Foraging in the Ant-Lion *Myrmeleon mobilis* Hagen 1888 (Neuroptera: Myrmeleontidae): Behavioral Flexibility of a Sit-and-Wait Predator

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The relative effects of foraging benefits (food intake) and costs (disturbance = pit destruction) on growth rate and foraging behavior of larvae of the ant-lion Myrmeleon mobilis *were investigated. In a laboratory experiment second-instar larvae were subjected to combinations of three rates of feeding and three rates of disturbance. Pit relocations were generally rare but occurred more often in starved larvae. Disturbance rate had no significant effect on pit relocation rate. Feeding rate was a major determinant of the energy allocated in pit construction and maintenance (positive relationship). In a second experiment third-instar larvae encountered changing rates of disturbance. Pit size was reduced as a response to increased rates of disturbance. Disturbance had no detectable effect on growth. In general, M.* mobilis *larvae were cost-conservative foragers.*

INTRODUCTION

The larvae of many species within the family Myrmeleontidae are sit-and-wait predators that capture arthropod prey in conical pit-traps dug in loose substrate. As unreproductive feeding stages nearly all of the ant-lion's behavioral traits are directly related to foraging (Heinrich and Heinrich, 1984). Therefore and because of the fact that it is easy to define and measure these traits, ant-lions are ideal subjects for testing general theories of foraging and intraspecific com-

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petition (McClure, 1976; Griffiths, 1980, 1986, 1993; Heinrich and Heinrich, 1984).

Foraging theory assumes that, within a certain range of environmental conditions, and taking into account functional limitations of the forager (e.g., its limited ability to collect and process information), foraging individuals behave optimally with respect to maximizing their fitness (Pyke, 1984; Stephens and Krebs, 1986). As foraging conditions vary both spatially and temporally in most natural habitats, a forager's set of behavioral traits should show an appropriate amount of flexibility to maximize foraging efficiency. Simplified, pit-trapping ant-lions may respond behaviorally to changing environmental conditions in three general ways. First, the parameters determining pit morphology can be modified, e.g., by altering the diameter and depth of a constructed pit or by altering the amount of energy allocated in pit maintenance. Second, ant-lions might alter the amount of time that is spent pit-trapping. And third, they can relocate their pits. This experimental study addresses the question of how larvae of the ant-lion *Myrmeleon mobilis* make use of these alternative possibilities when faced with varying levels of foraging benefits (food intake) and costs (disturbance = pit destruction).

Pit morphology is a major determinant of capture success in ant-lions. Capture success increases with pit diameter (Wilson, 1974; Griffiths, 1980) and pit slope (Lucas, 1982). Furthermore, for a given arthropod abundance in a specific habitat, the prey encounter rate will inevitably increase with the pit diameter. Griffiths (1986) suggests that an optimal pit size exists for a given size of larva which maximizes the net rate of energy gain. His experiments provide evidence for the hypothesis that pit construction activity depends on both past and present foraging success in African *Macroleon quinquemaculatus* and that pit size is generally determined by energy gains (food intake) and costs (e.g., disturbance) (Griffiths, 1986). In captivity as well as under natural conditions ant-lions occasionally can be observed to relocate their pits. Prolonged starvation is known to trigger movements in some species (Heinrich and Heinrich, 1984; Matsura and Murao, 1994), whereas others rather die at the base of their pits (Matsura, 1987). Generally, ant-lions should move their pits if the benefits of moving exceed the costs, e.g., the danger of predation while moving or the risk of not finding any suitable site. Possible benefits include increased foraging success and decreased likelihood of disturbance (Griffiths, 1986).

An ant-lion's foraging behavior should reflect the benefits and costs encountered at its particular foraging site. In the present experimental study both variables, food availability (benefits) and frequency of disturbance (costs), were manipulated to evaluate their influence on growth rate and foraging behavior of *Myrmeleon mobilis* larvae. Effects on three variables were studied: probability of pit relocation, pit diameter, and time until reconstruction of pits following disturbance.

