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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 km^2 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 km^2; 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 km^2; 32°11'35"N 34°49'14"E) and Afeka caves (0.0067 km^2; 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 boarders). 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; Abràmoff 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