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Adaptive short-term changes in pit design by antlion larvae (*Myrmeleon* sp.) in response to different prey conditions

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Predators that live in environments with variable prey availability should be capable of modifying their behaviour in order to maximize their consumption rate. Sit-and-wait predators that use passive traps should modify trap architecture depending on the local conditions of prey availability. We quantified the short-term behavioural response of *Myrmeleon* sp. larvae in their pit-trap design in response to different experimentally modified prey conditions. The larvae (1) increased the diameter of the trap (which should increase prey encounter rates) but not the depth of the trap when prey were absent or scarce and, (2) increased the depth of the trap (which should minimize the probability of prey escape) under high availability of prey that were capable of escaping from the pit trap. *Myrmeleon* sp. larvae are thus capable of quickly adapting to different types and availability of prey. This behaviour could have been selected as a strategy to survive in poor environments with unpredictable prey availability.

KEY WORDS: antlion, behavioural plasticity, Costa Rica, *Myrmeleon* sp., sit-and-wait predators, trap design.

INTRODUCTION

The quantity and quality of food resources available to predators often changes in space and time. Consequently, natural selection will favour a predator's ability to rapidly adjust its capture mode to fit changes in the availability and type of prey. In animals that use pit traps, behavioural adjustments may involve modifications to the physical characteristics of the traps, or their location. *Myrmeleon* lar-

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vae (Neuroptera Myrmeleontidae) are sit-and-wait predators that build such pit traps. These traps are conical pits dug in dry soils. A larva rests quietly and is covered with fine dust or sand at the bottom of the trap where it waits for prey to fall into the trap. These insects are commonly known as antlions because they prey mainly ants (WILSON 1974, GRIFFITHS 1980, GOTELLI 1996). As a sessile predator, an antlion larva is entirely dependent on prey activity: its development and survival depends on prey falling into their traps, and such events are generally sporadic and unpredictable (GRIFFITHS 1980, 1986, 1991). Consequently, when a larva is starved for long periods, it abandons its trap and digs another one in a new location (GRIFFITHS 1980, 1986). Because predation risk may increase when they move to another location, and pit construction is energetically expensive (WILSON 1974, GRIFFITHS 1980, LUCAS 1985), we expect that antlions might modify the design of the trap in response to decreased food availability before moving to a new location. In this investigation, we quantify the behavioural response of *Myrmeleon* sp. to experimentally manipulated conditions of prey type and availability.

Features of pit architecture, such as diameter, slope, and depth, influence success in prey capture (WILSON 1974; GRIFFITHS 1980, 1986). A successful capture (i.e., prey consumption) depends on both efficiency in trapping prey (an encounter) and on minimizing the probability that the prey escapes (retention). These two components should have selective consequences for the design of the trap. For example, augmenting the diameter of the trap increases the probability of encounter, while a steeper slope and a greater depth increase the probability of prey retention (GRIFFITHS 1980, 1986).

Our objective was to experimentally determine the ability of *Myrmeleon* sp. larvae to respond to short-term changes in prey type and availability. We predicted that (1) under low prey density or when prey are absent the larva would increase trap diameter, and (2) under high density conditions using prey that are capable of escaping, the larva would increase the depth and/or the inclination of the wall (Table 1).

MATERIAL AND METHODS

We conducted this research at Palo Verde National Park, Costa Rica (10°N, 85'W), which includes part of the southernmost Middle American tropical dry forest. We collected 40 larvae of *Myrmeleon* sp. from different sites within the forest. Each larva was measured and placed in an individual container (60 cm in diameter and 25 cm deep) filled with fine soil from the same areas where the larvae were collected. As soon as the larvae were placed in

Table 1.

Treatments and expected short-term effects in trap design (see text for explanation).

Treatment	Changes expected in traps
T1: absence of prey	increase in diameter
T2: few prey (4 ants/24 hr), none escape	increase in diameter
T3: many prey (18 ants/24 hr), none escape	no changes
T4: many prey (18 ants/24 hr), all escape	increase in depth and/or inclination of the wall

containers, all started to dig traps. Approximately 2 hr later, digging activity ceased. Six hours later (all without digging activity), we assumed that the traps were finished. For each trap, we measured the diameter, depth (in mm), and the angle of the wall (angle of repose). The angle subtended by the pit was calculated from pit diameter and the vertical depth of the pit. Then we randomly assigned the containers to one of four treatments (10 traps in each). Traps did not differ initially in the variables measured among treatments (F = 1.05, $P = 0.38$ for diameter; F = 1.11, $P = 0.36$ for depth; F = 1.44, $P = 0.25$; F = 1.06, $P = 0.40$ for angle of wall, one-way ANOVA in all cases).

The treatments (T1, T2, T3, and T4) were 24 hr simulations of different conditions involving the arrival rates of ant prey, and the prey types that occur in nature: (T1) no prey were presented, (T2) one ant was placed in the trap every 360 min, (T3) one ant was placed in the trap every 80 min; and (T4) one ant was placed in the trap every 80 min, but we made sure they escaped before captured. In this case, we eventually took out the ant from the pit using a forceps. Antlion larvae in T2 and T3 receive *Pseudomyrmex spinicola*, a relatively small (ca 5 mm long) and abundant ant species in the study area. Due to their small size, *P. spinicola* rarely escape from *Myrmeleon* traps. For T4, we used *Ectatomma ruidum*, a larger ant (ca 10 mm long) that is also abundant, and which normally escapes from *Myrmeleon* traps (pers. obs.). The first three treatments were designed to simulate different situations of prey availability (absent, low, and high) of ants that are readily retained once they fall into a trap. The fourth treatment was designed to simulate the condition in which prey are abundant but difficult to retain (i.e., high encounter probability but low retention probability) in order to determining the possible changes in trap depth and/or wall angle (see Table 1). In all cases the ant prey was placed in the trap with forceps to standardize prey introductions, a technique following GRIFFITHS (1980, 1986) and WILSON (1974). We ran the experiment for 24 hr, and then measured the diameter, depth, and angle of each trap. We used repeated measures ANOVA to determine changes in the variables before and after the manipulation of density and type of prey. A significant interaction between time (before and after) and treatment would indicate that antlions under some treatments altered their pits more in 24 hr than those under other treatments.

