

# The pit-trapping foraging strategy of the ant lion, *Myrmeleon immaculatus* DeGeer (Neuroptera: Myrmeleontidae)

Bernd Heinrich and Margaret J.E. Heinrich

Department of Zoology, University of Vermont, Burlington, Vermont 05405, USA

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**Summary.** Larvae of *Myrmeleon immaculatus* in large pits captured both large and small prey, while larvae in small pits captured only the small prey. Larvae in small pits did not respond to large ants, although they always responded by sand-flinging to small ants. Larvae in medium-sized pits often captured large ants only after prolonged and vigorous sand-flipping. Larvae in large pits usually captured large ants with relatively little sand-flipping. Pit enlargement and pit relocation in the laboratory were not significantly correlated with reduction of rations in the first 3 weeks after a pit was built. However, after a month without food, larvae on the average moved once every 10 days, built successively smaller pits, and moved longer distances before building a new pit. In the field pits were dug primarily in response to microclimatological factors and possibly edge-effects. The presence or absence of suitable prey at a site, per se, had no effect on whether or not a larva would dig a pit there. We conclude that these sit-and-wait predators have a relatively large repertoire of behavior that enhances their foraging success, and we contrast it with previously made optimal foraging models relating to pit locations, pit relocations, pit size and ant lion responses.

## Introduction

The larvae of many species within the family Myrmeleontidae are semisedentary predators that capture small arthropod prey in pit-traps dug in loose sand. Their unique method of foraging enables ant lions to capture a wide range of prey types, including many that are much larger and/or faster than the larvae themselves.

While the novelty of their pit-trapping technique has long been of fascination to naturalists (Turner 1915; Doflein 1916; Wheeler 1930), ant lions have also recently been identified as highly appropriate subjects for testing current general theories of foraging and intraspecific competition (Wilson 1974; McClure 1976; Griffiths 1980a, b). This is largely because of the relative ease of defining and measuring behaviors associated with pit-trapping. Additionally, these animals are reproductively inactive, non-territorial and appear to suffer little predation; hence, nearly all of their activities are directly related to foraging.

Ant lions could conceivably have considerable flexibility in their foraging behavior. Pit size, frequency of pit enlargement, duration of tending a given pit, pit location, and vigor of response to potential prey which fall into their pits are all variables which could affect the costs and benefits of foraging. Recent studies on the ecology of ant lions have addressed the question of their foraging 'optimality' (Wilson 1974; McClure 1976; Griffiths 1980a, b). However, these authors arrive at contradictory sets of conclusions.

We undertook this study with the primary goal of trying to clear up the confusion of what ant lions are and aren't doing, and to try to gain insight into the evolution of pit-building behavior.

## Materials and methods

All of the ant lions of this study were derived from an approximately 100 m long stretch of south-facing sandy beach of Mallets Bay on Lake Champlain near Burlington, Vermont. The ant lion larvae were located in a strip of sand approximately 4–15 m from the shoreline of the lake, where the vegetation began to join the beach. Ant lion larvae from this site were also observed after being transferred into beach sand placed on a south-facing slope of a hill in Maine.

Pit diameters and depths were measured to the nearest mm. Mass of ant lions was determined to the nearest 0.1 mg using a Roller-Smith Precision torsion balance. Soil and air temperatures were taken with a thermocouple probe and read to the nearest 0.5 °C with an Omega Engineering thermocouple read-out meter.

We experimentally examined prey-capture in the field by releasing ants of known size near pit rims. Response of larvae to prey and the success or failure of attempts to capture the prey was scored in those instances where the ant ran into the pit. (Ants that were dropped directly into the centers of pits were nearly always captured immediately and had almost no chance of escaping. Thus, we were careful to avoid data from such unnatural situations in our analysis). Only first encounters were used to determine capture success.

We censused natural prey capture in the field by examining the corpses at the periphery of pits. In addition, we directly observed 100 pits 1 h a day for 5 days and recorded natural prey encounters and capture success.

In addition to the field observations, we conducted several summer-long experiments in the laboratory. For these, one larva each were placed in at least 7 cm of sand in open cardboard boxes, most of which were 0.2 m<sup>2</sup>. Although ambient temperature was not controlled, all experimental groups for a given experiment were observed simultaneously, so variations in temperature should not affect differences detected between groups. Statistical significance was determined by Student's *t*-test and by  $\chi^2$ , as appropriate.

