

1 Sand throwing in a pit-building antlion larva from a soil mechanical 2 perspective

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4 Sebastian Büsse^{1*}, Thies H. Büscher¹, Lars Heepe¹, Stanislav N. Gorb¹ & Hans Henning
5 Stutz²

6
7 ¹ Functional Morphology and Biomechanics, Institute of Zoology, Kiel University, Kiel,
8 Germany

9 ² Department of Engineering, Geotechnical Engineering, Aarhus University, Aarhus,
10 Denmark

11
12 *Corresponding author: sbuesse@zoologie.uni-kiel.de

13 14 **Abstract**

15 Sandy pitfall traps are an elaborate construction to capture prey and antlions are well-known
16 representatives of this predation technique. From a soil mechanical perspective, antlions
17 exploit the interactions between the particles of their habitat and engineer a stable trap. This
18 construction is close to the unstable state, where a prey item will immediately slide towards
19 the center - towards the ambushing antlion - when accidentally entering the trap. This method
20 is efficient, but requires permanent pit maintaining. According to the present knowledge,
21 antlions throw sand at their prey, to distract it, and/or cause sand slides towards the center of
22 the pit. Using sand throwing and escape experiments, as well as finite element analysis, we
23 supported this hypothesis. Furthermore, we added new hypothesis about maintaining the
24 pitfall trap. We showed that sand that accumulates in the center of the pit will be continuously
25 removed, which lead to the slope maintenance close to an unstable condition. This avoids
26 self-burial of the antlion, as well as decreasing the chance of prey item escapes by keeping
27 the slope angle steep. This demonstrates the interaction of an insect larva with its abiotic
28 environment from a novel perspective and adds further insights into longstanding
29 entomological hypotheses.

30
31 **Keywords:** *Euroleon nostras*, self-stratification, soil mechanics, finite element modelling,
32 prey capturing, predatory strike, trap-building predators, angle of repose

33 34 **Background**

35 Trap-building is a highly specialised, but comparably uncommon, hunting strategy within the
36 animal kingdom (Franks et al. 2019). Most trap-building invertebrates employ silk in their
37 constructions, with orb-web spiders probably being the most prominent example (Denny

38 1976; Vollrath and Knight 2001). These invertebrates successfully use silk to capture prey
39 (Lin et al. 1995; Krink and Vollrath 2000; Venner et al. 2006). In contrast, the construction of
40 traps without the employment of silk is best known in wormlions (Diptera: Vermileonidae) and
41 antlions (Neuroptera: Myrmeleontidae), using sand to dig a pitfall trap (Fig. 1 B,C) (cf. Adar et
42 al. 2016) with a few exceptions (cf. Dejean et al. 2005). Even though the trap-digging
43 strategy in antlions (spiral digging) is considered more effective in comparison to central
44 digging in wormlions (Tuculescu 1975; Franks et al. 2019), pitfall trap building strategies of
45 worm- and antlions represent an excellent example for convergent evolution of behaviour
46 (Miler et al. 2018).

