# Efficiency of antlion trap construction 

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#### Abstract

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.

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Key words: animal construction, antlion pit, sit-and-wait predation, physics of sand, psammophily.

## 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 timeconsuming. Spiders are the main group of trap-building animals, with over 10000 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 $0.5 \mathrm{~mm} \times 0.5 \mathrm{~mm}$ ) (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:

$$
\begin{equation*}
\left(x-O_{\mathrm{x}}\right)^{2}+\left(y-O_{\mathrm{y}}\right)^{2}-\left(z-O_{\mathrm{z}}\right)^{2} \tan ^{2}[(\pi / 2)-\alpha]=0, \tag{1}
\end{equation*}
$$

The parameter $\alpha$ 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 ( $\alpha_{\mathrm{c}}$ ), which cannot be achieved because of the physical properties of sand. $\alpha_{\text {WO }}$ is the theoretical angle without off-centring.
$\left(O_{\mathrm{x}}, O_{y}, O_{z}\right)$ 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):

$$
\begin{equation*}
\mathrm{RMSE}=\sqrt{\mathrm{RSS}} / n \tag{2}
\end{equation*}
$$

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 coordinates 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 $\left(47^{\circ} 21^{\prime} 16.36^{\prime \prime} \mathrm{N}, 0^{\circ} 42^{\prime} 16.08^{\prime \prime} \mathrm{E}\right.$, 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 SDS 190027, particles of 100 to $300 \mu \mathrm{~m}$ in size). The antlions were placed in square Perspex boxes $(11 \times 11 \times 6 \mathrm{~cm}) 16 \mathrm{~h}$ 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

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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 threedimensional 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 offcentred position is exaggerated for the purpose of illustration.
conditions of controlled temperature $\left(24.4 \pm 1.7^{\circ} \mathrm{C}\right)$ and humidity ( $43.7 \pm 6.3 \%$; mean $\pm$ 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, twodimensional 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 $(8 \mathrm{~cm}$ 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, $\alpha_{c}$, corresponds to the value of the drained angle of repose by a crater. The mean RMSE value obtained, RMSE $_{\mathrm{c}}$, 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 $\alpha_{c}$ and $\operatorname{RMSE}_{c}$ as follows:

$$
\Delta_{\text {angle }}=\alpha_{\mathrm{c}}-\alpha \quad \text { and } \quad \Delta_{\mathrm{RMSE}}=\mathrm{RMSE}-\mathrm{RMSE}_{\mathrm{c}} .
$$

## 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 $\pm 95 \%$ 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 offcentring. As off-centring was observed in all cases, we also investigated the values of trap angle and RMSE in the absence of off-centring ( $\alpha_{\text {wo }}$ and RMSE wo ). A linear model accounting for changes in $\Delta_{\text {angle }}$ as a function of off-centring $\left(R^{2}=0.42\right.$, $F=15.93, P<0.001, N=24$ ) predicted that, in the absence of off-centring, $\Delta_{\text {angle }}$ would be significantly different from zero (intercept: $\Delta_{\text {angle }}=4.5279 \pm 1.2674^{\circ}, t=7.409, \quad P<0.001$ ) (Fig. 3A). The theoretical angle $\alpha_{\text {wo }}\left(37.0594 \pm 1.2674^{\circ}\right)$ is therefore significantly smaller than the crater angle $\alpha_{c}$ ( $41.6085 \pm 0.2366^{\circ} ; N=30$ ). The study of the distribution of angles measured on antlion constructions showed that the mode was located in the confidence interval of $\alpha_{\text {wo }}$ (Fig. 4). Only one trap had an angle greater than the upper limit of this confidence interval. Similarly, linear regression $\left(R^{2}=0.6136, F=34.94\right.$, $P<0.001, N=24$ ) was used to predict $\Delta_{\text {RMSE }}$ in the absence of off-centring (Fig. 3B). The predicted $\Delta_{\text {RMSE }}$ in the absence of off-centring did not differ significantly from zero (intercept: $\Delta_{\text {RMSE }}=0.0359 \pm 0.0533 \mathrm{~mm}, t=1.396, P=0.177$ ). The theoretical RMSE, $\quad \mathrm{RMSE}_{\mathrm{wo}}=0.2478 \pm 0.0533 \mathrm{~mm}$, is therefore not significantly different from the $\mathrm{RMSE}_{\mathrm{c}}$ of $0.2098 \pm 0.0130 \mathrm{~mm}$ ( $N=30$ ). 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 $\Delta_{\text {angle }}$ (A) and $\Delta_{\text {RMSE }}$ (B) as a function of offcentring. 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 $\Delta_{\text {angle }}$ and $\Delta_{\text {RMSE }}$ in the absence of off-centring, making it possible to obtain $\mathrm{RMSE}_{\mathrm{wo}}$ and $\alpha_{\mathrm{wo}}$ : $\mathrm{RMSE}_{\mathrm{wo}}=$ $\Delta_{\text {RMSE }}(0)+$ RMSE $_{c}$ and $\alpha_{\text {wo }}=\alpha_{\mathrm{c}}-\Delta_{\text {angle }}(0)$.
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 $\alpha_{\text {wo }}$ and $\alpha_{c}$, and the dotted lines indicate the $95 \%$ confidence intervals for these angles.

