

# The effect of previous experience on trap construction and movement distance in a pit-building predator

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**Abstract** Wormlion larvae are sit-and-wait predators that construct cone-shaped pits in sandy patches to capture prey. Wormlions select microhabitats that feature favorable conditions for pit construction, in a similar way to other trap-building predators, like spiders and antlions. We investigated whether wormlions exhibit an experience-based behavioral plasticity in their pit construction behavior. In a laboratory experiment, pit sizes and relocation distances were compared between larvae that experienced either a period of unfavorable conditions, i.e., surface obstacles, shallow or coarse sand, or a period of favorable conditions, i.e., clear, deep, and fine sand and were able to construct pits undisturbed. We expected that wormlions experiencing improving conditions would build larger pits than those experiencing deteriorating conditions. In addition, we expected that larvae experiencing unfavorable conditions would be less choosy in their new microhabitat and move over shorter distances. We observed a certain effect of recent experience on the trap-building behavior; however, it was not consistent among treatments. Additionally, we detected a correlation between larval body mass, relocation distance, and pit area. These findings might suggest that past experience does not influence wormlion foraging behavior in a simple manner but that different types of experience induce different behavioral responses.

**Keywords** Trap-building predators · Vermileonidae · *Vermileo* · Wormlion · Foraging

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## Introduction

The choice of a suitable habitat has a critical effect on animal fitness. Selection favors those individuals that succeed best at obtaining reliable information about the environment by using their senses and accordingly choose a habitat that maximizes resource uptake, survival, and reproduction (Brown 1988; Morris 1989). During their lifetime, individuals may acquire critical information regarding their environment. Therefore, an animal's previous experience and habitat familiarity might play a major role in influencing its behavior later on (Wolf et al. 2009). A plastic behavioral response can be advantageous over a "hard-wired" (fixed, regardless of conditions) behavior when the environment changes predictably within the lifespan of an individual but changes unpredictably between generations (Stephens 1993; Snell-Rood 2013). Too much variation causes the learned behavior to lose its utility, while too little variation makes a hard-wired behavior more suitable (Kerr and Feldman 2003; Cunningham and West 2008).

Variation in experience resulting from differing habitat conditions can generate evolutionarily and ecologically relevant variation in behavior. For example, experience with a certain prey type can greatly increase a predator's foraging efficiency of feeding on that particular prey (Ibrahim and Huntingford 1992). Similarly, experience in a particular habitat can induce specialization, increasing patch use success (shown in bluegill sunfish; Werner and Hall 1974). Another way an animal's experience can affect its behavior is directly through the animal's physiology. For example, in the ant *Temnothorax albipennis*, a worker's decision whether to remain inside the nest or go outside and forage is affected both by the individual's fat reserves and by the recent experience (Robinson et al. 2012). "The silver spoon effect" hypothesis predicts that animals in a poor physiological condition will be less selective when choosing habitats and mating partners

(Stamps 2006). For example, parasitoid wasps that develop and emerge from a less preferred host have increased acceptance to that host as adults (Vos and Vet 2004).

Most studies that have investigated the effect of experience on habitat choice have focused on the relationship between natal experience and behavior during the dispersive, adult stage. This type of behavior is of interest to evolutionary biologists, as it might influence dispersal and speciation (Davis 2008). Insects and birds are particularly suitable for this type of research, as their early life stages are usually immobile as opposed to the adult flying, dispersive stage. Because experience can be used shortly after exposure to a specific environment, it can have a large adaptive value even in short-lived species like most insects (Anderson and Anton 2014). In insects, relatively few studies have focused on the relationship between experience and behavior solely within the larval stage. Of these, many have focused on Lepidopteran larvae, which prefer plants on which they have already fed over plants on which they have not fed (Saxena and Schoonhoven 1982; Carlsson et al. 1999). For example, naïve larvae of the moth *Manduca sexta* feed and grow successfully on a variety of plants, but after a period of feeding experience on a natural host plant, they become specialist feeders (Saxena and Schoonhoven 1982).

