

Article

Comparison of wormlion behavior under man-made and natural shelters: urban wormlions more strongly prefer shaded, fine-sand microhabitats, construct larger pits and respond faster to prey

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Abstract

Urban habitats differ from their natural surroundings in various aspects, such as a higher temperature and a distinct species composition. It is therefore not surprising that animal behavior too differs between these habitat types. We studied the foraging and habitat selection behavior of a pit-building predator, a wormlion, originating from either an urban or a more natural site. Wormlions occur in nature under structures that provide shelter from sunlight and rain, such as caves, and are also common in cities, occurring under artificial shelters. Wormlions construct pit-traps to hunt arthropods, and the pits constructed by urban wormlions were larger than those constructed by wormlions from caves. Urban wormlions responded faster to prey falling into their pit, probably leading to a higher capture success. We suggest that these 2 findings indicate the higher investment of urban wormlions in foraging, resulting from the higher abundance of potential prey in the city. Urban wormlions were choosier regarding their preferred microhabitat. While both fine sand and shaded microhabitats were preferred by wormlions, urban wormlions demonstrated a greater preference for such conditions. We suggest that relocation is more likely to lead wormlions in cities to find microhabitats of a higher quality compared with wormlions inhabiting caves. This is probably due to the larger areas in the city available for wormlions. Wormlions from the caves possessed more lipids, suggesting that they employ a conservative growth strategy, intended to contend with the uncertainty of prey arrival, in contrast to the city, where potential prey are more abundant.

Key words antlions, habitat selection, habitat structure, optimal foraging, trap-building predators

Cities usually differ from their adjacent surroundings in various biotic and abiotic ways, such as higher temperature, more polluted soil, and higher light pollution and noise levels (Peng et al. 2011; Sauerwein 2011; Swaddle et al. 2015). Cities also contain non-seasonal food and water resources (Beckmann and Berger 2003;

Bateman and Fleming 2012), plausibly leading to the occurrence of “urban specialists,” such as doves and sparrows (McIntyre 2000; Shochat et al. 2004; Evans et al. 2009). Seasonal changes in temperatures, food and water availability are moderated in cities compared with their surroundings, enabling longer growth seasons

(Sukopp 1998; Shochat et al. 2006). Cities can therefore resemble each other more than they resemble their immediate natural surroundings.

In addition to the differences in species composition between cities and more natural habitats, there has been accumulating evidence in recent years of intraspecific differences in life history, behavior, and physiology, focusing mostly on vertebrates (Chamberlain et al. 2009; Bonier 2012; Lowry et al. 2013). Taking sparrows as a case study, urban sparrows are more aggressive, bolder, take higher risks while foraging, and sing at a higher frequency in order to overcome background noise; but they are also smaller than those in rural or more natural habitats (Wood and Yezerinac 2006; Liker et al. 2008; Tsurim et al. 2008; Scales et al. 2011). Regarding arthropods, only a few studies have compared between arthropods in urban and more natural habitats (McIntyre 2000). Those that did so demonstrated a higher thermal tolerance of insects in the city than in the more rural areas (Angilletta et al. 2007; Diamond et al. 2017, 2018; but see Bar-Ziv and Scharf 2018). Studies also demonstrated interference of city noise with sounds made by prey, making it harder for predators to detect prey, and for females to recognize sounds produced by males when calling them (Lampe et al. 2014; Wu and Elias 2014; Bent et al. 2018). The differences between animals in urban versus natural habitats could stem not only from adaptation to urban conditions but also from phenotypic plasticity, and it is important to separate between the 2 mechanisms (Atwell et al. 2012; Lampe et al. 2014; Donihue and Lambert 2015).

We compared wormlion populations (Diptera: Vermilionidae) originating from under artificial, man-made shelters, located in an urban habitat, with those from caves, occurring in more natural habitats. Wormlions are fly larvae that construct pit-traps in loose soil and prey on any small arthropod prey that fall into their pit (Wheeler 1930; Devetak 2008a, 2008b). Their hunting behavior is similar to that of the unrelated pit-building antlions (Neuroptera: Myrmeleontidae), together presenting an example of convergent evolution (Dor et al. 2014), though dissimilarities also exist (e.g., wormlions are able to capture smaller prey than co-occurring antlions of the same size and prefer more strongly fine sand; Miler et al. 2018, 2019). Wormlions occur at high densities in cities all over Israel, whereas their habitat in nature is either the soil in caves or below cliff overhangs. They occur strictly under shade, provided by artificial or natural shelter, and prefer shade when given a choice (Adar et al. 2016; Katz et al. 2017). We hereafter refer to an “urban habitat” as a site in which wormlions occur under man-made shelter, whereas we define a “natural habitat” as a site in which wormlions occur in caves.

