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Wormlions prefer both fine and deep sand but only deep sand leads to better performance

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Abstract

Wormlions are small fly larvae that dig pits in loose soil to trap their prey. Similar to other trap-building predators, like spiders and antlions, they depend on the habitat structure for successful trap construction and prey catch. We examined whether sites at which wormlions are present differ in sand depth and particle size from nearby sites, at which wormlions are absent. Next, in the laboratory we manipulated both sand depth and type (fine vs. coarse) to determine their joint effect on microhabitat preference, the size of the constructed pit, wormlion movement, and their latency to respond to prey. We expected better performance by wormlions in fine and deep sand, and the sand in wormlions' natural sites to be finer and deeper. However, in only partial agreement with our expectations, wormlion sites featured finer sand but not deeper sand. In the laboratory, wormlions preferred both fine and deep sand, and moved more in shallow and coarse sand, which we interpret as an attempt to relocate away from unfavorable conditions. However, only deep sand led to larger pits being constructed and to a faster response to prey. The preference for fine sand could, therefore, be related to other benefits that sand provides. Finally, body mass was a dominant factor, interacting with the preference for both deep and fine sand: deep over shallow sand was more favored by large wormlions and fine over coarse sand by smaller ones. Our results suggest that several factors should be incorporated when studying microhabitat selection.

Key words: antlions, habitat selection, habitat structure, substrate, trap-building predators, Vermileo

Habitat selection—the process through which animals choose where to settle—has great impact on survival and reproduction (Tregenza 1995; Gunnarsson et al. 2005). Choosing the most suitable conditions is important for animals, and other choices can lead to suboptimal performance. A mismatch between the preferred habitat and the one that provides the highest fitness is common, and have been explained in various ways, such as ecological traps, conflicting demands taken into account by animals, individual experience, and frequency-dependent selection (reviewed in birds in Chalfoun and Schmidt 2012). While choosing a suitable habitat, animals take into consideration biotic and abiotic factors, such as the habitat quality, conspecific density, predation risk, and temperature (Rosenzweig 1981; Huey 1991; Grand and Dill 1999). Past studies often focus on the biotic characteristics of the habitat, whereas relatively neglecting

the effect of abiotic features on habitat selection (Huey 1991; Halliday and Blouin-Demers 2014).

Ground-dwelling animals, like those inhabiting sandy habitats, are greatly affected by the features of their substrate. Burrows in sand, for example, are efficient in providing thermal refuge for birds and lizards in sandy habitats (Pough 1970; Williams et al. 1999), and the depth to which they can dig is therefore critical. The effects of substrate depth and particle size, as 2 potentially important abiotic factors for ground-dwelling animals, have not been the focus of much research. The few studies include the effect of sand particle size on the performance of parasitic nematodes infecting moths, with optimal performance being found in mid-size particles (Blackshaw and Senthamizhselvan 1991), and the strength of this abiotic effects being species-specific (Gruner et al. 2007). Similarly, adding coarser particles to sand impairs the

predation success of fish on substrate-dwelling insects in rivers and lakes (Brusven and Rose 1981).

Pit-building predators are small insect larvae that construct conical pits in loose soils in order to trap arthropod prey (Scharf et al. 2011). They belong to 2 unrelated insect families—antlions (Neuroptera: Myrmeleontidae) and wormlions (Diptera: Vermileonidae)—demonstrating together a fine example of convergent evolution (Miler et al. 2018). Antlions have been much more often studied than wormlions (Dor et al. 2014). Therefore, most of the cited literature when discussing pit-building predators will refer to antlions, although we study wormlions. Antlion literature is nevertheless relevant here, due to the high similarity in the foraging method between the 2 taxa. Pit-building predators greatly depend on the abiotic features of their habitat for their success (Scharf and Ovadia 2006), but not all species perceive their habitat similarly. Two co-occurring antlion species, for example, differ in their preferred substrate, with each species constructing larger pits in its preferred substrate and being more likely to capture prey there (Barkae et al. 2012). Several antlion species prefer fine sand of small particle size when given a choice (Allen and Croft 1985; Loiterton and Magrath 1996; Botz et al. 2003; Farji-Brener 2003). The definitions of “fine” and “coarse” sand differ between studies (cf. Farji-Brener 2003; Matura et al. 2005), and when given a choice between 2 options of sand (“fine” vs. “coarse”), there is rarely a reference to the natural habitat (but see Farji-Brener 2003). Even when such a reference is given, the threshold separating between “fine” and “coarse” sand is usually not justified. In general, there are large differences among antlion species in their preferred sand type and particle size, as well as difference in the level of specialization or the breadth of preference (Devetak and Arnett 2015).

