

Foraging behaviour of a neglected pit-building predator: the wormlion



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Wormlion larvae (Diptera: Vermileonidae) construct conical pits in fine loose soils and ambush arthropod prey. Their hunting strategy resembles that of pit-building antlions (Neuroptera: Myrmeleontidae), offering a classical example of convergent evolution, as they belong to different orders of insects. However, compared with other trap-building predators, spiders and antlions, the foraging behaviour of wormlions is almost unknown. In this study we used a combination of field observations and laboratory experiments to close this gap and investigate how hunger and ecological factors such as density and spatial pattern affect pit size, that is, how they shape investment in foraging and indicate competition between neighbouring larvae. We found slight, mainly decreasing, changes in pit size with hunger, with no change in response to prey. Surprisingly, body mass and length were not tightly correlated with pit size, unlike in antlions and spiders. Other factors, in addition to body mass and size, affect pit size, as the correlation between pits constructed in the field and in the laboratory was strong. The evidence for competition was mixed. On the one hand, we detected, in the laboratory, a change towards a regular spatial pattern with increasing pit densities, as expected, suggesting interference competition. On the other hand, we detected, in the field, a positive correlation between the sizes of neighbouring pits, and a negative correlation in the laboratory between pit size and distance to the nearest neighbour, both indicating clustering in favourable microhabitats, and not supporting strong competition. We discuss our findings in comparison with other trap-building predators and locate them within the general framework of foraging theory.

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Although most animals in nature actively search for their prey, a large number of predators do not and instead merely choose a suitable location for ambush (Huey & Pianka, 1981; Perry & Pianka, 1997; Uetz, 1992). Sit-and-wait predators invest less energy in searching for prey and have a lower metabolic rate, but they also exhibit lower encounter rates and need to endure longer starvation periods (Elimelech & Pinshow, 2008; Huey & Pianka, 1981; Nagy, Huey, & Bennett, 1984). Many animals across various taxa can switch between the two foraging modes. Theoretical and empirical studies suggest that prey abundance and size, hunger level, body condition and movement velocity and directionality of both predators and prey play a role in determining which foraging mode such predators will employ (e.g. Elimelech & Pinshow, 2008; Helfman, 1990; Scharf, Nulman, Ovadia, & Bouskila, 2006). Some models have emphasized the importance of prey capture variance. Caraco and Gillespie's (1986) model, for instance, suggests that the sit-and-wait strategy has a higher variance of success than the active foraging mode; thus, the sit-and-wait strategy is probably

employed when the requirement for food exceeds the expected extent of prey capture, leading the predator to become more risk prone.

Trap-building arthropod predators are a subgroup of sit-and-wait predators, and employ a unique foraging strategy (Ruxton & Hansell, 2009). Active foragers should search for food as long as the marginal cost of searching is lower than the benefit, the chance of prey capture (Brown, 1988; Mitchell, Abramsky, Kotler, Pinshow, & Brown, 1990). The investment in trap construction and maintenance is analogous to the investment in searching for prey by active predators, because trap construction is an energetically expensive process (Lucas, 1985a; Tanaka, 1989; but see Elimelech & Pinshow, 2008, for a lower cost). Thus, trap-building predators should present a flexible strategy of investment in traps, and maximize foraging gain as much as possible, by adjusting trap size (Scharf, Lubin, & Ovadia, 2011). The costs of foraging are expected to be lower (e.g. the perceived cost of predation) and the benefit from successful foraging is expected to increase (the value of each prey caught) when animals are hungrier (Brown, 1988). Empirical evidence demonstrates varying changes in foraging activity with starvation, as some animals reduce their activity with starvation while others first increase activity before decreasing it (reviewed in Wang, Hung, & Randall, 2006). Trap-building predators usually

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increase their traps with starvation (before exhaustion) and neglect them with satiation (e.g. Herberstein, Craig, & Elgar, 2000; Lomascolo & Farji-Brener, 2001; Lubin & Henschel, 1996). Hungry trap-building predators respond faster to prey (Persons, 1999; Scharf, Barkae, & Ovadia, 2010) and consume a higher proportion of the prey items caught (Lucas, 1985b; Samu, 1993). Similarly, the cutoff distance below which an ambushing lizard responds to prey becomes greater when prey are scarce (Shafir & Roughgarden, 1998).

The investment in foraging depends not only on hunger level but also on competition with nearby foragers. While strong interference competition should lead to a decrease in foraging intensity, as it reduces the benefit and increases the cost of foraging, exploitation competition has a complex effect, because it is expected to reduce both the benefit and the cost. The effect on foraging intensity thus depends on whether the marginal cost has been reduced more than the benefit (Mitchell et al., 1990). Indeed, empirical evidence is mixed, with animals either increasing or decreasing foraging intensity with increased density or competition (cf. Abramsky & Pinshow, 1989; Grand & Dill, 1999). Trap-building predators experience both exploitation and interference competition with increasing conspecific density. 'Shadow competition' (individuals closer to a source of food reduce its availability to those further away; Wilson, 1974; Lubin, Henschel, & Baker, 2001) is equivalent to exploitation competition, while fights over suitable places for trap construction and sand throwing while constructing/maintaining pits are examples of interference competition (Day & Zalucki, 2000; McClure, 1976).