Two previous studies in the same habitats studied here demonstrated differences between the urban and the natural sites under study (Bar-Ziv and Scharf 2018; Bar-Ziv et al. 2018). Among other differences between the 2 habitats under study, the 2 habitats also differ in their arthropod composition. According to a single evaluation in late spring in the studied habitats, ants comprise a larger proportion of the arthropods occurring at the urban sites than in or next to caves, and ants at the urban sites are smaller and more abundant (Bar-Ziv et al. 2018). Such small ants are more easily captured and constitute suitable prey for wormlions in the city, possibly explaining why they are able to reach a larger size in the city than in caves (Bar-Ziv et al. 2018). Urban wormlions can therefore construct larger pits simply because they themselves are larger: there is a positive correlation between body mass and pit size in both antlions and wormlions (Griffiths 1980; Dor et al. 2014). Alternatively, urban wormlions might have a higher expectation of prey arrival, leading to a higher investment in foraging or larger pits, even after correcting for body mass. While no differences in either heat or cold tolerance were detected among sites (Bar-Ziv and Scharf 2018), behavioral differences may exist.

The goal here was to test for behavioral and physiological differences between wormlions from urban and natural habitats and to explain any such differences found. We tested for differences in the constructed pit area, response time to prey, movement under unfavorable conditions, preference for specific microhabitats (shaded vs. lit, deep vs. shallow and fine vs. coarse sand), and lipid content. We hypothesize that urban wormlions should invest more in foraging, because prey are more available in the studied urban habitat than in caves (Bar-Ziv et al. 2018). We predicted that urban wormlions would construct larger pits irrespective of body mass and respond faster to prey, both indicative of a higher investment in foraging. We also hypothesized that urban wormlions should be more selective when choosing a site for pit construction, because there are more suitable sites available for pit construction in cities and they present better hunting opportunities. Previous studies found that wormlions prefer dry, fine, deep, shaded, and obstacle-free sand (Devetak and Arnett 2015; Adar et al. 2016; Bar-Ziv et al. 2019; Scharf et al. 2018; Miler et al. 2019). Such preferences however are not fixed but depend on interactions with other factors. For example, habitat shape, conspecific density, and temperature affect to which extent wormlions prefer shaded sites (Katz et al. 2017; Katz & Scharf 2018). Specifically, we predicted that urban wormlions would move more when encountering an unfavorable microhabitat and that urban wormlions would be choosier between favorable and unfavorable conditions, that is, dry versus wet, fine versus coarse and shaded versus lit sand, respectively. Finally, we hypothesized that urban wormlions are in a better physiological condition, and predicted them to contain more lipids than those from caves for 2 reasons: 1) suitable prey is more abundant in cities and urban wormlions probably capture prey more frequently and store the energy as fat; 2) urban wormlions reach a larger final size prior to pupation than those from natural sites. We expected the large size to be reflected also in larger body reserves.

Materials and Methods

Wormlion collection and habitats-of-origin

We collected wormlions in November 2018 from 3 adjacent sites: (a) Tel Aviv University (0.5044 km²; 32°6'45"N, 34°48'15"E), an urban site, in which wormlions occur under man-made shelters (Figure 1); (b) Shmaryahu caves (0.0153 km²; 32°11'35"N 34°49'14"E) and Afeka caves (0.0067 km²; 32°07'46"N 34°48'34"E). Shmaryahu caves are located in a town park, 9 km north to Tel Aviv University. Afeka caves are located in a natural area, 1 km north of the outskirts of Tel Aviv. Wormlions occur in caves at both latter sites (Figure 1), which even if not entirely free of human influence, represent a more natural habitat than the Tel Aviv University campus. The sites have already been characterized and compared in 2 previous studies, regarding temperature, soil type and cover, plant and arthropod species diversity, wormlion abundance, wormlion mass, and wormlion average pit size in the field (Bar-Ziv and Scharf 2018; Bar-Ziv et al. 2018). The studied wormlion species is not yet described, but there is only a single wormlion species in Israel (Freidberg A, personal communication).