Although the effect of sand depth on pit-building predators has been considerably less studied than sand particle size, antlions have been shown to construct larger pits and move over shorter distances in deep than in shallow sand (Loria et al. 2008; Scharf et al. 2009). Movement over long distances is usually interpreted in trap-building predators as a sign for low suitability of the current site for ambushing prey, and can be triggered by both biotic and abiotic factors (reviewed in Scharf and Ovadia 2006). Larger pits enable capturing larger prey and reduces the likelihood of prey escaping the pit (Griffiths 1980; Lucas 1982; Heinrich and Heinrich 1984; Scharf et al. 2018; but see Lomascolo and Farji-Brener 2001). Another gap in the literature relates to the effect of body mass on preference for different substrates in pit-building predators in particular, and in ground-dwelling insects in general. Body mass is a key trait, affecting both survival and reproduction (Stockhoff 1991; Honěk 1993; Renault et al. 2003). It is also often involved in tolerance of abiotic stress (e.g., larger insects tolerate desiccation stress better than smaller ones; Le Lagadec et al. 1998; Fouet et al. 2012). There is, therefore, good reason to assume an effect of body mass on preference and performance also in respect to sand type and depth.

Wormlions are highly abundant in cities all over Israel and generally in the Mediterranean, found beneath man-made shelters (Ludwig et al. 2001; Dor et al. 2014), whereas their natural habitat is either in caves or cliff overhangs (Wheeler 1930, ch. 5; Devetak 2008b). Wormlions are a neglected trap-building predator in regard to research, and there is only a little available evidence of their habitat preferences. When wormlions are given a choice, they prefer fine, deep and dry sand, clear of any obstructions (Devetak 2008a; Adar et al. 2016; Devetak and Arnett 2015; Scharf et al. 2018). They also prefer shaded over lit microhabitats, although this preference also depends on the microhabitat shape and temperature (Katz et al. 2017; Katz and Scharf 2018).

There were 2 main goals in this study. First, we performed field observations to uncover whether sites beneath man-made shelters where wormlions are present differ regarding sand depth and particle size from sites at which wormlions are absent. We expected sites inhabited by wormlions to have deeper, finer sand than sites with no wormlions. Second, we performed 3 laboratory experiments, examining the combined effect of sand depth and particle size on pit construction, latency to respond to prey, and microhabitat choice by wormlions. We expected wormlions to prefer fine and deep sand, because both may contribute to the construction of larger pits, and consequently to faster response to prey, translated to more efficient prey capture. Even though our field observations did not point to differences in sand particle size between wormlion-present and absent sites (see Results), we still expect wormlions to prefer fine sand, based on past studies with a similar species (Devetak 2008a; Devetak and Arnett 2015).

Materials and Methods

The studied species is undescribed yet (*Vermileo* sp.), but according to a Dipteran specialist, there is only a single wormlions species in Israel (A. Freidberg, personal communication). Wormlions occur in dense groups (hereafter, “clusters”) only below a cover providing full shade. Their clusters are similar to clusters of the ecologically comparable pit-building antlions (called “antlion zone”; Gotelli 1993).

Field observations: characterization of sand particle size and depth

Our goal was to compare sand particle size and depth at sites where wormlions are present and absent, hypothesizing that wormlion clusters would be characterized by occupying finer, deeper sand. We collected 150 mL of sand from each of 22 sites: 12 samples from wormlion clusters and 10 samples from sites of loose sand under full shade with no visible pits (wormlion present vs. wormlion absent sites). The wormlion absent sites were up to a few 10 of meters from wormlion present sites and there was no observable difference between the 2 site types. We did not choose wormlion absent sites that are immediately adjacent to wormlion present sites, because they are often not suitable for wormlions (either too little sand or insufficient shade). The soil was collected from a single point (an approximation of the site’s center) using a measuring cup. The cup reached the ground below the sand in all collections, which was only a few cm deep. All sites were observed located beneath man-made shelters at Tel Aviv University (32°6′45″N, 34°48′15″E) and were within a limited area of ~0.50 km². The distance between the most remote sites was less than 1 km. Each sand sample was dried for 48 h at 60°C and then weighed (Precisa BJ410, accuracy of 0.01 g). Sand density is the ratio between mass and volume, with higher mass in equal volume comprising higher density, which in this case suggests more sand particles in the 150 mL sand samples. The sand samples were then passed through 5 sieves filtering sand particle sizes in descending size (710, 500, 250, 105, and 63 μm; similar to Devetak and Arnett 2015). We separately weighed the sand of the 6 different particle size ranges obtained in this process. To determine sand depth, we placed 2 measuring tapes crossing the wormlion cluster along its longer axis, and measured using a ruler the sand layer depth in evenly distributed points along this axis. In each cluster, we measured 10 points (5 points across each measuring tape), with 13 and 12 wormlion present and absent sites being measured. The sites were identical to those used to measure sand particle size, plus 3

additional sites. We averaged the 10 sand depths in each cluster to achieve a single value per cluster (to avoid pseudoreplications).

