

Comparison of wormlions and their immediate habitat under man-made and natural shelters: suggesting factors making wormlions successful in cities

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ABSTRACT

Wormlions are fly larvae that construct pit-traps in loose soil and ambush prey that fall into their pits. They occur in high numbers in cities, below any man-made shelter providing protection from direct sunlight, such as a concrete roof with a thin layer of sand at the ground. Their natural habitat is either caves or any natural structure that provides full shade. We characterized a large urban habitat and compared it to two natural habitats, where wormlions occur in caves. Wormlions were abundant in all studied habitats. Our goals were to understand whether wormlions in the urban habitat perform better than in the natural habitats, and to suggest differences between the habitats that may contribute to their success under man-made shelters. Wormlions in the city reached larger size before pupation, and wormlion clusters there were larger. The studied urban habitat contained more concrete and perennial plants, while the natural habitats comprised of more annuals. We suggest that this concrete, covered with a thin layer of sand, leads to large areas suitable for wormlions. Furthermore, ants were more common in the urban habitat than the natural habitats, referring to their relative proportion of all arthropods collected. We suggest that these small ants provide suitable prey for wormlions, especially in the early stages of their development, when wormlions are limited by prey size. This could explain why they reach larger size prior to pupation. Pits were probably larger because they were constructed by larger individuals. In conclusion, we suggest that wormlions present an interesting case of an insect pre-adapted to urban life.

1. Introduction

The first 30 years of the 21st century are expected to experience a vast transformation of natural habitats to cities, and by 2030 over 5 million km² of natural area will become urban (Seto et al., 2012). Cities can dramatically alter their local environment, with their impact felt far beyond the space they occupy (Grimm et al., 2008). Cities differ from natural surroundings in various abiotic aspects. For example, the soils inside and outside of cities often differ in composition and age (Schleuß et al., 1998), due to physical disturbance, coverage by impervious surfaces, fertilization, and irrigation, all common in cities (Pouyat et al., 2003). Wind velocity is reduced in cities owing to buildings, cities are affected by light pollution, and temperatures within cities rises with increasing human population (Oke, 1973; Hough, 1995; Gaston et al., 2013). These abiotic differences have strong consequences for the city flora. Plant species richness can be higher in cities than the natural surroundings, due to the introduction of exotic plants, while the richness of native plants in cities is generally lower than that in the surrounding areas (Zipperer et al., 1997; Wania et al., 2006; McKinney,

2008).

While many animals are negatively influenced by cities (Fattorini, 2011; Reis et al., 2012), some animals adapt to urban habitats and thrive in cities (Maklakov et al., 2011; Bateman and Fleming, 2012). Other species, such as those living inside buildings, are probably pre-adapted to such lifestyle, explaining their success (Martin et al., 2015). Cities do not only pose stress on animals, but may improve their conditions, by offering more available water, food and shelter (Davies, 1977; Bateman and Fleming, 2012). “Urban specialists”, such as cockroaches and pigeons, take advantage of such available resources (McIntyre, 2000; Sacchi et al., 2002).

Most studies on urbanization have focused on the biodiversity and macroecological aspects (e.g., Clemants and Moore, 2003; Chace and Walsh, 2006), but there has been a growing interest in how animals populating both habitats differ in their traits (Shochat et al., 2006). For example, urban and rural populations of the same bird species behave differently: urban populations are bolder, more aggressive, and sing at a higher pitch than non-urban populations (Slabbekoorn and Peet, 2003; Nemeth and Brumm, 2009; Evans et al., 2010). However, most such

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studies have focused on birds, with less attention given to arthropods (Møller, 2008; Reis et al., 2012; McDonnell and Hahs, 2015, but see McIntyre, 2000). Insects have a short generation time and can thus adapt to a rapidly changing environment, such as in cities.

Studies on insects in urban vs. natural habitats revealed that the diversity of insects in cities is lower. In some cases, only one species gains dominance and spreads through the habitat (Weller and Ganzhorn, 2004; Sadler et al., 2006). Generally, small arthropods are more dominant in urban sites while large arthropods are more dominant in rural sites (Kotze et al., 2011). Insects of the same species can also differ in body size and shape between urban and natural habitats. Female grasshoppers from an urban habitat, for instance, are 10% heavier than their conspecifics from a natural habitat (Gomez and Dyck, 2012). Other studies demonstrated behavioral or physiological differences between insects from urban and natural habitats, such as grasshoppers next to a busy road call louder than those from more tranquil locations (Lampe et al., 2014), or city ants tolerating heat better than those from more rural sites (Angilletta et al., 2007; Diamond et al., 2017).

Our goal here was to compare the environmental conditions experienced by urban and natural populations of wormlions (Diptera: Vermileonidae). Wormlions build pit-traps in loose soil and ambush the small arthropods that fall into them (Wheeler, 1930; Devetak, 2008). Wormlions are abundant in cities all over Israel and are common also in natural habitats (Dor et al., 2014; Bar-Ziv and Scharf, 2018). We focused on two representative habitat types: urban, under man-made shelters, mostly buildings providing protection against direct sunlight and rain, and natural, in caves (Fig. 1; Supplementary material, Fig. S1). We first tested whether wormlions are indeed more abundant under man-made shelters than in caves, whether they construct larger pit-traps and differ in their body mass. If so, we tested several biotic and abiotic factors that might explain this difference, such as suitable substrate for constructing pits and available arthropod prey.

