanese antlions may be due to its small body size as FURUNISHI and MASAKI (1982) described. GRIFFITHS (1985) also noted that smaller species of antlion larvae in Tanzania complete their life cycle within a single dry season while larger species need two dry seasons to reach the full larval size.

Although the date of cocoon formation was remarkably variable among *M. bore* larvae because of the difference in prey consumption, adult emergence was synchronized under natural daylength and uncontrolled room temperature (Fig. 5). We pointed out two reasons for this synchronization; one is temperature and the other is a physiological factor related with body size. A smaller cocoon formed late in the season due to food shortage must experience high temperatures in midsummer. Moreover, there is a tendency for smaller cocoons to develop faster, and the adult size correlates with cocoon size (Fig. 9 in this paper and GRIFFITHS, 1985). On the other hand, a larger cocoon formed early in the season by consuming enough prey would have a longer cocoon stage owing to lower temperatures and a lower developmental velocity. As a result, the adult emergence will be more synchronized under the conditions of natural temperature and daylength, even though the prey consumption varies between individuals.

Larvae that consumed only a small amount of prey would have to enter a second hibernation. It is evident from this study that the photoperiod during the third instar is one of the important factors determining whether or not they form a cocoon without entering hibernation again. FURUNISHI and MASAKI (1981) examined the influence of daylength, temperature and food consumption on the development of '*Myrmeleon formicarius*' larva, and found that more than half of the larvae did not form a cocoon at a photoperiod less than LD 15 : 9. Their species is not *M. formicarius* but *M. bore*, because their identification was based on BABA (1953) whose classification should be revised (see MATSURA, 1987 b). In our experiments all third instar larvae at short-days of LD 12 : 12 or 13 : 11 formed a cocoon, though the period of the third instar was prolonged. This may be due to the difference in experimental conditions. We reared each antlion at 25°C and fed one chironomid larva every day, FURUNISHI and MASAKI (1981) reared at 21°C and gave one larva of *Plodia interpunctella* every 14 days. Therefore not only photoperiod but also feeding rate and temperature are important factors governing cocoon formation in *M. bore*.

It may be necessary for an antlion to attain a certain body weight in order to form a cocoon. GRIFFITHS (1985) reported that the large sized antlion, *Macroleon quinquemaculatus* in Tanzania, did not pupate unless it reached about 100 mg. He suggested that the larva requires a minimum level of fat in order to survive the pupal stage. Since most species of adult antlions are predacious (MATSURA, 1989; STANGE, 1970), the fat stored during the larval stage must be consumed during not only in the pupal but also early adult stage. The body weight of third instar larva of *M. bore* must reach the threshold of cocoon formation before daylength

becomes shorter than 14 hours. Otherwise it cannot form a cocoon before a second hibernation because both the shortening daylength and lowering temperature with the progress of season would inhibit cocoon formation.

In summary, the developmental rate of the antlion larva varies among individuals owing to a variation in feeding rate, but it is controlled in nature by environmental factors such as daylength and temperature. Moreover, after cocoon formation, it is controlled both by temperature and by the physiological effect of pupal body size. These mechanisms would ensure synchronous adult emergence in natural habitats.

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