

AN EXPERIMENTAL STUDY ON THE FORAGING BEHAVIOR OF A PIT-BUILDING ANTLION LARVA, *MYRMELEON BORE*

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INTRODUCTION

The quantity of food resources used by predators often changes both in space and time. As a result, the effectiveness of foraging strategies for many predators is especially important to the fitness of these animals. There are wide variety of predatory foraging tactics, from sit-and-wait tactics to widely-foraging tactics (PIANKA, 1978). Among them, pit-building antlion larvae are typical sit-and-wait predators, and several aspects of their prey capture have been investigated recently (GRIFFITHS, 1980, 1986; LUCAS, 1982, 1985; WILSON, 1974). However, the relation between energy gain and pit movement has received little attention. An antlion larva requires energy to change an ambush-site in traveling and constructing a new pit. LUCAS (1985) reported that the metabolic expenditure during pit constructions in antlion larvae (*Myrmeleon carolinus* and *M. crudelis*) was about 10 times as great as resting metabolic rates. This suggests that they should move less compared with other arthropod predators whose movement costs are lower (JANETOS, 1982b).

In order to test this hypothesis, I conducted three experiments, using pit-making antlion larvae, *Myrmeleon bore* TJEDER. This species is small-sized (approximate body weight of the 3rd instar larva, 30–60 mg) and lives mainly in the seaside dunes in Japan. I first released the antlion larvae in artificial sands, and observed the construction and the relocation of pits under the condition that antlions were capable of capturing prey freely. Secondly, I examined the difference of pit relocation rate between fed and nonfed antlions in the laboratory. Thirdly, I reared *M. bore* larvae separately without food supply, and examined pit relocation, pit enlargement and survival periods.

FORAGING BEHAVIOR OF *M. BORE* LARVAE IN ARTIFICIAL SANDS

Artificial sands (135 × 135 cm) were made in the middle of the ground under a semi-cylindrical frame (5 × 6 × 3 m), covered with vinyl sheet on the roof. The frame was built in a grass field at the campus of Kyoto Kyoiku University. Twenty-three antlions (3rd instar larvae) were released uniformly on the sands. They were satiated fully by feeding on large bagworms (*Clania variegata*) the day before. Two antlions did not burrow into sand and died on the surface of the sands, probably because of extreme high temperature on the sand surface in the daytime.

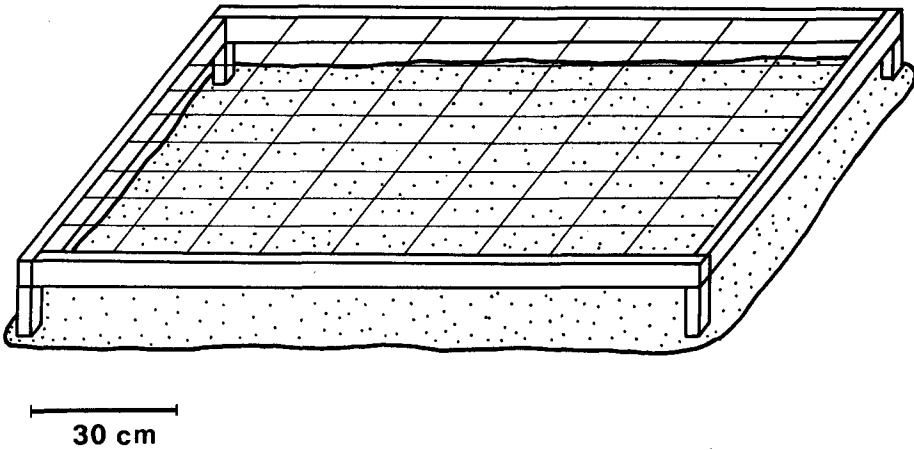


Fig. 1. Artificial sands constructed in the ground to research the pit relocation of the antlions. A frame in which threads were stretched at a 15 cm interval was set above it to measure the position of the pits.

I set a square frame in which threads were stretched at a 15 cm interval above the sands (Fig. 1), and recorded positions and sizes of pits of the antlions every day. Observation was carried out at 10:00–12:00, then corpses of prey discarded at the periphery of pits were collected. Various kinds of arthropods entered onto the sands because the lower part of the surrounding walls of the frame was opened 50 cm from the ground.

