Acta Scientiarum

http://periodicos.uem.br/ojs/acta
ISSN on-line: 1807-863X
Doi: 10.4025/actascibiolsci.v41i1.45871

ZOOLOGY

Effect of asymmetric competition on distance among *Myrmeleon brasiliensis* (Návas, 1914) (Neuroptera: Myrmeleontidae) larvae

Tatiane do Nascimento Lima*, **Luciane Gomes Freire and Dariany Cristina Aristides de Lima**

Laboratório de Estudos da Biodiversidade, Universidade Federal de Mato Grosso do Sul, Rua Oscar Trindade de Barros, 740, 79200-000, Aquidauana, Mato Grosso do Sul, Brazil. *Author for correspondence. E-mail: tatianenlima@gmail.com

ABSTRACT. In cases of asymmetric competition, larger individuals of many animal species have a greater probability of acquiring territory, gaining initial access to resources and finding a mate in comparison to smaller individuals. The competition among larvae of the antlion *Myrmeleon brasiliensis* (Neuroptera, Myrmeleontidae) is observed in the search for space for the construction of traps, in the forage for prey, and in the occurrence of cannibalism. The body size of the larvae is proportional to the size of the traps and the success of predation. Thus, larger specimens are better competitors in terms of capturing preys (asymmetric competition). The aim of the present study was to determine the effects of asymmetric competition in *M. brasiliensis* regarding the distance among these larvae. The study was developed in a permanent reserve area, located in the municipality of Aquidauana, from the Mato Grosso do Sul state, Brazil. For the laboratory experiments, we collected *M. brasiliensis* larvae and placed two larvae in plastic pots. The observations occurred by the visual search of traps, when a larva was seen in the diameter of its trap and the trap of its closest neighbor. Next, the trap size and the distance between them were measured for a period of 15 days. The results of the present study demonstrate that the largest *M. brasiliensis* larvae were outside the clusters. Within these clusters, the larvae moved away from each other because of the size of their traps, as the larger the neighboring larvae the greater the distance between them. Thus, the asymmetric competition between *M. brasiliensis* (larger larvae are better competitors) suggests a spatial arrangement among the larvae that is guided by the variable size of the trap.

Keywords: antlion; foraging; intra-specific competition; traps.

Received on December 14, 2018.
Accepted on April 2, 2019.

Introduction

Individuals of the same species have similar requirements in terms of growth, reproduction and survival, which generates competition when the demand for resources exceeds the immediate supply (Nicholson, 1954; Varley, Gradwell, & Hassell, 1973; Hassell, 1975; Young, 2004; Pfennig & Pfennig, 2012). Thus, a specific characteristic, such as the size of the individual, can represent a competitive advantage. In this type of interaction, which is denominated as asymmetric competition, larger individuals of many species have a greater probability of acquiring territory, gaining initial access to resources and finding a mate in comparison to smaller individuals (Polis, 1980; Lawton & Hassell, 1981; Prado, Bede, & Faria, 1993).

Larval forms of antlions (Neuroptera, Myrmeleontidae) are sit-and-wait predators that built traps in sandy soil to capture their prey (Nonato & Lima, 2011). Competition among antlion larvae is seen in the quest for space to build their traps, in the search for prey and in the occurrence of cannibalism (Lima, 2016). To minimize the effects of competition, the larvae demonstrate spatial distribution that ranges from random to uniform, depending on the need to increase the density of the groups (Lima & Faria, 2007). Moreover, a minimum distance between larvae is maintained to diminish the effects of the sand particles tossed by neighboring larvae during the maintenance of the pit (Simberloff, King, Dillon, Lowrie, Lorence, & Schilling, 1978; Lima, 1998).