The Species

M. mobilis occurs in the southeastern United States and larvae are generally found in finer soils in sheltered areas (Lucas and Stange, 1981), e.g., at the base of small cliffs, underneath protruding roots of trees, or under various artificial shelters (e.g., car shelters). Occasionally large aggregations are observed. Food availability and the frequency of disturbances are likely to vary both spatially and temporally in the ant-lion's natural habitit. Seasonal variation in general arthropod abundance is probably a major determinant of food availability, but the exact spatial placement of the pit may also be important. In high-density aggregations foraging success is likely to be affected by intraspecific exploitation competition (Wilson, 1974; Griffiths, 1980, 1993). Disturbance (partial or complete destruction of the pit) may come from various sources, e.g., from inanimate objects falling into the pits, large animals, or simply bad weather conditions such as rainfall or strong wind. Rainfall is a major source of disturbance in aggregations of a Panamanian species of *Myrmeleon* (personal observation). In certain circumstances there might also be a tradeoff between the two factors. Pit sites are relatively exposed and therefore suitable in terms of their prey encounter rate (e.g., pits placed in the periphery of aggregations) are likely to be prone to disturbance.

The behavioral patterns of pit construction of second- and third-instar larvae of *M. mobilis* are very similar to those described for *Myrmeleon immaculatus* by Tuculescu *et al.* (1975). The average pit size of 6-day-old pits of well-fed, undisturbed second-instar larvae is 34.8 ± 7.4 mm (range, 18–48 mm; $N = 24$). Third-instar larvae construct larger pits (43.5 ± 6.0 mm; range, 27–53 mm; $N = 24$; t test, $P < 0.0001$). In third-instar larvae there is a positive linear correlation between pit diameter and depth ($r^2 = 0.84$, $P < 0.0001$).

MATERIALS AND METHODS

All larvae of *M. mobilis* were collected from a large aggregation at Duke field station, Durham, North Carolina, and kept individually in 16 × 12 × 6-cm plastic boxes filled with substrate (minimum depth, 4 cm) from their original site. Nonflying *Drosophila melanogaster* (mutation "curly") served as reliable and uniform food (0.7–1.5 mg). To ease handling, the flies were immobilized with ethyl acetate or CO_2 before they were dropped into the pits. Disturbance was simulated by simply refilling the pits with substrate from the edge of the pit. A piece of cardboard was used for that purpose. Pit destruction did not alter the position of larvae within their boxes and was usually carried out in the early afternoon. Pit diameter was measured to the nearest millimeter using calipers. In the common case that the pits were slightly elliptical, I recorded the shortest diameter.

All larvae were kept under the same climatic conditions at a fixed photo-period of 12 h. Room temperature varied between 20 and 24°C. During daytime the substratum in the plastic boxes was additionally heated (up to 28–30°C) by 150-W light bulbs, which were installed 1.2 m above the experimental setup. The relative humidity in the room varied between 40 and 70%.

Two experiments were carried out.

Forty-Eight-Day Combined Treatment Experiment

Second-instar larvae were randomly assigned to nine groups, each contain-ing 12 individuals. Three rates of feeding (every second day, every sixth day, starvation) were combined with three rates of disturbance (none, every sixth day, every second day). Before the experiment was started all larvae were fed one *Drosophila* per day for 5 days. All larvae were weighed at the beginning of the experiment and after 48 days. I recorded the location of the pits of all larvae every second day during the whole experiment. For this purpose the available arena (15 × 12.5 cm) was divided into 2.5 × 2.5-cm subsquares. An ant-lion was recorded as "moved" if the center of its pit was found at least two subsquares away from its original position. Additionally, I kept the surface of the substratum smooth to be able to detect the tracks of moving larvae. Usually both methods yielded consistent results and allowed detection of movements. The pit diameter of all larvae was measured every 6 days before pits of the disturbance groups were destroyed. To assess treatment effects on the time the individuals were actively foraging (had active pits), I observed larvae following disturbance. On days 12, 18, 24, 30, 36, and 42 of the experiment, when pits of all disturbed larvae were destroyed, I counted the number of individuals that had started reconstruction until 20 and 60 min after disturbance and the number of individuals that had completed reconstruction after 60 min.

