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Why are antlion larvae rare under the leaf litter? Testing the hypothesis of improper trap maintenance

¿Por qué las larvas del león de las hormigas son tan raras bajo la hojarasca? Probando la hipótesis del mantenimiento inadecuado de las trampas

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Abstract

1. Understanding why animals avoid some locations is needed to improve the theory of habitat selection. This is key in semi-sedentary organisms, such as antlion larvae, because once established they rarely move, and their performance largely depends on local environmental conditions.
2. Antlion larvae are sit-and-wait predators that build conical pitfall traps in sandy soils to capture passing prey. They clean constantly their traps, expelling soil, prey carcasses and debris out of the pit to maintain their trapping success. Therefore, we propose that they avoid soils with leaf litter because leaves hinder the maintenance of their pits; a hypothesis that has not yet been tested.
3. We first demonstrated that antlion larvae (*Myrmeleon inmaculatus*) are rare from soils with leaf litter in a tropical semi-deciduous forest in Mexico. We then experimentally tested the effect of leaf litter on pit maintenance by adding debris in 90 antlion traps, 45 of which were covered with a leaf, and 45 remained uncovered. Two hours after adding the debris, we recorded its location and quantified the variation in depth and diameter of the pits.
4. Larvae in uncovered traps were twice as effective at cleaning up the debris than larvae in covered traps. Furthermore, in just 2 h, covered traps were on average 21% shallower than control traps, probably because unsuccessful attempts to clean debris caused sand slides to fill the pit partially.
5. Leaf litter seems to hinder the proper maintenance of antlion traps, explaining at least partially, why these animals are rare under leaf litter.

KEYWORDS
habitat avoidance, Myrmeleontidae, sit-and-wait predator, tropical dry forest

INTRODUCTION

Habitat selection depends on multiple factors, both those that benefit animal fitness and those that imply costs to it (Morris, 2003; Rosenzweig, 1981). However, as most studies focus on the positive factors of habitat selection, those that promote habitat avoidance are scarce and not well understood (Feder & Forbes, 2007; Forbes et al., 2005). Filling this knowledge gap is particularly relevant for organisms with limited mobility, given that once established, they rarely move and thus their growth, survival and reproduction strongly depend on the local environmental conditions. In semi-sedentary organisms, establishment in unfavourable sites should be penalised by natural selection because its relocation capacity is energetically costlier and limited compared to more mobile animals (Pinter-Wollman & Brown, 2015; Scharf & Ovadia, 2006). For example, leaf-cutting ant nests are rare in floodable sites because these areas negatively impact leaf-cutting foraging and survivorship (Farji-Brener et al., 2018; Rodríguez-Planes & Farji-Brener, 2019; Sendoya et al., 2014). Therefore, semi-sedentary organisms can be considered optimal subjects to study the causes of habitat avoidance and thus, to improve our understanding of the mechanistic basis of habitat selection (Lubin et al., 1993; Morris, 2003).

Antlion larvae (Neuroptera: Myrmeleontidae) are an excellent system for studying the causes of habitat avoidance for several reasons. First, these larvae are easy to find in the field because of their conspicuous pitfall traps and their aggregated spatial distribution (Figure 1). Antlions are site-and-wait predators that build conical pits in sandy soils and wait for prey, usually ants, to fall in them (Heinrich & Heinrich, 1984; Lucas, 1982). Antlion larvae are usually grouped in areas with fine-grained soils, without leaf litter and sheltered from the rain (Farji-Brener, 2003; Farji-Brener & Amador-Vargas, 2020; McClure, 1976), forming 'antlion zones' (Gotelli, 1993). Second, pit traps are easy to measure and manipulate. Finally, even though antlions rarely relocate their traps because pits are energetically costly to build (Crowley & Linton, 1999; Gotelli, 1996; Griffiths, 1980; Lucas, 1985), they can move at a short distance away to avoid unfavourable places (Matsura & Takano, 1989; Scharf & Ovadia, 2006). For example, when antlions were offered two soil types, they actively avoided the coarser soil and searched for the more suitable fine soil to build traps (Farji-Brener, 2003). In summary, the ease of finding larvae in the field and measuring and manipulating their traps, together with the high cost of relocation, make antlions an ideal organism for evaluating the causes of habitat avoidance.

