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Effects of Slope and Particle Size on Ant Locomotion: Implications for Choice of Substrate by Antlions

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ABSTRACT: Antlions construct conical, mechanically unstable pits in sand for prey capture. If ants (a major prey item) have difficulty walking on inclined sand surfaces, this may explain the effectiveness of their capture by this trap design. We investigated the degree to which locomotion of ants is impaired on sandy slopes. The locomotion of ants, physical characteristics of sand, steepness of antlion pit walls, and sand-size preference of antlion larvae were evaluated using four size fractions of sand (0.1–0.25, 0.25–0.50, 0.50–0.71, and 0.71–1.0 mm diameter). An ant's probability of falling when walking on a sandy slope increased with increasing slope angle or decreasing sand-particle diameter. For a given particle size and angle of inclination, larger ants were more likely to fall and roll uncontrollably than smaller ants. The maximum inclination above horizontal (angle of repose) for sand of different particle sizes was measured. The angle of repose was higher for the finest sand fraction than for the three coarser sand fractions, but did not differ among these three coarser fractions. In each sand fraction, the steepness of pits constructed by antlions was not significantly different from the angle of repose. Antlion larvae preferentially built pits in the two finer sand-size fractions.

KEY WORDS: Antlion, biomechanics, locomotion, *Myrmeleon crudelis*, prey capture

Most forms of effective locomotion minimize uncontrolled movements such as slipping or rolling that generate unpredictable postures or displacements. A sandy slope is an environment that may interfere with controlled locomotion, because sand grains slide when forces are exerted on the surface during locomotion. This interference with locomotion is exploited by antlion (Neuroptera: Myrmeleontidae) larvae which build mechanically unstable conical pits in sand that function in prey capture.

An antlion pit slopes to a single point at the bottom, where the antlion waits for prey (Fig. 1A). Pits with steeper sides are generally assumed to capture and retain prey more effectively (Lucas, 1982; Allen and Croft, 1985; Griffiths, 1986; Lucas, 1989). Steeper sides may hypothetically be achieved by building in finer sand, because the maximum angle of a slope (the angle of repose) will depend in part on the size of the constituent particles due to adhesive forces that are more significant at smaller sizes. It is known that pit-building behavior of antlion larvae differs with coarseness of substrate; it has been demonstrated that *Myrmeleon pictifrons* Gerstaecker larvae do not build normal pits in sand with particle diameters below or above certain values (0.125 mm and 1.0 mm, respectively) (Kitching, 1984). In addition, when given choices between two sand-size fractions, antlions built pits preferentially in the finer sand (*M. diminutus* Esben-Petersen and *M. pictifrons*, Allen and Croft, 1985; *M. acer* Walker, Loiterton and Magrath, 1996).

Ants (Hymenoptera: Formicidae) are numerically the most important prey items of antlion larvae (Lucas and Brockmann, 1981). Because ants are very agile at moving around on a variety of substrates, including rapidly scaling smooth vertical surfaces, interference with their locomotion by a sloping sandy surface might seem unlikely. Lucas (1982) did show that increasing slope angle and decreasing sand-particle size independently slowed exit of ants from pits in some cases; however, the artificial pits used were constructed by

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compressing sand, which may have facilitated ant locomotion. In order to evaluate more accurately any adverse effects on ant locomotion, the present study evaluated the tendency of ants to fall while walking on sandy slopes of different angles and particle sizes, using non-compressed sand. Slope angle and particle size may have different effects on ant locomotion, and both are evaluated separately in this study. In addition, the angles of antlion pits were measured and compared to the angles of repose for the four sand-size fractions. Precise estimates of slope angle are necessary for interpreting the role of physical factors in pit morphology and function, and therefore we used a more reliable and accurate method for slope measurement which avoids problems encountered in previous studies.

Methods

Experimental animals

Larvae of *Myrmeleon crudelis* Walker were collected from Bay County, FL and maintained at a 16:8 L:D cycle under 18–25°C, on a diet of fruitflies (Diptera: Drosophilidae) and flour beetle (Coleoptera: Tenebrionidae) larvae. Identification of antlion larvae was based on Lucas and Stange (1981). Individuals ranged in size from 3.5 to 58.7 mg, and were mostly second and third (final) instar larvae (mean = 22.8 mg, standard deviation = 11.0 mg, $n = 67$).

