



# Pitfall vs fence traps in feeding efficiency of antlion larvae

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## Abstract

Larvae of pit-building antlions are expected to be more efficient at capturing prey than those of non-pit-builders. To test this prediction, feeding behaviors were compared in the same experimental conditions among pit-building *Baliga micans* and *Myrmeleon bore*, and non-pit-building *Distoleon contubernalis*. The number of prey eaten did not differ between species. *D. contubernalis* larvae used the walls of the experimental chamber as fence traps to capture prey. In the field, they were also found near edges of natural barriers, such as rocks, stones, tree roots, and plant stems. Artificial pitfall traps captured more arthropods near the edges of fences than farther from them. Larvae of the two pit-building species were located in the central part of the experimental chamber. In their natural habitats, the number of arthropods captured by artificial pitfall traps increased with pit size; thus, larger pits may be more efficient for capturing prey. In conclusion, pit-building and non-pit-building antlion larvae are both efficient hunters; the former hunt efficiently by making larger pitfall traps, and the latter do so by waiting for prey at the edge of the natural fences along which arthropods walk.

**Keywords** Foraging strategy · Myrmeleontidae · Neuroptera · Prey availability · Sit-and-wait predator

## Introduction

Some species, but a monophyletic group, of antlions (Neuroptera: Myrmeleontidae) construct conical pitfalls and wait at the bottom for prey to fall in (Badano et al. 2017). This type of sit-and-wait predation is efficient in terms of capture success without costs of actively searching for or pursuing prey (Scharf et al. 2011). Antlion pitfalls can be easily found in dunes of sand or loose soil, and therefore many studies have examined antlion feeding behavior (Griffiths 1980, 1982; Matura 1986; Kuszewska et al. 2016; Miler et al. 2018), pit structure and function (Fertin and Casas 2006; Devetak et al. 2012; Humeau et al. 2015), spacing (Morisita 1959; Griffiths 1991), microhabitat and substrate selection (Morisita 1952; Matura et al. 2005; Devetak and Arnett 2015; Barkae et al. 2017), pit relocation (Heinrich and Heinrich 1984; Matura 1987; Matura and Takano

1989; Matura and Muraio 1994; Scharf and Ovadia 2006; Loria et al. 2008; Tsao and Okuyama 2013), thermal biology (Ábrahám 2003; Antoł et al. 2018), and life cycle (Furunishi and Masaki 1981, 1982, 1983; Griffiths 1985; Matura 1986; Matura et al. 1991).

However, larvae of most groups of antlions do not make pitfalls, but rather sit and wait just beneath the substrate to capture prey (Badano et al. 2017), which makes it difficult for researchers to find them in the field. Therefore, the following few studies have revealed their feeding behaviors and general biology. The larvae of *Brachynemurus* spp. capture prey successfully within 2 mm of their bodies (Cain 1987). The larvae of *Nophis teillardii* also capture prey passing within a few millimeters of their ambush sites (Simon 1985). The feeding behaviors of larval *Neuroleon microstenus* are less stereotypical, particularly in prey-carcass clearing, than those of pit-building species (Klokočovnik and Devetak 2014). Predator existence affects the frequency of ambush site relocation in *Lopezus fedtschenkoi* (Loria et al. 2008). The larvae of *Brachynemurus* spp. move around the open sandy habitat when temperatures exceed 45 °C by sunshine (Cain 1987). In *Furgella intermedia* and *Palpares annulatus*, however, larvae migrate vertically in the sand at high sand-surface temperatures in the daytime (Van Zyl et al. 1996). In *Distoleon contubernalis*, eggs can tolerate relatively high

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temperatures, up to 37.5 °C (Matsura et al. 2001). The larvae of *Nophis teillardii*, *Synclisis baetica*, *Distoleon tetragrammicus* and *Neuroleon microstenus* prefer substrates with a certain particle size (Devetak and Arnett 2015).

In general, larvae that build pits are expected to capture prey more efficiently than those that do not, although the latter relocate their ambush sites more frequently because they do not bear the cost of making and maintaining pits (Elimelech and Pinshow 2008; Scharf et al. 2011; Lima and Silva 2017). The pitfall traps are relatively easy to construct, but they have two main disadvantages: they require a specific microhabitat, and they also may not retain larger prey unless the antlion is present at the bottom of the pit (Ruxton and Hansell 2009). Thus, antlions must remain in their traps, rendering them vulnerable to predators and parasitoids that cue on the traps (Ruxton and Hansell 2009; Tsao and Okuyama 2012). Therefore, antlions face a trade-off between hunting efficiency and predation/parasitism risks. However, reports on predation/parasitism of antlions are scarce, so this aspect is quite speculative. Only a few studies show that antlion larvae are preyed upon by scrub-jays (Hauber 1999), ants (Gatti and Farji-Brener 2002), carabid beetles and wolf spiders (Loria et al. 2008), and two groups of parasitoids (Baba 1953; Baba et al. 1987; Matsura and Takano 1989; Matsura et al. 1998; Uchôa and Missirian 2014).

The present study was conceived with a rare opportunity to observe and collect a sufficient number of larvae of non-pit-building species. We compared feeding efficiency between this non-pit-building species, *Distoleon contubernalis* (McLachlan, 1875), and pit-building species, *Baliga micans* (McLachlan, 1875) and *Myrmeleon bore* (Tjeder, 1941). Our results show that the larvae of *D. contubernalis* captured prey as efficiently as pit-building species. This unexpectedly efficient feeding rate may be due to the structure of their ambush sites, which have natural barriers acting as “fence traps” to capture prey. This foraging strategy has not been reported previously in antlion larvae.

