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PREDATOR-PREY INTERACTIONS IN ANTLIONS: TRANSMISSION OF VIBRATIONAL SIGNALS DEEP INTO THE SAND*

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Abstract - Trap-building antlion larvae dig conical pitfall traps in sand for catching small arthropods. The larvae detect them according to substrate vibrations produced by the movement of the prey on sand surface. While most studies have been devoted to surface waves, here we elucidate the role of vibrations travelling in deeper sand layers. We demonstrate that an antlion larva, even when buried deep in the sand, is capable to detect its prey and it consequently reacts attacking it. Both, pit builder and non-pit-builder antlions respond to signals travelling deep into sand. This kind of the signals have not yet been measured so far. We conducted measurements of artificial signals and signals produced by walking insects (prey) with an accelerometer buried in the substrate. We addressed the following question: Do sand properties have any impact on the signal transmission? Particle size highly affects signal transmission. Sand is a filter for higher frequencies. Smaller are the sand particles, more intense is the filtering, which means that fine sand is a more efficient filter. However, low frequency signals are still propagated to a certain distance and they are biologically relevant for prey detection.

Key words: antlion, Neuroptera, substrate vibration, predatory behaviour, pit builders, non-pit-builders

Izvleček – INTERAKCIJE MED PLENILCEM IN PLENOM PRI VOLKCIH: PREVAJANJE VIBRACIJSKIH SIGNALOV GLOBOKO V PESEK

Ličinke volkcev lijakarjev gradijo v pesku stožčasto oblikovane lijakaste pasti za lov drobnih členonožcev. Ličinke jih zaznavajo na osnovi vibracij podlage, ki jih plen proizvaja med hojo po peščeni površini. Medtem ko je bila večina raziskav posvečena površinskim valovom, pa mi osvetljujemo vlogo vibracij, ki potujejo v globlje plasti peska. Ugotavljamo, da celo globoko v podlago zakopana ličinka lahko zazna plen in se odzove nanj z napadom. Oboji – lijakarji in nelijakarji – se odzivajo na signale, ki potujejo globoko v pesek. Te vrste signalov doslej še niso merili. Z akcelerometrom, zakopanim globoko v substrat, smo merili umetne signale in signale, ki nastajajo zaradi hoje žuželke. Zastavili smo si naslednje vprašanje: Ali imajo lastnosti podlage vpliv na prevajanje signalov? Velikost delcev podlage zelo vpliva na njihovo prevajanje. Pesek filtrira signale visokih frekvenc. Manjši so peščeni delci, močnejše je filtriranje, kar pomeni, da je fini pesek učinkovitejši filter. Kljub temu se signali nizkih frekvenc prevajajo na določenih razdaljah in so biološko pomembni pri zaznavanju plena.

KLJUČNE BESEDE: volkec, Neuroptera, vibracije podlage, plenilsko vedenje, lijakarji, nelijakarji

*Dedicated to Matija Gogala on the occasion of his 80th birthday / Posvečeno 80-letnici Matije Gogala

Introduction

Antlions (Myrmeleontidae) are a family of the order Neuroptera with a remarkable diversity in larval ecology. Most antlion larvae live in dry, loose soil and sand, and this sand-dwelling or psammophilous habit, which required fossorial adaptations, was probably a key factor in the radiation of Myrmeleontidae into the largest family of Neuroptera (Mansell 1996, 1999, Badano et al. 2017, 2018). Only in a small number of antlion species, the larvae construct pitfall traps, thus they are considered strict sit-and-wait predators, while the majority of sand-dwelling antlion species ambushes prey just beneath the sand surface, without a pit (Mansell 1996, 1999, Klokočovnik and Devetak 2014). Psammophilous antlion larvae prefer special microhabitat, fine sand or loose soil, and many species even require a particular combination of fine sand and shelter from rain and sun (Scharf et al. 2011).

The antlion larvae detect prey according to substrate vibrations produced by the movement of the prey on sand surface (Devetak et al. 2007, Devetak 2014). While most studies on sand dwelling arthropods using substrate vibration signals have been devoted to the study of surface (Rayleigh) waves, i.e. a type of surface acoustic or vibrational waves that travel along the surface of solids (e.g. Brownell 1977, Brownell & Farley 1979, Gogala 1985, Aicher & Tautz 1990, Devetak et al. 2007), here we elucidate the role of vibrations travelling in deeper sand layers. Until now, deep sand vibrations relevant for sand dwelling arthropods have not yet been evaluated.

