ARTICLE

Optimal pit site selection in antlion larvae: the relationship between prey availability and pit maintenance costs

Taka Hayashi[1] · Kina Hayashi[2] · Noriko Hayashi[3] · Fumio Hayashi[4]

Abstract

Traps are an efficient method of capturing prey for ambush predators, but trap building and maintenance are costly. We describe suitable hunting sites for pit-building antlion larvae living in sand dunes based on its cost–benefit relationship. In the field, antlion pits were located near natural barriers, such as cliffs, rocks and vegetation, but not closest to these barriers. Our results show that this pattern of pit location did not differ between populations; neither with or without the influence of a specific dipteran parasitoid of antlion larvae. Artificial pitfall traps deployed in their habitats revealed that invertebrates move along barriers, likely through thigmotaxis (wall hugging or wall-following), and drop sands in the traps set at barrier edges. In the laboratory, repeated artificial destruction of pits from larval antlions induced frequent pit relocation and rebuilding. This task reduces life history parameters, such as the larval growth and food conversion rates, suggesting a high cost of pit maintenance. Thus, antlion pits might shift away from barrier edges where more prey is available but pit destruction occurs more frequently due to wall-following invertebrates. Such disturbance may explain why antlions are not located closest to these barriers.

Keywords Cost–benefit relationship · Myrmeleontidae · Neuroptera · Optimal hunting site · Parasitic bee fly

Introduction

Many predatory animals exhibit an ambush or sit-and-wait mode of predation. This mode is more efficient when the encounter rate of prey is higher due to high mobility and density of prey, and directional prey movement (Helfman 1990; Scharf et al. 2006; Ross and Winterhalder 2015). It is also suggested a hump-shaped pattern linking prey abundance and foraging mode, i.e., ambush predation is more efficient in low and high densities of prey whereas in the middle range active predation is better (Scharf et al. 2009, 2011). Ambush predators must decide where to hunt (Smith et al. 2020) and how long to wait for prey (Wearmouth et al. 2014). Trap building is an efficient method of capturing prey as for example known from pit-building antlion and wormlion larvae, as well as web-building spiders; however, building and maintaining the traps carries energetic costs (Scharf et al. 2011). Larval antlions (Neuroptera: Myrmeleontidae) are typical ambush predators, some species build conical pitfall traps on sand and loose soil to efficiently capture prey that fall into the traps, while others lay in wait just beneath the land surface with no trap (Scharf and Ovadia 2006; Scharf et al. 2011; Badano et al. 2017).

Individuals of these predators can change ambush sites. The pit-building antlion larvae also relocate their pits. Pit relocation is triggered by both population density-independent and -dependent factors. For example, antlion larvae avoid substrates with particle sizes that are too fine or large (Simberloff et al. 1978; Botz et al. 2003; Devetak and Arnett 2015). They prefer substrates that are suitable for pit building in terms of particle size (Farji-Brener 2003; Matsura et al. 2005; Devetak 2008; Devetak et al. 2012; Klokočovnik

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et al. 2012) and soil type (Barkae et al. 2012). Wet soil is avoided (Simberloff et al. 1978) and sand moisture of 9–17% is preferred (Fukada and Nisimura 2021). Sand depth (shallow or deep) affects pit relocation rates (Loria et al. 2008; Adar et al. 2016). High predation risk (i.e., the presence of predators) decreases pit relocation rates (Loria et al. 2008). The relocation rate increases under the conditions of starvation (Simberloff et al. 1978; Heinrich and Heinrich 1984; Griffiths 1986; Rosenberg 1987; Matsura and Murao 1994; Eltz 1997). Relocation based on prey availability also occurs in antlion larvae (Matsura 1987; Scharf and Ovadia 2006; Scharf et al. 2011).

Population density-dependent pit relocation occurs at high population densities. Larvae relocate their pits more frequently with increasing larval density, and the pits become more uniformly distributed (Matsura and Takano 1989) or expand outward if additional area is available (Linton et al. 1991; Day and Zalucki 2000). One response to density is frequent sand tossing by larvae into neighboring pits (Simberloff et al. 1978; Matsura and Takano 1989; Day and Zalucki 2000). Sand tossing is essential to maintain efficient traps in which prey will slip to the center, where the head of the antlion larva is positioned (Lucas 1989; Loiterton and Magrath 1996; Fertin and Casas 2006; Franks et al. 2019; Büsse et al. 2021). In *Myrmeleon persimilis*, however, artificial sand tossing into the antlion pit reduced the larval pit relocation rate (Tsao and Okuyama 2013). This contradictory result is predicted by the individual-based ESS model, which states that under conditions where prey is not randomly distributed and antlion larvae can learn it from their past foraging experiences, they continue to stay in neighborhoods where food availability is likely higher than in other open areas (Tsao and Okuyama 2013).

Here, a cost–benefit approach is useful when analyzing antlion's decision to relocate between ambush sites, because pit building and maintenance is costly (Elimelech and Pinshow 2008). The resting metabolic rates of antlion larvae are much lower than expected for similar-sized poikilothermic invertebrates, suggesting low energy demand to survive prolonged periods of starvation (van Zyl et al. 1997). Moreover, respiration rates after a week of starvation are around 20% of those before starvation (Matsura and Murao 1994). However, metabolic rates during pit construction are twice as high (Elimelech and Pinshow 2008), or even 10–15 times higher (Lucas 1985), than resting metabolic rates.

In general, not all invertebrates are suitable sources of food. Antlion larvae, similar to other sit-and-wait predators, are considered opportunistic predators that take whatever falls into their pits, as long as it is of suitable size. Although this is likely for large than small larvae (Heinrich and Heinrich 1984), inedible invertebrates should be considered a source of disturbance rather than a food source (Scharf et al. 2010). The movement of invertebrates (also small vertebrates, such as lizards) in and around antlion pits results in pit destruction and the energy cost of repair is predicted to increase as encounter rates with invertebrates increase. The cost is not only of repair but also the antlions might miss hunting opportunities, while the pit is destroyed (a missed-opportunity cost). Invertebrates often exhibit thigmotaxis (wall-hugging or wall-following behavior) and move along a barrier (Creed and Miller 1990; Patt and Pfannenstiel 2009; Kohler et al. 2018; Doria et al. 2019). Thus, artificial pitfall traps captured more invertebrates when set along an artificial barrier than in open areas (Jingu and Hayashi 2018).

In this study, we examined the effect of pit distance from a barrier edge on invertebrate abundance. First, the pit distribution patterns relative to barrier edges were examined for two antlion species, *Myrmeleon bore* and *M. taiwanensis*, at six study sites in Japan. Second, destruction rates were assessed according to the amount of substrate that fell into artificial conical traps placed at various distances from an artificial barrier (wooden board) in the field. We assumed that more sand dropped into the conical trap when more invertebrates walked along the barrier edge and climbed the pit walls. At the same time, artificial pitfall traps were placed at various distances from the artificial barrier and the trapped invertebrates were compared in terms of number and mass. In the laboratory, we examined how pit destruction affects pit relocation frequency and distance, as well as behavior and life history variables, such as the larval feeding rate, larval period, and adult size.

