

RESEARCH ARTICLE

Fine sand particles enable antlions to build pitfall traps with advanced three-dimensional geometry

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ABSTRACT

Pit-building antlion larvae are predators that construct pitfall traps in fine sand. We used three-dimensional laser scanning and geometric morphometrics to reveal the shape of antlion pits of two antlion species, analysed the particle size composition of sands from the different natural habitats, and measured the slope angles of the pits of the two species. In most antlions, the pits are structured as a simple inverted cone, as in *Myrmeleon hyalinus*, studied here. The other antlion studied, *Cueta lineosa*, constructs a unique pit composed of two inverted truncated cones inserted into one another, which feature substantially steeper walls than the pits of any other antlion studied to date. Pit stability depends on the slope inclination, which oscillates between the maximum angle of stability and the angle of repose. The angles in *C. lineosa* substrates were larger than those in *M. hyalinus* substrates. One reason for the steeper walls is the greater proportion of fine sand in the natural sand inhabited by *C. lineosa*. However, video-recording revealed that both the natural sand of *C. lineosa* and the finest sand tested had a higher maximum angle of stability than any of the other substrates studied here. Furthermore, experiments with pits built in different substrates revealed that the shape of the pit is variable and depends on the structure of the sand. *Myrmeleon hyalinus* displayed a more flexible pit construction behaviour than *C. lineosa*. The present demonstration of such differences in pit characteristics contributes to understanding how these two species co-exist in the same habitat.

KEY WORDS: 3D laser scanning, Pit geometry, Pit-building antlion, Maximum angle of stability, Angle of repose, Geometric morphometrics

INTRODUCTION

Predators capture prey using a variety of strategies. For example, while some predators chase after the prey, others just choose an ambush site and wait for the prey to enter their attack range (Huey and Pianka, 1981). Among those searching for prey, some spot the prey from a large distance, such as birds of prey, while for others the prey is hidden, and detection takes place only with tactile contact, such as shorebirds searching for prey buried in the sand (Vahl et al., 2005; Jones et al., 2007). Trap-building predators hunt prey using traps and are a sub-group of ambush predators (Scharf et al., 2011). This is a rare strategy in the animal kingdom, with less than 1% of terrestrial animals constructing traps, and such construction is

restricted to invertebrates (Ruxton and Hansell, 2009). Trap construction is performed by spiders, caddisfly larvae and glowworms by means of secretions used to build a net or a similar sticky trap (Ruxton and Hansell, 2009). In contrast, antlions and wormlions build conical pitfall traps in dry sand and loose soil (Wheeler, 1930; Mansell, 1996, 1999). As an example of convergent evolution, carnivorous plants can be considered trap-building predators, using ‘pitfall’, ‘sticky’ or ‘suction’ traps (Ellison, 2020).

Antlion (Neuroptera: Myrmeleontidae) larvae are sit-and-wait predators, occupying a variety of habitats. Most species of antlion larvae live in sand and the majority are free-living, i.e. non-pit-builders, with pit-builders representing only a small proportion. In general, pit-building antlions prefer fine over coarse sand (reviewed in Devetak and Arnett, 2015), with a few notable exceptions. Additionally, they prefer dry over wet sand (Gotelli, 1993; Freire and Lima, 2019; Miler et al., 2019). Ants are the main prey of antlions in nature (Griffiths, 1980; Lucas, 1986; Matsura, 1986; Crowley and Linton, 1999; Humeau et al., 2015). In most antlion species, the pit, which presents an efficient trap for prey, is shaped like an inverted cone. Constructing pits provides antlions with some advantages over non-pit-building antlion species (Griffiths, 1980; Mansell, 1996): the pit reduces the need to pursue prey actively and it leads the prey directly to the antlion’s jaws. Furthermore, the pitfall trap impedes the escape of prey and increases the amount of time the prey is available to the antlion (Lucas, 1989; Mansell, 1996). In addition to catching prey, pit-traps can also provide shelter from the extreme desert temperatures in soil exposed to direct sunlight (Marsh, 1987; Gotelli, 1993). However, pit construction bears some costs: the energetic expenditure on pit construction (Lucas, 1985; Elimelech and Pinshow, 2008), being restricted to habitats that contain a suitable substrate for pit construction, and being reluctant to relocate the pit and move to a more profitable ambush site (see Matsura, 1987, for an extreme example of no pit relocations until death). Furthermore, under certain conditions, the non-pit-building strategy has also been documented to be highly successful, despite expending more energy in the pursuit of prey (e.g. Tsao and Okuyama, 2012; Klokočovnik and Devetak, 2014; Jingu and Hayashi, 2018).

Efficient trap design is crucial for prey capture success and requires a major investment in terms of time and energy (Lucas, 1985). Natural selection should act to minimize trap construction costs by optimizing trap architecture. The pit is dug by the antlion larva, including backward movements accompanied by sand-tossing behaviour (Youthed and Moran, 1969; Tuculescu et al., 1975; Topoff, 1977; Lucas, 1982; Klokočovnik et al., 2012). Sand-tossing comprises violent jerks of the head and mandibles to excavate the sand. The antlion starts by excavating the initial furrow (i.e. first circular furrow of the pit) and continues with spiral movements towards the centre (i.e. deepening) until the pit is finished. Spiral pit construction by antlions is more efficient than the

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List of symbols and abbreviations

w%	weight percent
α_m	maximum angle of stability
α_r	angle of repose
Θ_b	angle of the back wall (<i>M. hyalinus</i>)
Θ_f	angle of the front wall (<i>M. hyalinus</i>)
Θ_l	angle of the lateral wall (<i>M. hyalinus</i>)
Θ_{pb}	angle of the back wall of the primary cone
Θ_{pf}	angle of the front wall of the primary cone
Θ_{pl}	angle of the lateral wall of the primary cone
Θ_r	angle of the ramp
Θ_{sb}	angle of the back wall of the secondary cone
Θ_{sf}	angle of the front wall of the secondary cone
Θ_{sl}	angle of the lateral wall of the secondary cone

central digging used by the ecologically similar wormlions (Franks et al., 2019). Following pit construction, the antlion waits hidden at the bottom of the pit, covered with fine sand; its head, with the eyes, antennae and part of the jaws, is usually visible. Several design features affect the efficiency of prey capture: pit size, slope of the pit walls, size of the sand particles, and the physical properties of sand as a granular medium.