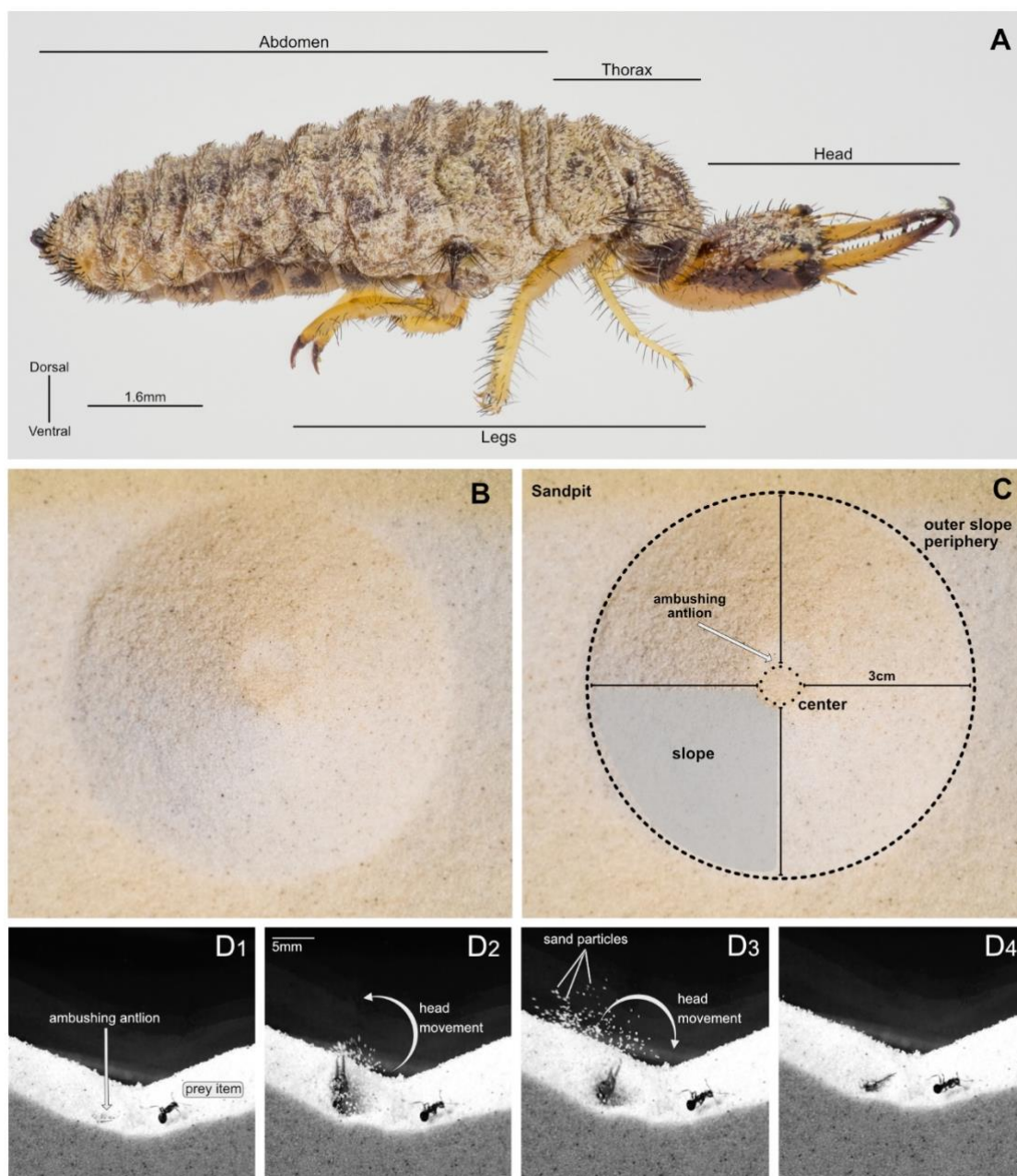
47
48 Generally, ground-dwelling animals which inhabit sandy habitats are strongly affected by the
49 physical characteristics of the substrate. Sand is a collection of particles interacting with each
50 other via contact forces. Here, spontaneous organisation (Rosato et al. 1987; Möbius et al.
51 2001) faces natural stratification (Bak et al. 1987; 1988), which leads to an irregular solid-
52 pore system (Herrmann 1998). Whereas the number of pores in granular media influences
53 the stress-deformation behaviour to a great extent, loose packing of granular particles leads
54 to an instable construct that can easily reach an unstable state (Terzaghi 1943, Miura et al.
55 1997). Here more voluminous sand grains show a larger angle of repose (definition see
56 "Methods: Terminology") than less voluminous grains, and all interact with the successive
57 sand layers (Makse et al. 1997).

58
59 The juvenile stages of most antlion species (Myrmeleontidae) utilise exactly this soil
60 mechanics phenomenon. The laval antlion (Fig.1 A) is a pit-building ambush predator
61 (Franks et al. 2019). The hunting success of it largely depends on the abiotic factors of its
62 habitat (Scharf and Ovadia 2006; Bar-Ziv et al. 2019), such as sand grain size and
63 distribution, and the majority of antlion species prefer sand with a comparably small particle
64 size (Allen and Croft 1985; Loiterton and Magrath 1996; Botz et al. 2003; Farji-Brener 2003).
65 Suitable substrates will enable the construction of considerably larger pits (Barkae et al.
66 2012), resulting in the ability to capture larger prey and reducing the risk of prey escapes
67 (Griffiths 1980; Lucas 1982; Heinrich and Heinrich 1984; Scharf et al. 2018). The relationship
68 between sand properties and slope is the key difficulty for prey items captured in a sandy
69 pitfall trap, as shown for the ant species *Aphaenogaster subterranea* (Latreille, 1798). This
70 species copes with the unstable substrate with a gait pattern transition from the tripod gait to
71 the metachronal wave pattern (Humeau et al. 2019). Changing the gait to the one involving a
72 higher number of legs (e.g. metachronal wave) is known from other insects adapting to
73 challenging attachment conditions (e.g. walking on the ceiling), and thus risking to lose their
74 grip to the substrate (Gorb and Heepe 2017; Büscher and Gorb 2019). Thus, the pitfall trap

75 of an antlion is a mechanically unstable construction, and its capturing success is increasing
76 with increasing slope angles and positively affected by decreasing sand particle size (Botz et
77 al. 2003). Exploiting the instability of the slope, the trap's morphology (Fig. 1 B,C) is used to
78 facilitate hunting prey of very different kind and size (cf. Gepp and Hölzel 1989). The larval
79 antlion is ambushing in the vertex of the pit (Lambert et al. 2011), where it is throwing sand,
80 using fast flicks of its head (Fig. 1 D₁-D₄; Griffiths 1980; Gepp and Hölzel 1989; Lambert et
81 al. 2011). This behaviour intends the distraction of escaping prey and more importantly,
82 causes small sand slides to trap the prey and translocate it to the center of the vertex –
83 respectively towards the antlion (Griffiths 1980).