## Materials and methods

### Laboratory observations

A total of 88 larvae of pit-building *B. micans* were collected at a denuded slope along small trails in a secondary deciduous forest near the Sayama-ko Lake, Tokyo, Japan (35°45'40"N, 139°23'05"E) on 5 May 2016, 10 September 2016, and 3 September 2017. At this site, the larvae made pits on the surface of dry soil around exposed tree roots (Fig. 1a). A total of 54 larvae of pit-building *M. bore* were collected from the dry bed of the Tama-gawa River in Akiruno, Tokyo, Japan (35°42'45"N, 139°19'45"E) on 26 April 2017 and 5 September 2017. Larval *M. bore* was

found on the open parts of sands where gramineous plants grow in patches (Fig. 1b). A total of 62 larvae of non-pit-building *D. contubernalis* were collected at the seashore in Nagahama, Miura Peninsula, Kanagawa, Japan (35°11'18"N, 139°37'02"E) on 4 May 2016, 5 September 2016 and 15 September 2017. This open, sandy site is surrounded by large rocks and scattered vegetation (Fig. 1c). Although the larvae of *M. bore* and *D. contubernalis* are usually found in the same seashore areas (Hayashi 2013; Ezawa and Tsurusaki 2015), these species did not coexist at our study sites.

Dorsal photographs of the collected larvae were taken on 1-mm graph paper. The larvae were then reared individually in glass vessels (40 mm in diameter, 60 mm in height for smaller larvae; 60 mm in diameter, 90 mm in height for larger larvae). The lower halves of the vessels were filled with sand or soil obtained from the collection sites. To avoid serious desiccation, 3 ml water was added to the vessels twice a week. Larvae were maintained in a large insect rearing room at 25 ± 1 °C with a 14-h light/10-h dark photoperiod. Twice a week, they were fed live chironomid larvae, *Prophiloceris akamusi* (Tokunaga, 1938), at their final instar. The chironomids were maintained in water at 4 °C. After behavioral observations, most larvae were reared to adulthood. Species identification of larvae and adults was based on Hayashi (2013) and Sekimoto (2014).

Behavioral trials were recorded using three video cameras (HDR-SR7, Sony, Tokyo, Japan). The larvae were placed in a plastic chamber (Fig. 2; 150 mm in diameter, 65 mm in height). The lower 30 mm of the chamber was filled with light-colored beach sand to standardize the substrate quality and to enable us to distinguish animals from the substrate during nighttime observations. Antlion larvae were placed individually at the chamber's center in the late afternoon, and video recording began just before dark on the next day, when three live larval crickets, *Gryllus bimaculatus* De Geer, 1773, with head widths of 0.82–1.84 mm (1.12 ± 0.06,  $N=30$ ) were introduced to the central part of the chamber. The chamber was covered with a clear glass plate (Fig. 2) and a millimeter scale was put beside the chamber. Larval crickets are suitable prey for antlion larvae (Baba 1953; Matsura 1986) because they walk on the sand surface without digging or flying, which offering a simple situation of prey availability. The night-shot function of the video camera was used at night, and larval behaviors were recorded for 13 h covering the whole 10-h dark phase. The diurnal activity patterns of antlion larvae are not well known, although a few studies have revealed that they capture prey at any time of the day (Matsura 1986), metabolize at a nearly constant rate throughout the day (Van Zyl et al. 1997), and select illuminated or shaded habitats depending on the situation (Scharf et al. 2008). We did not observe feeding behaviors of the larvae not making pitfalls (in *B. micans* and *M. bore*) or not opening their mandibles (in *D. contubernalis*) on



**Fig. 1** Habitats of the antlion species. **a** Pitfall-building *Baliga micans*, **b** pitfall-building *Myrmeleon bore*, and **c** non-pitfall-building *Distoleon contubernalis*

the day of video recording. These larvae molted into next instar larvae or prepupated after 10 or more days, during which time they did not feed. Newly molted larvae were also avoided because they did not eat prey for several days. Each larva was subjected to one behavioral trial. Ultimately, the feeding behaviors of 55 *B. micans*, 46 *M. bore*, and 51 *D. contubernalis* larvae were analyzed.

The larval instars were identified by using the photographs to measure head width between the left and right outer eye margins and mandible length from the tip to the outer base (HW and ML, respectively, in Supplementary Fig. 1). In Japanese antlion species, the 2nd- and 3rd-instar larvae are abundant in spring to early summer and the 1st-instar larvae increased from summer (Furunishi and Masaki 1981, 1982, 1983; Matura et al. 1991). In *B. micans* and *M. bore*, the maximum and minimum pitfall diameters were measured on screen shots of the videos using Picture Motion Browser software (Sony, Tokyo, Japan), and the average value was used to estimate the pit diameter (Fig. 2). The minimum linear distance from the center of the pit (or the larval head in non-pit-building species) to the wall of the observation chamber was measured to estimate the “ambush

sites” (Fig. 2). When larvae captured crickets, the duration from capturing to releasing it was measured to estimate “feeding time” (but impossible for some larvae because of unclear pictures), and the minimum linear distance from the capture site to the chamber wall was measured to estimate “feeding sites”.

### Ambush sites in the fields

The distance from the pit center to the edge of a natural barrier (e.g., rocks, stones, tree roots, or grass stems) was measured using a ruler for all *B. micans* pits found in the field on 10 September 2016 and 21 May 2017. On 26 April 2017, the pits of *M. bore* were also measured. Individual larval instars were not identified because the pit size overlapped among instars (Supplementary Fig. 1).

On 20 October 2016, the habitat surface was carefully searched by sifting of sand with a wire-meshed sifter. When larval *D. contubernalis* was found, the minimum distance from the larval head position to the natural barrier edge was measured.



**Fig. 2** Chamber used for the observation of larval antlion behavior (150 mm in diameter, 65 mm in height, sand 30 mm in depth) with three larval crickets introduced as live prey (arrows). Pit size was determined using the longest and shortest distances between pit edges, and the minimum distance from the pit center (larval ambush site) to the plastic wall was measured. A scale is included at the left

The substrate particle sizes were determined by sieving of dried samples with standard sieves, as in Matura et al. (2005) (fine, diameter < 0.25 mm; medium, 0.25–0.5 mm; coarse, 0.5–1 mm; very coarse, 1–2 mm; gravel, > 2 mm), and each size class was expressed as percent weight of the total sample.

### Prey availability

Prey availability was assessed using artificial pitfall traps. At study sites inhabited by *B. micans* and *M. bore*, cylindrical plastic vessels of various diameters (15, 30, and 72 mm) were used to examine the effects of pit size on prey capture on 4 June and 3 September 2017, and 9 June and 4 September 2017 for the respective species. All were done on fine days. The three sizes of vessels were buried at ca. 30-cm intervals (Supplementary Fig. 2A), and 10 sets of these traps were placed at more than 1-m intervals. The vessels were not baited. After 24 h, the vessels were recovered and brought to the laboratory of Tokyo Metropolitan University, Hachioji, Tokyo. Animals in the vessels were killed by placing them at  $-20\text{ }^{\circ}\text{C}$  for 2 h. Each sample was identified to the family level and fresh weight was determined to the nearest 0.001 g using a microbalance (BL-320H, Shimadzu, Kyoto, Japan).