Prey capture success depends on the slope of the pit walls. Several authors have studied the most appropriate physical properties of sand for pit-building antlions (Lucas, 1989; Robinson and Friedman, 2002; Botz et al., 2003; Crassous et al., 2017; Franks et al., 2019). The slope of the pit depends on the sand slope stability, and it has been assumed that antlions rely on avalanches caused by prey falling into the trap. Only recently, Humeau et al. (2019) demonstrated that ants walking in the area of the pit rim, near the avalanche threshold, tend to slide considerably but do not cause avalanches. The inclination of the pit walls impairs the ant's movement, as suggested earlier (Botz et al., 2003) and confirmed only recently (Humeau et al., 2019). The sand-tossing by the antlion, however, does cause avalanches. Consequently, prey capture is accelerated owing to the steepness of the pit walls and the avalanches caused by the antlion itself. The pit walls are constructed to incline at an angle close to the avalanche angle of sand (Botz et al., 2003; Crassous et al., 2017).

Two or more pit-building species (antlions or wormlions) often co-occur in the same habitat (Griffiths, 1991; Miller et al., 2018; Klokočovník et al., 2020). The most thoroughly studied example to date is that of two antlion species: *Myrmeleon hyalinus* and *Cueta lineosa*. In the Eastern Mediterranean (e.g. Cyprus, Albania and Israel) these two species often occur sympatrically (Barkae et al., 2012; Devetak et al., 2013; Badano et al., 2018). Despite their sympatric occurrence, they do not usually share their microhabitats, demonstrating spatial segregation. *Cueta lineosa* prefers open soil surfaces exposed to direct sunlight, whereas *M. hyalinus* inhabits shaded microhabitats (Scharf et al., 2008; Barkae et al., 2012; Rotkopf et al., 2013; Ovadia et al., 2020). This does not hold true in the western Mediterranean, where *M. hyalinus* occurs also in open habitats (Badano and Pantaleoni, 2014). The antlions also differ in their preference for soil type (Barkae et al., 2014): *M. hyalinus* in the eastern Mediterranean inhabits both sand- and loess-derived soils, although preferring sandy soils. In contrast, *C. lineosa* only inhabits fine-grained soil such as loess, while avoiding coarse-grained sandy soils. There are further differences in the niche axes between the two species: *C. lineosa* is more tolerant of starvation and heat than *M. hyalinus* and is also more tolerant of variation in the rate of prey arrival (Rotkopf et al., 2012; Barkae et al., 2017). That said,

M. hyalinus is a better hunter and is more successful in direct competition (Barkae et al., 2012; Ovadia et al., 2020).

The objective of the present study was to describe the three-dimensional (3D) geometry of the pits of the two species. Pit geometry refers to the general shape of the pit, whether it is composed of a single unit or several, and the pit slope. The pit geometry might be affected by the sand particle size and by examining the pit geometry in different substrates, we take account of it.

MATERIALS AND METHODS**Study species and particle size composition of the natural substrate**

We focused on the two most abundant pit-building antlion species in Cyprus: *Myrmeleon hyalinus* Olivier 1811, and *Cueta lineosa* Rambur (1842). Thirty *M. hyalinus* larvae were collected near Agios Sergios/Yeni Boğaziçi, Cyprus, in sand dunes close to the sea, from the pits built in a shelter of trees (35°11'24"N, 33°54'09"E; location 1), and 28 larvae were collected in fine sand in the vicinity of tufts of herbs (35°11'41"N, 33°54'03"E; location 2). Thirty-one individuals of the other highly common pit-builder in Cyprus, *C. lineosa*, were obtained from an open area exposed to direct sunlight near Agios Sergios (35°11'22"N, 33°54'11"E; location 3), and 27 larvae were collected in an exposed area with fine sand and loess on Golden Beach in the Karpas Peninsula (35°38'29.9"N, 34°32'29.8"E; location 4). Mean \pm s.d. body mass was 29.9 \pm 4.3 mg for *M. hyalinus* larvae ($n=36$) and 65.1 \pm 5.1 mg for *C. lineosa* larvae ($n=23$).

The antlion larvae were brought to the Laboratory of Animal Physiology and Ethology, Maribor and kept in individual plastic containers (diameter 20 cm, height 8 cm) filled with sand from their natural microhabitat, separated to avoid cannibalism. The larvae were fed once a day with worker ants of the species *Lasius niger* and *L. fuliginosus*.

To understand the role of sandy substrate regarding the instability of the pit walls, we analysed the particle size composition of sands originating in the antlions' natural habitats. Sand samples were collected using a 12 ml volume spoon (for details, see Devetak and Arnett, 2015). Three such samples were taken from the substrate of each pit and transferred to the laboratory, where they were dried for 2 weeks at room temperature (26 \pm 2°C) and 25% relative humidity.

Substrate fractions differing according to the particle sizes were determined by sieving dry sand samples with standard sieves as used previously (Devetak and Arnett, 2015). Fractions composing a certain substrate were then weighed using a scale (Kern and Sohn GmbH, Balingen, Germany; accuracy of 0.001 g). Finally, fractions were expressed in weight percent (w%). According to the particle size composition, each sample was characterized as a mixture of the following fractions with particle sizes: ≤ 60 , 61–110, 111–230, 231–540, 541–1000, 1001–1540, 1541–1750, 1751–2200 and ≥ 2201 μ m. We calculated for each location the weighted mean of the sand particle size and the coefficient of variation (CV). The latter, if small, indicates that the particle sizes are relatively homogeneous, while large values of CV indicate that the particle sizes are more heterogeneous.

Slope angle measurements

The stability of a sandy heap is characterized by two angles – the angle of repose (α_r) and the maximum angle of stability (α_m). During a continuous pouring of sandy material, the slope angle oscillates between the two values, i.e. between the upper and lower bounds (Robinson and Friedman, 2002).

To measure the slope angles of sands, a modified Hele–Shaw cell was used (Jaeger et al., 1989; Botz et al., 2003). A cylindrical container (110 mm diameter, 30 mm high) made of cardboard was filled halfway with 140 ml dried sand and rotated slowly until an avalanche occurred. During the rotation of the container, the slope of the sandy heap was video-recorded. Two circular parallel planes partly composed of a transparent plastic foil enabled observation and video-recording of the avalanching sandy slope. Water level, kept in a separate container in the background of the Hele–Shaw cell, served as a reference to facilitate the measurements of both angles (α_r , α_m). From the video recordings, angles were determined to the nearest degree using NIS-Elements D 4.20 software.

