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ORIGINAL RESEARCH ARTICLE

Foraging behavior plasticity in antlion larvae *Myrmeleon brasiliensis* (Neuroptera, Myrmeleontidae)

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Abstract

The biotic and abiotic factors of an ecosystem exert an influence on the behavior and survival of organisms, which adapt to changes in these factors to ensure their reproduction and survival. Phenotypic plasticity regards any type of change induced by the environment without the need for genetic modifications. The aim of the present study was to evaluate whether the investment of the antlion, *Myrmeleon brasiliensis* (Neuroptera, Myrmeleontidae) in trap building is a phenotypic response that changes according to the surrounding environment. Larvae were observed in their natural environment (control), in a simulated natural environment (below tents) and after being transplanted to the laboratory. We found that the investment in trap size is a plastic phenotypic response in *M. brasiliensis* larvae and this behavior varies in accordance with the location in which the larvae build their traps. In areas with protection for the traps, greater investment was made in the size of the trap and consequently increased the success in capturing prey.

Keywords Mirmeleontini · Phenotype · Sit-and-wait predators · Trap

Introduction

The biotic and abiotic factors of an ecosystem exert an influence on the behavior and survival of living beings. It is important to understand how organisms adapt to changes in these factors to ensure their reproduction and survival (Farji-Brener 2003; Lima and Faria, 2007). Therefore, it is also important to understand the relations between adaptive and non-adaptive phenotypic plasticity (Hoffman et al. 2001; Klokocovnik et al. 2015).

Phenotypic plasticity regards any type of change induced by the environment without the need for genetic modifications (Scheiner 1993; Via et al. 1995). Plastic responses are not always adaptive, but phenotypic plasticity can be adaptive if it is a mechanism through which relative fitness is maintained in response to a variable and involves morphological, physiological or behavioral responses (Klokocovnik et al. 2012; Thompson 1991).

For organisms that exhibit less mobility, changes in the environment exert a more direct influence on their mode of life. Sit-and-wait predators are considerably more affected by changes in the environment compared to active organisms (Lima and Lopes 2016; Orians 1991; Scharf et al. 2011). An example are antlion larvae, sit-and-wait predators, which builds cone-shaped traps in dry sandy soils and remains buried awaiting a prey, such as small arthropods that move over the surface of the soil and fall into the traps (Franks et al. 2019; Lima and Faria 2007).

The occurrence of antlion larvae is the result of laying eggs by female, soil temperature, protection for the traps, density and the distribution of food sources (Freire and Lima 2019; Gotelli 1993; Morrison 2004; Ngamo et al. 2016). In present study, we investigate whether the investment in trap building is a plastic phenotypic response that varies according to the surrounding environment. For such, the following hypotheses were tested: 1) antlion larvae *Myrmeleon brasiliensis* (Neuroptera, Myrmeleontidae) in environments with greater protection invest more in trap size; and 2) antlion larvae *M. brasiliensis* in environments with greater protection have greater success capturing prey.

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Materials and methods

The first part of the study was conducted in a Permanent Protection Area (800 ha) of Brazilian biome *Cerrado*, located in the municipality of Aquidauana, MS, Brazil (20°26′06″S, 55°39′35″W). The annual mean temperature and rainfall are approximately 26 ºC and 1250 mm, respectively.

Mapping was performed in an area of a nature reserve to determine distribution of *Myrmeleon brasiliensis* larvae (Návas 1914) (Neuroptera, Myrmeleontidae). After the determination of the distribution of the larvae, two canvas tents with a bamboo frame were assembled measuring 3 m in length × 1.5 m in width × 4 m in height. These tents were used to simulate protected environment under which the antlion larvae could build the traps protected from the rain, leaves and other falling vegetal matter. The litter and superficial soil (3 cm depth) were removed from the area under the tents, leaving only the exposed sandy soil without any antlion.

The study was initiated six months after the installment of the tents. For such, we measured the diameter of the traps of 50 larvae that were under the tents (simulated natural environment) and another 50 that were in a natural environment in the area surrounding the tents (control). After measuring the traps, the larvae were transplanted individually in plastic bags with a little sand from the place. In the laboratory, body size (head-abdomen) was measured and the larvae were placed individually in plastic pots measuring 20 × 10 cm containing sand from the collection site. After 24 h (in the laboratory), the diameter of the traps was measured again. Paired t-tests were performed to compare the investment in the size of the sampled traps: in the tents (simulated environment) x in the laboratory and outside the tents (natural environment) x laboratory.