In this study, we investigated the experience-dependent behavior of wormlion larvae. Wormlions are predators that construct pits to trap small arthropods and feed on them, similarly to pit-building antlions. Because wormlions and antlions belong to two different insect orders, this presents a fine case of convergent evolution (Dor et al. 2014), and both pit-building predators can be compared to web-building spiders, which similarly use traps to hunt prey (Scharf et al. 2011). Antlion pit construction behavior is affected by abiotic factors that might influence their capture success, such as soil type and depth (Hauber 1999; Scharf et al. 2008; Liang et al. 2010; Barkae et al. 2012; reviewed in Scharf et al. 2011). Spiders and antlions change their trap dimensions or other trap characteristics following experience with different prey types (Herberstein and Heiling 1999; Lomascolo and Farji-Brener 2001; Tso et al. 2007; but see Olive 1982), and improve their capture success with experience (Nakata 2007; but see Scharf et al. 2010). Additionally, antlions can learn to associate a cue (falling sand) with a prey item falling into their pit, which leads to more efficient prey consumption and faster larval development (Guillette et al. 2009; Hollis et al. 2011). Furthermore, both spiders and antlions relocate their traps more often when exposed to a lower prey arrival rate than previously experienced (Olive 1982; Jenkins 1994).

We performed two experiments to study the effect of prior experience and its interaction with current conditions on pit area and habitat selectivity. As highly sedentary predators, it may be adaptive for wormlion larvae to be able to compare their current conditions to their previous experience; we

therefore expected that current and previous conditions would interact to affect the behavior. Specifically, deteriorating and improving conditions were expected to lead to smaller or larger pits being constructed, respectively, since the probability of capturing prey may be higher in improving conditions, and the larvae are thus expected to invest more in foraging. According to the silver spoon effect (Stamps 2006), we expected that larvae with past experience of favorable conditions to invest more effort in relocating and therefore move over greater distances when exposed to unfavorable conditions than larvae with prior experience of unfavorable conditions, which are expected to be less selective.

## Methods

### Study animal and collection

Wormlions (Diptera: Vermilionidae) are sand dwelling, sit-and-wait, predaceous insect larvae that feed on other small arthropods (Devetak 2008a, b; Fig. 1). Once a small arthropod falls into the pit, it collapses the sand around it, alerting the predator, which then strikes and feeds on its prey. Wormlion habitat choice is most affected by abiotic factors such as light, sand depth, and sand particle size (Devetak 2008a; Devetak and Arnett 2015; Adar et al. 2016). Being highly sedentary, and most commonly found in shaded sandy patches (Devetak 2008b; Dor et al. 2014; Adar et al. 2016), wormlions have



**Fig. 1** **a** An image of a wormlion (*Vermileo* sp., undescribed) larva under a binocular and **b** an image showing wormlion pits in their natural environment

relatively predictable local environmental conditions. However, small objects, such as debris and stones, can fall onto the pit and impede its construction, and sand can be shifted by wind.

Wormlion larvae were collected from sandy patches under residential buildings in north Tel Aviv, west of Tel Aviv University. The larvae were placed in the laboratory in individual plastic cups (diameter of 4.5 cm) filled with 3 cm deep sand. Before the experiments, each wormlion larva was fed with a small flour beetle larva (*Tribolium castaneum*) and then left for 3 days to standardize the hunger level. Wormlions were weighed using an analytical balance (accuracy of 0.1 mg) to determine their body mass. Pit areas and movement distances were measured by photographing the sand and analyzing the photographs using the software ImageJ (Abràmoff et al. 2004). A piece of millimetric paper was included in the photos as a scale.

