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Pit relocation by antlion larvae: a simple model and laboratory test

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Summary

We generated a computer model to analyse the effects of 'shadow' competition for sit-and-wait predators, particularly antlion larvae. The model used a simple foraging assessment rule to determine the quality of an antlion's location, and antlions relocated randomly in their habitat when a location proved to be of low quality. Shadow competition, or competition for food caused when one sit-and-wait predator intercepts moving prey before a second sit-and-wait predator is encountered, was incorporated into the model by restricting antlions to a bounded arena, and having prey for the antlions enter from the arena periphery. Antlions responded to shadow competition by relocating their pits to peripheral areas of their habitat. This peripheral accumulation of pits was most pronounced when antlion densities were high, and when prey availabilities were intermediate. An experimental test with the antlion *Myrmeleon immaculatus* supported the importance of shadow competition as a cause of observed pit distributions. Only the treatment which incorporated shadowing had pit distributions near the periphery, while the pit distributions in the control treatments did not differ from randomly generated distributions. We conclude that shadowing can influence sit-and-wait predator distributions when the prey distributions and movement patterns generate the conditions necessary for shadowing. But when prey availability is unpredictable, making assessment of patches difficult, or when prey do not originate in the periphery of the habitat, other factors, such as temperature or moisture, could be more important.

Keywords: Sit-and-wait predators; predator distribution; antlion larvae; *Myrmeleon immaculatus*; Kentucky; invertebrate predation; interference

Introduction

Sit-and-wait predators, including filter feeders, marine entangling predators and ambush predators, rely more on the movement of their prey than on their own movement to generate encounters. With many of these predators (i.e. spiders, caddisfly larvae and antlion larvae), increasing energy intake tends to increase fitness because higher energy intake leads to larger adult body size and increased reproduction (Wise, 1975; Vollrath, 1980; Hinton, 1981; Griffiths, 1985). Maximization of energy intake requires that sit-and-wait predators must find the right location for intercepting prey. Finding this best location could cost relatively little energy (antlion larvae; Lucas, 1985) or, as in some sheet weaving spiders, could have a high energy cost.

The search method of sit-and-wait predators makes them susceptible to a particular type of interference competition called 'shadowing' (Wilson, 1974). Shadowing occurs when one sit-and-

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wait predator intercepts or interrupts the flow of prey to another simply by being 'upstream' in that flow. This type of competition should affect predator dispersion patterns.

There is some evidence of such competition in filter feeding blackfly larvae and in some species of web-building spiders. Hart (1986) found that blackfly larvae, which filter fine particles from streams, were hyperdispersed on the substrates in the streams, and that they exhibited aggressive behaviour toward their upstream neighbours. He speculated that the upstream neighbours reduced the flow of particles to the downstream neighbour by decreasing local current velocity and increasing turbidity of flow. The aggressiveness of these larvae seemed to be a response to reduced access to food due to the upstream neighbour's shadow.

The evidence for shadow competition is not as clear for spiders, in part because the flow of prey to spiders is not as unidirectional as it is for blackfly larvae. However, several investigators have shown that spider webs tend to be hyperdispersed in a habitat (Riechert *et al.*, 1973; Riechert, 1974; Wise, 1979; Gillespie, 1987), and that spiders tend to move their webs to areas of higher prey availability (Turnbull, 1964; Riechert, 1976; Olive, 1982; Gillespie, 1987). The cause-and-effect relationship between web hyperdispersion and competition for prey is not established in most cases and is often considered secondary (Riechert and Tracy, 1975; Wise, 1983).

Antlion larvae of the family Myrmeliontidae are sit-and-wait predators that build conical pits in sand or loose soil and use these pits to trap prey. Wilson (1974) hypothesized that the observed dispersion patterns of antlion larvae reflect their reaction to shadow competition. Antlion larvae could reduce shadow competition and increase the probability of encountering prey by moving their pits away from other antlion pits and towards the source of prey (often the periphery of the suitable habitat). Wilson termed these peripheral distributions 'doughnuts' because the pits were in a ring around the periphery of the habitat with no pits in the centre. Alternative explanations for the antlion dispersion patterns include substrate heterogeneity, mutual avoidance of pit destruction caused by the pit maintainance activities of neighbours (sand throwing: Simberloff *et al.*, 1978), and temperature (Heinrich and Heinrich, 1984; Lucas, 1985).

