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ECOLOGICAL RESEARCH

The Feeding Ecology of the Pit-making Ant Lion Larva, *Myrmeleon bore*: Feeding Rate and Species Composition of Prey in a Habitat

Toshiaki MATSURA, *Department of Biology, Kyoto Kyoiku University, Fushimi-ku, Kyoto, 612 Japan*

Abstract

The prey species composition and feeding rate of the pit-making ant lion larva, *Myrmeleon bore* Tjeder, which inhabits open sandy areas, were examined. Not less than 30 prey species, most of which were ants, were collected during a research period of 1.5 years. First instar larvae most often (81.1%) captured ants. Although 3rd instar larvae captured larger-sized prey than individuals of any other instar, they also captured small prey. The feeding rate of 3rd instar larvae was estimated by using the frequency of observed predation (FOP; (no. of ant lions handling a prey)/(total no. of pits observed)), the prey-handling time and the rhythm of daily foraging activity. FOP of *M. bore* larvae was constant on the whole from spring to autumn. It was estimated that each captured 1.25 prey per day on average during this period. This estimate, however, was the feeding rate for days on which there was no rain. Assuming that the larvae cannot capture prey due to pit destruction when there is more than 10 mm of rainfall per day, the figure was reduced to 1.03 prey/day. The estimated feeding rate was evaluated with reference to larval foraging behavior.

Key words: Ant lion; Feeding rate; Foraging behavior; Predation; Prey species.

Introduction

Most arthropod predators are generalists which feed on various kinds of prey items (Townsend and Hildrew, 1979; Nentwig, 1980; Polis, 1980), because the available biomass of one prey species is rarely high and constant enough to maintain a predator population. It is significant for understanding the ecological characteristics of predators, e.g. foraging strategy or numerical response, to investigate the feeding rate of predator in nature and the types of prey species. To date, however, investigations of this kind have been rather few, and precise feeding rates of predators in natural habitats have rarely been estimated yet except for a few species (Lawton, 1970; Kiritani et al., 1972; Hildrew and Townsend, 1982; Matsura and Nagai, 1983).

Species composition of prey and prey consumption for the larvae of a caddisfly, *Plectrocnemia conspersa* were estimated from the gut contents (Hildrew and Townsend, 1982), and those for the nymphs of a dragonfly, *Pyrrhosoma nymphula* were estimated by using fecal remains. Even with these predators we cannot easily observe them capturing prey in their natural habitats. The advantage of studying pit-making ant lion larvae is that their feeding behavior can be directly observed because of their longer prey-handling time and the ease of finding their pits.

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Myrmeleon bore Tjeder which was used in this study is one of the types of pit-making ant lion larvae inhabiting sand dunes, and is a common species in Japan (Kuwayama, 1959). It is a univoltine species and overwinters in all its larval instar stages (Matsura, in preparation). In this study, I first determined the species composition of prey items and showed the seasonal change of frequency of observed predation. Then using these data, the feeding rate of *M. bore* larvae in their natural habitat was estimated.

Research Area and Methods

The research site was a sandy area of waste ground in an abandoned filtration plant at Fushimi-ku in Kyoto City. It contained five empty water-purification tanks, the bottoms of which had been deeply filled with sand. Each tank was partitioned by concrete walls 30 cm wide and 2 m high. Sparse patches of plant species including a mugwort (*Artemisia vulgaris* L.) and a Japanese knotweed (*Polygonum cuspidatum* Sieb. et Zucc.) grew along the walls, but no vegetation covered the central parts of the sandy areas. Ant lion larvae lived only in the peripheral regions of the sandy areas and around the patches of grass.

The research area was surrounded by a bamboo thicket (at the south end), a forest of Japanese red pine (at the west end) and grassy plots composed of *Solidago altissima* L. (at the north and the east ends). Adults of *M. bore* probably rested in the forested areas during the day.