For the first set of experiments, we collected 50 wormlions from Afeka and Shmaryahu caves and 60 from Tel Aviv University, which we weighed (XT 220 A, Precisa Gravimetrics, Dietikon, Switzerland; accuracy of 0.1 mg), and placed in cups (diameter of 5.5 cm) filled with 3 cm of sand. We used sand from a construction shop to avoid damaging the wormlions' habitats and to ensure that the sand was homogenous, and because in some caves there was

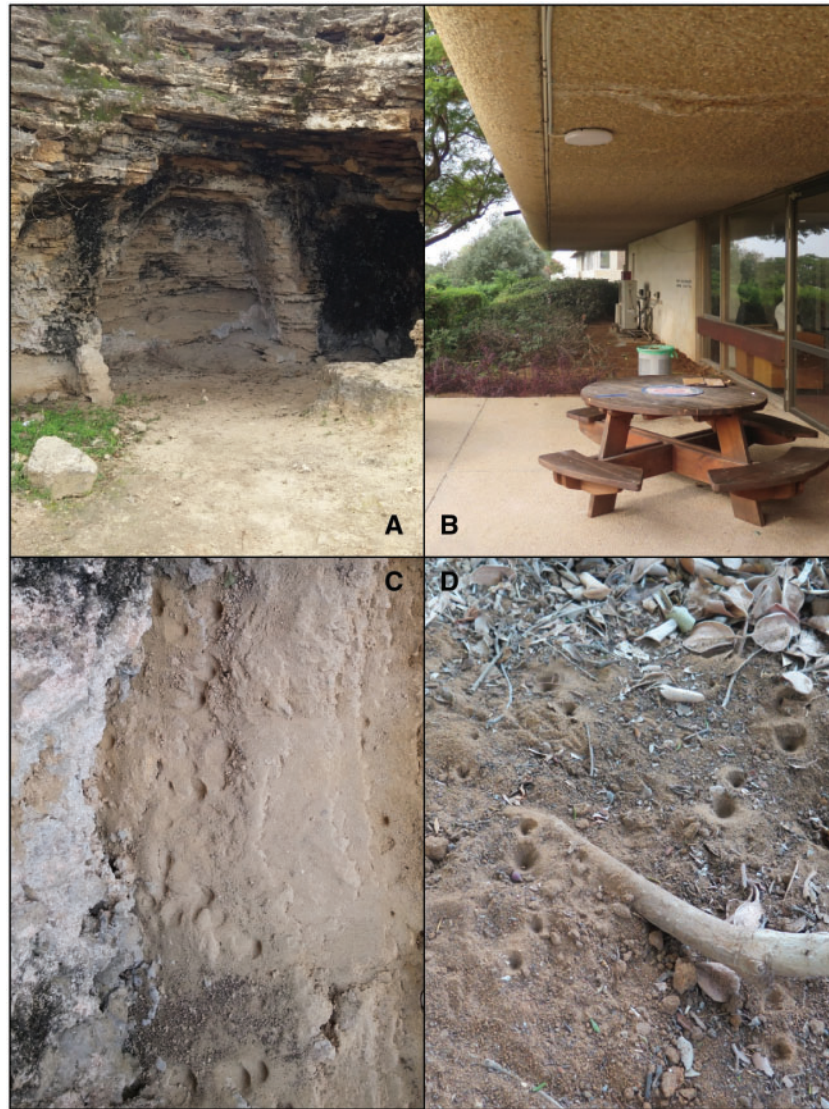


Figure 1. Photos of the 2 habitats, (A) one of the Shmaryahu caves, a natural habitat of wormlions, and (B) the ground below the central library at Tel Aviv University, representing an urban habitat for wormlions. Wormlions occur under natural or artificial shelter. Pits constructed at each of the sites: (C) the natural site, and (D) the urban site.

insufficient sand for our requirements. Wormlions collected in the 2 habitats did not differ in their body mass ($F_{1, 108} = 1.343$, $P = 0.249$; 0.0072 ± 0.0038 g; mean ± 1 SD; range: 0.0015–0.0193 g). Wormlions were given 48 h to acclimate to the laboratory conditions (27.5°C, 12: 12 L: D) before the first set of experiments began. For the second set of experiments, we collected 60 wormlions from Tel Aviv University and the same number from the 2 other sites together. They were brought to the laboratory, weighed and placed in cups, similar to the first set of experiments. Here too, there was no mass difference between the wormlions from the 2 habitats ($F_{1, 113} = 3.048$, $P = 0.083$; 0.0096 ± 0.0052 g; mean ± 1 SD; range: 0.0021–0.0269 g). No permits are required for wormlion collection.