Statistical analysis

Sand particle size was compared in 2 ways. First, we used a *t*-test to compare the sand masses (of equal volumes) between wormlion present and absent sites. Next, we performed a principal component analysis (PCA) on z-transformed masses of the 6 sand particle size ranges (Gotelli and Ellison 2004, ch. 12). The first and second Principal Components (PCs) were then compared using 2 separate *t*-tests. Sand depth was compared by first averaging the 10 depth measurements for each wormlion present or absent site (to obtain a single average sand depth value per cluster), and then applying a *t*-test on square-root transformed depths (due to their right-skewed deviation from normal distribution).

Experiment 1: the effect of sand particle size and depth on pit area and response to prey

Wormlions ($n = 180$) were collected in April 2018 in a single site at Tel Aviv University. Here and in the following experiments wormlions were not fed prior to the experiment and their hunger level represents well that found under natural conditions. They were weighed (accuracy of 0.1 mg), and individually assigned in a full-factorial design to 6 sand depths (0.5, 1, 1.5, 2, 2.5, and 3 cm), and 2 sand types (fine and coarse, particles of 105–250 μm and 250–500 μm , respectively; 12 treatment combinations; 15 replications per treatment). We used this specific cut-off point, because the characterization of sand particle size had revealed that ~85% of the sand fell within one of these 2 ranges of particle size (see “Results” section). The sand was purchased from a construction shop in order not to destroy the wormlions’ habitats and to ensure that the sand was as homogenous as possible, as we required a large quantity of sand, which could not be obtained from any one site alone. After 24 h, we photographed the constructed pits and measured their area using the software ImageJ (Abràmoff et al. 2004). Next, we dropped into the pit of each wormlion a pharaoh ant as prey (*Monomorium pharaonis*) of ~0.15 mg, collected at Tel Aviv University. Pharaoh ants resemble the similar-sized ants that comprise the majority of prey of wormlions under natural settings, though it is unknown whether wormlions prey on pharaoh ants. We recorded the latency to wormlion response to the prey by sand flicking. Wormlion response usually results in ant capture (Scharf et al. 2018). We recorded the test as “failed”, if the wormlion did not respond within 60 s or if the ant escaped the pit. Room temperature was $24.5 \pm 0.5^\circ\text{C}$ and light cycle was 12:12 L:D, both are similar to the natural conditions in the collection month. Following the experiments, which were non-lethal, wormlions were released in their collection sites that contained fine sand under shelter. No permission is required to collect wormlions.

Statistical analysis

1) We tested using an Analysis of Covariance (ANCOVA) whether body mass, sand type, and sand depth affected pit area. Body mass and pit area were both square-root transformed due to their deviation from normal distribution (skewed to the right). Here and in all analyses, we started with a saturated model (including all possible interactions) and gradually removed non-significant interactions, according to the lowest F values. The final model incorporated main effects, which were always included, and significant interactions. 2) We tested using logistic regression whether body mass, sand type and sand depth affected the likelihood of wormlions to respond to

prey (as a binary variable, yes/no). 3) We tested using an ANCOVA whether body mass, sand type and sand depth affected the response time to prey (only wormlions that responded to prey). Response time was log-transformed due to its deviation from normal distribution (skewed to the right).

Experiment 2: choice between deep and shallow sand

We collected 132 wormlions in May 2018 at Tel Aviv University from a different site than Experiment 1, in order not to collect the same individuals twice. We weighed them, and placed them individually in the center of aluminum trays (15 × 15 cm). The trays were divided into 2 halves of deep versus shallow sand (2 cm and 0.5 cm depth sand). The trays comprised either fine or coarse sand (particles of 105–250 μm and of 250–500 μm). We placed a single wormlion exactly in the middle of each tray. After 24 h, we photographed the trays and documented the wormlions’ chosen location (deep or shallow sand), pit area and movement. Movement was evident as tracks on the sand, and was estimated by dividing each tray using a 10 × 10 grid and measuring the number of cells containing wormlion tracks (0–100). Room temperature was $25.5 \pm 0.5^\circ\text{C}$ and light cycle was 12:12 L:D.

Statistical analysis

1) We tested using a one-sample *t*-test whether there was a preference for deep or shallow sand. The effect of sand type (fine or coarse) and body mass on the preference for deep sand was tested with a χ^2 test and a logistic regression, respectively. 2) The effect of mass, sand type, and the chosen sand depth on pit area was tested using ANCOVA. Non-significant 2-way interactions were gradually removed and the test was repeated. Body mass and pit area were log-transformed due to their deviation from normal distribution (right skewed). 3) The effect of body mass, sand type, and the chosen sand depth on movement was tested using ANCOVA. Movement was log-transformed (right skewed).

