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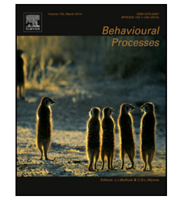

Consequences of the instar stage for behavior in a pit-building antlion

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ABSTRACT

Pit-building antlion larvae are opportunistic predators that dig conical pits in loose soils, and prey on small arthropods that fall into their traps. We investigated different behavioral traits of second and third instar larvae selected for similar body masses, while also exploring the behavioral consistency and personalities of the third instar stage. Second instar larvae constructed smaller pits than third instar larvae. The former also responded more slowly to prey and exploited prey less efficiently. Notably, all these instar-based differences disappeared after molting into the third instar stage. In addition, third instar larvae exhibited consistent behavior in their pit size, response times to prey and to less extent in relocation distances. We detected two axes of behavior. The first axis included a correlation between pit size, response time and prey exploitation efficiency, thus reflecting investment in foraging activity. The second axis seemed to represent a trade-off between response time and relocation distance, implying that individuals that responded more slowly to prey, relocated over larger distances. These results point to coordinated behavior reflecting different levels of investment in foraging, while also emphasizing the importance of instar stage, in addition to body mass, when studying the behavior of such organisms characterized by a complex life cycle.

1. Introduction

Individuals within a population often differ consistently in their behavior, and such differences can persist over time and across varying ecological contexts (e.g., Sih et al., 2004; Dingemanse et al., 2010). Behavioral variation can be maintained by different processes including frequency-dependent selection and changing environmental conditions (Réale et al., 2007; Pruitt and Riechert, 2012). Notably, most studies of animal personalities and syndromes, rather than emphasizing initial/known individual differences in body size, development stage or age, demonstrate how similar individuals that experience the same environmental conditions behave consistently and differently (e.g., Kortet and Hedrick, 2007; Modlmeier and Foitzik, 2011). However, especially in field-collected animals, it is often difficult to determine whether apparently similar individuals are indeed similar. For instance, differences related to developmental history usually remain uncovered, although they may dramatically affect various behaviors, such as activity level and boldness (Tremmel and Müler, 2013).

In arthropods, individuals of two successive instar stages may possess very similar body masses and dimensions. When the behavior of such individuals is studied while erroneously ignoring the instar stage, consistent individual differences based on personality might be detected. However, such consistency and behavioral differences are stage-dependent, and they may disappear when all individuals progress into the same instar stage. Although behavioral differences based on the instar stage and independent of body size may exist, they are rarely reported. Three examples include sharp between-instar differences in the predation avoidance behavior of grasshoppers in the presence of spider predators (Danner and Joern, 2003), foraging behavior differences between instar stages of a plant bug reflected in its feeding time and number of plants it attacks (Zink and Rosenheim, 2005), and differences in the latency to attack prey and resume movement after disturbance in spiders (Sweeney et al., 2013). In such cases, ignoring the instar stage and studying insect personality and consistency might lead to erroneous results.

In addition, morphology and body shape have consequences for behavior, even when the general body size is similar. For instance, sit-and-wait and widely foraging predators differ in their body shape (stocky vs. streamlined, respectively; Huey and Pianka, 1981; Meiri, 2010). Yet, the vast majority of personality studies ignore body shape, even when accounting for general body size or mass (e.g., Kortet and Hedrick, 2007; Modlmeier and Foitzik, 2011; Tremmel and Müler, 2013). Incorporating morphology could lead to a better understanding of behavioral differences among individuals. For instance, morphology can indicate on body condition

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(e.g., Stevenson and Woods, 2006), which is likely to have a strong influence on behavior (e.g., Tucker et al., 2007).

In this research, we investigated, for the first time, personalities and behavioral consistency of pit-building antlion larvae. These opportunistic predators hunt their prey by constructing conical pits in loose soils, while waiting for small arthropods to overstep their pit margins. Because they are not yet in a reproductive stage, they are an excellent model system to study foraging-related behavior. Our goals are: (1) To investigate behavioral differences between second and third instar larvae having similar body masses in spite of their different developmental stage. (2) Examine behavioral consistency of third instar larvae; consistency is the first step in determining animal personality (Bell et al., 2009). (3) Determine the personality (defined here as the nature of the correlation among behavioral traits) of third instar larvae. (4) Investigate possible effects of morphology on behavior.

In insects there is a tight positive correlation between body size and reproductive success (Honek, 1993). State-dependent models, considering both survival and reproduction, predict that when foraging aims at future reproduction and not mere survival, there is a benefit to increase effort and take further risks (Bednekoff, 1996). This especially holds true for sit-and-wait predators in advanced larval/juvenile stages, facing a minor starvation risk combined with uncertainty in respect to accumulating sufficient resources for reproduction. Antlion species develop through three instar stages. The third instar is the longest, comprising more than half of the larval period, and providing the main opportunity for the antlion to accumulate resources for reproduction. Thus, third instar larvae should exhibit high foraging activity and more risk-prone behavior compared to second instar larvae, which are perhaps more occupied with survival. Regarding antlion personality, we predicted that there should be a positive correlation between behaviors related to foraging, including pit size and response time to prey, and a negative correlation between these two traits and relocation tendency. We also posited that head width (hereafter, HW) and mandible length (hereafter, ML) should be positively correlated with pit size, as pits are constructed by throwing sand using the mandibles.