Figure 2 shows changes in the number of pits constructed, the number of pits moved and the cumulative number of pupated antlions. Although some antlion larvae did not construct pits for a few days after the release possibly because of satiation, all the antlions constructed pits on the 5th day. Pit relocation occurred during the initial 5 days except

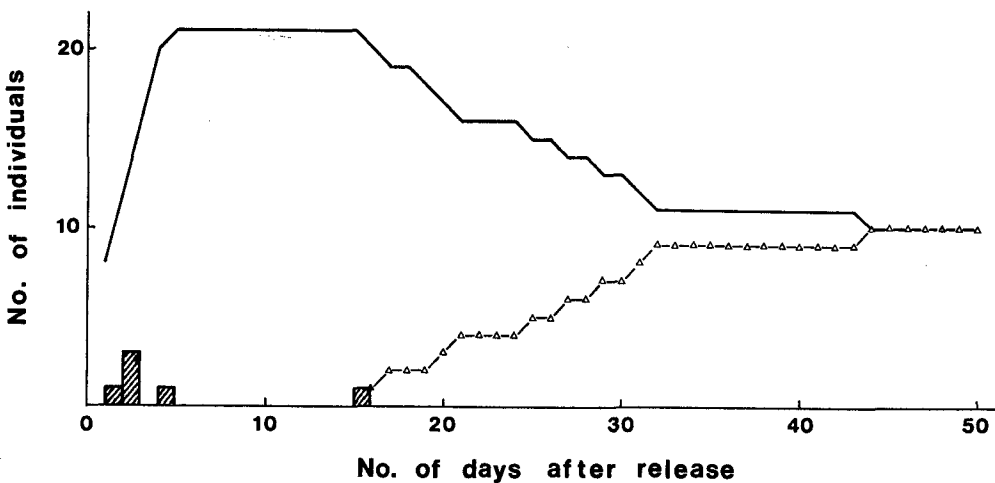


Fig. 2. Changes in the number of pits constructed by the antlion larvae (—), and the cumulative number of pupated antlion larvae (Δ). Shaded columns show the number of pits moved.

Table 1. Species composition of prey captured by the 3rd instar larvae of *M. bore* on the artificial sands.

Prey type	No. of individuals	% Frequency
Ants	127	58.0
Isopods	33	15.1
Beetles	20	9.1
Hemipterous insects	18	8.2
Spiders	10	4.6
Others	11	5.0
Total	219	100.0

for one pit movement on the 15th day. However, the total pit relocations was only six times. Decrease in the number of pits was mainly due to the pupation of the larvae. Nine of 10 antlions which had not pupated yet on the last day of the experiment had ambushed at the same positions for 50 days.

Two hundred and nineteen corpses of prey were collected during the experiment (Table 1). About 60% of the prey items were ants (*Tetramorium caespitum* and *Formica japonica*). The average daily number of prey captures per antlion larva was estimated by dividing the number of prey corpses collected by cumulated number of pits. The value was 0.3, i.e. the antlions captured one prey per about 3 days on the average. Small-sized corpses of prey, however, might be blown off and might not have been collected. Accordingly this estimate of prey capture may be slightly underestimated.

DO ANTLIONS CONCENTRATE INTO THE AREA WHERE THEY CAN CAPTURE MORE PREY?

To examine whether *M. bore* larvae concentrate into an area in which prey density is relatively high, I conducted the following experiment. Eight 3rd instar larvae of *M. bore* collected in the field were released into a container (30 × 30 × 10 cm) filled with sand to a depth of 5 cm. Six replications were made. The hunger level of the antlions was not regulated. A larva of *Chironomus* sp. (average body weight ± s.d.; 22.1 ± 3.9 mg) was given every 4 or 5 days to each pit which had been built in the left half (called 'fed area') of the containers. No prey was given to the other pits built in the right half ('nonfed area'). I measured the position of the pit center and the pit diameter before prey was given. The experiment was conducted in the laboratory under the conditions of 25 ± 1°C, 50–60% RH and 12L : 12D.