We studied the potential significance of shadow competition for antlion larvae by constructing a computer simulation of antlions foraging in arenas with uniform substrate and temperature. Antlions in our simulation used a simple rule of movement which involved assessment of the foraging, return of pit locations and random relocation when a pit was determined to be unprofitable. We also subjected laboratory populations of antlion larvae to shadow competition and examined the resulting pit distributions for evidence of a peripheral distribution of pits.

The antlion foraging model

Formulation

Wilson's (1974) original approach to understanding the relationship between shadow competition and antlion foraging behaviour, and therefore their pit dispersion, viewed the problem as an exercise in geometry: antlion larvae would maximize their energy intake by minimizing obstruction of their pit peripheries. The presence of neighbouring pits obstructs a portion of the periphery; the magnitude of this effect depends on both the size and proximity of neighbouring pits. An antlion would be totally shadowed if its pit were completely surrounded by other pits. Wilson then hypothesized that groups of antlions should collectively arrange their pits in the circular, or 'doughnut', configuration so that each antlion would have approximately half of its pit periphery (i.e. the outer half) unobstructed by its neighbours. Wilson's approach has been criticized as requiring group selection, and as being untestable (McClure, 1976; Simberloff *et al.*, 1978; Simberloff, 1979). Here, we specifically focus on how individual predator responses to shadow competition could lead to 'doughnut' distributions.

We incorporated the geometry of antlion foraging into a simulation model. We envisioned a group of antlion larvae living in a small circular arena of uniform sand. The periphery of the arena was impermeable to antlion larvae, but not to their prey. This scenario closely mimics local antlion habitat, where antlion larvae are found under overhangs of limestone cliffs (Linton, personal observation). The antlion larvae do not disperse from their small patch of sand, but many prey types move freely across the boundaries of the patch. Our antlion larvae were introduced into the simulated arena at random, with the qualification that pits were not allowed to overlap (the actual Pascal computer code used for our simulations can be obtained from Linton). Antlion pits could overlap and be truncated by the boundary of the arena (as when abutting rock surfaces in nature); only the centre of the pit was constrained to stay within the arena, and the portion of the antlion pit outside of the arena was ignored. All of the antlions had equal-sized pits.

Prey for the antlions were uniform in profitability (e.g., worker ants of one species). A fixed number of prey entered the arena sequentially during each feeding bout (one day). Each prey would begin to cross from a randomly chosen point on the arena periphery and would proceed straight across the arena in a randomly chosen direction. (Angles from 0° to 180° with respect to a tangent line at the entry point were randomly chosen from a continuous uniform distribution.) If the prey path intercepted an antlion's pit, the antlion captured and consumed that prey. If the path of the prey intercepted more than one antlion's pit, the antlion with the intercepting pit closest to the point where the prey entered the arena ate the prey. In local antlion habitat, prey generally come from outside the small patch of sand inhabited by antlions; ants do not nest within antlion habitat. For simplicity in the model, prey travel in straight lines; this approximates the behaviour of many potential antlion prey. This method of prey presentation incorporated the potential for shadow competition into the model.

Antlion foraging behaviour in our model was described by a simple assessment rule (as for other sedentary trap-building foragers; Stephens and Krebs, 1986). Any new pit location was assessed for a fixed period of time; thereafter, the antlion's feeding rate, in prey per day, was compared to the minimum feeding rate it would tolerate (the hunger threshold). This hunger threshold may represent the point at which antlions just become unable to replace their basal metabolic expenditure. If its realized feeding rate was greater than, or equal to, the hunger threshold, the antlion did not move. If the antlion's realized feeding rate was below the hunger threshold over any continuous feeding period as long as the assessment period, then the antlion moved to a new randomly chosen position in the arena. This movement was assumed to involve no significant energetic cost (Lucas, 1985; Linton, unpublished data) or predation risk (Wheeler, 1930; Lucas, 1985). After an antlion moved, a new assessment period for that antlion began.

We chose a satisficing algorithm to model the foraging behaviour of antlion larvae because it represented the conceptually simplest, assessment mechanism consistent with available data. This approach makes only relatively weak assumptions about the antlion's abilities to choose and assess pit locations. If antlions distribute peripherally using this foraging rule, optimization models would be more likely to achieve peripheral distributions over a greater range of antlion densities and prey availabilities. An optimal foraging rule would have a higher minimum feeding threshold (e.g. the environmental mean). Since patterns of antlion larval movement indicate that they do not closely track prey abundance patterns on a time scale relevant to our simulation (Heinrich and Heinrich, 1984), satisficing should adequately represent their foraging behaviour on this time scale.

