

Variations in the Pit Size of *Cueta sauteri* (Neuroptera: Myrmeleontidae) Larvae in Response to Past Pit-Building Experience and Food Limitation

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Shih-Hsiung Liang, Wan-Yu Lin, Yi-Ching Lin, Yi-Chih Chen, and Bao-Sen Shieh (2010) Variations in the pit size of *Cueta sauteri* (Neuroptera: Myrmeleontidae) larvae in response to past pit-building experience and food limitation. *Zoological Studies* 49(1): 102-107. Few studies on antlion species of Taiwan have been conducted to examine the pit structure of antlion larvae and their pit building responses to food limitations. Pit-building antlions may respond to food limitations by relocating their pits or altering their established pits. The present study attempted to describe pit structures built in the field and in captivity by the larvae of *Cueta sauteri*, an antlion species distributed in a prey-poor badland area of southern Taiwan, and compare pit sizes of fed and unfed antlions under different past pit-building experiences in a situation with restrictions on pit relocation. *Cueta sauteri* larvae exhibited similar pit-building behaviors and pit structures in both the field and laboratory. By controlling relocation and preventing pit building, the results of the present study indicated that both food limitations and past pit-building experience affected pit sizes of *C. sauteri* larvae. In a comparison between fed and unfed larvae, free-building larvae displayed no differences in pit sizes during 32 d of observation, while size differences were significant in those previously not free-building antlions after 22 d. We suggest that *C. sauteri*, a badland species, is more tolerant of food limitations than other antlion species found in prey-rich habitats. <http://zoolstud.sinica.edu.tw/Journals/49.1/102.pdf>

Key words: Antlion, *Cueta sauteri*, Pit size, Myrmeleontidae, Food limitation.

Pit building antlions (Neuroptera: Myrmeleontidae) construct conical traps in dry, loose substrate and wait for their prey at the bottom of the trap. These sit-and-wait antlions are ideal animals for testing the optimal foraging theory because it is easy to define and measure antlions' foraging traits such as pit size (Griffiths 1986, Eltz 1997, Elimelech and Pinshow 2008). Pit size, measured as the diameter of the trap surface, is one of the most important features in studying the foraging behavior of antlions (Griffiths 1980, Kitching 1984, Hauber 1999, Day and Zalucki 2000). According to the optimal foraging theory,

antlion larvae should optimize their pit size to maximize the net energy gain, a difference between the benefits of capturing prey and the costs of pit construction. Griffiths (1986) predicted that in poor food conditions, benefits of capturing prey would be reduced because fewer prey are caught and pit size would be expected to be smaller than the optimum for a given size of larva. Additionally, the costs of pit construction depend on past and present energy inputs by antlion larvae, and after pit destruction, previously well-fed larvae should construct larger-sized pits than would starved ones.

Because of the passive hunting tactic of

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antlion larvae, food limitation is a critical factor for the survival of these sit-and-wait predators, and has been widely used as a study treatment to investigate their foraging responses. Previous studies found that antlions may respond to food limitation by relocating pits to increase prey encounters or by altering pit sizes (Youthed and Moran 1969, Griffiths 1980, Rosenberg 1987, Jenkins 1994).

Pit sizes of antlions are affected by food limitation and also other factors such as past pit-building experience and relocation frequency (Hauber 1999). Therefore, the effect of food limitation on pit sizes is hard to justify without controlling for factors of past pit-building experience and relocation frequency. Additionally, given the varied abilities to tolerate starvation among species, a short period of food limitation, such as 8 d in the study of Hauber (1999), might not be long enough to evoke significant responses in antlion larvae of other species (Matsura and Murao 1994, Scharf and Ovidia 2006). Thus, more studies on different antlion species are required to further understand the variations in pit size of antlion larvae in response to food limitations.

In Taiwan, although over 20 species of antlions have been identified (Stange et al. 2002), almost no studies have been conducted to examine their pit structures or pit-building responses to starvation. Thus, the objectives of the present study were to describe pit structures built in the field and in captivity of larvae of *Cueta sauteri*, an antlion species distributed in a prey-poor badland area of southern Taiwan, and compare pit sizes between fed and unfed antlions under different past pit-building experiences in a situation with restrictions on pit relocation. We predicted that unfed antlions which had been starved and prevented from building pits for a period of more than 20 d should construct smaller pits than fed ones once they are allowed to build.

MATERIALS AND METHODS

Sampling area

Cueta sauteri larvae were observed and collected in Yanchao Township, Kaohsiung County, southern Taiwan. The study area is characterized by badland terrain with loose, fine sand and scarce vegetation. Air temperature ranged 26-35°C in the sampling area during the study period.