We addressed the following questions:

(i) Are the non-pit-builders sensitive to substrate vibrations produced by prey, similarly to the pit-builders?

(ii) Does the antlion buried into the deep layers of sand detect its prey moving on the surface?

(iii) How are vibrational signals propagated deep into the sand?

Material and Methods

Animals

The antlions used in the study were third-instar larvae of *Euroleon nostras* (Geoffroy in Fourcroy, 1785) (Fig. 1a) collected in Boč mountain and the surroundings of Maribor, Slovenia. Larval stages were determined by measuring head capsule width and body length (Devetak 2005, Devetak et al. 2005). The antlions used in behavioural observations belonged to the pit-building *Myrmeleon hyalinus* Olivier, 1811 which were collected in Salamis, Cyprus, and to the non-pit-builder *Synclisis baetica* (Rambur, 1842), which were instead collected in the Divjakë-Karavasta National Park, Albania (Fig. 1b). Prior to experiments, the larvae were kept in the laboratory, at room temperature, in natural sand within plastic cups (7 cm diameter, 9 cm height). Reactions of antlions were observed in presence of prey – such as: firebugs, *Pyrrhocoris apterus* (Linnaeus, 1758) and ants, *Lasius fuliginosus* (Latreille, 1798), both collected in Maribor, and mealworm beetles, *Tenebrio molitor* (Linnaeus, 1758), originating from our laboratory stock. Ants, *Lasius* sp., were used as food source. Feeding took place every day and one ant was delivered to each antlion.

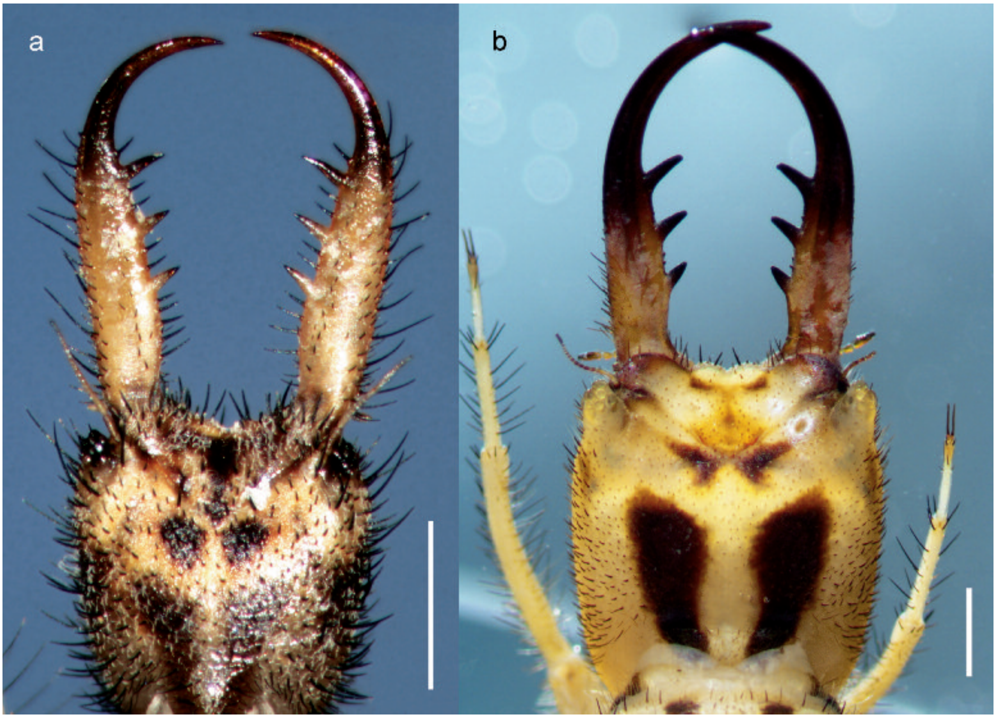

Fig. 1: The head of two antlion species, a pit-builder *Euroleon nostras* (a) and a non-pit-builder *Synclisis baetica* (b). Scale bar 1 mm.

