Efficiency of antlion trap construction

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Summary

Assessing the architectural optimality of animal constructions is in most cases extremely difficult, but is feasible for antlion larvae, which dig simple pits in sand to catch ants. Slope angle, conicity and the distance between the head and the trap bottom, known as off-centring, were measured using a precise scanning device. Complete attack sequences in the same pits were then quantified, with predation cost related to the number of behavioural items before capture. Off-centring leads to a loss of architectural efficiency that is compensated by complex attack behaviour. Off-centring happened in half of the cases and corresponded to post-construction movements. In the absence of off-centring, the trap is perfectly conical and the angle is significantly smaller than the crater angle, a physical constant of sand that defines the steepest possible slope. Antlions produce efficient traps, with slopes steep enough to guide preys to their mouths without any attack, and shallow enough to avoid the likelihood of avalanches typical of crater angles. The reasons for the paucity of simplest and most efficient traps such as theses in the animal kingdom are discussed.

Introduction

The use of traps for predation has evolved independently in several groups of animals (e.g. spiders, wormlion larvae, trichopteran larvae) (Alcock, 1972). This strategy reduces the amount of energy expended in hunting and chasing prey, but the construction of the trap is itself energy- and time-consuming. Spiders are the main group of trap-building animals, with over 10 000 species (Foelix, 1996). Despite considerable variation of web architecture, and the stunning beauty of some webs, very few studies have investigated the costs and benefits of web architecture (Opell, 1998; Craig, 1987; Craig, 1989; Herberstein and Heiling, 1998). The most recent comprehensive study, based on the large energy budget of the *Zygiella x-notata* spider, showed that a small increase in web size translates into a large increase in prey biomass, due to an increase in the likelihood of catching large and heavy prey (Venner and Casas, 2005). Thus, spiders clearly adapt their traps as a function of costs and benefits. The geometric complexity of spider webs, differences in material and structural properties and the re-ingestion of webs by many spiders make it difficult to study the optimality of construction of these structures. The geometric simplicity of the antlion (Myrmeleontidae) trap makes this model more accessible than spiders' webs for studies of the relationship between predation and the structure of the trap – the object of this study.

Several antlion species live in sandy habitats and their larvae dig funnel-shaped pits to catch small arthropods, primarily ants. The pits are dug starting from a circular groove, the antlion throwing sand with its mandibles. Afterwards, the antlion gradually moves down in a spiral from the circumference towards the centre, making the pit deeper and deeper (Tuculescu et al., 1987; Youthed and Moran, 1969). At the end of construction, the antlion is generally located at the trap centre. It may move away from the centre over time (personal observations). The antlion trap functions by conveying the prey towards the base of the trap (Lucas, 1982). When the prey arrives at the bottom of the pit, the antlion rapidly closes its mandibles. If the prey is not bitten at the first attempt and tries to climb up the walls of the trap, the antlion violently throws sand over it to destabilise it and attempts to bite it (Napolitano, 1998).

The costs inherent in trap-based predation can be minimised by choices concerning: (1) the location of the trap, (2) the 'giving up time', defined as the time for which the predator is prepared to wait before changing location and (3) the structure of the trap (Hansell, 2005). The location of the trap is determined on the basis of a number of criteria, including prey density (Griffiths, 1980; Sharf and Ovadia, 2006), soil granule size distribution (Lucas, 1982), the density of other animals of the same genus (Matsura and Takano, 1989) and disturbance

(Gotelli, 1993). In some species, the giving up time is determined as a function of the frequency of prey captured (Heinrich and Heinrich, 1984; Matsura and Murao, 1994). Antlions are also able to adapt the design of their trap (e.g. the diameter/height ratio) in response to variations in prey availability (Lomáscolo and Farji-Brener, 2001). The direct impact of the geometric design of the trap on the efficacy of predation at a given constant prey density remains unknown. This animal-built structure is constrained by the physical properties of the soil, in particular the crater angle, which is a physical constant of the sand that defines the steepest possible slope not leading to an avalanche (Brown and Richards, 1970). This angle should be distinguished from the talus angle, which is valid for a heap of sand. The crater angle is greater than the talus angle because it involves arch and buttress phenomena (Duran, 2000).

Attack behaviour (i.e. behaviour such as sand throwing and bite attempts) when the prey attempts to escape involves an energy cost for the antlion with respect to the situation in which the prey is conveyed immediately to the base of the trap and immobilised with the first bite. Cost of predation is minimal when there is no attack behaviour. Trap slope modifies prey movements: the weaker is the slope, the easier the locomotion is (Botz et al., 2003). We can thus expect a decrease of predation cost with trap angle (Fig. 1). The aims of this study were to define the efficiency of trap geometry in terms of attack behaviour.