The results of our simulation model depend on antlion density, pit size, prey availability, the duration of the assessment period, and the hunger threshold. Table 1 contains the default, or baseline, parameter values for our simulations. For the default runs we assumed that all antlions

Table 1. Parameters of the model.

Parameter	Default value
Diameter of the arena	40 cm
Density of antlions	160 larvae m^{-2}
Antlion pit diameter	5 cm
Prey availability	1 prey per antlion per day
Hunger threshold	0.333 prey per day
Assessment period	3 days
Length of simulation	30 days
Prey incidence*	entire periphery of arena

*The portion of the arena from which prey may enter.

were second instar *Myrmeleon immaculatus* larvae having circular pits 5 cm in diameter. (Of the second instar *M. immaculatus* pits measured locally, 65% were within 1 cm of that size; Linton, unpublished data). We established the density of antlions at 160 m^{-2} (Linton, unpublished field data). The hunger threshold and assessment period were estimated from the literature. Heinrich and Heinrich (1984) starved antlion larvae and found that 17% of them moved within 10 days, and Wilson (1974) found that his starved antlions had begun to move within 5 days. We therefore chose 3 days as the assessment period, representing roughly the minimum observed interval between moves. Heinrich and Heinrich also noted that antlions in the field averaged one prey capture every twelve hours. In a preliminary test, we observed a correlation between antlion movement rates and feeding rates only at lower feeding rates than those recorded by Heinrich and Heinrich (Linton, unpublished data). Therefore, antlions move again in the model after any time equal in duration to the minimum assessment period, if their cumulative feeding rate falls below one prey every 72 hours.

Detecting doughnuts

We used two criteria to evaluate whether a pit dispersion pattern was a ‘doughnut’. The first addressed whether the antlion locations were nearer the periphery than expected if the locations were randomly generated. For this we calculated the radial displacement from the centre of the arena of each antlion, which hereafter we refer to as the ‘antlion distance’. Antlion distances generated by random pit placement are biased towards larger radii by the greater areas of the arena at those radii. Because of this inherent negative skew of the antlion distance distribution, we used the median antlion distance as our measure of central tendency. This negative skew is exaggerated by the fact that antlion locations are nonoverlapping pits rather than points. For example, when our arena is divided into 2 equal areas, an inner circular core and an outer peripheral ring, more pits can be packed into the outer ring than in the inner core, because of the difference in the shape of the two areas. We determined the random expected median antlion distance by calculating the mean media of 15 000 randomly generated antlion distance distributions for each antlion density and pit size (see Sokal and Rohlf, 1981 for similar simulation techniques). For each combination of parameter values in the satisficing model, the mean median of ten replicate simulations was compared to the appropriate expected median antlion distance using a *t*-test.

The second criterion of a ‘doughnut’ distribution is that the antlions be distributed randomly around the circumference of the arena. In this case we calculated the angle between a fixed arena radius and the radius intersecting each pit centre, hereafter called the ‘antlion angle’. The antlion angles should be symmetrically distributed around a mean antlion angle of π, and a t-test was used to test if the mean antlion angle was different from π.

We concluded that antlion distributions were peripheral (approximated a 'doughnut') if: (i) the mean median antlion distance was significantly larger than expected, and (ii) the mean antlion angle was not significantly different from expected.

Model results and discussion

Figure 1 shows the mean median antlion distances from the default parameter set. They are graphed with the mean medians from a simulation of random movement by antlion larvae. (Twenty antlions with 5 cm diameter pits were moved randomly every day for 30 days. Antlion distances and angles were analysed as in the model simulations where antlions moved on the basis of hunger.) The mean antlion angles from neither simulation differed from the expected antlion angle. In fact, the mean antlion angle was never different from π when prey entered from the entire periphery of the arena. The mean median antlion distance from the randomly moved antlion pits never differed from the expected antlion distance (14.9 cm for 20 antlions with 5 cm diameter pits). The mean median antlion distance generated by the default parameters increased monotonically, approaching an asymptotic value of approximately 16.1 cm. These medians were larger than the expected median, indicating peripheral clustering, from day 7 to day 30. This peripheral clustering was caused by an accumulation of antlions that sharply reduced their movement frequency after randomly relocating to the arena periphery. This peripheral distribution of pits was not generated by group selection but by responses of individual antlions to shadow competition.