At least 10 replicates of avalanching were made for each of the four sand samples originating from the natural habitats of both antlion species (locations 1–4). We collected sands from pits of individual antlions. Additionally, the avalanche angles were measured in three artificial sand types, differing according to particle sizes (<110, 110–230 and 230–540 μm). Artificial sands were prepared using different samples of sand produced by Kema Puconci, Slovenia, with particle sizes of 0–4 mm, which were sifted to obtain the desired sand fraction. Before sifting, sand was dried for 2 weeks at room temperature. At least 10 replicates for each sand type were made.

Three-dimensional geometry of the antlion pit

A total of 24 *C. lineosa* pits and 24 *M. hyalinus* pits were scanned in the laboratory using a portable laser 3D Scanner Ultra HD (NextEngine, Santa Monica, CA, USA). The NextEngine desktop 3D laser scanner was released in 2006 and enables users to capture highly accurate 3D images of objects at a relatively low price (White, 2015). It uses structured light scanning, with a multi-laser technology and triangulation technique, employing four twin arrays of lasers and two cameras, which allow fast scanning and macro-image capture or wide field of view (for details, see <http://www.nextengine.com/products/scanner/specs#>).

Antlions were allowed to construct pits in their natural substrate. Each larva was in its own plastic container. A wooden frame was placed over the container to support the scanner. The scanner was laid onto the frame horizontally, with scanner lights and cameras facing down over the sand surface. Great care was taken to maintain a horizontal position of the sand surface and constant distance between the sand surface and the scanner. After the pits were scanned, 3D mesh models of pits were created in the ProScan ScanStudio software (NextEngine). The scans were rotated or tilted to achieve the most suitable view, which provided us with insight into the 3D geometry of the antlion pitfall trap. Angular measurements were taken between selected points using the measuring program of the NIS-Elements D 4.20 software (Fig. 1).

To analyse shape variability of the pits using geometric morphometric methods, only 3D scans without missing parts in the observed surface were used (10 *C. lineosa* pits and 12 *M. hyalinus* pits). The missing parts were methodological artifacts of 3D scanning. The 3D scanners have difficulties capturing transparent, shiny, dark or furry surfaces, as well as objects with holes, and in our case, steep slopes of pitfalls. Two-dimensional cross-sections of 3D images were captured running through the midline of the larva buried in the sand. On each 2D image, seven landmarks were digitized (for description, see Fig. 2C) using TpsDig2 software (Rohlf, 2015). To minimize the measurement variability, scanning and digitizing were conducted by one person. All pits were digitized twice to test for measurement error due to digitizing using Procrustes ANOVA (Klingenberg and McIntyre,

1998). The digitizing precision was adequate because the mean squares of variation among individual pits exceeded the digitizing error by more than 182-fold for size and 46-fold for shape.

Generalized Procrustes analysis (GPA) was applied to standardize size and remove differences in landmark configuration owing to position and orientation (Rohlf and Slice, 1990). Size information was preserved as centroid size (CS), which is the square root of the sum of squared distances between each landmark and the centroid of the landmark configuration (Bookstein, 1991), and shape information as Procrustes coordinates. A principal component analysis (PCA) was used to summarize and explore the patterns of variation among pits in the shape space. To visualize shape features associated with the most variation, a scatter plot of the first two principal components (PCs) was drawn. Shape changes along the first PC were presented by wire-frame graphs based on the thin-plate spline algorithm (Bookstein, 1991) using MorphoJ (Klingenberg, 2011).

Pit construction in different substrates

Antlions were placed individually in containers (diameter 20 cm, height 8 cm) filled with 6 cm of sand. In addition to natural sand, we also used three artificial types of sand with particle sizes <110, 110–230 and 230–540 μm . We scanned the pits constructed after 24 h. We used 25 larvae of each species in the experiment with natural sand; one larva of each species did not construct pits. Additionally, in the treatments with artificial sands, we used nine antlions of each species in each type of sand. Finally, we allowed six antlions of one species to build pits in the natural sand of the other species, and vice versa. We did not use the same individuals in different substrates.

Statistics

The normal distribution and homogeneity of the variances were tested using the Kolmogorov–Smirnov test. Because no substantial departures from normality and/or homoscedasticity (both $P > 0.05$) were found, between-group comparisons were carried out using *t*-tests and one-way MANOVAs. The number of shape variables used in MANOVA was reduced to the first five PCs, which explained 98.08% of the total variance in the pit shape. Statistical analyses were performed in SPSS 21.0 and GraphPad Prism 6 software.

RESULTS

Particle size composition of substrates in natural habitats

To determine whether the physical properties of the substrate influence pit geometry, we analysed sands from the two antlion species' natural habitats. Substrates inhabited by *C. lineosa* contained a 10-fold greater proportion of fine sand with particles <110 μm (15.2–38.2 w%) than the substrates of *M. hyalinus* sands (2.1–3.5 w%) (Table 1). Furthermore, the substrates inhabited by *C. lineosa* are more heterogeneous than those inhabited by *M. hyalinus*, as indicated by the CV of the sand particle sizes.

Functional three-dimensional geometry of the antlion pits

Field observations and scanning the pits in the laboratory of the two antlion species in their natural substrate revealed their 3D architecture. The pit of *M. hyalinus* was shaped as a simple inverted cone, reflecting a regular form of pits in most pit-building species, with significantly shallow sloped back walls and steeper front walls (*t*-test: $t=7.201$, d.f.=23, $P < 0.0001$) (Figs 1A,C and 2A). In contrast, the pit of *C. lineosa* was composed of two inverted truncated cones inserted into one another (Figs 1B,D and 2B). The primary cone, with a larger diameter, was close to the sand surface and featured lower-sloped walls. The secondary cone was excavated