Materials and methods

Three-dimensional analysis

We calculated the three-dimensional (3D) surface of the trap by measuring all three dimensions with a scanner system developed in the laboratory and inspired by the work of Bourguet and Perona (Bourguet and Perona, 1998). This system functions by projecting the shadow of a plane on the surface of the trap (Fig. 2A) (see supplementary material for the calculus details). A camera (Euromex VC3031) records the deformation of the shadow. The data were extracted as pixel co-ordinates in ImageJ (Abramoff et al., 2004) and were then processed digitally in the R environment. The surface of the trap was reconstructed by linear interpolation of the scattered points on a grid (with each square on the grid being 0.5 mm×0.5 mm) (Akima, 1996) (Fig. 2B). Various geometric parameters were calculated from this surface (Fig. 2C). The centre of the trap was identified as the lowest point of the surface, corresponding to the point at which all objects falling into the trap should arrive. The height of the trap is the difference in height between the centre and the mean height of the points on the rim of the trap. The data were subjected to least mean square adjustment on the conical surface given by the equation:

$$(x - O_x)^2 + (y - O_y)^2 - (z - O_z)^2 \tan^2 [(\pi/2) - \alpha] = 0 , \quad (1)$$

The parameter α is the mean angle with respect to the horizontal of the walls of the trap. The estimated points
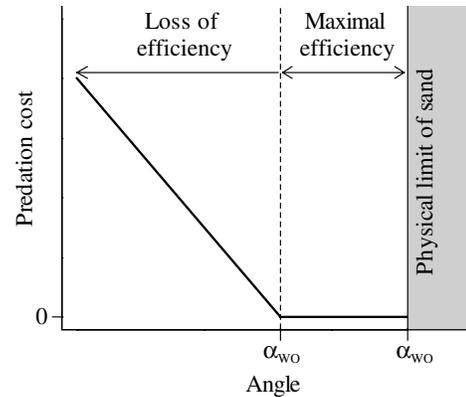

Fig. 1. Hypothetical relationship between predation cost and trap angle. The shaded part of the graph corresponds to angles greater than crater angle (α_c), which cannot be achieved because of the physical properties of sand. α_{WO} is the theoretical angle without off-centring.

(O_x,O_y,O_z) correspond to the summit of the inversed conical surface. The diameter was determined from the adjusted surface, at the mean height of the points of the rim of the trap. The goodness-of-fit of the data was assessed by determining the root mean square error (RMSE):

$$RMSE = \sqrt{RSS/n} , \quad (2)$$

where RSS is the squared sum of the residuals and n is the number of points on the surface of the trap. RMSE gives a mean difference in mm of the deviation from the adjusted conical model. As an example, a RMSE of 0.4 mm corresponds to a mean lack of conicity by about two grains of sand. The 3D co-ordinates of the head of the antlion (corresponding to the median point between the eyes) were calculated from the pixel co-ordinates on the image and by projection on the surface. The distance separating the head from the centre is referred to as off-centring (Fig. 2C).