FIGURE 1 Antlion pitfall traps in trail sandy soils around the biological station of the Yaakunah Kaax reserve, Mexico (red arrows on the left side) and a 50 × 50 cm plot in the nearest area naturally covered with leaf litter (right side).

Some environmental features can negatively affect the performance of antlion larvae and might determine habitat avoidance: soil compaction, rain and leaf litter. The avoidance of compacted soils with coarse-grained particles is not surprising, as these characteristics can limit trap building and result in smaller traps that capture fewer prey (Devetak et al., 2005; Farji-Brener, 2003; Gatti & Farji-Brener, 2002; Gotelli, 1993; Loiterton & Magrath, 1996; Lucas, 1982, 1985). Rain also limits trap building and its capture success decreases larvae activity and increases their mortality (Algarve et al., 2022; Freire & Lima, 2019; Griffiths, 1980, 1991; Scharf & Ovadia, 2006). But why are antlion larvae so rare under the leaf litter? Some studies propose that this pattern is related to the fact that leaf litter could cover the pits and thus reduce prey capture (Farji-Brener, 2003; Griffiths, 1980). However, there is another alternative but non-exclusive hypothesis that has not yet been empirically tested: the leaves covering the antlion traps may hinder their proper maintenance. Because traps must be kept clean to reduce the chance of prey escape from the trap, antlion larvae constantly clean their traps, expelling soil particles, prey carcasses and debris out of the pit (Büsse et al., 2021; Farji-Brener, 2003; Franks et al., 2019; Lomascolo & Farji-Brener, 2001; Lucas, 1982). Therefore, these larvae probably avoid building traps on soils with leaf litter because they make it difficult (or prevent) the proper maintenance of their pits.

Here we test this hypothesis in a tropical semi-deciduous forest from the Yucatan Peninsula, Mexico. We first verify whether the premise that antlion larvae are rare under leaf litter is correct in our study site. Then, we used a field experiment, including a large number of traps, to assess the impact of leaf litter on trap maintenance. If leaf litter hinders trap maintenance, it is feasible that the covered traps fill with the particles that larvae intend to expel. Therefore, we expect that expelling debris will be more difficult in covered traps, and thus, that these traps to be shallower after being experimentally covered with leaf litter.

MATERIALS AND METHODS

Study area

We conducted this research in the Yaakunah Kaax private reserve, municipality of Chemax, Yucatan, Mexico (20°45′16″ N, 87°41′54″ W), a flat limestone platform of karst topography located 55 km apart from the Caribbean Sea. The climate in the region is tropical subhumid, with yearly precipitation around 1200–1400 mm, and a dry season from February to May (<60 mm per month; INEGI, 2010). The mean annual temperature ranges between 24 and 26°C (INEGI, 2010). This reserve comprises ≈ 450 ha of tropical semi-deciduous forest, where some tree species (e.g., *Bursera simaruba*, *Ceiba* spp., *Ficus* spp., *Metopium brownei*, *Vitex gaumeri*) lose their leaves in the dry season (CONAFOR, 2014).

Antlion natural history and study species

Adult antlions are feeble fliers, active at night and short-lived. Females lay eggs in the soil. Since antlion larvae have limited mobility, females can maximise offspring fitness by ovipositing in suitable microhabitats (Scharf et al., 2009, 2011; Scharf & Ovadia, 2006). Depending on food availability, larval development is quite variable but probably requires >2–3 years to become an adult (Gotelli, 1993, 1997; Griffiths, 1980, 1991). The digging activity of antlions to build their traps includes backward movements just beneath the substrate surface. These backward movements are accompanied by periodic sand-tossing behaviour, consisting of rapid jerks of the head and mandibles and expelling the sand outside the trap (Franks et al., 2019; Lucas, 1982, 1989; Tuculescu et al., 1975; Youthed & Moran, 1969). After capturing prey, antlions suck out their prey's haemolymph and then expel the carcass out of their pits with their large mandibles (Lucas, 1982). Pit maintenance is vital to antlion larvae because irregular, shallow and smaller pits capture fewer prey (Farji-Brener, 2003; Heinrich & Heinrich, 1984; Lomascolo & Farji-Brener, 2001; Lucas, 1989). Pit maintenance implies expelling outside the trap soil particles produced by small sand slides, prey carcasses and small debris that occasionally fall into the trap. We worked with *Myrmeleon immaculatus*, one of the most frequent antlion species in the Yucatan state, Mexico (Bousquets, 1996; Contreras-Ramos & Rosas, 2014; Penny et al., 1997). This species is very common in sheltered and sandy microhabitats in the study area (Figure 1).