Seventy-Four-Day Disturbance Experiment

This experiment was carried out to test if *M. mobilis* larvae adjust pit size responding to a given rate of disturbance. Third-instar larvae (14.0 to 22.5 mg) were assigned to two groups, each containing 12 individuals. All larvae were fed one *Drosophila* every second day during the whole experiment. For the first 20 days and the last 18 days of the experiment they were also subject to an equally low rate of disturbance. Pits were destroyed every sixth day. Between day 18 and day 54 the disturbance rate of one group was shifted to a higher level (every second day). The diameters of 2-day-old pits of all individuals were measured every sixth day during the whole experiment.

M. mobilis larvae frequently enlarge their initial pits on subsequent days. Therefore an observed change in pit size following an increased rate of distur-bance might come from two behavioral responses: (i) changes in size of the

initial pit and (ii) an alteration of the likelihood of enlarging the initial pit. To evaluate these two possibilities the pits were measured daily for 6 days after the end of the treatment period (on days 55 to 60).

All larvae were weighed before and after the experiment.

RESULTS

Forty-Eight-Day Combined Treatment Experiment

Foraging Time

Pit reconstruction of disturbed larvae usually took place immediately after destruction. On days when reconstruction was observed an average of 50% of the disturbed individuals had started excavations after 20 min following destruction and 80% had done so after 1 h. Fifth-five percent of the larvae had already completed reconstruction during the first 60 min after disturbance. Only on rare occasions did ant-lions delay pit reconstruction until the next day. This response pattern was very stable throughout the whole experiment and did not depend on treatment (ANOVA, tests for effects of feeding rate, disturbance rate, and time: all N.S.). Even starved or highly disturbed larvae did not show measurable changes in response time toward the end of the experiment. Undisturbed larvae, aside from short interruptions while moving, maintained pits continuously throughout the experiment.

Pit Diameter

Figure 1 shows mean pit diameters of all groups as a function of time. Groups with the same rate of disturbance are plotted together. Measurements were carried out every sixth day of the experiment before pits of the disturbed groups were destroyed. As a result, the three graphs show changes in diameter of pits of three age classes depending on the disturbance regime [2 days (Fig. 1c, high rate), 6 days (Fig. 1b, low rate), and as old as the experiment (Fig. 1a, no disturbance)]. Therefore, the data can be used only to test for the effects of feeding rate. Only larvae that did not move or molt during the whole 48-day-period were included in the analysis. Linear regressions were calculated for each group. Coefficients and significance values are given in Table I.

Feeding regime had a strong effect on energy allocated in pit construction and maintenance. For all groups with an equal disturbance regime (equal pit age), the change of pit diameter over time (slope of regression line) was dependent on the feeding rate (two-way ANOVA with significant interactions between independent variables day and feeding rate: no disturbance, $F = 15.74$, $P < 0.001$; low rate of disturbance, $F = 26.45$, $P < 0.001$; high rate of disturbance, $F = 16.73$, $P < 0.001$). The general pattern of these results (well fed >
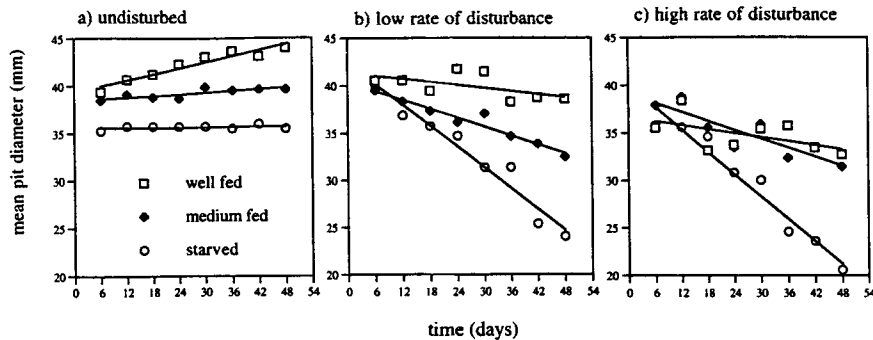
Fig. 1. Mean pit diameter of nine groups of second-instar larvae of *M. mobilis* as a function of time. Groups with identical disturbance regime are plotted together. Note that graphs show pit diameters of pits of three age classes depending on disturbance rate: (a) no disturbance, pits as old as the experiment; (b) low rate of disturbance, pits 6 days old; (c) high rate of disturbance, pits 2 days old. Coefficients and significance values of regression lines are given in Table I.