Behavioural experiments

Stage 2 and 3 larvae of *Euroleon nostra* Fourcroy (Neuroptera, Myrmeleontidae) were collected at Tours (47°21′16.36″N, 0°42′16.08″E, France) and raised in the laboratory for six months with constant nutrition provided. Larval stage was determined by measuring the width of the cephalic capsule (Friheden, 1973). *Lasius fuliginosus* Latreille (Hymenoptera, Formicidae) workers were used as prey in observations of predation behaviour, as carcasses of this species were frequently observed around traps in the field. The antlions were provided with sand of known particle size distribution (Fontainebleau sand SDS190027, particles of 100 to 300 μm in size). The antlions were placed in square Perspex boxes (11×11×6 cm) 16 h before the experiment. The traps constructed were thus studied the first time they were used. The boxes containing the animals were placed on a base mounted on ball bearings so that they could be correctly positioned for filming without disturbance. All experiments were carried out at the same time of day (between 10.00 and 10.30 hours), in
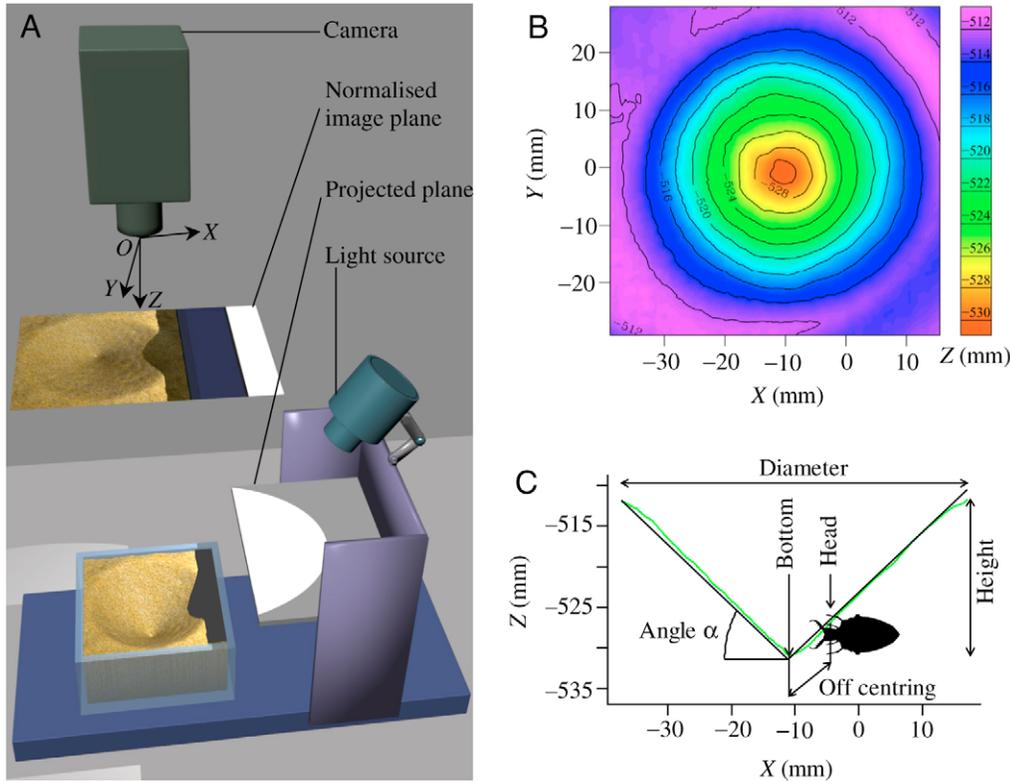
Fig. 2. Reconstruction and 3D measurements of an antlion trap. (A) Diagram of the set-up. The light source projects a shadow of the edge of the plane on the scene. The edge of the plane and the shadow are projected onto the normalised image plane of the camera, and the resulting image is used to reconstruct the three-dimensional scene in the camera's reference frame $O(X,Y,Z)$. (B) Reconstruction of the trap surface. (C) Geometric variables measured on the surface of the trap (green line) and on the conical surface (black line). The figured off-centred position is exaggerated for the purpose of illustration.

conditions of controlled temperature (24.4±1.7°C) and humidity (43.7±6.3%; mean ± standard deviation). We scanned the pits dug by the antlions before introducing an ant into the box, close to the trap. Predation sequences were filmed in their entirety with the same camera used to record the scan. These sequences were then analysed frame-by-frame (25 frames s^{-1}). The recording of the sequence continued until the death of the prey. Capture time was measured by counting the number of frames between the moment at which the prey arrived at the bottom of the trap and the moment at which the fatal bite was delivered. This final bite was followed by a specific pattern of behaviour, in which the ant was shaken and then buried in the sand. The cost of prey capture was quantified by counting the number of attempts to bite the prey or to throw sand over the prey for each predation sequence. Each attack behaviour entails a cost in terms of time and energy. To summarize, an experiment followed this sequence: we first put an antlion in a box of sand with known granular properties, it was allowed to dig a trap and 3D modelling of the trap was undertaken; we then put an ant in the box and analysed the attack behaviour and trap geometry.