In order to examine the feeding rate and species composition of prey taken by *M. bore* larvae, I observed pits of the ant lion larvae once a week from mid-June, 1982 to the end of December, 1983. The observation time during the day was about 10:00–12:00 in 1982 and about 15:00–17:00 in 1983. No marked difference in behavior of ant lion larvae and their prey species composition was noted between the two observation periods. For each survey, ant lion larvae concealing themselves under pits were picked up and examined to determine their instar. If a larva had been handling a prey, the corpse of the prey was collected in order to identify it and measure its body length.

The feeding rates of *M. bore* larvae were estimated from the frequency of observed predation (abbreviated as FOP), which was the ratio of the number of ant lion larvae handling a prey to the total number of larvae observed. FOP depends on the time taken by an ant lion larva in handling its prey and the daily rhythms of its hunting activity. In order to determine the handling time (the time between prey capture and the ejection of its carcass by the ant lion larva) for various types of prey, those were measured in the laboratory using 3rd instar larvae. Six types of prey (5 species) were used, i.e. an aphid (*Macrosiphum ibarae* Matsumura), ants (*Tetramorium caespitum* Linnaeus and *Formica japonica* Motschulsky), larvae of a fly (*Phaenicia serivata* Meigen) and large- and small-sized woodlice (*Armadillidium vulgare* Latreille). The experiment was conducted at 25±1°C and 40–60% RH.

The daily rhythm of hunting activity of *M. bore* larvae was examined on a sandy beach at Tango-Kitsu, about 110 km north-west of Fushimi-ku in Kyoto City. A 35-mm camera (Minolta X-700), with an automatic shutter-release mechanism timed to operate at regular given intervals, was placed at a height of about 40 cm above the pits. The interval between each photograph was 20 mins. This examination was conducted once a month from June to September, 1982 (June, 60 hours; July and August, 84 hours; September, 36 hours). Prey types and feeding times were determined from the resulting projected transparencies. Since the time of each photograph had been recorded on the film, it was possible to detect the time of day of the predation.

Larval pits were observed during the day (10:00–15:00) and the night (21:00–23:00) on the sandy beach of Tango-Kitsu in order to determine feeding patterns. These observations were made 2–4 times per month from June to September in 1982.

Results

Species composition of prey

Over the course of the 1.5-year study period, 483 prey corpses were collected and identified as to class (Table 1). At least 30 species of prey were collected and about 70% of prey corpses were ants (98% of the number of individuals among the Hymenoptera in Table 1 were ants). The ratio of the number of ants to the total number of prey was highest for the 1st instar larvae (about 80%).

The second most common prey type, for all instar stages, was hemipterous insects. These were composed mainly of apterous aphids and true bugs. Simpson's (1949) indices of diversity for the ant lion's prey were 1.49, 1.97 and 2.03 for the 1st, the 2nd and the 3rd instar larvae, respectively. Thus the diet of 2nd and 3rd instar larvae was more varied than that of 1st instar larvae. Only one ant lion larva was found among the prey collected, suggesting that cannibalism in *M. bore* larvae in the field is rare.

Most prey of *M. bore* larvae were surface-dwelling arthropods, among which ants were most important. Table 2 shows the species names and numbers of ants captured by each

Table 1. Species composition of prey captured by *M. bore* larvae.

Class	Order	Instar of larvae							
		1st		2nd		3rd		Total	
		No. of ind.	%	No. of ind.	%	No. of ind.	%	No. of ind.	%
Insecta	Hymenoptera	98	81.0	150	68.8	99	68.8	347	71.8
	Hemiptera	14	11.6	39	17.9	15	10.4	68	14.1
	Coleoptera	5	4.1	7	3.2	11	7.6	23	4.8
	Diptera	1	0.8	6	2.8	0	—	7	1.4
	Lepidoptera	0	—	4	1.8	3	2.1	7	1.4
	Orthoptera	0	—	1	0.5	3	2.1	4	0.8
	Blataria	1	0.8	0	—	1	0.7	2	0.4
	Dermaptera	0	—	0	—	2	1.4	2	0.4
	Neuroptera	0	—	1	0.5	0	—	1	0.2
Arachnoidea	Araneida	1	0.8	4	1.8	6	4.2	11	2.3
	Acarina	0	—	1	0.5	0	—	1	0.2
Crustacea	Isopoda	1	0.8	2	0.9	4	2.8	7	1.4
Chilopoda	Lithobiomorpha	0	—	3	1.4	0	—	3	0.6
	Total	121	100.0	218	100.0	144	100.0	483	100.0

