PIT-RELOCATION OF ANTLION LARVAE IN RELATION TO THEIR DENSITY

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INTRODUCTION

Most sit-and-wait predators stay longer within a more profitable patch (e.g. Olive, 1982; Inoue and Matsura, 1983; Formanowicz, 1987). As a result, the density of predators becomes higher in such a patch, but this concentration would be moderated by interference among the predators. Thus, spatial distribution of predators in a habitat is influenced both by distribution of prey and by mutual interference among predators.

Pit-building antlion larvae are one of the typical sit-and-wait predators like net-spinning spiders and caddis larvae. Matsura (1987) examined experimentally whether antlion larvae (*Myrmeleon bore* Tjeder) changed their ambush-sites depending upon a change in reward rate, and he showed that *M. bore* larvae rarely relocate their pits even though starvation progressed and they never concentrate into the profitable area.

Factors affecting pit-relocation of antlion larvae would be separated into biotic factors (e.g. feeding rate and density of antlions) and physical factors (e.g. sand temperature and water content of sand). Since it has been already demonstrated by Matsura (1987) that the feeding rate almost never affect the pit-relocation rate in *M. bore* larvae, we aimed to examine whether another biotic factor, i.e. density of antlion larvae influences the pit-relocation rate. The aims of this study are to clarify experimentally (i) relationship between the density of antlion larvae and the spatial distribution, (ii) whether or not high density of the larvae causes pit-relocation, and (iii) what mechanism causes the larvae to relocate their pits.

MATERIALS AND METHODS

M. bore is an univoltine antlion whose larva builds a pit mainly in open sands such as seaside dunes. The final i.e. third instar larvae of *M. bore* used in this experiment were collected from the seaside dune at Tango-Kitsu of Kyoto Prefecture in May 1983.

We filled 30 containers ($30 \times 30 \times 10$ cm^3) with sand to a depth of 5 cm, and released 2, 5, 10, 15, 20 and 30 larvae at the center of each container. Five replicates were made. Hunger level was not regulated directly but we selected as similar sized larvae

as possible, because the body length of antlion larva is closely related to its hunger level (MATSURA, unpublished). The position of the pit center and the pit diameter were recorded on the 1st, 2nd, 4th, 7th, 11th and 15th day after release. No prey was given to the larvae during the experiment. Although the number of antlions in some containers decreased due to cannibalism, we did not replenish them.

We analized the spatial distribution of larvae, using nearest neighbor distance (NND). To compare the distribution of the larvae in a container with a random distribution, the average NND when a given number of points are randomly distributed in the container was calculated by computer simulation (MELCOM 7000). The number of replications was 500 for the density of 2 points per container, and 400 for other densities. The position of each larva was measured in a unit of 0.5 cm, therefore we set 61×61 lattice points in the 30×30 cm^2 area and selected a given number of points at random. Marginal points were excluded from the selection because the larvae could never locate at those points.

As a direct cause of pit-relocation when the larval density became higher, we predicted the frequent dropping of sand-grains tossed by neighbor antlion larvae. This was tested as follows:

Eight containers ($20 \times 13.5 \times 7.5$ cm) were filled with sand to a depth of 5 cm, and the sand surface of each container was divided into six cells by standing cardboard perpendicularly on it (Fig. 1). A third instar larva of *M. bore* was released into each cell. All the larvae built pits till the third day after release, when the partition walls in 4 out of 8 containers were removed. The cardboard walls were high enough to ensure that sand thrown by any larva did not enter other larva's pit. Without the cardboard partitions, sand regularly entered pits from other larvae. We observed pit-relocation and/or change in the pit size every other day during 16 days.

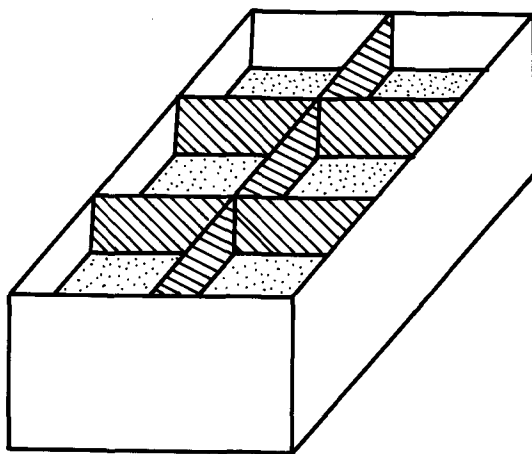These experiments were all conducted at $25 \pm 1°C$, 50–60% RH and 14L : 10D.