84

85 We here present a study of the soil mechanical behavior that ensure the antlion's prey
86 capturing success. Underlining the sandslide theory, mentioned above, on the one hand, we
87 present a supplementary hypothesis focusing on pit maintaining, on the other. Presumably,
88 the sand throwing will not only actively prevent the prey from escaping, but will also maintain
89 the required instability of the slope. The sand, which will accumulate at the center of the pit
90 by the movements of the escaping prey, will be removed and more importantly the slope will
91 be kept close to an unstable condition. This study exemplifies the benefits of an
92 interdisciplinary approach to evaluate a known phenomenon from the perspective of two
93 different scientific disciplines aiding in the understanding of the underlining mechanisms –
94 here of the sand throwing by antlion larvae.



95
96
97 Figure 1: Antlion and pitfall trap. A. Habitus of antlion larva (*Euoleon nostras*), lateral view. B-C.
98 Sandpit used from the antlion as pitfall trap. C. Same sandpit as in B including labels. D. Sand
99 throwing behaviour of the antlion by the flick of its head. D1-4. Time series based on single frames
100 obtained from high-speed videography: 1. Before the flick of the antlion head starts; 2. During the flick,
101 upwards movement of the antlions head; 3. During the flick, downward movement of the antlions
102 head; 4. After the flick of the antlion head.

103

104 **Methods**

105

106 *Terminology*

107 **Angle of repose:** Physically, the angle of repose is described as the angle at which a
108 transition between phases of granular materials happening. The adopted common definition
109 is the steepest slope angle of the unconfined granular material measure from the horizontal
110 axis.

111
112 **Friction angle:** The friction angle defines the frictional shear resistant of the soil dependent
113 of the normal effective stress.

114
115 **Cohesion:** The cohesion is the shear strength component of the soil that is independent of
116 the inter-particle friction.

117
118 **Mobilised friction:** This is the definition of the friction that was mobilised in the strength
119 reduction method using the finite element model.

120

121 *Sand throwing experiments*

122 Larvae of *Euroleon nostras* (Fourcroy, 1785) were kept in small ant-terrariums
123 (210x100x105mm) filled with sand (particle size: 125 µm). Prior the experiments, the antlion
124 had 24h for setting up their pitfall trap. We used small instars of the house cricket (*Acheta*
125 *domesticus* (Linnaeus,1758)) as well as black garden ants (*Lasius niger* (Linnaeus,1758) and
126 *L. fuliginosus* (Latreille, 1798)) to film the prey capturing process of the antlion larvae using
127 an Olympus OMD 10mkII digital camera (Olympus K.K., Tokyo, Japan) equipped with a
128 Leica 45mm macro lens (Leica, Wetzlar, Germany). For measuring the slope angles (N=9,
129 total sequences 16) and for further image processing, Affinity Photo and Affinity Designer
130 (Serif Ltd, Nottingham, United Kingdom) were used. The slopes before and after sand
131 throwing were compared via a paired t-test, as the data was normally distributed (according
132 to Shapiro-Wilk's test for normality, P=0.08), using SigmaPlot 12.0 (Systat Software Inc., San
133 José, CA, USA).

134

135 *Escape experiments*

136 For the escape experiments a small formicarium (210x100x105mm) was used to film house
137 crickets (*A. domesticus*) while trying to escape a conical half-shaped artificial pitfall trap. The
138 formicarium was filled with sand (particle size: 125µm) using a defined funnel to produce a pit
139 close to the unstable state. Furthermore, we used ants (*L. niger* and *L. fuliginosus*) to escape
140 from a conical artificial pitfall trap. To produce this pit a box was filled with sand (see above)
141 with a hole in the bottom to produce a pit close to the unstable state. The prey items were
142 filmed, using an Olympus OMD 10mkII digital camera (Olympus K.K., Tokyo, Japan)
143 equipped with a Leica 45mm macro lens (Leica, Wetzlar, Germany), while ascending the

144 slope of the pit (N=7). Furthermore, a house cricked was filmed, using a Go-Pro Hero 5
145 (GoPro Inc., San Mateo, US) in time lapse setting (1 frame/min), over the course of 12h by
146 trying to escape the pit (respectively the terrarium), without the maintaining of an antlion. For
147 measuring the slope angles and for further image processing, Affinity Photo and Affinity
148 Designer (Serif Ltd, Nottingham, United Kingdom) were used.

149

150 *Photography*

151 For stacked photography, we used a custom-made 3D-printed LED illumination dome system
152 (Bäumler et al. 2020) and an Olympus OMD 10mkII digital camera (Olympus K.K., Tokyo,
153 Japan), equipped with a Leica 45mm macro lens (Leica Camera AG, Wetzlar, Germany).
154 In general, all images were subsequently processed in Affinity Photo and Affinity Designer
155 (Serif Ltd, Nottingham, United Kingdom).