Antlions were fed first on the 4th day after release, when the number of pits constructed in the fed area was 3.0 ± 1.1 (mean ± s.d.) and that in the nonfed area was 3.5 ± 0.8 (Fig. 3). During 48 days the movement of a pit occurred only 7 times. No movement from the nonfed area to the fed area was observed, and movement from the fed area to the nonfed area occurred only once. The remainder was movement within the same area. Concentration of the pits into the fed area was never observed (Fig. 3).

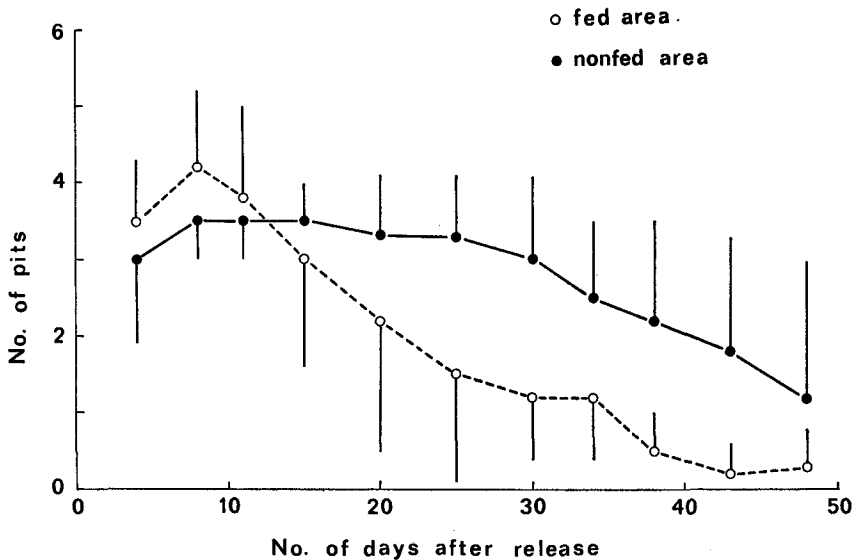


Fig. 3. Changes in the number of pits constructed in the 'fed area' (open circles) and in the 'nonfed area' (solid circles). Vertical bars show S.D.. See text for the details.

The number of pits in the fed area decreased due to pupation of the antlion larvae (Table 2). Decrease in the number of pits in the nonfed area was mainly due to death by starvation.

FORAGING BEHAVIOR UNDER THE STARVED CONDITIONS

In the experiment described above, there is a possibility that foraging behavior of *M. bore* larva was influenced by the existence of other individuals. Also the experiment was ended in 50 days, and thus the behavior of antlions without food >50 days was unknown. I aimed to clarify their behavior under starved conditions and their tolerance to starvation by rearing them separately without food till their death.

Second instar larvae of *M. bore* were collected from the habitat, and fed *Chironomus* larvae and mealworms. Newly moulted 3rd instar larvae were given mealworms every day for 3 days till satiation. Thirty antlions were released separately into containers (13.5 × 20.5 × 7.5 cm) filled with sand to a depth of 4 cm. I examined the position of pits and measured the pit diameters with vernier calipers every day. Death of each

Table 2. Comparison of the mortality rate and the number of pupae in *M. bore* larvae on the 48th day after the release between the fed and the nonfed antlions.

	Total no. of antlions	No. of antlions dead	% Mortality	No. of pupae
fed area	27	1	3.7	10
nonfed area	21	12	57.1	0