Traps usually become smaller with increasing density, even when space for the trap itself is not yet a limiting factor (e.g. Devetak, 2000; Griffiths, 1991), plausibly reflecting an increase in the cost of trap maintenance. In addition, the relocation rate of trap-building predators and the proportion of nontrap-building individuals increase with density (e.g. Day & Zalucki, 2000; Scharf & Ovadia, 2006). Parallel evidence for competition is provided in the shift in spatial pattern from random to regular with increasing density, as individuals try to maximize the distance to the nearest neighbour (Birkhofer, Henschel, & Scheu, 2006; Day & Zalucki, 2000; Matsura & Takano, 1989). Ant colonies, central-place foragers, respond similarly to competition, by increasing the distance to the nearest neighbours, in a process that results in a regular spatial pattern of ant nests (Ryti & Case, 1986). In all cases, maximizing the distance to neighbours should reduce the cost of foraging (by minimizing interference competition). Clearly, the effect of interference is moderated in rich habitats, where the distance to neighbours and territories held are smaller (e.g. spiders: Uetz, Kane & Stratton, 1982).

In addition to the well-studied web-building spiders and pit-building antlions, wormlions (Diptera: Vermileonidae) are a third group of such predators that has rarely been studied (a single ecological/nontaxonomical paper in ISI: Devetak, 2008a). Similar to antlions, wormlion larvae construct conical pits in loose soil and ambush small arthropods, mainly ants (Wheeler, 1930; Devetak, 2008a). This similarity to antlions, representing a clear example of convergent evolution, calls for comparisons in order to understand better the important biotic and abiotic factors relevant to their natural history, foraging and development. For instance, the vast majority of studies on trap-building predators have detected a positive correlation between body mass or size and trap size (e.g. Griffiths, 1986; Heinrich & Heinrich, 1984; Miyashita, 2005; Scharf, Golan, & Ovadia, 2009). However, it is unknown whether and to what extent body size affects trap dimensions in wormlions. Nothing is known about the importance of interference and exploitation competition, the effect of temperature or photoperiod and stress or starvation endurance.

We conducted a series of field observations and laboratory experiments in order to understand better the effect of external (density, spatial pattern) and internal (hunger, body mass and body size) factors on the foraging behaviour and competition of wormlion larvae, as reflected in their pit size and response to prey. Hunger and density manipulations were chosen because they are the most commonly tested factors affecting the pit size of antlions. Our working hypothesis was that both should affect the foraging behaviour of wormlions in seeking to maximize foraging gain and minimize foraging costs, when under starvation or competition conditions. We expected the following: (1) that the spatial pattern of wormlions in both the field and the laboratory would be random at lower densities but regular as density increases; (2) that a positive association would be found between pit size and distance to the nearest neighbour; (3) that pit sizes of the same individuals in the field and under laboratory conditions should be correlated, and there should be a positive correlation of both with body mass and length; and (4) that starvation would result in larger pits and faster responses to prey.

METHODS

Study Species and Collection Site

The wormlion species used in this study has not yet been formally described and is referred to here as *Vermileo* sp. (A. Freidberg, personal communication). It is probably very similar morphologically (especially in the larval stages) to its relative *Vermileo vermileo*, inhabiting the northern Mediterranean countries. The ecological or natural history differences between the studied species and its congeneric relatives are expected to be very minor. Wormlion larvae have a simple morphology compared with antlion larvae. They lack long mandibles, but have an elongated body shape with two protrusions from the main body part, the pseudopodium, which probably help in detecting and grasping the prey, and an abdominal comb, composed of several spines, which are probably used to anchor the wormlion in the sand (demonstrated for *V. vermileo*; Wheeler, 1930; Ludwig, Melzer, & Ehrhardt, 2001; Devetak, 2008b; Fig. 1). *Vermileo vermileo* larvae prefer finer sand than antlion larvae (Devetak, 2008a). There are probably six larval instars (Wheeler, 1930; the Sierra wormlion, *Vermileo comstocki*) and the pupal stage may last for up to a month, after which a very short-lived adult emerges (Wheeler, 1930; Devetak, 2008b).

Wormlion larvae were collected and photographed in July 2013 from Tel Aviv University, Tel Aviv, Israel, and the surrounding streets (32°6'54.35" N, 34°48'21.69" E), as well as in the city of Ramat Hasharon, 4 km northeast of the university. Wormlions were found only in fully sheltered places, on the sides of walls or buildings, in the shade. The substrate was always very fine sand, almost dust, which was usually only a few centimetres deep. Figure 1 shows two examples of collection sites. Note that some of the zones were disturbed by leaves, sticks, small stones and even shoe footprints, characterizing urban habitats. Wormlions were kept in the laboratory after the termination of the experiment, because we were interested in mating the adults for later research. The larvae were of different instar stages, but it is difficult to determine the stage based on allometry without knowing more about this species.

Experimental Design

Density and spatial pattern in the field

We first photographed 13 zones (Fig. 1a, b; mean zone area ± 1 SD: 0.272 ± 0.084 m²) and calculated pit density for each zone. We measured pit area and location using the software ImageJ