### Experimental setup

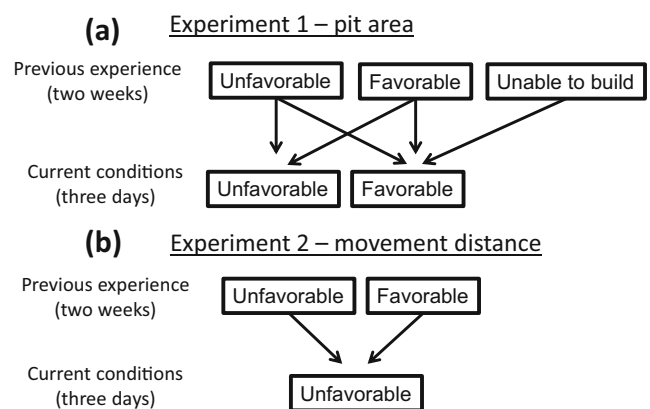
#### Experiment 1: the effect of recent larval experience on pit area

Wormlion larvae ( $n = 230$ ) were placed in individual plastic cups in a climate cabinet throughout the experiment (26 °C, ~50 % humidity). Each larva was randomly assigned to one of the five following initial treatments: (1) shallow sand (0.5 cm deep); (2) sand with surface obstacles (small pebbles; similar to Adar et al. 2016); (3) coarser sand (mostly >250 μm particles); (4) larvae unable to build pits (larvae which were placed in small closed Eppendorf vials, completely filled with sand); and (5) control, no disturbance, clear, fine (mostly <250 μm particles), and deep sand. The initial treatment lasted for 14 days, during which we monitored whether larvae had built pits and if so, we measured their area by calculating the area locked within a polygon in the photos. Pit areas were measured twice during the initial condition period: 24 h after placing the larvae in the cups (day 2), and again on day 5. One day before the second measurement, larvae were pulled out of their pits and thus forced to construct new ones. Pits were measured the second time to control for the effect of pulling the larvae out, regardless of a change in conditions. After a 14-day period, either the larvae remained under the initial conditions or their conditions were changed from favorable to any of the unfavorable treatments or vice versa. Our 11 treatments and sample sizes were performed as follows: Deteriorating conditions: from control to (1) shallow, (2) coarse, and (3) obstacles conditions. Improving conditions: from (4) shallow, (5) coarse, and (6) obstacles to favorable (control) conditions. Constant disturbance conditions: (7) shallow to shallow, (8) coarse to coarse, and (9) obstacles to obstacles ( $n = 20$  for each of these nine treatments). (10) Constant conditions without disturbance: control to control. (11) Larvae without past

building experience: Eppendorf (unable to construct a pit) to control ( $n = 25$  for treatments 10 and 11). Note that our design is not full factorial, because we were not interested in studying interactions between different, unfavorable, disturbance conditions (Fig. 2a). We were interested in testing the effect of improving or deteriorating conditions across multiple kinds of poor conditions. Pits were photographed and measured 24 h after the change (day 15). To explore the effect of initial treatment on pit area, we used two separate ANCOVA tests with  $\text{pit}_{\text{day} = 2}$  and  $\text{pit}_{\text{day} = 5}$  as response variables and treatment and body mass as binary and continuous explanatory variables, respectively. Since we detected a possible change in the effect of treatment with time, we used a single repeated measure ANCOVA to test for the effect of treatment, body mass, and time on the change in pit area from day 2 to day 5. After changing conditions (day 14), each treatment combination, based on initial and current conditions, received a code, for example, a larva that received coarse sand initially and favorable conditions as the current ones received the code CF. Statistically crossing initial and current conditions was impossible due to missing combinations. For the analyses, we used an ANOVA to test for the effect of previous conditions on pit area in favorable sand compared to each of the previous disturbance conditions, with body mass as a covariate. Pit areas were log transformed due to their deviation from a normal distribution. Average body mass did not differ among treatment groups. We used Tukey’s post hoc tests to examine differences among treatment groups.