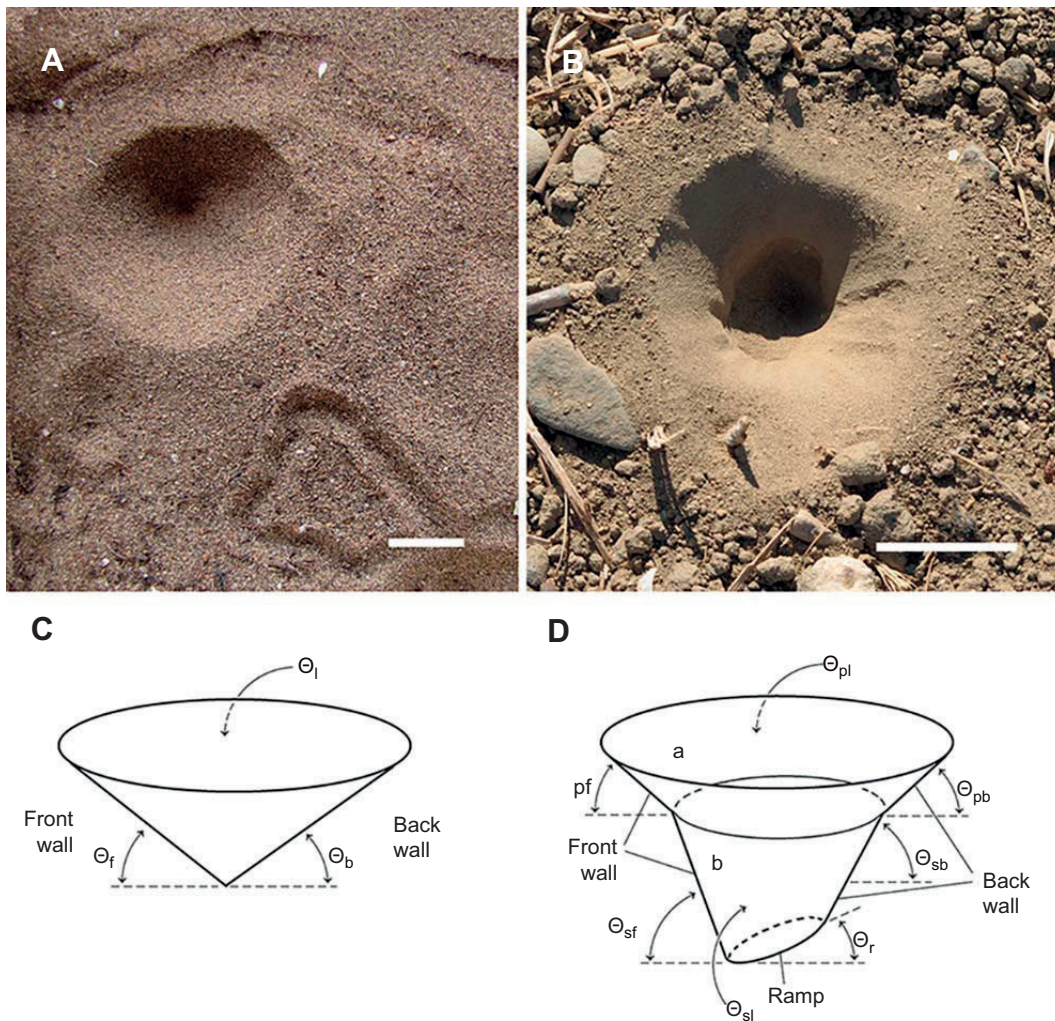


Fig. 1. Pits of antlions in their habitat. Pits of *Myrmeleon hyalinus* (A) and *Cueta lineosa* (B) in their natural sand, Cyprus (view from above). Three-dimensional architecture of the pits of *M. hyalinus* (C) and *C. lineosa* (D) (side view). Scale bars: 10 mm. a, primary cone; b, secondary cone; Θ_b , angle of the back wall; Θ_f , angle of the front wall; Θ_l , angle of the lateral wall; Θ_{pb} , angle of the back wall of the primary cone; Θ_{pf} , angle of the front wall of the primary cone; Θ_{pl} , angle of the lateral wall of the primary cone; Θ_r , angle of the ramp; Θ_{sb} , angle of the back wall of the secondary cone; Θ_{sf} , angle of the front wall of the secondary cone; Θ_{sl} , angle of the lateral wall of the secondary cone.

deeper into the substrate and featured steeper walls (Table 2). The front walls were steeper than the back walls of both cones (slope angles of primary cone: mean \pm 1 s.d.: front wall: 43.5 \pm 8.8 deg, back wall: 42.7 \pm 9.1 deg; secondary cone: front wall: 70.0 \pm 8.8 deg, back wall: 54.5 \pm 12.0 deg). A *t*-test revealed that the slopes of the front and back walls in the secondary cone differed from one another, while the slopes in the primary cone did not (primary cone: $t=0.4638$; d.f.=23, $P=0.6471$; secondary cone: $t=6.533$; d.f.=23, $P<0.0001$). The front wall of the secondary cone was the steepest wall of the pit (Table 2), with the angle of the front wall of the secondary cone in a few pits even reaching 90 deg. The antlions were buried in the sand below the ramp.

Myrmeleon hyalinus constructed significantly larger pits than *C. lineosa* ($F_{1,20}=20.44$, $P<0.001$). The two antlion species also differed in their pit shapes (Wilks' $\lambda=0.181$, $F_{5,16}=14.46$, $P<0.001$), which confirmed the results of the angular measurements. This difference is illustrated in a PCA scatter plot revealing a clear distinction along the first PC axis (explaining 59.9% of the total variance) (Fig. 2B). Pits constructed by *M. hyalinus* had a relatively narrow range of negative PC1 scores compared with pits constructed by *C. lineosa*, which had a wider range of positive PC1 scores

(Fig. 2B). The PCA scatter plot as well as the comparison of extreme (Fig. 2C) and average shapes (Fig. 2D) of both species showed that pits of *C. lineosa* were more variable in shape, more complex, relatively narrower and deeper than pits of *M. hyalinus*.

Pit construction in different substrates

To determine whether the species-specific structure of the pit is consistent across sand types or is plastic and easily influenced by varying the physical characters of the sand, we enabled antlions of each species to build pits in the sand typical of the natural habitat of the other species. Barkae et al. (2012) studied *M. hyalinus* and *C. lineosa* in the Israeli desert. They had suggested that whereas *M. hyalinus* is a habitat generalist, *C. lineosa* is a habitat specialist. We therefore expected *M. hyalinus* to cope better with the substrate of *C. lineosa* than vice versa. Although *C. lineosa* larvae did not build pits in substrates of *M. hyalinus*, larvae of the latter antlion did construct pits in the substrates of the other species, and their pit shape was even similar to that of *C. lineosa* (Table 3).