At the study site inhabited by *D. contubernalis*, five wooden boards (200 mm high, 400 mm long, 6.2 mm thick) were buried, to act as fences, 100 mm deep and more than 3 m apart. Cylindrical plastic vessels (27 mm in diameter,

$N=30$ ) were buried at 0, 10, and 20 cm from both sides of the board (Supplementary Fig. 2B). The vessels were not baited and recovered after 24 h. Animals in the vessels were killed by placing them at  $-20\text{ }^{\circ}\text{C}$  for 2 h, identified to the family level, and weighed to the nearest 0.001 g of fresh weight. Prey availability was assessed on two fine days on 24 May and 14 September 2017.

### Statistics

Values are shown as mean  $\pm$  standard errors (SE). Pearson's correlation coefficient was used to test the relationships between the sizes of the larvae and pitfalls in the two pit-building species. One-way analysis of variance (ANOVA) was used to compare the total prey weight per trap (or individual prey weight per trap) among the three sizes of artificial pitfall traps. One-way ANOVA was also used to compare the total weight of prey per trap (or individual prey weight per trap) among pitfall traps set at different distances from the artificial fence, and to compare the mean relocation distance among the three instars of the non-pit-building species. Two-way ANOVA was used to test the effects of instars and species of antlion larvae on the mean number of prey eaten, mean feeding time, and number of ambush site relocations. In this case, Levene's test was used to check the equality of variances. When variances were equal, the differences among mean values were analyzed by ANOVA  $F$  test, but when equality of variances could not be assumed at  $p < 0.05$ , Brown–Forsythe's  $F$  test was used (Brown and Forsythe 1974). Interspecific differences in the median distances between ambush sites and the edge of natural barriers were compared using the Kruskal–Wallis test with Scheffé's test for multiple comparisons. The distances from larval ambush sites to the wall of the observation chamber, and from larval predation sites to the wall, were analyzed for each species using chi-square ( $\chi^2$ ) tests.  $\chi^2$  tests were also used to detect differences between the observed and expected (equal) numbers of prey collected among pitfall traps of different sizes and distances from the artificial fence.

### Results

The particle size compositions (%) were as follows:  $30.7 \pm 1.0$  fine,  $25.7 \pm 1.1$  medium,  $22.0 \pm 0.6$  coarse,  $18.9 \pm 1.1$  very coarse, and  $2.6 \pm 1.0$  gravel at the site of *B. micans* ( $N=3$ );  $11.4 \pm 0.3$ ,  $47.1 \pm 1.8$ ,  $32.2 \pm 1.4$ ,  $7.9 \pm 0.8$ , and  $1.4 \pm 0.3$ , respectively, at the site of *M. bore* ( $N=3$ ); and  $23.6 \pm 0.6$ ,  $56.1 \pm 1.5$ ,  $16.8 \pm 1.3$ ,  $3.0 \pm 0.5$ , and  $0.5 \pm 0.2$ , respectively, at the site of *D. contubernalis* ( $N=3$ ). The composition of the substrates used in the experiments was similar to that of the *D. contubernalis* site ( $26.1 \pm 0.3$ ,

$50.6 \pm 0.8$ ,  $19.0 \pm 0.3$ ,  $3.5 \pm 0.2$ , and  $0.8 \pm 0.3$ , respectively,  $N=3$ ).

The three larval instars of all three species were discriminated by their head widths and mandible lengths (Supplementary Fig. 1). The head widths (mm) of the 1st-, 2nd-, and 3rd-instar larvae were  $0.925 \pm 0.015$  ( $N=30$ ),  $1.501 \pm 0.020$  ( $N=24$ ), and  $2.266 \pm 0.035$  ( $N=34$ ) in *B. micans*;  $0.709 \pm 0.007$  ( $N=16$ ),  $1.116 \pm 0.010$  ( $N=28$ ), and  $1.836 \pm 0.026$  ( $N=10$ ) in *M. bore*; and  $0.998 \pm 0.013$  ( $N=14$ ),  $1.634 \pm 0.020$  ( $N=21$ ), and  $2.606 \pm 0.025$  ( $N=27$ ) in *D. contubernalis*. The mandible lengths (mm) of the 1st-, 2nd-, and 3rd-instar larvae were  $1.252 \pm 0.016$  ( $N=30$ ),  $1.921 \pm 0.032$  ( $N=24$ ), and  $2.984 \pm 0.030$  ( $N=34$ ) in *B. micans*;  $1.098 \pm 0.008$  ( $N=16$ ),  $1.514 \pm 0.017$  ( $N=28$ ), and  $2.481 \pm 0.036$  ( $N=10$ ) in *M. bore*; and  $1.040 \pm 0.027$  ( $N=14$ ),  $1.588 \pm 0.022$  ( $N=21$ ), and  $2.543 \pm 0.024$  ( $N=27$ ) in *D. contubernalis*.