First set of experiments

1) Pit area: The wormlions were allowed to construct pits in a cup of 8.5 cm diameter filled with 3 cm of sand. We photographed the pits 24 h after they had been placed in the experimental cups and

measured their pit area using the software ImageJ (Abràmoff et al. 2004). The pits were then destroyed by shaking the cup, and we gave the wormlions an additional 24 h to reconstruct their pits, after which the pits were again photographed and measured. 2) Response time to prey: After photographing the pits for the second time, we dropped into each wormlion's pit a single pharaoh ant *Monomorium pharaonis* and measured the response time of the wormlion to the ant, by either sand flicking or moving in the pit (similar to Scharf et al. 2018). The ants were collected inside and around one of the buildings of the Faculty of Life Sciences at Tel Aviv University. This species is more common in the city than in more natural habitats, but other *Monomorium* species are common also in the natural habitat (Bar-Ziv et al. 2018). It is unknown whether wormlions prey on pharaoh ants in nature, but the 2 species co-occur and wormlions prey on other ant species of similar size. If the wormlion did not respond within 60 s or if the ant escaped the pit we recorded the test as “failed.” Wormlions were not allowed to capture and consume the prey. 3) Choice of shaded versus lit

microhabitat: Wormlions usually prefer shaded sand when given a choice (a study on urban wormlions: Adar et al. 2016). One day after measuring the response time to prey, we placed the wormlions individually in aluminum trays ($31 \times 10 \times 5$ cm), filled with 3 cm sand and divided into 2 halves: one half was completely shaded with a cover while the other remained exposed to a non-heat producing room light, about 2 m above the trays, and there was therefore no difference in temperature between the 2 halves of the tray. The wormlions were placed in the middle of the tray and their choice of location between the 2 microhabitats was documented after 24 h. Their choice could be clearly seen according to the pit constructed in the preferred location or to their tracks left in the sand (Adar et al. 2016). 4) Movement on shallow sand: Shallow sand induces elevated movement by wormlions (Bar-Ziv et al. 2019). We tested the wormlion's movement on shallow sand 1 day after the previous experiment, using the same trays, filled with 0.5 cm of sand. We placed the wormlion in the tray's center and photographed the tray after 24 h. We placed a grid of 20×5 cells on the photos and counted the cells covered by tracks in order to calculate the proportion of the tray area covered (Bar-Ziv et al. 2019). 5) Lipid content: We weighed the wormlions again (Boeco BBX22, Hamburg, Germany; accuracy of 0.01 mg), and then placed them in Eppendorf tubes and froze-killed them, after which they were dried for 48 h at 60°C . They were then weighed again to obtain their dry mass. Next, we added to each tube 1 mL petroleum-ether and let the solution extract the non-polar lipids for 5 days (Williams et al. 2011). We refilled the tubes daily, and we then dried them again at 60°C for 48 h and weighed them. The difference between the dry mass and the last mass measurement represents the absolute lipid content.

Second set of experiments

1) Choice of deep versus shallow microhabitat: Wormlions prefer deep sand when given a choice (a study on urban wormlions: Adar et al. 2016). They were placed individually in the center of a tray ($15 \times 15 \times 4$ cm), separated into 2 equal-size halves. One half was filled with 3 cm deep sand whereas the other contained only 0.5 cm sand. We documented the wormlion's choice after 24 h, which was visible according to the location of the constructed pit or the tracks. 2) Choice of fine-sand versus coarse-sand microhabitat: Wormlions usually prefer fine sand when given a choice (known for 2 species in urban sites: Devetak and Arnett 2015; Bar-Ziv et al. 2019). They were placed individually in the center of a tray ($15 \times 15 \times 4$ cm), filled with 3 cm deep sand passed through a sieve of $250 \mu\text{m}$. Sand composed of particles larger or smaller than $250 \mu\text{m}$ is hereafter referred to as "coarse" or "fine," respectively (similar to Bar-Ziv et al. 2019). We documented the wormlion's choice after 24 h. 3) Choice of dry versus wet microhabitat: Wormlions, at least urban ones, usually prefer dry sand when given a choice (Scharf et al. 2018). They were placed individually in the center of a tray ($15 \times 15 \times 4$ cm), filled with 3 cm deep sand. One half of the tray was moistened with 0.8 g water using a sprinkler (similar to Scharf et al. 2018). We documented the wormlion's choice after 24 h.

Statistical analysis

We tested the effect of habitat-of-origin (urban vs. natural/caves) and body mass on the area of the constructed pit on Days 1 and 2, the response time to prey, and movement on shallow sand using separate analysis of covariance (ANCOVA) tests. Pit areas on the second day, movement, and response time to prey deviated from a normal distribution. The first 2 were therefore square-root transformed whereas

the latter was \log_{10} transformed. The choices of wormlions for shaded versus lit, deep versus shallow, or fine-sand versus coarse sand microhabitats were analyzed using separate logistic regressions, with habitat-of-origin and body mass as explanatory variables. Absolute lipid content was compared between the 2 habitats using ANCOVA tests, with body mass and habitat as explanatory variables. Here, both lipid content and body mass deviated from a normal distribution and were square-root transformed in order to retain the link between the 2 linear. Negative values of lipid content were obtained for 7 cases, probably due to measurement error, and these values were removed from the analysis. We always included first the interaction of body mass and habitat-of-origin, which was removed if it was not significant, and the test was redone.