Presence of antlion larvae under leaf litter

To verify the premise that antlion larvae are rare under the leaf litter in the study area, we actively searched for antlion pits around de biological station of the Yaakunah Kaax reserve for 12 days at the end of the dry seasons (May 2023). We only found pits in open areas without leaf litter, such as forest trails and underneath the roofs of the station buildings. We then randomly selected 30 pits and located a plot of 50 × 50 cm in the nearest area naturally covered with leaf litter (~100 cm apart from the pits; Figure 1). We then carefully removed all the leaf litter from the plot and searched for antlion pits.

Field experiment: The effect of leaf covers on pit dimensions

To test whether the leaf litter hinders trap cleaning and maintenance, we selected 90 active antlion pits around the biological station. Antlion activity was confirmed by the direct observation of larvae movements within the pits and by the general condition of the trap (i.e., totally clean and with fine sand in the slopes). We then measured the diameter and depth of all traps using a calliper. After that, we carefully throw a rice grain into each pit from 5 cm height to simulate the fall of debris and stimulate the cleaning behaviour of antlion. Larvae often rapidly expel outside their pits any inert objects that fall in. We used a rice grain to standardise the weight and form of the debris across traps. Right after throwing the rice, we gently covered 45 traps with a dry leaf from the nearest leaf litter. Covered and uncovered traps (independent variable) were randomly assigned and were spatially interspersed in the study area. Two hours later, we recorded the location of the rice grain and measured again the diameter and depth of each trap. We choose to wait 2 h because this lapse is long enough to get a clear response since the larvae cleaning activity begins immediately after debris fall into the trap. Rice location (dependent variable) was categorised as: (i) inside the trap, (ii) on trap slopes or (iii) outside the trap. We calculated the difference (Δ, in percentage) in diameter and depth of each trap before and after the experiment using the following formula: Diameter change (Δ Diam.), in % = (Diameter before − Diameter after)/Diameter before × 100, and Depth change (Δ Dep.) in % = (Depth before − Depth after)/Depth before × 100. Hence, each pit was considered as its own control. Both Δ values were considered response variables, and with/without leaf litter as an independent factor. Negative Δ values imply that trap diameter or depth increased over time, whereas positive values indicate the opposite. Values around zero denote no change in size over time. The field experiment was done for 5 days at the end of the dry season (May 2023). The weather conditions did not change during the study period.

Data analyses

We determined whether the location of the rice grain depended on the presence of leaf litter covering the trap using a chi-square test of independence. To assess whether the mean differences in diameter and depth of the traps differed between covered and uncovered traps, we used *t*-student tests. The normality and homogeneity of

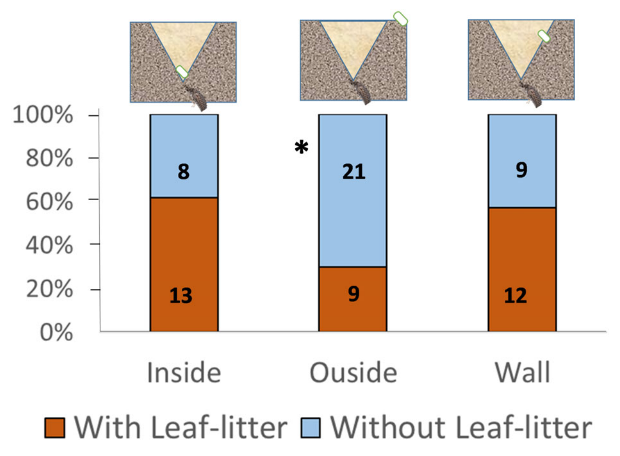

FIGURE 2 Absolute frequency (numbers within each bar) and percentage of each category of the rice grain location 2 h after being thrown into the antlion trap, in traps experimentally covered (orange) and uncovered (blue) by leaf litter. We considered three main categories: inside the pit, outside the pit and on the pit wall. (*) Mean statistically significant differences ($p = 0.04$).

variance of the data were confirmed prior to performing the *t*-tests. Data were analysed using *Statistica* 8.0®.