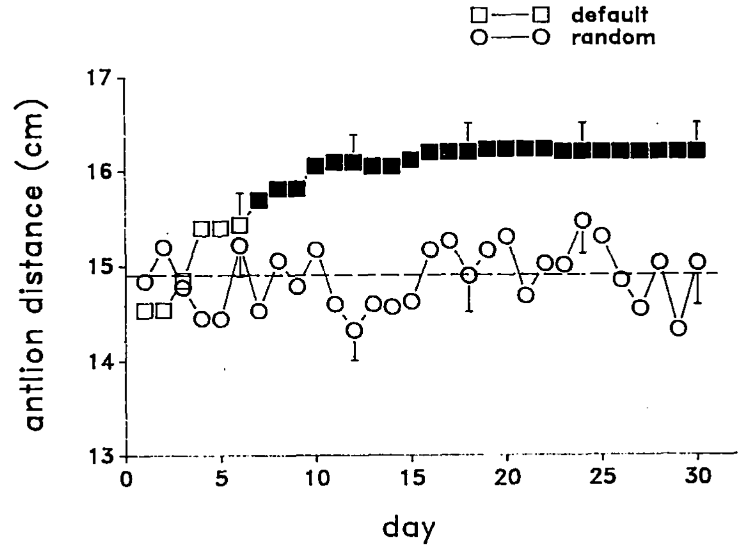

Figure 1. Results of model simulations for the default parameter set and random daily movement. The median antlion distances from the arena centre for ten runs were averaged daily and the mean median is graphed; the standard errors of the means are shown for days 6, 12, 18, 24, and 30. The solid horizontal line indicates the expected median distance from the centre for 20 randomly placed 5 cm diameter pits. Closed symbols indicate that the median antlion distance is significantly different from the median expected by chance, and the pit distribution approximates a 'doughnut'; the open symbols indicate that the pit distribution was not a 'doughnut'.