Experiment 3: choice between fine and coarse sand

We collected 132 wormlions in May 2018 at Tel Aviv University, weighed them, and placed them individually in the center of aluminum trays (15 × 15 cm). The trays were divided into 2 halves of fine versus coarse sand, and comprised either deep or shallow sand (values identical to Experiment 2). Experiment 3 differed from Experiment 2 in that wormlions chose between fine and coarse sand in either deep or shallow sand whereas in Experiment 2 they chose between deep and shallow sand in either fine or coarse sand. After 24 h, we photographed the trays and documented the wormlions’ chosen location (fine or coarse sand), pit area, and movement. All measurements, including temperature and photoperiod, were identical to Experiment 2 above.

Statistical analysis

1) We tested using a one-sample *t*-test whether there was a preference for fine or coarse sand. The effect of sand depth (deep or shallow) and body mass on the preference for fine sand was tested with a χ^2 test and a logistic regression, respectively. 2) The effect of mass, sand depth, and the chosen sand type on pit area was tested using ANCOVA. Non-significant 2-way interactions were removed and the test was repeated. Body mass was square-root transformed and pit area was log-transformed due to their deviation from normal distribution (right skewed). 3) The effect of body mass, sand depth, and the chosen sand type on movement was tested using ANCOVA. Movement was log-transformed (right skewed).

Results

Field observations: characterization of sand particle size and depth

The PCA resulted in 2 PCs with eigenvalues larger than one, which should be interpreted (Table 1; Jackson 1993). PC1 reflected a trade-off between the 2 coarsest particle ranges and all other ranges, and the larger values for this PC indicate a site of finer sand. PC2 reflected a trade-off between the mid-particle size range of 250–500 μm and all other size ranges. Wormlion-present sites contained finer sand than wormlion absent sites (a comparison of the PC1 between sites: $t = -2.500$, $df = 20$, $P = 0.021$; Figure 1a, b). This difference is the strongest comparing the largest particle size category, but there are also differences considering other size categories, such as the smallest one (Figure 1a). Comparison of PC2 between habitats indicated on the absence of differences ($t = -0.206$, $df = 20$, $P = 0.839$). Sand mass (of equal volume, 150 mL) differed between wormlion present and absent sites ($t = -2.965$, $df = 20$, $P = 0.008$; Figure 1c): sand in wormlion present sites was heavier, suggesting that it is composed of smaller particles. Regarding sand depth, there was no difference in the average sand depth between wormlion-present and absent sites ($t = -0.759$, $df = 23$, $P = 0.455$; mean \pm 1 SD: 3.1 \pm 2.0 cm).

Experiment 1: the effect of sand particle size and depth on pit area and response to prey

1) Wormlions constructed larger pits but only when sand depth was greater than 1 cm ($F_{1,137} = 6.624$, $P = 0.011$; Figure 2a), indicating on an interaction between body mass and sand depth. Sand type had no effect on pit area ($F_{1,137} = 0.359$, $P = 0.550$). There was no effect of sand depth and body mass as main effects on pit area ($F_{1,137} = 3.569$, $P = 0.061$; $F_{1,137} = 1.740$, $P = 0.189$, respectively). All other interactions were not significant and removed ($P > 0.348$).

Table 1. Loadings of the 1st and 2nd PC of the sand particle size PCA

Sand particle size range	PC1	PC2
λ	2.90	1.23
Percentage of variance explained	48.4	20.5
>710 μm	-0.8482	0.3841
500–710 μm	-0.3344	0.5386
250–500 μm	0.5550	-0.5970
105–250 μm	0.7361	0.2024
63–105 μm	0.7279	0.4653
< 63 μm	0.8312	0.4205