Table 2. Species of ants captured by each larval instar of *M. bore* and their frequencies.

Name	Instar of larvae							
	1st		2nd		3rd		Total	
	No. of ants	%	No. of ants	%	No. of ants	%	No. of ants	%
Tetramorium caespitum	93	94.9	126	86.9	59	60.8	278	81.8
Formica japonica	0	—	6	4.1	21	21.6	27	7.9
Pristomyrmex pungens	3	3.1	9	6.2	10	10.3	22	6.5
Camponotus japonicus	0	—	1	0.7	6	6.2	7	2.1
Iridomyrmex itoi	2	2.0	3	2.1	1	1.0	6	1.8
Total	98	100.0	145	100.0	97	100.0	340	100.0

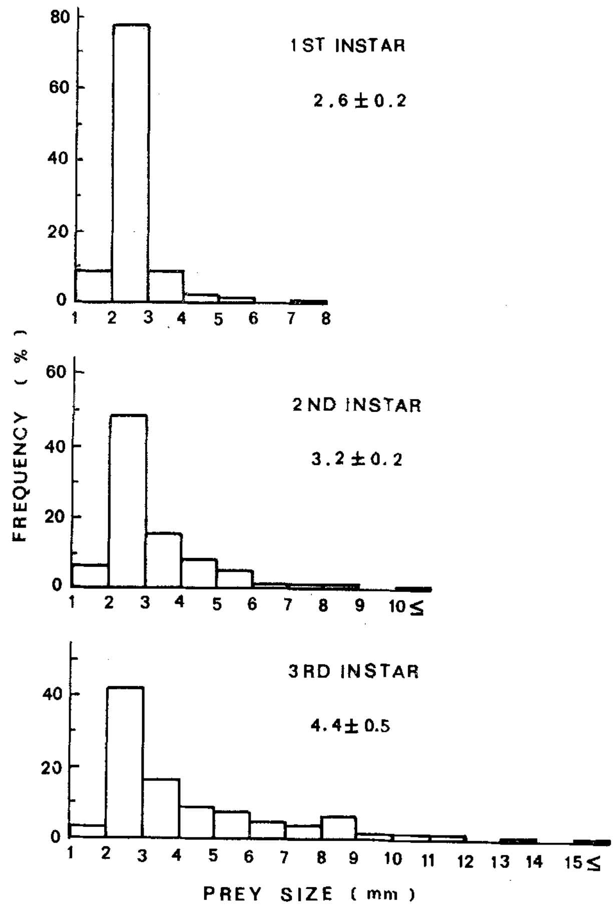

Fig. 1. Frequency distributions of body length of prey captured by ant lion larvae. Numerals in the figure indicate mean ± 95% C.L.

larval instar. For the 1st instar, a small ant, *Tetramorium caespitum* was the most frequently captured. Investigation by a pitfall trap method revealed that *T. caespitum* was the most dominant species among the surface-dwelling arthropods in the research area (Matsura and Yasuda, unpublished). Although the 2nd and 3rd instar ant lion larvae also captured this species most frequently, 3rd instar larvae captured a large proportion of a medium-sized ant, *Formica japonica* (length about 5 mm) and a large-sized ant, *Camponotus japonicus* (length about 8 mm).