Another disadvantage of pit builders is the higher probability of being parasitized (Ruxton and Hansell 2009; Tsao and Okuyama 2012). Antlions may face a trade-off between hunting efficiency and parasitism risk. Several studies have shown that pit-building antlion larvae are parasitized by parasitic bee flies (Diptera: Bombyliidae): *Villa myrmeleonostena* in Japan (Baba 1953; Baba et al. 1987; Matsura and Takano 1989; Matsura et al. 1998); *Micomitra stupida* around Europe, eastern Russia and the Middle East (Nartshuk et al. 2019); *Chrysanthrax pennyi* in Costa Rica (Evenhuis 2017); and *Paravilla* sp. in Brazil (Uchôa and Missirian 2014; Nonato et al. 2018). According to the observations of Baba (1953) and Matsura and Takano (1989), female *V. myrmeleonostena* oviposit from late summer to mid-autumn. Each egg is dropped while hovering around the antlion pit. If newly hatched larvae encounter antlion larvae of any instar, they enter a non-growing, endoparasitic stage within the host body. No differences in behavior or development have been detected between parasitized and non-parasitized antlion larvae (Baba 1953; Baba et al. 1987). Once the host antlion forms a cocoon and pupation occurs therein, the endoparasitic first-instar larva emerges and attaches to the ventral side of the thorax between the middle and hind legs of a newly formed host pupa, where the first-instar larva of the parasitic fly begins consuming the digested body of the host pupa.

After consuming the host pupal body (aside from pupal cuticle), the fully grown larva of the parasitic fly pupates in the host cocoon. The pupa of the parasitic fly has several hard spines located on its head (Fig. S1), which are used to open the host cocoon during the emergence of the fly (Baba 1953; Baba et al. 1987).

We are unaware of any study that has examined the rate of parasitism in antlions with regard to their spatial distribution pattern. At our two study sites, larvae of *M. bore* were parasitized heavily by the bee fly *V. myrmeleonostena* (Diptera: Bombyliidae) (Table 1, Fig. S1). Therefore, the relationship between the antlion pit distance from the barrier and the prevalence of the parasitoid was assessed in the field.

Materials and methods

Study sites and field data

Field data were collected on sunny and windless days from March 2020 to June 2021 at six study sites in Japan: North Tsugaru, Aomori Prefecture, northern Honshu; South Tsugaru, 10 km south of North Tsugaru on the same large sand dune; Ueda, Nagano Pref., central Honshu; Awajishima Island, located between Honshu and Shikoku; Yashima, Kagawa Pref., Shikoku; and Iriomotejima Island, located in the southern part of the Ryukyu Islands (Table 1). Field studies were conducted during two seasons in Awajishima and Iriomotejima (Table 1). All study sites were located within the upper part of sand dunes facing the sea, except

at Ueda, where the site faced a river, and vegetation including herbaceous plants and beach shrubs that present along cliffs on the inland side. A relatively homogenous habitat area, 100–200 m in length and parallel to the coast, was selected in each study site. The pit-building antlion species was *Myrmeleon bore* at five sites; at Iriomotejima, *M. taiwanensis* was present (Table 1). Antlion larvae did not occur at high density and two or more larval pits were rarely in close proximity. In North and South Tsugaru, the bee fly *V. myrmeleonostena* parasitized *M. bore* at high rates (Table 1).

The particle sizes of field-collected sand substrates ($N = 3$ from each study site) were determined through sieving of air-dried samples using standard sieves, as described by Matsura 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 in diameter), and each size class was expressed as a percentage of the total sample weight. Medium-sized sand dominated all study sites except for Awajishima and Yashima, where coarse sand was also abundant (Table 1).

Larvae of the studied antlions build conical pitfall traps on the surface of the sand substrates. To assess the locations of individual pitfalls in accordance with the method of Scharf et al. (2021), we measured the minimum distance from the pit edge to natural barriers, such as cliffs, rocks, vegetation (including herbaceous plants and beach shrubs), and dead tree branches. The pit diameter was also measured at its widest point.

Potential movements of invertebrates in sandy habitats occupied by antlions were assessed using a field sampling set consisting of an artificial fence and two types

Table 1 Six study sites with information regarding sampling date, habitats, antlion species, parasitoid prevalence, and substrate particle size composition (fine, < 0.25 mm; medium, 0.25–0.5 mm; coarse, 0.5–1 mm; very coarse, 1–2 mm; gravel, > 2 mm in diameter)

Study site	Date of study	Habitat	Antlion (% Parasitism by bee flies)		Substrate particle size compositions (% dry weight)				
					Fine	Medium	Coarse	Very coarse	Gravel
North Tsugaru	15–16 May 2021	Seashore	*M. bore* (40.4, $N^a = 47$)	Mean	28.9	62.4	7.4	0.4	0.9
				SE	0.4	0.1	1.0	0.1	0.6
South Tsugaru	15–16 May 2021	Seashore	*M. bore* (57.1, $N = 28$)	Mean	19.7	69.5	10.5	0.3	0.1
				SE	0.4	0.8	0.5	0.0	0.1
Ueda	8–9 June 2021	Riverside	*M. bore* (0, $N = 3$)	Mean	22.2	47.1	24.9	4.5	1.3
				SE	1.3	0.6	1.0	0.3	0.2
Awajishima	10–11 October 2020 and 22–23 April 2021	Seashore	*M. bore* (0, $N = 2$)	Mean	7.1	39.2	38.3	13.8	1.6
				SE	0.4	0.8	0.6	0.3	0.3
Yashima	21–22 April 2021	Seashore	*M. bore* (0, $N = 33$)	Mean	10.8	33.1	46.9	7.7	1.4
				SE	1.4	0.8	2.0	0.4	0.3
Iriomotejima	24–25 March 2020 and 29–30 September 2020	Seashore	*M. taiwanensis* (0, $N = 31^b$)	Mean	17.8	55.6	24.5	2.1	0.0
				SE	0.5	0.4	0.2	0.3	0.0

[a] Number of antlion larvae examined

[b] From Hayashi et al. (2020)

of artificial traps (Fig. 1). A wooden board (labeled wb in Fig. 1; 600 mm × 100 mm, 3 mm thick) was buried to a depth of 50 mm to act as the barrier. Four empty cylindrical plastic tubes (29 mm inner diameter, 115 mm deep) were buried to act as pitfall traps (labeled pft in Fig. 1) at 0, 100, 200, and 400 mm from the board edge (300 mm at Iriomotejima in March 2020). These tubes were empty, with no bait. An additional four conical substrate traps (labeled cst in Fig. 1) on the opposite side of the board were used for estimation of the amount of substrate, such as sand and fine plant debris, falling into each trap (44 mm diameter, 26 mm depth); these traps were prepared by cutting portions from a paper egg carton (1 mm thickness). The traps allowed invertebrates to walk along the inner wall without slipping to the bottom. These traps were buried at distances 0, 100, 200, and 400 mm from the board edge (300 mm at Iriomotejima in March 2020). After burial, the bottom of each trap was cleared using an airbrush for camera lens cleaning.