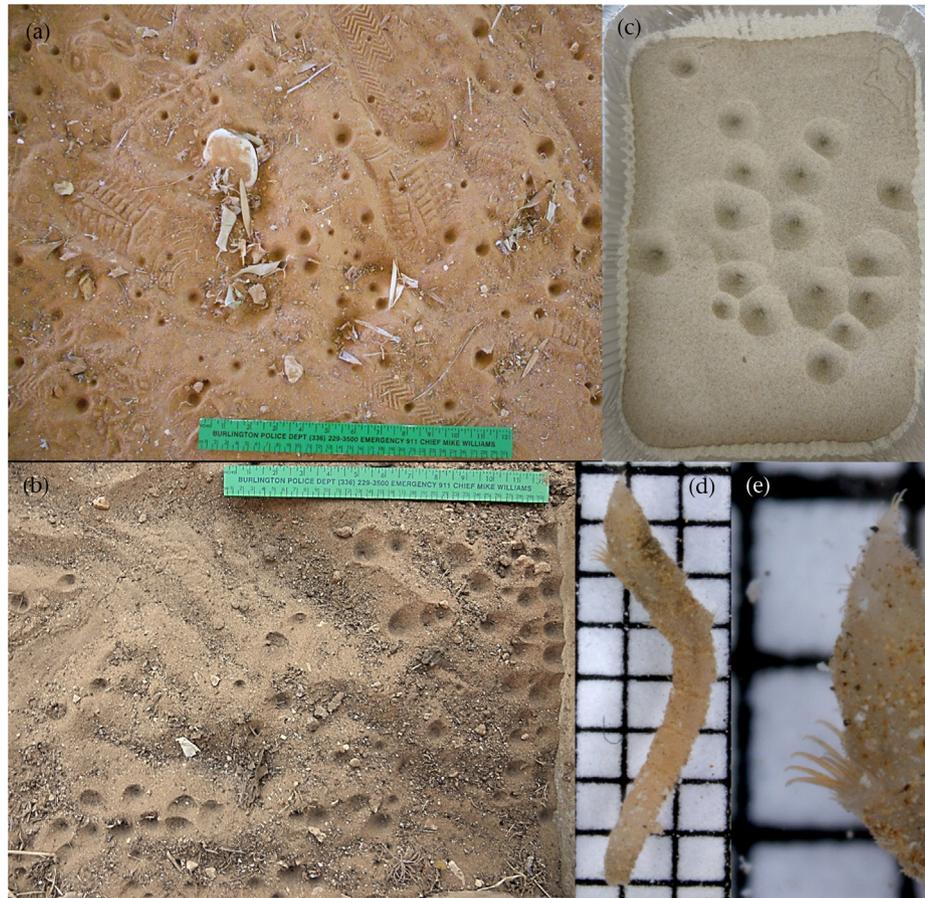


Figure 1. (a, b) Two examples of wormlion zones photographed and used to analyse the spatial pattern under natural conditions. The upper photo, with shoe footprints, demonstrates the high disturbance level that wormliions experience in urban environments. The ruler length is 30 cm. (c) Photo of the density experiment in the laboratory setting (here, second-highest density, 18 wormliions, in 23.5×17 cm aluminium tray). (d) A wormlion larva of advanced stage. Each square is 1 mm. The posterior part is at the top in the photo and in (e) is shown magnified. Note the abdominal comb, which probably assists in anchoring the wormlion in the sand.

(Abramoff, Magalhães, & Ram, 2004). We then calculated the spatial pattern for each zone using a null model written in MatLab v.7.8 (Mathworks, Natick, MA, U.S.A.). Null models maintain some of the data constant (here, the area dimensions and wormlion density), while randomizing the rest (wormlion positions), leading to a pattern that is expected in the absence of any driving mechanism (Gotelli & Graves, 1996). The null model randomly selected positions for the same number of wormliions in each zone and then calculated the mean distance to the nearest neighbour (hereafter, NND). This procedure was repeated 1000 times to create a randomly achieved mean NND distribution. We determined the spatial pattern (nearest-neighbour index; hereafter, NNI) by dividing the real, observed mean NND by the randomly expected NND (similar to Crist & Wiens, 1996; Scharf, Fischer-Blass, & Foitzik, 2011). Thus, values above 1 indicate a regular pattern, below 1 is clumped and around 1 is random. We referred to the spatial pattern as differing from random if 95% of the randomly obtained mean NND values were larger (clumped) or smaller (regular) than the observed mean NND in each zone (but we also considered 90% as a trend). We first used a linear regression to understand whether density correlated with the spatial pattern, and expected a shift to a regular pattern with increasing densities. We then calculated the relative pit area, by subtracting each pit area from the mean pit area value of each zone and dividing it by the zone mean value (to obtain deviations from each zone average pit area). We used a linear regression to test for a link between the NND (of the first to the third nearest neighbours) and pit area for all zones together and for

each zone separately. The distance between pits was calculated as the distance between both centres, minus the radius of the focal pit. This provides a measure of the interference from the neighbouring wormlion: the neighbour throws sand while maintaining its pit. However, the sand may fall in to any point in the pit of the focal individual and cause a disturbance. All statistics were performed using SYSTAT v. 12 (Systat Software Inc., Chicago, IL, U.S.A.).

Density and spatial pattern in the laboratory

We collected 240 wormlion larvae, fed each one with a small flour beetle larva, *Tribolium castaneum*, and 3 days later weighed and allocated them to one of four treatments. We allocated the wormliions to treatments according to body mass in order to keep the mean and variance of mass similar between treatments (test of body mass differences between treatments, one-way ANOVA: $F_{3,236} = 0.67, P = 0.57$). The treatments had densities of 6, 12, 18 and 24 individuals in an aluminium tray of 23.5×17 cm (Fig. 1c). Individuals were placed in the centre of each tray on day 1, using a cup of 6 cm diameter. We photographed the aluminium tray after 3 days (day 3) and measured pit locations and areas using ImageJ, similar to the field photo analysis. Each density had four replications (using different individuals). We calculated the spatial pattern using the same model described above. We examined (1) whether pit area and spatial pattern depended on density, using two linear regression tests; (2) whether there was a link between the relative pit area (pit area minus the mean pit area in the tray divided by the mean pit area) and NND using a linear regression; and (3) whether

pits closer to one of the tray edges differed in size from more central pits. During the laboratory experiments, wormlions were kept at room temperature (about 28 °C) under a 12:12 h light:dark photoperiod.