Wilson (1974) proposes that larvae are distributed in such a manner to maximize the effectiveness of catching prey items and reducing intraspecific competition. In experiments involving an artificial increase in density, McClure (1976) found a spatial distribution pattern with a clear tendency toward uniformity, which is believed to minimize competition. According to Simberloff et al. (1978), the sediment tossing into neighboring pits is a preponderant factor in the population dynamics, leading to the moving of a pit to a different location, which could increase the probability of cannibalism occurrence of, as larvae may fall into the trap of the neighboring larva. However, the effect of asymmetric competition among larvae with traps of different sizes on the distribution of antlion larvae pits has not previously been investigated.

The body size of the *Myrmeleon brasiliensis* larvae is proportional to the size of the traps and predation success (Missirian, Uchôa-Fernandes, & Fischer, 2006). Thus, larger individuals are better competitors regarding the capture of preys (asymmetric competition). The hypothesis raised in this study is that, in order to avoid the effects of asymmetric competition, smaller larvae must maintain distance from larger individuals. The aim of the present study was to determine the effects of asymmetric competition among *M. brasiliensis* on the distance between the larvae. The following parameters were investigated: 1) the effect of the size of the neighboring trap on the distance between larvae and 2) the size of larvae found within and outside of the groups. Laboratory experiments were also conducted to evaluate 3) the effect of the neighboring trap size on the distance between larvae.

Material and methods

Larvae of the antlion *M. brasiliensis* were studied and collected in a permanent reserve area (1.600.000 m^2) of the *Universidade Estadual de Mato Grosso do Sul*, located in the municipality of Aquidauana in the state of Mato Grosso do Sul, Brazil (20°26'06"S 55°39'35"W), where annual mean temperature and rainfall is approximately 26ºC and 1250 mm, respectively. The observations took place between August 2016 and January 2017. The area is characterized by vegetation of the savannah-like biome denominated *Cerrado* (Fina & Monteiro, 2013). The sandy soil is favorable to the construction of pits by the larvae (Lima & Faria, 2007).

The sampling method involved a visual search for *M. brasiliensis* traps along a trail, which measured approximately six km in length and approximately two meters in width. When a larva was sighted, we measured the diameter of its trap and the trap of its closest neighbor as well as the distance between traps (center to center). The larvae of *M. brasiliensis* that did not have a neighboring larva within a radius of 30 cm were considered isolated (outside of a group). The measurements were taken with the aid of digital calipers with a resolution of 0.01 mm.

For the laboratory experiments, *M. brasiliensis* larvae were collected with the aid of a spoon along with sand from the collection site. After that, we placed them in plastic bags and took to the Laboratory of Biodiversity Studies of *Universidade Estadual de Mato Grosso do Sul*, Aquidauana campus. In the lab, the body length (head-abdomen) and head capsule size were measured with the aid of digital calipers. The larvae were sorted and placed in plastic pots (15 x 10 cm) containing sand (500 gr) from the collection site. Two larvae were randomly selected for each plastic pot. Nineteen replicates were mounted, totaling 38 larvae. After placement in the plastic pots, the larvae were left for 24 hours to construct their traps. Next, the trap size and the distance between traps were measured for a period of 15 days.

To evaluate the effect of the neighboring traps size on the distance between larvae observed in the forest reserve and in the simulated experiment, the sum of the trap diameters was calculated (independent variable) and compared with the distance between larvae (dependent variable) by means of linear regression analysis. The Mann-Whitney test was used to evaluate the trap size (dependent variable) of *M. brasiliensis* larvae found within and outside groups (independent variable). Repeated-measures analyses of variance (ANOVA) were used to compare the distancing pattern (dependent variable) among *M. brasiliensis* larvae over time (independent variable) in the laboratory. All statistical analyses were conducted with the aid of the BioEstat 5.3 free software (Ayres et al. 2007).

Results

In the forest reserve, 93 *M. brasiliensis* larvae were sampled, of which 54 were grouped and 39 were isolated (no presence of other larvae in a 30-cm radius). The trap diameter was 29.35 ± 13.22 mm (mean ± standard deviation) among grouped larvae and 35.56 ± 4.89 mm among isolated larvae (n = 26). Thus, trap size was significantly larger among isolated larvae than those in groups (U = 742; n1 = 39; n2 = 54; p = 0.0155) (Figure 1).