Behavioural experiments

The response of the larvae, elicited by the sand vibrations of the prey, was recorded with a Sony HDR-CX 240E video camera, using a 16 GB SD card and a Sony HDR-CX 130 video camera, using a 32 GB SD card. To minimize disturbance, the camera was left unattended during recording.

Sand

Prior to treatment, antlions were kept in sand, originating from their natural habitat. In experiments, we used four sands differing in particle size (Table 1). The sands were obtained by sieving. The sand fractions were weighted and then, taking into account weight percentage of certain sand fraction, mean sand particle size was calculated (for details, see Devetak & Arnett 2015).

Table 1: Particle size of sands used in experiments.

	Particle sizes range	Mean particle size
Finest sand	60–230 μm	105 μm
Fine sand	230–540 μm	360 μm
Medium sand	540–1000 μm	770 μm
Coarse sand	1000–2200 μm	1650 μm

Production, recording, and analysis of the vibrational signals

The subject of the analyses were artificial and natural vibrational signals. Artificial signals were pure sine-wave pulses, with a 100-ms duration and a 25-ms amplitude ramp at the start and end of the pulse, to remove the transient onset/offset unwanted frequencies. Signals with the repetition rate of 1 s^{-1} and frequencies of 50, 100, 200, 300, and 500 Hz were applied to the sand surface using a sine wave oscillator Bistim 01 (Elestro, Slovenia) and B&K 2706 attenuator (Brüel & Kjaer, Denmark), connected to a B&K 4810 mini-vibrator. The sand surface was stimulated by direct contact with the tip of a cone (15 mm diameter, 45 mm length) mounted on the mini-vibrator (Fig. 2). The tip of the cone was sunk for 5 mm deep into sand. The source of natural vibrational signals was instead an insect walking or crawling on the sand surface.

To reduce noise from the surroundings, a plastic container filled with sand was placed on a sand layer, which in turn rested on cork, mineral-wool layer, and on a concrete plate supported by a mineral-wool layer. The experimental setup was placed on a vibration-free table, in an anechoic chamber. A plastic box (38 x 38 x 20 cm) was filled with sand. Artificial and natural vibrational signals were recorded within sand with a Brüel & Kjaer 4381 accelerometer buried inside the sand in the box at a certain depth of the substrate. The sensitive surface of the accelerometer was positioned