## Results

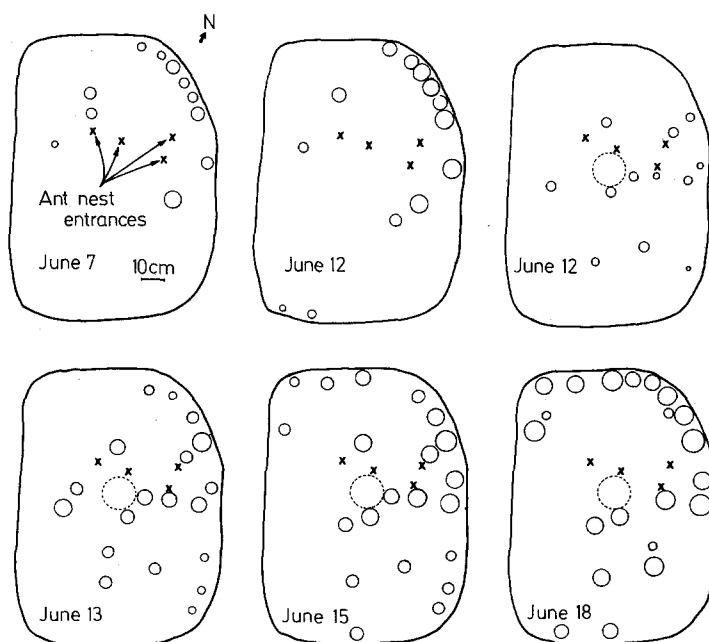
### Habitat

The pits can only be dug in loose, dry sand. Thus, suitable pit-sites are generally restricted to open sandy habitat. We found pits only along the beach close to the vegetation, and under bank or log overhangs.

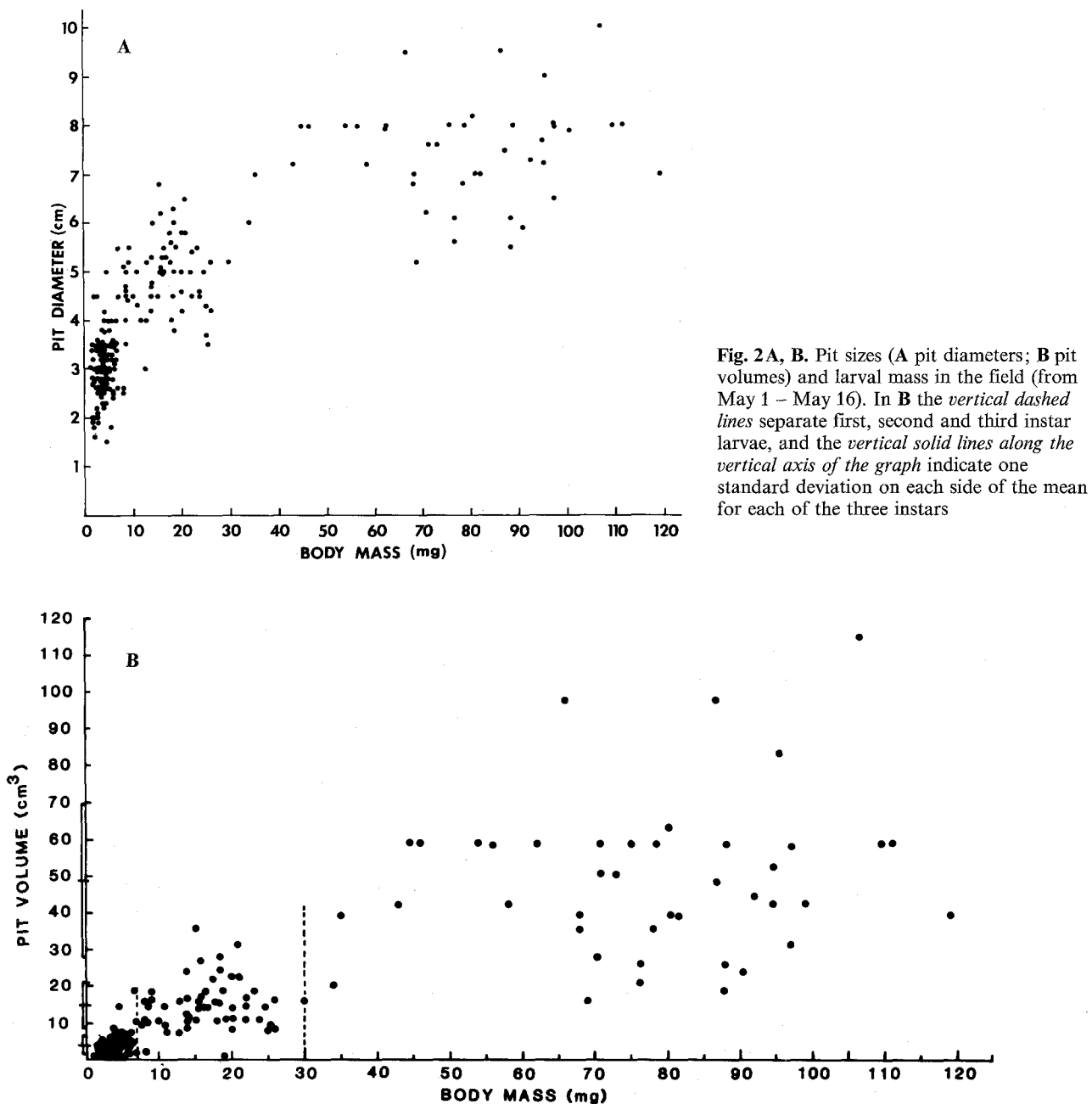
High temperature may be a constraining factor in open habitat. For example, on 5/4/81 at 1220 h we observed sand surface temperature of 57 °C on the beach. All the pits in direct sunshine at that time were inactive; the larvae had burrowed deeper, away from the apex of the pit, and the pits were partially filled in near the bottom. Other nearby pits in partial shade (at the vegetation edge) were not filled in and the larvae were in attendance at the pit apex. The highest concentration of pits we observed was in shade (at noon) under a tree trunk that lay nearly horizontally several cm above the sand.