#### Experiment 2: the effect of recent larval experience on movement distance

Similarly to the previous experiment, 150 wormlion larvae were placed in individual plastic cups in a climate cabinet



**Fig. 2** A scheme describing **a** experiment 1: the effect of recent larval experience on pit area and **b** experiment 2: the effect of recent larval experience on movement distance. Unfavorable conditions included one of the abiotic disturbances (shallow, coarse, or obstructed sand). Larvae in favorable conditions received the same fine, deep, and clear sand. During the 2-week period larvae were pulled out of their pits after 4 days and again when transferred to “current conditions”

under the same conditions. Each larva was assigned to one of four initial treatments: (1) shallow sand (0.5 cm deep), (2) sand with surface obstacles, (3) coarser sand, and (4) undisturbed control group (clear, fine, and deep sand). After a 14-day period, the larvae were individually placed in the center of large aluminum trays (25 × 20 cm) filled with sand. These trays contained either shallow sand, surface obstacles, or coarser sand (Fig. 2b). After 24 h the trays were photographed, and the trails made by the larvae while moving were measured. We compared the distances moved by larvae from each treatment to control larvae (clear, fine, and deep sand). For this purpose, we used three ANCOVA tests (one for each treatment against the control), including body mass and its interaction with treatment. We performed another ANCOVA test to determine whether the initial treatment (control vs disturbed) or disturbance type (shallow, coarse sand, or obstacles) affected the larvae's movement distance. Distances were square root transformed due to their deviation from a normal distribution (this transformation achieved a normal distribution [Kolmogorov-Smirnov test:  $P = 0.47$ ], while a log transformation did not [Kolmogorov-Smirnov test:  $P = 0.022$ ]).

## Results

### Experiment 1: the effect of recent larval experience on pit area

#### Initial conditions I

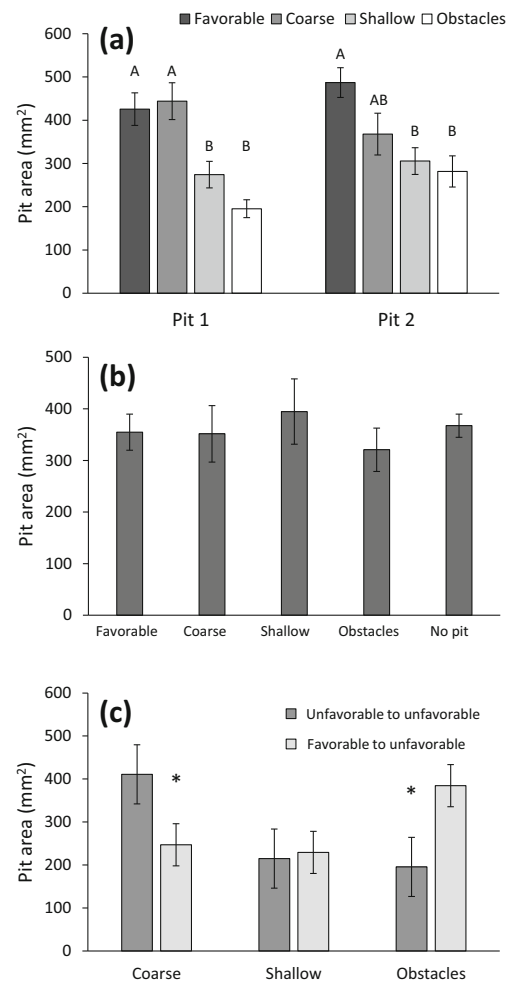
Initially, larvae exposed to surface obstacles or shallow sand conditions constructed smaller pits than those in the control and coarse sand groups ( $F_{3,119} = 10.96$ ,  $P < 0.0001$ ). Body mass had a positive effect on pit area ( $F_{1,119} = 7.67$ ,  $P = 0.0065$ ). The mass × treatment interaction was not significant ( $P = 0.15$ ), and was subsequently removed from the analysis.