When placed in artificial sand of differing particle sizes, *C. lineosa* constructed pits only in sand similar to the sand present in its own natural substrate. In contrast, the behaviour of

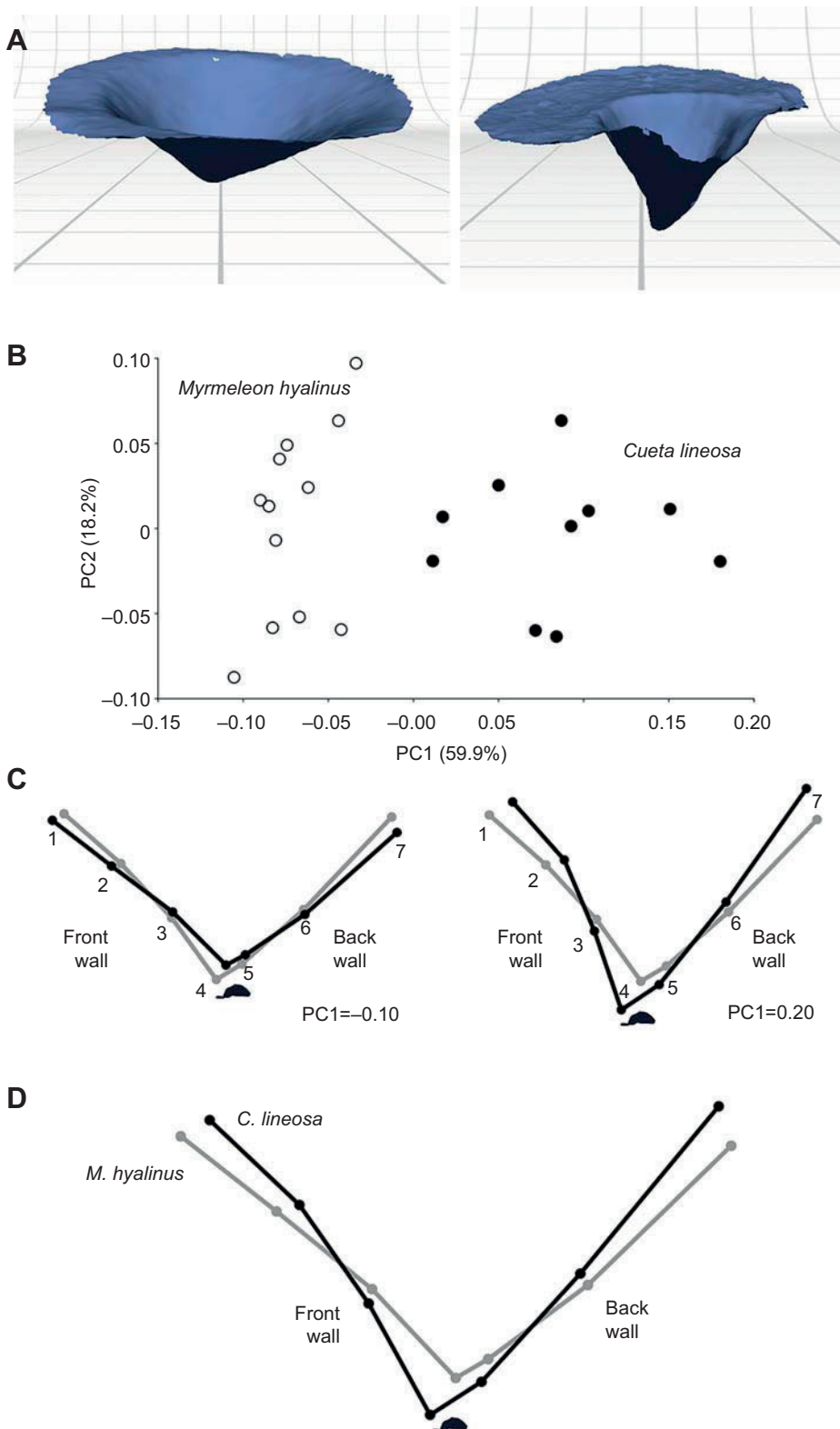


Fig. 2. Three-dimensional images and shape variability of the scanned pits. (A) Scanned pits of *M. hyalinus* (left) and *C. lineosa* (right) in natural sand, side view. (B) A scatter plot of the first two PCs (percentage of variance in parentheses) for antlion pits (empty circles – *M. hyalinus*, $n=12$ pits; filled circles – *C. lineosa*, $n=10$ pits). (C) Wire-frame graphs illustrating extreme shapes of the pits constructed by *M. hyalinus* (left; black line: $PC1=-0.10$) and *C. lineosa* (right; black line: $PC1=0.20$) compared with the mean shape (grey line: $PC1=0.00$). Landmark point descriptions: front wall: 1, rim of the pitfall; 2, one-third of the distance from 1 to 4; 3, two-thirds of the distance from 1 to 4; 4, the lowest point of the pitfall and front point of the ramp; back wall: 5, back point of the ramp; 6, half-way of the distance from 4 to 7; 7, rim of the pitfall. (D) Wire-frame graphs with average shapes of *M. hyalinus* (grey line) and *C. lineosa* (black line). An antlion in a lateral view is depicted at the base of the pits in C and D to show the body orientation with respect to the shape of the pit.

M. hyalinus was flexible and its pit shape depended on the granular structure of the sand: the front and back walls were steeper in finer sands (Fig. 3A). In the finest sand fraction with particles $<110\ \mu\text{m}$, *M. hyalinus* constructed pits shaped similarly to those of *C. lineosa*.

The angle of the front wall (Θ_f) of the pits built in the finest sand ($<110\ \mu\text{m}$) was much larger than in medium ($110\text{--}230\ \mu\text{m}$) and

coarse sand ($230\text{--}540\ \mu\text{m}$) (mean \pm s.e.m.: 60.4 ± 1.7 versus 46.4 ± 0.8 deg and 36.7 ± 1.1 deg, respectively; $n=7$ measurements in each sand type). The angle of the front wall differed among the different sands when all three sands were included (one-way ANOVA: $F_{1,24}=93.83$, $P<0.0001$, d.f.=46). There was a strong negative correlation between mean particle size and the angle of the front wall (Pearson's $r=-0.9188$, number of pairs=21; $P<0.0001$).

Table 1. Substrates in natural antlion habitats

	Particle size fraction (μm)									Homogeneity	
	<60	60–110	110–230	230–540	540–1000	1000–1540	1540–1750	1750–2200	>2200	Weighted mean	CV
<i>Myrmeleon hyalinus</i>											
Location 1	0.7 \pm 0.1	2.8 \pm 0.4	13.1 \pm 0.6	80.1 \pm 0.7	2.1 \pm 0.2	0.7 \pm 0.1	0.1 \pm 0.02	0.1 \pm 0.02	0.3 \pm 0.04	368.73	1.71
Location 2	0.4 \pm 0.02	1.7 \pm 0.1	12.6 \pm 0.6	77.6 \pm 0.3	6.5 \pm 0.2	1.2 \pm 0.1	0	0	0	387.15	1.89
<i>Cueta lineosa</i>											
Location 3	6.7 \pm 0.3	8.5 \pm 0.3	16.3 \pm 0.4	57.8 \pm 0.7	7.8 \pm 0.3	3.1 \pm 0.1	0	0	0	360.19	2.98
Location 4	13.2 \pm 0.3	25 \pm 0.6	17.5 \pm 0.7	42.9 \pm 0.7	0.9 \pm 0.06	0.4 \pm 0.02	0	0	0	236.33	3.10

Weight percent (w%) of a certain particle-size fraction is expressed as mean \pm 1 s.e.m. Number of samples $n=10$.