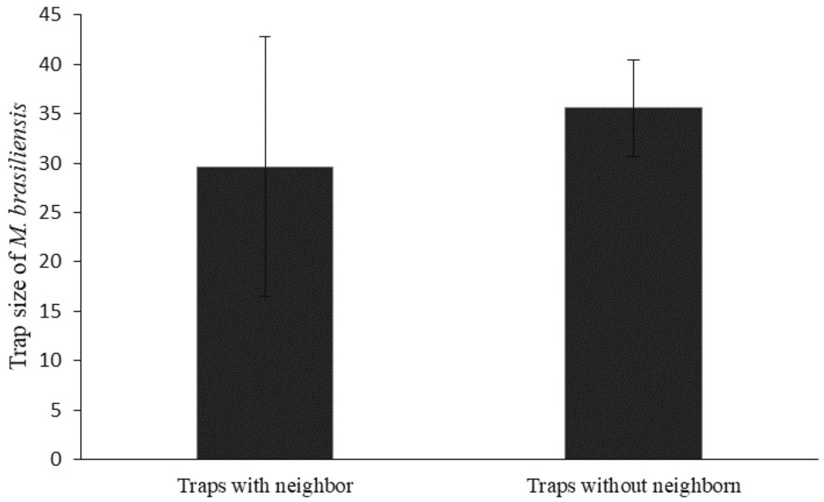

Figure 1. Trap size (mm) (mean ± sd) of grouped (with neighbor) and isolated (without neighbor) *Myrmeleon brasiliensis* larvae (U = 742; n1 = 39; n2 = 54; p = 0.0155).

The mean distance between the grouped *M. brasiliensis* larvae was 90.16 ± 60.24 mm. The high standard deviation demonstrates that some larvae were very close to one another (minimum distance: 29.93 mm), and others were quite distant from one another (maximum distance: 275 mm). The relationship between the sum of the trap diameters and the distance between neighboring larvae demonstrated greater distance between larger neighboring larvae ($r^2 = 0.26$; p = 0.0007; n = 44) (Figure 2).

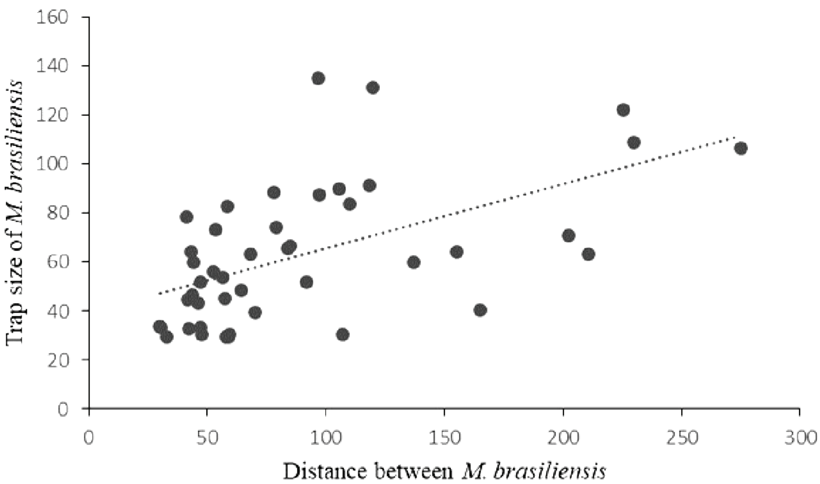

Figure 2. Relationship between the size of the neighboring trap (mm) and the distance (mm) between the *Myrmeleon brasiliensis* larvae ($r^2 = 0.26$; p = 0.0007; n = 44).