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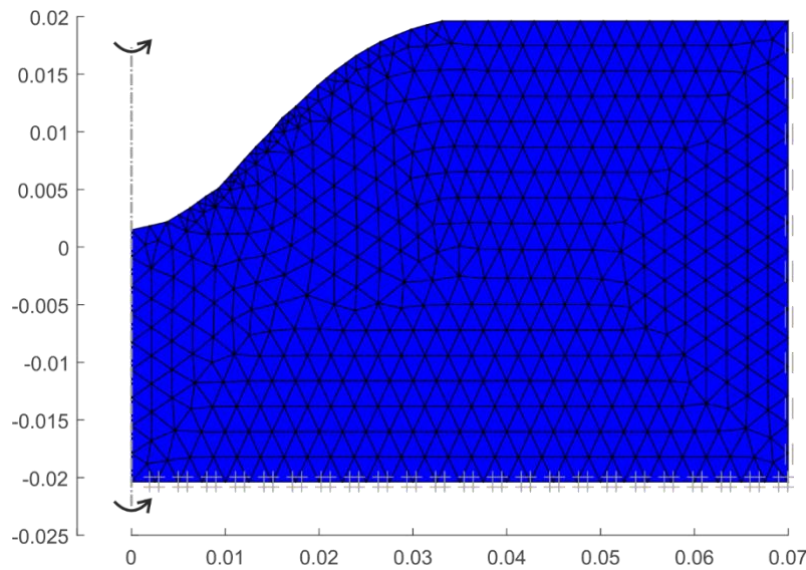
157 *Finite-element simulations*

158 The simulations are conducted using the finite-element method (FEM; commercial software
159 package OPTUM G2 2020, Copenhagen, Denmark). For studying the slope stability, the
160 strength reduction method has been applied to simulate the progressive failure of the sand
161 slope that is built by the antlion larvae as pitfall trap. The underlying principle of the strength
162 reduction method is that the initially assigned soil strength parameters will be reduced until a
163 failure occurs in the soil continuum. A detailed description of the strength reduction method is
164 given in e.g. Tschuchnigg et al. (2015a; 2015b). In short, the strength reduction method is
165 used to estimate the stability of a soil mechanical system by reducing systematically the
166 strength parameters of soil, namely cohesion and the friction angle. For the assessment of
167 the failure, the factor of safety (FoS) is used as:

$$168 \quad FoS = \frac{\tan \varphi'}{\text{mobilised } \tan \varphi'} = \frac{c'}{\text{mobilised } c'}$$

169 Where $\tan \varphi'$ is the effective friction angle of the soil and c' is the effective cohesion of the
170 soil. Herein, the friction angle and the cohesion describe the shear strength of a soil using
171 the concept of the Mohr-Coulomb failure criterion (Mohr 1900). The friction angle defines the
172 friction shear resistant of the soil dependent of the normal effective stress. The cohesion is
173 the shear strength component of the soil that is independent of the interparticle friction.
174 These are divided by mobilised friction and cohesion. The mobilised friction $\tan \varphi'$ and
175 cohesion describe the values that could be applied in the strength reduction method. $FoS < 1$
176 describe a failure and $FoS > 1$ describe a stable pit slope. The axisymmetric geometry of the
177 initial reference pit is shown in Figure 2. The boundary conditions at the bottom of the model
178 are fixed for all degree of freedoms, and the right side is a slider boundary condition.

179



180

181 Figure 2: Axi-symmetric mesh for the initial slope model, using 1000 (15-noded) elements. The soil
182 (blue) is modelled using the linear elastic – perfectly plastic Mohr-Coulomb model.

183

184 The model used in the simulations is the linear elastic-perfectly plastic Mohr-Coulomb
185 constitutive model, which have been proven to be sufficient for such ultimate limit state
186 simulations (Davis 1968, Tchuchnigg et al. 2015). The used geometry is chosen based on
187 the previously reported average antlion pits (e.g. Bongers & Koch 1981; Lucas 1982) and our
188 experimental setup.

189

190 In general, the following steps are conducted for each simulation:

- 191 1). The initial stress is applied and calculated.
- 192 2.) The initial geometry is analysed to estimate the initial FoS.
- 193 3.) The changed geometry is used to estimate the change in the FoS and the consequences
194 due to the sand throwing of the antlion larvae.

195

196 The reference configuration (Fig. 2) has an initial FoS= 1.096, and this means the slope
197 geometry is stable. For the more accurate prediction of the failure mechanisms and the FoS,
198 a mesh adaptivity step is applied with three adaptive iterations using the shear dissipation as
199 adaptivity control. The mesh adaptivity is a procedure using an adaptive meshing technique
200 to refine the mesh around the shear zone in which the plastic deformation is overdriven (Ortiz
201 & Quigley 1991). The mesh is refined according to the norm of the strain vector $\|\epsilon\|$. The
202 initial model shown in figure 2, shows a mesh consisting of 1000 elements; here, the model
203 is using a linear elastic – perfectly plasticity Mohr-Coulomb constitutive model (Mohr 1900).
204 The parameters used in the simulation are given in Table 1. In the mesh refinement step,
205 2000 elements are used.

