

Mapping the limits of trap construction: LiDAR quantification of substrate moisture effects on pit construction and quality morphometrics in *Myrmeleon* larvae

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Abstract

We examined the effect of substrate moisture on pit construction in *Myrmeleon* larvae across four treatments (0.0–1.5%). Construction success, pit diameter, and slope angle were quantified using LiDAR-derived morphometrics and analysed via χ^2 and ANCOVA. Increasing moisture significantly inhibited construction and reduced pit dimensions, with failures restricted to $\geq 1.0\%$ moisture. These results suggest a critical threshold in substrate suitability, highlighting potential climatic sensitivity within this unique predatory guild.

1 | Introduction

Predation through the construction of traps has independently evolved in a number of taxa (1), reducing energy expenditure otherwise involved in actively hunting prey (2). Invertebrate trap construction is dominated by Araneae and almost always involves the use of dedicated materials (namely silk) (3); the use of simple pitfall traps is a much rarer phenomenon, almost exclusively restricted to certain antlion (Neuroptera: Myrmeleontidae) and wormlion (Diptera: Vermileonidae) species (4). The former create conical pits in sandy substrate by manoeuvring backwards in a spiral pattern, excavating the site by flicking sand out with their mandibles (5).

A steep pit slope is a key predictor of prey capture success (6), with larvae tending to construct close to the angle of repose (the steepest stable angle before avalanche) (7). Increased diameter also benefits its constructor by increasing the probability of prey falling into the pit by chance, increasing the larva's effective area of discovery (8). Prey escape time has also been found to be significantly positively

associated with both slope angle and pit diameter (5). The biophysical properties of the substrate are therefore critical determinants of a pit's effectiveness; particle size is particularly well studied in this regard, with a preference for fine substrates established (6,9,10). Moisture is also a key factor in effective pit construction, with existing research suggesting a strong preference for dry substrates (11). Indeed, previous observational studies have found antlions to be highly sensitive to major rainfall events, with a dramatic negative effect on *Myrmeleon* sp. pit densities in exposed areas (12). Mechanistically, moisture introduces inter-particle cohesion through capillary action (13), increasing the energetic cost of excavation and potentially inhibiting construction entirely.

Antlions are significant sit-and-wait predators of ground-dwelling arthropods, exerting top-down control on prey populations (14). Our changing climate, and the resulting increased precipitation intensity in many regions (15), may negatively impact the foraging success and population viability of this key predator, with potential cascading effects on terrestrial invertebrate communities. This experiment aims to quantify the mechanistic link between substrate moisture and pit construction to better understand the potential vulnerability of these predators to a changing environment. We hypothesise that increasing substrate moisture will negatively impact antlion trap construction, resulting in: (i) a lower frequency of successful pit construction; (ii) a reduction in pit diameter; and (iii) a reduction in pit slope angle.

2 | Methods

40 *Myrmeleon* sp. larvae were collected from pits along a 160m stretch of unmade track southwest of Klipbokklop field station, South Africa (Fig. 1). Preliminary field measurements of 10 pits informed the required minimum depth (range: 1.3-3.0cm) and diameter (3.1-4.5cm) of the experimental containers. Additionally, 12kg of sandy soil was collected and sun-baked for 3 hours to achieve a baseline substrate. 300g of this was then added to each of 40 plastic bowls (5cm deep, 7cm diameter) and local spring water added in the following quantities to achieve 10 of each treatment: baseline (~0.0%) – none added; 0.5% – 1.5g added; 1.0% – 3.0g added; 1.5% – 4.5g added. Antlions were qualitatively categorised as small, medium or large in body size, and assigned across treatments evenly. Bowls were covered with plastic sheeting to minimise evaporation

