BIOTROPICA 34(3): 458–462 2002

Low Density of Ant Lion Larva (*Myrmeleon crudelis*) in Ant–Acacia Clearings: High Predation Risk or Inadequate Substrate?[1]

ABSTRACT

We experimentally determined whether the low density of antlion larvae found in ant-acacia clearings is due to high levels of ant predation or an inadequate substrate for pit-trap construction. Pit establishment was more affected by soil improvement than by the exclusion of ants, suggesting that soil condition is the main factor that affect antlions' density. The low density of this ant-predator in ant-acacia clearings may be considered as an indirect advantage of the ant's pruning behavior.

RESUMEN

Determinamos experimentalmente si la baja densidad de larvas del "león de las hormigas" en los claros de Acacia producidos por hormigas es consecuencia de los altos niveles de depredacion por hormigas o de la condicion del suelo alrededor de las Acacias. El establecimiento de las trampas del "león de las hormigas" estuvo más afectado por el mejoramiento del suelo que por la exclusión de las hormigas, sugiriendo que la condición del suelo es el factor más importante que afecta la densidad del "león de las hormigas". La baja densidad de este depredador de hormigas en los claros de Acacia puede ser considerada como una ventaja indirecta de la actividad "limpiadora" de las hormigas.

Key words: *abiotic constraints;* Acacia collinsii; *ants; ant lions; dry tropical forest;* Myrmeleon crudelis; *pit trap; predation.*

MANY ANIMALS ARE LIMITED IN MOBILITY. As a result, local conditions entirely determine their survival. Both abiotic (*e.g.,* temperature) and biotic factors (*e.g.,* predation and prey availability) may affect the fitness of such organisms and therefore, patterns of variation in their local abundance (Gotelli 1993, Crowley & Linton 1999). Because biotic and abiotic factors usually covary along spatial gradients, however, an experimental approach is necessary to reveal their relative importance and to explain why semisedentary animals of the same species are relatively abundant in some areas but scarce in others (Gotelli 1993). In this study, we experimentally explored whether the low density of semisedentary ant lion larvae found in ant–acacia clearings is due to high levels of predation or an inadequate substrate for pit-trap construction.

Myrmeleon larvae (Neuroptera: Myrmeleontidae) are sessile predators that dig conical pits in loose substrates to capture small arthropods that fall into the trap (Griffiths 1980). These larvae are commonly

---

[1] Received 27 September 2001; revision accepted 29 March 2002.

known as ant lions because they prey mainly upon ants (Griffiths 1980, Gotelli 1996). Adult ant lions are short-lived feeble flyers, and females lay eggs in the soil. Larval development is variable in duration, and larvae require 6–24 months to mature (Gotelli 1993). Ant lion larvae are sessile predators but semisedentary animals (Heinrich & Heinrich 1984). The larva moves along the soil surface to build a new trap 10–200 cm from the previous location every 5–70 days (AGF, pers. obs., Wilson 1974; Heinrich & Heinrich 1984; Crowley & Linton 1999).

It has been proposed that both food and space are limiting resources for ant lions (Gotelli 1997). As a sit-and-wait predator, an ant lion larva is entirely dependent on prey availability, which is generally sporadic and unpredictable (Griffiths 1980, 1986, 1991). Experimental increase in food availability can reduce the duration of larval life and increases adult body size (Heinrich & Heinrich 1984, Gotelli 1997). Furthermore, ant lions usually build their pits in sandy or loose soil along zones without litter cover (Wilson 1974; McClure 1976; Griffiths 1980, 1986, 1991; Gotelli 1993, 1996, 1997). Sandy soils are probably preferred by ant lions because they decrease the cost of pit construction and maintenance (Griffiths 1980, Lucas 1985, Gotelli 1993) and increase capture success (Lucas 1982). Bare ground is also preferred for pit construction because the presence of plant litter can cover ant lion pits, reducing the probability that prey fall into the trap (AGF, pers. obs.).

In the tropical dry forests of Costa Rica, ant lion pits are most commonly found on loose, bare soils near buildings and along forest trails (McClure 1976). This suggests that in the forest a suitable substrate for trap construction is another limiting resource in addition to prey availability (Gotelli 1993). Moreover, during the dry season when ant lion larvae are active, bare ground in the tropical dry forest is scarce because of the considerable abundance of dead leaves on the forest floor (McClure 1976); however, there is still a potentially favorable microhabitat in Neotropical dry forest for the establishment of ant lions: ant–acacia clearings.