Pit size in the field versus the laboratory

Using a calliper (accuracy of 0.1 mm), we measured the pit diameter of 51 wormlions in their natural habitat. Pit diameter was measured twice in two perpendicular measurements (similar to antlions: Scharf et al., 2009, 2010; Alcalay, Barkae, Ovadia, & Scharf, 2014). In the field, we also measured pit depth using a calliper. The same individuals were then collected, brought to the laboratory, weighed using an analytical balance XT 220A, Precisa Gravimetrics, Dietikon, Switzerland; accuracy of 0.1 mg), and placed in small cups (diameter of 6 cm) filled with 4 cm of sand brought from the habitat of origin. The constructed pits were measured on the following day (day 1). We used linear regression tests to investigate the link between body mass, pit size in the laboratory and pit size in the field (body mass versus pit size in the field, body mass versus pit size in the laboratory and pit size in the field versus pit size in the laboratory). We also compared the pit diameter and depth using a Pearson correlation. We used log-transformed body mass, as body mass was not normally distributed but skewed to the right.

Effect of hunger level on pit size and response to prey

We used the collected wormlions to test for the effect of hunger level on pit size and response to prey. We first fed 103 wormlions with a small flour beetle larva each. They were then weighed and photographed on the same day using a digital camera (Axiocam ICC5) connected to a stereomicroscope (Stereo Discovery V12, Zeiss, Oberkochen, Germany). We used the photos to measure the wormlion body's length (Fig. 1d). Three days later we allocated them to one of three feeding treatments. Each feeding treatment had a similar mean and variance of body mass (test of body mass differences between feeding treatments, one-way ANOVA: $F_{2,91} = 0.08$, $P = 0.92$). The first feeding treatment was that of complete starvation for 3 weeks (F0); in the second we provided a single prey item after a week, followed by starvation for 2 weeks (F1); in the third we provided a prey item every week (twice in total; F2). We measured pit diameter using a calliper four times: in the first week, 1 day (day 1) and 7 days (day 7) after placing the wormlions in the experimental cups; in the third week, 1 day (day 1) and 7 days (day 7) after the pits were destroyed in order to weigh the wormlions again. The response to feeding regime was compared among the three feeding treatments by two repeated measures ANCOVA tests, with body mass and treatment as the between-subject variables, time (day 1 versus day 7) as the within-subject variable and pit diameter as the response variable: (1) a test in the first week, when no difference was yet expected, and (2) a test in the third week, in which we expected starved wormlions to possess larger pits, controlling for body mass. Body mass was log-transformed to fit a normal distribution. To investigate whether body mass affected not only pit size but also the likelihood of constructing a pit, we used pit construction as a binary dependent variable (constructed/not constructed) and body mass as an explanatory variable, and applied a logistic regression test. We also calculated the 'odds ratio', which shows how a variation of one unit in body mass (log mass [mg]) affects the likelihood of pit construction.

After 3 weeks, we offered a prey item (*T. castaneum* larva) to each wormlion and recorded the time needed for it to start moving in an attempt to capture the prey. Since many wormlions did not react at all (within 1 min), we used the binary variable responded/not responded instead of response time, and examined how it was

related to treatment (with a chi-square test). We also used a logistic regression with response as the binary dependent variable and body mass as the explanatory variable to test the link between body mass and the likelihood of responding. The 'odds ratio' shows how a unit change in body mass (log mass [mg]) affects the likelihood of responding to prey.

Because in the first week the groups had not yet experienced different feeding treatments, we used day 1 and day 7 of the first week to explore which body trait, body mass or body length, was better correlated with pit diameter. For this purpose we used two linear regression tests (log-transformed body mass or length versus pit diameter).

RESULTS

Density and Spatial Pattern in the Field

Wormlion densities in the 13 photographed zones were $3.48 \times 10^{-2} \pm 1.07 \times 10^{-2}$ (mean \pm 1 SD) wormlions/cm² (see Table 1 for more information on the different zones). The spatial pattern was either regular (5/13 zones), tended towards regular (2/13 zones) or random (6/13 zones; Table 1). Density and spatial pattern (NNI) were not correlated (linear regression: $R^2 = 0.004$, $N = 13$, $t = -0.20$, $P = 0.84$), and neither were spatial pattern and the average pit area ($R^2 = 0.221$, $N = 13$, $t = 1.77$, $P = 0.10$). There was a positive correlation between the relative pit size and the relative pit sizes of the three nearest neighbours (first to third nearest neighbours: $R^2 = [0.070, 0.074, 0.040]$, $N = [1172, 1171, 1172]$, $t = [9.40, 9.68, 7.02]$, $P < 0.0001$ for all; see Fig. 2 for the first nearest neighbour). The NND (always reduced by the radius of the focal pit) was not correlated with relative pit area over all zones ($R^2 = 0.001$, $N = 1172$, $t = 1.20$, $P = 0.23$). A between-zone comparison showed that in three zones the link was positive (an increase in pit area with distance to the nearest neighbour), in three others negative, and in the other seven not significant (Table 1).

Density and Spatial Pattern in the Laboratory

The laboratory density treatments were below and above the average wormlion field density. The six and 12 individuals per aluminium tray (1.50×10^{-2} and 3.00×10^{-2} wormlions/cm²) were below the average (3.48×10^{-2}), while 18 and 24 individuals