Among the larvae taken to the laboratory, the mean body size was 5.4 ± 1.76 mm; the mean head capsule size was 1.5 ± 0.34 mm and the mean trap size was 32.38 ± 9.55 mm. Although an increase in the size of neighboring larvae led to greater distancing between traps, no significant change in the distance between traps was found over time. The mean distance between the larvae was 61.42 ± 13.29 mm on the first day and 65.96 ± 22.32 mm on the last day of the experiment (F = 0.97; GL = 2; p = 0.39).

Discussion

The data of the present study demonstrate that, with an increase the trap size, a greater distance occurs between the larvae of *M. brasiliensis*. Thus, it is observed that larger larvae are more isolated, whereas smaller larvae are observed in groups. The larvae of *M. brasiliensis* are grouped according to the reflex of the oviposition behavior of adult females and the heterogeneous distribution of suitable areas for the construction of traps (Lima & Faria, 2007; Lima & Lopes, 2016). However, with the development of the larvae, there is a greater distance among these organisms. For a small larva, remaining close to large larvae may represent less access to resources, since larger larvae are better competitors (asymmetric competition) (Nonato & Lima, 2011). Thus, the competition among *M. brasiliensis* may be generating a spatial distribution design that is guided by the size of the trap.

The distancing among antlion larvae may be a response to the trap building behavior and predation. During these processes, *M. brasiliensis* expels sand particles from the trap, which could end up destroying a neighboring trap, and leading to an energy expenditure on the part of the neighboring larva for the reconstruction of the damaged trap (Day & Zalucki, 2000; Nonato & Lima, 2011). Experiments conducted with *Myrmeleon acer* demonstrate that the minimum distance between larvae under conditions of high density was similar to the distance that the grains of sand reached during the construction of the pits (30 mm) (Day & Zalucki, 2000). In the present study, the minimum distance between *M. brasiliensis* larvae was 29.30 mm in the natural environment and 35.28 mm in the laboratory.

With the increase in trap size, which reflects the progression of larval instars, *M. brasiliensis* larvae were observed outside of groups (no presence of neighboring larvae within a 30-cm radius). Larvae that remain in groups are subject to competition for prey items, the destruction of their traps by neighboring larvae and cannibalism (Gotelli, 1993; Day & Zalucki, 2000; Lima, 2016). Isolated larvae avoid these problems, but at the cost of moving to a different location and reconstructing the trap (Lucas 1985; Lima & Silva, 2017). Thus, there must be a competitive advantage for larger larvae to forage farther from other *M. brasiliensis* larvae. For example, ants, which are the main food source for antlion larvae, avoid foraging near trap sites (Hollis, 2016). Thus, the relocation far from groups may minimize the effects of competition and maximize the capture of prey items.

Temperature is another factor that allows larger larvae to migrate outside groups. Larger antlion larvae are capable of withstanding hotter locations (Lucas, 1985; Fisher, 1989). Faria, Prado, Bede, and Fernandes (1994) found that the mean size of traps located in open areas was significantly greater than that of traps located in areas protected from direct sunlight. In the present study, grouped *M. brasiliensis* larvae were under the protection of the leaflets and fallen tree trunks, whereas larvae with larger traps were found in open areas exposed to direct sunlight.

Larger body size among larvae of *M. brasiliensis* leads to a higher probability of cannibalism. This is expected, since the success of predation is related to the increase in trap size, because larger individuals build larger traps (Lima & Faria, 2007). To minimize the effects of cannibalism, larvae distance themselves from each other, and this distancing increases with the increase of body size. Larger individuals are generally more voracious cannibals than smaller individuals. Consequently, smaller larvae are often eaten by larger individuals (Polis, 1980; Lima, 2016). The presence of cannibals may induce smaller conspecifics to avoid foraging in areas near large individuals (Persson & Eklov, 1995; Biro, Post, & Parkinson, 2003; Rudolf, 2006). Moreover, cannibalism structured by predator size exerts a strong influence on the dynamics of the population and community (Claessen, Roos, & Persson, 2000).