In contrast to the above observations along the beach of Lake Champlain where sand temperatures were almost always above 55 °C in noon sunshine, we observed apparent heat-seeking behavior in 25 larvae that we transplanted to a 70 × 100 cm sand patch we created at the edge of a small forest clearing, on a hill in Maine. In this patch of sand, temperatures at the surface did not exceed 46 °C in direct sunshine, and on May 16 (a week after they had been released) the larvae's pits were located primarily along those edges of the sand patch that received the most direct sunshine throughout the day. By June 12 most of the pits (9 out of 13 or 69.2%) were still located along the side of the patch that received the most direct sunlight during the day (Fig. 1).

We dug the ant lions from all of the 13 pits mentioned above and released them in the center of the same patch of sand to observe the subsequent placement of new pits. Within 4 h 12 new



**Fig. 1.** Pit location and pit diameters (drawn to scale) of a small population of ant lion larvae captive on a small patch of sand in an overgrown field on a hillside in Maine. The northern corner received the most direct sun throughout the day. The southwest side was shaded by shrubs. x's indicate entrance holes of an ant colony. On June 12 all of the ant lions from functional pits were excavated and released in the center of the plot (dashed circle), and by the next and subsequent days the newly-dug pits tended to be located away from the shaded portion, and along the periphery of the sunny side of the plot



pits had been dug, but only 3 of them were on the periphery of the sand patch. Three days later 21 occupied pits were visible (apparently at least 8 larvae were not occupying visible pits when the patch was observed on June 7 shortly after a rainy day), and on three observations over the next 5 days (Fig. 1) the percentage of the pits that were located in the patch periphery increased from 25% to 47.6, 57.1 and 66.6% respectively. The distribution of pits after the 5th day resembled the original distribution seen on May 16. As before, the side of the sand patch that received the fewest hours

of direct sunshine contained the fewest pits. The larvae made no apparent attempt to place their pits near these ant nest entrances (Fig. 1). A large *Formica* sp. colony (1 m diameter) was located within 2 m of the south-east corner of the plot, yet most of the pits were ultimately located at the northern end of the plot.

We do not know if ant lion larvae avoid each other in areas of suitable habitat. However, pits are commonly close enough together that while one larva is excavating its pit, it is flinging sand into the pit of another larva. When ant lion larvae

move about on the same surface they could enter the pits of neighbors, where they could potentially become prey, or be predators that take over the already made pits for their own use. It is likely, however, that ant lion larvae avoid direct contact. We observed that when larvae encounter a pit they turn away, moving along the pit periphery. If a larva is placed part-way into a pit it always backed out, rather than backing in. Larvae rarely entered and utilized another pit when we replaced them into an enclosure with other existing (unused) pits. Larvae dropped into an empty pit, whether their own or that of another, left the pit.

#### Pit size

In early spring (May 1-May 10) the diameters of pits in the field varied approximately 7-fold, from 1.5 cm to 10 cm, whereas larval mass varied 60-fold, from 2 mg to 120 mg. Thus, small larvae were tending disproportionately larger pits than large larvae.

In general, large larvae occupied larger pits than small larvae (Fig. 2). However, larvae of any given mass had pits varying 2-fold in diameter, while a pit of given diameter could contain larvae varying up to 10-fold in mass.

Pit diameter provides an indicator of how much surface area a larvae samples for prey, but pit volume gives a measure of the relative amount of work the larva invested to excavate the pit in order to trap in any one place. Pit volumes (calculated from measurements of pit depth and pit diameter) varied over 100-fold from 1 cm<sup>3</sup> to 115 cm<sup>3</sup>, and again showed considerable variation at any one body mass of occupying larva (Fig. 2B).

#### Prey capture in the field

Direct observations of prey capture in the field (from May 1-7) were made by five 1 h observation periods at a 0.63 m<sup>2</sup> plot originally containing 57 pits, and by another five 1 h observation periods at a 0.90 m<sup>2</sup> plot containing 48 pits. Additionally, we daily censused other pits in the study area for prey corpses.

In the two study plots the average daily number of pits under observation (104.6 pits) yielded 44 prey captures and 54 prey escapes during the 5 h of the 5 days. Thus, during the hours of observation (on sunny days, from 0940 h to 1625 h,  $T_a = 15-23^\circ\text{C}$ ) the average daily no. of prey captures for all of the 104.6 pits was 8.8. This corresponds to 0.084 captures per pit per hour; on the average, one of these pits captured one prey every 12 h.