Capture time was also correlated with off-centring ( $r=0.8992$, $t=13.3903, \quad P<0.001, N=24$ ), and this relationship was expressed in terms of a linear model $\left(R^{2}=0.8085, F=92.9\right.$, $P<0.001, N=24$ ) (Fig. 5). The intercept of this regression line was not significantly different from zero (intercept= $-0.5154 \pm 0.3571 \mathrm{~s}, t=-1.443, P=0.163, N=24$ ). 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 postconstruction 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 offcentring.
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 ( $\alpha_{\text {wo }}$ ) is significantly smaller than that defined by the physics of sand $\left(\alpha_{c}\right)$. Thus, before off-centring, the antlion constructs a trap that is perfectly conical but has an angle smaller than the crater angle. The angle $\alpha_{\text {wo }}$ 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 $\alpha_{\text {wo }}$. 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

| $\alpha$ | angle with respect to the horizontal of the trap |
| :--- | :--- |
| RMSE | root mean square error |
| $\alpha_{\mathrm{c}}$ | drained angle of repose by a crater |
| $\mathrm{RMSE}_{\mathrm{c}}$ | root mean square error by a crater at $\alpha_{c}$ |
| $\Delta_{\text {angle }}$ | difference between $\alpha_{c}$ and trap angle |
| $\Delta_{\text {RMSE }}$ | difference between trap RMSE and RMSE |
| $\alpha_{\mathrm{wo}}$ | theoretical angle without off-centring |
| $\mathrm{RMSE}_{\mathrm{wo}}$ | theoretical RMSE without off-centring |

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# A low cost 3D capturing system: an application for antlion pit architecture analysis 

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## 1. Set-up, description and principle

The principle involves projecting the shadow of a plane with a rectilinear edge on the surface and using the deformations of the shadow to estimate the three-dimensional points corresponding to this surface. The system has two parts (Fig. 1A): 1) an apparatus with a light source (Orbitec P80818) fixed above the plane used to generate the shadow; 2) a camera (Euromex VC3031) placed above the apparatus. The apparatus is moved on ballbearings along a fixed axis on a flat surface. Displacements are made millimetre-by-millimetre above the object to be scanned. The equipment is set up such that the axis along which the apparatus moves is parallel to the $X_{p x}$ axis of the image. The edge of the plane therefore moves parallel to the $Y_{p x}$ axis of the image, making it possible to simplify implementation (Fig. 2). The images comprising the scan are coded on a grey-scale level from 0 (white) to 255 (black) (Fig. 2A). The camera captures the deformations of the shadow, which are then digitised using a graphics card (ADSTech DVDXpress) for computer processing. A point on the edge of the plane $P$ is projected on a point $S$ on the shadow on the surface of the object (Fig. 1). The camera and the graphics card produce a digital image of the scene on which we find the points $S_{p x}$ and $P_{p x}$ (Fig. 2A). The method used involves estimating the three-dimensional coordinates of $S$ (the shadow) by reversing the process of image formation from the real scene to the digital image. These calculations lead to the generation of a 3D model of the object, as shown in Fig. 3.