medium fed > starved) is consistent among groups with different levels of disturbance. For undisturbed larvae, however, the situation is principally different. As pits were never destroyed, the graph shows the changes in mean diameter of the same pits over the entire duration of the experiment. Pits became significantly larger in well-fed and medium-fed larvae, while those of starved larvae did not change at all. In disturbed larvae the pit diameter remained unchanged in well-fed larvae but decreased in all other groups. Starved ant-lions generally showed the most pronounced reduction in pit diameter.

Table I. Coefficients and Significance Values for Diameter Regressions in Each Group of Second-Instar Larvae in the 48-Day Experiment (See Fig. 1)

Treatment (disturbance)/feeding rate	Slope	N	P (t statistic)	R^2
No/well	0.11	9	<0.001	0.90
No/medium	0.03	11	<0.05	0.64
No/starved	0.005	4	N.S.	0.08
Low/well	−0.05	7	N.S.	0.35
Low/medium	−0.15	11	<0.001	0.91
Low/starved	−0.36	6	<0.001	0.91
High/well	−0.09	8	N.S.	0.31
High/medium	−0.16	9	<0.05	0.87
High/starved	−0.39	5	<0.001	0.95

Pit Relocation

During the 48-day period 46 pit relocations were recorded. *M. mobilis* larvae did not move at all during the first 2 weeks of the experiment. In the following weeks the number of relocations increased progressively. The feeding regime strongly affected the individual likelihood of pit relocations (Kruskal–Wallis ANOVA by ranks, $H = 28.86$, $P < 0.0001$), with starved ant-lions accounting for 85% of all recorded movements. No further simultaneous testing of feeding treatments was done, but there appeared to be no difference between well-fed and medium-fed larvae. Disturbance had no effect ($H = 2.19$, N.S.).

Generally second-instar larvae of *M. mobilis* were extremely sessile and only relocated their pits when starved for a considerable time. Only 26 of 108 larvae (24%) moved at least once during the 48 days (19 of 36 starved larvae; 53%). Thirteen individuals, all in the starvation groups, moved more than once, two of them even four times. The average time between movements of individual ant-lions (residence time at new pit sites) was 8.3 days ($N = 21$; range, 2 to 24 days).

Treatment Effects on Growth and Survival

To assess the effects of the treatment combinations on growth of individual larvae, ratios of body weight before and after the experiment were calculated and analyzed with ANOVA. Changes of body weight during the experiment were strongly affected by feeding regime (ANOVA, $F = 126.22$, $P < 0.001$) but not by rate of disturbance ($F = 2.94$, $P > 0.05$). Well-fed larvae (one *Drosophila* every second day) nearly doubled their weight (75–101% increase), while starved larvae showed a clear reduction (33–41% decrease). Medium-fed ant-lions (one *Drosophila* every sixth day) hardly changed in body weight at all during the 48-day period. There was no indication that an increased rate of pit destruction results in a decreased growth rate. Undisturbed larvae showed the highest increase/lowest decrease in body weight in all feeding regimes, but there was no consistency of this trend among the groups with low and high rates of pit destruction (every sixth and every second day).

During the course of the experiment 13 larvae molted. This was indicated by a sudden stop of pit-tending activities approximately 6 days prior to the actual molting. Of the 13 individuals, 11 belonged to one of the well-fed groups and 2 were medium-fed. In general, mortality was very low ($N = 4$ deaths) during the course of the experiment. In all groups larvae constructed and maintained pits throughout the 48-day period.