During each sampling event, 10 or 12 field sampling sets (see Table 1) were placed 5–15 m apart at around 4–6 pm. The next morning (around 6–8 am), the pitfall traps were removed and capped, and the substrates within the conical pits were individually transferred to small paper packages. The surface activity of most arthropods living on sandy beaches is known to be nocturnal (Colombini et al. 1994, 1996; Jaramillo et al. 2003). The recovered pitfall tubes were stored at −30 °C for 1 day, and the trapped invertebrates were then sorted, identified to the family level (or order level for some groups; Table S1), and weighed to determine fresh weight. The substrates in the paper packages were dried at room temperature for 1 day, and then weighed.

Fig. 1 Field sampling set consisting of a wooden board (wb) acting as a barrier, four artificial pitfall traps (pft) used to collect invertebrates, and four conical substrate traps (cst) used to assess the amount of substrate falling into the pits; these two types of traps were buried in the sand at distances of 0, 100, 200 and 400 mm from the board

Artificial pit destruction and pit relocation

In the laboratory, following the methods of Eltz (1997) and Barkae et al. (2010), we examined how pit destruction affects pit relocation frequency and distance. Twenty 2nd-instar larvae of *M. bore* collected at North Tsugaru were reared individually in plastic tubes (29 mm inner diameter, 50 mm high, containing field-collected sand ca. 30 mm deep) at 25 ± 1 °C under uncontrolled day length (ca. 14 h of light). One live chironomid (the last-instar larva of *Propsilocerus akamusi*) was fed every other day. Twenty larvae were individually placed in large Petri dishes (174 mm inner diameter, 44 mm high, containing sand ca. 30 mm deep) approximately 1 week after molting into the 3rd instar. All larvae had made new pits by the next (1st) day. The pits of half of the larvae were fully filled with surrounding sand every evening (cf. artificial disturbance) and the pits of the remaining larvae were kept intact until the 5th day. This procedure of fully destroying the pit is comparable to disturbance in the field caused by large animals, such as toads, lizards and rodents stepping on the pit, and to the cumulative effects of partial destruction caused by frequent visits from relatively large arthropods, such as crabs, centipedes, beetles and earwigs. One live chironomid larva was provided on the morning of the 2nd and 4th days. A photograph of each Petri dish was taken from above every morning, and daily changes of the pit center location were measured to determine the minimum distance of pit relocation (Fig. S2). Finally, the sum of the four daily relocation distances was compared between the intact and experimentally buried pit groups.

Artificial pit destruction and life history

A total of 35 larvae were collected from Yashima ($N = 33$) and Awajishima ($N = 2$) on April 22, 2021. These larvae were reared individually in glass vessels (63 mm inner diameter, 86 mm high, containing field-collected sand ca. 40 mm deep) at 25 ± 1 °C under a 14 h:10 h light:dark cycle, with one live chironomid larva provided every other day. During this rearing, the 2nd-instar larvae ceased pit maintenance and feeding. After about 10 days, the newly molted last (3rd)-instar larvae constructed new pits and resumed feeding. These 27 larvae that built new pits during the period May 2–8 were used in the experiment examining the effects of frequent pit destruction on life history.

Larval body weight was measured on the day of new pit construction. Last-instar larvae of the chironomid *P. akamusi* undergo summer diapause in the lake bottom sediments from May to October (Yamagishi and Fukuhara 1972; Iwakuma and Yasuno 1983). In this experiment, we selected similar-sized chironomid larvae of 22.1 mg fresh weight ($N = 10$, SE = 0.9) among mass-cultured summer-diapausing larvae and provided them to the antlion larvae from the day

after new pit construction at 3-day intervals. The antlions were randomly separated into two groups, an intact-pit control group ($N = 13$) and an experimental group ($N = 14$), for which the pits were fully filled with the surrounding sand around 5 pm daily, except on feeding days.

Pit reconstruction behavior was recorded above the rearing glass vessels using the infrared detection function of a video camera (FDR-AX55; Sony, Tokyo, Japan) for 10 of the 14 antlion larvae in the experimental group. Individual larvae were monitored for 12 h after artificial pit destruction, beginning around 5 pm.

During rearing, the larvae ceased pit maintenance and feeding. In this study, the 3rd-instar larval period was defined as the time from the initiation of new pit construction to cessation of pit maintenance, and the prepupal and pupal period was the time between cessation of pit maintenance and adult emergence. After pit maintenance had ceased, the glass vessel was covered with vinyl, and a 70-mm wooden stick was placed in it to allow the emerged adults to climb and expand their wings. Adult emergence was checked daily until September 10, when the last adult emerged. On the day of emergence, adult body weight was measured followed by preservation in a freezer at $-30\,°C$. Subsequently, the sexes were determined based on genitalia, and head width (distance between the outer edges of eyes) and forewing length (from the basal part to the tip) were measured with slide calipers.

Pit location and parasitism

The preliminary data suggested that no parasitoids were present at four (Ueda, Awajishima, Yashima, Iriomotejima) of the six study sites. Therefore, the relationship between the antlion pit location and the parasitoid prevalence was examined at the North and South Tsugaru sites (Table 1). A total of 79 larvae, 51 from North Tsugaru and 28 from South Tsugaru, were collected randomly in the field on May 15 and 16, 2021, and the minimum distance from the barrier to the center of each pit was measured. These larvae were kept individually in plastic tubes (29 mm inner diameter, 50 mm high, containing field-collected sand ca. 30 mm deep) at $25 \pm 1\,°C$ under uncontrolled day length (ca. 14 h of light), and one live chironomid larva was provided every other day. Rearing continued until August 16, 2021. After the formation of cocoons, the plastic tube was covered with a small plastic bag and a 70-mm wooden stick was placed in it to allow the emerged adults to expand their wings. Emergence of adult *Myrmeleon* and parasitizing bee flies was checked daily. Upon emergence, the adults were stored in a freezer at $-30\,°C$, and their sexes were later determined based on the genitalia. Head width and forewing length were measured with slide calipers.