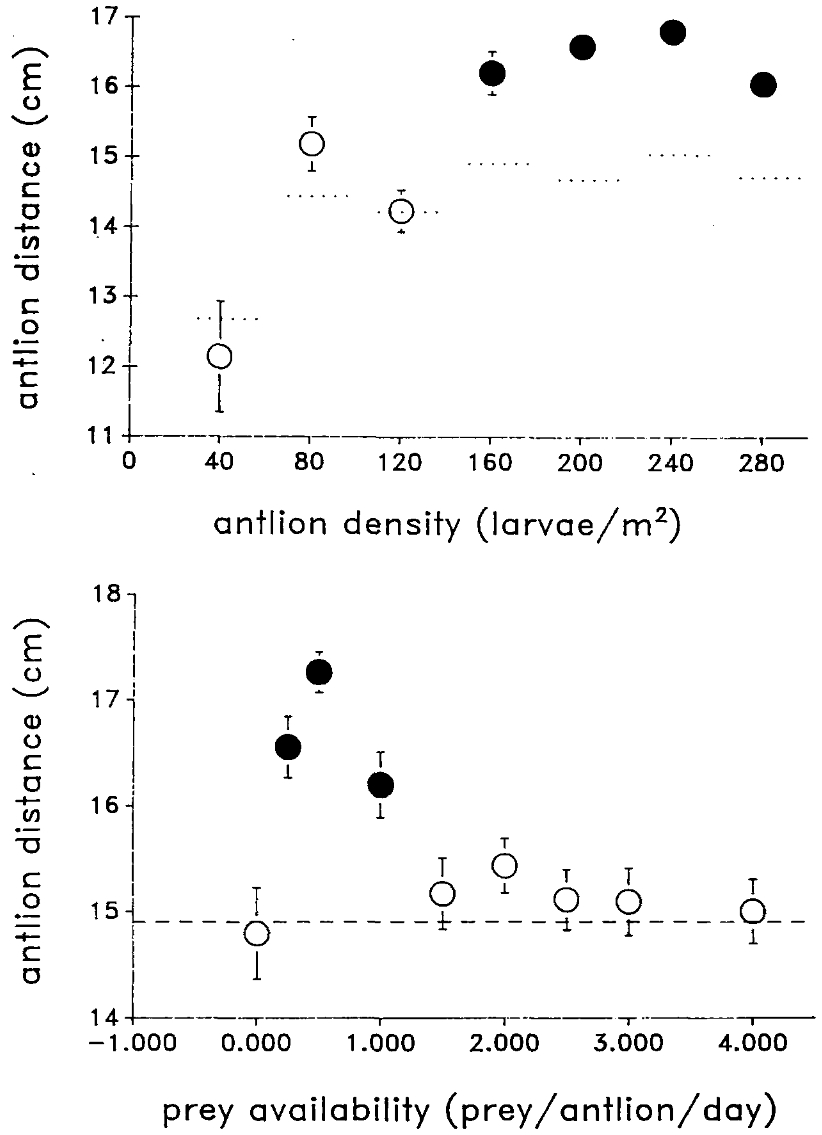

Figure 2. The mean median antlion distance from the arena centre (with standard errors) on day 30 (where closed squares indicate 'doughnut' distributions and open squares do not). A: versus antlion density (larvae m^{-2}) with prey availability and hunger threshold held at default values. Dotted lines indicate the random expected median for each density. B: versus prey availability with antlion density and hunger threshold held at default values. The horizontal line indicates the random expected median.

Effects of prey availability and of antlion density on the antlions' response to the hunger threshold were not completely independent. The reduced feeding rate resulted both from low prey availability and from shadowing, which in turn reflected both prey availability and antlion density. Increasing antlion density, while holding prey availability and hunger threshold constant, increased the median antlion distance towards a limit set by the radius of the arena (Fig. 2A). Peripheral clustering was only observed at higher densities of antlions, indicating interference in feeding between larvae: interior antlions were effectively shadowed at higher densities but not at lower densities. Altering pit size had the same effect as altering antlion density (not shown) because larger pits cast larger shadows toward the arena interior.

Altering the prey availability, while holding antlion density and the hunger threshold constant yielded significant peripheral clustering only at intermediate densities (Fig. 2B). As prey became very rare, the antlions could not reach their hunger threshold and therefore moved continuously. This seemingly maladaptive behaviour reflects the simple constant-threshold foraging rule that does not allow the hungry antlion to reduce its hunger threshold during food shortage (or to become quiescent, enter diapause, or pupate; these three methods of dealing with low food have not been documented in antlions). At high prey availabilities, the antlions consistently exceeded the threshold feeding rate and therefore moved very little, regardless of their initial pit locations or density. Therefore, only at intermediate prey availabilities were antlions more likely to move from interior locations than from peripheral ones, generating a net peripheral accumulation.

Finally, to simulate a situation in which prey tend to enter the arena from a particular direction, we restricted the prey entry to the 'first quadrant' of the arena boundary. The arena periphery associated with the rest of the boundary then became much less profitable for the antlions. Moreover, even individuals in the interior of the first quadrant would tend to encounter more prey than those elsewhere in the arena, at least until most of the first quadrant periphery was occupied by antlion pits. Because this restricted prey entry should tend to distribute antlion pits throughout much of the first quadrant, we expected the distribution of antlion distances to be indistinguishable from the random pattern, but antlion angles to be significantly smaller than expected. By day 5 of the simulations, the anticipated pattern had appeared (Fig. 3). This last