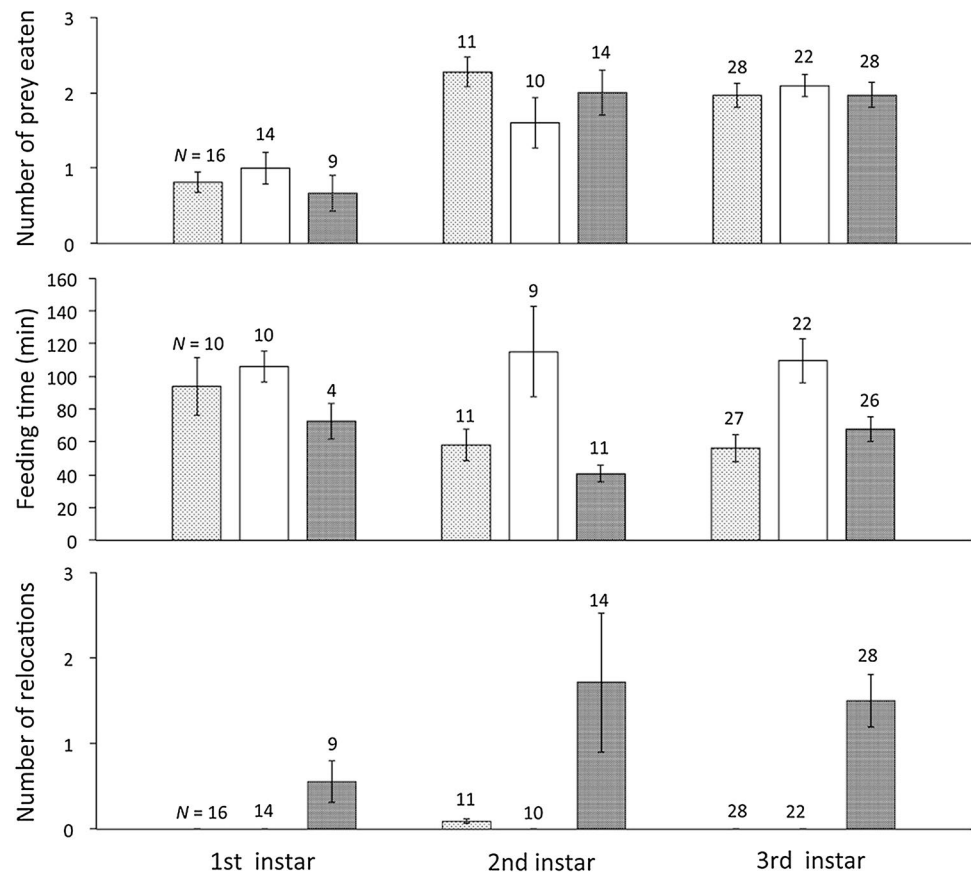
In pit-building species, the pitfall diameter (mm) increased with larval head width (Supplementary Fig. 1:  $r=0.634$ ,  $N=55$ ,  $p<0.01$  in *B. micans*;  $r=0.828$ ,  $N=46$ ,  $p<0.001$  in *M. bore*), but overlapped among the three instars:  $19.6 \pm 1.2$  ( $N=16$ ) in the 1st instar,  $36.3 \pm 5.3$  ( $N=11$ ) in the 2nd instar, and  $44.6 \pm 2.6$  ( $N=28$ ) in the 3rd instar in *B. micans*; and  $20.4 \pm 0.8$  ( $N=14$ ),  $33.9 \pm 1.9$  ( $N=10$ ), and  $45.4 \pm 1.9$  ( $N=22$ ), respectively, in *M. bore*.

The number of prey eaten differed among instars (Fig. 3: two-way ANOVA;  $F_{2,143}=27.74$ ,  $p<0.001$ ), but not among species ( $F_{2,143}=0.38$ ,  $p=0.68$ ) and species/instar interactions ( $F_{4,143}=1.15$ ,  $p=0.33$ ). Feeding time differed among the species (Fig. 3: Brown–Forsythe’s ANOVA;  $F_{2,121}=9.99$ ,  $p<0.001$ ), but not among instars ( $F_{2,121}=1.04$ ,  $p=0.36$ ) and species/instar interactions ( $F_{4,121}=1.29$ ,  $p=0.28$ ). The smaller species, *M. bore*, took longer to feed on individual prey across instars than the other two species.

The pit-building species did not relocate their pit sites, except for one observation of a 2nd-instar larva of *B. micans* (Fig. 3). The non-pit-building species usually relocated once as 1st-instar larvae, and twice as 2nd- and 3rd-instar larvae during 13-h video recordings (Fig. 3). Relocation rates differed between species (Brown–Forsythe’s ANOVA;  $F_{2,143}=15.59$ ,  $p<0.001$ ), but not among instars ( $F_{2,143}=1.28$ ,  $p=0.28$ ) and species/instar interactions ( $F_{4,143}=1.02$ ,  $p=0.40$ ).

The linear distances of ambush sites before and after relocation were 4.8–17.3 mm ( $13.8 \pm 2.3$ ,  $N=5$ ) in the 1st instar, 9.4–139.1 mm ( $51.1 \pm 7.9$ ,  $N=24$ ) in the 2nd instar, and 3.4–115.7 mm ( $50.7 \pm 4.6$ ,  $N=39$ ) in the 3rd instar. Smaller (1st instar) larvae relocated closer than larger ones (one-way ANOVA;  $F_{2,65}=3.14$ ,  $p=0.049$ ). Although the larvae of *B. micans* and *M. bore* can only walk backward when hiding

**Fig. 3** The mean ( $\pm$ SE) number of prey items eaten (upper), mean ( $\pm$ SE) feeding time on each prey item (middle), and mean ( $\pm$ SE) number of ambush site relocations (lower) in a 13-h video recording for the three instars of larvae of pit-building *Baliga micans* (dotted bars) and *Myrmeleon bore* (open bars), and non-pit-building *Distoleon contubernalis* (shaded bars). For statistical tests, see text