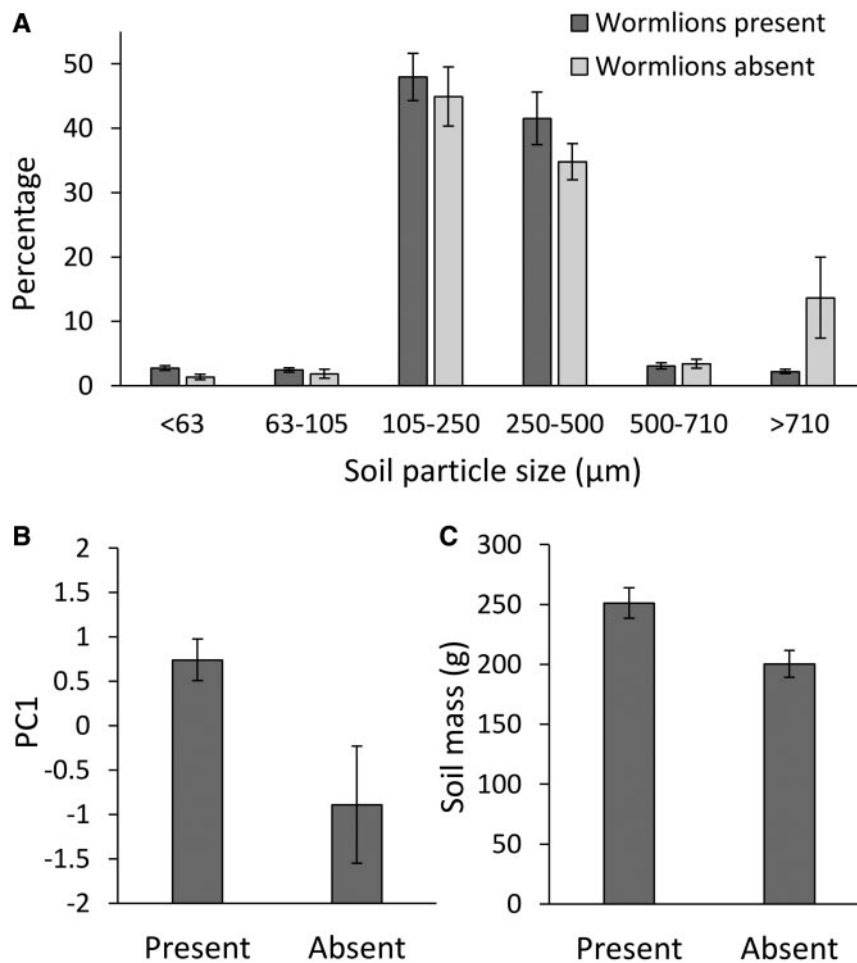


Figure 1. (A) Sand composition according to the different ranges of sand particle size at the sites, at which wormlions were present, and from which they were absent. (B) Differences between PC1 at wormlion-present and wormlion-absent sites. (C) Differences between sand mass of 150 mL sand samples from wormlion-present and wormlion-absent sites. Means \pm 1 SE are presented.

2) The likelihood to respond to prey in coarse sand increased with depth but decreased with depth in fine sand ($Z = -2.542$, $P = 0.011$; Figure 2b), due to an interaction between sand type and depth. The likelihood to respond to prey was not affected by sand type and depth as main effects ($Z = 1.957$, $P = 0.051$ and $Z = 1.537$, $P = 0.124$, respectively). The probability to respond to prey was similar among wormlions with different body mass ($Z = 1.623$, $P = 0.105$). All other 2-way interactions were not significant ($P > 0.103$). 3) Smaller wormlions and those in deeper sand responded faster to prey (Figure 2c, d), pointing to an effect of sand depth ($F_{1,111} = 5.906$, $P = 0.017$) and body mass ($F_{1,111} = 11.964$, $P < 0.001$). Response times did not differ between fine and coarse sand ($F_{1,111} = 1.402$, $P = 0.239$), and all other 2-way interactions were not significant as well ($P > 0.185$).

Experiment 2: choice between deep and shallow sand

1) Of the wormlions, 68.4% preferred deep sand ($t = 4.256$, $n = 116$, $P < 0.001$). This preference for deep sand was similar in fine or coarse sand ($\chi^2_1 = 1.766$, $df = 1$, $P = 0.184$), but increased with body mass ($Z = -2.265$, $P = 0.024$; mean ± 1 SE of wormlions in deep and shallow sand: 9.0 ± 0.7 and 6.5 ± 0.8 mg). 2) Pit area of larger wormlions was more strongly affected by the chosen sand depth than that of smaller ones ($F_{1,94} = 9.960$, $P = 0.002$; Figure 3a). This result indicates on an interaction between the chosen sand depth and body mass. Two other 2-way interactions were marginally significant: a) smaller wormlions constructed smaller pits, but this trend was more prominent in coarse than in fine sand (mass \times sand type: $F_{1,94} = 4.093$, $P = 0.046$); b) wormlions constructed larger pits in deep than in shallow sand, but this pattern was more prominent in fine sand ($F_{1,94} = 3.966$, $P = 0.049$). As main effects, larger wormlions constructed larger pits and larger

pits were constructed when deep sand was chosen ($F_{1,94} = 25.081$, $P < 0.001$ and $F_{1,94} = 14.417$, $P < 0.001$, respectively). However, sand type had no effect on the area of the constructed pit ($F_{1,94} = 3.220$, $P = 0.076$). 3) Wormlions moved over longer distances when they chose shallow sand than coarse sand ($F_{1,112} = 9.970$, $P = 0.002$), and when they chose coarse sand over fine sand ($F_{1,112} = 7.215$, $P = 0.008$; Figure 3b). Wormlions of different body mass moved over similar distances ($F_{1,112} = 0.105$, $P = 0.747$). All 2-way interactions were not significant and removed ($P > 0.104$).