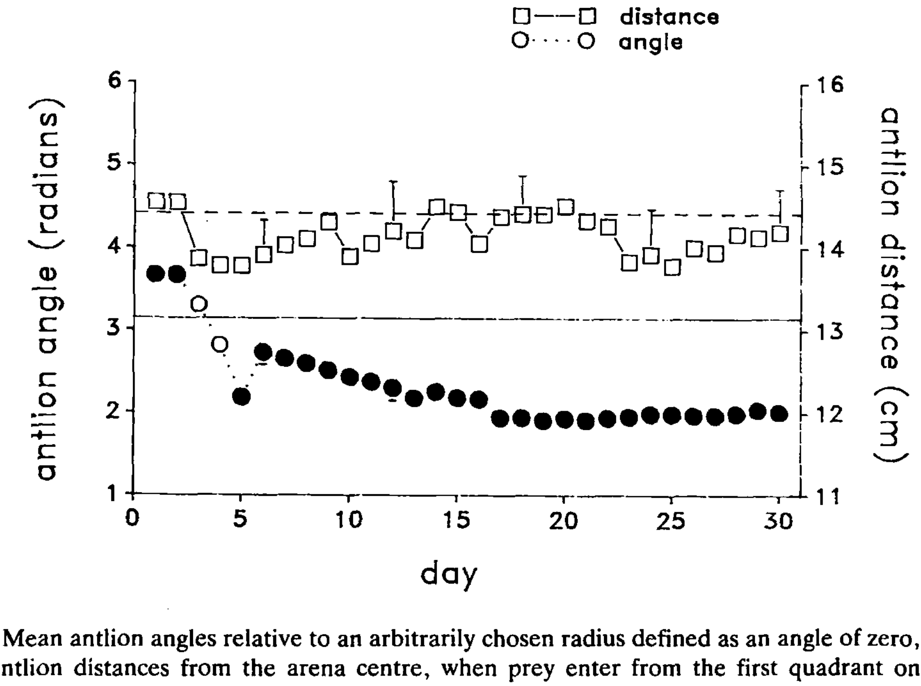

Figure 3. Mean antlion angles relative to an arbitrarily chosen radius defined as an angle of zero, and mean median antlion distances from the arena centre, when prey enter from the first quadrant only (0 to π radians). Standard errors are shown on days 6, 12, 18, 24 and 30 only. Dotted horizontal line indicates the random expected median antlion distance for 10 antlions with 5 cm diameter pits. The solid horizontal line indicates the random expected mean antlion angle. Closed symbols indicate a significant difference from the expected, open symbols do not.

result, when coupled with the previous results, showed that antlions in our simulations ended up in areas where the effects of shadow competition were reduced and the probability of feeding was high enough to meet their hunger threshold requirements.

Laboratory experiment

Methods

In June 1985, we collected 180 second instar *Myrmeleon immaculatus* larvae from the Red River Gorge in eastern Kentucky, USA. In the laboratory we randomly assigned 20 larvae to each of 9 circular plastic trays 40 cm in diameter, containing an 8 cm layer of uniform sand. This density of larvae (160 larvae m^{-2}) was within the range of field densities observed in the Red River Gorge (Linton, personal observation). Each tray was randomly assigned to one of three feeding treatments: shadow, random, and control.

In the shadow treatment, straight-line prey trajectories were generated randomly by computer, in the same fashion as in the simulation model, and the first antlion with a pit that intercepted the prey's trajectory was fed that prey. This method of feeding incorporated a stochastic prey availability and a pit location effect, because the antlions in the periphery of the tray were more likely to encounter the prey first. In the control, the larvae were fed a number of prey each day that depended only on their pit diameters. If the antlion's pit diameter was smaller than or equal to 60 mm, the antlion received one prey, otherwise it was fed two prey. Thus, the feeding regime in the control reflected differences in pit size but not in pit location or in random availability of prey. In the random treatment, each individual prey was randomly and independently assigned to a pit based on probabilities proportional to pit diameters but not on pit location. This can be visualized as having prey rain down on the tray at random; antlions with larger pits would tend to have more prey fall into their pits.

Since pit sizes could not be controlled, the total number of prey fed to a given tray was determined to be one prey for every antlion with a pit diameter less than or equal to 60 mm, and two prey for every antlion with a pit greater than 60 mm. Prey were vestigial-winged fruit flies (mean wet weight ± 1 SD, $n = 20$, is 2.413 ± 0.521 mg; antlion larvae extracted an average of 87.9% ± 3.1% of the wet weight from the flies). Dipterans, including mosquitos, blackflies, and deer flies and other tabanids, can be captured by antlion larvae (Linton, unpublished data). We assumed that fruit flies, from which antlion larvae extract approximately the same weight as small ants, would be well within the range of appropriate prey. Prey were dropped directly into antlion pits and were always captured. This allowed us to control the feeding regime of each treatment. When more than one prey per day was to be fed to an antlion, the feedings were at least an hour apart to ensure that all prey were eaten. The experiment was conducted for 30 days, 1 July to 30 July, 1985. Each morning the pit locations and diameters were measured for each tray and these data were used to determine that day's feeding schedule. The daily pit location data were used to generate antlion distances and angles, which were analysed exactly as in the model.