Seventy-Four-Day Disturbance Experiment

Third-instar larvae apparently adjusted pit size to an experienced rate of disturbance (Fig. 2a). Larvae in the treatment group (shift from a disturbance
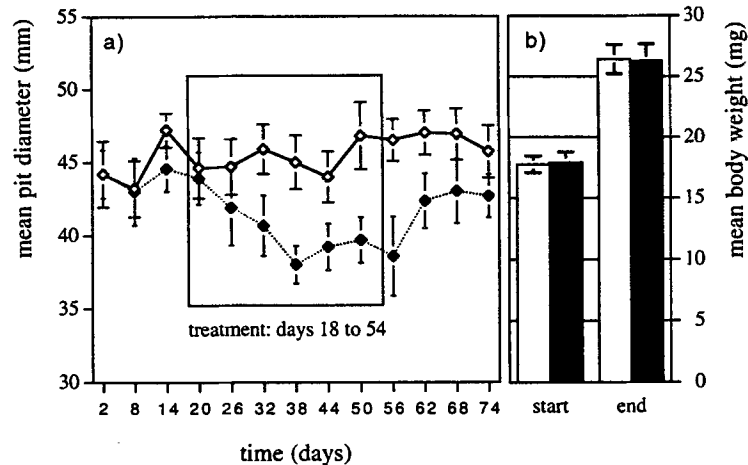
Fig. 2. Effects of an increased rate of disturbance on third-instar larvae of *M. mobilis* during the 74-day disturbance experiment: (a) mean pit diameter (and standard error) as a function of time of treatment (♦) and control (◇) larvae. Between day 18 and day 54 the rate of disturbance was shifted from low (every 6 days) to high (every 2 days) in the treatment group. Two-day-old pits were measured. (b) Changes in mean body weight (and standard deviation) of treatment (black) and control (white) larvae. Individuals were weighed at the beginning and at the end of the experiment.

rate of once every 6 days to once every 2 days) significantly reduced the diameter of their pits until day 56 (Kendall rank correlation; $t = -0.69$, $N = 9$, $P < 0.01$). No change was observed in the control group ($t = 0.33$, $N = 10$, $P > 0.05$). Only larvae that did not move during the experiment were included in that analysis. After 18 days of increased disturbance the rate of decrease in pit diameter seemed to slow down. Between day 38 and day 56 the mean pit diameter remained fairly constant at a level that was on average 6.7 mm (15%) below the corresponding measurements taken from the control group. This is equivalent to a 39% reduction of pit volume (calculations based on the positive linear correlation between pit depth and diameter). After the reestablishment of the original low rate of disturbance, the mean pit diameter increased again and approached a level found in the control group.

After the end of the treatment period the size development of the pits was monitored for 6 days (days 55 to 60, daily measurements) in both groups (Fig. 3). Larvae in the control group constructed large initial pits and did not enlarge them during the consecutive days (Kendall rank correlation; $t = 0.28$, $N = 10$, $P > 0.05$). Highly disturbed larvae, in contrast, built comparatively small initial pits. In this group, the mean pit diameter increased significantly within the 6 days ($t = 0.73$, $N = 9$, $P < 0.05$). However, the pit enlargements did not completely erase the overall difference between the two groups.
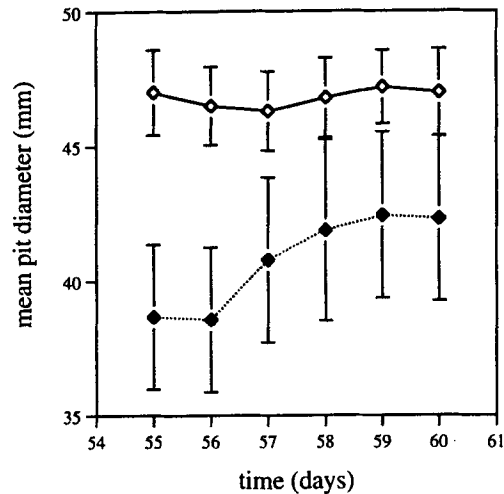
Fig. 3. Mean pit diameter of treatment (◆) and control
(◊) larvae on 6 consecutive days following the treatment
period (days 18 to 54; disturbance experiment). See text
for further specifications.