The effects of asymmetric interactions on population dynamics have been widely investigated. Bassar, Childs, Rees, Tuljapurkar, Reznick, and Coulson (2016) demonstrated that the difference in fish body length among the interacting individuals influences the outcome of competition. Cameron, Wearing, Rohani, and Sait (2007) noted that the intraspecific competition between large and small larvae of insects is asymmetric, with large larvae reducing the survival rate of small larvae rather than vice versa. It is interesting to note that, in all studies, as in the present study, intra- and interspecific competition was asymmetric, with large individuals dominating the interactions.

Conclusion

The results of the present study demonstrate that the largest *M. brasiliensis* larvae were outside the clusters. Within these clusters, the larvae move away from each other due to the size of their traps, as the larger the neighboring larvae the greater the distance among them. Thus, the asymmetric competition among *M. brasiliensis* (larger larvae are better competitors) suggests a spatial arrangement among the larvae that is guided by the variable size of the trap.

References

Ayres, M., Ayres, J. M., Ayres, D. L., & Santos, A. A. (2007). *Bioestat: Aplicações Estatísticas nas Áreas das Ciências Biológicas*. Belém, PA: Ong Mamiraua Brazil.

Biro, P. A., Post, JR., & Parkinson, E. A. (2003). From individuals to populations: Prey fish risk-taking mediates mortality in whole-system experiments. *Ecology, 84*(9), 2419-2431. doi: 10.1890/02-0416

Bassar, R. D., Childs, D. Z., Rees, M., Tuljapurkar, S., Reznick, D. N., & Coulson, T. (2016). The effects of asymmetric competition on the life history of Trinidadian guppies. *Ecology Letters, 19*(3), 268-278. doi: 10.1111/ele.12563

Claessen, D., Roos, A. M., & Persson, L. (2000). Dwarfs and giants: cannibalism and competition in size-structured populations. *American Naturalist, 155*(2), 219-237. doi: 10.1086/303315.

Cameron, T. C., Wearing, H. J., Rohani, P., & Sait, S. M. 2007. Two-species asymmetric competition: effects of age structure on intra- and interspecific interactions. *Journal of Animal Ecology, 76*(1), 83-93. doi: 10.1111/j.1365-2656.2006.01185.x

Day, M. D., & Zalucki, M. P. (2000). Effect of density on spatial distribution, pit formation and pit diameter of *Myrmeleon acer* Walker, (Neuroptera: Myrmeleontidae): patterns and processes. *Austral Ecology, 25*(1), 58-64. doi: 10.1046/j.1442-9993.2000.01032.x

Fisher, M. (1989). Ant-Iion life cycles in Nigeria. *Journal of Tropical Ecology, 5*(2), 247-250. doi: 10.1017/S0266467400003552

Faria, M. L., Prado, P. I. L., Bede, L. C., & Fernandes, G. W. (1994). Estrutura e dinâmica de uma população de larvas de *Myrmeleon uniformis* (Neuroptera: Myrmeleontidae). *Brazilian Journal Biology, 54*(2), 335-344.

Fina, B. G., & Monteiro, R. 2013. Análise da estrutura arbustivo-arbórea de uma área de Cerrado *Sensu Stricto*, município de Aquidauana – Mato Grosso do Sul. *Revista Árvore, 37*(4), 577-585. doi: 10.1590/S0100-67622013000400001

Gotelli, N. J. (1993). Ant Lion zones: causes of high-density predator aggregations. *Ecology, 74*(1), 226-237. doi: 10.2307/1939517

Hassell, M. P. (1975). Density-dependence in single-species populations. *Journal Animal Ecology, 44*(1), 283-295. doi: 10.2307/3863

Hollis, K. L. (2016). Ants and antlions: the impact of ecology, coevolution and learning on an insect predator-prey relationship. *Behavioural Processes, 139*(1), 4-11. doi: 10.1016/j.beproc.2016.12.002

Lawton, J. H., & Hassell, M. P. (1981). Asymmetrical competition in insects. *Nature, 289*(1), 793-795. doi: 10.1038/289793a0

Lucas, J. R. (1985). Metabolic rates and pit-constructions costs of two antlion species. *Journal Animal Ecology, 54*(1), 295-309. doi: 10.2307/4639

Lima, T. L., & Faria, R. R. (2007). Seleção de microhabitat por larvas de formiga leão *Myrmeleon brasiliensis* (Návas) (Neuroptera: Myrmeleontidae), em uma reserva florestal, Aquidauana, MS. *Neotropical Entomology, 36*(5), 812-814. doi: 10.1590/S1519-566X2007000500026.