Table 1

Summary of the 13 wormlion zones photographed and analysed

Zone ID	No. of wormlion pits	Area (cm ²)	NNI	NND (cm; mean \pm 1 SD)	Pit area (cm ² ; mean \pm 1 SD)	<i>t</i> , <i>R</i> ²
A	100	3759.3	1.053	3.374 \pm 2.335	2.181 \pm 1.558	4.168, 0.151
B	81	3139.2	0.961	3.128 \pm 1.671	1.121 \pm 1.010	2.021, 0.049
D	158	4471.1	0.986	2.711 \pm 1.431	1.529 \pm 1.053	-0.156, 0.001
E	117	2072.6	1.023	2.246 \pm 0.835	1.718 \pm 1.014	-3.200, 0.082
F	71	1760.9	1.016	2.678 \pm 1.058	3.310 \pm 1.770	-2.169, 0.064
G	65	1949.5	1.137	3.292 \pm 1.261	2.865 \pm 1.592	-2.442, 0.087
H	91	2916.4	<i>1.079</i>	3.191 \pm 1.483	2.588 \pm 1.534	-0.262, 0.001
I	89	3048.1	<i>1.073</i>	3.292 \pm 1.626	1.520 \pm 1.065	1.049, 0.012
J	67	2883.3	1.145	3.981 \pm 1.782	3.226 \pm 2.081	0.155, 0.001
K	61	2055.7	1.035	3.187 \pm 1.440	1.674 \pm 0.917	-0.629, 0.007
L	82	1485.4	1.111	2.483 \pm 1.215	0.963 \pm 0.681	2.848, 0.093
M	111	2797.7	1.105	2.889 \pm 1.754	2.040 \pm 1.895	-1.106, 0.011
N	80	3053.1	1.114	3.624 \pm 1.237	3.672 \pm 1.666	-1.162, 0.017

NNI (nearest-neighbour index) values in bold indicate a regular pattern ($P < 0.05$), those in italics indicate a trend towards a regular pattern ($P < 0.1$), while all other NNIs do not differ from random. Also shown are the *t* value and *R*² of the regression of NND (nearest-neighbour distance) versus relative pit area (significant values appear in bold).

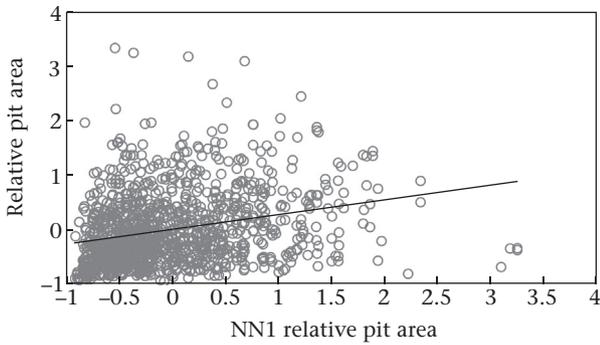


Figure 2. Correlation between the relative pit area of the first nearest neighbour (NN1) and the relative pit area of the focal wormlion. The relative pit area was calculated by subtracting the pit area from the mean pit area in each plot and then dividing by the mean pit area.

(4.51×10^{-2} and 6.01×10^{-2}) were above it. The spatial pattern was affected by density ($R^2 = 0.482$, $N = 16$, $t = 3.61$, $P = 0.003$; Fig. 3a): High densities were more regularly distributed than lower ones. Average pit area was negatively correlated with density ($R^2 = 0.275$, $N = 16$, $t = -2.31$, $P = 0.037$; Fig. 3b) but a polynomial equation of the second degree had a lower corrected Akaike’s information criterion, AICc: AICc = 1.365 and 0.456 for the linear and polynomial regression, respectively, resulting in a marginal difference of $\Delta AICc = 0.909$ in favour of the polynomial model. The NND (distance minus the focal pit radius) was negatively correlated with the relative pit area (all pits; $R^2 = 0.042$, $N = 222$, $t = -3.06$, $P = 0.002$; Fig. 3c). Neither density nor its interaction with NND was significant ($P > 0.68$). There was no correlation between the relative size of the nearest-neighbour pit and the relative pit size ($R^2 < 0.001$, $N = 222$, $t = 0.23$, $P = 0.82$). However, pit size was positively correlated with distance from the tray edge ($R^2 = 0.035$, $N = 222$, $t = 2.85$, $P = 0.005$; Fig. 3d).

Pit Size in the Field versus the Laboratory

Surprisingly, body mass was not correlated with pit diameter measured in the field ($R^2 = 0.040$, $N = 51$, $P = 0.16$). After we removed one outlier of the largest individual, deviating more than 2 SDs from the mean body mass, and repeated the regression test, the link became significant but was still weak ($R^2 = 0.082$, $N = 50$, $P = 0.044$; Fig. 4a). The results obtained for the pits built in the laboratory were similar ($R^2 = 0.098$, $N = 43$, $P = 0.041$; Fig. 4a). The trend was for a positive association, although it was weak and only marginally significant. The correlation between pits built in the field and in the laboratory was stronger ($R^2 = 0.142$, $N = 44$, $P = 0.012$; Fig. 4b). Pit diameter and depth in the field were tightly correlated ($r = 0.775$, $N = 51$, $P < 0.0001$). The pit diameter-to-depth ratio was normally distributed (Kolmogorov–Smirnov test: $P = 0.80$; mean ± 1 SD: 1.253 ± 0.250).

Effect of Hunger Level on Pit Size and Response to Prey

As expected, pit diameters did not differ between feeding treatments in the first week of the experiment, and neither treatment nor its interaction with body mass or day was significant (Table 2). Body mass was positively correlated with pit diameter, and pits on day 7 were naturally larger (Table 2). However, in the third week, after the feeding treatments, the three-way interaction, day*body mass*feeding treatment was almost significant, and both two-way interactions of feeding treatment*body mass and feeding treatment*day were significant (Table 2, Fig. 5a–c). Fed wormlions constructed larger pits than starved ones, with this difference between starved and fed individuals being more prominent for smaller individuals. This was consistent between day 1 and day 7 (Fig. 5c), although the relation between pit diameter and body mass was weaker on day 7 (Fig. 5a, b). In short, hungrier small larvae constructed smaller pits than more satiated small ones. Larger individuals tended to construct pits less, as a logistic regression