Results

Pit area

Urban wormlions constructed larger pits that were 24% and 29% larger than the pits constructed by wormlions from caves on the first and second day of testing, respectively (Day 1: $F_{1, 101} = 7.100$, $P = 0.009$; Day 2: $F_{1, 94} = 20.134$, $P < 0.001$; Figure 2A). Larger wormlions constructed larger pits on both days (Day 1: $F_{1, 101} = 11.765$, $P < 0.001$; Day 2: $F_{1, 94} = 21.227$, $P < 0.001$). The interaction of habitat and body mass was not significant in both cases and removed from the analysis ($P > 0.096$).

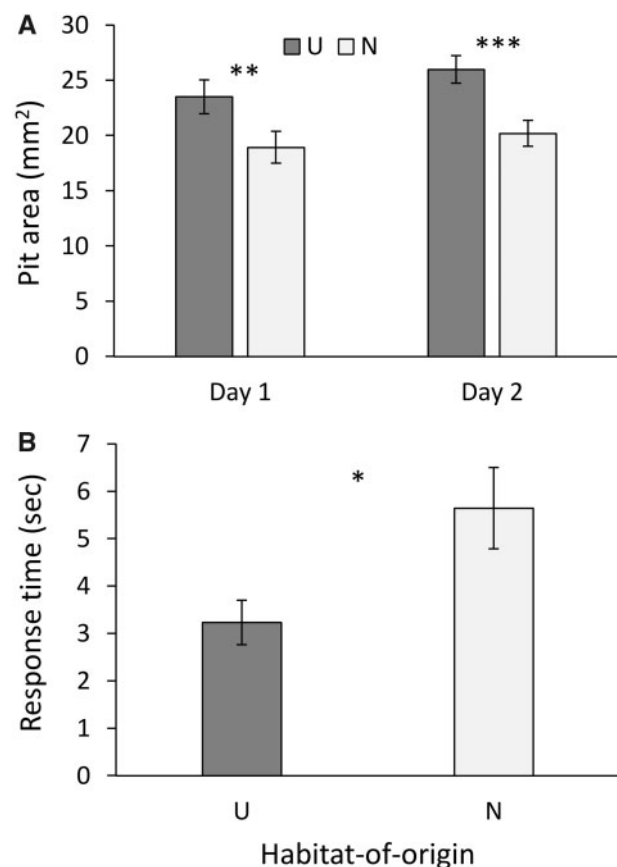


Figure 2. The effect of habitat-of-origin (urban vs. natural sites, U vs. N) on (A) the area of the constructed pit on 2 successive days; and (B) response time to an ant prey that was dropped into the pit. Means \pm 1 SE are presented. Asterisks indicate the significance level.

Response time to prey

Urban wormlions responded 43% faster to prey than those from caves ($F_{1, 85} = 4.639$, $P = 0.034$; **Figure 2B**), whereas body mass had no effect on response time ($F_{1, 85} = 0.554$, $P = 0.459$). The interaction term was also not significant ($F_{1, 84} = 2.398$, $P = 0.125$).

Movement on shallow sand

Neither the habitat-of-origin, nor body mass, nor their interaction had a significant effect on movement ($F_{1, 105} = 0.683$, $P = 0.411$, $F_{1, 105} = 0.002$, $P = 0.967$, $F_{1, 104} = 0.002$, $P = 0.965$, respectively).

Choice of shaded versus lit microhabitat

While urban wormlions preferred shaded microhabitats (73%), wormlions from the caves showed no such preference ($Z = 2.829$, $P = 0.005$; **Figure 3A**). Generally, smaller wormlions had a higher preference for shade than larger ones ($Z = 2.375$, $P = 0.018$). The interaction between habitat-of-origin and body mass was not significant ($Z = 0.373$, $P = 0.709$).