Measurement of crater angle

The measurement and definition of the drained angle of repose can be achieved by three types of analysis, each of which provides a slightly different angle: conical heap, two-dimensional slope and crater angle (Brown and Richards, 1970). By analogy with the funnel-shaped trap of the antlion, we chose to measure crater angle. This angle was measured on 30 artificial cones obtained by filling a circular box (8 cm in diameter, 2 cm high), in which a 1.19 mm hole had been made in the base, with the same sand as was used in the experiments described above. A crater is formed when the sand escapes *via* the hole. The angle of the slope of this crater is the crater angle. These cones were scanned and their surfaces were reconstructed and adjusted, based on conical area, as described above. Thus, for each artificial cone, we obtained a measurement of crater angle and a measurement of deviation from the model cone. The mean angle obtained, α_c, corresponds to the value of the drained angle of repose by a crater. The mean RMSE value obtained, $RMSE_c$, corresponds to the smallest deviation from the model cone, taking into account the precision of the apparatus and the size of the grains forming the surface. The values of crater angle and RMSE measured on the traps dug by the antlions were compared with α_c and $RMSE_c$ as follows:

$$\Delta_{angle} = \alpha_c - \alpha \quad \text{and} \quad \Delta_{RMSE} = RMSE - RMSE_c .$$

Statistical analysis

We assessed the correlations between various geometric, behavioural and predation variables, by calculating Pearson's correlation coefficients and carrying out Student's *t*-tests. We used linear models for the correlation between certain variables for which the significance of the correlation was tested by means of *F*-tests. The narrow range of angles measured allows us to apply a linear model without transformation (Batschelet,

1981). The significance of differences of variables between larval stage 2 and 3 was tested by means of Wilcoxon tests. The significance of the parameters generated by these models was assessed by means of Student's t-tests. All means and estimates are given with their 95% confidence interval (mean ± 95% confidence interval).

Results

Trap architecture

The values of RMSE are weak, from 0.18 mm to 0.71 mm, indicating that traps are never far from a perfect conical model. Out of 24 antlions, seven had an off-centring of less than 1 mm, and 15 had an off-centring less than 2 mm. Thus, off-centring is generally minimal, of the order of the size of its head. Diameter, height, angle, RMSE and off-centring measured on stage 2 larvae were not distinct from those measured on stage 3 larvae (respectively: $W=40$, $P=0.720$; $W=54$, $P=0.3311$; $W=84$, $P=0.494$; $W=43$, $P=0.1056$; $W=42$, $P=0.0933$; $N=24$). Angle was negatively correlated with RMSE ($r=-0.7248$, $t=-4.9350$, $P<0.001$, $N=24$). Angle was also negatively correlated with off-centring ($r=-0.6481$, $t=-3.9917$, $P<0.001$, $N=24$). RMSE was positively correlated with off-centring ($r=0.7833$, $t=5.9112$, $P<0.001$, $N=24$). Thus, the two geometric parameters, trap angle and RMSE, vary similarly with off-centring. As off-centring was observed in all cases, we also investigated the values of trap angle and RMSE in the absence of off-centring (α_{wo} and $RMSE_{wo}$). A linear model accounting for changes in Δ_{angle} as a function of off-centring ($R^2=0.42$, $F=15.93$, $P<0.001$, $N=24$) predicted that, in the absence of off-centring, Δ_{angle} would be significantly different from zero (intercept: $\Delta_{angle}=4.5279\pm1.2674°$, $t=7.409$, $P<0.001$) (Fig. 3A). The theoretical angle α_{wo} ($37.0594\pm1.2674°$) is therefore significantly smaller than the crater angle α_c ($41.6085\pm0.2366°$; $N=30$). The study of the distribution of angles measured on antlion constructions showed that the mode was located in the confidence interval of α_{wo} (Fig. 4). Only one trap had an angle greater than the upper limit of this confidence interval. Similarly, linear regression ($R^2=0.6136$, $F=34.94$, $P<0.001$, $N=24$) was used to predict Δ_{RMSE} in the absence of off-centring (Fig. 3B). The predicted Δ_{RMSE} in the absence of off-centring did not differ significantly from zero (intercept: $\Delta_{RMSE}=0.0359\pm0.0533$mm, $t=1.396$, $P=0.177$). The theoretical RMSE, $RMSE_{wo}=0.2478\pm0.0533$ mm, is therefore not significantly different from the $RMSE_c$ of 0.2098 ± 0.0130 mm ($N=30$). In the absence of off-centring, the antlion is therefore able to construct a perfectly conical trap with a slope shallower than the maximal slope permitted by the physics of sand.