Statistics

Values are shown as mean $\pm$ standard error (SE). Pearson's correlation coefficient was used to examine the relationships between the antlion pit diameter and distance from the natural barrier edge. This coefficient was also used for the relationship between the number or mass of trapped invertebrates per one side of the field sampling set and the amount of fallen substrates per opposite side of the field sampling set. The number of invertebrates per trap, their mass per trap, and the relative amount of fallen substrate per trap were analyzed using the Friedman test, with the post-hoc Dunn–Bonferroni multiple comparison test, to compare differences among four traps set at different distances in each sampling set. To detect differences in the distance between the natural barrier edge and antlion pit edge among the six study sites, the Kruskal–Wallis test and Steel–Dwass multiple comparison test were used. The Mann–Whitney U test was used to detect differences in the sum of daily pit center movements between the control (intact) and experimental (artificial pit destruction) groups of antlion larvae. Life history parameters, such as the sizes of last-instar larvae and adults, larval growth rate, and efficiency of food conversion were compared between the control and experimental pit-destruction groups, using Student's t test, because the data showed homogeneity of variance. A sex difference in adult body size was tested for using Student's t test. The emergence day data were compared between sexes using the Mann–Whitney U test. Differences in parasitism among the four groups distinguished according to pit distance from the barrier edge were tested using Fisher's exact test. These tests were performed using the IBM SPSS Statistics (ver. 25.0; IBM Corp., Armonk, NY, USA) and G∗Power 3.1 (University of Dusseldorf, Dusseldorf, Germany) programs, or using the base package of R 3.6.0 (R Core Team 2019).

Results

Field data

In the field, the pits were located near the natural barriers. The medians of the minimum distance from the barrier edge to the pit edge were 90–165 mm (Fig. 2), which differed among the six study sites (Kruskal–Wallis test; $\chi^2 = 14.9$, df $= 5$, $P = 0.011$). However, a statistically significant difference was only seen between Awajishima and Iriomotejima (Steel–Dwass test; $t = 3.18$, $P = 0.018$), and Awajishima and North Tsugaru ($t = 3.35$, $P = 0.011$). In common, pits at 0–15 mm (closest to the barrier) were less frequent than pits located more than 15 mm from the barrier, at all study sites (Fig. 2). Although larval instars were not determined by individual pit diameter (Fig. S3), there were positive
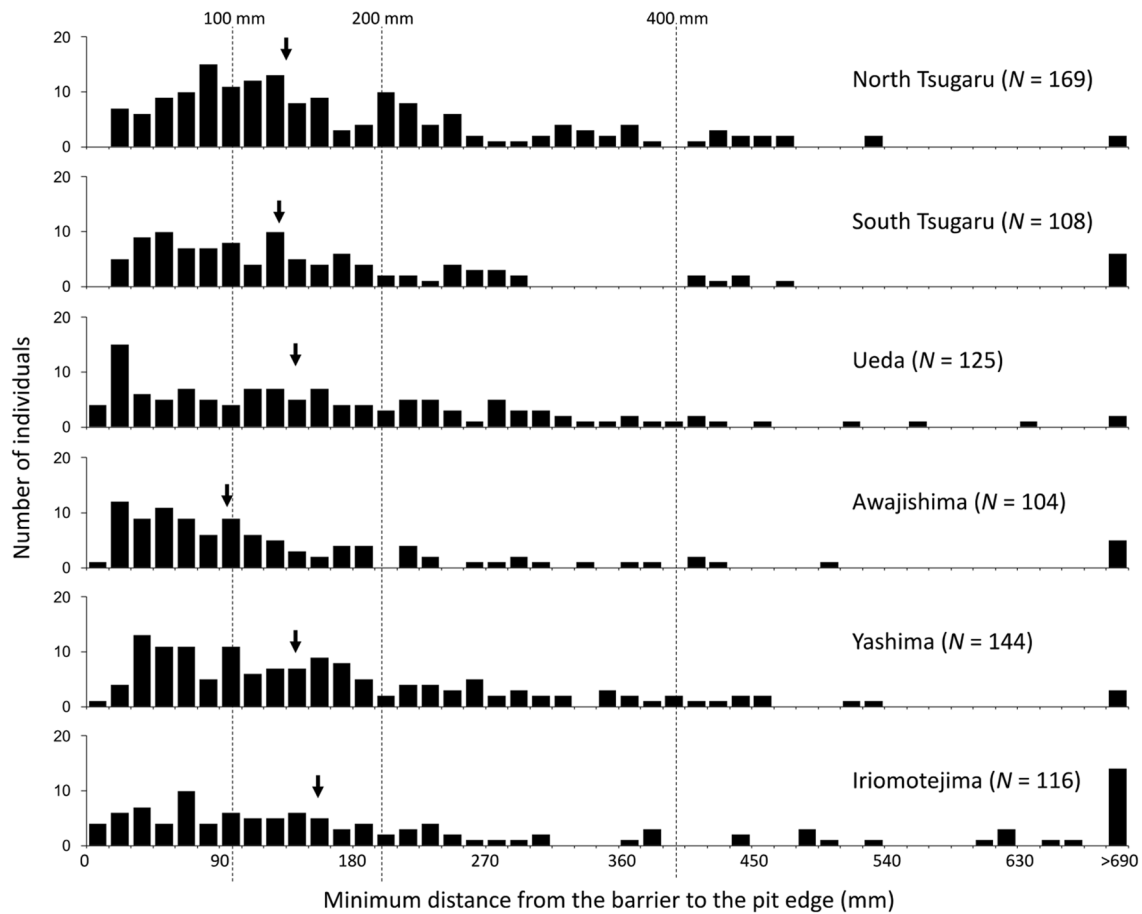
Fig. 2 Frequency distributions of distances from the antlion pit edge to the natural barrier edge at six study sites. Arrows indicate the medians and *N* is the number of pits observed

Table 2 Coefficients derived from Pearson's correlation analysis between the pit diameter and distance from the natural barrier edge and between the number or weight of trapped invertebrates per one side of the field sampling set and the weight of fallen substrates per opposite side of the field sampling set for each field sampling and all combined data

Study site (season)	Number of antlion pits examined	Correlation coefficient between pit diameter and pit distance from the barrier (*P*)	Number of field sampling sets	Correlation coefficient between the number of trapped invertebrates and the weight of fallen substrates in the traps (*P*)	Correlation coefficient between the weight of trapped invertebrates and the weight of fallen substrates in the traps (*P*)
North Tsugaru (May)	169	0.322 (<0.01)	10	0.503 (0.14)	0.623 (0.05)
South Tsugaru (May)	108	0.081 (0.41)	10	−0.328 (0.36)	0.313 (0.38)
Ueda (June)	125	0.224 (0.01)	12	0.374 (0.23)	−0.265 (0.41)
Awajishima (Apr.)	104	−0.068 (0.50)	12	−0.144 (0.66)	0.328 (0.30)
Awajishima (Oct.)	0	–	12	−0.275 (0.39)	0.449 (0.14)
Yashima (Apr.)	144	0.147 (0.08)	12	−0.280 (0.38)	0.746 (<0.01)
Iriomotejima (Mar.)	54	0.266 (0.05)	10	−0.075 (0.85)	−0.207 (0.57)
Iriomotejima (Sep.)	62	0.399 (<0.01)	10	−0.146 (0.69)	0.590 (0.07)
All	766	0.124 (<0.01)	88	−0.150 (0.16)	0.309 (<0.01)

correlation between the pit diameter and distance from the barrier edge on four sampling site/occasions and for all combined data (Table 2).