Field measurements

In the field at the study area, diameters of pits built by *C. sauteri* larvae ($n = 17$) were measured using Mitutoyo digimatic calipers (Model CD-6" CS) along both the north-south (N-S) and east-west (E-W) axes in Mar. 2005. The pit depth was determined from the center of the pit surface to the deepest point. After a pit was measured, the antlion was collected with a sieve (with a mesh size of 0.5 mm). The collected antlions were then marked, placed in a 20 ml vial, and carried back to the laboratory within 60 min.

Laboratory experiments

Pit structure

In the laboratory, the body length and head width of each individual were first measured. Body lengths of collected larvae ranged 4.1-8.2 mm, and each larva was classified as being in the 2nd or 3rd instar stage according to Wu (2006). Each antlion was then placed in a paper cup (with a height of 5.8 cm and width of 6 cm), and filled with sifted sand (up to a height of 4 cm) taken from the sampled area in which to freely build its pit. For the next 24 h, the number and ratio of successfully constructed pits were recorded every 30 min to evaluate if *C. sauteri* larvae could build its pit within a short period of time in the laboratory. The diameter and depth of each pit were also measured after 24 h of observation.

Pit construction and food limitation

We collected 40 larvae from the sampled area in Apr. 2005 and used them for the following experiments in the laboratory. Ten larvae were randomly assigned to one of 4 groups with different combinations of pit construction and food limitation treatments: (1) free-building/fed, (2) free-building/unfed, (3) not-building/fed, and (4) not-building/unfed. Larvae in the 1st group (free-building/fed) were individually placed in a paper cup filled with a 5 cm height of sifted sand from the sampling site, and each was fed 1 ant (*Tapinoma melanocephalum*) per day. Larvae in the 2nd group were also placed individually in a paper cup but were not fed. The diameter of each pit was measured once on the 2nd, 7th, 12th, 17th, 22nd, 27th, and 32nd d for the 1st and 2nd groups; the day on which a larva was placed into the cup was denoted the 1st d. Because 2 larvae in the 1st group and 3 in the 2nd group failed to build pits

on the 2nd d, the sample sizes were 8 for the 1st group and 7 for the 2nd group.

Larvae in the 3rd group (not-building/fed) were separately placed in small 20 ml glass vials with a diameter of 2 cm which had been filled with sifted sand from the collection site up to a height of 2 cm, and were fed 1 ant (*T. melanocephalum*) per day; antlions in the 4th group (non-building/unfed) were put in an identical container but were not fed. As evidenced by the skeletal remains of ants, antlions in the small vials were successful in capturing prey despite being prevented from building pits. A previous study by Wu (2006) indicated that *C. sauteri* does not display signs of starvation until a food shortage of at least 20 d. Therefore, on day 21, we transferred larvae of the 3rd and 4th groups from vials to paper cups to allow pit building, and subsequently recorded their pit diameters on the 22nd, 27th, and 32nd d. The feeding treatments for the 4 groups remained the same throughout the observation period. Because of limited space in the paper cups, pit relocation was restricted in the paper cups in this study.

Statistical analysis

Paired *t*-tests (2-tailed) were used to assess differences in pit structure for *C. sauteri* larvae between those in the field and in captivity. Linear regressions were used to evaluate the symmetry of pit structures in both locations. Two-sample *t*-tests (2-tailed) were used to examine body size differences between the experimental groups of antlion larvae. The non-parametric Mann-Whitney *U*-test was chosen to compare pit diameters between experimental groups. Because we predicted that fed antlions would construct larger pits than unfed ones, 1-tailed *p* values were examined in the Mann-Whitney *U*-test. All statistics were calculated using SYSTAT 11 (SYSTAT Software, Inc.).

RESULTS

Pit structures: field vs. captivity

Three antlion larvae built their pits within 1 h after they were placed in the paper cups in the laboratory ($n = 17$). Over 75% (13 of 17) of the larvae successfully built their pits within 3 h. All individuals had completed their pits within 15 h after they were placed in paper cups containing

sand.

Significantly greater E-W (diameter_(E-W)) and N-S (diameter_(N-S)) diameters were recorded in the laboratory (diameter_(E-W) = 21.6 ± 4.5 mm, diameter_(N-S) = 21.5 ± 4.7 mm) than in the field (diameter_(E-W) = 17.4 ± 5.3 mm, diameter_(N-S) = 17.2 ± 5.5 mm) (diameter_(E-W): $t_{16} = 7.1$, $p < 0.01$; diameter_(N-S): $t_{16} = 6.7$, $p < 0.01$). Additionally, greater pit depths were measured in the laboratory (13.7 ± 3.5 mm) than in the field (9.5 ± 3.5 mm) ($t_{16} = 6.2$, $p < 0.01$).