Choice of deep versus shallow microhabitat

Wormlions of both habitats preferred deep sand (68%). Neither the habitat-of-origin, nor body mass, nor their interaction had a

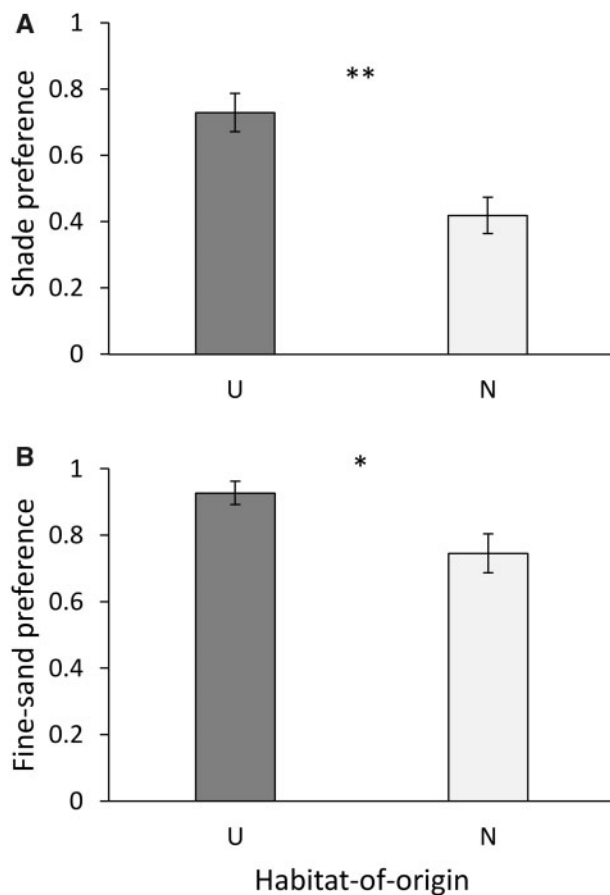


Figure 3. The proportions of wormlions preferring (A) shaded microhabitats, when given a choice between shaded and lit ones; and (B) fine-sand microhabitats, when given a choice between fine-sand and coarse-sand ones, according to the habitat-of-origin (urban vs. natural sites, U vs. N). Proportions ± 1 SE are presented. SE was calculated according to the formula: $\sqrt{\frac{p(1-p)}{n}}$, where p is the proportion and n is the sample size. Asterisks indicate the significance level.

significant effect on the choice of deep versus shallow sand ($Z = -0.541$, $P = 0.588$, $Z = 0.720$, $P = 0.471$, $Z = 0.379$, $P = 0.705$, respectively).

Choice of fine-sand versus coarse-sand microhabitat

While wormlions of both habitats preferred finer sand, this preference was stronger for urban wormlions (93% vs. 75% for the urban and natural habitats, respectively; $Z = -2.047$, $P = 0.041$; **Figure 3B**). There was a non-significant trend of smaller wormlions preferring fine sand, more than larger ones ($Z = 1.849$, $P = 0.064$), but the interaction was not significant ($Z = -0.666$, $P = 0.506$).

Choice of dry versus wet microhabitat

Wormlions of both habitats strongly preferred a dry microhabitat (87%). There was a significant interaction between habitat-of-origin and body mass in their effect on microhabitat choice ($Z = 2.058$, $P = 0.040$; **Figure 4**): whereas wormlion mass was similar across habitats-of-origin in both dry and wet microhabitats, urban wormlions that chose the wet microhabitat were larger than those wormlions from caves that chose it. As main effects, habitat-of-origin was marginally not significant ($Z = -1.926$, $P = 0.054$) and body mass was also not significant ($Z = -1.751$, $P = 0.080$).

Lipid content

Body mass was strongly and positively correlated with the absolute lipid content ($F_{1, 91} = 34.519$, $P < 0.001$). Urban wormlions contained almost 28% less lipids on average than those from caves ($F_{1, 91} = 7.086$, $P = 0.009$; **Figure 5**). The interaction term was not significant ($F_{1, 90} = 0.145$, $P = 0.704$).

Discussion

Urban and natural habitats greatly differ in various abiotic and biotic features. It is therefore of no surprise that animals in such different habitats demonstrate distinct phenotypes. We tested here for behavioral differences between urban wormlions and those originating from caves at more natural sites. Urban wormlions were found to construct larger pits and to respond faster to prey than those from caves. Both reactions plausibly indicate a higher investment in foraging and a stronger expectation of prey capture. Furthermore, urban

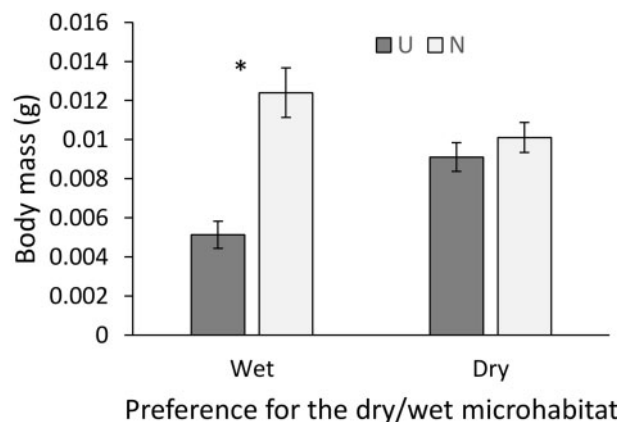


Figure 4. The interactive effect of habitat-of-origin and body mass on the proportion of wormlions choosing dry microhabitats, when given a choice between dry and wet ones. Means ± 1 SE are presented. Asterisks indicate the significance level.