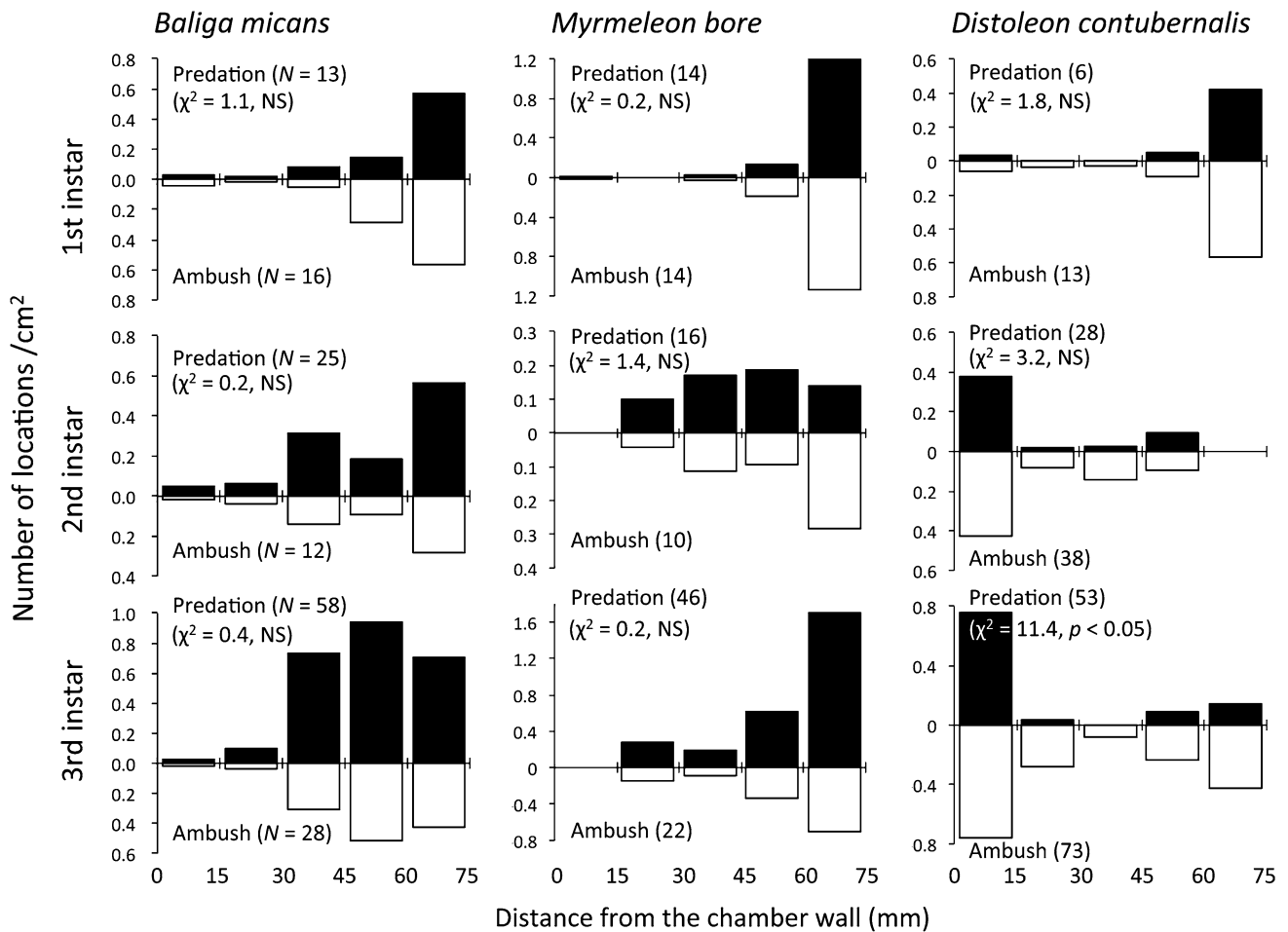
under substrates, the larvae of *D. contubernalis* can walk forward when relocating ambush sites and backward when hiding beneath the sands.

During 13-h video recordings, all ambush sites of the pit-building species were distributed near the center of the observation chamber, and all predation events occurred there (Fig. 4). In non-pit-building species, ambush sites of the 1st-instar larvae were located near the center, but those of the 2nd- and 3rd-instar larvae were close to the wall (Fig. 4). Predation events mostly occurred at these ambush sites. However, the ambush sites close to the wall of the 3rd-instar larvae were significantly more efficient in feeding than those near the center (Fig. 4).

In the field, 26.0% of non-pit-building *D. contubernalis* larvae were found close to natural barriers, such as rocks, stones, trees, and plants, and pit-building *B. micans* and *M.*

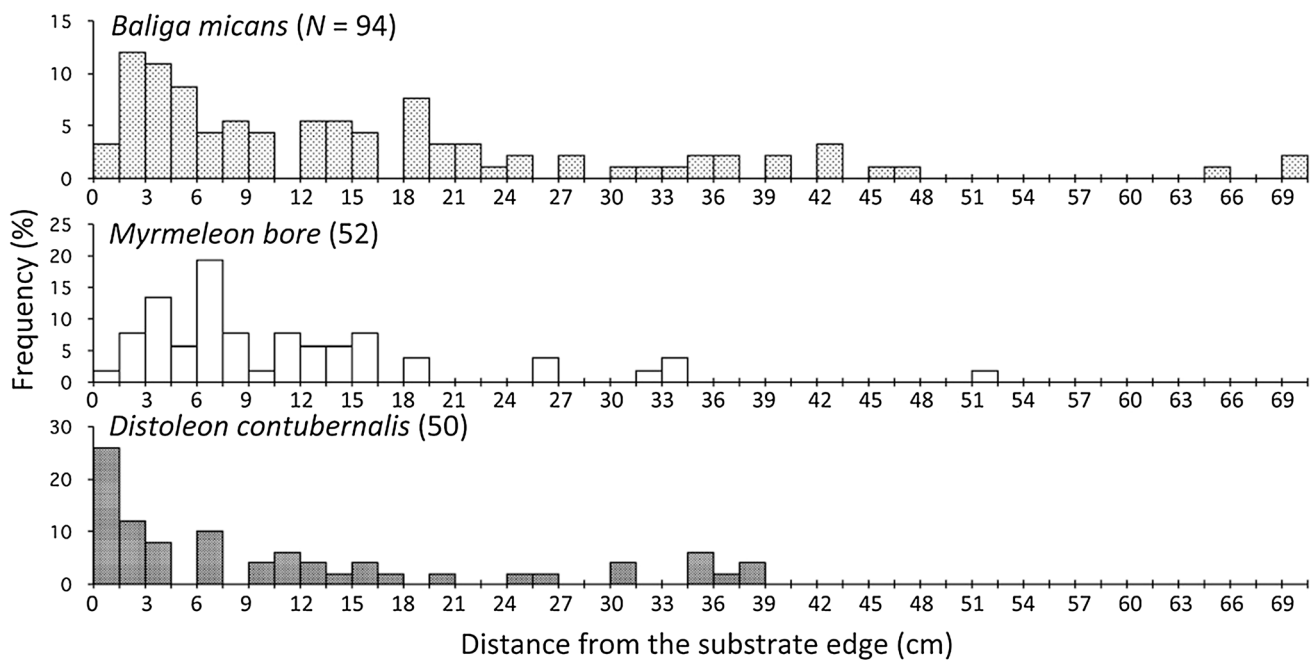
*bore* larvae were distributed farther away from such barriers (Fig. 5: median; 12.25 cm in *B. micans*, 7.50 cm in *M. bore*, 6.25 cm in *D. contubernalis*; Kruskal–Wallis test,  $\chi^2 = 6.98$ ,  $df = 2$ ,  $p = 0.030$ ). The distribution pattern of *D. contubernalis* differed from that of *B. micans* (Scheffé’s multiple comparison test;  $\chi^2 = 6.90$ ,  $p = 0.032$ ), whereas all other comparisons revealed no significant difference (*D. contubernalis* vs *M. bore*,  $\chi^2 = 1.65$ ,  $p = 0.44$ ; *M. bore* vs *B. micans*,  $\chi^2 = 1.41$ ,  $p = 0.49$ ).