#### Initial conditions II

After pulling the larvae out of their traps and forcing them to construct new pits in the same conditions, the results were similar, with the only difference being that of the coarse sand group constructing smaller pits that were not statistically different than the other groups ( $F_{3,108} = 8.46$ ,  $P < 0.0001$ ; Fig. 3a—pit 2). Body mass again had a positive effect on pit area ( $F_{1,108} = 9.32$ ,  $P = 0.0028$ ).

#### Switching conditions

After conditions were switched, all wormlions tested under favorable conditions constructed similarly sized pits, regardless of previous conditions (no effect of previous treatment on



**Fig. 3** a Initial pit areas in different abiotic conditions before (pit 1) and after (pit 2) pulling larvae out of their traps. Significant statistical differences are indicated by capital letters. b Pit areas in favorable conditions after switching conditions from all abiotic disturbance types (Coarse, shallow, obstacles, or unable to build). There were no differences in pit area based on previous experience. c Pit area before and after switching the conditions (unfavorable to unfavorable conditions, dark gray, vs. favorable to unfavorable conditions, light gray). Unfavorable conditions comprise coarse sand, shallow sand, and surface obstacles. Means of each disturbance treatment ±1 SE are shown; significant statistical differences are marked by asterisks

area:  $F_{4,70} = 1.06$ ,  $P = 0.38$ ; Fig. 3b). The effect of mass was again significant, with larvae of greater mass constructing larger pits ( $F_{1,70} = 10.27$ ,  $P = 0.0020$ ). The mass × treatment interaction was again not significant and removed ( $P = 0.61$ ). Interestingly, when constructing pits in coarse sand, larvae with previous experience in such sand constructed larger pits than those that previously experienced fine sand ( $F_{1,19} = 8.52$ ,  $P = 0.0088$ ; Fig. 3c). Mass and its interaction with treatment had no effect ( $P = 0.87$  and  $P = 0.28$ , respectively). In contrast, when constructing pits in obstructed sand, larvae with previous experience in obstructed sand constructed smaller pits than those previously in unobstructed sand ( $F_{1,20} = 14.94$ ,  $P = 0.0010$ ; Fig. 3c). Mass and its interaction with treatment

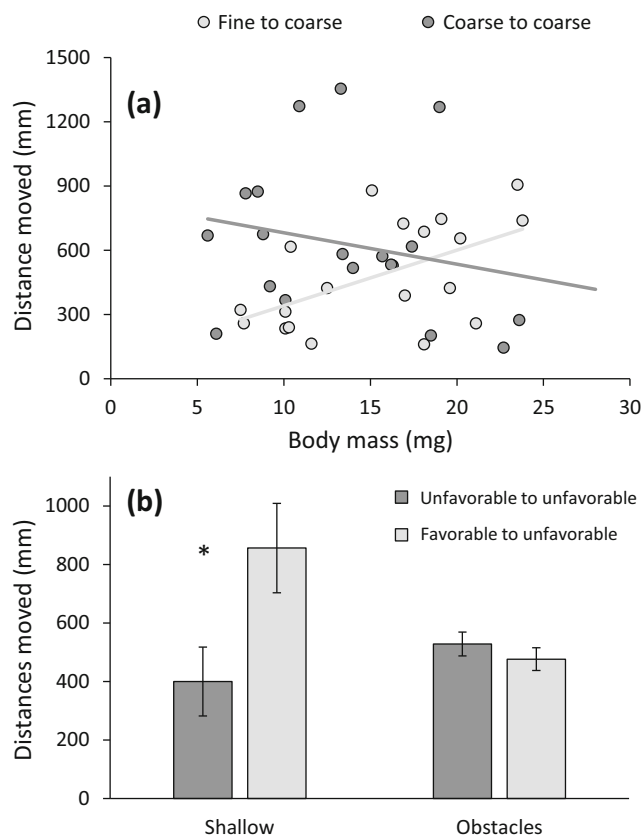


had no effect ( $P = 0.59$  and  $P = 0.47$ , respectively). Pit area in shallow sand was similar, regardless of previous conditions ( $F_{1,18} = 0.15$ ,  $P = 0.70$ ; Fig. 3c). Mass and its interaction with treatment had no effect ( $P = 0.49$  and  $P = 0.25$ , respectively).