Antlion larvae were observed in the natural environment of the reserve (control) and under the tents (simulated) to assess prey capture. Fifty larvae were observed in each environment (under the tent and natural environment). The diameter of each trap was measured and each larva was then observed for 30 min. The number of prey captured and size of the prey (head-abdomen) were recorded. For such, the predation behavior was observed until the death of the prey, which was then removed from the trap (with a forceps) and measured. After, the antlion larvae were collected and body size (head-abdomen) was measured. The capture success in the two environments was compared using the X^2 test. The relation between prey size, larva size and trap size was evaluated using linear regression. All measurements were made with a digital caliper (0.01 mm). The normality of the data was tested with the Kolmogorov Smirnov test. Analyses were performed in MyStat software program. Voucher specimens were placed in the Zoological Collection of the Universidade Federal de Mato Grosso do Sul (ZUFMS) at Campo Grande-MS.

Results

An increase in trap size after translocation to the laboratory was found for both the larvae collected from the natural environment (control) ($t = -7.81$; $p = 0.03$) (Fig. 1) and those collected from under the tents (simulated natural environment) ($t = -2.13$; $p = 0.03$) (Fig. 2). Mean trap size (± standard deviation) for larvae in the natural environment was 21.76 (± 12,89) mm and increased to 36.39 (± 15,81) mm after being translocated to the laboratory. Mean trap size for larvae under the tents was 26.87 (± mm 12,89) and increased to 29.76 (± 11,77) mm in the laboratory.

The success of capturing prey items was greater in the simulated environment (under the tents). The capture rate was 90% among the larvae under the tents and 66% among those in the natural environment ($X^2 = 8.39$; $p = 0.00$). Significantly positive relations were also found between trap size and prey size as well as between larva size and prey size in both environments (Table 1).

All prey caught were ants (Hymenoptera), with a mean body size of 3.20 mm and 3.45 mm in the simulated and natural environments, respectively. Regarding non-captured prey, potential prey items fell into the traps the majority

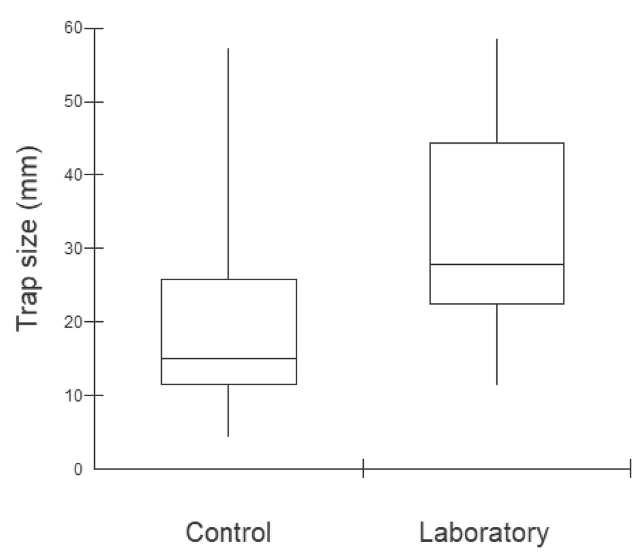

Fig. 1 Trap size (mean ± standard deviation) of *M. brasiliensis* larvae in natural environment (control) and after being translocated in the laboratory

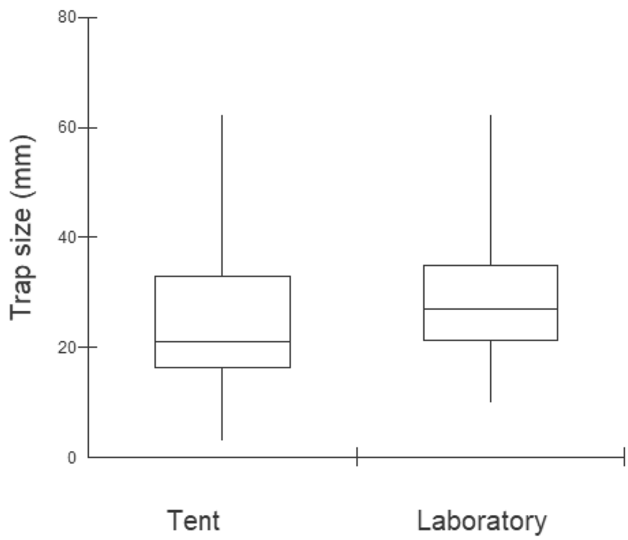

Fig. 2 Trap size (mean ± standard deviation) of *M. brasiliensis* larvae in simulated natural environment (under the tents) and after being translocated in the laboratory

of times, but not all *M. brasiliensis* larvae invested in the capture. Moreover, smaller larvae only consumed smaller prey items, whereas larger larvae consumed prey items of all sizes.