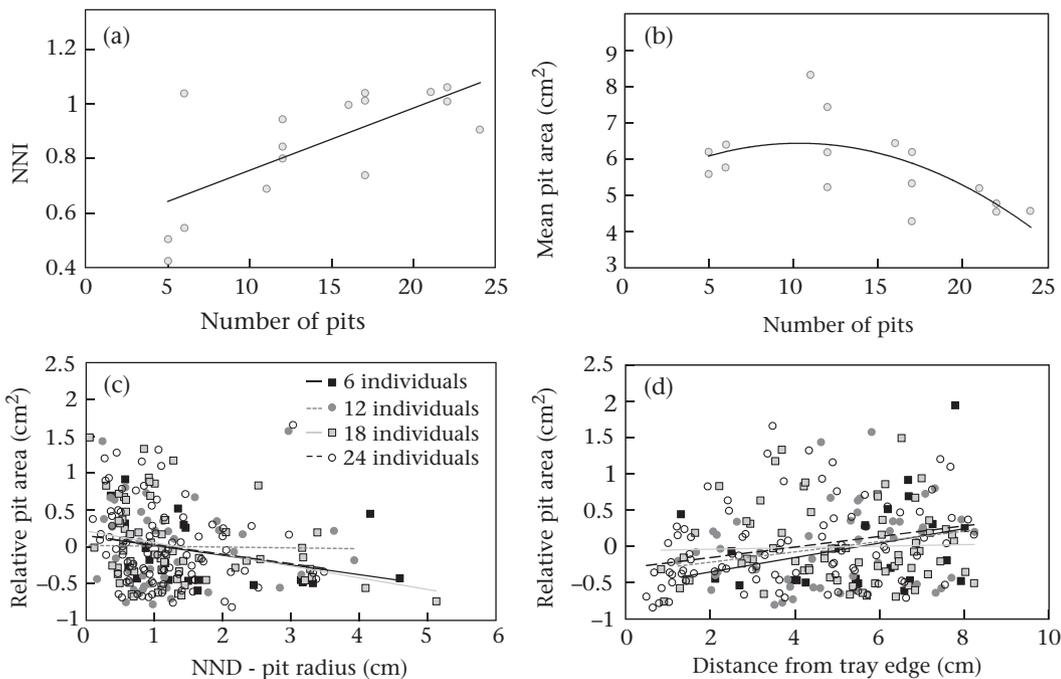


Figure 3. (a, b) Correlation between the number of pits in the laboratory density experiment and (a) the nearest-neighbour index (NNI) and (b) the mean pit area. (c, d) The relative pit area (difference of the pit area from the tray mean divided by the tray mean) and its correlation with (c) the distance to the nearest neighbour, corrected for the focal pit radius (NND – pit radius) and (d) the distance from the tray edge. Black, dark grey and light grey regression lines correspond to 6, 12 and 18 individuals, respectively, the dashed line to 24 individuals.

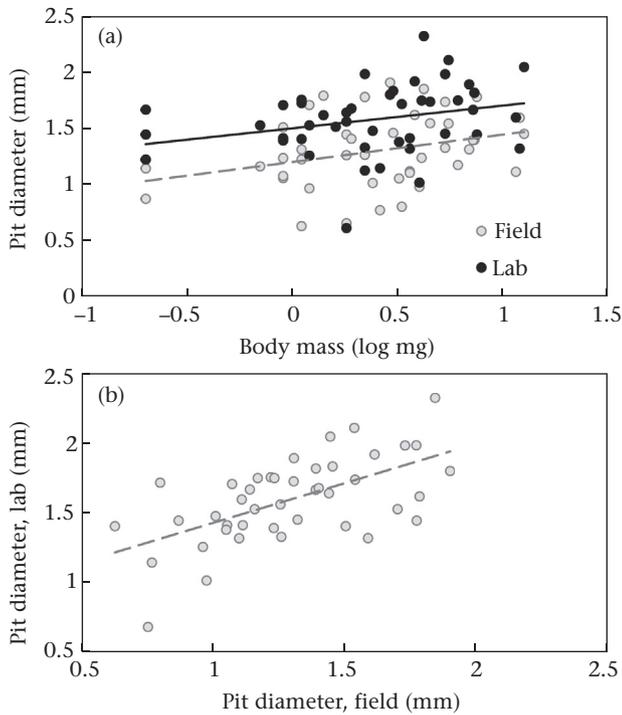


Figure 4. (a) Correlation between body mass and pit diameter under field (dashed line) and laboratory (straight line) conditions, and (b) correlation between pit diameter built under the two settings. Pits in the laboratory were measured on day 1.

showed that larger larvae were less likely to construct pits on day 1 ($Z = -2.84$, $P = 0.005$, odds ratio = 0.0143; Fig. 5d). This held true also for day 7, but with a much lower proportion of wormlions not having pits then (17/92 and 4/92 on day 1 and day 7, respectively).

Only 23 (out of 92) wormlion larvae responded within 60 s to a beetle larva offered as prey. Of these, 11 belonged to the unfed treatment and six each to the other two treatments (no significant difference between treatments: $\chi^2_2 = 2.03$, $P = 0.22$). However, a logistic regression showed that nonresponding wormlions were larger ($Z = -2.70$, $P = 0.007$, odds ratio = 0.0546; Fig. 5d).