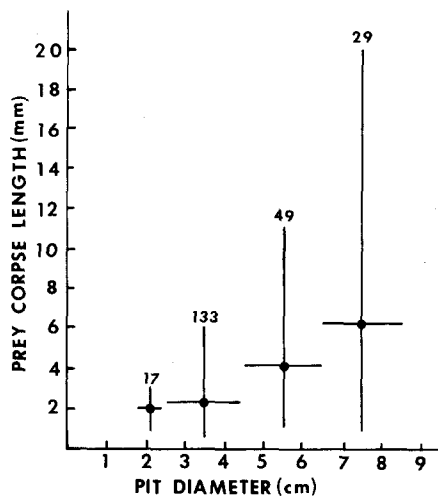


Fig. 3. Prey corpse lengths of observed captures or consumed prey near isolated pits in the field as a function of pit diameter. Vertical and horizontal lines indicate range. Numerals indicate number of prey in the respective size ranges of pit diameters

However, most of the prey (such as the mites and midges) under consideration here weighed less than a tenth of one mg. There was no consistent pattern in prey capture success during the day. In the times at which observations were initiated (0940, 1015, 1230, 1525, 1600 h), the combined prey captures (and escapes in parentheses) were 12(13), 5(10), 10(7), 7(9), and 10(6), respectively.

The majority (79) of the 228 observed prey were ants. In addition, the pits captured 36 spiders, 32 beetles, 27 midges, 21 red mites, 19 small wasps, two each of caterpillars, leafhoppers, millipedes and hemipteran bugs, and 6 other miscellaneous winged insects.

The largest pits caught the largest prey (Fig. 3). Pits near 2 cm diameter captured only prey 1-3 mm in length ( $\bar{x} = 1.9$  mm), while successively-larger pits captured larger prey, as well as the small prey. Mean prey length increased from 1.9, to 2.3, 4.1 and 6.2 cm, in pit diameters averaging 2.2, 3.5, 5.5 and 7.5 cm, respectively.

#### Larvae's response to prey

From the above data it was not clear whether the larvae in small pits did not attempt to capture large prey, or whether the small pits failed to hold the large prey. In order to systematically observe the larvae's response to differently-sized prey we staged encounters with small (*Leptothorax longispinosus*, length=3 mm, weight=<1 mg) and large ants (*Camponotus herculeanus*, length=9-

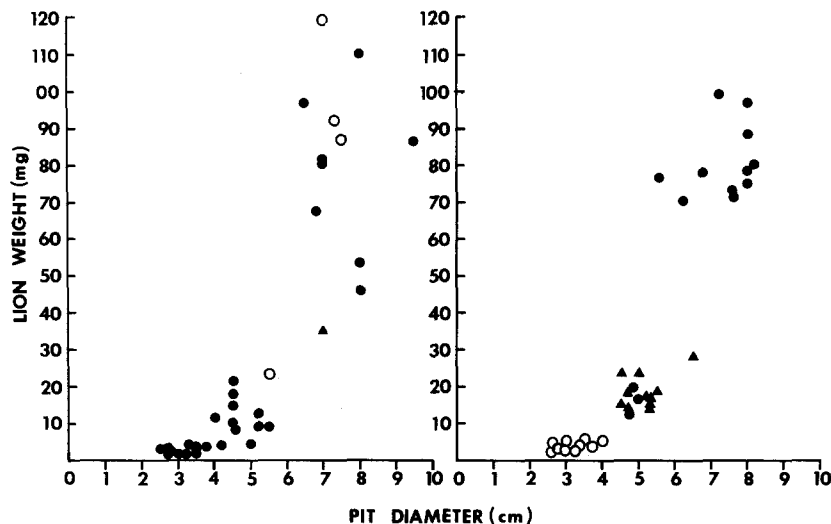


Fig. 4. The response of ant lion larvae of different weights (and/or different diameters of the pits they occupied) during staged encounters with small (left) and large ants (right). Left: *Leptothorax longispinosus* (length = 3 mm). Right: *Camponotus herculeanus* (length = 9–10 mm). ○: no response; ▲: sand flipping response but ant escapes; ●: successful capture of ant

10 mm, weight = 8–27 mg). The small ants did not escape from small pits (<5 cm diameter) with attending ant lion larvae from the first (presumably) larval instar (weighing <10 mg). When the small ants walked into the pits of the large (>30 mg) third instar larvae with pit diameters >6 cm, however, they sometimes escaped (Fig. 4). The small ants that escaped from the large pits often did not elicit the sand-flipping response of the attending larvae at the bottom of the pit.

In 10 encounters, none of the first instar ant lion larvae in pits of diameter from 2.5–4 cm captured the large ants, *C. herculeanus* (Fig. 4). However, none of these larvae responded by sand-flipping. The large ants did not escape from the large pits of third instar larvae, who invariably responded by sand-flipping until they captured the ant.

Whether or not a larva of a given body size and/or pit size captured an ant often dependent on the vigor of its sand-flipping response. First, second and third instar larvae that attempted to capture the small ants generally did so within 10 sand-flips (Fig. 5). Some (19%) of the third instar larvae did not respond at all to the majority (77%) made successful captures.