Discussion

We found that the investment in trap building by *M. brasiliensis* larvae is a plastic phenotypic response that varies in accordance with the environmental factors. We also found that this behavior affects the success rate in capturing prey. The expression of a behavior is influenced by intrinsic factors (e.g., dispersal capacity) and extrinsic factors (e.g., the availability of resources). In turn, both types of factors are influenced by the patterns of a habitat or patch within an ecosystem (Yahner and Mahan 2002). When the characteristics of the environment change, the behavior of organisms is modified. Thus, the attributes of the phenotype related to behavior are those that respond more quickly to changes in the environment (Relyea 2003; Briffa et al. 2008).

For trap-building animals, the construction characteristics of their traps are likely among the first behavioral variables to be affected. As trap building involves high energy expenditure (Harwood et al. 2003; Lucas 1985; Miyashita 2005), changes in the abundance of prey items or environmental disturbance to the trap can affect the investment of predators in the building and maintenance of these traps. When the antlion larvae were taken to the laboratory, both those from the natural environment and those that were under the tents built larger traps, which enables the inference that the investment in trap size is guided by the characteristics of the surrounding environment.

Table 1 Relations between size of *M. brasiliensis* larvae, trap size and size of prey items captured in natural environment (control) and simulated natural environment (tents)

	Larvae size		Trap size	
Environment	r^2	P	r^2	P
Natural	0.17	0.00	0.33	0.00
Simulated	0.18	0.00	0.14	0.01

The positive relation between trap size and capture success has been demonstrated in several studies (e.g., Day and Zalucki 2000; Faria et al. 1994; Griffths 1980, 1986; Lima and Faria 2007). However, we demonstrate here that *M. brasiliensis* larvae that build traps in protected environments invest more in trap size and therefore obtain greater success in capturing prey. For many authors (e.g., Lucas 1982; Mansell 1996, 1999; Fertin and Casas 2006; Mencinger-Vracko and Devetak 2008), antlion larvae build perfect traps for capturing prey, as the architecture of the trap in sandy soil sends the prey item directly to the larva. However, differences in the size of traps built by the same individual can affect the quantity and size of the prey captured. Experiments involving *Myrmeleon* sp. have shown that traps with diameters approximately eightfold larger than the size of the prey reduce its probability of escape by 50% (Dias et al. 2006).

Larvae accelerate their development to ensure greater success in capturing prey and can consequently invest more in body size. In many insect orders, the size of the adult has a strong genetic component that determines growth. For others, however, the size of the adult depends on the size of the larva and its nutritional quality (Boggs and Freeman 2005; Kolss et al. 2009). Thus, antlions whose traps were destroyed have less growth and consequently become smaller adults, which could affect their success at capturing prey as well as their reproductive success, since insect size tends to be related to the fecundity of females (Honek 1993; Sokolovska et al. 2000).

An increase in the size of *M. brasiliensis* larvae (and their traps) enables an increase in the size range of the prey. Larger larvae capture both small and large prey items. For example, larvae with trap diameters larger than 40 mm were observed capturing prey ranging in size from 2.12 to 4.92 mm. We also observed that when the prey was considerably large in relation to the size of the trap, the larvae often did not invest in its capture. The fact that antlion larvae mainly capture ants is common in the majority of environments – not *par excellence*, but due to their greater abundance (Elimelech and Pinshow 2008).

Antlion larvae perceive the presence of prey at a distance of few centimeters through vibrations in the soil due to its movements (Devetak et al. 2007; Mencinger-Vracko and Devetak 2008). Thus, the larva perceives the prey even before it falls into the trap. It is possible that this characteristic of detecting prey keep smaller larvae from investing in the capture of larger prey items. Organisms obtain information regarding the success of predation based on past foraging experiences (Guillette et al. 2009) and tend to adjust their behavior accordingly to obtain a larger energy return. Thus, upon perceiving that certain prey items cannot be captured, the antlion larvae simply do not attack and therefore save energy.

Interestingly, the greater success in capturing prey in a wider size range meant that larger *M. brasiliensis* larvae were less exposed to variations in the abundance of the sizes of prey items in the natural environment. This fact is important, as the capture rate by antlion larvae is low in the natural environment (Hauber 1999). The capacity to capture the entire variety of available prey enables larger larvae to ensure greater capturing success and consequently accelerate their development. This does not happen among larvae at the beginning of their development, which depend exclusively on the supply of small prey to be able to complete their larval development.

In conclusion, the investment in trap size is a plastic phenotypic response in *M. brasiliensis* larvae, as this behavior varies in accordance with the surrounding environment. Moreover, the choice of *M. brasiliensis* larvae regarding the size of the traps affects their success rate in capturing prey items, which is one of the most important variables of its foraging.

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