Two species of ants were collected locally, maintained on sugar water, and used within one week of collection (Fig. 2). *Camponotus* sp. (Formicidae) (Johnson County, KS) ranged in size from 2.2 to 11.6 mg (mean = 4.5 mg, standard deviation = 2.0 mg, $n = 38$). *Tapinoma sessile* (Say) (Formicidae) (Douglas County, KS) ranged in size from 0.35 to 0.87 mg (mean = 0.55 mg, standard deviation = 0.15 mg, $n = 16$). The ants used in this study are woodland species, which may lack special adaptations for walking on sandy slopes, but are still subject to predation by antlions.

Sand characteristics

Quartzitic sand (from the Ogallala formation) was collected from Rooks County, Kansas (39.5°N, 99.5°W) and was washed in tap water and dried before use. The moisture content of the sand was always less than 1% by weight (average loss of weight after drying at 90°C for 4 hours was 0.29%). Porosity of 30–50% and density of sand grains of 2.5–2.7 g/cc are typical for sand of this type. The sand was separated into four size fractions by sieving, resulting in particle diameter ranges of 0.10–0.25 mm, 0.25–0.50 mm, 0.50–0.71 mm, and 0.71–1.00 mm (Fig. 2). X-ray diffraction was used to analyze the mineral composition of the sand grains after grinding samples of each fraction to fine powder.

Angle of repose of sand

A cylindrical container (85 mm diameter, 25 mm height) was filled halfway with sand and rotated slowly and smoothly until an avalanche occurred (Fig. 1B). The angle above horizontal at which this collapse occurred (angle of repose) was measured to the nearest degree by this standard method (Jaeger *et al.*, 1989). Ten replicates were made for each of the four sand-size fractions. In addition, the angle of repose was measured for sand that had been caused to settle by shaking before rotating the sample, but the results were not significantly different from the unshaken sand samples ($P = 0.77$ for class variable "shake", two-way ANOVA with sand grade as other class variable, interaction term was not significant at $P = 0.65$, d.f. = 79 for entire model) and so the two data sets were combined ($n = 20$ for each sand-size fraction).