We deployed a total of 88 field sampling sets (Table 1, Fig. 1). The trapped invertebrates consisted mostly of insects (particularly beetles and ants), isopods, and spiders (Table S1). The number of invertebrates per trap was significantly higher in traps located 0 mm from the wooden board on three sampling site/occasions and for all combined data (Fig. 3). The fresh weight of invertebrates per trap varied greatly among traps owing to occasional capture of relatively large invertebrates. This value was higher in the traps set at 0 mm on one sampling site/occasion

and for all combined data (Fig. 4). The relative weight of substrate that fell into each four conical substrate traps of the sampling set was higher at 0 mm on two sampling site/occasions and for all combined data (Fig. 5). The total weight of fallen substrate per field sampling set was not correlated with the total number of trapped invertebrates per sampling set on any sampling site/occasion, but was positively correlated with the total weight of trapped invertebrates per sampling set on two sampling site/occasions and for all combined data (Table 2). Thus, the analyses for all combined data suggested that the invertebrates living in the sand dune with pit-building antlion larvae tend to move along the barrier and drop sand into the pit there.
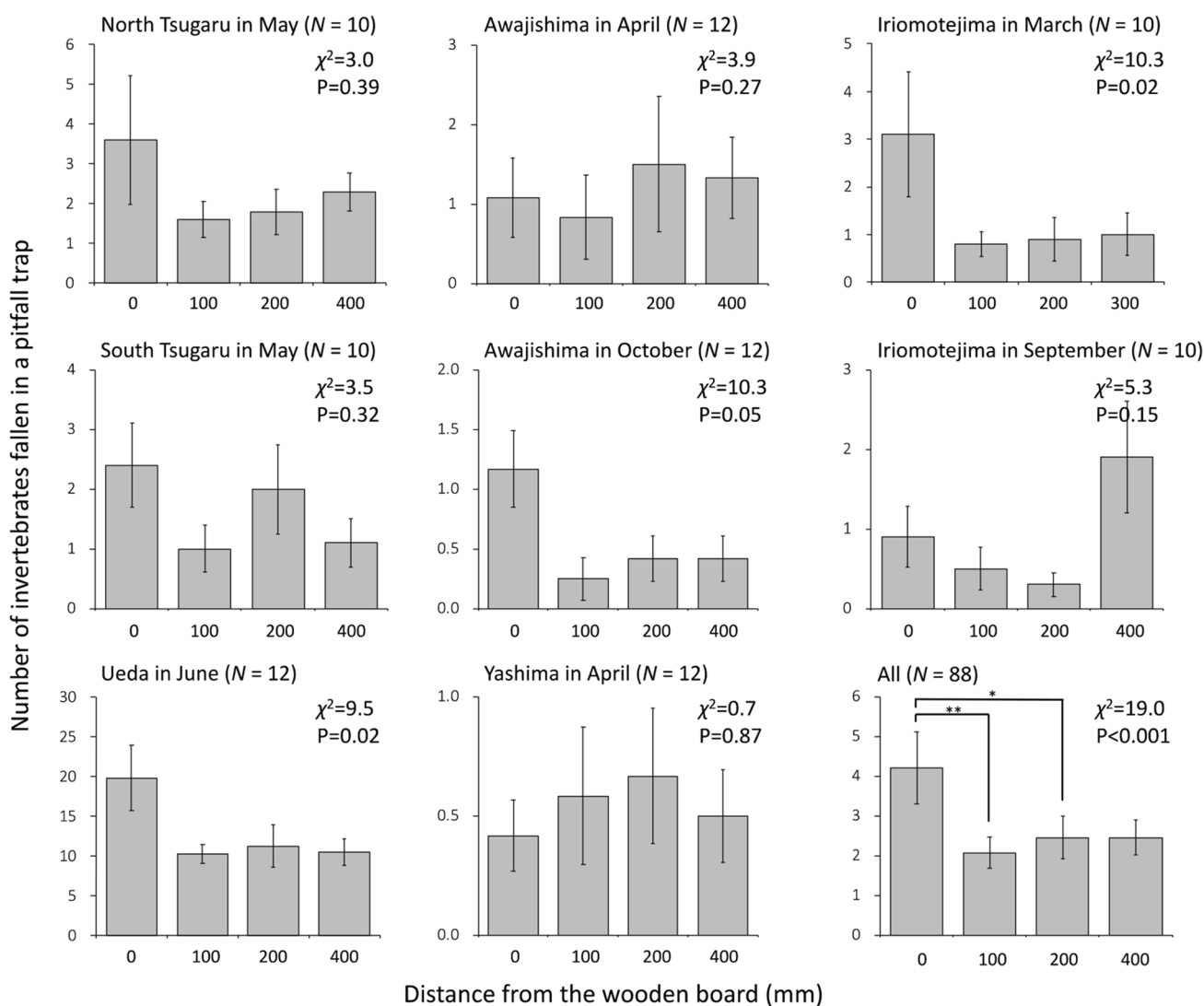
Fig. 3 Number of invertebrates (mean ± SE) per artificial pitfall trap (pft in Fig. 1) buried at 0, 100, 200, and 400 mm (300 mm in Iriomotejima in March) from the wooden board for each field sampling event, and for all data combined. N is the number of traps set at each distance. The results of the Friedman test (χ^2, P, df = 3 in any case) are shown. Asterisks show the results of post-hoc Dunn–Bonferroni multiple comparison test (*$P < 0.05$ and **$P < 0.01$)
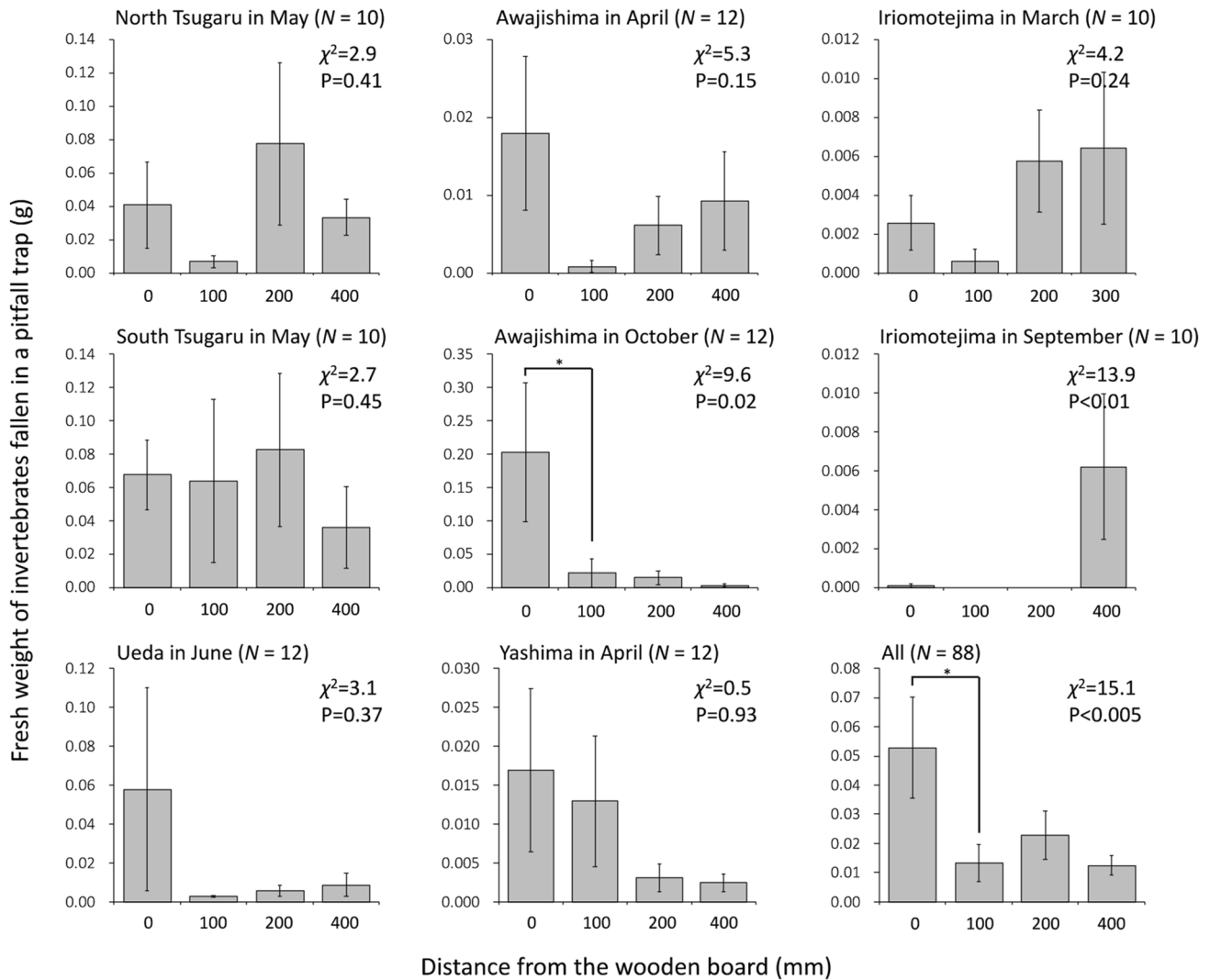
Fig. 4 Fresh weight of invertebrates (mean ± SE) per artificial pitfall trap (pft in Fig. 1) buried 0, 100, 200, and 400 mm (300 mm in Iriomotejima in March) from the wooden board for each field sampling event, and for all data combined. N is the number of traps set at each distance. The results of the Friedman test (χ^2, P, df = 3 in any case) are shown. Asterisks show the results of post-hoc Dunn–Bonferroni multiple comparison test (*$P < 0.05$ and **$P < 0.01$)