We expected to find more and larger wormlions in the city than the natural habitat. The soil in the city could be deeper and feature smaller particle size, both preferred by wormlions under laboratory conditions (Devetak, 2008; Adar et al., 2016). The urban habitat is also expected to possess a higher abundance of arthropods, due to irrigation and the higher plant diversity. City arthropods may be smaller and thus provide more available prey for wormlions, especially in their early stages. In short, we expect the urban habitat to provide better conditions for wormlions than the natural habitat, which would translate to higher abundance and larger size.

Studying the effect of urban habitats on soil-dwelling insects, using wormlions as a case study, can help in understanding the consequences of urbanization, because insects can serve as good bioindicators of human-induced environmental change (McGeoch, 1998; Frouz, 1999). Insects generally present an important food source for higher trophic levels. Finally, soil-dwelling insects are especially interesting because city soils are often polluted (Chen et al., 2005; Sauerwein, 2011).

2. Materials and Methods

2.1. Wormlions and their habitats

Wormlions are fly larvae (Diptera: Vermileonidae) that dig pit-traps in loose soil to hunt for arthropod prey. The larvae live for a year or more in soil, while the adult is short-lived (Adar and Dor, 2018). Adults mate and lay eggs in spring, beginning in late April (personal observation). Their foraging strategy is similar to the unrelated pit-building antlion (Wheeler, 1930; Scharf et al., 2011). Although wormlions are ambush predators, they relocate their pits if the current conditions are unsuitable, and actively prefer shaded, dry and deep soil of small particle size (Devetak and Arnett, 2015; Adar et al., 2016; Scharf et al., 2018). When choosing a suitable microhabitat, they simultaneously take into consideration several habitat features, such as

the level of shade and sand depth, obstacles on the ground and conspecific density, showing complex habitat choice (Adar et al., 2016; Katz and Scharf, 2018).

Wormlions occur in cities all around Israel, below man-made shelters, protecting against direct sunlight and rain (Dor et al., 2014). In natural habitats, they can be found in caves or below cliff overhangs (Bar-Ziv and Scharf, 2018), providing a similar shelter (Supplementary material, Fig. S1). We compared between these two habitats (hereafter, urban habitat vs. natural habitat). Our urban habitat is the whole area of Tel Aviv University (0.5044 km²; 32°6'45"N, 34°48'15"E). There are at least 20 separate wormlion clusters in this habitat, with a distance of 20–100 m between adjacent clusters, not all of them documented here. The caves are located in two smaller habitats: 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). The first is a park within a town and the second is located in an open area, about 1 km north to Tel Aviv. At least 12 separate caves in the two sites are populated by wormlions (9 and 3 in Shmaryahu and Afeka caves, respectively). The caves are located close to the city or within a town park; they were also used by men till the 4th century for burial (according to the Israel Antiquities Authority; http://www.hadashot-esi.org.il/Report_Detail_Eng.aspx?id=25250), and are therefore not fully natural. However, the goal was to compare the two common sites of wormlions in Israel, caves vs. man-made shelters, and for this purpose the difference between urban and natural shelters is clear. We used mostly the same clusters throughout the study, with some minor differences, depending on wormlion availability and construction taking place in the university. The studied habitats are located along the coastal plain of the southeastern Mediterranean Sea and experience a Mediterranean climate, with a dry, hot summer and rainy winter (Goldreich, 2003, ch. 2). Mean annual rainfall is ~550 mm, mean August and January temperatures are 25.5 °C and 12.3 °C, and altitude is 20–30 m (BioGIS, 2017). No permits were required to conduct the experiments.

2.2. Wormlion cluster size, pit area and body mass

We define wormlion cluster as a group of 20 or more wormlions that are located in vicinity to each other (mostly a distance of a few cm between individuals, but up to 1 m in rare cases). We selected 12 wormlion clusters in 12 caves in the two studied sites and 12 clusters under man-made shelters at Tel Aviv University in May 2018. We chose the largest clusters detected in both habitats. We first counted the number of wormlions in each cluster. We then measured the wormlion cluster area using two methods. Clusters under man-made shelters were bigger, and we therefore used a measuring tape to measure the rectangular that encompasses the wormlion pits (using the pits at the extremes as indicating cluster borders). Clusters in caves were relatively small and we therefore photographed the clusters with a scale and measured the rectangular area in which pits were detected (using the software ImageJ; Abramoff et al., 2004). Pits were then counted either in the field or based on the photos. In order to estimate the average pit area per cluster, we photographed in March 2017 18 and 12 wormlion clusters in caves and under man-made shelters, respectively. We measured in each photo 13–30 pits (19.9 ± 0.9 and 22.1 ± 5.5 under man-made shelters and in caves, respectively; Supplementary material, Fig. S2).

Wormlions were collected from the urban and natural habitats (man-made shelters and caves) in four occasions: May, October and December 2017 and March 2018 (N = 162, 99, 222 and 97, respectively) and then weighed (BOECO, BBX22, accuracy of 0.01 mg).

2.2.1. Statistical analysis

We used t-tests to compare the cluster size, cluster area, pit density (cluster size or number of pits divided by cluster area) and mean pit area between sites under man-made shelters and in caves. Next, we used two-way ANOVA with collection month and habitat as



Fig. 1. (a) The three habitats and their locations in central Israel (blue-yellow dots): (b) Tel Aviv University ($32^{\circ}6'45''\text{N}$, $34^{\circ}48'13''\text{E}$), the urban habitat, and the two natural habitats, (c) Shmaryahu Caves ($32^{\circ}11'35''\text{N}$ $34^{\circ}49'14''\text{E}$), and (d) Afeka caves ($32^{\circ}07'46''\text{N}$ $34^{\circ}48'34''\text{E}$). The yellow letters on Fig. 1a indicate the identity of the habitats in Fig. 1b–d.

explanatory variables and wormlion mass as the dependent variable. All response variables were \log_{10} -transformed to improve the conformity with the assumptions of parametric models (normality and heteroscedasticity).