Experiment 3: choice between fine and coarse sand

1) Of the wormlions, 76.1% preferred fine sand over coarse sand ($t = -6.481$, $P < 0.001$), and this preference did not differ when tested in shallow or deep sand ($\chi^2_1 = 0.347$, $P = 0.556$). Larger wormlions demonstrated a lower preference for fine sand than smaller wormlions ($Z = -2.182$, $P = 0.029$; mean ± 1 SE of wormlions in fine and coarse sand: 8.9 ± 0.7 and 11.7 ± 1.2 g). 2) Pit area was affected by both sand depth (larger in deep sand; $F_{1,96} = 107.832$, $P < 0.001$) and body mass ($F_{1,96} = 12.675$, $P < 0.001$), but not by the chosen sand type (fine or coarse; $F_{1,96} = 1.291$, $P = 0.259$). All 2-way interactions were not significant ($P > 0.110$). 3) Wormlions moved more when tested in shallow sand ($F_{1,112} = 42.471$, $P < 0.001$) and when the chosen sand was fine ($F_{1,112} = 5.442$, $P = 0.021$; Figure 4). Wormlions of different mass moved over similar distances ($F_{1,112} = 1.842$, $P = 0.177$).

Discussion

Sites at which wormlions were present contained sand of smaller particle size than sites at which wormlions were absent, reflected especially in the difference between those sites in the relative frequency of

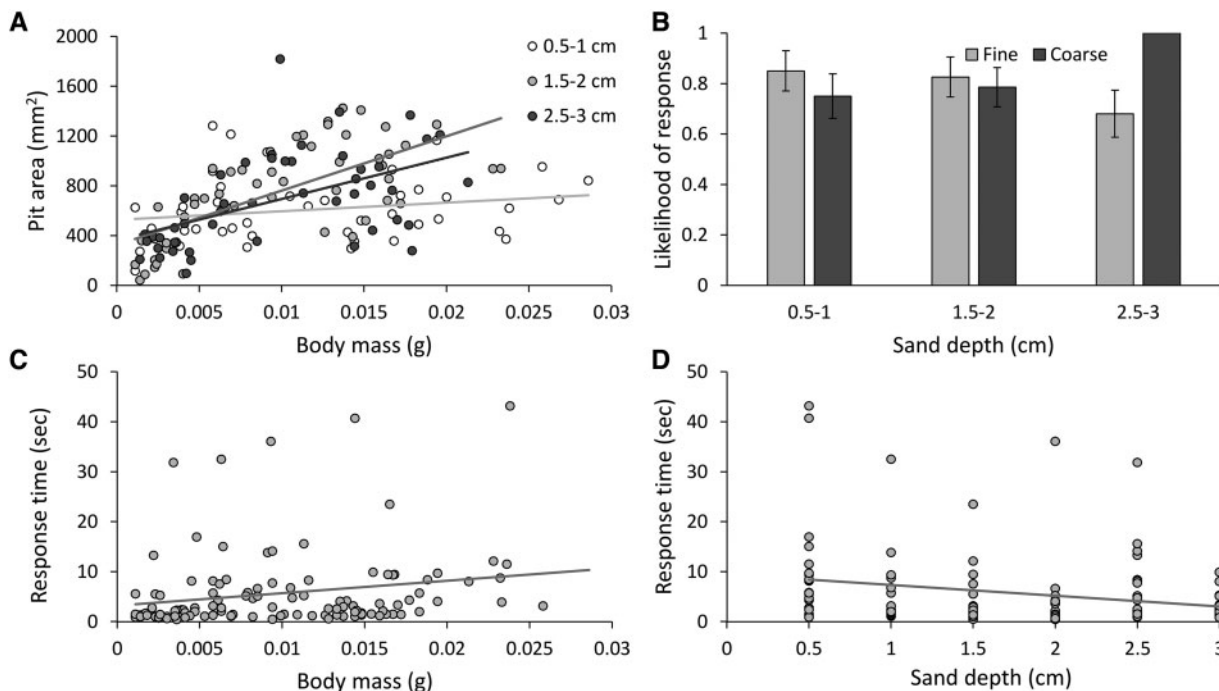


Figure 2. (A) The interactive effect of wormlion body mass and sand depth on the area of the constructed pit. The effect of mass was weaker in shallow sand. Sand depth is considered here as a categorical variable only for better visualization and as a continuous variable in the analysis. (B) The interactive effect of sand type and depth on the likelihood of wormlions to respond to prey: the likelihood increased with sand depth in coarse sand but showed the opposite pattern in fine sand. Standard errors are calculated according to the formula: $[p(1-p)/n]^{0.5}$. (C) The effect of body mass on the latency to respond to ant prey: smaller wormlions responded faster. (D) The effect of sand depth on the latency to respond to prey: wormlions in deeper sand responded faster.