The response of the larvae to the large ants, *C. herculeanus*, differed greatly. None of the first instar larvae responded to these ants. Seventy nine percent of primarily second instar larvae (weighing 14–25 mg) responded by sand-flicking, and 6.7% of these were successful in capturing these large ants. It is therefore unlikely that the first instar larvae have a chance of capturing one of those ants, no matter how vigorous their sand flipping.

All of the third instar larvae (70–100 mg) responded to *C. herculeanus*, and 92% of these made successful captures. One last instar larva made 48 sand-flicks before it captured the ant in its pit. These results suggest that the third instar larvae can usually expect a payoff if they respond vigorously enough.

#### Ant capture without pits

A large (last instar) ant lion larva moving on the sand leaves a 1 cm wide trough as a record of where it has been. The trough or track has a sharp apex, like a pit; it resembles a small pit with a longitudinal axis. The larva's mandibles protrude from the sand at the point of the "track".

We smoothed the sand in a tray and allowed a larva to move over it and leave tracks. Ants were then released into the tray. The small (2–3 mm long) ants often used the larva's tracks as walkways for several cm, and when an ant reached the ant lion it frequently was caught. Large (5–6 mm) long-legged ants, such as *Formica*, on the other hand, seldom oriented to the track and were seldom captured without the use of fully formed pits.

#### Feeding capacity

Although larvae in the laboratory appeared to be healthy after nearly 2 months without food, they also have the capacity to utilize many prey when given the opportunity, and to grow rapidly. Four larvae with a mean weight of 13.8 mg were fed a total of 22 ants (*Formica* sp.) of mean weight 4.38 mg in 2 days, and then reweighed 2 days after

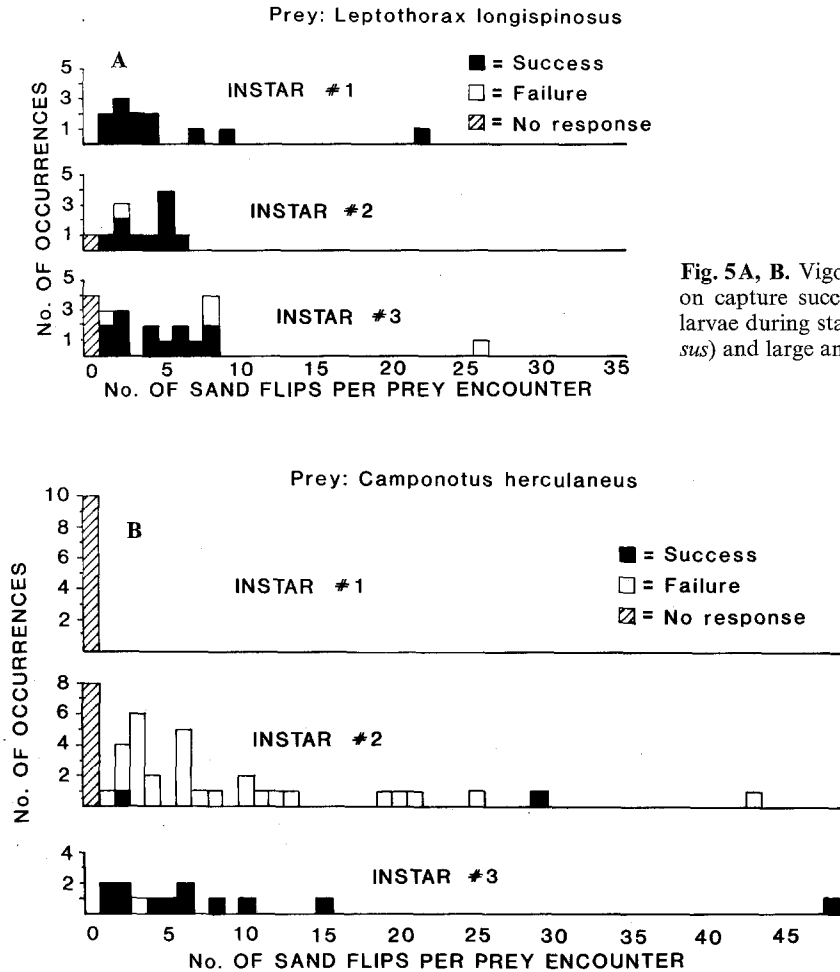


Fig. 5A, B. Vigor of response (in no. of sand flips) and effect on capture success of first, second and third instar ant lion larvae during staged encounters with small ants (*L. longispinosus*) and large ants (*C. herculeanus*)

the feeding. Their mean weight was now 25.8 mg. Thus, they had gained on the average 2.19 mg per ant eaten.

We fed a large (57 mg) larva 17 *Formica* ants, one after the other, in two days. The larva's weight increased to 98.0 mg, and it stopped tending its pit.

