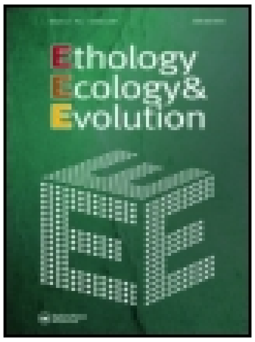

Ethology Ecology & Evolution

ISSN: (Print) (Online) Journal homepage: https://www.tandfonline.com/loi/teee20

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To cite this article: Alejandro G. Farji-Brener, Agostina S. Juncosa-Polzella, Daniela Madrigal-Tejada, Diego Centeno-Alvarado, Mariana Hernández-Soto, Mayori Soto-Huaira & Sebastián Gutiérrez-Cruz (2021): Antlion allometry suggests a greater importance of prey capture among first larval instars, Ethology Ecology & Evolution, DOI: 10.1080/03949370.2021.1893825

To link to this article: https://doi.org/10.1080/03949370.2021.1893825

Published online: 21 Mar 2021.

Ethology Ecology & Evolution, 2021
https://doi.org/10.1080/03949370.2021.1893825

Antlion allometry suggests a greater importance of prey capture among first larval instars

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Received 30 October 2020, accepted 28 December 2020

First larval stages require adequate feeding to reach subsequent instars. However, the accumulation of reserves is also important in the last larval instar because it is vital to pupate and successfully perform metamorphosis into adulthood. We indirectly determined the presence of changes in the relative importance of prey capture through larval ontogeny in the antlion larvae (Neuroptera Myrmeleontidae), a sit-and-wait predator with three instar stages that capture preys that fall into their pit-traps. We used scaling relationships between the size of body parts directly related to prey capture (prothorax) versus those that are not (thorax + abdomen). The prothorax (neck, head, and mandibles) is used in the pit building, prey capture, and re-capture, and pit cleaning. We measured the body parts of 70 larvae of *Myrmeleon crudelis* in a tropical rain forest of Costa Rica. The prothorax showed negative allometry: it was proportionally larger in the first than in the last instars. These results support the growth hypothesis, which states that food acquisition is key in the earlier stages of larval development. First instars can be more food-limited than later instars because they build small pit-traps where only very small arthropods can fall; have smaller mandibles and relatively lower grab force, increasing the probability of the prey escaping; and have smaller fat reserves and thus, are unable to resist long periods of starvation. This illustrates the relevance of using scaling relationships to better understand how ecological pressures change along ontogeny, emphasizing the role of food acquisition at earlier ontogenetic stages

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KEY WORDS: Costa Rica, foraging, *Myrmelon crudelis*, scaling relationships, sit-and-wait predators.

INTRODUCTION

The quantity and quality of ingested food are of key importance in the larval stages of many insects. An adequate diet allows better larval growth, faster transitions between instars stages, and larger body size as an adult (Scriber & Slansky 1981; Shafiei et al. 2001). However, in insects that develop through several instar stages, the relative importance of food acquisition may change according to the larval phase. Growing first stages require an adequate diet to reach the subsequent larval instars (Stockhoff 1993). Still, the accumulation of reserves is also particularly important in the last larval instar because it is vital to pupate and reach the metamorphosis into adulthood (Scriber & Slansky 1981; Shafiei et al. 2001). Consequently, food limitation in the first instars may restrict larval growth and the transition to the next larval phase, and food limitation in the last instar may reduce the pupation success (Shafiei et al. 2001). Determining the investment in foraging in the first and last larval stages can help us to understand which of these processes, growth or pupation, is most limited by food.

Antlion larvae (Neuroptera Myrmeleontidae) are a good model to test whether food acquisition is influenced more by growth or pupation. First, their larval phase includes several stages that can easily be identified by their size (Alcalay et al. 2014). During the 1–2 years as larva, antlions develop at least three instar stages before pupation with a size ranging between 2 and 20 mm (Scharf et al. 2008b). Second, it is easy to determine which body parts are directly involved in food acquisition, allowing the use of scaling relationships to indirectly determine whether the relative importance of foraging changes through larval ontogeny. The antlion larva has a very plump abdomen and a thorax bearing three pairs of walking legs. The prothorax is directly related with prey capture comprising a slender mobile "neck" for the large, square, flattened head, which bears an enormous pair of sickle-like mandibles (Griffiths 1980; Lucas 1989; Beponis et al. 2014; Franks et al. 2019). Antlion larvae are sit-and-wait predators that build conical pits in dry sand or loose soil to prey capture such as ants and other small insects. The digging activity includes backward movements that are accompanied by periodic sand-tossing behavior through rapid jerks of the head and mandibles (Lucas 1982; see https://www.youtube.com/watch?v=CWkfAyfBDHE). When the larva finishes building the pit, it rests at the bottom of it, waiting for a prey to fall in. When an ant or other prey falls into the pit, the antlion grabs the prey with its long piercing mandibles and sucks out the body fluids before discarding the body outside the pit. If the larva fails at capturing the prey on its first attempt, or if the prey attempts to climb out of the pit, the antlion tosses sand with violent flicks of its head. This causes small landslides carrying the victim back to the antlion's mandibles (McClure 1976; see https://www.youtube.com/watch?v=oUW05J5GYnw). Hence, the prothorax (neck, head, and mandibles) is the body part directly related to prey capture, because – as explained – it is used during pit building, prey capture, and re-capture, and pit cleaning.