Fig. 1. A container used to examine a cause for pit relocation.

Results

1. Influence of density on pit-building behavior

Not all antlion larvae released into the containers built pits. We term "pit construction rate" as a ratio of the number of pits constructed to the number of larvae alive in the container. The higher was larval density, the slightly smaller was this rate (Table 1). Especially more than 10% of larvae at the highest density did not build a pit during the experiment. Since every antlion larva at lower density made a pit, emergence of the non-pit-building antlions at higher density is clearly due to crowding.

Antlions which had abandoned their pits were sometimes captured by other antlions in the course of moving. The frequency of cannibalism was higher as the initial density of the larvae became higher (Table 2). However, it was 2.6 per container even at the highest density (30 larvae per container), and this value is equal to only 0.17 per day. At the density of 5 larvae cannibalism was observed only once, and this happened when the antlion larvae had been just released into the container.

In order to examine whether the antlion larvae changed position of their pits during 15 days, we calculated a "giving-up rate of pit", which is a rate of the number of pits abandoned at the ith time to the number of pits observed at the $(i-1)$th time. The larva that gave up ambushing beneath the pit either constructed a new pit or concealed itself beneath the sand surface at other ambush-site. We could not, however, judge which foraging tactic was adopted, because we could not look at any larva directly. Therefore we intended to evaluate a ratio of residence of the larvae from the giving-up rate of pit. Fig. 2 shows the giving-up rates of pits at each density. There is a tendency that pits were abandonded more frequently at higher densities (20 and 30 larvae/container). A ratio of larvae which had never relocated the pit during the experiment was almost inversely proportional to the initial density of the larvae, and only about one

Table 1. Changes in average pit construction rate (%) at each larval density.

Density	Day					
	1	2	4	7	11	15
2	100	100	100	100	100	100
5	100	100	100	100	100	100
10	100	94	100	91	94	91
15	88	92	97	96	97	95
20	77	86	92	100	100	100
30	48	80	91	81	84	88

Table 2. Number of cannibalism per container during 15 days at each initial larval density.

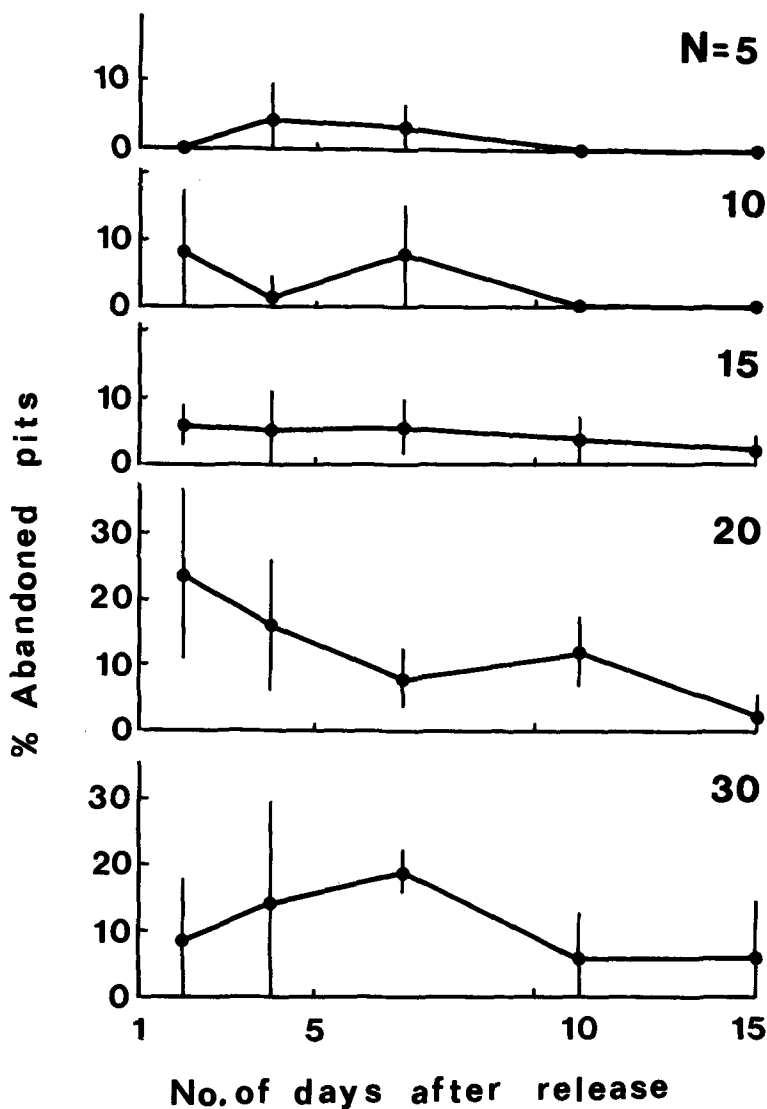|	Initial density					
	2	5	10	15	20	30
Av. no. of cannibalism	0	0.2	0	0.4	2.2	2.6
S.D.	0	0.4	0	0.9	1.5	1.5