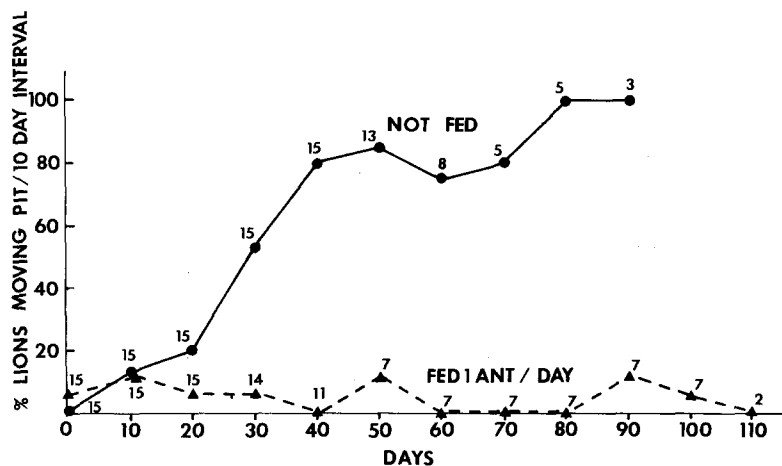
#### *Pit-building and prey-capture success*

The larvae are capable of rapid mobility, and digging is not a simple response to suitable sand. We released 106 larvae in the center of a 1.5–2.5 m diameter sandy area encircled by vegetation, having previously cleared all of the pits out of the surrounding area. Twenty one hours later highly curved trails were radiating in all directions from the release point, and 28 new pits were located within the area enclosed by the vegetation. (We do not know how many larvae travelled through the sand beyond the vegetation). Most of the 28 pits were near the edge of the vegetation. Few new

pits appeared over subsequent days. The density of pits (28 per 2 m<sup>2</sup> plot) was nearly 16 times less than that in a 0.5 m<sup>2</sup> section of one of our study plots, even though the same type of sand, from the same beach, was in both plots.

Does the presence of ants or their scent stimulate pit construction? We placed "clean" sand dug out of a gravel pit into two plastic trays with Fluon-coated sides. Fifty ants (*Formica* sp.) were placed into one of the trays for a half day, and then removed. We then placed 10 size-matched ant lion larvae into each of the two trays. (The larvae had been taken from the field 7 days before and kept in vials, without food). The next day, 17 h after having been placed into the trays with smooth sand, newly dug pits were observed in both trays. The tray that had held the ants contained 7 pits (diameter = 1.5–4.6 cm,  $\bar{x}$  = 3.0), while the "clean" tray had 8 pits (diameter = 2.4–5.4,  $\bar{x}$  = 4.8).

All of the pits in both the "clean" and the "ant-scent" tray were then destroyed, and 50 ants (*Formica* sp.) were added to the ant-scent tray.



**Fig. 6.** Pit relocation of fed (one 3.3 mg ant/day) and unfed larvae during successive 10 day intervals. The difference between fed and unfed is significantly different ( $P < 0.01$ ) at all intervals  $\geq 30$  days. The numbers refer to sample size. Declining sample size of unfed larvae is due to both pupation and death, and that of the fed larvae is due to pupation entirely

Within 10 min both trays contained 2 pits, and on the next day both trays had 6 pits. In the ant tray (with 30 ant corpses and no live ants evident) pit diameters were 2.5–5.0 ( $\bar{x} = 4.0$  cm). In the clean tray pit diameters ranged from 2.0–6.0 ( $\bar{x} = 4.0$  cm). These results suggest that neither the scent of ants nor the physical presence of ants is a necessary stimulus for pit construction.

Does previous prey-catching success or failure at a site affect mobility to a new site? We here experimentally reinvestigated the question of whether or not lack of success at any one pit causes the larva to abandon its pit and rebuild a pit elsewhere. Forty five ant lion larvae were taken from the field and each placed onto a 0.2 m<sup>2</sup> layer of beach sand in a separate cardboard box with open top in the laboratory. Within several hours most of the ant lions had dug their pits in this sand. All of the 45 ant lions were fed 1 ant (mean wt. = 3.3 mg) each day for 2 weeks. After that 15 of the ant lions were fed one ant (average wt. = 3.3 mg) per day, 15 were fed 2 ants per day, while the other 15 larvae were not fed. Each day the pit locations of the two groups were mapped, the pit diameters were measured, and the experiment was continued for the entire summer.

None of the ant lion larvae fed 2 ants per day relocated their pit. However, all had pupated within 30 days. The ant lions fed 1 ant per day grew relatively slowly, and two out of 15 had not yet pupated at the end of 110 days. On the average 5% of the larvae fed 1 ant/day moved during any 10 day interval, but there was no greater tendency to relocate after the first 10 days than after the 100th day where they were still rewarded with 1 ant/day.

Larvae had no greater tendency to abandon their pit and build another after they were 20 days

without food (Fig. 6). However, in the next and every succeeding 10 day interval the unfed larvae moved significantly ( $P < 0.01$ ) more often than fed larvae. From 40 to 60 days without food approximately 80% of the larvae relocated their pit during any one 10 day interval. Three larvae survived 3 months without food, and all of these larvae had moved their pit at least once at the end of the 8th and 9th 10 day intervals without food.