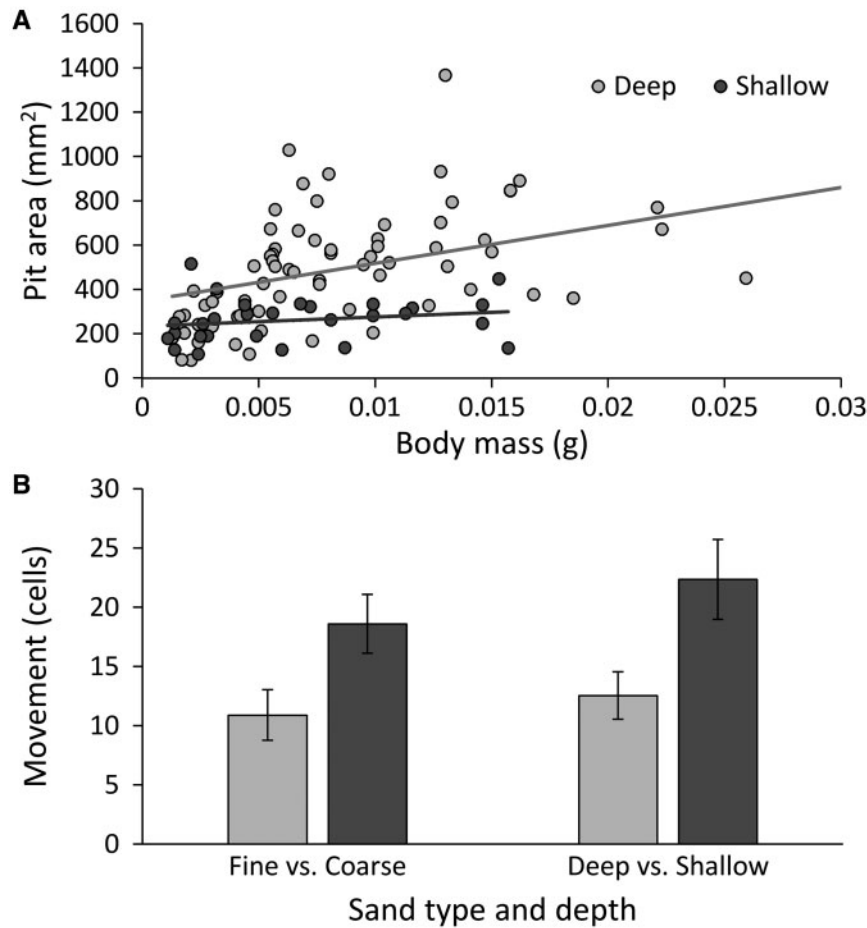


Figure 3. (A) The effect of wormlion body mass on pit area was stronger when deep sand was chosen than for shallow sand. (B) Wormlions moved longer distances in coarse sand (left) and shallow sand (right). Movement is calculated as the number of cells of 100 (a grid of 10×10 cells) in which the wormlions left traces. Means ± 1 SE are presented.

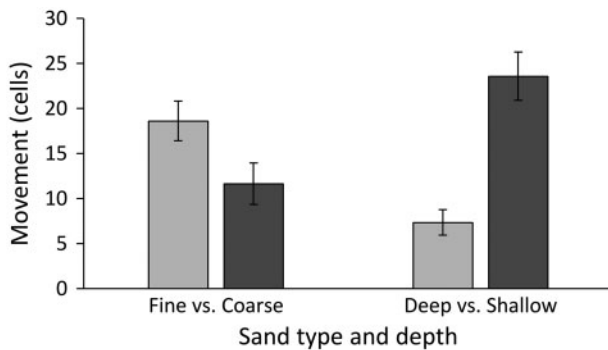


Figure 4. Wormlion movement in fine versus coarse sand (left) and deep versus shallow (right). Movement is calculated as the number of cells of 100 (a grid of 10×10 cells) in which the wormlions left traces. Means ± 1 SE are presented.

the finest and coarsest particles. Our field observations of wormlions occurring in sites of finer sand provide an indirect support for the preference of wormlions for fine sand. Our laboratory experiments provide a stronger support for this preference, irrespective of sand depth, because wormlions preferred fine sand in high proportions. This preference is mass-dependent, as smaller wormlions are choosier than larger ones. However, the preference for fine sand translated

neither to faster response to prey nor to larger pits constructed. Consequently, the exact advantage that fine sand apparently provides to wormlions remains to be uncovered. In contrast, while sand depth was similar between sites populated and unpopulated by wormlions, sand depth dramatically affected the size of the pits constructed and response time to prey, suggesting why deep sand was preferred under laboratory conditions. Body mass was also relevant here, as larger wormlions were choosier regarding sand depth, due to being more strongly limited by sand depth when constructing their pits.

Our study demonstrates that urban sites at which wormlions are present contain finer sand than that in nearby sites, from which they are absent. While the preference of wormlions for fine sand has been shown before (Devetak 2008a), our field observations suggest that this preference holds true also under natural conditions. Clearly, a correlation does not in itself indicate a preference, because the preference for finer sand could be correlated with some other factor, which is in turn preferred by wormlions. However, wormlions in the laboratory preferred fine over coarse sand. Such preference was evident in the wormlions' reduced movement in fine versus coarse sand, with increased movement being interpreted as an attempt to relocate away from unfavorable conditions. Trap-building predators move more frequently and relocate their trap more often under unfavorable conditions, such as interference or shortage of prey (Scharf and Ovadia 2006). Fine sand was more strictly preferred by smaller larvae. It is possible that particle size matters more to

smaller individuals, because the relative size of the wormlion versus the sand particles is lower.