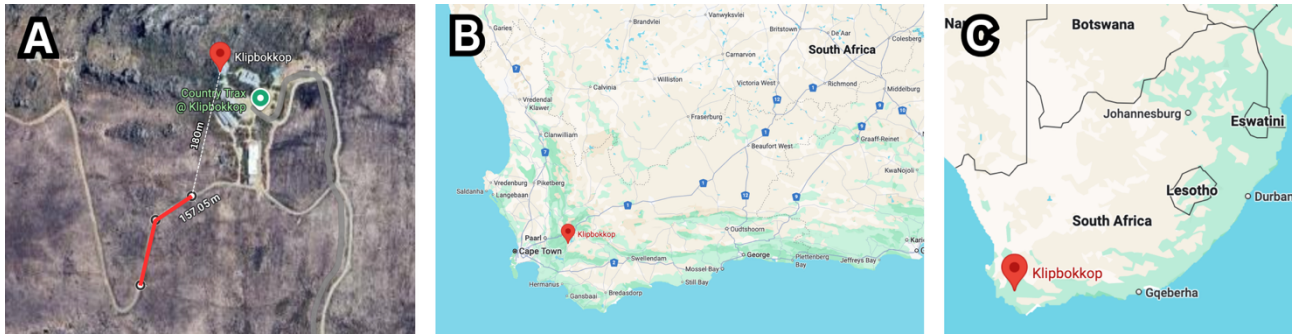


Figure 1. Site from which antlions were sourced (solid red line; NE terminal = 33°48'22.0"S 19°22'29.7"E) relative to Klipbakkop field station (Panel A), located in the Western Cape (Panel B), South Africa (Panel C). Map data from AfriGIS and Google.

while ensuring adequate ventilation, and left for 12 hours from 23:00 to 11:00 to coincide with peak pit-building activity (16).

LiDAR was chosen as a non-invasive method of assessing pit morphology through the creation of high-resolution 3D models, since traditional mechanical methods of measurement have been documented to disrupt pit morphology (8). Imaging was conducted using the *Scaniverse* app (Niantic, Inc.) on an iPhone 15 Pro Max, and pit diameter (the mean of 2 perpendicular measurements to account for the asymmetrical nature of most pits (17)) and slope length were independently measured by two observers using the digital model (Fig. 2A); values were only accepted if they were within 0.1mm of each other (and the mean taken), otherwise observers would reattempt. Slope angle was calculated using basic trigonometry: $angle = \arctan\left(\frac{\sqrt{slope^2 - radius^2}}{radius}\right)$. Once pits had been fully mapped, the larvae were extracted and multiple morphological measurements (Fig. 2B) were taken under an *Andonstar* digital microscope.

To assess whether there was a significant association between moisture treatment and successful pit construction, a Pearson's χ^2 test was performed. To analyse differences in morphology of constructed pits, two one-way ANCOVAs were performed, assessing the effect of substrate moisture treatment on (i) pit diameter and (ii) slope angle, while statistically controlling for antlion size (head width was used as a covariate due to its mechanistic relevance to the sand-flicking action used in pit