Our objective was to indirectly determine the existence of changes in the relative importance of prey capture through larval ontogeny using scaling relationships between the sizes of body parts that differ in their role in food acquisition (prothorax versus thorax + abdomen). If prey capture is equally relevant among instars, we expect that the size of these body parts changes at a similar rate (i.e., isometric scaling, $ß = 1$). Conversely, a negative allometry (i.e., $ß < 1$) will indicate that the body parts involved in prey capture grow more slowly than the rest of the body, and if so, prothorax would be proportionally smaller in the last than in the first's larval instar. Therefore, we expect this result if prey capture is more relevant during the first stages (i.e., the growth hypothesis). On the other hand, we expect a positive allometry (i.e., $ß > 1$) if prey capture is more important in the last larval instars (i.e., the pupation hypothesis) because this result will reflect that the body part involved in prey capture grows faster than the rest of the body, and thus, it is proportionally larger in the last larval stages allowing more and better prey capture.

MATERIALS AND METHODS

We conducted this study at La Selva Biological Station of the Organization for Tropical Studies (10°26′N, 83°59′W) in the Atlantic lowlands of Costa Rica, between January and February 2020 (dry season). The area is a tropical lowland wet forest that receives a mean annual rainfall of 4,000 mm (see McDade et al. 1994, for a full description). In this habitat, the most abundant antlion species, *Myrmeleon crudelis*, is very abundant in bare soils underneath roofs of the station buildings, where they are protected from rain and leaf litter (McClure 1976; Farji-Brener & Amador-Vargas 2020). We collected 70 larvae of *M. crudelis* of different sizes in different locations within the study site. Each larva was freeze and then measured at the scale of mm in the laboratory using digital photos, taking into account the body parts explained above (Fig. 1). We use the body length instead of body mass, because body length allows discriminating better among larval instars (Alcalay et al. 2014). To test whether the relative importance of prey capture changes through larval ontogeny, we determined scaling relationships between the size of prothorax versus the thorax + abdomen, from a linear regression analysis of log-transformed variables. We used ordinary least squares (OLS) instead of reduced major axis (RMA) regression because OLS regression is better suited to test for allometric relationships (Kilmer & Rodriguez 2017). Slope coefficients and their 95% CIs were determined (based on Gaussian errors) and compared with the predicted values under the assumption of isometric scaling, that is, that the size of parts change at the same rate ($ß = 1$ for linear vs linear measures).

RESULTS AND DISCUSSION

Larval size (total) ranged from 3.5 to 16.7 mm. The prothorax ranged from 1.6 to 6.8 mm, and abdomen + thorax ranged from 2 to 10 mm. The size of the prothorax of the larvae increased as the abdomen + thorax size increased, but at rates below those expected by isometry [i.e., with a slope < 1; $ß = 0.8$, (0.6–0.9), 95% confidence limits, $F_{2,\ 68} = 107.1$, $R^2 = 0.61$, $P < 0.001$, Fig. 2]. Moreover, in larvae smaller than 6 mm, the prothorax represented 50(± 4)% of its body length, but in larvae larger than 12 mm it represented only 42(± 1)% (Fig. 3).

Scaling relationships may reflect how biological form is shaped by ecological trade-offs (West et al. 1997). We found that the body section of antlion larva directly related in prey capture increases as the rest of its body increases, but at rates lower than expected by isometry. In accordance, this body part is proportionally larger in the first than in the last larval instars, suggesting a greater relative importance of prey capture in the first larval stages. These results support the growth hypothesis, which states that food acquisition is key in the earlier stages of larval development.