Results of the slope angle measurements

The angle of repose (α_r) and the maximum angle of stability (α_m) had the highest values in the finest artificial sand (particle size <110 μm) (Table 4). High values were noted also for the natural sand occupied by *C. lineosa* in the Karpas Peninsula (location 4). Low values of the angle of repose and the maximum angle of stability were characteristic for both substrates of *M. hyalinus*. Values in between were determined for two coarser artificial sands (110–230 and 230–540 μm) and the natural substrate occupied by *C. lineosa* in Agios Sergios (location 3).

In the finest sand, the angle of repose, the maximum angle of stability and the angle of the front wall of the pits built in the sand did not differ from each other (Fig. 3B). However, the three angles differed in the medium sand (110–230 μm) and in the coarse sand (230–540 μm) (Fig. 3B).

The angle of the front wall of the antlion pits built in the medium sand was greater than the maximum angle of stability in the same sand (t -test: $t=10.75$, d.f.=18, $P<0.0001$) and the angle of repose ($t=19$, d.f.=18, $P<0.0001$). In contrast, the angle of the front wall of the antlion pits built in the coarse sand did not differ from the maximum angle of stability in the same sand ($t=0.4256$, d.f.=15, $P=0.6764$), but was greater than the angle of repose ($t=5.645$, d.f.=19, $P<0.0001$).

The smaller the sand particles, the greater the pit slope angles. Similarly, both avalanche angles were negatively correlated with mean particle size of the sand (maximum angle of stability: Pearson's $r=-0.7627$, $n=37$, $P<0.0001$; angle of repose: $r=-0.7877$, $n=39$, $P<0.0001$), and strong relationships existed between sand particle size and avalanche angles.

Table 2. Angles of the pit walls of the pits of *M. hyalinus* and *C. lineosa* constructed in natural sand.

	Mean \pm 1 s.e.m.	Min.	Max.
Pit of <i>M. hyalinus</i>			
Pit diameter	30.0 \pm 0.5	25	34
Front wall (Θ_f)	41.9 \pm 0.7	34	46
Back wall (Θ_b)	36.3 \pm 0.7	30	42
Lateral wall (Θ_l)	37.6 \pm 0.6	31	42
Pit of <i>C. lineosa</i>			
Pit diameter	21.3 \pm 0.6	17	27
Primary cone			
Front wall (Θ_{pf})	43.5 \pm 1.8	27	59
Back wall (Θ_{pb})	42.7 \pm 1.8	28	60
Lateral wall (Θ_{pl})	43.1 \pm 1.6	32	55
Secondary cone			
Front wall (Θ_{sf})	70 \pm 1.8	55	90
Back wall (Θ_{sb})	54.5 \pm 2.6	32	75
Lateral wall (Θ_{sl})	53.2 \pm 1.2	43	66
Ramp (Θ_r)	31.2 \pm 1.9	10	43

Values of the angles in degrees, pit diameter in millimetres. For abbreviations, see Fig. 1. Twenty-four pits of each species were measured.

The shallower pits dug by *M. hyalinus* result from the low values of the angle of repose and the maximum angle of stability of its natural sand type. Fine particles enabled the stability of steeper walls in *C. lineosa*. Our measurements revealed that the highest maximum angle of stability occurred in the finest artificial sand (particle size <110 μm) and in the natural substrate of *C. lineosa*, which contained a high proportion (38 w%) of the sand fraction with particles <110 μm (Table 1); maximum angles of stability (mean values) were 62 deg (artificial sand) and 54 deg (natural sand).

DISCUSSION

In this study, we examined the pit shape of two common co-occurring pit-building antlion species in the eastern Mediterranean, *M. hyalinus* and *C. lineosa*. While the former prefers shaded microhabitats, at least in the population under study in the eastern Mediterranean, and is more general in its habitat use, the latter is exposed to direct sunlight and is more specialist. In contrast to orb-weaver spiders, which produce complex webs (Blackledge et al., 2011), most of the pit-building antlions construct simple funnel-like pits, shaped like an inverted cone (Griffiths, 1980; Lucas, 1989; Fertin and Casas, 2006). We have demonstrated here that the pitfall traps of *C. lineosa* larvae are composed of two inverted truncated cones inserted into one another. This antlion's pits are very steep, sometimes with almost vertical walls, rather than the funnel-like geometry of the pits in other antlion species. In contrast to *C. lineosa*, the pits of *M. hyalinus* revealed the typical morphology of traps of most pit-building antlion species. We have shown too that *M. hyalinus* is more behaviourally flexible than *C. lineosa* and constructs pits in a variety of substrates. Moreover, the pits of *M. hyalinus*, when constructed in *C. lineosa*'s typical substrates or in the finest artificial sand (with particles <110 μm), resembled those of the latter, further emphasizing the flexibility of *M. hyalinus*. We thus conclude that the pit shape constructed by *M. hyalinus* is strongly governed by the physical properties of the substrate.

Table 3. Angles of the pit walls of the pits of *M. hyalinus* built in the natural sand of *C. lineosa*

	Mean \pm 1 s.e.m.	Min.	Max.
Pit diameter	29.5 \pm 1	26	33
Primary cone			
Front wall (Θ_{pf})	42 \pm 0.6	41	45
Back wall (Θ_{pb})	40.2 \pm 0.8	38	43
Lateral wall (Θ_{pl})	41 \pm 0.4	40	42
Secondary cone			
Front wall (Θ_{sf})	61.3 \pm 0.5	60	63
Back wall (Θ_{sb})	47.2 \pm 0.9	45	51
Lateral wall (Θ_{sl})	49.7 \pm 1.1	47	55
Ramp (Θ_r)	29.5 \pm 1.6	25	36

Values of the angles in degrees, pit diameter in millimetres. For abbreviations, see Fig. 1. Six pits were measured.