The average body length of captured prey was smallest for the 1st instars and largest for the 3rd instars (Fig. 1). Prey of 2–3 mm body length were captured with the highest frequency by all larvae. *T. caespitum*, the most frequently captured prey species, was included within this range. The range of prey size captured by 3rd instar larvae was larger than for the other instars, implying no strong preference for a particular size of prey.

Estimation of feeding rate

If the daily feeding activity of ant lion larvae is constant, the probability (p) of finding an ant lion feeding at any time is

$$p = C \times T/24 \qquad (1)$$

where C is the number of prey eaten per day per ant lion larva and T is the average handling time (hours) per prey. Since

$$p = n/N = \mathrm{FOP} \qquad (2)$$

where n, N and FOP are the number of ant lions handling prey, the total number of pits observed and the frequency of observed predation (see Research Area and Methods), respectively, from formulas (1) and (2) we obtain

$$C = 24 \times \mathrm{FOP}/T \qquad (3)$$

If a daily feeding activity is not constant, we must calculate a ratio (r) of the frequency of observed predation at time t (FOP(t)) to the average frequency of observed predation per day (FOP(mean)). Namely,

$$r = \mathrm{FOP(t)}/\mathrm{FOP\ (mean)} \qquad (4)$$

Thus,

$$\mathrm{FOP(mean)} = \mathrm{FOP(t)}/r \qquad (5)$$

Substituting FOP(mean) for FOP in formula (3), we obtain

$$C = (24 \times \mathrm{FOP(t)})/(T \times r) \qquad (6)$$

Therefore it is only necessary to know the handling time per prey, the frequency of observed predation and the daily pattern of feeding activity to estimate the feeding rate per day per ant lion larva.

This estimation method is basically equivalent to "the sight-count method" by Kiritani et al. (1972), who devised it to evaluate predation by spiders on the green rice leafhopper. They estimated the number (n) of prey devoured by spiders by using the following formula;

$$n = (F \times C)/P \qquad (7)$$

where F is the observed frequency of feeding at a standard time, P is the probability of observing feeding given as the ratio of handling time in hours divided by 24, and C is the diurnal rhythm of feeding to give the proportion of feeding. From formula (7), the number of prey devoured by an individual spider is

$$n/N = (F \times C)/(N \times P) = (F \times 24)/(N \times T) \times C \qquad (8)$$

where N is the total number of spiders and T is the prey-handling time, and C and F/N are equivalent to $1/r$ and FOP(t), respectively.

As ant lion larvae are generalists, their eating time changes according to prey size and prey species. Table 3 shows handling times by 3rd instar larvae to which various types of prey were given. The range of average body length of prey items used in the experiment was 2.9–

Table 3. Handling times taken by 3rd instar ant lion larvae when given various types of prey.

Prey species	No. of individuals examined	Body length of prey (mm)*	Handling time (min)*	Range (min)
Ant (*Tetramorium caespitum*)	11	2.9±0.2	34.3±16.2	10–53
do. (*Formica japonica*)	14	4.9±0.3	52.9±9.5	36–67
Aphid (*Macrosiphum ibarae*)	15	2.8±0.3	25.6±8.3	14–41
Larva of fly (*Phaenicia sericata*)	6	11.0±0.7	353.2±128.4	238–593
Large-sized isopod (*Armadillidium vulgare*)	19	10.7±0.9	234.6±79.6	148–472
Small-sized isopod (do.)	7	8.1±0.1	148.4±47.5	90–229

*mean±S.D.