A larva could complete building a pit in 1 h or less. In order to determine whether or not foraging success had an effect on pit size we measured pit diameters in the laboratory in ant lions that were fed 1 ant/day, and in ant lions that were not fed. As previously indicated, pit sizes varied greatly depending on body mass. We therefore normalized pit size by comparing percent changes in diameter between maximal original pit size and the diameter of two-day old newly formed pits. In larvae that were fed 1 ant/day the diameter of a new pit (after 3 days) average 38.5% greater than the original. On the other hand, in larvae that had been without food for up to 40 days, the diameter of new pits averaged 50.1% greater than the original, while in larvae that had been without food for 50 days or longer the pit diameters averaged 28.9% smaller than the original. The trend for short-term food deprivation to result in larger pits, and long-term starvation to result in building small pits can also be seen by examining absolute pit diameter as a function of body mass (Fig. 7). The results (Figs. 6 and 7) indicate that when larvae are unsuccessful at their pit after about a month, and then build a new pit, they first build a larger pit than the one they had previously. However, if they are then still unsuccessful in capturing prey they continue to relocate pits more often, but build progressively smaller pits. Fed larvae always built a new pit with-

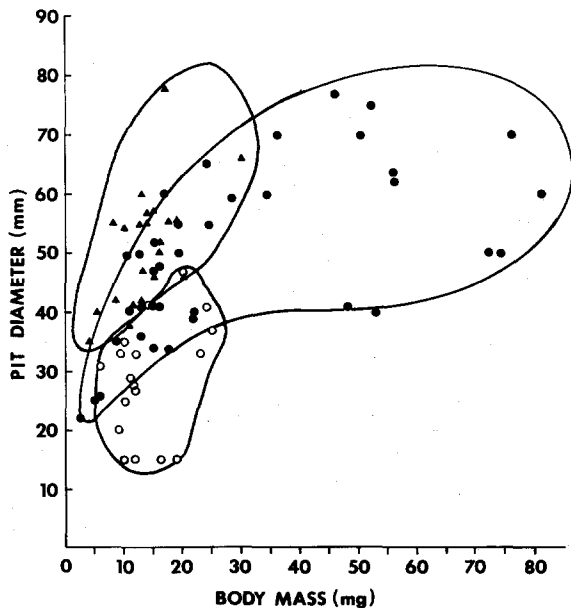


Fig. 7. Pit diameters (3 days after construction) as a function of body mass in ant lion larvae fed 1 ant/day (●), unfed for > 50 days (○), and unfed for < 40 days (▲). All three categories are significantly ( $P < 0.001$ ) different from one another

in one day after leaving their old pit, but larvae unfed for 50 days waited significantly ( $P < 0.05$ ) longer ( $x = 3.3$  days) before rebuilding.

It is doubtful that the small pits of unfed larvae are solely the results of diminishing strength. First, after pits were built the larvae often continued to enlarge them over subsequent days. However, the rate of increase was not significantly different ( $P > 0.2$ ) between larvae without food up to 40 days, those without food > 50 days, and those fed 1 ant/day. Secondly, fed larvae on the average moved only 51 cm (as determined by measuring trail length) before building a new pit, while larvae unfed for at least 50 days moved on the average 313 cm, a highly significant ( $P < 0.01$ ) difference. Both fed and unfed larvae flipped sand, building a groove in the sand to wherever they moved. In summary, fed larvae expended their time and energy building new pits, while larvae unfed for > 50 days locomoted relatively long distances without attempting to build a pit, and when they did build one it was small.

## Discussion

The foraging success of an ant lion larva conceivably depends on where its pit is located, how well it is constructed, as well as on how the larva responds to prey in the pit and to possible change

of prey availability through time. Some of the variables are interrelated, severely limiting the larva's options.

Because of biophysical constraints in pit construction (Lucas 1982) ant lion larvae that trap with pits are restricted to loose sand. In addition, sand subjected to direct solar radiation is subject to intense (> 50 °C) heating, and pits located at the edge of vegetation in shade should have less of a potential problem with excessive heat. However, rain showers that destroy pits are common, and a wet pit even if not destroyed, is totally ineffective. The more pits tend to be located in the open, the quicker the sand dries so that the larva can rebuild its pit and resume trapping. Our data indicate that the larvae are highly responsive to microclimatological factors in digging and maintaining their pits. Perhaps as a result of their demanding microhabitat specificity for the mechanics of pit construction and maintenance, it often happens that numerous pits are crowded so closely together that their rims touch.

We routinely observed pit densities so great that as one larva was enlarging its pit it was tossing sand into that of a neighbor's. Several other problems might arise from many ant lions being crowded closely together. First, since one ant lion is suitable food for another there is potential for cannibalism. Nevertheless, the potential exists that a larva, rather than building its own pit, usurps that of another. Our observations indicate, however, that larvae usually do not usurp pits of others. Indeed, when a larva wanders to the edge of another's pit it usually veers away. We speculate that usurpation of pits has not evolved because it is dangerous for any larva, regardless of size, to enter that of another. At least nat prey may be killed within 5 s after being bitten by an ant lion (Koch and Bongers 1981). The potential owner of the pit is hidden, and the larva, by having to crawl backwards (because of its large light pincers and anteriorly-directed body spines) advances toward its adversary with its soft exposed abdomen.