The arthropods collected from the artificial pitfall traps included mainly arachnids and insects common to all three study sites (Supplementary Table 1). In the habitats of pit-building antlions, the total number of trapped prey increased with the pit diameter (Fig. 6). However, the total prey mass per trap and the mean individual body weight of prey were not always correlated with the pit diameter, probably because



**Fig. 4** Distance from the plastic wall to the ambush sites (white bars) and predation sites (black bars) in an observation chamber 150 mm in diameter for the three instars of larvae of pit-building *Baliga micans* and *Myrmeleon bore*, and non-pit-building *Distoleon contubernalis*. All ambush and predation sites observed during 13-h video recordings are shown as the number of sites per unit area because

the area differed according to the distance from the wall (63.59 cm<sup>2</sup> in 0–15 mm, 49.46 cm<sup>2</sup> in 15–30 mm, 35.33 cm<sup>2</sup> in 30–45 mm, 21.20 cm<sup>2</sup> in 45–60 mm, 7.07 cm<sup>2</sup> in 60–75 mm). *p* values of chi-square tests of ambush and predation site frequencies are shown in parentheses (NS:  $p > 0.05$ )



**Fig. 5** Frequency distributions of the distances between ambush sites and the edges of natural barriers, such as rocks, stones, trees, and plants, in the habitats of pit-building *Baliga micans* (dotted bars) and

*Myrmeleon bore* (open bars), and non-pit-building *Distoleon contubernalis* (shaded bars)

of a great variation in individual prey size (Fig. 6). In the habitat of the non-pit-building antlion, the total number of trapped prey decreased with the distance from the artificial fence (Fig. 7). The total mass of prey per trap and the mean individual body weight of prey showed no clear relationship with distance (Fig. 7). A few prey had fresh body weights more than 0.1 g.

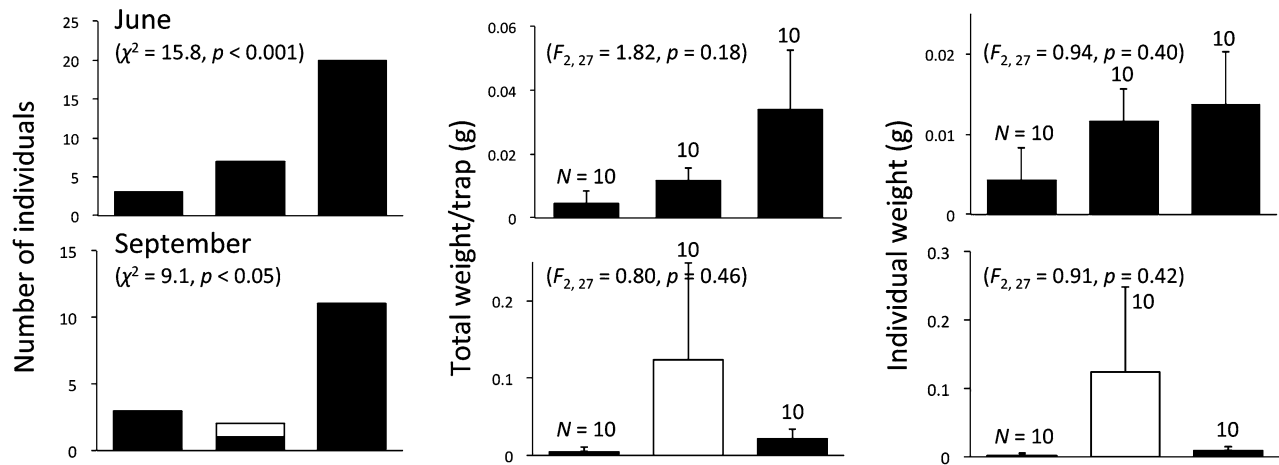
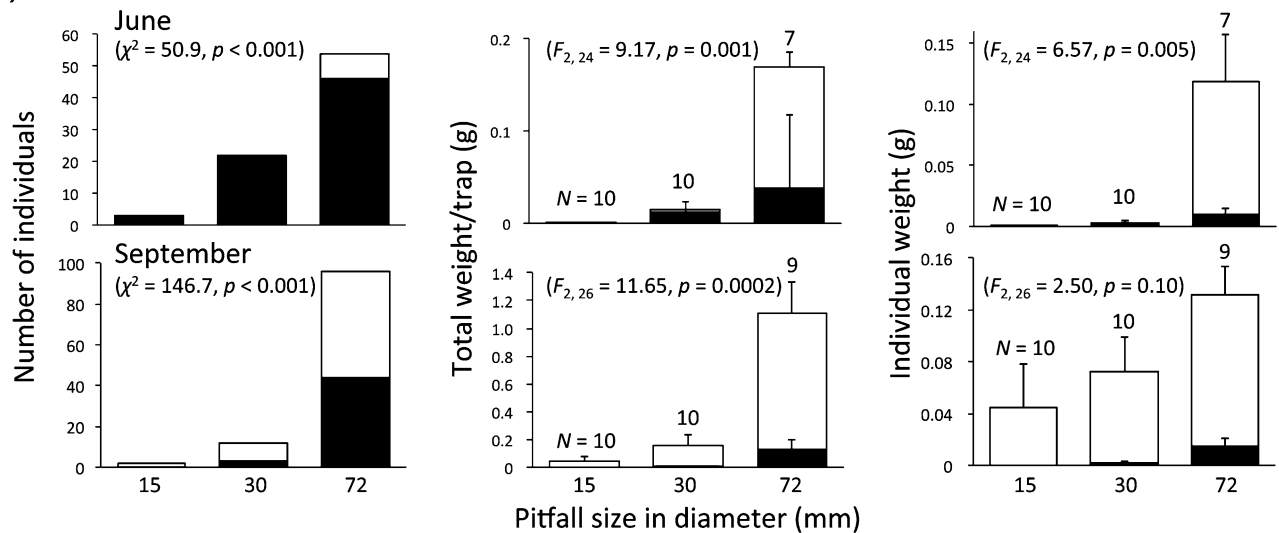
## Discussion