From the current design, however, it remains unclear how fine sand improves foraging success of wormlions, as the constructed pits and response time to prey were similar across sand types. It could be that wormlions start constructing pits faster in fine sand, which might give them some advantage by choosing more suitable locations in the microhabitat. This suggestion remains to be tested under field conditions. Regarding antlions, other studies have indicated some benefits provided by fine sand. Ants, an important prey of antlions and plausibly also of wormlions, escape better from pits dug in coarse than in fine sand (Allen and Croft 1985; Loiterton and Magrath 1996; Botz et al. 2003). Furthermore, since the steepest angle sand can be piled and stay stable (i.e., angle of repose) of fine sand is steeper than that of coarse sand, pits in fine sand are more easily constructed and maintained (Lucas 1982). In contrast to our findings with wormlions, Farji-Brener (2003) demonstrated that antlions constructed larger pits in finer sand. This might have been because of the high threshold (fine sand was considered there to be composed of particles <2 mm). Nonetheless, none of the proposed advantages of fine sand explain why some antlion species actually prefer coarse sand (Devetak and Arnett 2015). One should also consider the option of a choice, beneficial under natural settings but meaningless for wormlions in urban habitats. Other studies on habitat selection have sometimes detected a discrepancy between habitat preference and the habitat's payoff, in which preferred habitats do not lead to higher fitness or those leading to higher fitness are not necessarily preferred (Chalfoun and Martin 2007; Sadoti and Vierling 2010). This is sometimes the case under fast environmental change, such as that induced in urban environments (Frei et al. 2013), and might be relevant for wormlions in such habitats.

Interestingly, there was an interaction between sand type and depth in their effect on the likelihood to respond to prey. The likelihood decreased with depth in fine sand but increased with depth in coarse sand. This could perhaps be explained by the stronger attenuation of the vibrations triggered by the prey in fine than in coarse sand (Devetak et al. 2007). In shallow sand, the pits are limited in size and the difference between fine and coarse sand is small. In deep sand, larger pits can be dug, with a consequent difference in attenuation. Wormlions preferred deep sand to shallow sand in the laboratory, and the effect of depth was stronger than the effect of sand type. This was expressed in larger pits constructed in deeper sand, faster response to prey and less movement, which we interpret as high suitability of the chosen location. Nevertheless, the sand depth characterizing wormlion clusters was not deeper than that of the surroundings without wormlion presence. It could be that other factors are more important under field conditions, such as shelter from direct sunlight and rain. It could also be that pits dug in nature are smaller in size than those dug under laboratory conditions (Dor et al. 2014), moderating the benefits that deep sand provides to wormlions.

Body mass affected both the preference for fine sand and the preference for deep sand. Body mass also interacted with sand depth to affect pit size. All these interactions with body mass highlight the importance of referring to body mass when examining habitat choice and its consequences. Digging pits is easier for large individuals, as their posterior part, with which they dig in sand, is larger. Intraspecific variation in body size is relatively neglected in studies of habitat choice and its consequences, with a few exceptions. For example, smaller crayfish shifted their habitat preference to shallow water in the presence of other predatory fish, whereas larger crayfish

were little affected by the same predators and therefore showed no habitat change (Englund and Krupa 2000). Fine sand impaired the ability of a flatfish to bury itself below the sand, but this effect was much stronger for smaller than for larger individuals (Gibson and Robb 1992). Finally, a positive correlation was found between amphipod size and the size of the alga on which it is located (Hacker and Steneck 1990).

Our results indicating a strong preference for deep and fine sand support the existing literature on the importance of abiotic features of the habitat to all trap-building predators. Similar to antlions and wormlions that require a suitable substrate, spiders too need physical support for web construction (Glover 2013). Adding artificial structures providing physical support at natural sites led to an increase in the number of spiders constructing webs, whereas removing weeds, and thereby reducing structures enabling physical support, led to a decrease in the number of spider webs (Balfour and Rypstra 1998; McNett and Rypstra 2000). The next step should be testing the wormlion preference for deep versus shallow and fine versus coarse sand in the field. Preference under laboratory and field conditions might not be identical. For example, wormlion preference for dry microhabitats was stronger in the laboratory than in the field (Scharf et al. 2018). While studies on trap-building predators already provide answers regarding the effect of prey existence and abiotic features of the habitat on the site selection for trap construction, some potentially influencing factors remain to be uncovered. The probably most important of these factors is that of the effect of predators and parasites. Two studies have demonstrated a negative effect of predators on the constructed trap, but do not refer to the initial site selection (Li and Lee 2004; Loria et al. 2008). It is in any case important to examine several biotic and abiotic factors in parallel, as the interactions may also be meaningful, as indicated in this study.

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