Body length and body mass were both positively correlated with pit diameter, with no clear superiority to either of them: Body length explained pit diameter better on day 1 but the opposite held true on day 7 (log-transformed mass versus pit size: day 1: $R^2 = 0.052$, $N = 77$, $P = 0.046$; day 7: $R^2 = 0.040$, $N = 89$, $P = 0.061$; length versus pit size: day 1: $R^2 = 0.064$, $N = 77$, $P = 0.027$; day 7: $R^2 = 0.026$, $N = 89$, $P = 0.13$). Neither length nor mass explained

Table 2
The effect of hunger level on pit size

	Week 1			Week 3		
	<i>F</i>	<i>df</i>	<i>P</i>	<i>F</i>	<i>df</i>	<i>P</i>
Between subjects						
Treatment	0.57	2	0.57	4.94	2	0.01
Mass	5.90	1	0.018	4.77	1	0.032
Treatment*Mass	0.51	2	0.60	4.37	2	0.016
Within subjects						
Day	6.69	1	0.012	8.61	1	0.005
Day*Treatment	0.09	2	0.92	3.96	2	0.023
Day*Mass	0.03	1	0.87	0.92	1	0.34
Day*Treatment*Mass	0.06	2	0.94	3.07	2	0.053

Statistics are shown for the two repeated measure ANOVAs for the first week (prior to the experiment) and the third week (after the experiment). Significant results are in bold and marginally significant ones are in italics. Sample size is 77 (week 1) and 75 (week 3) wormlions.

much of the variance in pit size (2.6–6.4%). Body mass and length were tightly correlated (length versus mass: $R^2 = 0.746$, $N = 92$, $P < 0.0001$).

DISCUSSION

Wormlions only partially followed our foraging theory-related predictions. First, as in other trap-building predators, spiders and antlions, the spatial pattern became more regular with increasing densities, and pits became smaller, plausibly because of interference. This pattern was evident in the laboratory. In the field there was a positive association between neighbouring pits, thus not supporting competition between neighbours. As a response to hunger, wormlions did not build larger pits as had been expected, but even built smaller pits, especially the smaller individuals. Surprisingly, hungrier wormlions did not respond faster to prey. In contrast to both spiders and antlions, the association between pit size and body mass or body length was weak, and often even not statistically significant. Because there was a positive link between pit sizes in both the field and the laboratory, and both were only weakly affected by body mass, we suggest that pit size depends on other internal factors, which we did not investigate here.

Interference competition in trap-building predators is evidenced by the shift from a random to a regular spatial pattern with increasing densities in order to moderate the costs of interference in pit maintenance by neighbours (Birkhofer et al., 2006; Matura & Takano, 1989). This was also the case here, but only in the laboratory. The difference was perhaps caused by the range of densities tested in the laboratory, which was larger than that observed in the field. Other environmental factors, such as disturbance of leaves, stones, sticks and other objects, probably dictate the spatial pattern in the field much more than intraspecific interference competition does. The importance of such disturbances is known for antlions and can affect their density (Farji-Brener, Carvajal, Gei, Olano, & Sánchez, 2008). Note that the average wormlion densities observed in our study (348/m²) are higher than the antlion densities observed in their natural habitat (range 18.3–200 individuals/m² in different habitats around the globe; Matura & Takano, 1989; Gotelli, 1993; Day and Zalucki, 2000; Gatti & Farji-Brener, 2002; Morrison, 2004).

There was a positive spatial correlation of pit sizes in the field, meaning that larger pits were clustered together, as were smaller pits. This finding does not indicate a strong interference competition, as in such a case we would have expected a large pit to have a negative effect on the size of the neighbouring one. In addition, after we corrected for the size of each focal pit, the distance to the nearest neighbour had no link to its size, also not indicating (strong) competition. This positive association between size and distance to the nearest neighbour in sessile animals or central-place foragers is known, for example, in desert ant nests (Gordon & Kulig, 1996; Ryti & Case, 1986). However, a positive spatial correlation and large clustered nests found in other ant species was explained as a concentration of dominant colonies at sites of higher quality, while distancing colonies of lower competitive abilities (Scharf, Fischer-Blass, et al., 2011). The same explanation could hold true here: wormlions of better competitive ability cluster in the favourable areas while the subordinate ones are distanced. The spatial pattern is probably influenced by many additional factors. For instance, satiated spiders in habitats rich in prey maintain shorter distances to their nearest neighbours than spiders in poor habitats (e.g. Uetz, Kane, & Stratton, 1982).

In contrast to the field, there was no spatial correlation of pit sizes under laboratory conditions. However, pits further away from the tray edges were larger than those more adjacent to the edges. It could be that larger wormlions, or those in better condition, take