Lima, T. N. (2016). Cannibalism among *Myrmeleon brasiliensis* larvae (Návas, 1914) (Neuroptera, Myrmeleontidae). *Acta Scientiarum. Biological Sciences, 38*(4), 447-450. doi: 10.4025/actascibiolsci.v38i4.32822

Lima, T. N., & Lopes, F. S. (2016). Effect of density, disturbance and food on displacement of the *Myrmeleon brasiliensis* (Navás, 1914) (Neuroptera, Myrmeleontidae). *Ecología Austral, 26*(2), 166-170.

Lima, T. N., & Silva, D. C. R. (2017). Effect of energetic cost to maintain the trap for *Myrmeleon brasiliensis* (Neuroptera, Myrmeleontidae) in its development and adult size. *Brazilian Journal Biology, 77*(1), 38-42. doi: 10.1590/1519-6984.08715

McClure, M. S. (1976). Spatial distribution of pit-marking ant-lion (Neuroptera: Myrmeleontidae): density effects. *Biotropica, 8*(3), 179-183. doi: 10.2307/2989683

Missirian, G. B., Uchôa-Fernandes, M. A., & Fischer, E. A. (2006). Development of *Myrmeleon brasiliensis* (Navás) (Neuroptera, Myrmeleontidae), in laboratory, with different natural diets. *Brazilian Journal Zoology, 23*(4), 1044-1050. doi: 10.1590/S0101-81752006000400009

Nicholson, A. (1954). An outline of the dynamics of animal populations. *Austral Journal Zoology, 2*(1), 9-65. doi: 10.1071/ZO9540009

Nonato, L. M., & Lima, T. N. (2011). El comportamiento de predación de los estadios larvales de *Myrmeleon brasiliensis* (Neuroptera, Myrmeleontidae). *Revista Colombiana de Entomologia, 37*(2), 354-356.

Polis, G. A. (1980). The effect of cannibalism on the demography and activity of a natural-population of desert scorpions. *Behavioral Ecology and Sociobiology, 7*(1), 25-35.

Prado, P., Bede, L. C., & Faria, M. L. (1993). Asymmetric competition in a natural population of antlion larvae. *Oikos, 68*(3), 525-530. doi: 10.2307/3544921

Persson, L., & Eklov, P. (1995). Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. *Ecology, 76*(1), 70-81. doi: 10.2307/1940632

Pfennig, D. W., & Pfennig, K. S. 2012. *Evolution's wedge: competition and the origins of diversity*. Berkeley, CA: University of California Press.

Rudolf, V. H. (2006.) The influence of size-specific indirect interactions in predator-prey systems. *Ecology, 87*(2), 362-371. doi: 10.1890/05-0961

Simberloff, D., King, L., Dillon, P., Lowrie, S., Lorence, D., & Schilling, E. (1978). Holes in the doughnut theory: the dispersions of ant-lions. *Brenesia, 14-15*(1), 13-46.

Varley, G. C., Gradwell, G. R., & Hassell, M. P. 1973. *Insect population ecology*. Oxford, UK: Blackwell Scientific.

Wilson, D. S. (1974). Prey capture and competition in the antlion. *Biotropica, 6*(3), 187-193. doi: 10.2307/2989651

Young, K. A. (2004). Asymmetric competition, habitat selection, and niche overlap in juvenile salmonids. *Ecology, 85*(1), 134-149. doi: 10.1890/02-0402