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Foraging behaviour of a neglected pit-building predator: the wormlion

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Wormlion larvae (Diptera: Vermileonidae) construct conical pits in fine loose soils and ambush arthropod prey. Their hunting strategy resembles that of pit-building antlions (Neuroptera: Myrmeleontidae), offering a classical example of convergent evolution, as they belong to different orders of insects. However, compared with other trap-building predators, spiders and antlions, the foraging behaviour of wormlions is almost unknown. In this study we used a combination of field observations and laboratory experiments to close this gap and investigate how hunger and ecological factors such as density and spatial pattern affect pit size, that is, how they shape investment in foraging and indicate competition between neighbouring larvae. We found slight, mainly decreasing, changes in pit size with hunger, with no change in response to prey. Surprisingly, body mass and length were not tightly correlated with pit size, unlike in antlions and spiders. Other factors, in addition to body mass and size, affect pit size, as the correlation between pits constructed in the field and in the laboratory was strong. The evidence for competition was mixed. On the one hand, we detected, in the laboratory, a change towards a regular spatial pattern with increasing pit densities, as expected, suggesting interference competition. On the other hand, we detected, in the field, a positive correlation between the sizes of neighbouring pits, and a negative correlation in the laboratory between pit size and distance to the nearest neighbour, both indicating clustering in favourable microhabitats, and not supporting strong competition. We discuss our findings in comparison with other trap-building predators and locate them within the general framework of foraging theory.

Although most animals in nature actively search for their prey, a large number of predators do not and instead merely choose a suitable location for ambush (Huey & Pianka, 1981; Perry & Pianka, 1997; Uetz, 1992). Sit-and-wait predators invest less energy in searching for prey and have a lower metabolic rate, but they also exhibit lower encounter rates and need to endure longer starvation periods (Elimelech & Pinshow, 2008; Huey & Pianka, 1981; Nagy, Huey, & Bennett, 1984). Many animals across various taxa can switch between the two foraging modes. Theoretical and empirical studies suggest that prey abundance and size, hunger level, body condition and movement velocity and directionality of both predators and prey play a role in determining which foraging mode such predators will employ (e.g. Elimelech & Pinshow, 2008; Helfman, 1990; Scharf, Nulman, Ovadia, & Bouskila, 2006). Some models have emphasized the importance of prey capture variance. Caraco and Gillespie's (1986) model, for instance, suggests that the sit-and-wait strategy has a higher variance of success than the active foraging mode; thus, the sit-and-wait strategy is probably employed when the requirement for food exceeds the expected extent of prey capture, leading the predator to become more risk prone.

Trap-building arthropod predators are a subgroup of sit-and-wait predators, and employ a unique foraging strategy (Ruxton & Hansell, 2009). Active foragers should search for food as long as the marginal cost of searching is lower than the benefit, the chance of prey capture (Brown, 1988; Mitchell, Abramsky, Kotler, Pinshow, & Brown, 1990). The investment in trap construction and maintenance is analogous to the investment in searching for prey by active predators, because trap construction is an energetically expensive process (Lucas, 1985a; Tanaka, 1989; but see Elimelech & Pinshow, 2008, for a lower cost). Thus, trap-building predators should present a flexible strategy of investment in traps, and maximize foraging gain as much as possible, by adjusting trap size (Scharf, Lubin, & Ovadia, 2011). The costs of foraging are expected to be lower (e.g. the perceived cost of predation) and the benefit from successful foraging is expected to increase (the value of each prey caught) when animals are hungrier (Brown, 1988). Empirical evidence demonstrates varying changes in foraging activity with starvation, as some animals reduce their activity with starvation while others first increase activity before decreasing it (reviewed in Wang, Hung, & Randall, 2006). Trap-building predators usually

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increase their traps with starvation (before exhaustion) and neglect them with satiation (e.g. Herberstein, Craig, & Elgar, 2000; Lomascolo & Farji-Brener, 2001; Lubin & Henschel, 1996). Hungry trap-building predators respond faster to prey (Persons, 1999; Scharf, Barkae, & Ovadia, 2010) and consume a higher proportion of the prey items caught (Lucas, 1985b; Samu, 1993). Similarly, the cutoff distance below which an ambushing lizard responds to prey becomes greater when prey are scarce (Shafir & Roughgarden, 1998).

The investment in foraging depends not only on hunger level but also on competition with nearby foragers. While strong interference competition should lead to a decrease in foraging intensity, as it reduces the benefit and increases the cost of foraging, exploitation competition has a complex effect, because it is expected to reduce both the benefit and the cost. The effect on foraging intensity thus depends on whether the marginal cost has been reduced more than the benefit (Mitchell et al., 1990). Indeed, empirical evidence is mixed, with animals either increasing or decreasing foraging intensity with increased density or competition (cf. Abramsky & Pinshow, 1989; Grand & Dill, 1999). Trap-building predators experience both exploitation and interference competition with increasing conspecific density. ‘Shadow competition’ (individuals closer to a source of food reduce its availability to those further away; Wilson, 1974; Lubin, Henschel, & Baker, 2001) is equivalent to exploitation competition, while fights over suitable places for trap construction and sand throwing while constructing/maintaining pits are examples of interference competition (Day & Zalucki, 2000; McClure, 1976).