2.3. Ground cover and plant diversity

The ground cover and plant diversity were measured in November 2016 – February 2017. We constructed grids of 40×100 m, with 40 interior squares of 10×10 m in all habitats (similar to Abramsky et al., 1985). We used four grids at Tel Aviv University, covering most of it, representing the urban habitat including man-made shelters. We used three grids in the natural habitat including the caves (two grids in Kfar Shmaryahu and one in Afeka), covering all caves and the area in-between in both sites. Since the direction and exact area of measurement was randomly selected (see below), we measured both inside caves and under man-made shelters as well as the surrounding area. In each grid, we selected 20 squares in a “chess-board” pattern, which ensured that the area is fully and uniformly covered (Supplementary material, Fig. S3). We used a measuring tape (10 m length), chose four random

directions, and documented ground cover four times from each chosen square center along the 10 m transect. We referred to four ground cover types: soil, perennial plants, annual plants, and constructed area (hereafter, concrete). Concrete cover reflects the intensity of the urban influence on the habitat. To characterize plant diversity, we documented the identity of the first plant we encountered in a random direction. We repeated this procedure four times per each square (80 replications per grid).

2.3.1. Statistical analysis

We performed a Principal Component Analysis (PCA) on the z-transformed four types of ground cover (soil, perennial plants, annual plants, and concrete) and then used a t-test to compare between habitats. Considering plant species, we used the rarefaction method on individuals to estimate species richness (Gotelli and Colwell, 2001), and then characterized the diversity profile (Bunge and Fitzpatrick, 1993) to describe whether and how diversity differs between the habitats. We used the Hill's diversity indices, where diversity is calculated using several indices (such as the Shannon index, Simpson's index and Berger-Parker index; see Hill, 1973 for the full equation and its development)

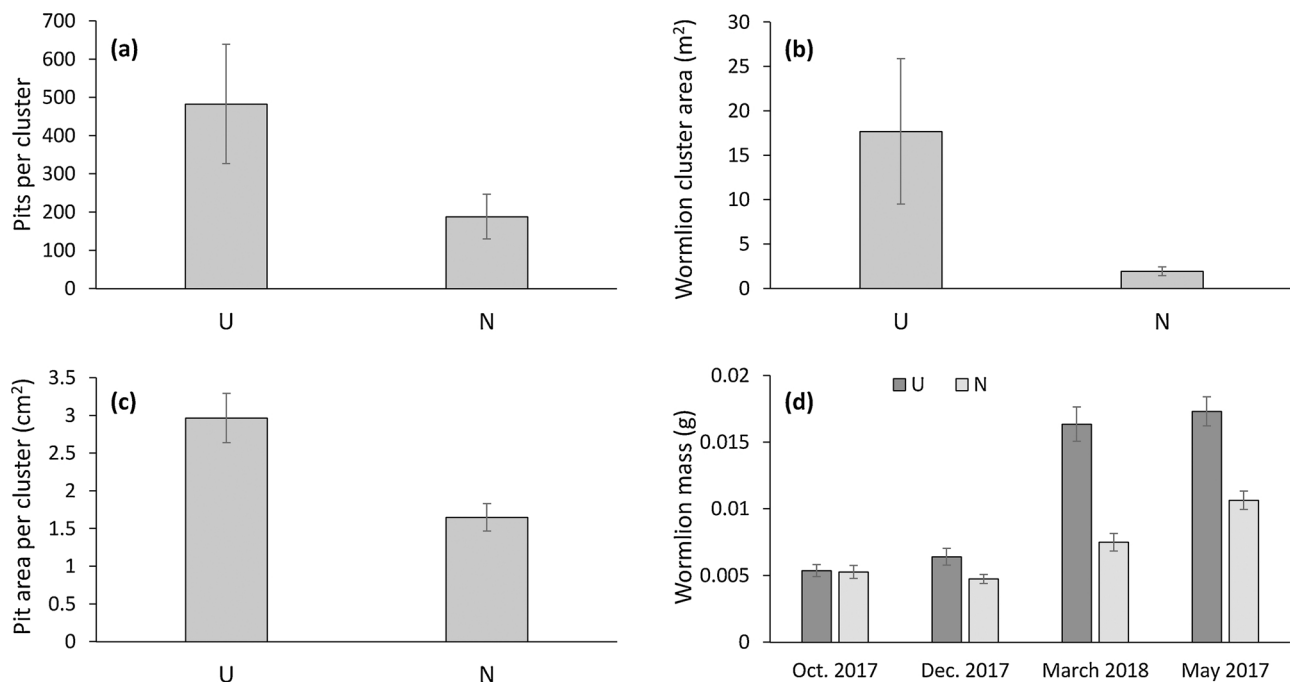


Fig. 2. Differences between the urban (U) and natural (N) habitats in: (a) the number of pits per cluster, (b) the area of wormlion clusters in the two habitats, (c) pit area per cluster, and (d) wormlion mass, collected in different months. Means \pm 1 SE are presented.

across q values. q represents diversity level, and modifies the contribution of rare species to the diversity calculation. When q is higher, the contribution of rare species to diversity decreases and thus diversity is more impacted by the evenness component. Plotting the diversity against q results in the diversity profile of a community, used to compare the contribution of rare and common species to diversity across the urban and natural habitats.