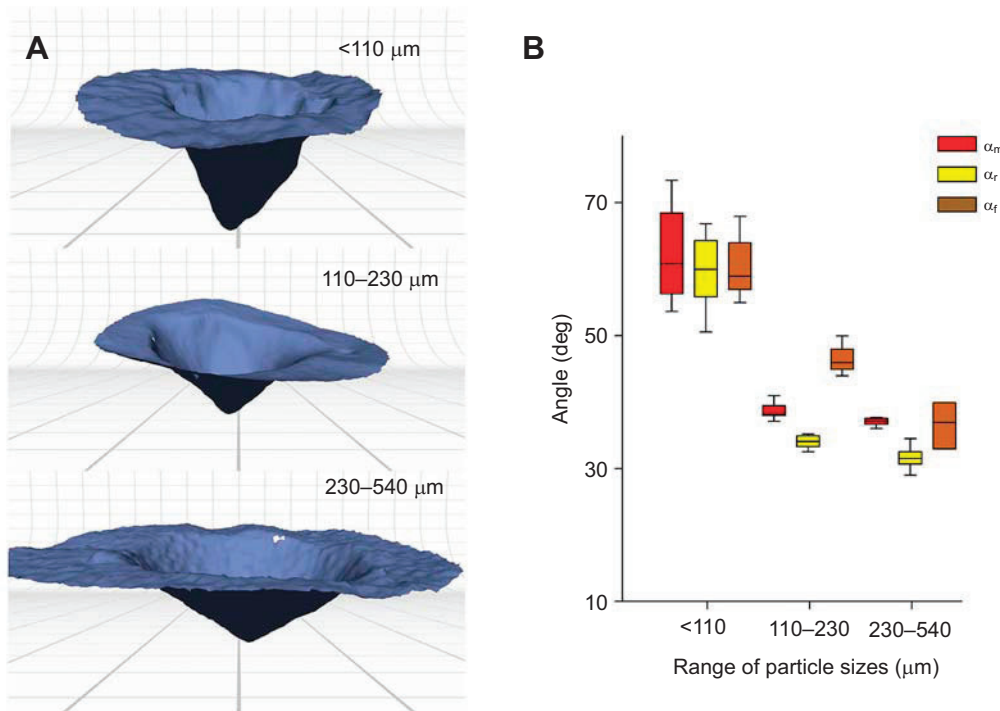


Fig. 3. Effect of sand particle size on the pit shape constructed by *M. hyalinus*. (A) Sand particle sizes strongly affected the pit slope of *M. hyalinus* in artificial sand. (B) Angle of the front wall of the pits (α_f) constructed in artificial sand correlated with maximal angle of stability (α_m) and angle of repose (α_r). Lines across boxes are medians, lower and upper boundaries are first and third quartiles, and adjacent whiskers are the lowest and highest values. In each sand type, seven measurements of the three angles were conducted ($n=7$). In the finest sand (i.e. artificial sand with particle size range of $<110 \mu\text{m}$), the three angles did not differ from each other (one-way ANOVA, $F_{1,24}=0.6280$, $P=0.5405$, $R^2=0.04019$, d.f.=46). In contrast, the three angles in the medium sand (110–230 μm) and coarse sand (230–540 μm) did differ (one-way ANOVA: medium sand: $F_{1,24}=208.5$, $P<0.0001$, d.f.=46; coarse sand: $F_{1,24}=40.96$, $P<0.0001$, d.f.=46).

To our knowledge, this is the first study in which a 3D-laser scanner was used as a tool to analyse the 3D geometry of antlion pits. The 3D-laser scanner allowed us to produce 3D models of pits quickly (approximately 3 min per scan at the lowest quality, 2000 points inch^{-2}) and in real-time without any manual movements of the scanner or pits. When the protocol was optimized, the process of scanning and digitizing (3D scanning, trimming of the 3D scan, 2D image capture and landmark digitizing) took approximately 15 min per pit. In 2006, Fertin and Casas (2006) introduced a low cost 3D capturing system for the analysis of the antlion pit architecture. There are some limitations to the 3D-laser scanner used in our study. The technique faces problems when confronted with shiny or dark surfaces. The 3D capturing system used by Fertin and Casas (2006) faced similar difficulties. As image analysis was based on the detection of a shadow, a texture giving an image with too many shadow pixels might result in too many erroneous points (Fertin and Casas, 2006). However, both imaging systems are highly sensitive, with the maximum resolution at the range of 0.1 mm. The higher cost of our system is a disadvantage compared with the cheaper methodology used by Fertin and Casas (2006).

Most antlions construct simple pits and only a few species construct complex ones. One example of a complex, uniquely shaped pit is that constructed by an Australian antlion, *Australeon manselli* (formerly *Callistoleon manselli*), which comprises several trenches

leading to the main pit (Mansell, 1988; Matsura and Kitching, 1993). In *Isoleon pumilio*, the larva constructs one of the most elaborate pitfall traps known in antlions (Stange et al., 2003), albeit only in very specialized substrates featuring a thin layer of loose sand over the compacted sand (hardpan). The larva first excavates the compacted sand at the top to create a small funnel and then constructs a tube leading down to a second layer of loose sand below, where a second funnel is built (Stange et al., 2003). This architecture makes it very difficult for a small arthropod to escape after falling into the trap. Stange et al. (2003) described the pit in *Cueta* sp., which consists of a funnel, at the bottom of which a small tubular extension contains some fine loose sand. The larva can move easily both to the bottom and to the side of the pitfall trap to evade predators and avoid overheating. When disturbed, the antlion moves into a small side burrow at the bottom of the tube (Stange et al., 2003).

It has long been known that antlion larvae can discriminate between substrates differing in particle size (Youthed and Moran, 1969; Lucas, 1982, 1986; Kitching, 1984; Allen and Croft, 1985; Loiterton and Magrath, 1996; Botz et al., 2003; Farji-Brener, 2003; Devetak et al., 2005; Farji-Brener et al., 2008; Klokočovník et al., 2012; Devetak and Arnett, 2015). Egg-laying females choose the most convenient oviposition substrate in respect to particle size, and this has been shown to be the most important factor governing the spatial distribution of individuals in the habitat (Miller, 1990;

Table 4. Angle of repose (α_r) and the maximum angle of stability (α_m) of a slope in natural and artificial sands

	α_r (deg)	α_m (deg)	n
Natural sand: <i>M. hyalinus</i> (Cyprus: Salamis, location 1)	28.2 \pm 1.1	35.1 \pm 1.2	15
Natural sand: <i>M. hyalinus</i> (Cyprus: Salamis, location 2)	30.1 \pm 1.0	34.5 \pm 1.3	15
Natural sand: <i>C. lineosa</i> (Cyprus: Salamis, location 3)	33.8 \pm 1.3	41.1 \pm 1.6	11
Natural sand: <i>C. lineosa</i> (Cyprus: Karpas Peninsula, location 4)	47.6 \pm 2.9	54.0 \pm 2.1	10
Sand with particles $<110 \mu\text{m}$	59.6 \pm 5.3	62.1 \pm 6.2	12
Sand with particles 110–230 μm	34.1 \pm 0.8	38.8 \pm 1.1	13
Sand with particles 230–540 μm	31.6 \pm 1.3	37.1 \pm 0.5	10

All values are means \pm s.e.m. n , number of measurements.