Impact of trap geometry on predation cost

All ants were captured during the experiments, ensuring a finite capture time. Out of 24 antlions, seven displayed no attack behaviour to catch their prey, and five used attack behaviours consisting of only one sand throwing or bite attempt. We did not observe avalanches triggered by ant struggle. Capture time was positively correlated with the
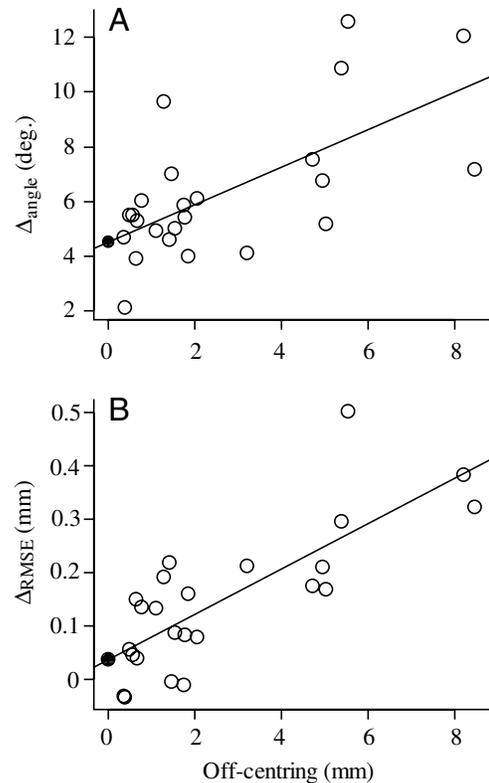

Fig. 3. Changes in Δ_{angle} (A) and Δ_{RMSE} (B) as a function of off-centring. The straight line corresponds to the linear model fitted on the data. The open circles are data points and the closed circles are the predicted values of Δ_{angle} and Δ_{RMSE} in the absence of off-centring, making it possible to obtain $RMSE_{wo}$ and α_{wo}: $RMSE_{wo}=\Delta_{RMSE}(0)+RMSE_c$ and $\alpha_{wo}=\alpha_c-\Delta_{angle}(0)$.

number of times sand was thrown ($r=0.9292$, $t=11.79$, $P<0.001$, $N=24$), and with the number of attempts to bite the prey ($r=0.7349$, $t=5.0824$, $P<0.001$, $N=24$). Capture time was a linear function of the number of times sand was thrown and the number of attempts to bite the prey ($R^2=0.9329$, $F=145.9$, $P<0.001$, $N=24$). Capture time was therefore considered to represent the cost of predation, as it is known that the number of times sand is thrown has a strong effect on predation cost (correlation between capture time and number of times sand thrown: $r=0.9292$, $t=11.7899$, $P<0.001$, $N=24$; correlation between capture time and number of biting attempts: $r=0.7348753$, $t=5.0824$, $P<0.001$, $N=24$). We then focused primarily on correlations between capture time and geometric variables. There was no difference in capture time between stage 2 larvae and stage 3 larvae ($W=38.5$, $P=0.05651$, $N=24$). Once the prey had fallen into the trap, the capture cost was totally independent of the size of the trap. Indeed, capture cost was not correlated with trap diameter ($r=0.1846$, $t=0.8812$, $P=0.3878$, $N=24$) or trap height ($r=-0.0616$, $t=-0.2894$, $P=0.7750$, $N=24$). Capture time was negatively correlated with angle ($r=-0.5545$, $t=3.1254$, $P<0.001$, $N=24$) and positively correlated with RMSE ($r=0.6793$, $t=4.3416$, $P<0.001$, $N=24$).
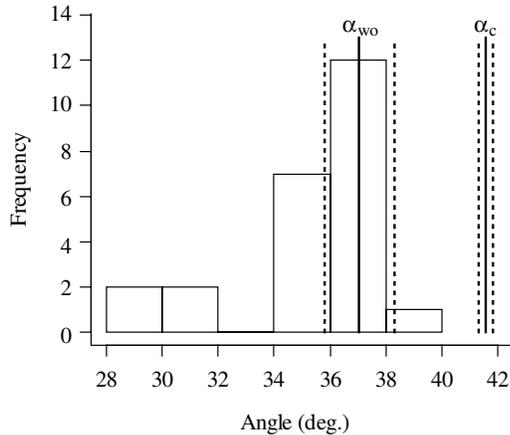
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Fig. 4. Distribution of the angles achieved in antlion constructions. The number of classes is given by Yule's formula (k=5.53). The bars with solid lines correspond to α_{wo} and α_c, and the dotted lines indicate the 95% confidence intervals for these angles.

Capture time was also correlated with off-centring (r=0.8992, t=13.3903, P<0.001, N=24), and this relationship was expressed in terms of a linear model (R^2=0.8085, F=92.9, P<0.001, N=24) (Fig. 5). The intercept of this regression line was not significantly different from zero (intercept= –0.5154±0.3571s, t=–1.443, P=0.163, N=24). Thus, a capture time of zero can be obtained only if there is no off-centring (i.e. the trap must be perfectly conical).