Artificial pit destruction and pit relocation

A video recording of pit reconstruction behavior in small glass vessels (63 mm inner diameter) revealed that the larvae appeared on the surface around 11.0 min ($N = 10$, SE = 3.7, range 3–31) after artificial pit destruction and undertook new pit construction for 48.3 min ($N = 10$, SE = 6.1, range 19–75).

The sum of distances of pit center relocation in successive 5 days in a large Petri dish (174 mm inner diameter) was 91.5 mm ($N = 10$, SE = 22.6, range 38.0–234.6) in the experimental (artificial pit destruction) groups of antlion larvae and 23.1 mm ($N = 10$, SE = 5.2, range 9.7–65.7) in the control (intact) group of larvae, which differed significantly (Mann–Whitney U test, $Z = 3.40$, $N_1 = 10$, $N_2 = 10$,

$P < 0.001$). Thus, frequent pit destruction caused movement of larvae.

Artificial pit destruction and life history

In males, but not females, the larval growth rate (mg/day) and efficiency of food conversion (mg/prey) differed between the pit destruction and control groups (Table 3), suggesting that pit reconstruction is costly for antlions.

Pit location and parasitism

In North and South Tsugaru located at a large continuous sand dune, 40.4% and 57.1% of antlion larvae were parasitized by bee flies (Table 1). The prevalence of bee
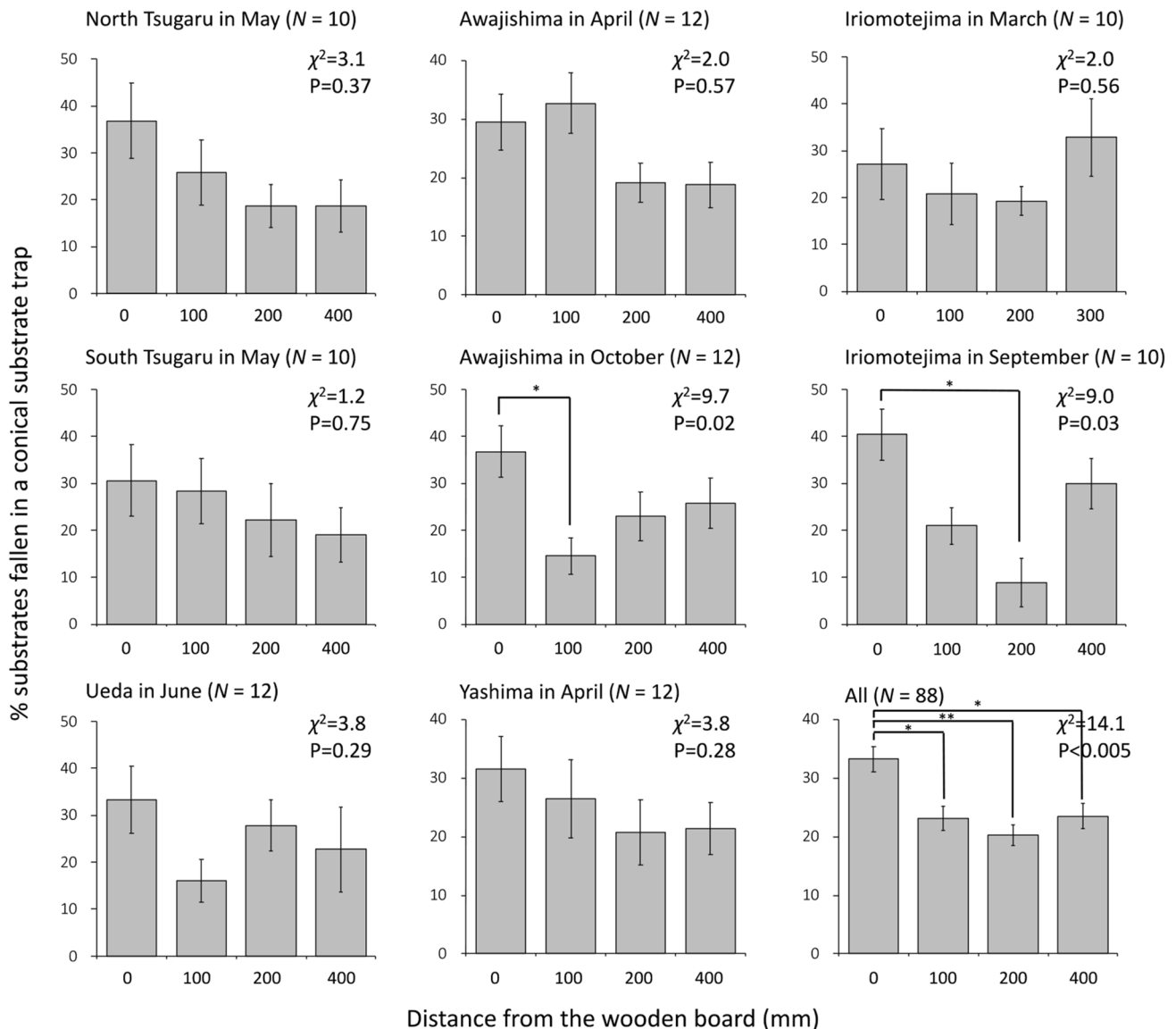
Fig. 5 Proportion (mean ± SE) of total substrate that fell into each of the four conical substrate traps in a field sampling set (cst in Fig. 1) buried 0, 100, 200, and 400 mm (but 300 mm in Iriomotejima in March) from the wooden board for each field sampling event, and for all data combined. *N* is the number of traps set at each distance. The results of the Friedman test (χ^2, *P*, df = 3 in any case) were shown. Asterisks show the results of post-hoc Dunn–Bonferroni multiple comparison test (*$P < 0.05$ and **$P < 0.01$)

flies did not differ among the five groups of antlion larvae with their pits at different distances from the natural barriers (Fig. 6; Fisher's exact test, $P = 0.33$). In all cases, one bee fly emerged from a single host. The first emergence of *Myrmeleon* adults occurred on June 23, and the last on July 30, whereas the emergence of bee flies occurred during July 12–28 (Fig. S4). Antlions exhibited protandrous (early male) emergence patterns (Mann–Whitney U test, $Z = 2.31$, $N_1 = 19$, $N_2 = 16$, $P = 0.02$), while male and female bee flies emerged simultaneously ($Z = 1.69$, $N_1 = 15$, $N_2 = 19$, $P = 0.09$). The mean head width of *Myrmeleon* adults was 3.56 mm ($N = 19$, SE = 0.02) and the

mean forewing length was 28.08 mm ($N = 19$, SE = 0.14) in males. Females were larger than males in terms of head width (3.71 mm, $N = 16$, SE = 0.04) and forewing length (30.39 mm, $N = 16$, SE = 0.27) (Student's *t* test: $t = 3.34$, df = 33, $P = 0.002$ for head width; $t = 8.08$, df = 33, $P < 0.0001$ for forewing length). Adult bee flies had similar head widths in both sexes; 2.60 mm ($N = 15$, SE = 0.02) in males and 2.58 mm ($N = 19$, SE = 0.03) in females ($t = 0.53$, df = 32, $P = 0.60$). The forewing length of bee flies differed between sexes, at 8.20 mm ($N = 15$, SE = 0.10) in males and 8.56 mm ($N = 18$, SE = 0.10) in females ($t = 2.52$, df = 31, $P = 0.017$).

Table 3 Comparison of life history parameters (mean ± SE) between the control (intact) and experimental (pit destruction on 2 of 3 days by filling with sand) groups of 3rd (last)-instar antlion larvae

Sex	Pit treatment	Initial body weight (mg fresh weight) of the 3rd-instar larva	Number of prey eaten at the 3rd instar	Number of days in which the pit was destructed with sands	Duration of the 3rd instar with a maintained pit (days)	Duration of prepupal and pupal stages	Body weight of the just emerged adult (mg fresh weight)	Head width of the emerged adult (mm)	Forewing length of the emerged adult (mm)	Growth rate (mg/day)	Efficiency of food conversion (mg/prey)
		W1	Np		T		W2			(W2−W1)/T	(W2−W1)/Np
Male											
N = 8	Control	21.50	8.75	0.00	25.38	37.88	55.38	3.86	29.39	1.32	3.83
(SE)		(1.87)	(0.59)	(0.00)	(1.63)	(8.66)	(3.99)	(0.07)	(0.50)	(0.07)	(0.17)
N = 9	Destructed	21.89	9.56	18.00	27.56	31.44	51.22	3.84	29.46	1.05	3.03
(SE)		(1.11)	(0.53)	(0.99)	(1.50)	(5.00)	(2.94)	(0.04)	(0.29)	(0.09)	(0.28)
P in t test		0.86	0.32	–	0.34	0.52	0.41	0.83	0.90	0.04	0.03
Female											
N = 5	Control	24.00	11.40	0.00	33.20	46.40	67.60	4.05	31.54	1.35	3.91
(SE)		(1.14)	(0.81)	(0.00)	(2.58)	(9.29)	(1.81)	(0.04)	(0.48)	(0.16)	(0.41)
N = 5	Destructed	24.20	12.40	23.80	37.20	37.40	66.60	4.08	32.41	1.14	3.43
(SE)		(1.20)	(0.81)	(1.46)	(2.27)	(11.16)	(3.01)	(0.04)	(0.29)	(0.08)	(0.24)
P in t test		0.91	0.41	–	0.28	0.55	0.78	0.62	0.16	0.26	0.34