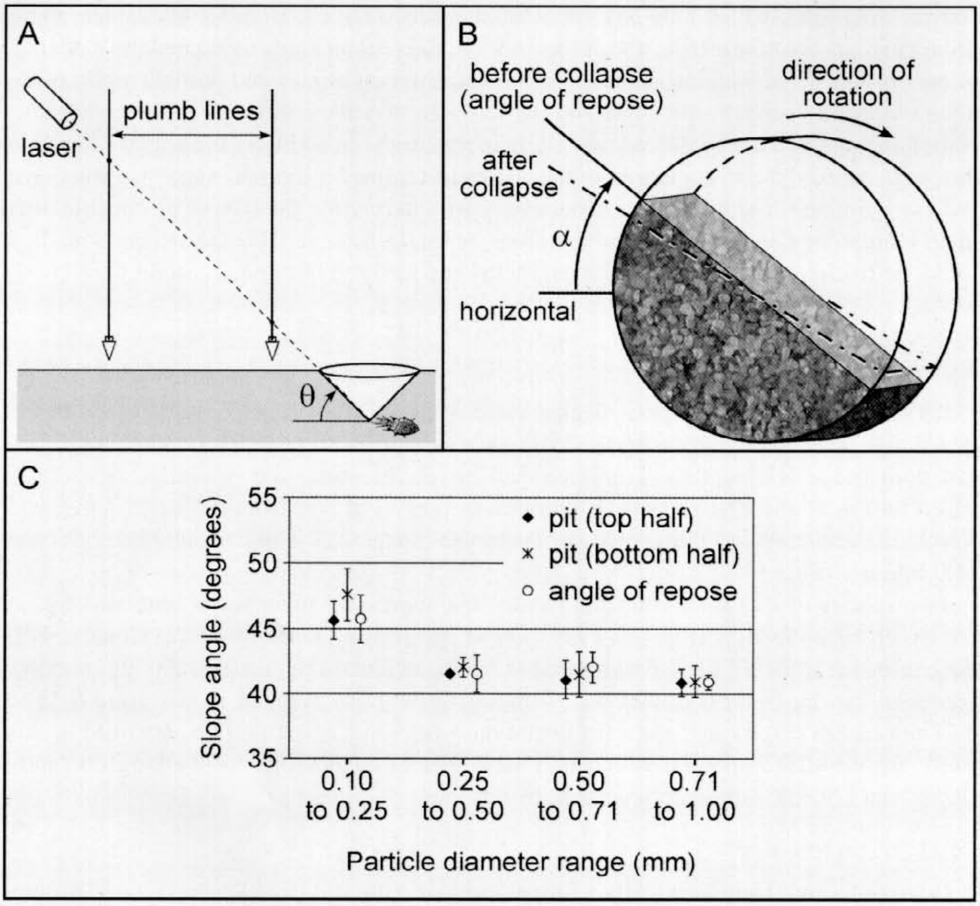

Fig. 1. **A.** A laser and two plumb lines were used to measure the angle of antlion pits (θ) as explained in the text. The location of an antlion below its pit is indicated. **B.** A standard technique for measuring the angle of repose (α) for a particulate medium is to rotate a cylindrical container half-filled with the medium until the slope becomes unstable and collapses (e.g., Jaeger *et al.,* 1989). **C.** The angle of the antlion pits (θ) was the same as the angle of repose (α) for the four sand-size fractions ($\bar{x} \pm 2$ SE, for each sand-size fraction $n = 20$ for angle of repose and $n = 7$–9 for pit angles).

Angle of antlion pits

The slope angle of antlion pits in each of the four sand fractions was measured without disturbing the pits, one and four days after introduction of the antlion to the sand ($n = 7$–9 for each fraction, 32 pits total, all larvae were >15 mg in mass). The angle was measured by rotating a laser (power < 5 mW, Model SNF-XXX, Lasiris Inc., St-Laurent, Québec) until the beam just grazed the side of the pit from rim to bottom. The angle of the laser was measured by moving two plumb lines into the path of the laser so that the beam intersected marked points on the plumb lines (Fig. 1A). The angle of the laser beam was calculated from the known horizontal and vertical distances between these points on the plumb lines. Some pits (34%) differed perceptibly in the angle of the top and bottom halves of the pits, and both angles were recorded. Angle was measured to the nearest degree; the standard error of the mean for repeated measurements on single pits was 0.4° ($n = 4$ pits, 10 measurements on each).

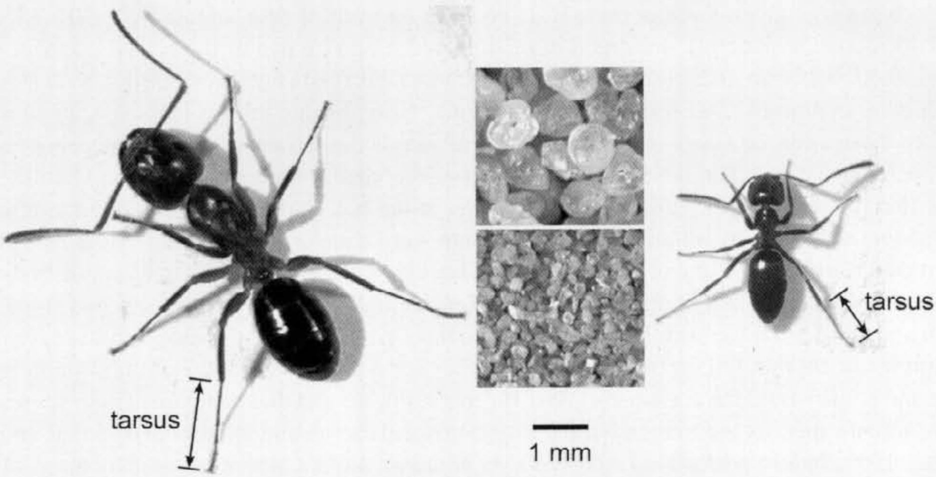

Fig. 2. The two ant species used for these measurements differed in size (left: *Camponotus* sp.; right: *Tapinoma sessile* (Say)). The average diameter of coarser sand particles (top) was comparable to the tarsal length of the smaller ants and approximately half the tarsal length of the larger ants (hind legs). The average diameter of finer sand particles (bottom) was approximately one-quarter the tarsal length of the smaller ants and one-eighth the tarsal length of the larger ants.