Discussion

Off-centring is the distance between the head and the lowest point of the trap. This off-centring is the result of post-construction actions: after constructing its trap, the animal moves, triggering one or several avalanches of various sizes. Off-centring therefore leads to a deviation from the perfect cone shape and a decrease in trap angle as a result of the
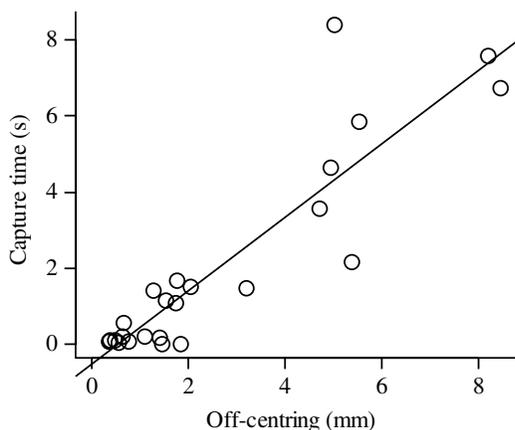

Fig. 5. Linear changes over time in capture as a function of off-centring.

avalanches. Greater off-centring is associated with more frequent and/or larger avalanches, leading to a simultaneous decrease in angle and increase in RMSE. The loss of conicity indicates deviations from a perfect conical surface due to dips and humps in the trap surface. A loss of smoothness of the trap surface may make it easier for the prey to climb back up the trap. Similarly, the angle of the slope may affect the displacement of the prey (Botz et al., 2003). This would explain why off-centring affects capture cost: the prey arrives at a point out of reach of the mandibles of the antlion and can move about more easily within the trap. Off-centring therefore seems to be the key factor determining predation cost. Thus, off-centring leads to a loss of architectural efficiency that is compensated for by attack behaviour.

We can now revisit our hypothetical model of costs and benefits of the pit construction on the basis of our results (Fig. 1). In the absence of off-centring, the trap is perfectly conical and the angle (α_{wo}) is significantly smaller than that defined by the physics of sand (α_c). Thus, before off-centring, the antlion constructs a trap that is perfectly conical but has an angle smaller than the crater angle. The angle α_{wo} therefore corresponds to the shallowest slope allowing prey to be captured as efficiently as possible. The antlion gains no advantage in terms of efficiency from building a trap with an angle greater than α_{wo}. Any perturbation leading to avalanches leads to higher maintenance cost. Thus the slope angle targeted by the antlion can be somewhat shallower than the crater angle. As described in the Introduction, the animal constructs its trap by defining an initial diameter and then digging down in a spiral to the bottom of the funnel (Tuculescu et al., 1987; Youthed and Moran, 1969). The creation of perfect traps requires that the antlion begins with an initial perfect circle, digs itself down with a spiral movement, and stops before reaching the crater angle. We do not know the stimuli used for making this decision, but the production of avalanches and/or the forces acting on the numerous mechanosensors on the body may be used.

Pits are the simplest possible type of trap, and their rarity remains puzzling (Hansell, 2005). This foraging strategy is not new. These insects changed habitat before the fragmentation of Gondwana, moving from the trees to sand (i.e. from arboreal life style to psammophily) and pit construction was the key to the emergence of a small but successful group within the Myrmeleontidae, the Myrmeleontini (Mansell, 1996; Mansell, 1999). Other groups that developed later, including the Palparini, did not adopt this strategy, but have also been successful. Pit construction does not require specific morphological adaptations. Wormlion larvae (Diptera, Vermileonidae, *Vermileo*), which have no legs or strong mandibles, also construct pits in sand (Wheeler, 1930). Thus, insect larvae of all morphologies are potentially able to build such traps. Finally, the type of prey and the microhabitat requirements are not necessarily unusual or restrictive in any way. It therefore remains a mystery why such simple traps have so rarely been adopted by the animal kingdom.

List of abbreviations

α	angle with respect to the horizontal of the trap
RMSE	root mean square error
α_c	drained angle of repose by a crater
$RMSE_c$	root mean square error by a crater at α_c
Δ_{angle}	difference between α_c and trap angle
Δ_{RMSE}	difference between trap RMSE and $RMSE_c$
α_{wo}	theoretical angle without off-centring
$RMSE_{wo}$	theoretical RMSE without off-centring

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