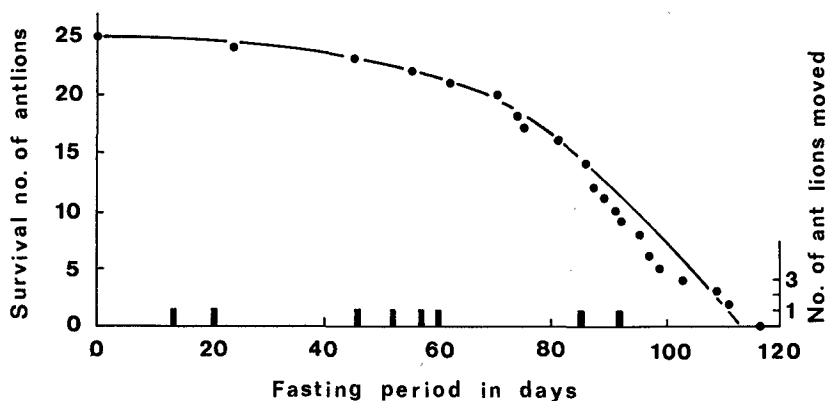


Fig. 4. The survival curve of *M. bore* larvae under starved conditions, fitted by eye. A solid column shows a pit relocation.

antlion larva was indicated by a flattened pit base. Occasionally the corpse appeared on the sand surface. When the death of larva was uncertain, I picked it up and examined directly. It was put again on the center of pit if alive, but such an emaciated larva never moved away from the released position. This experiment was conducted under the conditions of $25 \pm 1^\circ\text{C}$, 50–60% RH and 14L : 10D.

$$\bar{x} \pm 95\% \text{C.L.} = 83.9 \pm 9.3$$

$$n = 25$$

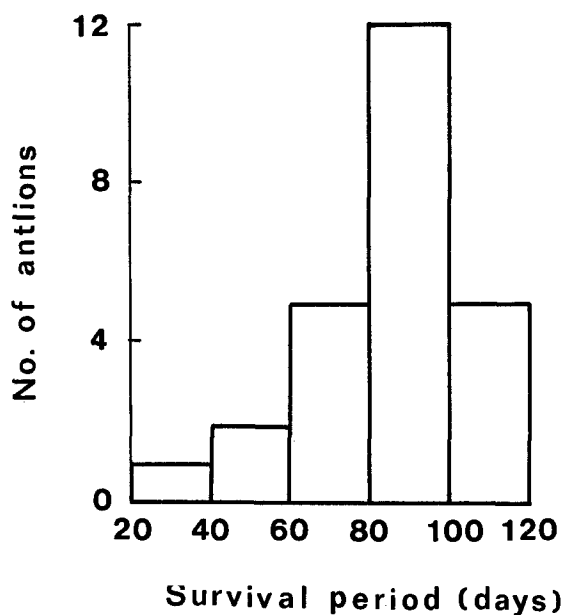


Fig. 5. Survival period of *M. bore* larvae under starved conditions.

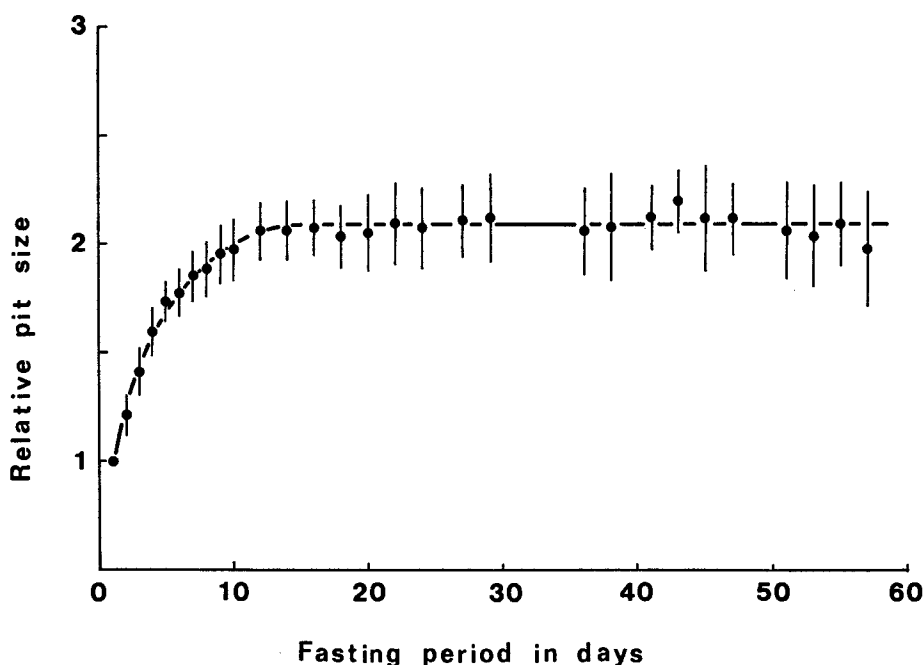


Fig. 6. Pit-enlargement by the antlion larvae with a progress of starvation. The pit size was expressed by a ratio of the pit diameter to that of the first constructed pit.