Previous studies of the function of conical pitfall traps built by antlion larvae have emphasized their efficiency in capturing prey (Scharf et al. 2011). Pit size increases with body size and instar, and the larger larvae can consume larger prey items (Griffiths 1980, 1986; Heinrich and Heinrich 1984; Matsura 1986; Hauber 1999; Scharf et al. 2009; Barkae et al. 2012; Humeau et al. 2015; Miler et al. 2018). In the field, pit-building antlion larvae consume a variety of species of arthropods (Baba 1953; Matsura 1986), and sometimes capture prey that exceed their own body size (Tsurusaki et al. 2012). In our study, the pit size of *B. micans* and *M. bore* increased with larval head width. In our field surveys, a variety of arthropods, such as spiders and insects, fell into the artificial pitfall traps, despite the lack of bait. Larger traps captured more prey than did smaller traps. Thus, pit-building antlion larvae can capture more prey by using larger pitfalls. However, the individual and total masses of prey did not

always increase with the diameter of the traps, due to the larger degree of variation in prey size.

However, pit building and maintenance are energetically costly. Although antlion larvae generally have low metabolic rates, their expenditure during pit constructions is about 10 times their resting metabolic rate and increases with pit diameter (Lucas 1985). If the traps are experimentally destroyed 3 times a week, the larval period becomes longer and eclosed adults are smaller than control adults, suggesting that the maintenance of pits is costly (Lima and Silva 2017). Therefore, antlion larvae rarely relocate after they have built pits (Scharf and Ovadia 2006). However, relocation rates are increased after starvation for more than 30 days in *Myrmeleon immaculatus* (Heinrich and Heinrich 1984), 72 days in *M. bore*, 54 days in *M. formicarius*, and 25 days in *Baliga micans* (Matsura and Murao 1994). Limited food availability also increases the relocation rates (Griffiths 1986; Hauber 1999; Tsao and Okuyama 2013). The presence of neighbors, simulated experimentally by tossing sand into the pits, decreases the relocation rates in *M. persimilis* larvae (Tsao and Okuyama 2013). Light/dark conditions also influenced the relocation rates (Scharf et al. 2008). In our observations, pit relocation occurred once in *B. micans* and never in *M. bore*, which is supported by the findings of Matsura (1987) and Matsura and Murao (1994).

The risks of predation and parasitism may increase with pit occupation (Ruxton and Hansell 2009; Tsao and Okuyama 2012). Florida scrub jays feed on pit-building antlion

*Baliga micans**Myrmeleon bore*

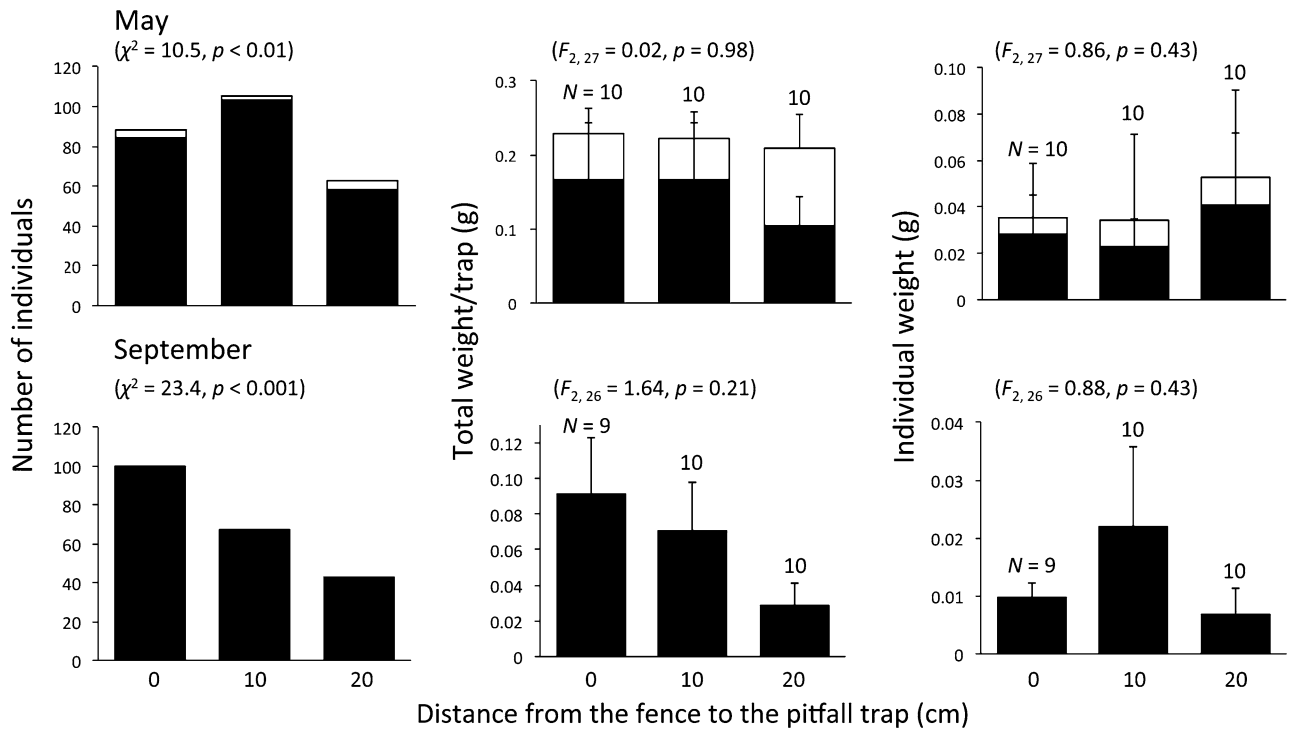
**Fig. 6** Prey captured in June and September by three sizes (15, 30 and 72 mm in diameter) of cylindrical artificial pitfall traps in the habitats of pit-building *Baliga micans* and *Myrmeleon bore*. The total number of prey collected by 10 traps, the mean (+SE) fresh weight of total prey per trap, and the mean (+SE) fresh weight of