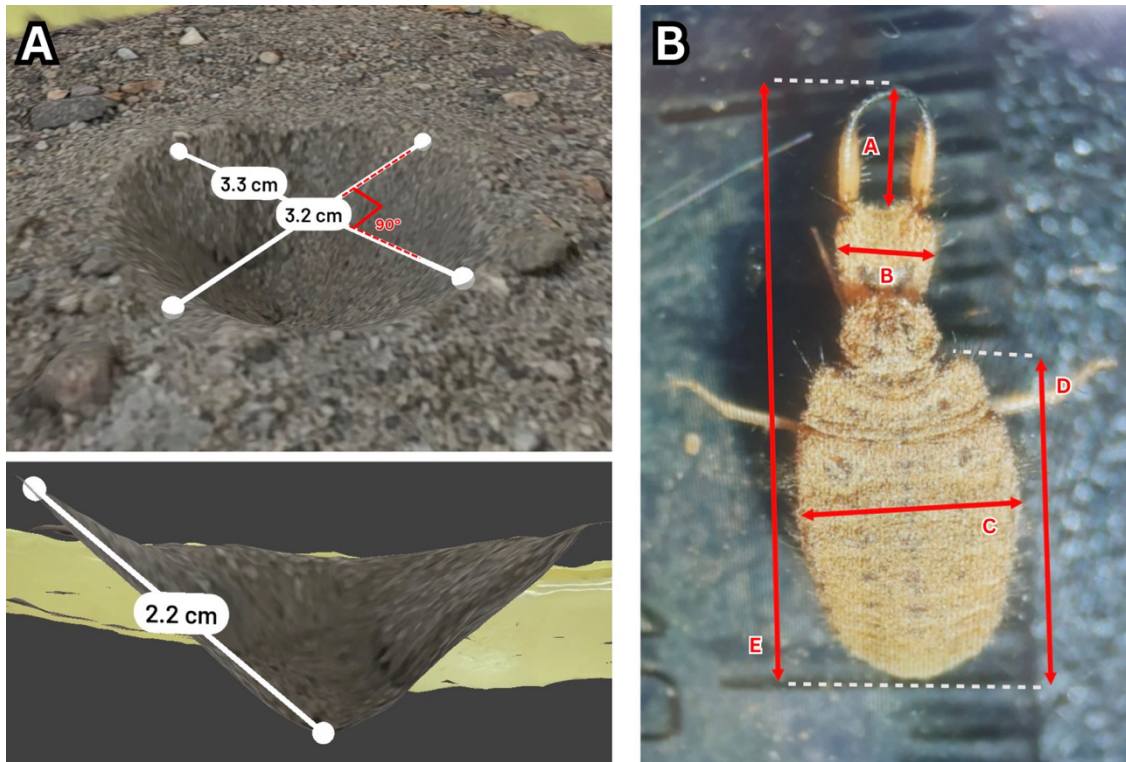


Figure 2. Physical measurements taken of pits (panel A: perpendicular diameters (top) and slope length (bottom) measured using scale 3D LiDAR models) and larva body morphology (panel B: mandible length (A), head width (B), body width (C), abdomen + thorax length (D) and total body length (E) measured under a digital microscope).

construction, and preliminary correlation analysis found all body morphometrics to be highly colinear). Model assumptions were checked and no violations found. Post-hoc pairwise comparisons were conducted on estimated marginal means with Tukey's HSD. All analyses were conducted in RStudio v2025.09.1+401.

3 | Results

Of the 40 antlions, 31 successfully constructed pits as of 11:00 the following morning; descriptive statistics for these can be seen in Table 1. The only bowl in the baseline treatment group with no pit was found to have no antlion larva present during subsequent excavation; it was assumed that this individual had escaped and so was excluded from statistical analyses. The eight true construction failures occurred exclusively in the higher moisture treatments: three in the 1.0% substrate and five in the 1.5%, representing failure rates of 30% and 50% respectively. The likelihood of an antlion constructing a pit was found to be significantly associated with substrate moisture treatment ($\chi^2 = 10.79, p = 0.009$).

Table 1. Descriptive statistics of antlion pit morphology across four substrate moisture treatments. Mean and standard deviation are shown for pit diameter and pit slope. The maximum possible number of pits constructed per treatment was 10, with the exception of 0.0% ($n = 9$).

Moisture (%)	Pits constructed	Diameter (cm)		Slope (°)	
		Mean	SD	Mean	SD
0.0	9	2.56	0.52	37.04	10.53
0.5	10	2.34	0.87	33.13	10.69
1.0	7	1.66	0.77	22.68	5.81
1.5	5	1.18	0.31	24.90	6.73

For the 31 constructed pits, a one-way ANCOVA revealed a significant effect of moisture on average pit diameter ($F(3, 26) = 5.55, p = 0.004$). The covariate, larval head width, did not have a significant effect ($F(1, 26) = 0.46, p = 0.505$). Post-hoc pairwise comparisons revealed that pits constructed in the baseline 0.0% moisture treatment were significantly wider than those in the 1.5% treatment ($p = 0.008$). Similarly, pits in the 0.5% moisture treatment were significantly wider than those in the 1.5% treatment ($p = 0.023$). No other pairwise differences were statistically significant (Fig. 3A).

The second ANCOVA revealed that substrate moisture also had a significant effect on pit slope angle ($F(3, 26) = 4.03, p = 0.018$). Again, larval head width was not a significant predictor ($F(1, 26) = 0.53, p = 0.471$). Pairwise comparisons showed that