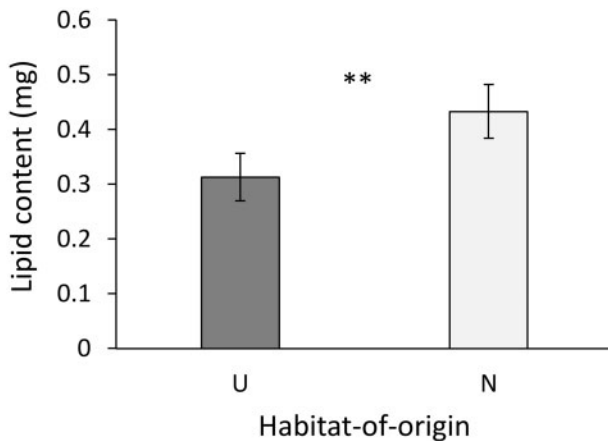


Figure 5. Absolute lipid content of the wormlions according to the habitat-of-origin. Means \pm 1 SE are presented. Asterisks indicate the significance level.

wormlions were more selective regarding their preferred microhabitat, expressed in higher proportions choosing shaded over lit microhabitats and fine-sand over coarse-sand microhabitats. These results match previous findings indicating that the studied urban habitat is richer in potential prey for wormlions and that those occur in high numbers in cities (Bar-Ziv et al. 2018). The tested urban wormlions contained fewer lipids than those from caves, indicating that urban wormlions employ a riskier growth strategy: they are more ready to invest in growth and deplete their body reserves because they have a greater expectation of a constant supply of prey. In comparison, wormlions in caves are probably more conservative in their growth strategy, because the potential arrival of prey is less predictable than in the city. A word of caution is necessary here, because the number of our studied populations is low. Although we perceive our urban and more natural populations to represent well their type, more solid conclusions could be only reached after replicating the comparisons of urban versus more natural populations that occur next to each other.

Bar-Ziv et al. (2018) found that urban wormlions are larger than those in natural habitats and construct larger pits under natural conditions, but it is unclear from that study whether the higher body mass of urban wormlions can explain this difference. We found here the same pattern after controlling for body mass—urban wormlions of similar mass to wormlions from caves still construct larger pits. We interpret the construction of larger pits as a higher investment of urban wormlions in hunting. Similarly, antlions and spiders with greater expectations of encountering prey construct larger traps (Nakata 2007; Scharf et al. 2010). Expectations of prey arrival clearly affect decision-making in sit-and-wait predators. For example, antlions relocate their pits faster when prey arrivals stop abruptly rather than gradually (Jenkins 1994); spiders construct larger or smaller webs depending on their expectation of capturing larger versus smaller prey (termite swarms vs. small flies; Sandoval 1994). Pit-building predators are expected to construct a trap if its construction and maintenance costs are returned by sufficient prey capture (Scharf et al. 2011). If this does not hold true, the constructed trap should be smaller, saving energetic costs, or the pit-builder should relocate, searching for a microhabitat richer in prey (Griffiths 1980; Eltz 1997; reviewed in Scharf and Ovadia 2006). Because the studied urban sites contain more abundant prey for wormlions than the surrounding natural habitats and because wormlion clusters are less dense in the urban sites probably relaxing intraspecific competition for space and prey (Bar-Ziv et al. 2018),

wormlions expect to gain more prey, on a regular basis, and larger traps should thus be constructed and maintained. Constructing a larger pit is beneficial in the presence of prey, as it increases the detection range of the pit-building predator, impairs the escape of prey from the pit, and enables it to capture larger prey (Griffiths 1980; Lucas 1982; Heinrich and Heinrich 1984; Scharf et al. 2018).