**Experiment 2: the effect of recent larval experience on movement distance**

*Movement in coarse sand*

Coarse sand interacted with body mass to affect movement distances ( $F_{1,34} = 5.99$ ,  $P = 0.020$ ; Fig. 4a): mass had no effect on movement when wormlions had previous experience in coarse sand but did have a positive effect on movement in the group that experienced fine sand. Individuals experiencing coarse sand moved over longer distances than ones experiencing favorable conditions ( $F_{1,34} = 7.94$ ,  $P = 0.008$ ), but the effect of mass was not significant ( $F_{1,34} = 0.31$ ,  $P = 0.58$ ).



**Fig. 4** **a** The interaction between the changing conditions (fine sand to coarse sand) or constant coarse sand and the body mass and their effect on movement distances. **b** Movement distances when conditions remain unfavorable (either coarse sand, shallow sand, or surface obstacles; dark gray), or change from favorable to unfavorable (light gray). Means of each disturbance treatment  $\pm 1$  SE are shown; significant statistical differences are marked by asterisks

*Movement in shallow sand*

Previous experience in favorable conditions led to longer movement distances in shallow sand than did previous experience in the less favorable shallow sand ( $F_{1,35} = 4.22$ ,  $P = 0.047$ ; Fig. 4b). The effect of mass and the interaction term were not significant ( $F_{1,35} = 0.19$ ,  $P = 0.66$ ;  $F_{1,34} = 0.30$ ,  $P = 0.59$ , respectively).

*Movement in obstructed sand*

Previous experience in favorable sand or sand with surface obstacles had no effect on movement distance ( $F_{1,40} = 0.65$ ,  $P = 0.42$ ; Fig. 4b). Body mass and the two-way interaction were also not significant ( $F_{1,40} = 2.51$ ,  $P = 0.12$ ;  $F_{1,39} = 1.08$ ,  $P = 0.30$ , respectively).

**Discussion**

In contrast to our expectations, we could not detect a consistent response by wormlions to deteriorating or improving conditions and behavior was mainly dictated by current conditions. Previous experience in coarse sand induced the construction of larger pits in the same conditions. In contrast, previous experience with obstructed sand induced the construction of smaller pits in those conditions. Experience in shallow sand had no effect on the later constructed pit size; neither did the previous inability to construct a pit at all. When constructing a pit for the first time, however, without prior experience in the lab, abiotic conditions did have an effect on larval pit areas. Larvae in the favorable conditions (control) group constructed larger pits than the abiotic disturbance groups, after controlling for the positive effect of body mass. Regarding movement distance, there were two important findings: the group experiencing deep sand first moved over longer distances when switched to shallow sand than the group that had experienced shallow sand as initial conditions. Additionally, changing from fine to coarse sand led larger larvae to move over longer distances, while body mass had no effect on movement for larvae remaining in coarse sand. These two latter results are the only ones supporting our expectation for increased selectivity when conditions deteriorate. While our initial expectation was not met entirely, we do have some evidence for the effect of previous experience on wormlion behavior. However, this effect is not as simple as we predicted and varies in different experience conditions.

The abiotic conditions we used as disturbances are known to affect the behavior of wormlion larvae (Adar et al. 2016). Wormlions move over greater distances when conditions are unfavorable and, when given a choice, larvae select the undisturbed habitats in greater proportions (Adar et al. 2016). This is similar to the behavior of antlions and spiders (Lubin et al.