Matsura et al., 2005). The larvae search for the most convenient substrate within a microhabitat and move over short distances.

The slope dynamics and stability of a pits' slope are crucial for understanding the unique architecture of the antlion trap and the difference between the two species studied here. Robinson and Friedman (2002) studied the angle of repose (α_r) and the maximum angle of stability (α_m) of a slope of sand using monosized grains. They demonstrated a strong relationship between the slope angles and particle shape, and that particle size distribution affects the slope angle and avalanching mode.

The angles of the pit walls in *M. hyalinus* ranged between 36.3 and 41.9 deg, with slightly lower values for the maximum angle of stability (34.5–35.1 deg) of the sand from its natural habitat (Table 4). This can be explained by the similarity in both the composition and avalanching angles of the natural substrates and of the artificial sands with particles larger than 110 μm . Natural *M. hyalinus* sand also contained a greater fraction of sand with particles >110 μm (Table 1), as also measured by Botz et al. (2003) in similar-sized artificial sands. Low values of the angle of repose and the maximum angle of stability of sands inhabited by *M. hyalinus* explain the shallower pits in this species. In contrast, the much steeper walls in *C. lineosa* pits (53.2–70 deg in the secondary cone) can be explained by the substantially higher angle of stability of the sand it inhabits (41.1–54 deg). A larger fraction of the finest particles (<110 μm) in *C. lineosa* sands explains the higher values of the maximum angle of stability. Similarly to the natural sand, the finest artificial sand used in the present study (with particles <110 μm) had a high mean value of the maximum angle of stability (62.1 deg; Table 4). These findings are also supported by Lucas (1982), who observed pit construction in *Myrmeleon crudelis*. Fine sand particles tend to stick to the pit walls, while large grains fall into the centre of the pit. Consequently, the pit walls are lined with the finer sand, which contributes to the stability of the pit.

In *C. lineosa* pits, the angles of the front wall had much greater values (mean of 70 deg) than the maximum angle of stability for its natural sands (41.1 and 54 deg; Tables 1 and 4), probably owing to the larval activity. Antlions are known for sand segregation during pit building, discarding the larger particles from the pit, which means that only fine particles remain, thereby increasing the stability angle of the pit walls (Lucas, 1982). In *C. lineosa* pits, we found the sand to have a higher proportion of fine particles (than *M. hyalinus* pits), which could enable the animal to discard the bigger particles and build the steeper walls of the pit. With the finest artificial sand (with particles <110 μm), we demonstrated a high mean value of the maximum angle of stability (62.1 deg; Table 4). Antlion larvae permanently maintain the shape of their pits and when necessary, deepen them. When sand collapses into the pit, the antlion excavates it out with violent flicks of the head and prothorax. In addition, the measurement method could contribute to different maximum stability angles in the same granular material (Jones and Pilpel, 1966; Arias García et al., 2011). For experimental determination of the maximum angle of stability, we used a dynamic method (rotating cylinder), which gives lower values than static methods (pit construction could be paralleled with static methods), where shearing forces of surrounding mass and inter-particle forces at small grain sizes contribute to greater stability of the slope (Jones and Pilpel, 1966; Wouters and Geldart, 1996). Other factors such as the shape of the particles also have an important influence on the repose angle (Arias García et al., 2011); however, in this study, we did not analyse this parameter. The possible advantage of the pit dug by *C. lineosa* with steeper walls remains to be examined in a future study.

Analysis of the 3D architecture of the pits of both species revealed an asymmetric nature of the trap. Lucas (1989) explained the role of the slope asymmetry of the pit in *M. crudelis*. During an escape attempt, ants tended to travel to a steeper wall of the pit when an antlion was present (Lucas, 1989). In artificial pits containing no antlions, ants attempted to escape in the direction of a lower-sloped wall.

The two studied antlion species co-exist in the same habitat and employ a similar trap-hunting tactic to capture their prey. A criterion for the co-existence of two similar species is that of differentiation across at least one axis of their niche. Classical examples refer to either spatial or temporal segregation (i.e. the two species occupy distinct microhabitats in the same habitat or one species is diurnal and the other is nocturnal; Kotler and Brown, 1988; Ziv et al., 1993; Chesson, 2000). There is already some evidence for niche differentiation between the two studied species. *Cueta lineosa* is a high-temperature specialist and, consequently, it has an advantage over *M. hyalinus* when exposed to direct sunlight. Furthermore, *C. lineosa* is more efficient in its energy budget, losing less mass during starvation, and gaining mass faster during feeding (Rotkopf et al., 2012). *Cueta lineosa* also copes better with high variability in prey arrival as it can deal with several prey items almost simultaneously (Barkae et al., 2017). However, *C. lineosa* suffers from a serious disadvantage: it fails in direct competition with *M. hyalinus*, expressed in lower survival owing to one-sided intra-guild predation and slower growth (Ovadia et al., 2020). When we enabled antlions of one species to build pits in the natural sand of the other species, only *M. hyalinus* built pits in the sand of the heterospecific, and its traps were similar to those of *C. lineosa*. We thus conclude that the shape of the pit is plastic and strongly depends on the structure of the sand. This finding supports a prior suggestion that *M. hyalinus* is more general in its habitat use than *C. lineosa* (Barkae et al., 2012). The present study has also demonstrated that *M. hyalinus* hunts prey better over a wider range of microhabitats than *C. lineosa*.

Here, we have contributed to existing studies indicating possible differences in the niches of the two species. In addition to the differences described above, we demonstrate that the two species differ in the shape of their constructed pits. It remains to be determined whether different prey items are caught in the pits of the two studied species, which would contribute an additional axis in their ecological niche. It also remains to be tested whether other co-occurring pit-building antlion and/or wormlion species similarly differ in their pit geometry.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: D.D., T.K.; Methodology: D.D., J.P., T.K.; Formal analysis: D.D., J.P., T.K.; Investigation: D.D., J.P., T.K.; Resources: D.D., I.S.; Data curation: D.D., J.P., T.K.; Writing - original draft: D.D., J.P., I.S., T.K.; Writing - review & editing: D.D., J.P., I.S., T.K.; Visualization: D.D., J.P., I.S., T.K.; Funding acquisition: D.D.

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