Traps usually become smaller with increasing density, even when space for the trap itself is not yet a limiting factor (e.g. Devetak, 2000; Griffiths, 1991), plausibly reflecting an increase in the cost of trap maintenance. In addition, the relocation rate of trap-building predators and the proportion of nontrap-building individuals increase with density (e.g. Day & Zalucki, 2000; Scharf & Ovadia, 2006). Parallel evidence for competition is provided in the shift in spatial pattern from random to regular with increasing density, as individuals try to maximize the distance to the nearest neighbour (Birkhofer, Henschel, & Scheu, 2006; Day & Zalucki, 2000; Matsura & Takano, 1989). Ant colonies, central-place foragers, respond similarly to competition, by increasing the distance to the nearest neighbours, in a process that results in a regular spatial pattern of ant nests (Ryti & Case, 1986). In all cases, maximizing the distance to neighbours should reduce the cost of foraging (by minimizing interference competition). Clearly, the effect of interference is moderated in rich habitats, where the distance to neighbours and territories held are smaller (e.g. spiders: Uetz, Kane & Stratton, 1982).

In addition to the well-studied web-building spiders and pit-building antlions, wormlions (Diptera: Vermileonidae) are a third group of such predators that has rarely been studied (a single ecological/nontaxonomical paper in ISI: Devetak, 2008a). Similar to antlions, wormlion larvae construct conical pits in loose soil and ambush small arthropods, mainly ants (Wheeler, 1930; Devetak, 2008a). This similarity to antlions, representing a clear example of convergent evolution, calls for comparisons in order to understand better the important biotic and abiotic factors relevant to their natural history, foraging and development. For instance, the vast majority of studies on trap-building predators have detected a positive correlation between body mass or size and trap size (e.g. Griffiths, 1986; Heinrich & Heinrich, 1984; Miyashita, 2005; Scharf, Golan, & Ovadia, 2009). However, it is unknown whether and to what extent body size affects trap dimensions in wormlions. Nothing is known about the importance of interference and exploitation competition, the effect of temperature or photoperiod and stress or starvation endurance.

We conducted a series of field observations and laboratory experiments in order to understand better the effect of external (density, spatial pattern) and internal (hunger, body mass and body size) factors on the foraging behaviour and competition of wormlion larvae, as reflected in their pit size and response to prey. Hunger and density manipulations were chosen because they are the most commonly tested factors affecting the pit size of antlions. Our working hypothesis was that both should affect the foraging behaviour of wormlions in seeking to maximize foraging gain and minimize foraging costs, when under starvation or competition conditions. We expected the following: (1) that the spatial pattern of wormlions in both the field and the laboratory would be random at lower densities but regular as density increases; (2) that a positive association would be found between pit size and distance to the nearest neighbour; (3) that pit sizes of the same individuals in the field and under laboratory conditions should be correlated, and there should be a positive correlation of both with body mass and length; and (4) that starvation would result in larger pits and faster responses to prey.

METHODS

Study Species and Collection Site

The wormlion species used in this study has not yet been formally described and is referred to here as *Vermileo* sp. (A. Freidberg, personal communication). It is probably very similar morphologically (especially in the larval stages) to its relative *Vermileo vermileo*, inhabiting the northern Mediterranean countries. The ecological or natural history differences between the studied species and its congeneric relatives are expected to be very minor. Wormlion larvae have a simple morphology compared with antlion larvae. They lack long mandibles, but have an elongated body shape with two protrusions from the main body part, the pseudopodium, which probably help in detecting and grasping the prey, and an abdominal comb, composed of several spines, which are probably used to anchor the wormlion in the sand (demonstrated for *V. vermileo*; Wheeler, 1930; Ludwig, Melzer, & Ehrhardt, 2001; Devetak, 2008b; Fig. 1). *Vermileo vermileo* larvae prefer finer sand than antlion larvae (Devetak, 2008a). There are probably six larval instars (Wheeler, 1930; the Sierra wormlion, *Vermileo comstocki*) and the pupal stage may last for up to a month, after which a very short-lived adult emerges (Wheeler, 1930; Devetak, 2008b).

Wormlion larvae were collected and photographed in July 2013 from Tel Aviv University, Tel Aviv, Israel, and the surrounding streets (32°6′54.35″ N, 34°48′21.69″ E), as well as in the city of Ramat Hasharon, 4 km northeast of the university. Wormlions were found only in fully sheltered places, on the sides of walls or buildings, in the shade. The substrate was always very fine sand, almost dust, which was usually only a few centimetres deep. Figure 1 shows two examples of collection sites. Note that some of the zones were disturbed by leaves, sticks, small stones and even shoe footprints, characterizing urban habitats. Wormlions were kept in the laboratory after the termination of the experiment, because we were interested in mating the adults for later research. The larvae were of different instar stages, but it is difficult to determine the stage based on allometry without knowing more about this species.

Experimental Design

Density and spatial pattern in the field

We first photographed 13 zones (Fig. 1a, b; mean zone area ± 1 SD: 0.272 ± 0.084 m^2) and calculated pit density for each zone. We measured pit area and location using the software ImageJ