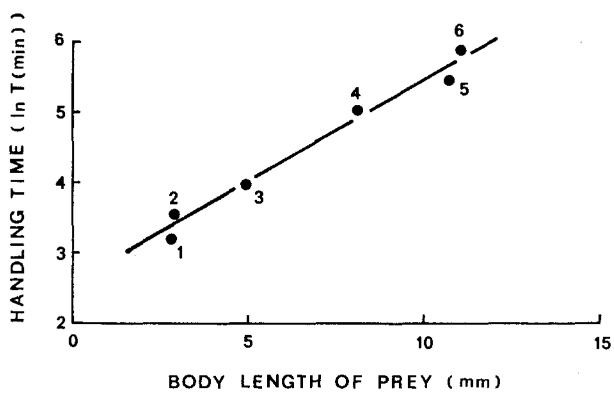

Fig. 2. Relationship between body length of a prey and the time taken by an ant lion in handling it. Handling time (min) is shown by natural logarithmic scale. 1, *M. ibarae*; 2, *T. caespitum*; 3, *F. japonica*; 4, small-sized *A. vulgare*; 5, large-sized *A. vulgare*; 6, *P. sericata*.

11.0 mm. Average handling times varied according to prey size (i.e. the minimum handling time was about 25 minutes and the maximum was about 7 hours). However, the relationship between the body length of prey (L, mm) and the natural logarithm of the handling time ($\ln T$, min) could be described by a linear equation, irrespective of the kind of prey (Fig. 2). The regression equation is

$$\ln T = 2.554 + 0.290L \qquad (r = 0.98) \tag{9}$$

Namely,

$$T = 12.858 \exp(0.290L) \quad \text{(min)} \tag{10}$$

Since the average body length of prey captured by the 3rd instar larvae in the research area was 4.4 mm, the average eating time is estimated as below:

$$T = 12.858 \exp(0.290 \times 4.4)/60 = 0.768 \quad \text{(hours)} \tag{11}$$

Next, the frequency of observed predation by each larval instar during the day (FOP(day)) is shown in Table 4. Since there is a similar tendency between FOP(day)s in 1983 and 1984, I used the pooled data. Average frequencies of observed predation were less than 5% for any larval instar and that of the 1st instar was significantly less than that of other instars (1st vs.

Table 4. Frequencies of observed predation (FOP (day)) by each larval instar during the day. FOP means (no. of ant lions handling a prey)/(total no. of pits observed) in a survey.

Year	Instar	% FOP (day)*	Range (%)	No. of surveys conducted	Average no. of larvae observed per survey*
1982	1st	3.38±1.16	0–7.14	17	125±29
	2nd	5.40±1.44	0–10.24	18	135±40
	3rd	4.96±1.54	0–12.50	18	97±20
1983	1st	2.17±1.39	0–11.54	21	82±26
	2nd	4.39±1.04	0–8.93	26	81±17
	3rd	4.43±2.32	0–20.69	22	56±10
Total	1st	2.71±0.88	0–11.54	38	101±18
	2nd	4.80±0.81	0–10.24	44	103±19
	3rd	4.67±1.36	0–20.69	40	75±13

*mean±95% C.L.

2nd instar, $t = 5.001$, $P<0.001$; 1st vs. 3rd instar, $t = 4.684$, $P<0.001$). As the relationship between prey sizes and handling times was examined only for 3rd instar larvae, only the feeding rate of the 3rd instar was estimated in the present paper. From Table 4, FOP(day) of the 3rd instar is