Statistical results (P) of t tests between the two groups are shown in male and female, respectively
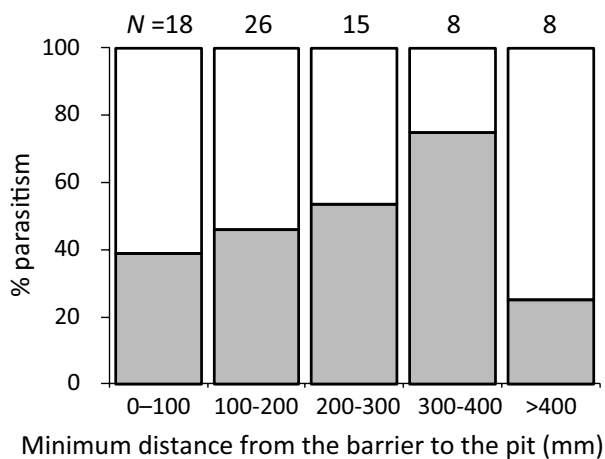
Fig. 6 Prevalence (%) of parasitism by bee flies among antlion larvae building their pits at various distances from natural barrier edges. *N* indicates the number of larvae in each 100-mm distance group

Discussion

Invertebrates living in sand dune, such as insects, spiders and crustaceans, were trapped most extensively along the artificial barrier in terms of both number and in mass, although not in all cases; at some sites no link between distance from the barrier and prey capture was observed (Figs. 3 and 4). The large number of invertebrates captured along the barrier may be due to thigmotactic (wall-hugging or wall-following) behavior, which is known in cockroaches (Creed and Miller 1990), crickets (Doria et al. 2019), carabid beetles (Langan et al. 2001), ants (Dussut-our et al. 2005), spiders (Patt and Pfannenstiel 2009), and crustaceans (Kohler et al. 2018). The idea of more prey available next to barriers have been also suggested regarding wormlions (Scharf et al. 2021). Thus, hunting along the barrier may be an optimal strategy through which antlion larvae could increase hunting success. However, not all invertebrates are suitable prey and inedible invertebrates are a source of disturbance rather than food (Scharf et al. 2010). We used conical artificial pits to evaluate pit destruction (Fig. 1) and the results showed that pits set closest to an artificial barrier accumulate more sand and fine plant debris (Fig. 5), probably due to intense activity of wall-following invertebrates. When sand and plant debris fall into the pit, antlions must maintain it by tossing them outside the pit with their head (Elimelech and Pinshow 2008). They can also remove relatively large debris (64–1,000 mm^3 rubber pieces in the experiments) that fall into the pits by moving backward with the debris contacted by the posterior or dorsal part of the abdomen (Tanaka and Ono 1973). In tropical dry forests, the amount of leaf litter negatively affects the density of antlions, probably due to damage to their pits caused by unsettled plant litter that is moved by the wind (Farji-Brener et al. 2008). Thus, pit-building antlion larvae may incur additional costs due to building along the edge of a natural barrier, as they must repair their pits often due to frequent destruction caused by invertebrates moving along the barrier edge and other unsettled materials. We must pay more attention to such costs of habitat selection by pit-building antlion larvae.

Avoiding areas rich in prey, solely because the prey disturbs the pit, may occur only when prey is highly abundant. If prey is not abundant, antlions should build pits closest to barriers theoretically. However, the pit distribution patterns in our field surveys suggested that antlion larvae avoid pit building closest to natural barriers at all sites (Fig. 2). If pit relocation occurs most often following pit destruction, the relocation rate would be higher for pits built along barriers. In our laboratory experiments conducted in a small area, artificial pit burial with sand induced new pit construction that is taking a rather long time (11 min before starting and 48 min to complete a new pit). In a large area, a new pit was often constructed at a different site from the previous. The larvae selected the new site by moving backward on the sand surface (Fig. S2). The sum of the daily distance between destroyed and reconstructed pit centers was much greater for larvae whose pits were buried compared to larvae in intact-pits. Such disturbance may explain why antlion pits are not located closest to barriers in nature. Antlion pits might shift away from the barrier edge, where pit destruction occurs more frequently due to wall-following invertebrates. Once the pits relocate away from the barrier, the larvae escape pit disturbance and rarely relocate from there. In general, the larger (late instars) larvae spend for longer time (Matsura et al. 1991) and experience more frequent disturbance than the smaller (early instars) larvae, which may explain the positive correlation between the larval pit size and distance from the barrier edge (Table 2). Avoidance of pit building along the barrier may not be applied for non-pit-building antlion larvae. Most larvae of such non-pit-building antlion, e.g., *Distoleon contubernalis*, hide in the sand for hunting prey closest to the barrier (Jingu and Hayashi 2018).

The effect of pit disturbance on the probability of pit relocation has been described in several other antlion species, but those studies assessed density-dependent processes, such as sand tossing by neighbors (Simberloff et al. 1978; Matsura and Takano 1989; Day and Zalucki 2000). Frequent pit destruction due to tossed sand generally induces frequent pit relocation. However, contrasting results have been reported in *Myrmeleon hyalinus* (Barkae et al. 2010). Weekly sand disturbance over 9 weeks, caused by shaking of the tray until existing pits were fully covered with sand, reduced the larval pit relocation rate relative to the non-shaken control. In *M. persimilis*, artificial sand tossed into the antlion pit (0.25 mL sand, 4 times/day at 2-s intervals) reduced the number of larval pit relocations per 30 days (Tsao and Okuyama 2013).

These differing behavioral responses to pit destruction should be examined carefully in the future.

Pit destruction can be considered a long-term cost in terms of the life history. The larvae of *M. brasiliensis* whose pits were disturbed had longer larval periods, shorter pupal periods, and emerged as smaller adults than intact-pit larvae (Lima and Silva 2017). In this experiment of *M. brasiliensis*, one *Drosophila* fly was provided daily and the pit was buried completely three times per week; on feeding day, burial was performed more than 1 h after feeding. In *M. mobilis*, in contrast, long-term (over 48 days) pit disturbance every other day had little effect on larval growth rates under all feeding regimes tested; unfed, one *Drosophila* fly every second or sixth day (Eltz 1997). In our experiment, one live chironomid larva was provided at a 3-day interval and the pit was buried completely once a day, excluding feeding days, during the last-instar larval stage. The pit destruction group of larvae required more prey and a longer period to complete that stage than the undisturbed control (Table 3). Finally, significant reductions in larval growth rate and prey conversion efficiency occurred with frequent pit destruction (Table 3). Such differing effects among species may depend on the experimental methods, particularly the timing of pit destruction, as suggested by Barkae et al. (2010), who found that the relative growth rate of *M. hyalinus* larvae over 9 weeks differed among three groups: no disturbance, complete pit destruction weekly prior to feeding, and complete pit destruction weekly after feeding.

At our two study sites, larvae of *M. bore* were parasitized by the bee fly *V. myrmeleonostena*. The emergence of adult parasitic bee flies occurs later than adult emergence of host *Myrmeleon* (Matsura et al. 1998; Nonato et al. 2018), as confirmed in our study (Fig. S4). No significant association was found between the distance of the pit from the natural barriers and the parasitism rate (Fig. 6), suggesting that avoidance of parasitism is not an important factor with respect to the distribution of antlion pits. This is the first examination of parasitoids as the potential factors affecting the spatial distribution of antlion larvae.

Declarations

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

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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