206 Table 1: Parameters used in the finite-element simulations for the Mohr-Coulomb model (grey zones
207 do not influence the strength reduction method)

Material	Cohesion c [kPa]	Friction angle φ [°]	Dilatancy [°]	E-modulus [MPa]	Poisson's ratio [-]
Sand initial	0	34.5	0	20	0.2
Sand reduced density	0	29	0	20	0.2

208
209 In total, six different simulations were conducted. In these simulations, the slope geometry
210 was changed to simulate the throwing behaviour of the antlion larvae (Case 1 & 2). In two
211 simulations, the soil was simulated with reduced friction angle zones (Case 3 & 4), based on
212 the looser soil state. This looser state is based on the assumption of generation of looser soil
213 zones due to the sand throwing behavior. This was done to screen the effect, when there is
214 no volume loss in the sand. In the last two simulations, the change in geometry (sand
215 throwing) and change in density was applied (Case 5 & 6). Based on the sand throwing
216 experiments and the experimental observations. The modelling assumption here is that a
217 looser granular packing has a smaller angle of friction (Mitchell & Soga 2005). The changes
218 in the geometry and the changes in the areas with smaller friction angles are indicated in
219 Table 2.

220
221 Table 2: Change in model areas to simulate the six different case via strength reduction method

Case	Area of slope geometry change [mm ²]	Area of change in friction angle [mm ²]
1	4.64	-
2	3.40	-
3	-	15.66
4	-	8.19
5	4.64	12.13
6	3.40	11.48

222
223 This selection aims to model the different effects induced on the soil by the antlions sand
224 throwing behaviour, to study the effect of the antlion trap/pit slope stability. The figures were
225 prepared with MATLAB (R2019b, The Mathworks Inc., Natick Massachusetts) using the data
226 files form OptumG2.

227
228 All experiments and simulations were conducted considering a dry sand character, the effect
229 of partially saturation of the soil was not studied.

230

231 **Results**

232 We used the insights from biological experiments considering the soil mechanical properties
233 of the antlions' trap building and combined these with finite element simulations to identify
234 the underlying soil mechanical behaviour.

235

236 *Sand throwing experiments*

237 After allowing the antlion larvae to set up a pitfall trap for 24h, all formicariums for the
238 experiment exhibited a sandpit ready to capture prey. After inserting a prey item into the
239 terrarium, the antlions start throwing sand (Fig. 1, supplemental videos 1-3), when noticing
240 the vibrations of the prey. The sand throwing can start without visible sand movement, but
241 becomes more frequent (sand throwing and therefore sand movement), when the prey item
242 changes the slope geometry and especially when moving sand from the slope towards the
243 center of the pit (respectively towards the ambushing antlion). The sand throwing of the
244 antlion usually causes small sand slides (supplemental video 1) distracting the prey and/or
245 causing the prey sliding towards the center of the pit (supplemental video 2). However, it
246 becomes obvious that these sand slides also recover the steepness of the sandpit's slope -
247 smoothed by the movement of the prey or the antlion itself (Fig. 3, supplemental video 3).
248 The average slope angle before sand throwing of the antlion is $27.3 \pm 2.7^\circ$ (min. 22.5° ,
249 max. 31.5°), the average slope angle after sand throwing of the antlion is $31.1 \pm 2.1^\circ$
250 (min. 26.5° , max. 34.5°) resulting in an average slope angle change of 3.44° (min. -1° , max.
251 7°). The sand throwing of the antlion results in a significantly steeper slope after the action
252 (paired t-test, $t=-8.095$, d.f.=8, $N_{1,2}=9$, $P \leq 0.001$).

253



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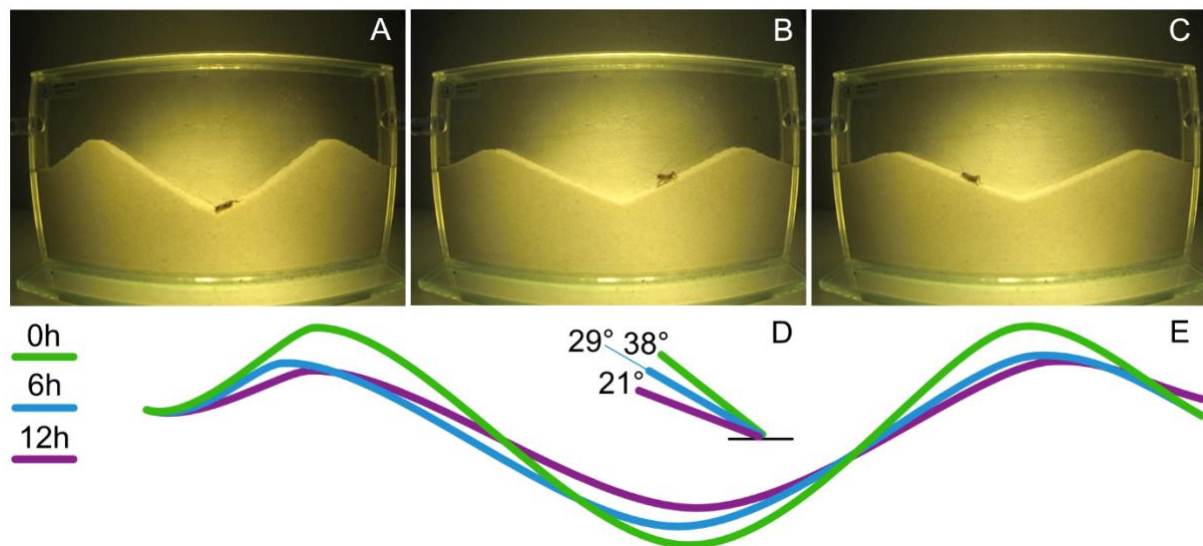
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256 Figure 3: Slope of a sandpit before and after sand throwing by the antlion. A. Already leveled slope
257 (caused by the prey item, house cricket on the left side) before the sand throwing of the antlion. Red
258 line indicates the slope angle of 25.5°, the grey line indicates the reference angle. B. Slope after the
259 sand throwing of the antlion. Blue line indicates the new slope angle of 31°, red line of the old slope
260 angle in transparent, the grey line indicates the reference angle. C. Box-whisker-plots of initial (before)
261 and resulting (after) slope angles of the pit. The line represents the median, the box and whiskers the
262 10, 25, 75 and 90 % percentiles, respectively. * $P \leq 0.001$, paired t-test.