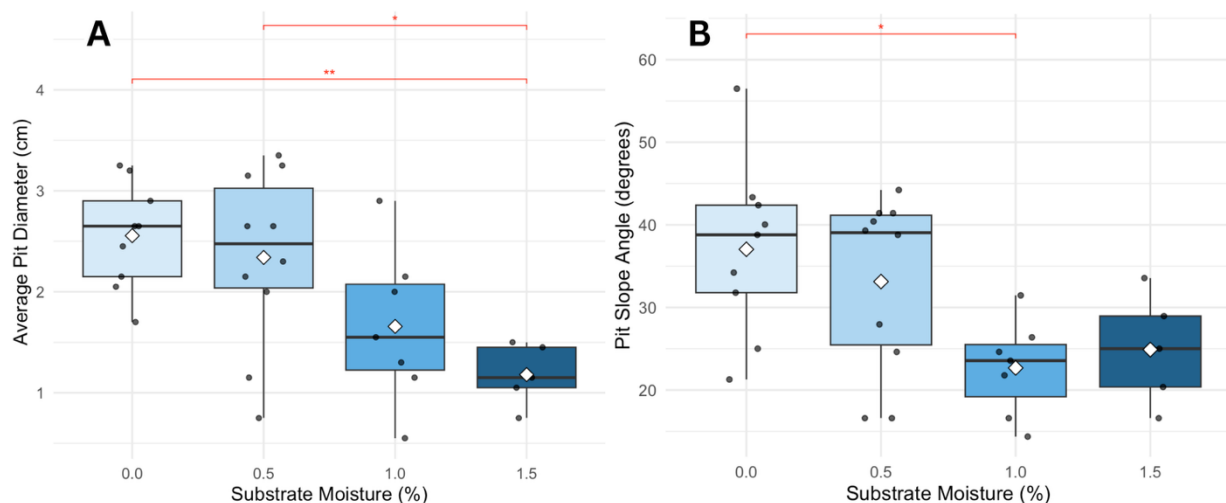


Figure 3. Boxplots depicting the distribution of diameter (panel A; mean of two perpendicular measurements) and slope angle (panel B) values for antlion pits across four substrate moisture treatments ($n = 10$, except for 0.0% where $n = 9$). Horizontal lines within each box indicate the median, the diamond the mean, and the upper and lower edges of the box the interquartile range (IQR). Significant post-hoc Tukey comparisons are indicated by red brackets: * = $p < 0.05$; ** = $p < 0.01$.

antlions in the 0.0% moisture treatment created significantly steeper pits than those in the 1.0% treatment ($p = 0.026$). No other treatment groups differed significantly from one another in slope angle (Fig. 3B).

4 | Discussion

These findings support the notion that increased substrate moisture both inhibits pit construction and reduces pit quality in antlion larvae. Since reduced slope angles and diameters are known to lower prey-capture efficiency (5,6,8), this suggests a direct fitness cost under excessively moist conditions. This aligns with the preference for dry microhabitats observed previously (11) and explains documented population declines following major rainfall events (12). Specifically, construction failures occurred exclusively at $\geq 1.0\%$ moisture, indicating a potential threshold in tolerance between 0.5% and 1.0%. Similarly, significant reductions in both diameter and angle were only observed between combinations of one of 0.0 or 0.5% and 1.0 or 1.5%; there were no significant pairwise differences between either morphometrics of the 0.0% and 0.5% nor the 1.0% and 1.5% treatments, again suggesting the existence of a threshold in suitability in the 0.5% to 1.0% range.

These results should be considered in the context of the considerable diversity within Myrmeleontidae, the most diverse Neuropteran family, with around 191 genera (18). Many genera likely exhibit different local adaptations to substrate moisture: for example, *Euroleon nostras* shows even poorer moisture tolerance than *Myrmeleon* (9), while others will likely be more robust. Nevertheless, increased extreme precipitation events (15) are likely to pose challenging across the family, as rapid climatic shifts outpace evolutionary adaptation.

Further larger-scale studies should employ finer moisture gradients, particularly within the 0.5-1.0% range to identify any precise threshold our data alludes to, and quantify moisture more accurately using oven-dry gravimetry and/or calibrated TDR/FDR probes for volumetric water content. Introducing multiple particle sizes and substrate types may also reveal interactive effects between moisture and other biophysical factors, helping to translate these preliminary findings into real-world insights as to the resilience of these fascinatingly resourceful and ecologically important invertebrates.