The interaction between acacias trees and *Pseudomyrmex* ants is an obligate mutualism: the acacia provides food (nectar and protein bodies) and nest sites (thorns) to the ant colony, and the ants protect the tree from herbivores and cut foreign plants that sprout within 40 cm of the host acacia (Janzen 1966, 1967). Consequently, it is common to find acacias in starkly defined clearings in the forest. Sometimes a group of several acacias can support only one colony of *Pseudomyrmex* ants, and the colony maintains a zone of 10 to 80 m^2 free of vegetation and plant litter. In those cases, the ants frequently walk on the soil surface, moving between the acacias' trunks. Therefore, the ant–acacia clearings represent a microhabitat that is apparently favorable for pit establishment but is uncommon in the dry forest: bare ground for pit construction and high abundance of predictable, potential prey (*Pseudomyrmex* ants rarely escape from an ant lion trap into which they fall; Lomascolo & Farji-Brener 2001). Ant lions, however, have relatively low density in acacia clearings. Ant lion pit densities reach only 1.6 /m^2 in acacia clearings, whereas in bare soil along forest trails they reach 18.3/m^2 (AGF, pers. obs.). Why? There are at least two non-mutually exclusive reasons for this low density. First, soil associated with acacia clearings commonly remains compacted and has a persistent crust. Larvae are probably unable to penetrate soil crusts and/or dig in soils that are too compacted (Gotelli 1993). Second, *Pseudomyrmex* workers occasionally succeed in capturing insect prey in the nest area (Hölldobler & Wilson 1990), including ant lion larvae that are relocating their traps (AGF, pers. obs.; Lucas & Borackman 1981). Therefore, *Pseudomyrmex* ants can be either prey of ant lions (if they fall into an active pit) or their predators (if they find the larvae moving along the soil surface). In this study, we experimentally tested whether the low density of ant lion larvae in ant–acacia clearings was a consequence of high predation levels or an inadequate soil condition for pit construction.

The study was carried out in February 2001 during the dry season in Palo Verde National Park (10°N, 85W), a tropical dry forest located in the Guanacaste Province, Costa Rica. Characteristic trees include *Bursera simaruba*, *Pithecellobium saman*, *Guazuma ulmifolia*, and *Spondias mombin*, and there are large areas with the understory ant–plant *Acacia collinsii*. Mean annual rainfall is 1500–2000 mm and highly seasonal. Almost no rain falls from November to May and many plants drop their leaves. Mean annual temperature is 27°C.

Seven clearings (*ca* 50 m^2) with *ca* six acacia trees in each one were chosen near the Palo Verde field station operated by the Organization for Tropical Studies (OTS). These clearings were separated by *ca* 20 m, and each one was inhabited by only one *Pseudomyrmex spinicola* colony. In all the clearings selected, we confirmed the presence of *P. spinicola* ants walking on the soil surface. To assess the effect of soil

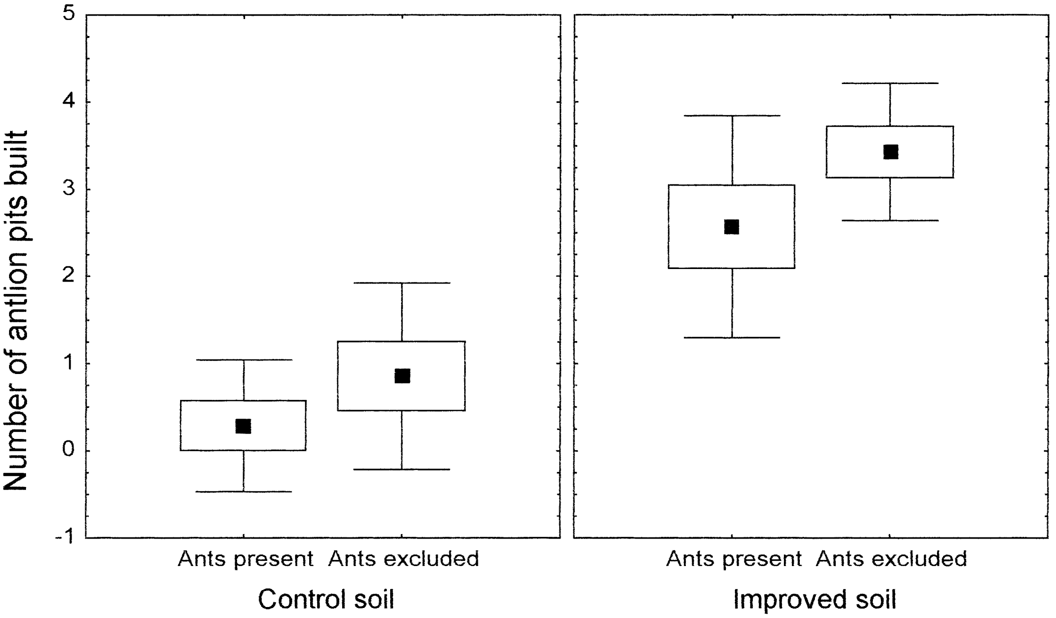

Figure 1. Number of ant lion pits constructed per treatment (4 = 100%) in ant–acacia clearings (see text for further explanations). Black points indicate the mean, boxes the standard error, and the error bars the standard deviation.