263

264 *Escape experiments*

265 The restructuring of the sand topography within the artificial sandpits reveals the influence of
266 the distortion, a prey item causes without the influence of maintaining the pit by the antlion
267 (Fig. 4, supplemental video 4 and 5). The escape efforts of the prey item can cause serious
268 damage to the sandpit geometry, especially to the slope angle. The slope in the 12h
269 experiment decreases from 38° over 29° after 6h, to 21° after 12h (Fig. 4, supplemental
270 video 4). However, even single events (one walk of a cricket or ant on the slope) can cause
271 sand movements and therefore changes in the overall slope geometry. Sand is pushed
272 downwards, towards the center of the slope by every step of the prey item. Every step is,
273 therefore, changing the slope geometry slightly, as well as pushes small volumes of sand to
274 the center of the pit. The influence of several steps of the prey item accumulates over time.
275 Consequently, with an increasing dwelling time of the prey in the pit, the change of the
276 sandpit geometry leads to an increasing chance of its escape (supplemental video 5).
277



278
279 Figure 4: Escape experiment: house cricket over the course of 12h in a formicarium. A-C. Change of
280 the artificial pit geometry over the course of 12h. A 0h. B 6h. C 12h. D. Change of the slope angle over
281 the course of 12h, green line after 0h, blue line after 6h and violet line after 12h. E. Change of the
282 artificial sandpit geometry over the course of 12h shown as schematic, green after 0h, blue after 6h
283 and purple after 12h.

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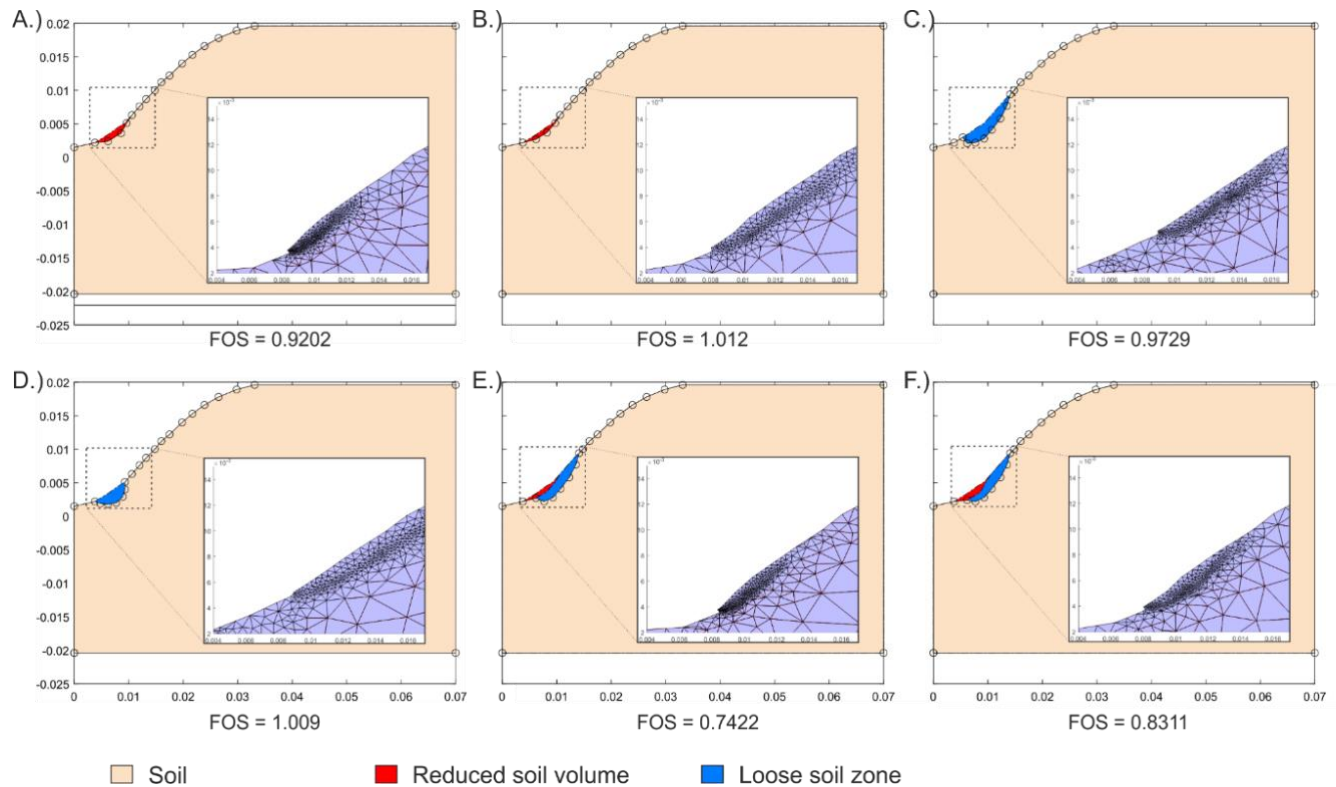
285 *Finite-element analysis*