Highly symmetrical pits were found in both the field (diameter_(N-S) = 0.99 diameter_(E-W) - 0.06 , $R^2 = 0.89$, $p < 0.01$, $n = 17$) and the laboratory (diameter_(N-S) = 0.99 diameter_(E-W) + 0.10 , $R^2 = 0.92$, $p < 0.01$, $n = 17$). Larval body lengths (6.1 ± 1.6 mm) were positively correlated with pit diameters_(N-S) in both the field ($n = 17$, $R^2 = 0.73$, $p < 0.01$) and laboratory ($n = 17$, $R^2 = 0.81$, $p < 0.01$).

Laboratory experiments

Before the experiments began, body lengths of larvae in the 2 free-building groups (free-building/unfed vs. free-building/fed) did not significantly differ ($t_{13} = 1.69$, $p > 0.05$), and neither did those in the not-building groups (not-building/unfed vs. not-building/fed) ($t_{18} = 1.64$, $p > 0.05$). For the free-building groups, despite feeding treatments, the size of the established pits gradually increased over time (Fig. 1). In addition, no significant differences were found between the fed and unfed groups on 7 measurements of pit sizes during 32 d of observation (day 2: Mann-Whitney $U = 31$, $n = n_1 + n_2 = 15$, $p = 0.364$; day 7: $U = 25$, $n = 15$, $p = 0.364$; day 12: $U = 18$, $n = 15$, $p = 0.124$; day 17: $U = 34$, $n = 15$, $p = 0.244$; day 22: $U = 21$, $n = 13$, $p = 0.5$; day 27: $U = 31$, $n = 14$, $p = 0.203$; day 32: $U = 24$, $n = 12$, $p = 0.146$) (Fig. 1). In the not-building groups, in which antlion larvae had been prevented from pit construction for 22 d, fed larvae constructed significantly larger pits than did unfed larvae when they were allowed to build pits (day 22: $U = 67$, $n = 18$, $p = 0.010$; day 27: $U = 78$, $n = 19$, $p = 0.004$; day 32: $U = 84$, $n = 19$, $p = 0.001$) (Fig. 2).

DISCUSSION

Larvae of the antlion *C. sauteri* have pit-building behaviors similar to other antlion species in both the field and laboratory. As for the rebuilding time, our study showed that *C. sauteri* built pits

within 15 h after they were placed in paper cups containing sand, in agreement with Wheeler (1930) who suggested that 10-15 h is enough for antlion larvae to rebuild their traps. Greater pit sizes and depths were built in captivity than in the field by *C. sauteri* larvae. This difference may have resulted from finer and looser particles of sieved sand which was carried back to the laboratory (Gatti and Farji-Brener 2002, Farji-Brener 2003), and less disturbance by other animals or wind in captivity. *Cueta sauteri* larvae built highly symmetrical pits in both the field and laboratory despite variations in pit diameters and depths. A more-symmetrical pit maximizes the pit surface area for any given perimeter. This may enable the antlion to increase its prey encounters. Body lengths of *C. sauteri* larvae were positively correlated with pit sizes in both the field and captivity as found for many antlion species (Heinrich and Heinrich 1984, Griffiths 1986, Hauber 1999, Scharf et al 2009). Thus, *C. sauteri* larvae exhibited similar pit-building behaviors and pit structures in both the field and laboratory. The finding of a similarity in pit construction between the field and laboratory supports the notion that the pit-building behavior of *C. sauteri* is suitable for study in the laboratory, such as with spatial distribution and optimal foraging models (Heinrich and Heinrich 1984).

For *C. sauteri* larvae, the present study demonstrated that variations in pit sizes were associated with both previous pit-building experience and food limitation. For the free-building groups, despite feeding treatments, the size of established pits gradually increased over time, indicating that antlions subsequently enlarged

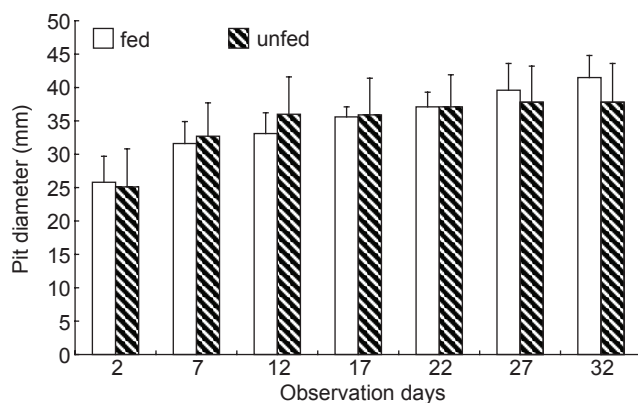


Fig. 1. Variations in mean pit diameters (\pm S.E.) between the fed and unfed groups on 7 measurements of pit sizes during 32 d of observation in the laboratory of free-building antlion *Cueta sauteri* larvae. * $p < 0.05$; ** $p < 0.01$.