RESULTS

We did not find any antlion trap in any of the 30 sampling plots, thus supporting the idea that antlion larvae are rare (if present) under leaf litter. On the other hand, all sampled traps were of similar dimensions before the experiment. Before covering half of the traps with a leaf, the diameter and depth of the traps assigned as treatments were similar to those assigned as controls (3.21 ± 0.10 vs. 3.18 ± 0.11 cm in diameter, $n = 45$, $t = 0.20$, $p = 0.84$; and 1.51 ± 0.06 vs. 1.56 ± 0.06 cm in depth, $n = 45$, $t = 0.52$, $p = 0.60$; mean ± SE). After 2 h, we located the rice grain in 72 of 90 traps (80%); in the remaining 18 traps, the rice grain was probably buried inside the pit and/or was impossible to find. Considering only these 72 traps, we found significant differences in the rice grain location between covered and uncovered traps. While 55% of the rice grains were expelled outside the pit in traps uncovered by leaves, only 26% were expelled out in covered traps ($\chi^2 = 6.22$, *d.f.* $= 2$, $p = 0.04$; Figure 2).

Even though trap dimensions were similar in both treatments before the experiment, we found that in just 2 h, covered traps were on average 21% shallower and slightly narrower than control traps (Figure 3). At the end of the experiment, traps covered with leaf litter

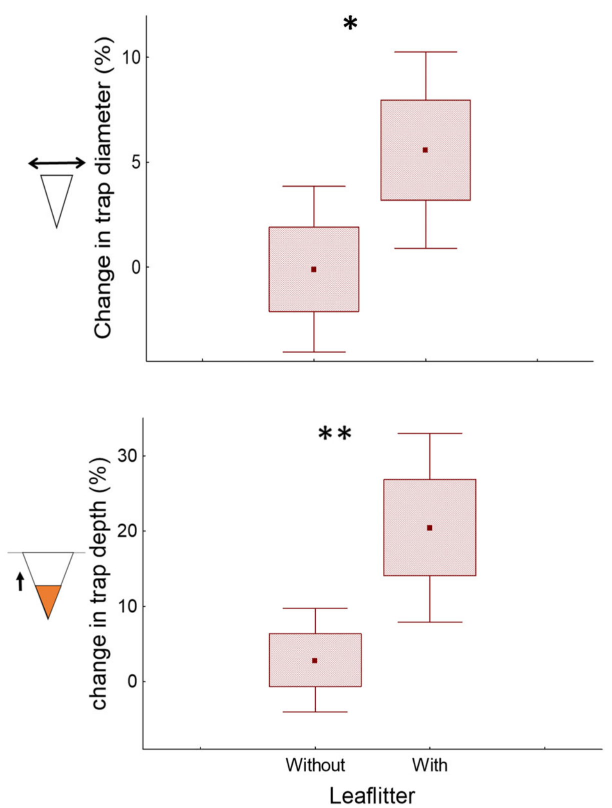

FIGURE 3 Changes (Δ, in percentage) in diameter and depth of antlion pits covered and uncovered with leaf litter. Positive Δ values imply that diameter and depth decreased when covered with leaf litter (*t*-tests, $^{**}p = 0.02$, $^{*}p = 0.07$).

were shallower than control traps (depth change: 21 ± 6% vs. 3 ± 3%, mean ± SE; $t = 2.4$, *d. f.* $= 88$, $p = 0.02$) and showed a trend to be narrower (diameter change: 5.6 ± 2.4% vs. −0.1 ± 2%; $t = 1.8$, *d. f.* $= 88$, $p = 0.07$). In other words, covered traps suffered a reduction of ~21% of their depth, while control ones only a ~5%. Even more, several traps experimentally covered with leaf litter were almost filled with soil particles in only 2 h.