$$\mathrm{FOP(day)} = 0.0467 \tag{12}$$

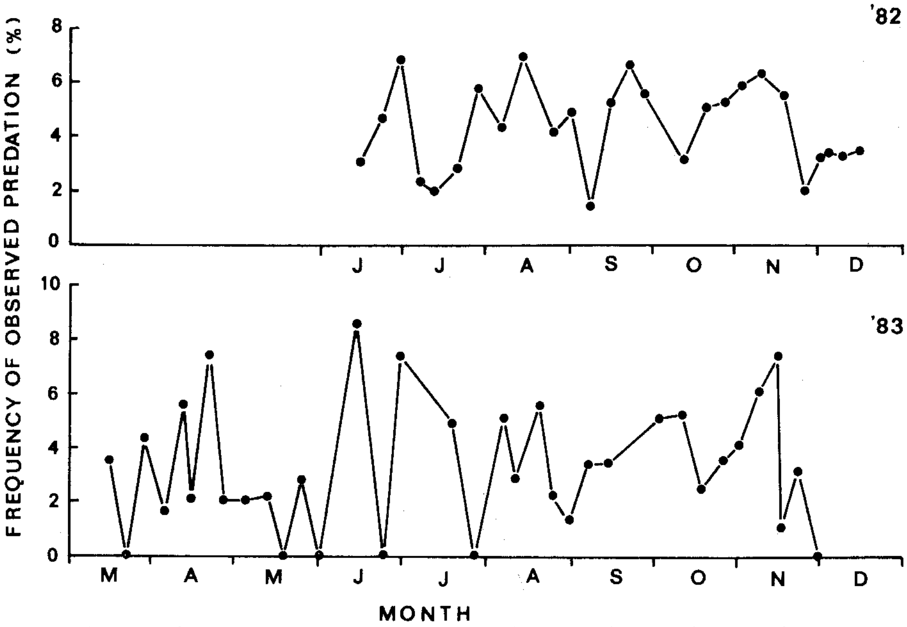

Fig. 3. Seasonal changes in the frequency of observed predation for all instars of *M. bore* larvae.

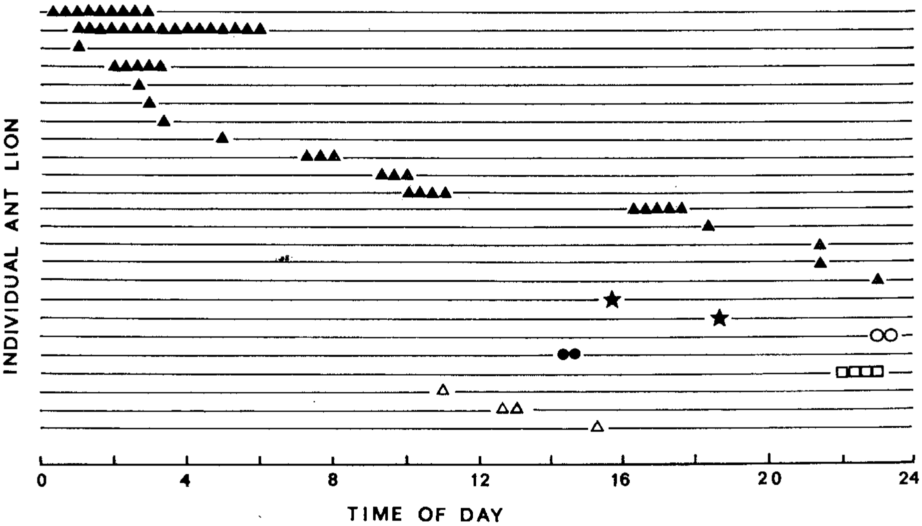

Fig. 4. Daily feeding activity of *M. bore* larvae. Each horizontal line represents one individual ant lion larva and each symbol indicates that the ant lion was eating a prey: ▲, *Tylos granulatus* (Isopoda); ★, ant; ○, Diplopod; ●, spider; □, leafhopper; △, unknown.

Although this is a mean value throughout the year, little seasonal change was found in FOP (day) (Fig. 3). Ant lion larvae did not prey at a higher rate in a specific season but captured prey constantly throughout the year, although FOP(day) was variable from day to day.

Two kinds of investigations were carried out on the daily rhythm of feeding activity of *M. bore* on the sandy beach at Tango-Kitsu. Figure 4 shows the daily feeding activity of the ant lion larvae. A horizontal line represents each ant lion, and various symbols indicate that an ant lion was eating a prey at the time a photograph was taken. Six kinds of prey items were detected in all. Since the average eating time per prey by the 3rd instar larvae was more than 20 minutes, as mentioned before (Table 3), almost all the predation could be captured by photographs taken at 20-minute intervals. Figure 4 shows that *M. bore* larvae are neither diurnal nor nocturnal, and can capture prey at any time of day.