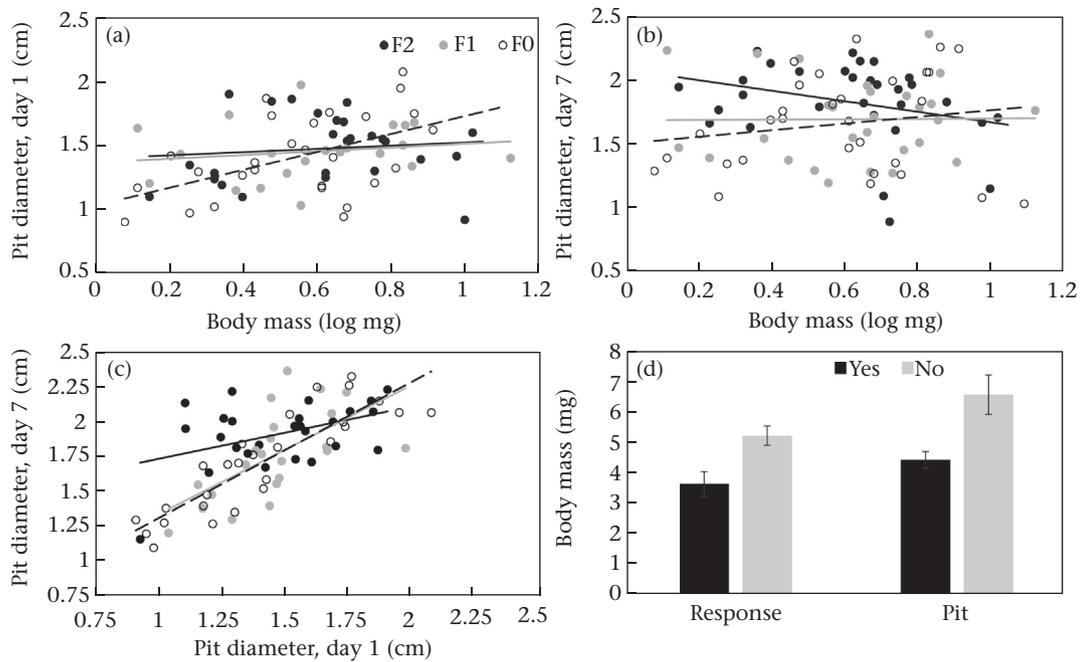


Figure 5. The interaction between feeding treatment, body mass and pit diameter. F0, F1 and F2 indicate unfed, fed once and fed twice after 2 weeks (a) on the first day and (b) on the seventh day. (c) The relation between the pit diameter on the first day and seventh day after pit construction. The dashed regression line corresponds to F0, the grey line to F1 and the black line to F2 in (a–c). (d) The difference in body mass between wormlions that responded or did not respond to a suggested prey item and those that constructed or did not construct a pit. Error bars indicate SE.

over the areas where they were initially placed, and the smaller individuals, or those in worse condition, move away after losing the competition for initial sites. The core–periphery preference could be based on keeping inferior individuals at a distance from the safer, preferred centre, or on a trade-off between safer microhabitats (centre of the group) versus microhabitats that are risky but richer in prey (periphery; summarized in Krause & Ruxton, 2002). The reduction in pit size with density in the laboratory offers additional support for the expectation of mutual interference, as also shown for antlions and spiders (e.g. Day & Zalucki, 2000; Devetak, 2000; Matura & Takano, 1989). We suggest that pit construction and maintenance involve sand throwing, leading to disturbance and encouraging pit relocation. Indeed, in antlions and spiders relocations increase with density, as individuals try to move away from the dense habitat where they pay high foraging costs from interference (e.g. Day & Zalucki, 2000; Griffiths, 1991; Smallwood, 1993). The next step should be to investigate how hunger level affects the spatial pattern. When animals are satiated the benefit of capturing prey decreases, making relocation to less dense sites and pit construction both energy consuming and risky, and thus less profitable.

Hungry active foragers search more intensely for prey (Bell, 1991; Claver & Ambrose, 2003), while trap-building predators enlarge their traps when needing prey (Lubin & Henschel, 1996; Herberstein et al., 2000; Lomascolo & Farji-Brener, 2001; and other references in Scharf, Lubin, et al., 2011). Hungry predators also respond faster to prey (Nakata, 2007; Scharf et al., 2010). The effect of hunger in our experiment, however, was weak, and in the opposite direction. First, the probability of a wormlion responding to prey after a 1-week or a 3-week period of starvation was not significantly different. Second, the change in pit size was minor, and contradicted our predictions: satiated individuals, especially of small body mass, constructed larger pits than hungrier small individuals. In addition, the correlation between pit size on day 1 and on day 7 was the weakest for the satiated group, as the maximal pit

size was reached after 7 days for this group, almost irrespective of body mass. In comparison, hungrier wormlions showed a stronger correlation between pit sizes on day 1 and day 7. Sit-and-wait predators have lower metabolic rates than their actively foraging relatives (Nagy et al., 1984). Trap-building predators, and especially antlions, have very low rates as well (Lucas, 1985a; Tanaka, 1989), and they can endure starvation for months (Scharf & Ovadia, 2006). It is possible that the wormlions not receiving prey in this experiment entered an ‘energy-saving’ mode, and reduced their activity in order to preserve energy, in the absence of food. Third, lack of response/activity could be related to a decrease in activity before moulting (Griffiths, 1986). Wormlion larvae plausibly have six instar stages (Wheeler, 1930), so some of the tested individuals could have started to moult. Finally, the starvation treatment might not have been harsh enough, and more prominent differences might have been obtained if the wormlions had been starved for longer.

In general, pit size was only weakly affected by body mass or length in both field and laboratory. This is in strong contrast to other trap-building predators, for which up to 87% of the variance in pit size was explained by body size (e.g. Scharf et al., 2009). The correlation found between pit sizes in the field and the laboratory suggests that pit size could be consistent, and perhaps influenced by physiological condition (Elimelech & Pinshow, 2008), as part of a multitrait correlation (Alcalay et al., 2014), or a consequence of past experience (Liang, Lin, Lin, Chen, & Shieh, 2010). A combination of field and laboratory experiments is important in order to understand whether the patterns and processes observed in the laboratory are also reflected in the field. We found that the increased regularity of the spatial pattern was evident mainly in the laboratory, and the spatial pattern in the field could be affected much more by other factors, such as abiotic disturbance (e.g. leaf litter). In addition, we detected a similar correlation between body mass or size and pit size both in the field and under laboratory conditions. Since wormlions sometimes coexist with antlions and exploit a

similar niche, it would be interesting to study their mechanisms of coexistence. Devetak (2008a) suggested that such a mechanism might be that of a distinct preference for different sand particle size, with wormlions preferring finer sand. We suggest, in short, that wormlions demonstrate a different balance point on the trade-off between tolerance to biotic and abiotic stress: they are probably less sensitive to intraspecific competition than antlions but more sensitive to the physical characteristics of the microhabitat. This suggestion still remains to be tested.

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