their pits over time (Griffiths 1980). Based on 7 measurements during 32 d of observation, pit sizes of free-building larvae did not differ between the fed and unfed groups. This might be because *C. sauteri* larvae constructed similarly sized initial pits on day 2 between the fed and unfed groups (with only 2 d of food shortage) and then subsequently enlarged those initial pits without pit relocation, which was controlled for in the present study. The energy expenditure of pit enlargement is definitely smaller than that of pit relocation and can be afforded by unfed larvae even after a long period of food shortage. Thus, no significant difference in pit size was found even after 32 d of food shortage between fed and unfed groups in the present study. On the contrary, for those *C. sauteri* larvae that had previously been prevented from building pits, after being allowed to build on day 22, unfed larvae (with 22 d of food shortage) had less energy left to construct an initial pit and therefore built pits significantly smaller than fed ones.

In this study, no significant difference in trap size was recorded for free-building *C. sauteri* larvae between the fed and unfed groups during 32 d. This differs from studies of Eltz (1997) and Hauber (1999) where significant differences in pit diameters were found between fed and unfed larvae after 6 d of food shortage in free-building *Myrmeleon mobilis* and *M. carolinus*. Two hypotheses, including species variations in starvation tolerance and site variations in prey availability, may explain these divergent results.

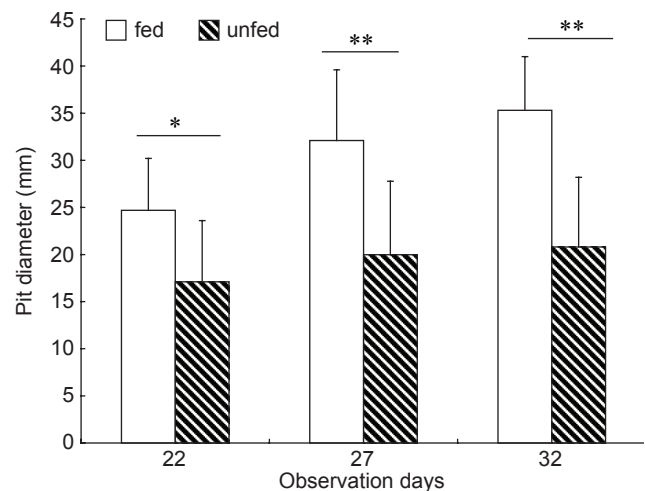


Fig. 2. Variations in mean pit diameters (\pm S.E.) between the fed and unfed groups on 3 measurements of pit sizes when they were allowed to build pits in the laboratory of previously not-building antlion *Cueta sauteri* larvae. * $p < 0.05$; ** $p < 0.01$.

First, our study species *C. sauteri*, a badland species, may be more tolerant of food limitations than are *M. mobilis* and *M. carolinus*. Wu (2006) observed that times which prey handling, killing, and sucking lasted were all significantly decreased only after 20 d of starvation in *C. sauteri* larvae. Additionally, Zyl et al. (1997) found that resting metabolic rates of *Cueta* sp. larvae were < 1/10 of the expected values for similarly sized poikilothermic invertebrates. Due to their low energy demands, antlion *Cueta* sp. larvae can survive prolonged periods of starvation. Second, site quality such as prey availability in the original habitats of antlions may have shaped their pit-building behaviors. Several studies suggested that higher metabolic rates and starvation mortalities were measured from antlions in relatively prey-rich habitats than those from prey-poor habitats (Lucas 1989, Matsura and Murao 1994, Crowley and Linton 1999). Hauber (1999) reported that the estimated daily predation rate was 1.7 prey items/pit for *M. carolinus* at the Archbold Biological Station (FL, U.S.A.) based on recording a successful predation event within 1.5 h of observation. For our study species of *C. sauteri*, the living habitat is characterized as a badland terrain with open, fine sand and scarce vegetation. No prey capture was observed at any pit during 4 h of collection time of *C. sauteri* larvae in the field; prey abundance was low in the badland habitat compared to the habitat of *M. carolinus*.

In conclusion, by controlling relocation and preventing pit building, this study indicated that food limitation and past pit-building experience were both related to variations in pit size for larvae of the antlion *C. sauteri*. Two hypotheses were suggested to explain the differences of results between our study and other studies. Our study species, *C. sauteri*, a badland species, may be more tolerant to food limitation than other species found in prey-rich habitats.

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