The criterion for statistical evidence of peripheral clustering by antlion larvae on a daily basis was the same as in the model analysis: there were no mean antlion angles different from the random expected mean antlion angle, and no median antlion distances were significantly greater than the expected median distance ($p < 0.05$). In addition to the analysis of daily pit distributions as in the model analysis, we tested for differences between feeding treatments in their degree of peripheral clustering. On each day, we ranked the arenas from highest to lowest in median antlion distance, and used an exact randomization test (by enumeration, Sokal and Rohlf, 1981, p. 788ff) to evaluate two hypotheses. (1) To address the effect of stochastic versus deterministic prey availability, we compared the random treatment to the control. The two-tailed prediction that the random and control treatments differ in median antlion distance is corroborated only when all three medians of one treatment exceed those of the other. (There are 6!/3!3!, or 20, possible permutations of tray order. Only 2 of the permutations, all control median antlion distances longest or all random treatment longest, ($p = 0.1$ (2/20)), provide even weak statistical support.) (2) If shadow competition contributed to peripheral clustering, then we would expect the shadow treatment to result in distributions more peripheral than those found for the random treatment and the control. The one-tailed prediction that shadow treatment should generate larger median antlion distances than the other two treatments is corroborated only when shadow treatment medians are the three largest, or three of the four largest, from the nine arenas (the 4 most peripheral of the 84 possible permutations of trays, $p = 0.0476$).

Results

None of the feeding groups exhibited a monotonic increase in median antlion distance (Fig. 4); all fluctuated considerably (compare with Fig. 1). The variability in the number of occupied pits through time probably contributed to these fluctuations in median distance. Antlions in laboratory culture do not always maintain their pits (Linton, unpublished), and these unmaintained pits were not included in the analysis. Also, near the end of the experiment some of the larvae had pupated and therefore did not have pits. Median antlion distances for the random and control treatments were different from expected ($p < 0.05$) on only one day each. In contrast, the shadow treatment median antlion distance was significantly larger than expected on 19 days of the 30 day experiment. The gross pattern of the shadow treatment medians through time did not closely resemble that shown by the model (default, Fig. 1) because the medians did not increase monotonically to an asymptote. An approximately steady state distribution of pits at the periphery was reached much sooner than in the model.

On three of the 30 days of observation (days 1, 8, and 9) one of the arenas contained fewer than

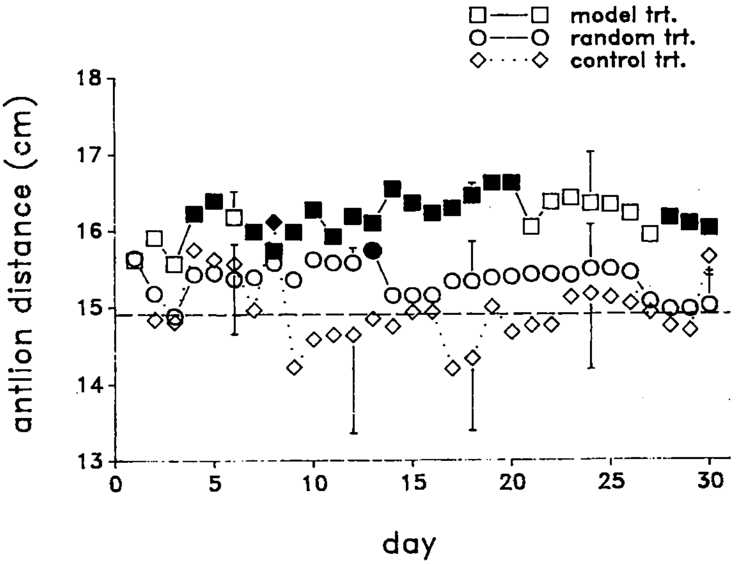

Figure 4. Mean median antlion distances from the arena centre for the feeding groups in the experimental test of shadow competition. Standard errors are given on days 6, 12, 18, 24 and 30 only. Closed symbols indicate 'doughnut' distributions and open symbols do not. The horizontal line indicates the median distance expected by chance.

six pits, making the median calculation unreliable; these days were ignored in the exact randomization analysis. In none of the other 27 days did the random treatment differ from the control; neither treatment had all median distances larger than the medians of the other ($p > 0.1$). We thus detected no evidence that randomness of prey availability alone is sufficient to alter the distributions of pits in the experimental arenas. But on 11 of the 27 days, including the last three days, the model treatment accounted for three of the four highest medians among all nine arenas ($p < 0.05$), providing additional evidence for shadow effect on antlion pit distributions.