Unfortunately, precise daily feeding rhythms of ant lions were not obtained from this research due to the small number of pits observed. However, observations were conducted to determine at which period of day or night ant lion larvae captured more prey (Table 5). There was little difference between the species composition of prey captured during the day and that captured at night, although the proportion of ants in the diet was higher during the day and the proportion of isopods was higher during the night. FOP values in the day were generally higher than those in the night. Using these values, r, i.e. the correction rate considering a daily change of FOP, was calculated as follows:

$$r = 2.58/[0.5\times(2.58+1.85)] = 1.165 \qquad (13)$$

This means that FOP in the day was 1.165 times higher than the mean value of FOP per day.

By substituting formulas (11), (12) and (13) for formula (6), we can obtain the estimates of the feeding rate (C):

$$C = (24\times 0.0467)/(0.768\times 1.165) = 1.25 \qquad (14)$$

That is, the 3rd instar larvae of *M. bore* in this habitat captured 1.25 prey whose body size was 4.4 mm per day on average during the period from spring to autumn. However, this is the value estimated on the basis of no rain falling during the whole day. Ant lion larvae cannot capture prey on rainy days since their pits are destroyed by rain. Moreover, they cannot make pits unless the sand dries after it has rained. Therefore their actual feeding rates would seem to be lower than this value.

Table 5. Comparison of frequencies of observed predation (FOP) between during the day and the night.

Date	Day			Night		
	No. of pits observed	No. of ant lions handling a prey	% FOP	No. of pits observed	No. of ant lions handling a prey	% FOP
June 6	652	17	2.61	451	10	2.22
June 7	657	14	2.13	561	14	2.50
July 11	103	2	1.94	—	—	—
July 12	272	15	5.51	190	7	3.68
Aug. 20	—	—	—	84	3	3.57
Aug. 21	287	10	3.48	349	4	1.15
Aug. 22	513	7	1.36	360	0	0.00
Aug. 23	462	10	2.16	605	4	0.66
Sept. 28	1833	34	1.85	1119	17	1.57
Sept. 29	1037	23	2.22	1419	19	1.34
mean	—	—	2.58	—	—	1.85
S.E.	—	—	0.41	—	—	0.42

Discussion

Heinrich and Heinrich (1984) investigated the foraging strategy of the *M. immaculatus* larva, a similar ant lion that constructs a pit in open sands. They roughly estimated feeding rate in the field to be 0.084 captures/h/pit, i.e. one prey every 12 h. In the present study, it was estimated that 3rd instar larvae of *M. bore* captured, on average 1.25 prey/day/pit, the body length of the prey being 4.4 mm. Although the larvae become satiated with one large captured prey, the density of larger prey is probably lower than that of smaller prey. Accordingly, the encounter rate with larger prey would be lower. On the other hand, although smaller prey occur at a higher density in ant lion habitats and the encounter rate with their pits is also higher, ant lion larvae do not become satiated with a single smaller prey because of the smaller biomass per individual. Therefore there may be great variation among individuals in the actual feeding rate of ant lion larvae.

Even light rain destroys the pits of *M. bore* larvae and causes foraging behavior to stop. The length of the foraging interruption period is dependent on the level of rainfall and the weather following the rain. Although the precise foraging period in days per year is not known, I roughly calculated an annual foraging period for *M. bore* larvae on the assumption that they maintain a pit except on days when there is a certain level of rainfall.

Since 3rd instar larvae of *M. bore* are active mainly during the period from April to October in Kyoto City, their potential foraging period can be regarded as 214 days. If they cease pit construction when daily rainfall is more than 10 mm, the active foraging period can be estimated as below.