DISCUSSION

This study confirms that antlion larvae are rare in soils covered by leaf litter. This pattern was already described in several studies (Farji-Brener et al., 2008; Farji-Brener & Amador-Vargas, 2020; Gatti & Farji-Brener, 2002; Griffiths, 1980). The novel contribution here was to experimentally demonstrate that such a pattern can be related to the fact that leaf litter hinders the adequate maintenance of their pitfall traps; as we found that after adding debris (a grain of rice) within 90 traps, larvae in traps uncovered by leaf litter were twice as effective cleaning up the debris than larvae in traps covered with leaf litter. Also, in just 2 h, covered traps were on average 21% shallower than uncovered ones, suggesting that repeated (and unfruitful) attempts to clean up the debris probably caused sand slides toward the centre of the pit. All this evidence can explain, at least, partially why antlion larvae are rare under leaf litter.

Almost all maintenance tasks are disturbed when traps are covered with leaf litter. As described above, the antlion pitfall trap is an inverted cone dug into sandy soils, where the larva waits for prey to fall at the vertex of the pit. Since antlions usually build their pits near the condition of physical equilibrium, the slope of the pit is highly unstable and sensitive to disturbance (Büsse et al., 2021; Lucas, 1982, 1989). To keep an adequate pit depth and stable slope, larvae need to regularly clean sand out of the pit. This sand-throwing behaviour is also required after prey capture because movements of prey and larvae can cause small landslides that change the shape of the pit (Griffiths, 1980; Lomascolo & Farji-Brener, 2001; Lucas, 1982). In addition to that, larvae also need to expel the carcasses of captured prey and debris that occasionally fall inside the trap to keep it in optimal condition (Beponis et al., 2014; Lucas, 1982). Our results strongly suggest that a leaf litter cover interferes with all of these maintenance activities because soil particles, prey carcasses and debris that the larva attempts to remove from the trap can bounce off the litter covering the trap and fall back into the pit.

The gradual filling of the trap due to the difficulty of expelling the particles to the outside determines as we demonstrated here, shallower and slightly narrower pits. We found that in just 2 h of being covered with a leaf, pits were ~21% shallower than the uncovered pits, suggesting that this effect could be greater if the leaf cover remains longer, as it probably does in nature. The pit filling was so great, in certain cases, that the mean diameter of the traps also tended to get smaller after the experiment. This negatively affects larval performance through, at least, two ways. First, antlions need to invest more energy to keep their pit functional, which has a negative impact on larval performance (Griffiths, 1986; Lucas, 1985). Moreover, the chance of prey falling into a pit is reduced, while the larvae are doing pit maintenance, because the activity of expelling sand can warn of the presence of a trap before the prey can fall into it (Bar et al., 2022; Gotelli, 1996; Hollis, 2017). Second, shallower pits probably capture fewer prey because prey can escape easier from small than from large traps (Farji-Brener, 2003; Lomascolo & Farji-Brener, 2001; Scharf et al., 2011). In summary, placing their pitfall traps under leaf litter prevents the proper maintenance of the pit, potentially limiting larval performance. Consequently, it is logical that antlion larvae are rare under leaf litter.

There are, however, other alternative, but non-exclusive explanations, aside from the restriction of proper trap maintenance, why antlion larvae may be so rare under leaf litter. First, potential prey, such as ants, can walk on the leaves and thus avoid falling into the larvae pits that are under the leaf litter (i.e., leaf litter may decrease the probability of prey capture; Farji-Brener et al., 2008; Farji-Brener & Amador-Vargas, 2020; Griffiths, 1980). However, this logical idea has yet to be empirically tested. Even more, it has been documented that small ants often walk through the leaf litter (Farji-Brener et al., 2004; Yanoviak & Kaspari, 2000), so they could eventually fall into the traps. Second, leaf litter cover can make it difficult for adult antlions to oviposit, although larvae can, at least to some extent, relocate their pits (Crowley & Linton, 1999; Gotelli, 1997; Scharf et al., 2009, 2011; Scharf & Ovadia, 2006). Hence, the presence of leaf litter hindering the oviposition may explain the origin, but not the maintenance, of why antlion larvae are so rare under leaf litter. Finally, the type of substrate under leaf litter may be coarser or more compacted than in open areas, making hampering trap construction more difficult. Preliminary observations do not support this hypothesis (Farji-Brener et al., 2008; Gatti & Farji-Brener, 2002), but additional data are required to reject this idea. Although all these ideas may play a role in driving the spatial distribution of antlion traps, we were able to experimentally demonstrate that leaf litter strongly hinders trap maintenance. Thus, we offer support to a novel and poorly understood and documented mechanism, which can be added to those already existing to explain why these larvae are so rare under leaf litter.