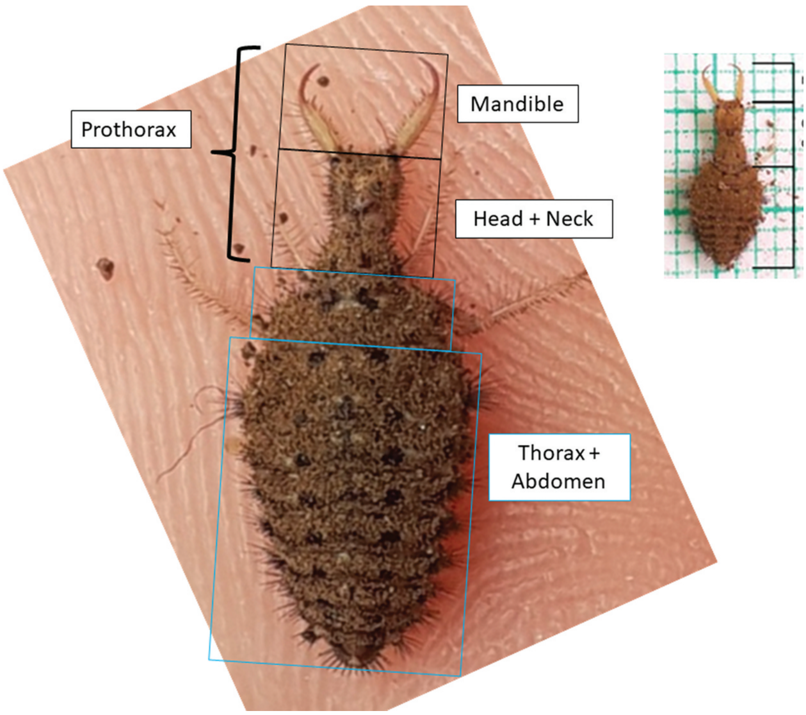

Fig. 1. — Body parts of measured antlion larvae to determine scaling relationships between the size of body parts directly related and unrelated to prey capture (prothorax and thorax + abdomen, respectively). The prothorax (neck, head and mandibles), is used in the pit building, prey capture and recapture, and pit cleaning. Larvae were obtained in the field, freeze and then measured using digital photos.

A number of reasons support the idea that first instars of antlion larvae can be more food-limited than later instars. First, small larvae build small pit-traps in where only very small arthropods can fall (Griffiths 1980; Alcalay et al. 2014; A.G. Farji-Brener personal obs.). Therefore, a large portion of potential prey never falls into the pit-traps of first larval stages. Second, the small mandibles and the relatively lower grab force of the first instar larvae increase the probability that prey escape after falling into the trap (Lomáscolo & Farji-Brener 2001). Finally, first instar larvae have less fat reserves than later instars, and thus often cannot resist long periods of starvation. Conversely, larvae of the latter instars build larger pits, respond faster to prey, capture larger preys and show an enhanced capacity to recapture prey, consume higher proportions of the captured prey, and have more fat reserves than larvae from the first instar stages (Griffiths 1980; Lomáscolo & Farji-Brener 2001; Farji-Brener 2003; Scharf et al. 2009a; Alcalay et al. 2014). Despite that the quantity of food needed for a small larva is obviously less than for a big one, all these reasons support the idea that first instars have relatively higher food restrictions than the last stages.

This study has limitations, but it also has strengths. The main limitation is the absence of experimental evidence supporting that first larval instars are more food-

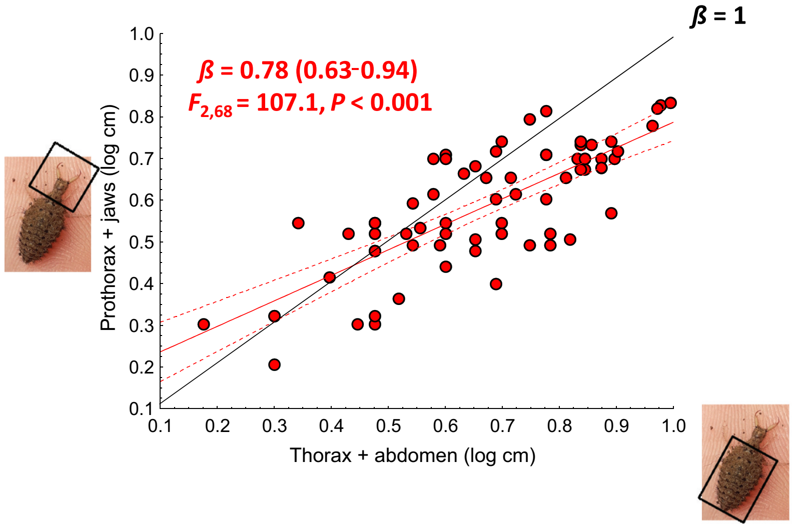

Fig. 2. — Scaling relationship between the length of body parts directly involved in prey capture (prothorax) and the body parts that are not directly involved (thorax + abdomen, in mm) all axes are log-transformed. Confidence limits (95%) are shown. The black line represents the expected slope under isometry (β = 1 for linear vs linear).