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Fig. 2. Periodical changes in the rate of abandoned pits at each larval density.

third antlion larvae at higher densities maintained their original pits (Table 3).

From these resuts, it was clarified that the density of antlion larvae affected more remarkably residence rate of the pits rather than it did the pit construction rate.

2. Spacing of the antlion larvae

If we write $\bar{r}_E$ as a mean of NND's for random distribution, and $\bar{r}_A$ as a mean of observed NND's in the experiment, then $\bar{r}_A < \bar{r}_E$ means contagious distribution and $\bar{r}_A > \bar{r}_E$ means uniform distribution (CLARK and EVANS, 1954). The NND of randomly distributed points decreased rapidly with density (Fig. 3). When there is no mutual in-

Table 3. Residence rate (a ratio of the number of individuals which have never relocated pits till the end of experiment to the number surviving) at each density of antlion larvae.

	Initial density					
	2	5	10	15	20	30
No. surviving	10	24	45	71	87	131
No. of resident pits	8	22	37	39	31	41
% residence	80.0	91.7	82.2	54.9	35.6	31.3

terference among the antlion larvae, the average NND at every density must follow this curve. However, values of $\bar{r}_A$ at lower density levels were smaller than those of $\bar{r}_E$. This is because we had released the antlion larvae in a mass at the center of container and also they did not disperse to a long distance from the released point. On the other hand, values of $\bar{r}_A$ at heigher density levels were larger than those of $\bar{r}_E$, and they seem to be approximately constant independent of the larval density.

Fig. 4 shows a relationship between the density of antlion larvae and the pit diameters on the 7th day after release. The regression coefficient in a linear regression
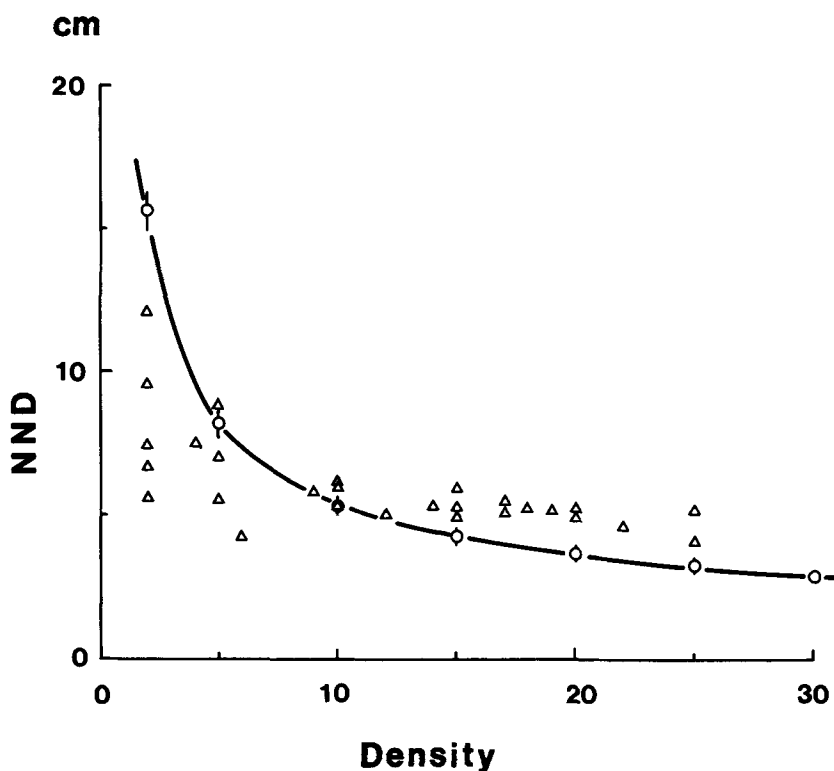