RESULTS AND DISCUSSION

Myrmeleon sp. larvae responded quickly to different conditions in prey availability and prey type. In a 24 hr period, the larvae changed the trap characteristics in ways that would increase their consumption rate (Table 2). Additionally, none of these changes were correlated with larval body size (diameter: $R^2 = 0.04$, F = 1.48; depth: $R^2 = 0.05$, F = 1.75 ; angle: $R^2 = 0.01$, F = 0.43; $P > 0.19$ in all cases).

The larvae that captured many prey (T3) did not change the features of their trap. This pattern may result because the larvae invested much time in feeding thus reducing the time available for changing pit architecture. Nonetheless, we observed that these larvae had enough time between feeding periods that could have been used for modifying their traps. Consequently, this result supports the idea that the larvae in T3 did not change the design of the trap because of the rate of prey consumption. A high consumption rate implies a relatively efficient trap design. Larvae that either did not capture prey at all or had low prey capture rates significantly increased their trap diameter, a modification that increased the probability of prey encounter. Given that even small increases in pit width can increase prey capture rates (see GRIFFITHS 1980), the increment obtained in our experiment (6-9 mm) may greatly increase the probability of prey capture under natural conditions. From these experiments we want to point out that: (1) the increase in diameter (T1 > T 2 > T3) followed an inverse relation with respect to the abundance of ants offered to

Table 2.

Mean (± 1 SD) of the diameter, depth, and wall angle of the traps of *Myrmeleon* sp. larvae in each treatment, before (above) and after (below) the experiment was conducted.

	No prey	Few prey, none escape	Many prey, none escape	Many prey, all escape
Diameter	43.3 ± 9.5	40.9 ± 4.6	38.4 ± 9.0	37.7 ± 7.1
(mm)	52.4 ± 5.0*	46.8 ± 3.1*	44.5 ± 7.4	49.0 ± 5.1*
Depth	19.1 ± 5.6	19.0 ± 3.6	19.1 ± 5.6	15.6 ± 4.6
(mm)	23.6 ± 2.7	21.6 ± 2.8	19.3 ± 4.7	23.6 ± 1.4*
Angle	50 ± 5	47 ± 5	46 ± 4	51 ± 8
(°)	48 ± 3	47 ± 3	49 ± 4	48 ± 3

Source of variation (df)	pit diameter	pit depth	wall angle
Treatment (3)	1.65	0.99	0.55
Before/after (time) (1)	88.41 **	17.23 **	0.03
Time × treatment (3)	4.30 **	3.20 *	1.85

Summary of results of repeated-measures ANOVAs (F values) designed to test the effect of different availability and type of prey (treatments) on pit design (see text for more explanation). * = $P < 0.05$, repeated measures ANOVA; ** $P < 0.01$.

these predators (none, few, many). This finding supports the idea that the antlions can rapidly respond to improved rates of prey capture. (2) None of the *Myrmeleon* sp. larvae in treatments T1-T3 significantly changed the depth of the traps, suggesting that larvae can change only those features of the trap that are expected to increase consumption rate.

In contrast to our original prediction, none of the larvae changed the angle of the pit trap in response to experimental manipulations. Modifications to the angle of repose are probably constrained because steeper walls are harder to maintain (see Lucas 1982). However, trap depth was increased significantly by larvae from which all prey escaped. An increase in depth reduces the probability of escape (Griffiths 1980, 1986). Therefore, this result again supports the idea that the larvae change those characteristics of trap design that lead to an increased probability of capture. In this instance the perception of the *Myrmeleon* sp. larva could be that its trap is efficient enough for the ants to fall into but inefficient in retaining them, so the larvae respond quickly with an average increase of 51% in trap depth. This increment is not a result of the experimental manipulation, because each time that the larva fought to retain a prey, the walls partially slid down and trap depth decreased. Consequently, an increase in depth of the traps at the end of the experiment resulted from active behaviour of the larvae. Trap diameter also increased significantly in this treatment. We argue that such an increase is a consequence of the increase in depth. Increasing the depth without an increment in diameter will initiate a landslide of the walls when the angle becomes too acute. Maintaining the angle of repose imposes limitations on the modifications of trap and diameter (LUCAS 1982). In addition, the modification of a trap to minimize the probability that prey escape is beneficial only if such a change does not reduce the probability that prey falling into a trap.

The results of this experiment are the opposite to those reported by GRIFFITHS (1986), who found that trap diameter was reduced after holding larvae for a 15-day period of starvation. The different temporal scale and the positive relation between size of the larva and size of the trap (WILSON 1974; MCCLURE 1976; GRIFFITHS 1980, 1986; GOTELLI 1997) may explain such differences. After long periods of low feeding regimes the larvae have relatively lower development, and build smaller traps than larvae under better feeding regimes and consequently bigger in body size (GRIFFITHS 1980, 1986). The short-term responses of *Myrmeleon* sp. we found differed from middle term responses (see also HEINDRICH & HEINDRICH 1982), and these modifications were independent of the size of the larvae. This implies that the changes in the trap design were not the result of morphological variation or growth of the larvae, but of their ability to adapt to different situations of prey availability and type. This flexible behaviour has possibly been selected as a way to survive in poor environments with unpredictable prey availability.

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