2.4. Soil composition and soil depth

We collected in March 2017 150 ml of soil from each area in the two habitats, where wormlion clusters were spotted (12 and 19 sites under man-made shelters and in caves, respectively). Each soil sample was dried for 48 h at 60 °C and then weighed (Precisa BJ410, accuracy of 0.01 g). Density is the ratio between mass and volume, with higher mass in equal volume comprising a higher density, which in this case means more soil particles in the 150 ml soil samples. The soil samples were then passed through five sieves filtering soil particle sizes in descending size (710, 500, 250, 105 and 63 μ m). We separately weighed the soils of the six different particle size ranges obtained in this process. To determine soil depth, we placed two measuring tapes across wormlion cluster, and measured using a ruler the soil depth in evenly distributed points along this axis. In each cluster we measured 10 points (5 points across each measuring tape), with 13 sites under man-made and the same number in caves.

2.4.1. Statistical analysis

Soil composition was analyzed in two ways. First, we used a t -test to compare the soil masses (of equal volumes) between wormlion clusters in the two habitats. Next, we performed a Principal Component Analysis (PCA) on z -transformed masses of the six soil particle size ranges. The first PC was then compared between the two habitats using a t -test. Soil depth was compared by first averaging the 10 depth measurements for each wormlion cluster, and then applying a t -test on \log_{10} -transformed depths (due to their right-skewed deviation from normal distribution).

2.5. Arthropod diversity and abundance

Arthropod collection in the field took place for two days in mid-May 2017. In and around caves, we placed 200 pitfall traps, 100 in each site (550 m² each), and in the urban habitat, under and around man-made shelters, we placed 200 pitfall traps divided into two areas (870 m² and 1300 m²). Each pitfall trap comprised a round 120 ml, $d = 6$ cm² plastic cup, buried 5–8 cm in the ground with its top exposed. The distance between pitfall traps was ~ 1 m. We collected arthropods in two successive cycles of 24 h (800 traps; 100 pit-fall traps per 4 areas \times 2 days). The arthropods in each pitfall trap were classified to the order level and were counted. Hymenoptera (almost only ants) was the most frequent order captured. We distinguished among three size categories of ants: large, medium and small, according to the size of the individual. The distinction of size categories was done by two independent observers by size estimation without weighing the ants. However, size categories were separable and clear, without much overlap: small, medium and large ants = 0.21 ± 0.03 , 1.89 ± 0.16 and 5.69 ± 0.28 , respectively (mg; mean \pm 1 SD). Arthropods, separated to order level for each pitfall trap, were dried and weighed (BOECO, BBX22, accuracy of 0.01 mg). Next, we focused on the most frequent order, Hymenoptera, and identified all individuals to the species level (Kugler, 1984). 30 and 25 traps of the urban and natural habitats, respectively, were not recovered and removed from further analysis.

2.5.1. Statistical analysis

We first compared between the two habitats the following variables: (1) The number of occupied traps (a χ^2 test). (2) Excluding empty traps, the number of individuals that had fallen into each trap (Kruskal-Wallis test). (3) The relative proportions of the main different arthropod orders (χ^2 test). (4) The number of ants that had fallen into the traps (Kruskal-Wallis test); and (5) frequency of the ant size categories (small, medium, large; Kruskal-Wallis test). We then assessed order richness and species richness, when focusing on ants, in the two habitats using the rarefaction method (Gotelli and Colwell, 2001). Next, we characterized the diversity profile to describe whether and how diversity differs between the habitats in arthropod orders and ant species.

3. Results

3.1. Wormlion cluster size, body mass and pit area

Clusters under man-made shelters were bigger than those in caves regarding the number of pits ($t = -2.282$, $df = 22$, $p = 0.033$; Fig. 2a) and area ($t = -4.278$, $df = 22$, $p < 0.001$; Fig. 2b). Pit density was lower under man-made shelters ($t = 4.122$, $df = 22$, $p < 0.001$; 4.02 ± 0.77 pits/m² and 12.11 ± 2.53 pits/m² under man-made shelters and in caves, respectively; mean \pm 1 SE). Pits in clusters under man-made shelters were on average larger than those in caves ($t = -3.441$, $df = 28$, $p = 0.002$; Fig. 2c). Collection month and habitat interacted to affect wormlion mass ($F_{3,572} = 3.142$, $p = 0.025$; Fig. 2d): while wormlions were similar in mass in October, the mass differences between habitats (larger under man-made shelters) increased in December and reached its peak in March, after which it declined a bit in May. Main effects were significant too: Wormlions were heavier in March and May than October and December ($F_{3,572} = 12.255$, $p < 0.001$) and were heavier under man-made shelters than in caves ($F_{1,572} = 48.654$, $p < 0.001$).