Fig. 3. Relationship between the pit density and NND. Open circle shows a mean of NND's between randomly distributed points obtained by computer simulation. Triangle shows an observed average NND per container. Vertical bar represents 95% C.L..
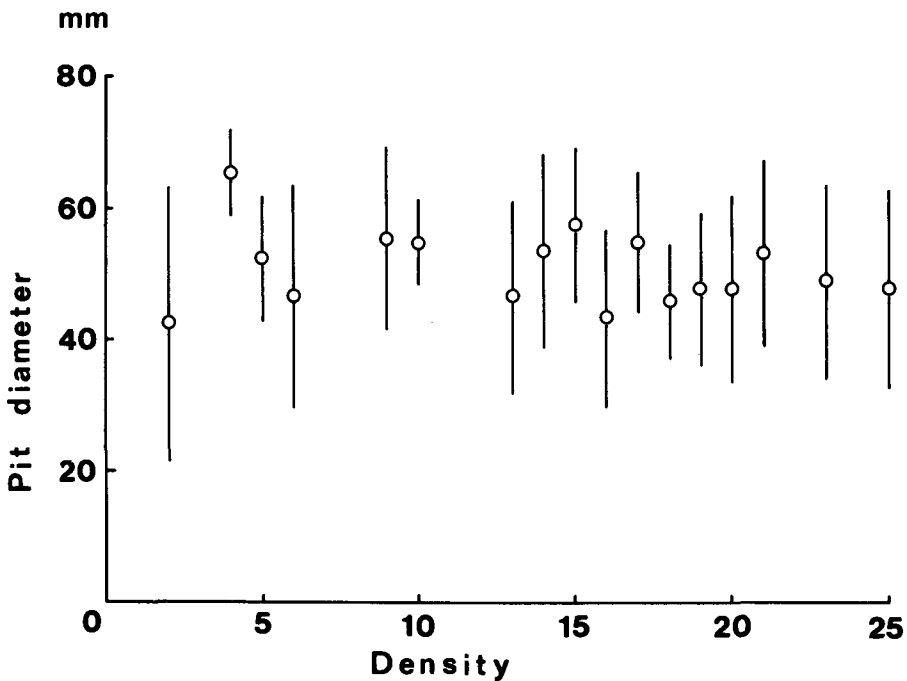
Fig. 4. Pit diameters (mean ± S.D.) at each larval density.

analysis for the density and the pit size was not statistically different from zero ($P>0.05$, F-test). The average pit diameter in *M. bore* larva was about 50.8 mm regardless of the pit density. This value is approximately equal to the average NND of pits at higher larval densities. This indicates that most pits of *M. bore* larvae rarely overlap each other due to mutual interference even though pit densiy became high. The bases of pits at the higher densities were buried a little with sand tossed by neighbor antlion larvae.

3. Mechanism of mutual interference

The density (6 larvae per container) in the second experiment corresponds to 20 larvae/30 × 30 cm^2 in previous experiment, thus it belongs to high density level. In the four containers with partition walls, only one out of 24 antlions that had constructed a pit within a cell changed the position of the pit once during 16 days. On the other hand, pit-relocation occurred 5.0 ± 2.2 (mean ± S.D.) times per container during 16 days in the four containers without partition walls, and 1.25 antlions per container were killed by other larvae. Only 4 larvae out of 24 never relocated their pits during the experiment. Thus, the frequent dropping of sand grains tossed by other larvae clearly motivated the pit-relocation of *M. bore* larvae.

Discussion

The experimental results indicate that crowding of *M. bore* larvae affected markedly residence rate of the pits. In Japan, there are four species of antlions whose larvae build a pit (MATSURA, 1978), and *M. bore* larva seems to be one of the most actively pit-building antlion larvae. Although YOUTHED and MORAN (1969) reported that African mymeleontid larva, *Myrmeleon obscurus* built a smaller size of pit with increased crowding of larvae, in the case of *M. bore*, their pit size was approximately constant independent of the larval density (Fig. 4). That is, they actively constructed a pit even though under high larval density. Increment of the larval density means not only reduction of distances between individuals but also increment of the number of surrounding pits. As a result, dropping of sand grains tossed by other larvae became frequent with increased larval density. From the result of the second experiment, it is clear that frequent dropping of sand grains into a pit caused pit-relocation. This is the reason why *M. bore* larvae often relocated their pits at high density.

