



# Mother doesn't always know best: Maternal wormlion choice of oviposition habitat does not match larval habitat choice



Shay Adar, Roi Dor\*

School of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv, Israel

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## ABSTRACT

Habitat choice is an important decision that influences animals' fitness. Insect larvae are less mobile than the adults. Consequently, the contribution of the maternal choice of habitat to the survival and development of the offspring is considered to be crucial. According to the “preference–performance hypothesis”, ovipositing females are expected to choose habitats that will maximize the performance of their offspring. We tested this hypothesis in wormlions (Diptera: Vermileonidae), which are small sand-dwelling insects that dig pit-traps in sandy patches and ambush small arthropods. Larvae prefer relatively deep and obstacle-free sand, and here we tested the habitat preference of the ovipositing female. In contrast to our expectation, ovipositing females showed no clear preference for either a deep sand or obstacle-free habitat, in contrast to the larval choice. This suboptimal female choice led to smaller pits being constructed later by the larvae, which may reduce prey capture success of the larvae. We offer several explanations for this apparently suboptimal female behavior, related either to maximizing maternal rather than offspring fitness, or to constraints on the female's behavior. Female's ovipositing habitat choice may have weaker negative consequences than expected for the offspring, as larvae can partially correct suboptimal maternal choice.

## 1. Introduction

Habitat choice is an important decision that animals make, and one that influences their survival and reproduction (Rosenzweig, 1981; Morris, 1989; Halliday and Blouin-Demers, 2014). When choosing among possible habitats, animals take into account multiple factors. Spiders, for example, evaluate prey and water availability, vegetation structure, and predation risk when choosing a site for their web (Gillespie, 1987; Ward and Lubin, 1993; Blamires et al., 2007). The ideal free distribution (IFD) model assumes that animals have an ideal/perfect knowledge of the environment, so that they can choose the habitat with the highest quality, and that they are free to move without restraint from one habitat to another (Tregenza, 1995). This is clearly an over-simplification of reality. Mobility, for example, is a limiting factor, restricting the ability of animals to freely choose among habitats. For example, even if adults and larvae of the same holometabolous insect generally prefer the same habitat, the larvae might choose it less often due to their reduced mobility, higher search costs, and more limited knowledge of the environment (Stamps et al., 2005). In such cases, the ovipositing females have a greater effect on habitat choice than the larvae.

When choosing a site for oviposition, the female insect should

ideally select a suitable location that will allow uninterrupted larval growth till adulthood, especially since larval mobility is often more limited than that of adults (e.g., Shikano et al., 2010). This idea, that female insects should choose sites on which their larval offspring will perform best, was termed the “preference–performance hypothesis” (Thompson and Pellmyr, 1991; Koricheva and Haukioja, 1994). In a meta-analysis on herbivorous insects, Gripengberg et al. (2010) provided strong support for this hypothesis, which was found for example in caddisflies (Bovill et al., 2013), beetles (Landvik et al., 2016), and butterflies (Friberg et al., 2015). However, mismatches between the preferences of the ovipositing female and the larvae are common too (e.g., beetles: Clark et al., 2011; Hufnagel et al., 2017; butterflies: Underwood, 1994; Marchioro and Foerster, 2014; flies: Scheirs et al., 2000; whiteflies: Jiao et al., 2012).

The interests of the ovipositing female and the offspring are similar, as both profit if the larvae grow successfully, but are nevertheless not identical. This is due to, among others, the common life-history trade-off between current vs. future reproduction (e.g., Candolin, 1998), because the female plausibly has more than a single egg to lay, is limited in time, and has to optimize as best as possible her “oviposition strategy”. Therefore, the decision related to an individual egg might not in itself be optimal (Thompson, 1988).

\* Corresponding author at: School of Zoology, Faculty of Life Sciences, Tel Aviv University, 69978 Tel Aviv, Israel.  
E-mail address: roidor@tauex.tau.ac.il (R. Dor).

We studied here the habitat choice of ovipositing wormlion females and its effect on offspring investment in foraging. Wormlions (Diptera: Vermilionidae) are flies whose larvae dig pit-traps in loose soil, and ambush and prey on small arthropods that fall into their pits (Wheeler, 1930; Devetak, 2008), similar to pit-building antlions (Neuroptera: Myrmeleontidae). In the two taxa, the larvae live for a year or even longer, while the adult is short-lived (Scharf et al., 2009; Dor et al., 2014). Pit size represents the investment in foraging of pit-building predators (Lucas, 1985; Scharf et al., 2011), and capture success is correlated with pit size in antlions (Griffiths, 1980). In wormlions, pit size was found to be correlated with body size of the larvae, disturbance level, starvation, and habitat quality (Dor et al., 2014; Scharf and Dor, 2015; Adar et al., 2016a). Many studies have described and examined the habitat preferences of wormlion and antlion larvae. Wormlion larva prefer dark, obstacle-free habitats with deep and fine sand (Devetak, 2008; Adar et al., 2016b), probably because this allows them to dig larger pits (Adar et al., 2016a). Antlion larva show a species-specific preference for a variety of habitats, differing for example in substrate type and sand particle size (Barkae et al., 2012; Devetak and Arnett, 2015). That said, no study has examined the habitat choice of adult wormlions and, to the best of our knowledge, no study has carried out any experiments with adult wormlions; while the habitat choice of antlion adults has only very rarely indeed been studied. Matura et al. (2005) presents an elegant experiment demonstrating that in antlions that both the ovipositing females and the larvae preferred the same habitat (sand of medium-sized particles).