References

1. Alcock J. The evolution of the use of tools by feeding animals. *Evolution*. 1972;26(3): 464. <https://doi.org/10.2307/2407020>.
2. Fertin A, Casas J. Efficiency of antlion trap construction. *Journal of Experimental Biology*. 2006;209(18): 3510–3515. <https://doi.org/10.1242/jeb.02401>.
3. Ruxton GD, Hansell MH. Why are pitfall traps so rare in the natural world? *Evolutionary Ecology*. 2009;23(2): 181–186. <https://doi.org/10.1007/s10682-007-9218-0>.
4. Franks NR, Worley A, Falkenberg M, Sendova-Franks AB, Christensen K. Digging the optimum pit: antlions, spirals and spontaneous stratification. *Proceedings of the Royal Society B: Biological Sciences*. 2019;286(1899): 20190365. <https://doi.org/10.1098/rspb.2019.0365>.
5. Lucas JR. The biophysics of pit construction by antlion larvae (Myrmeleon, Neuroptera). *Animal Behaviour*. 1982;30(3): 651–664. [https://doi.org/10.1016/S0003-3472\(82\)80135-8](https://doi.org/10.1016/S0003-3472(82)80135-8).
6. Devetak D, Podlesnik J, Scharf I, Klenovšek T. Fine sand particles enable antlions to build pitfall traps with advanced three-dimensional geometry. *Journal of Experimental Biology*. 2020; jeb.224626. <https://doi.org/10.1242/jeb.224626>.
7. Crassous J, Humeau A, Boury S, Casas J. Pressure-dependent friction on granular slopes close to avalanche. *Physical Review Letters*. 2017;119(5): 058003. <https://doi.org/10.1103/PhysRevLett.119.058003>.
8. Griffiths D. The feeding biology of ant-lion larvae: prey capture, handling and utilization. *The Journal of Animal Ecology*. 1980;49(1): 99. <https://doi.org/10.2307/4279>.
9. Klokočovník V, Bantan T, Devetak D. Substrate choice in antlion larvae: the combined effect of particle size and moisture. *Journal of Insect Behavior*. 2025;38(2): 18. <https://doi.org/10.1007/s10905-025-09882-1>.
10. Farji-Brener AG. Microhabitat selection by antlion larvae, *Myrmeleon crudelis*: effect of soil particle size on pit-trap design and prey capture. *Journal of Insect Behavior*. 2003;16(6): 783–796. <https://doi.org/10.1023/B:JOIR.0000018320.99463.ee>.
11. Burgess MG. Sub-optimal pit construction in predatory ant lion larvae (*Myrmeleon* sp.). *Journal of Theoretical Biology*. 2009;260(3): 379–385. <https://doi.org/10.1016/j.jtbi.2009.05.026>.
12. Morrison LW. Spatiotemporal variation in antlion (Neuroptera: Myrmeleontidae) density and impacts on ant (Hymenoptera: Formicidae) and generalized arthropod foraging. *Annals of the Entomological Society of America*. 2004;97(5): 913–922. [https://doi.org/10.1603/0013-8746\(2004\)097%255B0913:SVIANM%255D2.0.CO;2](https://doi.org/10.1603/0013-8746(2004)097%255B0913:SVIANM%255D2.0.CO;2).
13. Mitarai N, Nori F. Wet granular materials. *Advances in Physics*. 2006;55(1–2): 1–45. <https://doi.org/10.1080/00018730600626065>.
14. Gotelli NJ. Ant lion zones: causes of high-density predator aggregations. *Ecology*. 1993;74(1): 226–237. <https://doi.org/10.2307/1939517>.

15. Dore MHI. Climate change and changes in global precipitation patterns: what do we know? *Environment International*. 2005;31(8): 1167–1181. <https://doi.org/10.1016/j.envint.2005.03.004>.
 16. Chakradhari P, Pati AK, Parganiha A. Time of the day variability in pit-building behavior of antlion larvae. *Journal of Ravishankar University (PART-B)*. 2024;37(1): 22–31. <https://doi.org/10.52228/JRUB.2024-37-1-2>.
 17. Lucas JR. The structure and function of antlion pits: slope asymmetry and predator-prey interactions. *Animal Behaviour*. 1989;38(2): 318–330. [https://doi.org/10.1016/S0003-3472\(89\)80093-4](https://doi.org/10.1016/S0003-3472(89)80093-4).
 18. Kuznetsova VG, Khabiev GN, Anokhin BA. Cytogenetic study on antlions (Neuroptera, Myrmeleontidae): first data on telomere structure and rDNA location. *Comparative Cytogenetics*. 2016;10(4): 647–656. <https://doi.org/10.3897/CompCytogen.v10i4.10775>.
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