3.2. Ground cover and plant diversity

The first PC explained 45.4% of the variance (eigenvalue of 1.81) and was composed of a trade-off between the ground cover of annual plants and concrete ($PC1 = 0.902 \times \text{concrete} - 0.979 \times \text{annual plants} + 0.112 \times \text{perennial plants} + 0.168 \times \text{soil}$). High values of PC1 indicated on more concrete cover and less cover of annual plants. The habitat surrounding man-made shelters consisted of higher PC1 values than that in and around caves ($t = -11.703$, $df = 138$, $p < 0.001$; Fig. 3). Plant richness was much higher in the urban habitat than in the natural habitat (Fig. 4a), when sample size is identical. In total, we identified 15 species more in the urban habitat than in the natural habitat. When using q diversity profile, the natural habitat showed a smaller plant diversity as q increased, indicating that the diversity of the plant species found in the natural habitat was much smaller than that in man-made areas. In turn, the urban habitat had a higher decrease in plant diversity while q increased, indicating that the urban habitat was much less even in species than the natural habitat (Fig. 4b). The most common plant in the natural habitat was *Narcissus tazetta* (28 individuals), found only in this habitat, while in the urban habitat the most common plant was *Carissa* sp. (14 individuals), found in small numbers also in the cave habitat. *Cupressus*, *Lantana*, and *Olea europaea* were relatively common too and found in both habitats (Supplementary material, Table S1).

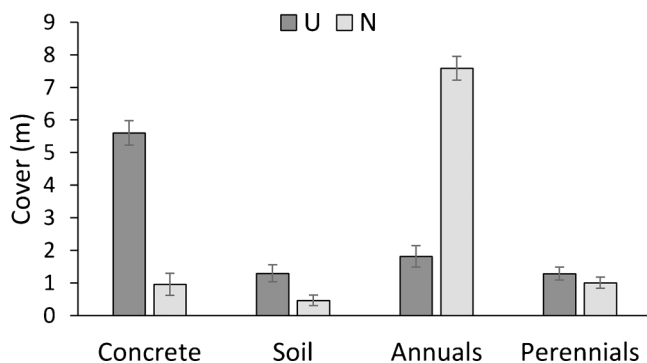


Fig. 3. The concrete, soil, perennial and annual plant cover in the urban and natural habitats. Dark grey and light grey indicate the urban and natural habitats, respectively.

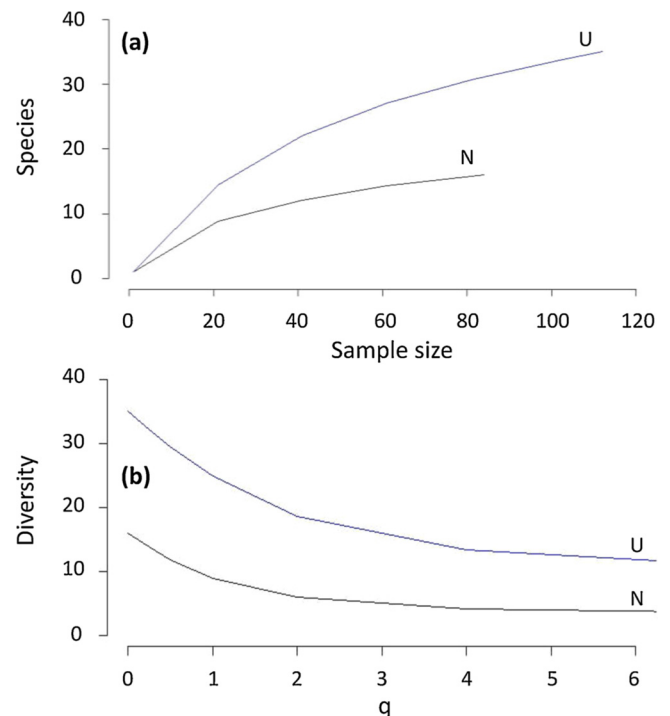


Fig. 4. The differences in (a) plant richness and (b) plant diversity between the urban and natural habitats.

3.3. Soil composition and soil depth

Soil mass (of 150 ml samples) collected in different clusters did not differ between man-made shelters and caves ($t = -1.619$, $df = 24$, $p = 0.118$; 223.85 ± 40.92 g and 251.24 ± 41.74 g, respectively; mean \pm 1 SD). The first principal component of the PCA on the ranges of particle sizes explained 47.9% of the variance with an eigenvalue of 2.87. PC1 reflects a trade-off between the three coarsest and three finest particle ranges ($PC1 = 0.579 \times [> 710 \mu\text{m}] + 0.669 \times [500-710 \mu\text{m}] + 0.508 \times [250-500 \mu\text{m}] - 0.809 \times [105-250 \mu\text{m}] - 0.803 \times [63-105 \mu\text{m}] - 0.729 \times [< 63 \mu\text{m}]$). Larger values for this PC indicate a site of coarser soil. Clusters under man-made shelters and in caves did not differ in their PC1 values ($t = 1.628$, $df = 24$, $p = 0.117$), indicating no difference in soil particle size between habitats. Average soil depth was similar in caves and under man-made shelters ($t = 1.550$, $df = 24$, $p = 0.134$; 2.37 ± 1.04 cm and 3.23 ± 1.69 cm, respectively; mean \pm 1 SD).