An additional potential problem of crowding due to microhabitat specificity is competition for food. McClure (1976) presumes a larva constructs its pit at a maximum distance from a neighboring pit. Wilson (1974), in contrast, speculates that competition in ant lions for food is "a simple exercise in geometry" of pit locations, and that the "optimal" pattern reducing competition between pits in a circular patch of sand is to line the periphery in a "doughnut configuration." We do not



question that this configuration could, indeed, be the "optimal" one in an ideal world where prey is delivered only from the periphery. However, we routinely observed the entrances of ant nests in the midst of patches of sand, and the ant lions captured a large number of flying insects, yet the pits were still located at the patch periphery. We sometimes also observed pits in "doughnut" configuration along the edge of vegetation, but this arrangement can also be attributed to microclimatic factors, as well as an edge effect. Larvae released into the center of a patch of sand moved to the edge of the sand and followed it. Larvae that dug pits after having travelled a given distance would automatically produce a doughnut configuration, given a sufficient number of pit relocations in a confined space. Wilson (1974) supposes that ant lion larvae monitor competition, and subsequently produce "optimal" pit distributions, by using their own hunger as a sensory cue. We found, however, that the "doughnut" configuration was usually formed within 3–4 days, while ant lions that had not fed did not relocate more frequently than fed larvae until at least 3 weeks without food.

We had previously reported that in the ant lion, *M. immaculatus*, pits are enlarged and/or relocated with the same frequency by fed and unfed larvae (Eppstein and Heinrich 1981). We report here, however, that this is a wrong conclusion derived from observations of larvae that were unfed for only 3 weeks. Our present data indicate that although unfed larvae do, indeed, remain relatively sedentary for 3 weeks without food, they became significantly more mobile, moving their pit on the average once every 10 days, if they remain unfed for 2–3 months. Like orb-weaving spiders (Olive 1982), also sit-and-wait predators operating traps, they move when their ration of victims becomes significantly reduced relative to previous rations. However, when food-deprived for sufficiently long durations, the large third instar larvae have the option of pupating that is not available to younger larvae.

Since large pits are seemingly more effective than small pits in aiding the larvae to capture prey, a larva could potentially increase its prey-catching ability by making a larger pit. We routinely observed that larvae that had moved first dug a small pit (for their mass), and then enlarged it over the next several days, and again later as the larva grew bigger. However, larvae that remained unfed long enough at any one pit did not enlarge their pit and eventually moved more often and constructed ever-smaller pits. This strategy suggests the larvae

engage in a relatively long-term sampling of the environment.

Not all of an ant lion larva's foraging behavior is restricted to pit construction. Pit "operation" is also essential for successful prey capture. When a potential prey is struggling it causes vibrations and releases sand grains that tumble down onto the larva's head and wide open mandibles. When the larva is enlarging the pit it hurls the sand back and to one side. But when it is attempting to capture prey it scoops up sand and hurls it alternately right and left. The sand that is tossed up helps to maintain small sand-slides that cause the victim to slide down into the pit. The smallest larvae did not attempt to flip sand to bring down the largest ants, possibly ultimately because the larvae are not immune from damage from the ants (Lucas and Brockman 1981) or because they could not capture them. The intermediate-sized larvae either did not flip or they flipped long and vigorously. They were only sometimes successful in capturing the large ants. The large larvae in large pits, on the other hand, were usually able to capture the large ants with relatively little sand-flipping. But in those instances where they were not immediately successful, they persisted until their victim was captured. The larvae in this case had nothing to lose by a maximum sand-flipping response since the investment of time and energy, given the large pit, almost invariably resulted in a payoff. Our results, however, differ from Griffiths (1980a) who observed much higher experimental capture success rates, presumably due to the fact that he dropped his ants directly into the center of the pits. In the field ants seldom drop immediately to the bottom of the pit without a struggle, and ant lions grab ants without sand-flipping only when the ants are dropped directly into their mandibles.

Is there an "optimal" prey size? Our results are in agreement with Wilson's (1974) who found that the larvae are highly non-selective predators. The large larvae are able to capture larger prey than the smaller, in addition to the small prey that the small larvae also capture. It does not necessarily follow, however, that the large larvae's ability to capture more food necessarily gives them an "advantage over the smaller larvae" (Wilson 1974) because the larger larvae require more food before they can grow because of greater metabolic maintenance costs (Griffiths 1980a). Wilson (1974) states that "the animal's life cycle appears to cause it to grow until it attains the optimal size as a food getter, but no further before metamorphosing." We doubt this, unless it can be shown that the

largest larvae with the largest pits suffer an increasing rate of energy debit.

In summary, although we cannot confirm all of the "optimal foraging" mechanisms that have so far been proposed for ant lion larvae, we nevertheless report a variety of behavior that should enhance their foraging success.

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