At the beginning and at the end of the experiment all larvae were weighed
and growth ratios were calculated. In both groups larvae showed an average
increase in body weight of 48% (range for individuals, 31–63%) after 74 days.
Increased disturbance treatment had no effect on growth. Growth ratios were
essentially equal in the treatment and control group (Fig. 2; t test; $t = 0.26$,
N.S.).

DISCUSSION

Prolonged starvation (>2 weeks) resulted in an increased likelihood of pit
relocation in $M.$ $mobilis$ larvae. In contrast, both well-fed and medium-fed larvae
exhibited an extremely sessile foraging strategy and almost never relocated their
pits. Well-fed larvae showed the expected strong increase in body weight during
the experiment and their reluctance toward relocations is not surprising. How-
ever, in the case of medium-fed larvae the treatment was by far less beneficial.
A zero mean growth rate was tolerated for 48 days without increasing the like-
lihood of movements. Increased rates of disturbance equally failed to provoke
pit relocations.

Why are $M.$ $mobilis$ larvae that sedentary? Faced with inferior foraging
conditions (high costs, low benefits) at a given pit site, an ambushing larva can
either reduce foraging costs (e.g., build smaller pits) and endure present con-

ditions or engage in increased foraging activity (e.g., move) to improve its situation quickly. *M. mobilis* larvae clearly preferred cost reduction. In the present study the changes in pit diameter over time in second-instar larvae was strongly dependent on feeding regime. Reduced food availability resulted in smaller pits. Furthermore, third-instar larvae reduced pit size as a response to increased disturbance. These results are in agreement with Griffiths' (1986) pit size model developed for *Macroleon quinquemaculatus*, which assumes that pit size is determined by energy inputs and costs. Another way of diminishing foraging costs is the reduction of the respiratory rate while ambushing. Recently, Matsura and Murao (1994) showed that larvae of three species of ant-lions (*Myrmeleon bore*, *M. formicarius*, and *Hagenomyia micans*) considerably reduced their respiration rates following the onset of starvation (76 to 84% reduction). No data exist for *M. mobilis*.

A cost minimizing strategy, however, will produce some shortcomings, too. Decreased pit size, e.g., will have a negative effect on future prey encounter rates and/or capturing success (Griffiths, 1980, 1986; Heinrich and Heinrich, 1984). Low metabolic rates might influence the ability of larvae to handle large prey and therefore also reduce capturing success. However, cost reduction will be an advantageous strategy if there is a high probability that an encountered food deprivation derives from temporal rather than spatial variation in prey abundance. In this case the alternative strategy, pit relocation, will not result in the expected increase in food intake. I hypothesize that the foraging behavior of *M. mobilis* larvae has evolved mainly to track temporal variation in prey abundance in its seasonal habitat. To respond to spatial variation larvae would need to sample the habitat for obtaining a reliable estimate of general prey abundance. This would imply frequent pit relocations, which are not observed in *M. mobilis* and most other ant-lion species investigated so far. It is reasonable to assume that in terms of food availability, the environment represents a black box to a foraging ant-lion. In this respect ant-lions seem to differ principally from other trap-building sit-and-wait predators, e.g., orb-weaving spiders (Olive, 1982) and net-spinning caddis larvae (Townsend and Hildrew, 1980), which are less sedentary. The observed infrequent pit relocations in *M. mobilis* are not likely to serve as a means of obtaining an estimate of the average prey availability in the habitat but rather appear to be a last desperate measure to escape starvation. Matsura and Murao (1994) suggest that larvae of *Hagenomya micans* follow a certain "giving-up time rule" that involves pit relocation at a fixed level of exhaustion, e.g., measured as a certain rate of decrease in body weight. Such a state-dependent shift in behavioral response might be based on a shift in the currency that a foraging larva attempts to maximize. After prolonged starvation lifetime becomes a limiting factor and ant-lions should abandon their cost-conservative foraging strategy, which is designed to maximize long-term energy gain. Instead they should shift to a strategy that is more costly in terms

of short-term energy expenditure but minimizes the risk of starvation (see Real and Caraco, 1986; Stephens and Krebs, 1986).

ACKNOWLEDGMENTS

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