## 2. Three-dimensional modelling of an object

### 2.1 Data extraction from images

The scan of an object comprises a series of images that record successive deformations of the shadow on the object. Each image is transformed into a binary image using the ImageJ program, with a threshold value giving a coded black (255) and white (0) image (Abramoff et al., 2004) (Fig. 2B). The co-ordinates of the points forming the edge of the shadow and the edge of the plane were extracted from each image, using an algorithm developed in ImageJ. Each point on the edge of the projected shadow $S_{p x}\left(X s_{p x}, Y s_{p x}\right)$ is associated with a point on the edge of the plane $P_{p x}\left(X p_{p x}, Y p_{p x}\right)$ (Fig. 2). It should be noted that for the set-up used, $Y s_{p x}=Y p_{p x}$. Processing of the entire image gave a series of paired points $\left(S_{p x}, P_{p x}\right)$.

### 2.2 Transformation of pixel data into metric data

The model of camera used was of the pinhole type (Heikkilä and Silvén, 1997). This type of camera model defines a normalised image plane, corresponding to a focal plane with a focal distance fixed at 1 (Fig. 1). A point in space within the field of the camera is projected onto the plane on which the image is formed, and the CCD sensor encodes the image in pixels. The transformation therefore involves finding the metric co-ordinates of the points $\left(S_{c} P_{c}\right)$ on the normalised image plane based on the pixel co-ordinates of the points $\left(S_{p x}, P_{p x}\right)$. The transformation of a point on the digital image into a point on the image in the normalised plane requires the use of the intrinsic parameters of the camera. These parameters were estimated by calibration of the camera with the Camera Calibration Toolbox for Matlab ${ }^{\circledR}$ (Bouguet). The transformation of a given point $\left(X_{p x,} Y_{p x}\right)$ from the pixel image into a point $\left(X_{n}, Y_{n}\right)$ on the normalised plane image is given by the following linear relationship:

$$
\left[\begin{array}{c}
X_{p x} \\
Y_{p x} \\
1
\end{array}\right]=K\left[\begin{array}{c}
X_{n} \\
Y_{n} \\
1
\end{array}\right] \text { with } K=\left[\begin{array}{ccc}
f_{x} & \beta f_{x} & X o_{p x} \\
0 & f_{y} & Y o_{p x} \\
0 & 0 & 1
\end{array}\right]
$$

The matrix $K$ is referred to as the camera matrix. It includes all the parameters intrinsic to the pinhole model camera. The point $\left(X o_{p x}, Y o_{p x}\right)$ is the principal point in the pixel image, $f_{x}$ and $f_{y}$ correspond to focal distances, expressed in pixels, corresponding to the axes $X_{p x}$ and $Y_{p x}$, respectively. $\beta$ is the skew coefficient defining the angle between the axes $X_{p x}$ and $Y_{p x}$. The co-ordinates, in pixels, of the points extracted from the image were converted into metric coordinates on the normalised image plane with equation [1].

The model of camera also defines the distortion parameters that can be used to rectify the distortion caused by the objective lens. A second transformation is used to correct the points on the normalised image field. There are no analytical solutions for the correction of lenses based on distortion coefficients. We therefore used a recursive method (Melen, 1994; Heikkilä, 2000). On the normalised image plane, the corrected co-ordinates $\left(X_{c}, Y_{c}\right)$ are approximated based on the distorted co-ordinates $\left(X_{n}, Y_{n}\right)$ as follows:

$$
\left[\begin{array}{c}
X_{c} \\
Y_{c}
\end{array}\right]=\left[\begin{array}{c}
\frac{X_{n}-\left(2 p_{1} X_{n} Y_{n}+p_{2}\left(r+2 X_{n}^{2}\right)\right)}{1+k_{1} r+k_{2} r^{2}+k_{3} r^{3}} \\
\frac{Y_{d}-\left(2 p_{2} X_{n} Y_{n}+p_{1}\left(r+2 Y_{n}^{2}\right)\right)}{1+k_{1} r+k_{2} r^{2}+k_{3} r^{3}}
\end{array}\right] \text { with } r=X_{n}^{2}+Y_{n}^{2} \text { [2] }
$$

where $k_{1}, k_{2}$ and $k_{3}$ are the coefficients of radial distortion and $p_{1}$ and $p_{2}$ are the coefficients of tangential distortion. This calculation is repeated 20 times, with $\left(X_{n}, Y_{n}\right)$ replaced by the $\left(X_{c}, Y_{c}\right)$ values from the previous iteration in each case. These two transformations were carried out in succession: conversion of the pixel co-ordinates into co-ordinates on the normalised image plane followed by correction for lens distortion.