3.4. Arthropod diversity and abundance

Most of the captured arthropods belonged to the Hymenoptera (74.4%), Araneae (8.4%), Ixodoidea (6.4%), Coleoptera (4.9%) and Isopoda (1.8%), together totaling 95.9% of the captured arthropods. The numbers of occupied traps was similar in urban and natural habitats (219 and 245, respectively; $\chi^2 = 2.993$, $p = 0.083$). The number of individual arthropods caught per pitfall trap was similar in both habitats ($U = 27,106$, $p = 0.844$). However, arthropod composition differed between habitats (proportion of different orders captured; $\chi^2 = 340.54$, $df = 5$, $p < 0.001$; Fig. 5a). The most striking difference was the proportion of Hymenoptera (mostly ants): 89% in the urban habitat vs. 58% in the natural habitat. In parallel, the natural habitat contained more individuals of all other above-mentioned orders (for the full list of orders see Supplementary material, Table S2). Considering arthropod orders, the urban habitat was richer than the natural habitat (Fig. 5b). The urban habitat was less even in arthropod orders, as the decrease in arthropod diversity was stronger when q was high (high q

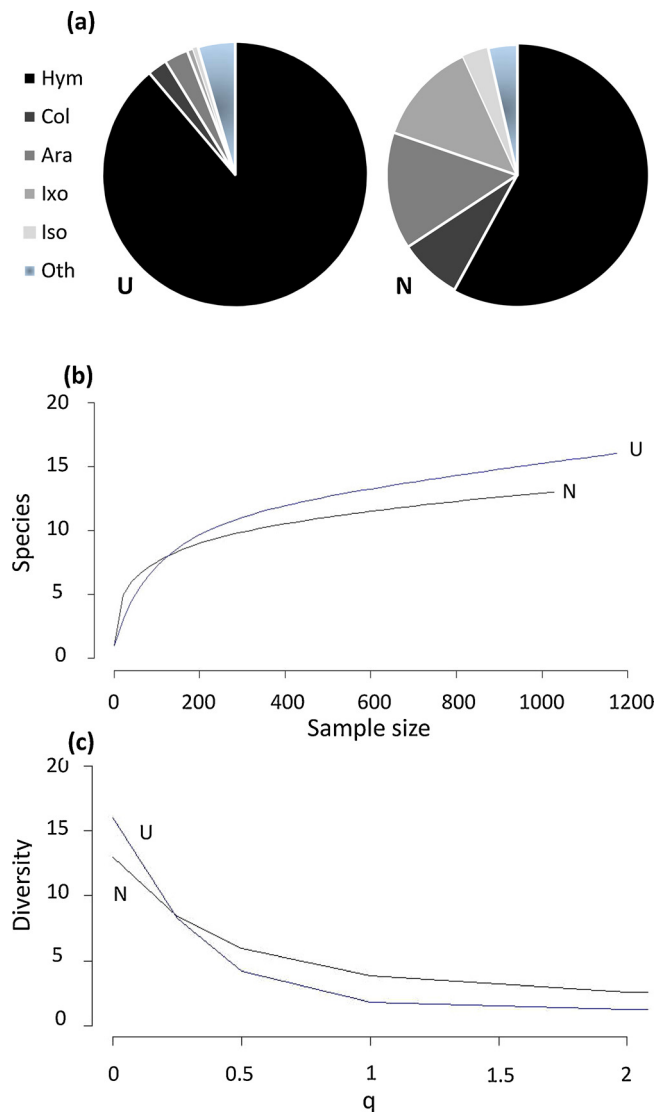


Fig. 5. (a) Proportions of the main arthropod orders found in the urban (U) and natural (N) habitats. Hym = Hymenoptera, Col = Coleoptera, Ara = Araneae, Ixo = Ixodoidea, Iso = Isopoda. (b) Order richness. (c) Order diversity.

values = rare species have a weaker effect). The natural habitat was a little more diverse than the urban habitat (Fig. 5c).

We next concentrated on the largest captured arthropod order, Hymenoptera. The vast majority of collected individuals were ants (1638 of 2202). Ants were more abundant in the city (1043 vs. 595 collected individuals; $\chi^2 = 62.433$, $df = 1$, $p < 0.001$). We counted the number of ants of each size category (small, medium and large) in the two habitats and found that small ants were more abundant in the urban habitat than in the natural habitat, while large ants were more abundant in the natural habitat ($\chi^2 = 357.166$, $df = 2$, $p < 0.001$; Fig. 6a). Only a minority of the ant species occurred in both habitats (*Cataglyphis niger* comp., *Camponotus fellah*, *Messor* cf. *ebeninus* and *Monomorium mayri*). Most ant species occurred in only one of the two habitats. For example, a common ant species in the urban habitat was *Pheidole indica* with no representation in the natural habitat, and an opposite example is several *Monomorium* species, common in the natural habitat but absent from the city. For the full list of species, see Supplementary material, Table S3. The natural habitat was richer than the urban habitat considering the ant species (Fig. 6b). Considering arthropod orders, the urban habitat was richer than the natural habitat, when using the rarefaction method on individuals (the test included