All habitats have associated costs and benefits. Therefore, identifying the habitat features that denote both advantages and disadvantages is paramount to better understanding the basis of habitat selection (Morris, 2003). In this case, leaf litter cover may represent benefits but also costs to antlion larvae. Leaf litter can protect traps from rain and excessive solar radiation, both factors that limit trap construction and larval feeding activity (Algarve et al., 2022; Farji-Brener, 2003; Farji-Brener & Amador-Vargas, 2020; Freire & Lima, 2019; Gotelli, 1993; Klein, 1982; Lucas, 1985; Miler & Scharf, 2022). But as already explained, leaf litter can also limit the prey capture, and the oviposition rate by adult females (not studied here), and make essential activities for trap maintenance more difficult (as we demonstrated here). The low abundance of antlion larvae under leaf litter strongly suggests that the costs outweigh the potential benefits. This may impact antlions at larger spatial scales. For example, the geographical distribution of antlions may be restricted in forests with abundant leaf litter. In these areas, larvae could be forced to inhabit only litter-free microhabitats.

Using antlion larvae as a model organism, we describe here a novel mechanism that may explain an overlooked but relevant aspect of habitat selection: habitat avoidance (Feder & Forbes, 2007; Forbes et al., 2005). It is generally argued that an organism decides where to reside based on positive habitat preferences. However, animals use both positive and negative cues from habitats when evaluating their environment (Sim et al., 2012). Thus, understanding why animals avoid certain habitat is also key, not only to better understand the complete process of habitat choice but also to predict changes in their geographical ranges under the scenario of rapid landscape change due to anthropogenic disturbances.

AUTHOR CONTRIBUTIONS

Alejandro G. Farji-Brener: Conceptualization; investigation; writing – original draft; writing – review and editing; formal analysis; supervision. **Merly Yenedith Carrillo-Fajardo:** Writing – review and editing; data curation. **Jorge Tanit Rodríguez-Malacara:** Writing – review and editing; data curation. **Víctor Arroyo-Rodríguez:** Funding acquisition; writing – original draft; supervision; resources.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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REFERENCES

Algarve, B.B., Graciolli, G. & Lima, T.N. (2022) Influence of rainfall regime in the Cerrado biome on the maintenance of traps built by *Myrmeleon brasiliensis* (Navás) (Neuroptera: Myrmeleontidae) larvae and the morphology of adults. *Iheringia. Série Zoologia*, 112, 1–8.

Bar, A., Marom, C., Zorin, N., Gilad, T., Subach, A., Foitzik, S. et al. (2022) Desert ants learn to avoid pitfall traps while foraging. *Biology*, 11(6), 897.

Beponis, L.M., O'Dea, R.E., Ohl, V.A., Ryan, M.P., Backwell, P.R., Binning, S.A. et al. (2014) Cleaning up after a meal: the consequences of prey disposal for pit-building antlion larvae. *Ethology*, 120(9), 873–880.

Bousquets, J.L. (1996) In: Aldrete, A.N.G., Soriano, E.G., Papvero, N. & Morrone, J.J. (Eds.) *Biodiversidad, taxonomía y biogeografía de artrópodos de México: hacia una síntesis de su conocimiento*. Mexico DF: Universidad Nacional autónoma de México, Instituto de Biología.

Büsse, S., Büscher, T.H., Heepe, L., Gorb, S.N. & Stutz, H.H. (2021) Sand-throwing behavior in pit-building antlion larvae: insights from finite-element modeling. *Journal of the Royal Society Interface*, 18(182), 20210539.

Comisión Nacional Forestal (CONAFOR). (2014) *Inventario estatal forestal y de suelos – Yucatán 2013*. Ciudad de México, México: Secretaría de Medio Ambiente Recursos Naturales.

Contreras-Ramos, A. & Rosas, M.V. (2014) Biodiversidad de Neuróptera en México. *Revista Mexicana de Biodiversidad*, 85, 264–270.

Crowley, P.H. & Linton, M.C. (1999) Antlion foraging: tracking prey across space and time. *Ecology*, 80(7), 2271–2282.