General discussion

We explicitly designed both the computer model and the laboratory test to incorporate the potential for shadow-driven pit distributions: antlions were constrained to the circular arena and prey entered from outside the arena. Antlions in the periphery of the arena could interfere with the flow of prey to interior antlions merely by being 'upstream'. We also specifically controlled substrate and temperature to eliminate those factors as causes of pit distributions. The model simulation, which used a simple rule for pit relocation based on hunger, demonstrated that when antlion density was high or prey availability was intermediate, antlions clustered at the periphery of their habitat. Peripheral clustering of pits was seen in the laboratory test only when shadow competition was imposed. This clustering was not caused by the sand throwing pit maintainance activities of the antlions suggested by Simberloff *et al.* (1978). We did not observe any violent sand throwing in our experiment, but even if we had, we would have predicted that all treatments would have shown peripheral clustering.

The analogue of the 'doughnut' distribution in aquatic filter feeding invertebrates would be hyperdispersion in the suitable habitat in streams. In high density populations, maintaining hyperdispersion might require active defence of a territory. Hyperdispersion has been seen in both blackfly larvae (Hart, 1986, 1987) and hydropsychid caddisfly larvae (Hildrew and Townsend, 1980). Our model would predict that in areas where prey are superabundant, these filter feeders should not hyperdisperse but should be highly aggregated on the best substrate with good access to prey. Lake outlets are known to be areas where seston quality and quantity is high (Richardson, 1984; Oswood, 1979). Species of blackfly larvae that regularly inhabit lake outlet areas do not defend territories and can be found in very high densities (Wotton, 1988). But downstream from the lake outflow, or in streams that originate from springs or snow melt, the prey availability is much lower and blackfly larvae are frequently hyperdispersed (Hart, 1987). Hydropsychid caddisflies are similarly highly aggregated at lake outlets (Malmqvist and Bronmark, 1985; Richardson, 1984; Oswood, 1979) but assume a hyperdispersed distribution when in areas with lower prey availability (Hildrew and Townsend, 1980).

The prey for antlion larvae and spiders approach from many directions. Spider webs, in particular, can intercept prey in all three spatial dimensions, but little is known about the distribution of prey trajectories. When prey trajectories were multidirectional and the problem of pit dispersion was multidirectional, the predicted pattern can be clustering at the periphery. But when prey trajectories were more unidirectional (Fig. 3) the pattern can be quite different. Without more information about prey movement patterns, it would be very difficult to predict what sort of three dimensional arrangement of webs would be expected under shadow competition. Spiders are frequently hyperdispersed and are highly aggressive defenders of their webs under intermediate prey conditions, but they tend to tolerate much closer aggregations with high prey availability (Gillespie, 1987; Uetz, 1988). In fact, when prey are abundant, some species of spiders exhibit a primitive colonialism in which silk is shared (Gillespie, 1987; Uetz, 1988).

We have modelled antlion pit dispersion as a two dimensional problem, with all prey travelling on the horizontal plane of the arena surface. Under these conditions, shadow competition can generate doughnuts, yet some field populations of antlion larvae have not been found in doughnut distributions (Simberloff *et al.*, 1978; McClure, 1976), even at high antlion densities. In some cases, the behaviour of the dominant prey taxa may be responsible for this. Though many antlion prey, such as ants, carabid larvae and caterpillars (Heinrich and Heinrich, 1984; Griffiths, 1980; Linton, personal observation), could move horizontally across the antlion habitat from the periphery, as in our model, others may not. Antlions also feed on aerial prey, such as flies, moths and spiders (Heinrich and Heinrich, 1984; Linton, personal observation); or on ants with nest entrances within patches of antlion habitat. The use of these prey could diminish or eliminate shadow effects.

We have demonstrated that foraging needs can influence antlion pit distributions when other possibly important factors, such as physical heterogeneity of the habitat, are controlled. With other sit-and-wait predators, an interplay of various factors determines the predator's microhabitat preferences. Riechert (1976) and Wise (1975) both showed that prey availability influences spider distributions, but both found that other factors, such as temperature, were more important. Since trap-building sit-and-wait predators seldom leave their traps and therefore cannot escape harsh physical conditions, physical factors should be very important in determining trap location. Antlion larvae, *Myrmeleon immaculatus*, seem to select covered spots for their pits; either for shade to prevent overheating (Lucas, 1985), or for protection from rain to prevent drowning or interrupted feeding (Linton, unpublished). The importance of physical factors should be accentuated when prey supply is unpredictable, due to limited information on both quality of patches and on presence of competitors. We have evidence that actual prey availability for antlion larvae is highly variable through time (Linton, 1988). These foragers may be influenced more by physical factors, which they may be able to assess much more accurately, than by their poorly predictable prey supply. Additional empirical studies and models are needed to evaluate these possibilities more fully.

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