According to "Rika Nenpyo, 1983" (in Japanese), the average number of days when the rainfall in Kyoto City exceeded 10 mm between April and October was 37 days (1951–1980). Therefore the active foraging period of the 3rd instar larvae of *M. bore* is

$$214-37 = 177 \text{ (days)}$$

Thus the actual feeding rate of *M. bore* larvae when considering the inactive period due to rainfall is estimated as

$$1.25\times 177/214 = 1.03 \text{ (prey)}$$

The feeding rate therefore tends to be overestimated using formula (6). It is presumed that ant lion larvae can capture prey at any time of the day, although the length of the foraging period seems to change seasonally. *M. bore* larvae make pits in open sandy areas where surface temperature varies remarkably with both the day and the month. In mid-summer, pits of *M. bore* larvae were rarely found in sunny areas, most being concentrated in shady areas around patches of grass. I observed that ant lion burrowed deeper under their pit base to avoid heat when the sand temperature had become too high. During this time, they would therefore not recognize the existence of a small-sized prey even it it dropped into the pit. Conversely, in early spring or late autumn, the larvae aggregated in sunny areas because the sand in shady areas tended to become wet. The larvae might cease foraging activity during the night in these colder seasons because of low sand temperature. Thus, the potential period of foraging varies with season and appears to be less than 24 hours.

Cannibalism by *M. bore* larvae was observed only once (Table 1) in spite of their high density. This low rate of cannibalism in the field suggests that the larvae rarely move a pit and tend to avoid neighboring pits. Heinrich and Heinrich (1984) observed that when the larva of *M. immaculatus* encountered another pit, it turned away, moving along the pit periphery. I have found experimentally that *M. bore* larvae rarely move even if starving and that most of them die of hunger without moving from one position (Matsura, in preparation). Ant lion larvae seem to move their pits in response to microclimatological factors rather than changing prey densities (Heinrich and Heinrich, 1984).

In the present study it was found that *M. bore* larvae in the field captured a variety of prey species and their feeding rate was estimated. In order to evaluate the feeing level, i.e. whether or not the larvae are starved in their habitats, it is necessary to obtain their maximum feeding rate in the laboratory and to know the ratio of an observed feeding rate to the maximum one. Such an evaluation of the feeding level of ant lion larvae in the field would lead to an understanding of the ecological characteristics of these unique predacious insects.

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References

HEINRICH, B. & HEINRICH, M. J. E. (1984) The pit-trapping foraging strategy of the ant lion, *Myrmeleon immaculatus* DeGeer (Neuroptera: Myrmeleontidae). Behav. Ecol. & Sociobiol. **14:** 151–160.

HILDREW, A. G. & TOWNSEND, C. R. (1982) Predators and prey in a patchy environment: a freshwater study. J. Anim. Ecol. **51:** 797–815.

KIRITANI, K., KAWAHARA, S., SASABA, T. & NAKASUJI, F. (1972) Quantitative evaluation of predation by spiders on the green rice leaf-hopper, *Nephotettix cincticeps* Uhler, by sight-count method. Res. Popul. Ecol. **13:** 187–200.

KUWAYAMA, S. (1959) On the genera *Myrmeleon* and *Grocus* in Japan and adjacent territories. Kontyû **27:** 66–69.

LAWTON, J. H. (1970) Feeding and food energy assimilation in larvae of the damselfly *Pyrrhosoma nymphula* (Sulz.) (Odonata: Zygoptera). J. Anim. Ecol. **39:** 669–689.

MATSURA, T. & NAGAI, S. (1983) Estimation of prey consumption of a mantid, *Paratenodera angustipennis* (S.) in a natural habitat. Res. Popul. Ecol. **25:** 298–308.

NENTWIG, W. (1980) The selective prey of linyphiid-like spiders and of their space webs. Oecologia **45:** 236–243.

POLIS, G. A. (1980) The effect of cannibalism of the dragonfly and activity of a natural population of desert scorpions. Behav. Ecol. & Sociobiol. **7:** 25–35.

SIMPSON, E. H. (1949) Measurement of diversity. Nature **163:** 688.

TOWNSEND, C. R. & HILDREW, A. G. (1979) Resource partitioning by two freshwater invertebrate predators with contrasting foraging strategies. J. Anim. Ecol. **48:** 909–920.