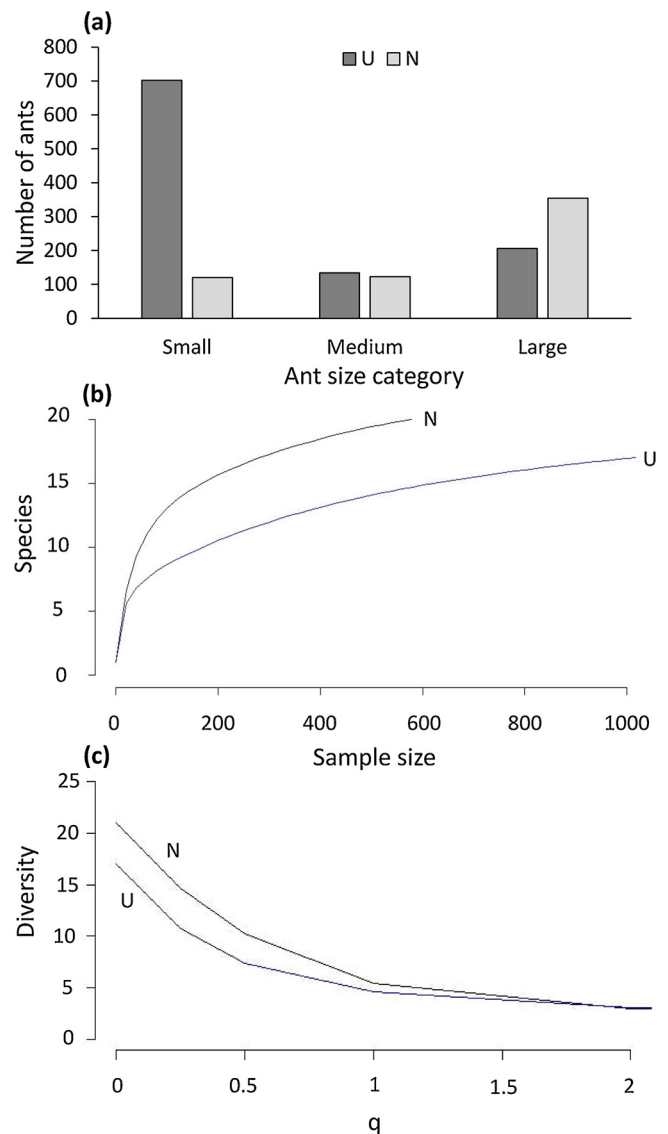


Fig. 6. (a) Number of ants found divided into size categories, small, medium and large ants = 0.21 ± 0.03 , 1.89 ± 0.16 and 5.69 ± 0.28 , respectively (mg; mean ± 1 SD), (b) ant species richness, and (c) ant species diversity.

1028 repeats). Regarding the ant species, diversity was higher in the natural habitat (the test included 597 repeats). More specifically, in low q values, when the contribution of rare ant species is high, the natural habitat is more diverse than the urban one. However, the difference diminishes in high q values (Fig. 6c).

4. Discussion

Characterizing the biotic and abiotic features of each habitat is the first step towards better understanding phenotypic variation in the same species. We focused here on pit-building wormlions, as a possible case study for other soil-dwelling arthropods, and characterized two habitats in which wormlions occur: under man-made shelters in the city and in caves, or urban vs. natural habitats, respectively. We concentrated on habitat features that are most likely to influence wormlions, such as soil characteristics and arthropod composition that serve as potential prey. Man-made shelters provided a more suitable habitat for wormlions than caves of two main reasons. First, the urban habitat consists of more suitable sites for pit construction than the natural habitats. Second, the urban habitat includes many more small ants than the more natural habitats, and prey size could be a limiting factor for

wormlions. It is therefore of no surprise that wormlions perform better in cities. Specifically, wormlion clusters in the urban habitat were larger in area and number, wormlions grew to a larger size and they constructed larger pits, which are probably translated to larger prey captured and to lower likelihood of prey escape.

4.1. Wormlion cluster size, body mass and pit area

While wormlions in fall were of similar size in both habitats, size differences in favor of the urban habitat were already detectable in winter and even larger in spring, when the wormlions start pupating. After pupation started, size differences somewhat diminished, as the largest individuals pupated first. This observation suggests that the higher abundance of small ants indeed serve as suitable prey for city wormlions, leading to a higher growth rate, larger body upon pupation and perhaps faster growth. This should lead to higher fitness, owing to the oviposition of more eggs by females and higher competitiveness by males (Partridge and Fraquhar, 1983; Honěk, 1993; Kingsolver and Huey, 2008). The larger pits constructed by wormlions could stem from larger body size, though the correlation in the field between wormlion and pit size was weak (Dor et al., 2014). It could also indicate that wormlions are located in a preferable habitat, because wormlions construct larger pits in their preferred conditions (Katz et al., 2016; Bar-Ziv et al., in press). Wormlion clusters under man-made shelters are larger, both in area and number, and less dense (possibly indicating on lower competition for prey) than in caves. This provides further evidence for the suitability of city habitats for this soil insect.

4.2. Soil characterization

The soil in the urban and natural habitats did not differ, neither in depth nor in particle size. The urbanization process typically adds new, younger sand, while also altering the chemical and biological soil features (Schleuß et al., 1998; Pouyat et al., 2003). We therefore expected a difference between habitats. Wormlions prefer in the laboratory fine and deep sand (Devetak, 2008; Adar et al., 2016). Furthermore, sites at which wormlions are present contain finer soil than sites of which they are absent, and deeper soil enables the construction of larger pits and faster response times to the prey (Bar-Ziv et al., in press). Since man-made shelters provide overall a better habitat for wormlions, we might have expected to detect deeper and finer soil there than in caves. This, however, did not come true. The absence of difference between habitats suggests that both sand depth and composition do not pose a serious limitation to wormlion occurrence, after crossing some minimal threshold. This remains to be tested. The pits constructed are therefore larger not because the soil provides more suitable soils (i.e., it is not deeper or of a finer particle size), but probably only because wormlions in the city are larger.