Response to prey was faster in the city. Faster response to prey usually improves capture success (e.g., Linley 1995; Hesselberg and Vollrath 2006). This is especially true in pit-building predators, because they do not chase after a prey that has successfully escaped the pit. A previous study with the same predators and potential prey, has demonstrated that the ants escape artificial pits (with no wormlion present) within the first minute after falling in high proportions (25–65%, depending on pit size; Scharf et al. 2018). In short, no or slow response translates to losing foraging opportunities. Therefore, why would wormlions at natural sites respond more slowly to prey? It could be that smaller pits and lower response time is a by-product of lowering the metabolic rate, which is perhaps a beneficial strategy when prey are scarce. In analogy, sit-and-wait lizards encounter prey less frequently than widely-foraging ones and also display lower metabolic rates (Huey and Pianka 1981; Nagy et al. 1984). Furthermore, predators seasonally adjust their activity levels to those of their prey (Zielinski et al. 1983; Christian et al. 2007). A higher activity or metabolic rate in the city could also be the outcome of higher temperatures there, as shown for our study sites (Bar-Ziv and Scharf 2018). Comparing metabolic rates between wormlions from cities and from natural sites could therefore be of interest. Other studies have demonstrated that urban *Daphnia* possess a faster life-style (Brans and De Meester 2018), which might also indicate differences in metabolic rate.

Urban wormlions were more selective regarding where to construct a pit. While wormlions generally prefer shade, deep sand, and fine sand (Adar et al. 2016), the preference of urban wormlions for shaded, fine-sand microhabitats was greater. Sites populated by wormlions in cities are larger and less dense than those in natural habitats, which probably make a higher diversity of microhabitats available for wormlions. This could lead to higher selectivity by city wormlions, since their choices matter more than in caves, where they are limited to a small space, because they may reach a more favorable site. Shade and fine sand are of value to wormlions for different reasons. Shade is probably preferred for preventing sand from reaching too high a temperature. The preference for shade evidently increases with increasing temperature (Katz et al. 2017). Fine sand is preferred, at least for antlions, due to making the maintenance of pits easier, enabling the construction of steeper pits than in coarse sand, and making it harder for prey to escape the pits (Lucas 1982; Allen and Croft 1985; Loiterton and Magrath 1996; Botz et al. 2003). In accordance, the soil in urban sites populated by wormlions is finer than that in immediately adjacent sites, from which wormlions are absent (Bar-Ziv et al. 2019). It will be interesting to examine whether there is a higher variance of available soils in the city, which makes it profitable for wormlions to be more selective, compared with those in caves. In other words, wormlions at the natural sites might simply be unable to reach microhabitats of finer sand by means of relocation, and this limitation would result in a decrease in choosiness.

The preference for dry microhabitats was strong for all wormlions, but the minority of them choosing the wet microhabitat differed in body mass between habitats-of-origin: smaller wormlions from natural sites but larger wormlions from urban sites preferred more strongly the dry microhabitat. Wet microhabitats are

unfavorable owing to the faster escape of prey and the smaller pits that are being constructed under such conditions (Scharf et al. 2018). Wet microhabitats are also unfavorable for the other group of pit-building predators—antlions (Gotelli 1993; Miler et al. 2019). We consider it more reasonable for the smaller wormlions, which are weaker competitors, to choose the unfavorable microhabitat in order to avoid competition (Andren 1990; Tregenza 1995). This is indeed what took place in the city, but did not hold true for wormlions from the natural sites. It could be that urban wormlion populations, occurring in higher numbers and larger clusters, are more exposed to intraspecific competition. We also expected urban wormlions to relocate more frequently when facing unfavorable conditions (shallow sand), but there was no difference based on habitat-of-origin. The reason for this could be that shallow sand is too unfavorable a condition, because it prevents wormlions in most cases building a pit, leading to little choice but to relocate.

Finally, urban wormlions were leaner than those originating from caves. This contradicted our expectation and somewhat also contradicted our claim that urban habitats are more suitable for wormlions than natural ones. First, it could be that urban wormlions invest greater energy in growth at the expense of accumulating body reserves. This enables urban wormlions to reach a larger mass prior to pupation. Clearly, investing in growth requires abundant and predictable prey arrival, which the city indeed provides, in containing many ants of small size, which are suitable prey for wormlions (Bar-Ziv et al. 2018). Shochat (2004) has presented a similar explanation in birds. City birds possess an energetic “overdraft” because they can count on a predictable influx of food. In natural areas, a bird must have some energetic reserves, because the timing of finding the next food is less predictable. While some birds of urban and natural habitats reflect this notion (Liker et al. 2008; Meillère et al. 2015; Dulisz et al. 2016), we are not aware of any support in an insect model system. Future studies should perhaps determine for how long the behavioral differences and the difference in lipid content between urban wormlions and those from natural sites persist under laboratory conditions. They should also test whether urban wormlions living in energetic “overdraft” is also reflected in other physiological differences between the 2 wormlion populations, such as starvation tolerance. It could be that whereas urban wormlions reach larger final size under average urban conditions, any deviations from such conditions involving stress would more negatively affect urban wormlions due to their lower body reserves.

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