condition and predation level on ant lion establishment, as well as the interaction between them, we conducted the following field experiment. In each clearing, we randomly located four circular 20 cm radius plots (*ca* 0.13 m^2) in a 2 × 2 factorial design: *P. spinicola* ants present and excluded crossed with improved soil present and absent. We excluded *P. spinicola* ants using a cardboard ring with petroleum jelly (Vaseline) along its border. The success of this ring as an ant barrier had been previously tested. The physical condition of the soil was improved by breaking the soil crust and transforming the first 15 cm of soil into a fine-particle substrate using a screen sieve. Thus, each clearing included the following four treatments: (1) ants excluded on improved soil; (2) ants excluded on control soil; (3) ants not excluded on control soil; and (4) ants not excluded on improved soil.

We collected ant lion larvae (*Myrmeleon crudelis*) *ca* 1 cm long (probably second and third instars) from different sites in the forest. Four ant lion larvae were randomly selected and carefully placed into their assigned soil plot early in the morning. A total of 112 larvae was used in the field experiment (4 per treatment, 16 per clearing, 7 clearings). The construction of pits was monitored every four hours during two days, time enough for larvae to construct their pits (McClure 1976, Heinrich & Heinrich 1984, Lomascolo & Farji-Brener 2001). The number of pits constructed per treatment in each clearing was scored at the end of the experiment (4 = 100%) and analyzed as a two-way ANOVA randomized block design. Ants and substrata were designated as main (fixed) effects and acacia clearings as blocks (random). Treatment effects were tested over the block × treatment interaction. Data were arcsine square-root transformed before analysis.

Pit establishment was more affected by the soil condition than by the exclusion of *Pseudomyrmex* ants. The number of pits was significantly greater in the soil-improved plots than in control soils ($F_{1,\,18} = 41.3$, $P < 0.0001$; Fig. 1), but there were no significant differences in the number of pits between ant-exclusion and non-exclusion plots ($F_{1,\,18} = 3.6$, $P = 0.10$; Fig. 1). Clearings (block effect) and the interaction between soil condition and ants were also not statistically significant ($F = 0.38$ and 0.12, respectively; both $P > 0.73$).

Although the effect of ants was statistically nonsignificant ($P = 0.10$), ant lion densities were slightly higher when ants were excluded than when they were present. This suggests that the ants may be acting as predators for the ant lion larvae; however, the number of pit traps built in the improved-soil plots was between 4- and 11-fold greater than for traps built in control-soil plots (Fig. 1), suggesting that soil condition is the main factor that affects ant lion density in ant–acacia clearings. Larvae on control soils appeared to be unable to bury themselves. They moved rapidly until they encountered a shaded crevice in the soil crust, in which the larvae made no apparent attempt to place their pit. In contrast, larvae on improved soils immediately started to dig traps. Moreover, low density of ant lions in ant–acacia clearings appears to be a result of the interaction between an inadequate substrate for trap construction and temperature. Soil surface temperature in clearings is, at midday, greater than the lethal limits registered for ant lions (AGF, pers. obs.; Marsh 1987; Lucas 1989). Ant lions that remain under direct sun can die in three minutes (Gotelli 1993); however, if the substrate is loose (as the improved soils in our experiment), ant lions can avoid thermally stressful conditions by moving to cooler refuges below their pits (Marsh 1987).

This study confirmed experimentally that ant lion density and distribution is strongly affected by the availability of an adequate substrate for pit building (Boake *et al.* 1984, Gotelli 1993). Nevertheless, it is important to consider other causes for this pattern that were not tested in this study. For example, the low density of pits in ant–acacia clearings can be also a consequence of the low oviposition rate of adult ant lions in these areas; however, larvae are very mobile and often travel long distances to relocate their pit (Heinrich & Heinrich 1984, Crowley & Linton 1999). Consequently, female oviposition behavior may contribute to initial variation in pit density, but not to its maintenance.