Since 5 of the 30 antlions used in the experiment became pupae, I omitted them from the calculation. This fact, however, suggests that some *M. bore* larvae can become pupae if they feed on enough prey during a few days after the second moult and even if they gain no food thereafter.

Figure 4 shows the survival curve of *M. bore* larvae and the frequency of pit relocation under starved conditions. Satiated antlion larvae survived for 83.9 days on the average under starved conditions, which suggests *M. bore* larvae are extremely tolerant of starvation (Fig. 5). The maximum survival period was 116 days. Although the antlions were given no water during the experiment, the survival period might have been prolonged still more if water had been given to them.

It is remarkable that pit relocation occurred only 8 times during the experiment of more than 100 days (Fig. 4). Since one antlion larva relocated twice, 7 antlions changed the position of pits. That is, 72% of the antlions (18/25) used in the experiment have never relocated their pits. *M. bore* larvae which never changed the ambush-sites died of starvation at the bottom of pit in the end.

Though *M. bore* larvae rarely changed their ambush sites, they flipped sand at the bottom of pit, as a result the pits were enlarged with the progress of starvation (Fig. 6). The pit size was saturated because of the limitation of sand-flip capacity and weakening from starvation.

DISCUSSION

In general, even for ambush-type predators, the frequency of change in position of the ambush-site is higher in areas of low prey density and lower in high prey density areas. This has been shown with such predacious arthropods as orb-weaving spiders (OLIVE, 1982; JANETOS, 1982a), a diving beetle larva (FORMANOWICZ, 1982) and a praying mantid (INOUE and MATSURA, 1983). However, *Myrmeleon bore* larvae rarely relocate their pits, i.e. they do not adopt a flexible tactic which changes an ambush-site in response to a change in prey capture rate.

Though I have not examined the pit-relocation rate of *M. bore* larvae in nature, I infer that there will be no relation between the pit-relocation rate and the prey capture rate. According to WILSON (1974), HEINRICH and HEINRICH (1984) and MATSURA (1986), ants are the most important prey of antlion larvae occurring in open sandy habitat. Nevertheless it has never been observed that antlions concentrate near entrances of ant nests where more ants are walking about (HEINRICH and HEINRICH, 1984; MATSURA, unpublished). Pit relocation of *M. bore* larvae in a natural habitat would not be due to a decline of prey capture rate but probably due to other factors, for example, heterogeneity of temperature or water content of sand among microhabitats. It is necessary hereafter to examine the distribution of their pits in the field in relation to microclimatic factors.

It would be surely wasteful for antlions occurring in such a uniform and stable habitat as open sands to relocate their pits frequently. This is because under such environmental conditions they could not expect an increase in prey-capture rate unless they moved a long distance. However, I have rarely observed long distance tracks by *M. bore* larvae in nature. Unlike other ambush predators that use no traps, the energetic cost accompanied with movement of ambush-site in antlion larvae includes expenditure not only in traveling but also in constructing a new pit, and the latter requires a much higher energy expenditure (LUCAS, 1985). Antlion larvae cannot travel while sampling prey, and neither can they capture prey unless building a pit. From a viewpoint of cost-benefit relations, it seems non-adaptive to respond sensitively to a decline of prey-capture rate and to relocate the pits frequently.

In order to adopt a tactic that does not change a position of ambush-site even if food resource becomes poor for a long period, the animal should have a trait highly tolerable to starvation. *M. bore* larvae were highly tolerable of starvation compared with other arthropod predators (e.g. 26.7 days in a praying mantid; MATSURA, 1981): they lived for 83.9 days without food. *M. bore* larva may have a tactic that endures starvation by reducing greatly the metabolic rate, as do the net-spinning spiders (ANDERSON, 1974).