individual prey are shown. *Black bars* represent prey with fresh body weight < 0.1 g. As some traps in the *M. bore* habitat were accidentally disturbed or lost after 24 h, the total number of prey is adjusted to 10 traps

larvae, locating their pits and preferentially attacking those with larger pits (Hauber 1999). Ants are potential enemies of antlions in ant-acacia areas of Costa Rica (Gatti and Farji-Brener 2002). Carabid beetles and wolf spiders also attack antlion larvae in laboratory settings (Loria et al. 2008). Two groups of parasitoids, Chalcididae (Hymenoptera) and Bombyliidae (Diptera), can infect up to 50% of pit-building antlion larvae (Baba 1953; Baba et al. 1987; Matsura and Takano 1989; Matsura et al. 1998; Uchôa and Missirian 2014). If the parasitoids use pitfalls as a cue to locate their hosts, pit holders may suffer serious costs of parasitism (Matsura et al. 1998). We did not see any predation or parasites during our field surveys or laboratory rearing.

However, larvae of most antlion species do not build pits. Those that live in dunes, seaside and riverine sands, and dry forest soils can hide just beneath the surface and wait for prey to pass within the radius of their open mandibles. They might use sand-borne vibrations to locate their prey as pit-builders do (e.g., Devetak et al. 2007; Fertin and Casas 2007; Kuszevska et al. 2016) and visual signals of prey with their eyes that are more protruded than pit-builders (e.g., Devetak et al. 2010). However, prey capture must occur within a few millimeters of the antlion's body (Lucas 1982; Simon 1985; Cain 1987; Crowley and Linton 1999). Therefore, the feeding efficiencies of non-pit-builders are expected to be lower than those of pit-builders under the same conditions.



*Distoleon contubernalis*

**Fig. 7** Prey captured in June and September by cylindrical artificial pitfall traps set 0, 10 and 20 cm away from the artificial wooden board in the habitats of non-pit-building *Distoleon contubernalis*. The total number of prey collected by 10 traps, the mean (+SE) fresh

weight of total prey per trap, and the mean (+SE) fresh weight of individual prey are shown. *Black bars* represent values for prey with fresh body weight < 0.1 g. As one of 10 traps was accidentally lost after 24 h, the total number of prey is adjusted to 10 traps

To compensate for lower feeding efficiency, non-pit-builders relocate their ambush sites more frequently than pit-builders (Elimelech and Pinshow 2008). In our observations, only one pit-building larva relocated its pit, and non-pit-building larvae walked (1–2 times/13 h on average) short distances (14–50 mm according to instars) to change their ambush sites.

Feeding time differed among the species examined in this study. Across instars, the smallest species (*M. bore*) spent more time handling prey than did any other species. However, the number of prey items eaten was unexpectedly similar among species. This may be caused by the fact that larvae of non-pit-building species use “fence traps” to capture prey, which is a previously undescribed feeding strategy of antlion larvae. They tended to ambush around the edge of our laboratory chamber. Although the ambush sites in pit-building species were distributed near the center of the chamber, those in non-pit-building species were distributed close to the chamber wall, excepting the less-mobile 1st instar. Our observation period (< 24 h) may have been insufficient for the 1st-instar larvae to establish ambush sites farther from their release sites. The 3rd-instar larvae with ambush sites close to the wall fed more efficiently than did those near the center. Moreover, our field surveys demonstrated that

non-pit-builders are found frequently at the edges of natural barriers. Ground-dwelling arthropods are potential prey items for antlion larvae, and those trapped by the artificial pitfalls were most abundant near the experimentally buried fences. Arthropods living in such open habitats may be nocturnal and prefer to walk along the edges of barriers because of thigmotactic behavior (Creed and Miller 1990; Patt and Pfannenstiel 2009). Therefore, the feeding rates may be higher at the edges of natural barriers than in open habitats.

Interestingly, antlion larvae are reported to change feeding modes from ambush under substrate to pitfall trap construction in *Myrmecaelurus* sp. (Elimelech and Pinshow 2008), *Myrmecaelurus trigrammus* (Devetak et al. 2013), and *Myrmeleon persimilis* (Tsao and Okuyama 2012). In our study, some pit-building larvae stopped repairing pits and ate little or hid under substrates without making pits when introduced to the new rearing vessels. However, this behavior seems to reflect physiologically inactive stages of their normal development, rather than an alternative ambush strategy. These larvae molted to the next instar or prepupated after a relatively long period.

In this study, we used the same substrate for behavioral observations despite differences in particle size composition among habitats. *B. micans* builds pits in fine soil, but

the other two species live in sand of medium particles. Larvae of *M. bore* are known to select substrates with medium particles (Matsura et al. 2005). Sand particle size affects the distance of prey detection through vibration signals (e.g., Devetak 2014) and prey escaping behaviors from pits (e.g., Lucas 1982; Allen and Croft 1985); therefore, a more detailed comparison of interspecific larval feeding rate is needed.

In conclusion, pit-building and non-pit-building antlion larvae are both efficient in capturing prey. The former makes larger conical pitfall traps and waits for prey, and the latter waits for prey at the edges of the natural fences along which arthropods walk. In the future, we need to examine how common such fence trapping is among non-pit-building antlion species. The way in which antlions arrange themselves in space may depend on female oviposition sites. They lay eggs one by one in beach sand at depths of 7.5 mm in pit-building *M. bore* and 10 mm in non-pit-building *D. contubernalis* (Matsura et al. 2001). Therefore, larvae of non-pit-building species might occur at the edges of natural barriers because of movement after hatching, whereas pit-building antlion larvae occupy places close to oviposition sites. Future studies should examine interspecific spatial partitioning in habitats where they coexist.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** This article does not report on any study with human participants performed by any of the authors.

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