Particle size choice tests

Twenty-four plastic boxes (170 mm length, 120 mm width, 60 mm height) were each temporarily partitioned into four quadrants of equal size. Each quadrant in a box was filled to a depth of 40 mm with a different sand-size fraction. The partitions were then removed, and the boxes were gently tapped from beneath to smooth out the sand surface. Spatial orientation of fractions in boxes was alternated to avoid bias of unknown factors. An antlion was weighed and dropped through a funnel (to randomize starting orientation) onto the center point of the sand surface in each box. The boxes were then covered with clear plastic lids and left undisturbed.

One and four days after introduction of antlions into the boxes, the sand-size fraction containing the center of a pit was recorded (if a pit had been built). Any other sand-size fractions containing visible antlion trails were noted. During pit construction, antlions move in large loops (Tuculescu *et al.,* 1975), and therefore some individuals in our particle size choice trials would have encountered more than one sand-size fraction during pit construction. The center of the pit identified the size fraction primarily used in construction.

As a control for the choice tests, 41 additional boxes were filled to the same depth (40 mm) with a single size fraction of sand (n = 10–11 for each sand fraction). An antlion was introduced to each box and pit building was assessed (all larvae were >14 mg in mass).

Ants walking on sandy slopes

A small plastic box (95 mm length, 80 mm width, 15 mm height) was filled with sand (each of the three sand fractions was used in turn), and the sand surface was smoothed by sliding a straight edge across the top of the box. A semicircular piece of filter paper (15 mm radius) served as a starting platform for the ants in the center of the sand surface and was held onto the sand surface by a wooden toothpick stake. The box was placed on a larger board which was slowly inclined and held in place using a pulley, thereby inclining the sand surface.

Each ant was given three opportunities to walk on each of four angles (25°, 30°, 35°, and 40° above horizontal), presented in random order, and on one of three sand-size fractions (0.10–0.25 mm, 0.25–0.50 mm, 0.71–1.00 mm). Forty-six ants were used in total (for each combination of sand fraction and angle: n = 10 replicates for the large species, n = 5–6 replicates for the small species). An ant was weighed, then released onto the paper on the inclined surface. The behavior of the ant was recorded with a video camera from the time that it left the paper until it reached an edge of the box or returned to the paper again. Behaviors exhibited by an ant during a replicate were categorized: "falling" (loss of upright position due to rolling or flipping onto its back), "walking" (moving at least one body length), and "sliding" (in upright position). For each combination of particle size and slope, each ant was scored for each behavior over the three trials that comprised a replicate. For example, an ant that fell on two of the three trials for a particular combination of particle size and slope would have a score of 0.67 for that replicate and that behavior. These scores were transformed as recommended for proportional data (arcsin(squareroot)), Sokal and Rohlf, 1995) before performing ANOVA's. In addition, any incidence of "avalanching" of the sand was recorded.

Eight ants were placed singly into boxes of sand in which antlions had already built pits. Each ant was videotaped as it fell into a pit; the videos were examined frame-by-frame for particle dislodgement on the sides of the pit.

Statistical analyses

Statistical analyses were run using SAS software (SAS Institute, 1996) except for chi-square tests, which were calculated by hand (Sokal and Rohlf, 1995).

Results

Angle of repose of sand

The angle of repose differed significantly among the different size fractions; a one-way ANOVA of the angle of repose was highly significant when all four sand-size fractions were included (P = 0.0001) (Fig. 1C, open circles). However, this result is due entirely to the steeper slopes attained by the finest sand fraction (average 45.8°, n = 20), as the angle of repose of the three coarser sand fractions did not differ significantly from each other (one-way ANOVA excluding finest sand fraction P = 0.40; average angles 41.0 – 42.1°).