4.3. Ground cover and plant diversity

The highest coverage of concrete was in the urban habitat. Although cities often have negative effects on animals, some animals can flourish in cities if they are already pre-adapted to it (e.g., Grzes and Okrutniak, 2016). We suggest that the city provides large areas suitable for wormlions, and that wormlions are pre-adapted to city life. Such shelters provide protection from direct sun, wind, rain and predators also to other animals (Frankie and Ehler, 1978; Bateman and Fleming, 2012; Martin et al., 2015). Bare soil was also abundant in the urban habitat, which wormlions require to construct pits. In the two natural habitats, loose soil is less available, due to the generally lower soil cover. Furthermore, the required shade occurs only in caves or next to rocky overhangs. The annual plant cover was greater in the natural habitat and plants could have supported many small arthropods, which could have served as potential prey for wormlions. This, however, did not hold true, because small ants, for example, were more common in the

urban habitat and not in the natural habitat.

The urban habitat was more diverse in perennial plant species than the natural habitats, but this diversity mostly stemmed from exotic, non-native plants. Similarly, a third of the plants occurring in north-eastern USA cities and over half of those in European cities are non-native (Clemants and Moore, 2003; La Sorte et al., 2008). The higher perennial plant diversity in the city, however, did not translate to higher arthropod diversity (see next section), even though higher plant diversity might be expected to support a larger diversity of herbivore arthropods (Siemann et al., 1998; Haddad et al., 2009). The higher plant diversity in the city possibly led to a higher arthropod richness compared to the natural habitat. Ant species richness, in contrast, was higher in the natural habitat (see next paragraph). Diversity did not show the same pattern as richness: arthropod orders and ant species were both more diverse in the natural habitat than the urban habitat.

4.4. Arthropod diversity and abundance

Hymenoptera, almost only ants, comprised 74% of the arthropods caught, with 89% in the urban habitat and 58% in the natural habitat. Aranea and Coleoptera were the two other large taxa (~13%). Arthropod abundance was higher in the city than in the natural habitat. We suggest that the higher abundance of wormlions in the city follows the general higher abundance of arthropods there, with especially high proportion of ants, serving as potential prey for wormlions. The abundance of predator arthropods, such as spiders, in the natural habitat is higher than in the city, and they are not only harder for the wormlions to capture, but they may even compete with wormlions for the same prey. Beetles, much more common in the natural habitat, are also hard to prey on, due to their thick cuticle, and some predatory ones can compete with wormlions over prey, similar to spiders. Finally, city habitats might be segmented to patchworks of various plant species, in contrast to the natural habitat, in which one plant species is dominant (Grimm et al., 2008; Dunn and Heneghan, 2011). Potential prey are therefore constrained to specific areas, providing wormlions with more opportunities to capture them. Furthermore, herbivorous insects have little reason to enter caves, where wormlions occur in nature, and the abundance of shelter in the urban habitat may enable the wormlion to draw closer to its potential prey.

The arthropod and ant diversities were higher in the natural habitat. This is in contrast to the higher order richness and abundance in the city. Other studies have shown contradicting results. Some studies have reported a lower species richness and lower abundance in cities (Weller and Ganzhorn, 2004; Rango, 2005); other studies have reported a higher diversity of arthropods in cities (Frankie and Ehler, 1978; McIntyre, 2000; Haddad et al., 2009); and yet, other studies have reported an opposite trend of a decline in diversity with urbanization (Venn et al., 2003; Croci et al., 2008; Su et al., 2011). This latter pattern is more similar to our results, and may be typical of a habitat that has been relatively recently urbanized. In the city, there are fewer ant species, which are also less diverse. This can affect wormlion foraging. It may enable wormlions to specialize on a more limited number of prey species and capture them more easily than in the natural habitat. Consequently, wormlions in the city may forage more efficiently.

Ants, comprising most of the arthropods captured in our pitfall traps, are smaller in the city than in the natural habitat and probably better serve as prey for wormlions, especially for the first wormlion instar stages. Indeed, wormlions construct smaller pits and capture smaller prey than co-occurring antlion species, and this fact indicates the importance of small prey in habitats populated by wormlions (Miler et al., 2018). The diet of the ecologically similar pit-building antlion comprises over 70% ants (Simon, 1988), and we assume that the wormlion diet is also based on ants. Generally, city arthropods are smaller than those found in more natural habitats (Kotze et al., 2011). The ant species richness was higher in the natural habitat, but the number of individuals per species was higher in the natural habitat. The

urban habitat had mostly a dominant ant species, common overall (*Pheidole indica*), which is also a small ant species, 0.79–1.44 mm (Kugler, 1984). In comparison, the most abundant ant species is a large one (*Cataglyphis niger* comp., 7–10 mm).

5. Conclusions

The urban habitat plausibly provides a more suitable environment for wormlions, as wormlions in this habitat were larger and more abundant, and constructed larger pits than in the natural habitat. Larger larvae should emerge as larger adults following pupation, laying more eggs or better competing for females. The city is rich with a large number of arthropods, especially small ant species, which can serve as suitable prey for wormlions. It also provides wormlions more available area for pit construction, indicated by the larger wormlion clusters in cities than natural habitats.

Although we mostly focused here on the suitability of the urban habitat for wormlions, our findings improve our general understanding of habitat features in the city and the adjacent natural habitats. We believe it is important to refer to many environmental features in urban ecology studies, because together they provide a more comprehensive understanding of the urban-natural habitat differences. For example, there might be a relationship between plant abundance, soil traits, and arthropod abundance, as our data suggest. Furthermore, the findings from this case study are intriguing because they suggest that the urban environment provides an advantage to some, pre-adapted insect species, in contrast to others. It will be interesting to study whether other soil-dwelling insects present a similar pattern.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.zool.2018.08.004>.

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