Devetak, D., Špernjak, A. & Janžekovic, F. (2005) Substrate particle size affects pit building decision and pit size in the antlion larvae *Euroleon nostras* (Neuroptera: Myrmeleontidae). *Physiological Entomology*, 30(2), 158–163.

Farji-Brener, A.G. (2003) Microhabitat selection by antlion larvae, *Myrmeleon crudelis*: effect of soil particle size on pit-trap design and prey capture. *Journal of Insect Behavior*, 16(6), 783–796.

Farji-Brener, A.G. & Amador-Vargas, S. (2020) Plasticity in extended phenotypes: how the antlion *Myrmeleon crudelis* adjusts the pit traps depending on biotic and abiotic conditions. *Israel Journal of Ecology and Evolution*, 66(1–2), 41–47.

Farji-Brener, A.G., Barrantes, G. & Ruggiero, A. (2004) Environmental rugosity, body size and access to food: a test of the size-grain hypothesis in tropical litter ants. *Oikos*, 104(1), 165–171.

Farji-Brener, A.G., Carvajal, D., Gei, M.G., Olano, J. & Sanchez, J.D. (2008) Direct and indirect effects of soil structure on the density of an antlion larva in a tropical dry forest. *Ecological Entomology*, 33(2), 183–188.

Farji-Brener, A.G., Dalton, M.C., Balza, U., Courtis, A., Lemus-Domínguez, I., Fernández-Hilario, R. et al. (2018) Working in the rain? Why leaf-cutting ants stop foraging when it's raining. *Insectes Sociaux*, 65, 233–239.

Feder, J.L. & Forbes, A.A. (2007) Habitat avoidance and speciation for phytophagous insect specialists. *Functional Ecology*, 21, 585–597.

Forbes, A.A., Fisher, J. & Feder, J.L. (2005) Habitat avoidance: overlooking an important aspect of host-specific mating and sympatric speciation? *Evolution*, 59(7), 1552–1559.

Franks, N.R., Worley, A., Falkenberg, M., Sendova-Franks, A.B. & Christensen, K. (2019) Digging the optimum pit: antlions, spirals and spontaneous stratification. *Proceedings of the Royal Society B*, 286(1899), 20190365.

Freire, L.G. & Lima, T.N. (2019) Effect of rain on trap building by *Myrmeleon brasiliensis*. *Entomologia Experimentalis et Applicata*, 167, 561–565.

Gatti, M.G. & Farji-Brener, A.G. (2002) Low density of ant lion larva (*Myrmeleon crudelis*) in ant-acacia clearings: high predation risk or inadequate substrate? *Biotropica*, 34(3), 458–462.

Gotelli, N.J. (1993) Ant lion zones: causes of high-density predator aggregations. *Ecology*, 74(1), 226–237.

Gotelli, N.J. (1996) Ant community structure: effects of predatory ant lions. *Ecology*, 77(2), 630–638.

Gotelli, N.J. (1997) Competition and coexistence of larval ant lions. *Ecology*, 78(6), 1761–1773.

Griffiths, D. (1980) The feeding biology of ant-lion larvae: growth and survival in *Morter obscurus*. *Oikos*, 34(3), 364–370.

Griffiths, D. (1986) Pit construction by ant-lion larvae: a cost-benefit analysis. *The Journal of Animal Ecology*, 55(1), 39–57.

Griffiths, D. (1991) Food availability and the use and storage of fat by antlion larvae. *Oikos*, 60(2), 162–172.

Heinrich, B. & Heinrich, M.J. (1984) The pit-trapping foraging strategy of the ant lion, *Myrmeleon immaculatus* DeGeer (Neuroptera: Myrmeleontidae). *Behavioral Ecology and Sociobiology*, 14, 151–160.

Hollis, K.L. (2017) Ants and antlions: the impact of ecology, coevolution and learning on an insect predator-prey relationship. *Behavioral Processes*, 139, 4–11.

Instituto Nacional DE Estadística Y Geografía (INEGI). (2010) *Compendio de información geográfica municipal 2010*. Chemax, Yucatán: Instituto Nacional de Estadística y Geografía.

Klein, B.G. (1982) Pit construction by antlion larvae: influences of soil illumination and soil temperature. *Journal of the New York Entomological Society*, 90(1), 26–30.