286 The results of the conducted finite element analysis are shown in Figure 5. The first two initial
287 cases (case 1 and 2; Fig. 5 A,B, see also Table 2) demonstrate the effect of a factor of safety
288 (FoS) reduction, based on a slight change in the slope geometry. Depending on this
289 geometry change (case 2, Figure 5 B), the FoS can result in a value below 1.0, which
290 indicate an unstable slope (initial slope geometry FoS = 1.096). This change in the slope
291 angle could be observed in the sand throwing experiments (see Figure 3 A, B). Herein, a

292 local change of the slope geometry can generate an unstable slope. In figure 5 (C,D), the
293 results of the cases 3 and 4 with a pure change in density are simulated without a change in
294 the slope geometry. Here it can be seen that a change in density may be caused by the
295 movement and throwing behavior of the ambushing antlion and can lead to an unstable
296 condition.

297 Generally, local changes do not necessarily lead to an unstable situation (see Fig. 5 D; FoS,
298 1.009). Whereas, a combination (cases 5 and 6) of a change in the slope geometry (case 1
299 and 2; Fig. 5 A,B) with a change in density of the soil (represented by a change in the friction
300 angle; case 3 and 4) leads to an unstable condition. Cases 5 and 6 (Fig. 5 E,F) are the most
301 realistic natural scenarios compared to the described sand throwing experiments. In both
302 cases, the FoS is below 1.0, which indicates an unstable slope.

303



305 Figure 5: Results for the Cases 1 – 6 (A.-F.) with the indicated change of the reduced soil volume (in
306 red), the changed zones for the friction angle (in blue) and the results, shown as failure surfaces with
307 different adaptive meshes, which demonstrate the failure mechanisms.

308

309 Besides an adaptive remeshing was used to refine the mesh around plastic zones in the soil.
310 The use of the remeshing technique lead to small element sizes close to zones of localized
311 deformations (shear zones). Therefore, the meshes shown in figure 5 indicate the different
312 failure geometries and shear zones, which are similar to the geometries in the sand throwing
313 experiments (Figure 3 and supplementary video material).

314

315 **Discussion**

316 The results of the sand throwing and escape experiments are combined with the finite
317 element simulations to underline the resulting hypothesis as well as add a new soil-
318 mechanical hypothesis. The sand throwing behaviour of antlion larvae is used during pit
319 building (Bongers & Koch 1981) as well as prey capturing (Griffiths 1980). During pit building,
320 the antlion sorts the sand grains towards a preferably smaller grain size (Allen and Croft
321 1985; Loiterton and Magrath 1996; Botz et al. 2003; Farji-Brener 2003) by the sand throwing,
322 which allows for larger and more stable pits (Barkae et al. 2012). Further, during prey
323 capturing, the sand throwing is used to cause small sand slides that displace the prey item
324 towards the ambushing antlion (Griffiths 1980). However, a prey item can cause significant
325 structural damage to the pit's geometry (cf. escape experiments). Therefore, pit maintaining
326 is vital for the antlions prey capturing success. Since antlions usually built their pits close to
327 the natural equilibrium condition of the slope (Botz et al. 2003) given by the angle of repose
328 of the granular media (Allen and Croft 1985; Loiterton and Magrath 1996; Botz et al. 2003;
329 Farji-Brener 2003), the pit's slope is highly unstable and delicate to disturbances (Lucas
330 1982). Here, without the maintenance by the antlion, the slopes are unstable and the prey
331 causes an irreversible deformation to the slope angle (slope angle reduction; Fig. 4).
332 Therefore, without constant maintaining of the pitfall trap (during prey contact), the antlion
333 befalls self-burial and the slope angle shallows (Fig. 4), so that a prey item can more easily
334 escape. However, the capturing success is increasing with an increasing slope angle causing
335 a prey item more likely to slide towards the center of the pit (Botz et al. 2003). As indicated in
336 the sand throwing experiment, the slope inclination increases by the sand throwing behaviour
337 of the antlion leading to retaining an unstable state (Fig. 3), the fact highly supporting the pit
338 maintaining hypothesis.

339

340 From a soil mechanical perspective, the soil state is changing from looser to a denser state
341 as the thrown sand causes a reorganization of the particles along the slope of the trap. The
342 sandparticles sliding towards the center of the pit are rearranged during this relocalisation
343 and come to rest in a denser conformation. The finite element simulation supports our
344 observations and experiments, because only a combined mechanism (cases 5 and 6,
345 change in density and sand volume) brings the slope to an unstable state from an initial
346 stable one (mean slope angle change of 3.44° , Fig. 3), as the factor of safety (FoS) of 0.74
347 (case 5) and 0.83 (case 6) clearly shows. On the other hand, the finite element simulations
348 underline the previous hypothesis that the sand throwing causes small sandslides (Griffiths
349 1980), as also shown in the supplemental videos (1 and 2). Here the change of FoS under 1
350 (unstable state) in the simulation is indicating that the sand indeed slides towards the center

351 of the pitfall trap. Additionally, sand slides may provide the information to the sensory system
352 of the predator about an optimal repose angle of the pit.