2. Methods

2.1. Study species

We collected *Myrmeleon hyalinus* (Neuroptera: Myrmeleontidae) larvae under different tamarisk trees and brought them to the laboratory. Larvae were identified according to the key presented in Simon (1988). The collection site, Nahal Secher (31°06′N, 34°49′E), is a sandy area 15 km south of Beer-Sheva, Israel. *M. hyalinus* is the most abundant pit-building antlion in Israel. The larvae inhabit a wide range of sandy soils, but they prefer constructing their pits in shaded areas located under trees or bushes (Simon, 1988). *M. hyalinus* attains body masses of up to 0.06 g before pupating (Scharf et al., 2008a). Individuals spend most of their lives as larvae (lasting ∼1 year), enter pupation (lasting ∼1 month), and then emerge as short-lived and weak-flying adults (lasting ∼1 week) (Scharf et al., 2009a).

2.2. Experimental design

The study included two experiments, of which the first included two phases: (1a) investigating the behavioral consequences of the instar stage by comparing the behavior of second and third instar larvae. (1b) Testing whether the differences between the instars diminish when the larvae are all at the third instar, and exploring the behavioral consistency and syndromes in third instar larvae. (2) Studying within-instar stage behavioral differences of second instar larvae differing in body mass.

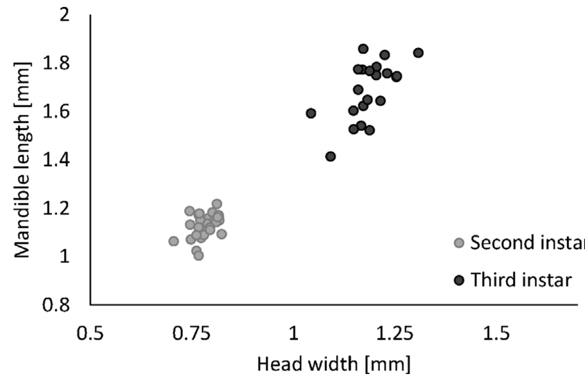

Fig. 1. Mandible length vs. head width of second and third instar larvae. The separation between the two instar stages is clear, based on this figure. Note that body mass of all antlion larvae was very similar.

Prior to all experiments, antlions were fed weekly with one flour beetle larva (mean larva mass of 2.5 mg) for three successive weeks, weighed using an analytical scale (CP224S, Sartorius AG, Göttingen, Germany; accuracy of 0.1 mg), and then starved for seven days in small plastic cups (diameter of 4.5 cm, filled with about 3 cm of sand). This procedure allowed standardizing the physiological state of the larvae prior to the experiment (Scharf et al., 2009b). All experimental tests were conducted under identical day/night photoperiod (12:12 h), temperature of 21.9 °C and relative humidity of 49.3% (averages of three daily measurements in the test room). Larvae were photographed using digital camera (Micropublisher 5.0, QImaging, Surrey, BC, Canada) connected to a Nikon stereoscope (SMZ 800, Nikon, Kawasaki, Japan). Using the program ImageJ (a public domain Java image processing program, National Institute of Mental Health, Bethesda, Maryland, USA) we measured ML, HW and abdomen width (hereafter, AW).

2.2.1. Experiment 1

We selected 50 individuals with similar initial body mass (mean mass ± 1 SD: 6.0 ± 0.5 mg, N = 50; range: 5.1–6.9 mg). Body mass of 5.0–7.0 mg is the range in which *M. hyalinus* second instar larvae molt and progress to the third and final instar stage (Scharf I, unpublished data). The morphological trait discriminating best between the larval stages is HW (Simon, 1988; Scharf et al., 2008a). By plotting the HW against ML, we could distinguish between second (N = 29) and third instar (N = 21) larvae (Fig. 1). The study included two phases: At the beginning, individuals were similar in mass (second instar: mean mass ± 1 SD: 5.8 ± 0.5 mg, N = 29; third instar: mean mass ± 1 SD: 6.2 ± 0.5 mg, N = 21). The overlap in body mass between the instars is limited, and although we selected small third instar larvae and large second instar larvae, there was a significant difference in average body mass between the two groups (t-test: $t_{41} = -2.79$, P = 0.0075); however, the effect size was very small (∼6.5%). In comparison, differences within the whole mass range of second instar larvae could reach ∼300% (this study). At the end of the first phase, the larvae were fed once a week until all second instar larvae progressed to the third stage and reached similar body masses (individuals collected as second instar: mean mass ± 1 SD: 8.5 ± 1.2 mg, N = 24; individuals collected as third instar: mean mass ± 1 SD: 9.2 ± 1.3 mg, N = 16). Six individuals died and four were either heavier or lighter more than 50% than the group's average; therefore, they were excluded from the second phase of the experiment in order to maintain similar average and low variance of body mass between the two groups.