### 2.3 Surface reconstruction

The corrected points on the normalised image plane $S_{c}\left(X s_{c}, Y s_{c}\right)$ and $P_{c}\left(X p_{c}, Y p_{c}\right)$ were calculated from the image points $S_{p x}\left(X s_{p x}, Y s_{p x}\right)$ and $P_{p x}\left(X p_{p x}, Y p_{p x}\right)$. The points $S_{c}\left(X s_{c}, Y s_{c}\right)$ and $P_{c}\left(X p_{c}, Y p_{c}\right)$ are the projections of the spatial points $S\left(x_{S}, y_{S}, z_{S}\right)$ and $P\left(x_{P}, y_{P}, z_{P}\right)$ in the camera's reference frame:

$$
\left[\begin{array}{c}
z_{S} X s_{c}  \tag{4}\\
z_{S} Y s_{c}
\end{array}\right]=\left[\begin{array}{l}
x_{S} \\
y_{S}
\end{array}\right][3] \text { and }\left[\begin{array}{c}
z_{P} X p_{c} \\
z_{P} Y p_{c}
\end{array}\right]=\left[\begin{array}{l}
x_{P} \\
y_{P}
\end{array}\right] \text { [4] }
$$

The aim was to define analytically the point on the edge of the shadow $S\left(x_{S}, y_{S}, z_{S}\right)$ in the camera's reference frame as a function of the co-ordinates of the points $S_{c}\left(X s_{c}, Y S_{c}\right)$ and $P_{c}\left(X p_{c}, Y p_{c}\right)$, the angle of incidence $\alpha$ of the light source with the axis x of the camera's reference, and the equation of the plane in space. The equation of the plane projected in the camera's reference frame is defined as follows:

$$
z_{P}=a x_{P}+b y_{P}+c \text { [5] }
$$

expressing $z_{p}$ as a function of $P_{c}\left(X p_{c}, Y p_{c}\right)$ based on equations [3], [4] and [5] :

$$
z_{P}=\frac{c}{1-a X p_{c}-b Y p_{c}} \text { [6] }
$$

The projection of the point $P$ on the point $S$ by the light source gives (Fig. 1B):

$$
\tan \alpha=\frac{z_{S}-z_{P}}{x_{P}-x_{S}}
$$

The equations [3], [4], [6] and [7] can be used to define the three-dimensional co-ordinates of the point $S$ in the camera's reference frame as a function of the points $S_{c}$ and $P_{c}$ and the parameters of the apparatus $(\alpha, a, b, c)$ :

$$
z_{S}=\frac{c\left(1+X p_{c} \tan \alpha\right)}{\left(\left(1-a X p_{c}-b Y p_{c}\right)\left(1+X s_{c} \tan \alpha\right)\right)}[8], x_{S}=z_{S} X s_{c} \text { [9] and } y_{S}=z_{S} Y s_{c} \text { [10] }
$$

The pairs of points ( $S_{p x}, P_{p x}$ ) extracted from the series of images were treated according to the process described above, to obtain a collection of three-dimensional points located on the surface of the scanned object. Akima's linear interpolation was used to reconstruct this surface using a grid with 0.5 mm squares (Akima, 1996).

### 2.4 Device calibration

The apparatus was calibrated and its parameters $(\alpha, a, b, c)$ estimated using a rod connecting two points $A$ and $B$ separated by a $d_{r e f}$ of 21.182 mm . The rod was placed in $N$ different positions in the field of the camera $(N=60)$. At each position $i$ the shadow of the plan was projected successively on the two points $A$ and $B$ of the rod. For position $i$, the co-ordinates in the camera's reference frame $A_{i}\left(x_{A i}, y_{A i}, z_{A i}\right)$ and $B_{i}\left(x_{B i}, y_{B i}, z_{C i}\right)$ were calculated as described above. The distance $d_{i}$ between $A_{i}$ and $B_{i}$ is calculated as follows:

$$
\begin{equation*}
d_{i}=\sqrt{\left(x_{A i}-x_{B i}\right)^{2}+\left(y_{A i}-y_{B i}\right)^{2}+\left(z_{A i}-z_{B i}\right)^{2}} \tag{9}
\end{equation*}
$$

This distance $d_{i}$ is a function of the parameters $(\alpha, a, b, c)$ and equals $d_{r e f}$ if and only if $(\alpha, a, b, c)_{\text {estimated }}=(\alpha, a, b, c)_{\text {real }}$. The method for estimating $(\alpha, a, b, c)$ was based on least squares minimisation:

$$
\operatorname{RSS}(\alpha, a, b, c)=\sum_{i=1}^{i=N}\left(d_{r e f}-d_{i}\right)^{2} \quad[10]
$$

This estimation was carried out in the $R$ environment ( R Development Core Team 2004), using a quasi-Newtonian method (Byrd et al., 1995).