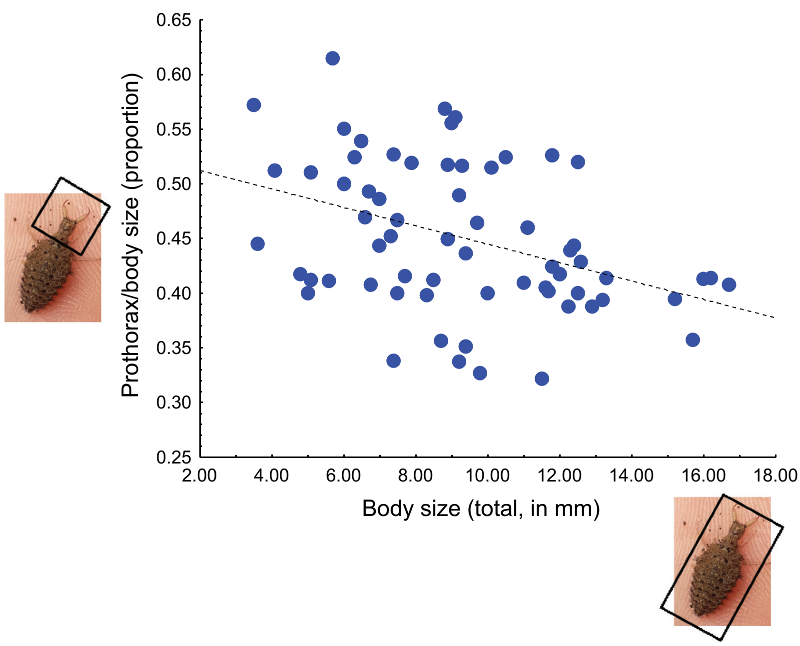

Fig. 3. — A description of how the relative proportion of prothorax/thorax + abdomen decreases as total body size increases.

limited than the latter larval stage. Experiments that measure the effects of food deprivation in first and third larval instars are needed to support the evidence found in this work. However, other works through experimental and observational evidence also support the idea that first larval instars are strongly food-limited (Griffiths 1980; Lomáscolo & Farji-Brener 2001; Arnett & Gotelli 2003; Scharf et al. 2009a; Alcalay et al. 2014). Second, the fact that smaller larvae have relatively large heads and mandibles may be consequence of other reasons aside from a stronger food limitation in first instars. For example, the efficiency of the feeding apparatus may change non-linearly as size increases, so the marginal gains from increasing the size of the feeding apparatus might be smaller for bigger animals than smaller ones. Alternatively, bearing large mandibles might be costly for large larvae for reasons not related with foraging. Finally, the body proportions may change just for ontogenetic reasons as, for example, gonads (surely found in the thorax and abdomen) might be more developed in the later stages as larvae approach adulthood. These alternative hypotheses deserve more study. Despite these potential limitations, the pattern we found (i.e., that the size of body part related with pit building and prey capture was proportionally larger in the first than in the last instars) come from a large sampling effort, which covers enough variation in larval size in order to detect reliable scaled relationships. Finally, with the use of relatively easy measurements, we were able to detect temporal patterns in antlion larvae which are difficult to perceive in short time periods, such as changes in the growth of body segments involved in different ecological roles.

Several studies on insect development detected that the relevance in food acquisition may change along larval ontogeny, and evidence supports both, the growth and the pupation hypotheses (Stockhoff 1993; Shafiei et al. 2001). Our results that the body part related to prey capture is proportionally larger in smaller larvae than in larger ones, together with previous comparative and experimental evidence (Griffiths 1991, 1993) suggest that, in antlion larvae, earlier larval stages are more restricted by food than last larval stages. However, studies in other pit-building and non-pit building antlion species showed the opposite pattern: the relative size of the head + mandibles increases relatively more than the abdomen with development (Scharf et al. 2008a, 2009b). These contradictory results suggest that we need more comparison among antlion species with different life history to better understand how and why food limitation might change among larval instars. Our results illustrate the relevance of using scaling relationships to better understand how ecological pressures change along ontogeny, emphasizing the role of food acquisition at earlier ontogenetic stages.

ACKNOWLEDGEMENTS

We thank the Organization for Tropical Studies (OTS) for logistic support. We thank to five anonymous reviewers for helpful comments on an earlier version of this article.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

FUNDING

The Organization for Tropical Studies partially funded this work via logistic support.

AUTHOR CONTRIBUTIONS

A.G. Farji-Brener conceived the ideas, designed the methodology, analyzed the data, and led the writing of the manuscript. All authors collected the data, contributed critically to the drafts and approved the final manuscript.

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