Prey capture by *M. bore* larvae completely depends upon prey mobility because they cannot pursue prey. However, they are unlikely to go without prey for long periods of time. Actually, they had captured one prey/3 days/pit in the artificial sands constructed in the field as shown in my first experiment, and the feeding rate of the 3rd instar larvae in a natural habitat was estimated to be 1.03 prey/day/pit (MATSURA, 1986). PIANKA

(1978) pointed out that the existence of prey in high density was one of the necessary conditions for a sit-and-wait tactic by a predator to be successful. *M. bore* is univoltine antlion (MATSURA, unpublished) whereas most other antlions in Japan require 2 or 3 years to complete their development (BABA, 1953; FURUNISHI and MASAKI, 1982). This shorter duration of the development in *M. bore* suggests that the food resource is rich in the habitat, i.e. open sands, although it may also be related to its small size at maturation. *M. bore* is the most common antlion larva occurring in high density at seaside dunes in Japan. Prosperity of this species might suggest that its extremely sedentary foraging tactic is not unsuccessful under the current environmental conditions. Since the population density of *M. bore*, however, would be governed by various factors, we cannot conclude it. More detailed population study of *M. bore* is necessary hereafter.

SUMMARY

Foraging behavior of a pit-building antlion larva, *Myrmeleon bore* TJEDER was investigated experimentally to elucidate the relation between the feeding level and pit relocation.

1. In artificial sands constructed in the field the 3rd instar larvae of *M. bore* rarely changed the positions of their pits, though several antlions had moved actively until they constructed pits. The average feeding rate was 0.3 prey/day/pit, and about 60% of prey captured were ants.

2. To examine whether or not *M. bore* larvae concentrate into the area where they can capture more prey, 8 antlions were released into each of 6 boxes filled with sand. I divided the sand surface of each box into two half areas, then gave prey to the pits built in a half area and gave no prey to the pits built in the other half. During the 50-day observation period, nonfed antlions never moved into the area where prey were given.

3. The 3rd instar larvae were reared separately without food. Even under starved conditions they rarely relocated their pits until death. The average duration of survival period was 83.9 days.

4. The experimental results indicate that *M. bore* larvae adopt a tactic of sedentary ambushing. These larvae exhibit low movement rates which are independent of prey capture rates.

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巣穴形成型アリジゴク (クロコウスバカゲロウ *Myrmeleon bore*) の 捕食行動に関する実験的研究

松 良 俊 明

開けた砂地に巣穴をつくるアリジゴク, クロコウスバカゲロウ幼虫 (*Myrmeleon bore* TJEDER) の捕食行動を, 擬餌レベルと巣穴移動との関係を中心に実験的に研究した。

1) 人為的につくった半野外条件下の砂場に3齢のアリジゴク(23個体)を放し50日間観察したところ, 数個体は巣穴をつくるまでの間活発に動いたものの, ほとんどのアリジゴクは巣穴を全く移動させなかった。その間のアリジゴクの平均捕食量は0.3匹/日/巣穴であり, 餌の約60%はアリであった。

2) より多くの餌を捕獲できる場所へアリジゴクが集中するかどうかを調べるために, 砂を入れた箱(30×30×10 cm)へ8匹ずつ放した。容器内の左半分にてきた巣穴には4, 5日に1匹の割合でアカムシを与えたが, 右半分にてきた巣穴には全く何も与えなかった。50日間の実験期間中に, 絶食区のアリジゴクが給餌区へ移動することは全くなかった。

3) 3齢のアリジゴクを絶食条件下で単独飼育した。このような条件下でも巣穴を移動させる個体はほと

んどなく、大部分のアリジゴクは死ぬまで1度も巣穴位置を変えなかった。平均生存日数は83.9日であった。また絶食がすすむにつれて巣穴サイズは一定レベルまで増大した。

4) これらの実験結果から、クロコウスバカゲロウ幼虫は餌の捕獲率の増減にとられない、非常に定着的な待ち伏せ型捕食戦術を採用していると結論された。