Loiterton, S.J. & Magrath, R.D. (1996) Substrate type affects partial prey consumption by larvae of the antlion *Myrmeleon acer* (Neuroptera: Myrmeleontidae). *Australian Journal of Zoology*, 44(6), 589–597.

Lomascolo, S. & Farji-Brener, A.G. (2001) Adaptive short-term changes in pit design by antlion larvae (*Myrmeleon* sp.) in response to different prey conditions. *Ethology Ecology and Evolution*, 13(4), 393–397.

Lubin, Y., Ellner, S. & Kotzman, M. (1993) Web relocation and habitat selection in desert widow spider. *Ecology*, 74(7), 1915–1928.

Lucas, J.R. (1982) The biophysics of pit construction by antlion larvae (Myrmeleon, Neuroptera). *Animal Behaviour*, 30(3), 651–664.

Lucas, J.R. (1985) Metabolic rates and pit-construction costs of two antlion species. *The Journal of Animal Ecology*, 54(1), 295–309.

Lucas, J.R. (1989) The structure and function of antlion pits: slope asymmetry and predator-prey interactions. *Animal Behavior*, 38(2), 318–330.

Matsura, T. & Takano, H. (1989) Pit-relocation of antlion larvae in relation to their density. *Researches on Population Ecology*, 31, 225–234.

McClure, M.S. (1976) Spatial distribution of pit-making ant lion larvae (Neuroptera: Myrmeleontidae): density effects. *Biotropica*, 8(3), 179–183.

Miler, K. & Scharf, I. (2022) Operant conditioning in antlion larvae and its impairment following exposure to elevated temperatures. *Animal Cognition*, 25(3), 509–518.

Morris, D.W. (2003) Toward an ecological synthesis: a case for habitat selection. *Oecologia*, 136, 1–13.

Penny, N.D., Adams, P.A. & Stange, L.A. (1997) Species catalog of the Neuroptera, Megaloptera, and Raphidioptera of America north of Mexico. *Proceedings of the California Academy of Sciences*, 50, 39–114.

Pinter-Wollman, N. & Brown, M.J. (2015) Variation in nest relocation of harvester ants is affected by population density and food abundance. *Behavioral Ecology*, 26(6), 1569–1576.

Rodríguez-Planes, L.I. & Farji-Brener, A.G. (2019) Extended phenotypes and foraging restrictions: ant nest entrances and resource ingress in leaf-cutting ants. *Biotropica*, 51(2), 178–185.

Rosenzweig, M.L. (1981) A theory of habitat selection. *Ecology*, 62, 327–335.

Scharf, I., Golan, B. & Ovadia, O. (2009) The effect of sand depth, feeding regime, density, and body mass on the foraging behavior of a pit-building antlion. *Ecological Entomology*, 34(1), 26–33.

Scharf, I., Lubin, Y. & Ovadia, O. (2011) Foraging decisions and behavioral flexibility in trap-building predators: a review. *Biological Reviews*, 86(3), 626–639.

Scharf, I. & Ovadia, O. (2006) Factors influencing site abandonment and site selection in a sit-and-wait predator: a review of pit-building antlion larvae. *Journal of Insect Behavior*, 19, 197–218.

Sendoya, S., Silva, P.D. & Farji-Brener, A.G. (2014) Does inundation risk affect leaf-cutting ant distribution? A study along a topographic gradient of a costa Rican tropical wet forest. *Journal of Tropical Ecology*, 30, 89–92.

Sim, S.B., Mattsson, M., Feder, J.L., Cha, D.H., Yee, W.L., Goughnour, R.B. et al. (2012) A field test for host fruit odour discrimination and avoidance behaviour for *Rhagoletis pomonella* flies in the western United States. *Journal of Evolutionary Biology*, 25(5), 961–971.

Tuculescu, R., Topoff, H. & Wolfe, S. (1975) Mechanisms of pit construction by antlion larvae. *Annals of the Entomological Society of America*, 68(4), 719–720.

Yanoviak, S. & Kaspari, M. (2000) Community structure and the habitat templet: ants in the tropical forest canopy and litter. *Oikos*, 89, 259–266.

Youthed, G.J. & Moran, V.C. (1969) Pit construction by myrmeleontid larvae. *Journal of Insect Physiology*, 15(5), 867–875.

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