1993; Farji-Brener 2003), which also modify their behavior according to past experience (see Introduction). Hence, we expected the wormlions to adjust their foraging investment according to recent conditions they experience. However, wormlions were not consistently affected by previous conditions, either favorable or unfavorable ones. In our first experiment, experience in coarse sand caused an increase in pit size when current conditions were favorable, as we predicted. In contrast, experience in obstructed sand caused a decrease in pit size. Perhaps a difference between these two types of abiotic disturbances is the time it takes the larvae to perceive them. Surface obstacles might have a longer-lasting response because not encountering them does not mean they are absent from the near environment. The reason larvae which had experienced obstacles might invest less in foraging for a longer period than larvae experiencing coarse sand might be that coarse/shallow sand can be sensed immediately, even before constructing a pit, unlike surface obstacles which might be mostly sensed when pit construction has already begun and can be avoided or discarded by large larvae. Perhaps a longer period in initial conditions than the one we used, while allowing the larvae to construct more pits, can make the response to obstacles more similar to that of the response to coarse sand. In shallow sand conditions, larvae that experienced favorable conditions moved over longer distances than larvae that experienced shallow sand. This matched our prediction, but no such trend was observed in the other disturbance treatment groups. Coarse sand and obstacles might make movement itself more costly, unlike shallow sand which should not influence it to a high degree; therefore, larvae experiencing obstacles or coarse sand may reduce their movement not because of reduced selectivity in the context of trap efficiency but due to the cost of relocation itself.

Responding to different environmental conditions might not always be the best strategy, and a fixed response could be preferred. If the environment changes too quickly, faster than the ability of individuals to follow such changes, it is perhaps advisable to use a constant strategy, which suits most situations on average. Olive (1982), for example, showed that some species of spiders do not change their web design when encountering different prey types, although other species do so. Changing the behavior following a period of experience might not occur not because it is not adaptive but because of its high cost. Maintaining long memory ability is costly, as shown for fruit flies selected for long memory, which exhibited a faster decrease in fecundity with age and elevated aging (Kawecki 2010). Furthermore, “forgetting” is also valuable, so predators, for example, should be “forgotten” when they are absent and normal activity can be resumed (Pamminer et al. 2011). In short, it might be non-beneficial or even costly for wormlions to maintain longer memory, and each microhabitat should consequently be treated based only on its current properties.

From similar experiments on antlions, however, it was concluded that pit-building experience has an influence on pit area, with larvae previously unable to construct pits having smaller traps than expected when compared to free-building ones (Hauber 1999; Liang et al. 2010). The main differences between those experiments and the ones presented here are that (1) pit building experience in those experiments encompassed only the ability/disability to construct a pit, irrespective of other abiotic conditions, and (2) food limitation was also manipulated and was shown to affect pit-building behavior. Other studies on improving or deteriorating conditions and their effect on behavior usually use food to simulate improvement/deterioration. For instance, flour beetles grown under a poor diet were more accepting of the same poor diet than those grown under a rich diet (Van Allen and Bhavsar 2014). Well-fed antlions, on the one hand, enlarge their pits compared to underfed ones (Hauber 1999; Liang et al. 2010), and even receiving prey cues, without actually consuming any prey, can lead to an increase in pit size (Scharf et al. 2010; also spiders: Nakata 2007). On the other hand, all trap-building predators strongly respond to the abiotic properties of their microhabitat, usually even more strongly than to prey, because trap use will be less efficient under unsuitable conditions (Liao et al. 2009).

Trap-building predators are known to experience high variation in the amount of incoming prey and are adapted to endure long periods of starvation. It is possible that this variance in the amount of incoming prey can induce an experience-based response better than the abiotic conditions used in our experiments. However, it might be hard for an individual predator to determine whether a current shortage of prey is global or only local, based only on prey arrival rate. This distinction is important because relocating is beneficial only if the shortage is local (Scharf et al. 2011). Directly examining the influence of feeding regime experience on trap construction behavior of wormlions may yield further interesting results.

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