There are two different interpretations concerning the spacing of antlion larvae. WILSON (1974) had investigated the spatial distribution of pits constructed by *Myrmeleon* larvae at open sands in Costa Rica, and offerred a "doughnut theory" which is that the optimal arrangement of the pits for reducing competition is to line along the circumference of a circle. According to WILSON (1974), the probability of capturing prey by an antlion larva is reduced by the existence of neighbor pits, because most prey animals walking into a patch of sand would be captured by pits at the periphery of the patch. WILSON (1974) showed some spatial distribution data of pits in the field as the proof of his hypothesis.

However, McCLURE (1976) attained a different conclusion from WILSON's (1974). He suggested that WILSON's "doughnut theory" involved unrealistic assumptions, i.e. (i) prey always enter a patch of sand only from its perimeter, (ii) prey approach pits with equal probability from all direction, and (iii) arthropod prey walk on the sand in a straight line. We agree with McCLURE's (1976) criticism, because many winged insects were found among prey of antlion larvae (MATSURA, 1986) and they seem to land on the sand surface from above the pits. Moreover, although WILSON (1974) claimed the arrangements of pits in the field were doughnut-shaped (his Figures 5 and 6), they does not appear particularly doughnutty to us (SIMBERLOFF *et al.*, 1978).

As an alternative interpretation for spacing of antlion larvae, McCLURE (1976) offerred a "spatial uniformity hypothesis", that is, the spatial arrangement of pits at high densities becomes uniform which is optimal pattern to decrease competition for prey capture among antlion larvae.

McCLURE (1976), however, confused the distribution of "pits" with that of "antlion larvae *per se*". Because he analized the spatial arrangement of "pits" by using the nearest neighbor method assuming points and this method underestimates expected nearest neighbor distance for circle (SIMBERLOFF, 1979). We also used the

nearest neighbor method assuming points in the present study, but we discriminated the distribution of larvae *per se* from that of pits, and consider it is more appropriate for the purpose of detecting mutual interference among antlion larvae to adopt the nearest neighbor method assuming points rather than circles.

Both WILSON (1974) and McCLURE (1976) described that antlion larvae had avoided each other at higher density in order to decrease competition for prey among them. Most sit-and-wait predators change their ambushing-sites depending upon decrease in capture rate of prey (e.g. INOUE and MATSURA, 1983; OLIVE, 1982), but *M. bore* larvae rarely relocated their pits even under starved conditions, i.e. they adopt a sedentary ambushing tactic independent of prey capture rate (MATSURA, 1987). Therefore we consider that the proximate factor for *M. bore* larvae causing uniform distribution pattern is not to gain more prey. They may relocate them only for the purpose of avoiding a physical disturbance such as frequent dropping of sand into a pit.

Most densities in third instar larvae of *M. bore* in natural habitats are less than 10 larvae per quadrat ($30 \times 30 cm^2$) (MATSURA, unpublished). It is clear from Table 3 that pit-relocation rate is low in the density of less than 10 larvae. The daily giving-up rate of pits in the field was approximately 2 to 6% (MATSURA, unpublished data). Thus, factors other than both starvation and high density possibly affect pit-relocation of *M. bore* larvae in the field.

The only natural enemy of *M. bore* larvae we have found is a Dipteran parasitoid, Bombyliidae sp., which emerges from the cocoon of *M. bore*. There is no remarkable difference in behavior and ecology between the antlion larva parasitized by it and non-parasitized one. Natural enemies of *M. bore* larvae may rarely affect relocation of pits directly. Other factors such as the distribution pattern of eggs laid by the adults and the heterogeneity of water contents and/or temperature of sands may be important ones affecting spatial distribution of *M. bore* larvae. The importance of micro-climatological factors upon the spatial distribution of antlion larvae in the field was suggested by HEINRICH and HEINRICH (1984). Investigation focussing on a relationship between physical environmental factors of habitat and foraging behavior of *M. bore* larave would be necessary hereafter.

SUMMARY

Of the biotic factors potentially affecting the foraging behavior of pit-building antlion larvae, *Myrmeleon bore* TJEDER, we focussed on the density effects and examined experimentally influences of larval density on pit construction behavior, spatial distribution and pit relocation rate. Moreover the mechanism of mutual interference among larvae was examined.

1. After releasing 2, 5, 10, 15, 20 and 30 third instar larvae of *M. bore* at the center of each container ($30 \times 30 \times 10 cm^3$) filled with sand, we measured number of pits, pit diameter and position of pit base.