353

354 **Conclusions**

355 We challenged the prevailing hypothesis on antlion sand throwing by investigating the
356 mechanism with a combination of sand throwing observations, escape experiments as well
357 as finite element simulations. Our results support the existing hypothesis that small sand
358 slides displace the prey item towards the ambushing antlion (Griffiths 1980), but furthermore
359 add a soil mechanical perspective to this behaviour: pitfall traps of antlion larvae are
360 mechanically unstable constructions, where the prey capturing success increases with an
361 increasing slope angle. We show that a prey item can considerably change the slope
362 geometry (flatten the slope) in the course of 12 h (if no antlion is involved; see. Fig. 4).
363 Furthermore, the sand throwing experiments reveal significantly higher slope angles after the
364 sand throwing (if a prey item is involved; see Fig. 3). We hypothesize, that sand throwing
365 functions as the trap maintenance mechanism, to keep the critical slope angle and
366 counteracts self-burial of the antlion itself.

367

368 **Ethics:** Insect specimens used in this study are not protected, and no ethical statement is
369 necessary. **Data accessibility:** All raw data will be uploaded to Dryad

370 **Authors' contributions:** SB, LH, SNG and HHS designed the project and developed the
371 concept of the study. THB and SB reared the antlions. SB and THB performed the high-
372 speed video recordings and the experiments. SB and THB analysed the biological
373 experiments and performed the statistics. HHS performed the finite element analysis. HHS
374 and LH formulated the physical principles and analysed the finite element analysis. SB,
375 THB, SNG and HHS wrote the manuscript. All authors agree to be held accountable for the
376 content therein and approve the final version of the manuscript.

377 **Competing interests:** We declare we have no competing interests.

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384

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523

524 **Table legends**

525

526 **Table 3:** Parameters used in the finite-element simulations for the Mohr-Coulomb model (grey zones
527 do not influence the strength reduction method).

528

529 **Table 4:** Change in model areas to simulate the six different case via strength reduction method.

530

531 **Figure legends**

532 **Figure 1:** Antlion and pitfall trap. A. Habitus of antlion larva (*Euroleon nostras*), lateral view. B-C.
533 Sandpit used from the antlion as pitfall trap. C. Same sandpit as in B including labels. D. Sand

534 throwing behaviour of the antlion by the flick of its head. D1-4. Time series based on single frames
535 obtained from high-speed videography: 1. Before the flick of the antlion head starts; 2. During the flick,
536 upwards movement of the antlions head; 3. During the flick, downward movement of the antlions
537 head; 4. After the flick of the antlion head.

538

539 **Figure 2:** Axi-symmetric mesh for the initial slope model, using 1000 (15-noded) elements. The soil
540 (blue) is modelled using the linear elastic – perfectly plastic Mohr-Coulomb model.

541

542 **Figure 3:** Slope of a sandpit before and after sand throwing by the antlion. A. Already leveled slope
543 (caused by the prey item, house cricket on the left side) before the sand throwing of the antlion. Red
544 line indicates the slope angle of 25.5°, the grey line indicates the reference angle. B. Slope after the
545 sand throwing of the antlion. Blue line indicates the new slope angle of 31°, red line of the old slope
546 angle in transparent, the grey line indicates the reference angle. C. Box-whisker-plots of initial (before)
547 and resulting (after) slope angles of the pit. The line represents the median, the box and whiskers the
548 10, 25, 75 and 90 % percentiles, respectively. * $P \leq 0.001$, paired t-test.

549

550 **Figure 4:** Escape experiment: house cricket over the cause of 12h in a formicarium. A-C. Change of
551 the artificial pit geometry over the cause of 12h. A 0h. B 6h. C 12h. D. Change of the slope angle over
552 the cause of 12h, green line after 0h, blue line after 6h and violet line after 12h. E. Change of the
553 artificial sandpit geometry over the cause of 12h shown as schematic, green after 0h, blue after 6h
554 and purple after 12h.

555 **Figure 5:** Results for the Cases 1 – 6 (A.-F.) with the indicated change of the reduced soil volume (in
556 red), the changed zones for the friction angle (in blue) and the results, shown as failure surfaces with
557 different adaptive meshes, which demonstrate the failure mechanisms.

558

559 **Supplement**

560

561 Supplementary Video 1: Sandslides caused by antlion

562

563 Supplementary Video 2: Sandslides caused by antlion and relocalisation of prey item

564

565 Supplementary Video 3: Slope change caused by prey item with antlion

566

567 Supplementary Video 4: Slope change caused by prey item without antlion over the cause of
568 twelve hours (12h experiment)

569

570 Supplementary Video 5: Ant escaping a antlions pitfall trap, without active antlion