The angles of the antlion pits built in any sand-size fraction were not significantly different from the angle of repose determined for that sand fraction using the rotating cylinder method (Fig. 1C). As found for the angles of repose, the angles of antlion pits differed between the finest sand fraction and the three coarser sand fractions, which did not differ from each other (two-way ANOVA of angle P = 0.95 for pit vs. angle of repose comparison, P = 0.0001 for sand-size fraction including all four sand fractions; one-way ANOVA of angle of antlion pits P = 0.56 excluding finest sand-size fraction). There was a small but significant trend for a steeper slope at the bottoms of the pits (average difference 0.8°, P = 0.006, n = 32) (Fig. 1C), especially in the finer sand.

Effects of sand angle and particle size on ant locomotion

Ant locomotion was adversely affected both by finer sand particles and by steeper angles (Fig. 3) (3-way ANOVA with three class variables: sand grades, 3; ant species, 2; and angles of slope, 4; $P < 0.0001$ for all three class variables for both Type I and Type III SS, two of the four possible interaction terms were significant at the P = 0.05 level). In par-

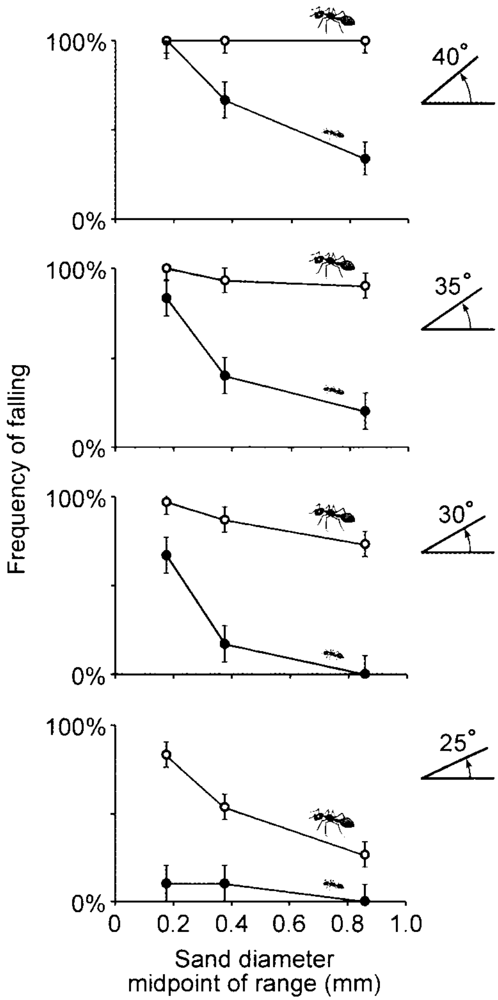

Fig. 3. A higher proportion of the ants of the larger species fell than ants of the smaller species while walking on most sand-size fractions and angles of inclination (larger ants: open circles, $\bar{x} \pm 2$ SE, $n = 10$ for each point; smaller ants: closed circles, $\bar{x} \pm 2$ SE, $n = 5$–6 for each point). Note that only the steepest angle (40°) is typical of antlion pits.

ticular, the larger ants always fell (rolling to the bottom) when attempting to walk on a 40° sand slope (somewhat less steep than natural antlion pits) for all sand-size fractions. (A slope >40° was too unstable to maintain for these ant locomotion measurements.) The steep slope (40°) had less of an effect on the smaller ants; on the coarser sand fractions they were able to walk without falling in about half of the trials.

Falling was the most frequent deviation from normal locomotion. After an initial loss of balance, ants rarely recovered but continued tumbling and rolling to the bottom. Sliding occurred much less often, in only 6% of the trials for both the large and small ants. There was no clear relationship between frequency of sliding and sand-size fraction or angle of slope.