Although abiotic factors appear to be responsible for the low density of ant lions in clearings, there are several biotic consequences of this pattern. First, ant lions are denied access to areas where food is more predictable and abundant, and thus cannot achieve an ideal free distribution with respect to food resources. Similar foraging constraints have been described for ant lions in central Oklahoma (Gotelli 1993), desert spiders (Riechert & Tracy 1975), and some ant species (Bestelmeyer 2000), in which thermal stress limits activity to the most unproductive habitats or times of the day. Second, the probability of competition and cannibalism, very frequent in the high-density aggregations of ant lions (Wilson 1974, Lucas 1989, Gotelli 1997), decreased in ant–acacia clearings. Thus, larval performance in ant–acacia clearings may increase. Third, ant lion predator aggregations are an important biotic constraint on foraging activity and nest placement of ants (Gotelli 1996). A low ant lion density in ant-acacia clearings may decrease the risk of death for *Pseudomyrmex* workers. It has been suggested that the pruning action of *Pseudomyrmex* ants promotes host growth (Janzen 1966, 1967), acts as natural fire breaks in dry environments (Janzen 1967), and removes bridges through which alien ants can attack the resident colony (Davidson *et al.* 1988). Our results suggest another indirect advantage of this ant's behavior. The ant's pruning activity in acacia clearings increases soil desiccation and compactness, and causes the formation of soil crust, which in turn maintains low density of this ant predator.

We thank M. "larva" Tadey, H. Vasconcelos, G. Barrantes, M. Aizen, A. Illes, W. Wcislo, N. Gotelli, and an anonymous reviewer for their comments. We are also grateful to the Organization for Tropical Studies for logistic support.

Bestelmeyer, B. 2000. The trade-off between thermal tolerance and behavioral dominance in a subtropical South American ant community. J. Anim. Ecol. 69: 998–1009.

Boake, C., D. Andow, and K. Visscher. 1984. Spacing of ant-lions and their pits. Am. Mid. Nat. 111: 192–194.

Crowley, P., and M. Linton. 1999. Ant lion foraging: tracking prey across space and time. Ecology 80: 2271–2282.

Davidson, D. W., J. T. Longino, and R. R. Snelling. 1988. Pruning of host plant neighbors by ants: an experimental approach. Ecology 69: 801–808.

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

———. 1996. Ant community structure: effects of predatory ant lions. Ecology 77: 630–638.

———. 1997. Competition and coexistence of larval ant lions. Ecology 78: 1761–1773.

Griffiths, D. 1980. The feeding biology of ant lion larvae. Prey capture, handling and utilization. J. Anim. Ecol. 49: 99–125.

———. 1986. Pit construction by ant lion larvae: a cost–benefit analysis. J. Anim. Ecol. 55: 39–57.

———. 1991. Food availability and the use of storage of flat by ant lion larvae. Oikos 60: 162–172.

Heinrich, B., and M. Heinrich. 1984. The pit-foraging strategy of the ant lion, *Myrmeleon immaculatus* degeer (Neuroptera: Myrmeleontidae). Behav. Ecol. Sociobiol. 14: 151–160.

Hölldobler, B., and E. O. Wilson. 1990. The ants. Belknap Press, Cambridge, Massachusetts.

Janzen, D. 1966. Coevolution of mutualism between ants and acacia in Central America. Evolution 20: 249–275.

———. 1967. Fire, vegetation structure and the ant–acacia interaction in Central America. Ecology 48: 26–35.

Lomascolo, S., and A. G. Farji-Brener. 2001. Adaptive short-term changes in pit design by ant lion larvae (*Myrmeleon* sp.) in response to different prey conditions. Eth. Ecol. Evol. 13: 393–397.

Lucas, J. 1982. The biophysics of pit construction by ant lion larvae (Myrmeleon, Neuroptera). Anim. Behav. 30: 651–664.

———. 1985. Metabolic rates and pit construction costs of two ant lion species. J. Anim. Ecol. 54: 295–309.

———. 1989. Differences in habitat use between two pit-building ant lion species: causes and consequences. Am. Mid. Nat. 121: 84–98.

———, AND H. BROCKMAN. 1981. Predatory interactions between ants and ant lions (Hymenoptera: Formicidae and Neuroptera: Myrmeleontidae) J. Kans. Entomol. Soc. 54: 228–232.

MARSH, A. 1987. Thermal responses and temperature tolerance of a desert ant-lion larva. J. Therm. Biol. 12: 295–300.

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

RIECHERT, S., AND C. TRACY. 1975. Thermal balance and prey availability: bases for a model relating web-site characteristics to spider reproductive success. Ecology 56: 265–284.

WILSON, D. S. 1974. Prey capture and competition in the ant lion. Biotropica 3: 187–193.

María Genoveva Gatti

Laboratorio de Ecología Funcional
Depto. de Biología, Pabellón II Piso 4
FCEyN–UBA, Ciudad Universitaria
(C1428EHA), Bs. Aires, Argentina

and

Alejandro G. Farji-Brener[2]

Lab. Ecotono, Depto de Ecología, CRUB.
Unidad Postal Universidad del Comahue, (8400) Argentina

---

[2] Corresponding author; e-mail: alefarji@crub.uncoma.edu.ar; alefarji@yahoo.com

---

[1] Received 1 March 2002; revision accepted 7 May 2002.