## 3. System precision

Table 1 shows estimates of the parameters of the apparatus and their precision. The director coefficients $a$ and $b$ are very close to zero, because, in the set-up used, the camera is positioned with respect to both the horizontal and the projected plane.

The precision of the apparatus was estimated using the same rod used for calibration. This rod was placed in 60 positions different from those used for calibration and, for each position $i$, the distance $d_{i}$ between the points A and B was calculated. The difference between $d_{i}$ and $d_{r e f}$ depended on the exact repositioning of the points A and B in space. At each position, we calculated the absolute error: $\varepsilon_{i}^{a}=\left|d_{\text {ref }}-d_{i}\right|$ and the relative error: $\varepsilon_{i}^{r}=\frac{\left|d_{\text {ref }}-d_{i}\right|}{d_{\text {ref }}} \times 100$. The absolute error was $\varepsilon^{a}=98.0737 \pm 18.5969 \mu \mathrm{~m}$ (mean $\pm 95 \%$ confidence interval), corresponding to a maximum error of $117 \mu \mathrm{~m}$ in the calculation of the distance between the two points. The relative error was low: $\varepsilon^{r}=0.4630 \pm 0.0878 \%$ (mean $\pm$ $95 \%$ confidence interval), or a maximum of $0.55 \%$. In the context of this study, the precision of the instrument corresponds to less than the diameter of a grain of sand.

## 4. Conclusion

This apparatus provides high-level precision at low cost (about \$40) and made it possible to analyse in detail the geometry of antlion traps (Fig. 4). This technique is competitive with respect to other available techniques. Profilometric lasers are much more expensive. The simplicity of the calculations with our method makes it possible to generate a three-dimensional model with a large number of points. Photogrammetry, which requires correlation between the images of at least two cameras, may become particularly cumbersome if a large number of points are required.

The principal limitation of our technique concerns the texture of the object used. As image analysis is based on the detection of a shadow, a texture giving an image with too many shadow pixels could result in too many erroneous points. However, this could readily be corrected by dusting the object with white powder or using a more powerful white light. Image processing with contour detection algorithms could also be used to overcome these problems of "dark" textures. It should be noted that lasers also face similar problems when confronted with dark or shiny surfaces.

## References

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## Tables and figures

| Parameters | Estimates | Standard deviation |
| :--- | :--- | :--- |
| $\alpha$ | 0.9580 | 0.0126 |
| $a$ | 0.0186 | 0.0165 |
| $b$ | 0.0071 | 0.0150 |
| $c$ | 484.6556 | 3.7518 |

Table 1: Estimates of the parameters of the apparatus. Standard errors were estimated by inversing the Hessian matrix obtained when $\operatorname{RSS}(\alpha, a, b, c)$ was minimised.


Figure 1: (A) Diagram of the set-up. The light source projects a shadow of the edge of the plane of the scene. The edge of the plane and the shadow are projected onto the normalised 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) Diagram explaining the calculation of $S\left(x_{S}, y_{S}, z_{S}\right)$ in the plane $(X, Z)$ of the camera's reference frame, as $\mathrm{y}_{\mathrm{s}}=\mathrm{y}_{\mathrm{p}} . O$ is the optical centre of the camera and $Z$ is the optical axis.


Figure 2: (A) Image extracted from the video obtained with the camera. (B) The same image after binary transformation. 1: Scanned surface, here an antlion trap; 2: Shadow; 3: Projected plane. The algorithm developed in ImageJ processes the pairs of pixel co-ordinates $\left(S_{p x,} P_{p x}\right)$.


Figure 3: Diagram of the various steps in the three-dimensional modelling of an object. The thick arrows show the steps to be followed when reconstructing an object.


Figure 4: Examples of two antlion trap topographies. (A) Trap with a low off-centring. (B) Trap with a high off-centring.