When avalanches occurred, they happened after (rather than before) ants fell and therefore did not cause the loss of controlled locomotion. This was clear from frame-by-frame

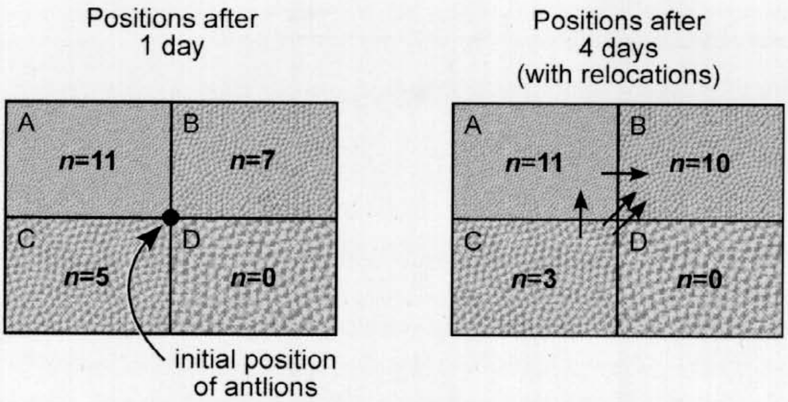

Fig. 4. Four sand-size fractions were arranged in quadrants in boxes, with an antlion introduced at the center of each box as shown (left). The number of individuals that built pits in each quadrant are indicated for one (left) and four (right) days after the introduction of the antlions into the boxes (="day zero"). A–D represent finest to coarsest size fractions sequentially. Each small arrow (right) indicates the relocation of a single antlion between days one and four.

examination of video recordings of ants walking on both the inclined sand surfaces and antlion pits. Avalanches were rare after falls by the smaller ant species (2%) and occurred 27% of the time after falls by the larger ant species. The greater frequency of avalanching for the larger ants may be caused by the greater force (weight) exerted on the sand through the tarsi, causing dislodgement of a greater number of sand grains and catastrophic failure of the surface. When ants of the larger species fell into antlion pits, the ants were captured by the antlions without any avalanche occurring ($n = 8$; 2 in each sand-size fraction).

Choice of sand size

Antlions were able to assess particle size either directly or indirectly: when given a choice between four size fractions of sand they preferentially constructed pits in the two finer fractions (Fig. 4) (chi-square test of equal numbers of pits in each fraction, d.f. = 3, $P = 0.0122$ for $t = 1$ day, $P = 0.0025$ for $t = 4$ days, where $t = 0$ is the start of the trial). In addition, three antlions relocated to finer sand and one antlion relocated to coarser sand during the five days of the trial (Fig. 4, right). Trails were usually found in more than one quadrant (79% of trials), indicating that more than one sand-size fraction had been encountered by the antlions. The particle size chosen was not related to antlion size; midpoint of chosen particle size range regressed against antlion mass (abscissa) resulted in a slightly negative slope with a very small correlation coefficient ($r^2 = 0.04$, $n = 16$ antlions).

Preferential building in finer sand does not mean that these antlions were incapable of building pits in the coarser fractions; when placed in boxes containing a single sand-size fraction, 75% of the antlions in the two coarser size fractions built pits within 24 hours, and all had built pits within 5 days ($n = 10$ for each). Similarly, in the two finer sand-size fractions, 95% of the antlions built pits within 24 hours ($n = 10$–11 for each).

Chemical assays

The vast majority of sand grains for all size fractions were composed of quartz with minor accessory mineral grains such as orthoclase (potassium feldspar) that are commonly found in sands derived from granite. The differences in mineral composition between the different sand-size fractions were sufficiently small that they were not quantifiable by X-ray diffraction methods.

Discussion

In natural habitats, antlion larvae may encounter sandy areas that are sorted (e.g., by wind) into patches of varying particle sizes. Antlions are capable of discriminating between patches of sand differing in particle size, building pits preferentially in finer sand (Lucas, 1986; Loiterton and Magrath, 1996; and present study). Pits built in finer sand may be more effective in prey capture if finer sand can support steeper walls in a pit and if this steeper angle results in greater prey capture or retention.