2.   More than 80 % of antlion larvae at each density always constructed pits, and the rates of larvae that had not constructed pits rose in proportion to the density.   Pit size was approximately constant independent of the density.

3.   The density of *M. bore* larvae clearly affected the residence time of the pits, i.e. more larvae frequently relocate pits with increasing larval density.

4.   To analyze the spatial distribution pattern of the larvae in a container, nearest neighbor distance (NND) was measured.   Comparison between the observed NND and the expected value for NND in random distribution obtained from computer simulation suggested that high larval density produced a uniform distribution owing to their mutual interference.

5.   The result of an experiment to examine the mechanism of mutual interference among larvae showed that frequent dropping of sand into a pit tossed by neighbor antlion larvae causes a pit-relocation.

REFERENCES

Clark, P.J. and F.C. Evans (1954)   Distance to nearest neighbor as a measure of spatial relationships in populations.   *Ecology* **35**: 445–453.

Formanowicz, Jr, D.R. (1982)   Foraging tactics of larvae of *Dytiscus verticalis* (Coleoptera: Dytiscidae): the assessment of prey density.   *J. Anim. Ecol.* **51**: 757–767.

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

Inoue, T. and T. Matsura (1983)   Foraging strategy of a mantid, *Paratenodera angustipennis* S.: mechanisms of switching tactics between ambush and active search.   *Oecologia* **56**: 264–271.

Matsura, T. (1986)   The feeding ecology of the pit-making antlion larvae, *Myrmeleon bore*: feeding rate and species composition of prey in a habitat.   *Ecol. Res.* **1**: 15–24.

Matsura, T. (1987)   An experimental study on the foraging behavior of a pit-building antlion larva, *Myrmeleon bore*.   *Res. Popul. Ecol.* **29**: 17–26.

Matsura, T. (1987)   Nomenclature of the Japanese pit-building antlions (Neuroptera, Myrmeleontidae).   *Kontyû* **55**: 543–548.   (In Japanese with English summary)

McClure, M.S. (1976)   Spatial distribution of pit-making ant lion larvae (Neuroptera: Myrmeleontidae): density effects.   *Biotropica* **8**: 179–183.

Olive, C.W. (1982)   Behavioral response of a sit-and-wait predator to spatial variation in foraging gain.   *Ecology* **63**: 912–920.

Simberloff, D., L. King, P. Dillon, S. Lowrie, D. Lorence and E. Schilling (1978)   Holes in the doughnut theory: the dispersion of ant-lions.   *Brenesia* **14–15**: 13–46.

Simberloff, D. (1979)   Nearest neighbor assessments of spatial configurations of circles rather than points.   *Ecology* **60**: 679–685.

Wilson, D.S. (1974)   Prey capture and competition in the ant lion.   *Biotropica* **6**: 187–193.

Youthed, G.J. and V.C. Moran (1969)   Pit construction by Myrmeleontid larvae.   *J. Insect Physiol.* **15**: 867–875.

密度に関連したアリジゴクの巣穴移動

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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* TJEDER）の捕食行動に影響を与えている生物的要因のうち，密度効果に焦点を当て，巣穴形成行動・空間分布・巣穴移動率に対するアリジゴク密度の影響について実験的に調べた．さらに，幼虫間の相互干渉のメカニズムについても調べた．

1. 砂を満した容器（$30 \times 30 \, \text{cm}^2$）の中央に，クロコウスバカゲロウの3齢幼虫をそれぞれ2匹，5匹，10匹，15匹，20匹，30匹放し，できた巣穴の数や，巣穴直径，巣穴底の位置を測定した．

2. どの密度区でも80％以上のアリジゴクが常に巣穴をつくったが，つくらなかった個体の割合は密度に比例して高くなった．しかし巣穴サイズは密度に関係なくほとんど一定であった．

3. 幼虫の密度は明らかに巣穴の定着時間に影響を与えた．すなわち密度が高まると多くの個体はしばしば巣穴位置を変えた．

4. 容器中の幼虫の空間分布を分析するため，最近接距離 (NND) を測定した．NND の観察値と，コンピュータ・シミュレーションによって求めたランダム分布のときの NND の期待値を比較した結果，幼虫は高密度になると相互干渉のせいで一様分布を示すことがわかった．

5. 幼虫間の相互干渉のメカニズムを調べた実験の結果，近接する他の個体によって放り投げられた砂粒の頻繁な落下が，巣穴移動の直接原因であることがわかった．