Antlion (and wormlion) pits are easy to detect and often occur in clusters, termed “antlion zones” (Gotelli, 1993). There is a discussion in the literature as to whether the females or the larvae are more responsible for the clumped spatial pattern demonstrated by the larvae (Scharf and Ovadia, 2006). While the larvae are more directly and severely affected by such decisions, the adults are able to fly and therefore move better and possess a better knowledge of potential suitable sites. Based on our knowledge of larval habitat preference (Adar et al., 2016b), we predicted that the ovipositing wormlion females would prefer deep, obstacle-free habitats. Since pit size is affected by sand conditions (Adar et al., 2016a), we expected that the pits dug in the favored habitat would be larger.

## 2. Methods

We collected ca. 200 wormlion larvae during March–June 2016 from five sand patches in Tel Aviv. This species has not yet been formally described but has recently been the subject of several foraging and habitat selection studies (Dor et al., 2014; Scharf and Dor, 2015; Adar et al., 2016b). Larva were kept together in aluminum trays, and were fed twice a week with a single red flour beetle larva (*Tribolium castaneum*). Within the next two months the larvae pupated, and each pupa was separately placed in a plastic cup. Following eclosion, we determined the sex of the wormlion adult (the last abdominal segment is wider in females than in males). 53 Pairs of male and female flies were placed one day following eclosion in net cages (30 × 30 × 30 cm) and were allowed to mate. The cages contained aluminum trays filled with sand to allow female oviposition (25 × 20 cm; preliminary assays showed that wormlion females lay eggs in these trays; Fig. 1). Both the eggs and the recently hatched larvae are extremely small and hard to detect in the sand. Therefore, after both adult flies had died (within a few days) the trays were removed from the cages and monitored for the construction of pits by the newly-hatched larvae.

Each cage contained two possible trays for female oviposition: (1) favored habitat comprising regular, clear sand (> 2 cm deep; previous work showed that sand deeper than 1.5 cm is considered deep enough; Adar et al., 2016b), or (2) unfavored habitat, with either shallow (1 cm deep) or obstructed sand (small pebbles on the sand surface) as abiotic disturbances (Fig. 1). The number of observed pits in the favored habitat was compared to that in the unfavored habitat. Additionally, the

newly-hatched wormlions were fed once a week and changes in pit size and number were monitored over two weeks. To achieve this, we photographed the trays, counted the number of pits, and measured their area using the ImageJ software (Abramoff et al., 2004).

### 2.1. Statistical analysis

We used a Wilcoxon sign test to compare the number of larvae in the favored and unfavored habitat for each of the ovipositing females, and to compare between the mean pit area of all pits dug in the favored and unfavored habitats after two weeks. We used non-parametric tests due to the small sample size ( $n = 11, 10$ ) and deviations from a normal distribution (Kolmogorov-Smirnov test:  $P < 0.05$ ).

## 3. Results

Only 21 adult wormlion pairs, of the 53 pairs used, mated and produced surviving offspring (identified through the appearance of new small pits, typically 5–10 days after mating). The number of pit-constructing offspring varied greatly among pairs (Table 1). Out of the females that laid eggs, almost all had oviposited in both trays, representing both the favored and the unfavored (either shallow or obstructed sand) habitats. In only four cases (out of 21) no pits were found in one of the trays, which was always the one with the unfavored habitat (two in the obstacle treatment and two in the shallow sand treatment; Table 1). We could not detect significant differences in the number of larvae between the favorable and unfavorable microhabitats (obstacles:  $Z = 1.54$ ,  $P = 0.12$ ; shallow sand:  $Z = 0.05$ ,  $P = 0.96$ ; lumped together, favored vs. unfavored habitats:  $Z = 1.16$ ,  $P = 0.25$ ).

Mean pit area differed between the favored and unfavored habitats when the two treatments were lumped together ( $Z = -2.11$ ,  $P = 0.035$ ): pits constructed in the preferred habitats were larger (Fig. 2). Tested separately, pits differed between shallow and deep sand ( $Z = -2.07$ ,  $P = 0.038$ ), but not between obstructed and obstacle-free sand ( $Z = -0.56$ ,  $P = 0.58$ ).

## 4. Discussion

In contrast to our expectation of a similar habitat choice by the ovipositing females and the larvae, we could not detect a significant preference of ovipositing females for the same habitat favored by the larvae. The wormlion larvae, in comparison, in about 85% of the cases revealed a preference for deep, obstacle-free sand over shallow or obstructed sand (Adar et al., 2016b). The negative implications of the female choosing the unfavored, inferior habitat is later reflected in the smaller pits constructed by the larvae. Larger pits, at least in the ecologically similar antlions, enable the larvae to capture larger prey items without compromising over smaller prey items (Scharf and Ovadia, 2006). The larvae therefore might pay a price (e.g., slower development) for a suboptimal habitat choice by their mothers.

In contrast to antlions, in which both the ovipositing females and the larvae demonstrate a similar preference (Matura et al., 2005), wormlion females were less selective. Explanations for this behavior can be roughly divided into that of being adaptive for the female, adaptive for the offspring, or non-adaptive for both. An adaptive explanation from the female perspective is that she is expected to maximize her fitness (raise as many offspring as possible) and not that of each individual offspring (Scheirs et al., 2000; Mayhew, 2001). It is possible that wormlion adult females are more constrained by time (they indeed have a short lifespan) and less by the number of eggs available. In such cases, theory predicts that females should be less choosy in their host choice (Doak et al., 2006). In other words, females should settle for oviposition sites that are of lower quality but more easily accessible. Another possible adaptive explanation from the female perspective is that of maternal bet-hedging, which takes place under unknown or changing conditions (Marshall and Uller, 2007). For

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