Previous studies have suggested these points but have not presented conclusive data. For example, the slopes of the pits are typically estimated from the depth and width of the pits using unspecified methods (e.g., "depth was measured" Allen and Croft, 1985; Loiterton and Magrath, 1996). Such rough trigonometric estimates will result in imprecise slopes, especially when width and depth are measured without reference to true horizontal or vertical. This may explain why the reported angles of repose for antlion pits using such methods are extremely variable and include values (e.g., 53° from Allen and Croft, 1985) that exceed the maximum angle expected for dry sand of that particle size (≤45°). A slope estimated from depth and width measurements may also be less accurate because such a method assumes a constant (straight) slope from top to bottom and radial symmetry of the pit (pits may be asymmetric; Lucas, 1989). Although Lucas (1989) also used width and depth measurements to estimate pit slope, his measurements were referenced to gravity (using a vertical plumb line) rather than local topography and therefore should be more reliable. Our noninvasive method aligning a laser with the sides of antlion pits provided a more accurate estimate of the slope relative to a true horizontal as well as allowing us to identify any changes in the slope from top to bottom.

Studies purporting to show a relationship between slope and prey capture success have not completely separated the effects of particle size and slope angle. For example, Loiterton and Magrath (1996) showed that ants placed in the bottom of artificial pits escaped more rapidly from less steep pits constructed of coarser sand, but whether this shorter escape time was due to the angle or the particle size (or both) is unknown. As an exception, Lucas (1982) separated these confounded factors by constructing artificial pits into which ants were placed and timed until they climbed out. While Lucas (1982) reported strong effects of both particle size and slope on the time for ants to leave these pits, the pits were formed by pressing a conical mold into the sand and therefore the ants had a compressed surface on which they may have walked more easily, in contrast to the noncompressed surface used in this study.

Our results (Fig. 3) suggest that pits built in fine sand would be more effective in prey capture than those built in coarse sand; the adverse effects on ant locomotion would be due both to the effects of smaller particles (ease of dislodgement) and increased steepness. These two potentially confounded factors (particle size and steepness) were separated by measurement of ant locomotion for all combinations of particle size and substrate angle. We would expect enhanced prey capture whether the pit was merely lined with finer sand (as found by Lucas, 1982) or constructed entirely of finer sand (Loiterton and Magrath, 1996). It follows from our data that pits built in coarser sand would be expected to catch the larger ants but would more rarely catch the more numerous small ants, such that potential prey species will be directly linked to microhabitat choice.

For every angle we tested, the finest sand resulted in the greatest proportion of prey falling. However, when given a choice, antlions were just as likely to build pits in slightly coarser sand (0.25–0.50 mm diameter), on which ants could walk more easily. The highest angle at which the sand fractions could be tested was slightly less than their angles of repose, and therefore the performance of real pits may be slightly better than expected from the simulations at 40°. Note that there will be a lower limit to particle size for pit construction; below a critical size (~0.1 mm diameter), particles start to act as powders, becoming airborne or showing adhesive interactions, making pit construction more difficult.

Antlions built pits in all size fractions when offered no alternative, indicating that the scarcity of pits in coarser sand fractions was not the result of a mechanical inability on the part of the antlions. It follows that the antlions were able to perceive a difference between the 0.25–0.50 mm sand and the 0.50–0.71 mm sand. No evidence was found of discrimination between the two finest fractions (0.10–0.25 mm and 0.25–0.50 mm). Our findings of discriminatory abilities by *M. crudelis* are consistent with results from two-choice tests conducted by Allen *et al.* (1985), Lucas (1986), and Loiterton and Magrath (1996).

For a pit to function effectively in prey capture, a potential prey item should fall or slide from the upper edge to the bottom, where the antlion is concealed. Sand grains on a slope are physically braced by other sand grains in a complex way that makes it difficult to predict forces that would cause dislodgement or avalanches (Vanel *et al.*, 1999). Sand grains that rotate or become dislodged may cause an ant to slip and fall down a slope. In our trials, dislodgement of individual sand grains always occurred immediately before ants lost their balance and rolled to the bottom, as seen in frame-by-frame analysis of regular and high-speed videography of ants walking on sand inclined to different angles. Using the same technique, we confirmed that this is also the case for ants walking into real antlion pits (with steeper sides); that is, dislodgement of a few sand grains, rather than avalanches, caused the ants to fall down the slopes.

Using a novel noninvasive method for measuring the angle of antlion pits, we found that pit steepness does not vary over a wide range of relevant particle sizes. This suggests that the primary benefit of choosing finer sand for pit construction is not a steeper pit, but ease of dislodgement of individual particles on the slope which leads to prey tumbling into the pit.

Acknowledgments

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