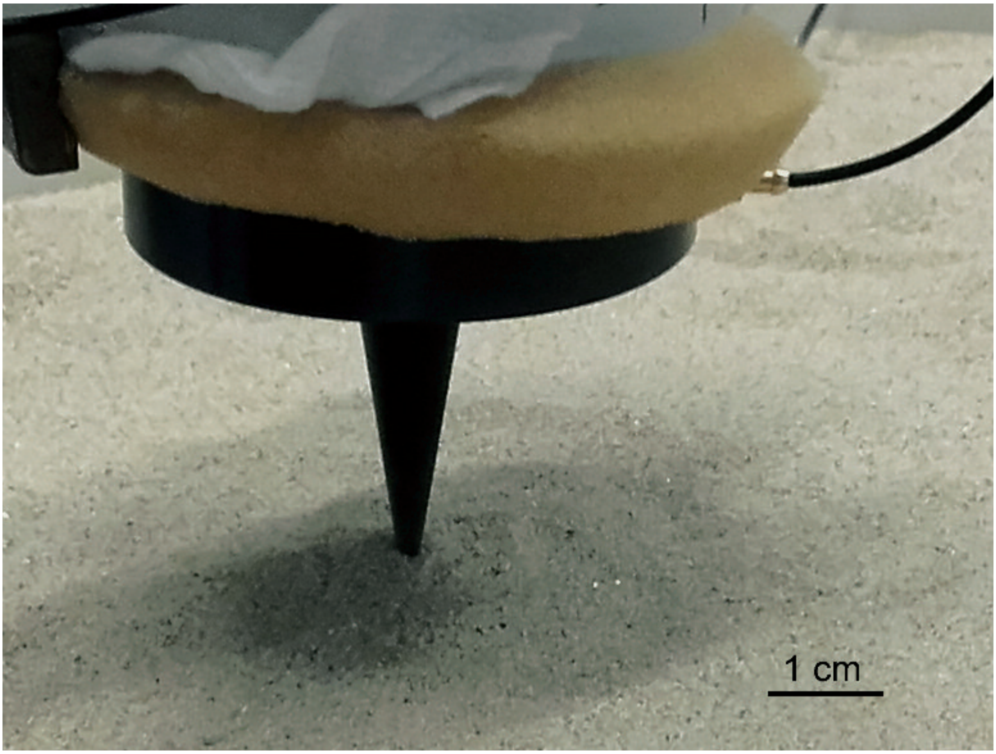

Fig. 2: Mini-vibrator Brüel & Kjaer 4810 in close contact with the sand surface at a tip of the cone.

parallel to the sand surface, so the sensitive axis of the accelerometer was orientated towards the source of vibrations. The accelerometer was connected to a B&K 2525 measuring amplifier and a personal computer.

Recordings were analysed using Avisoft SASLab Pro software (Avisoft Bioacoustics, Germany). All frequency analyses (Fast Fourier Transform) were performed using acceleration values of vibratory signals as the input parameter.

Results

Predatory behaviour

While the predatory behaviour of pit-building antlions has been thoroughly described by a number of authors (for reviews see Scharf & Ovadia 2006; Devetak 2014), there is a remarkable lack of information on the behaviour of non-pit-builders. Here, we describe the responses to the presence of prey in a non-pit-builder, i.e. *Synclisis baetica*. In this species, two prey-catching behaviours were observed, namely (i) immediate grasping the prey without previous pursuit, and (ii) active pursuit followed by grasping (Figs. 3-4).

Fig. 3: Predatory behaviour in a non-pit-builder, *Synclisis baetica*: immediate grasping the prey without previous pursuit: *a* an ant approaching the agape jaws of the antlion, *b* attack, *c* grasping, *d* submersion. Numbers represent time frames in seconds. In *a*, the antlion’s jaws are clearly visible.

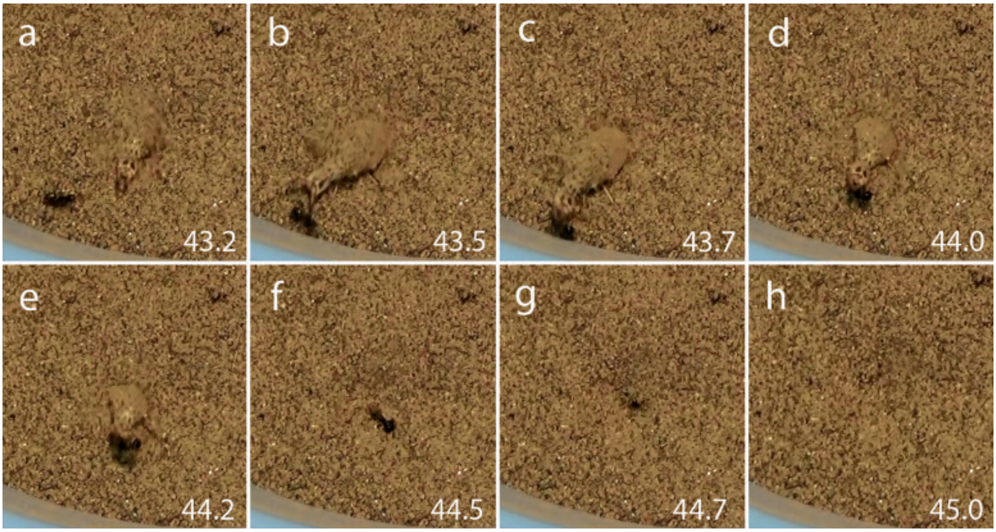

Fig. 4: Predatory behaviour in a non-pit-builder, *Synclisis baetica*: active pursuit followed by grasping: *a-b* pursuing prey, *c* grasping, *d-e* retreat, *f-h* submersion. Numbers represent time frames in seconds.

(i) Immediate grasping the prey without previous pursuit.

When an ant was gently dropped on the sand surface, the antlion larva detected the locomotory activity of the prey and moved closer to the surface. Therefore, the larva reacted to the presence of the prey without previous visual detection. The predator waited motionless just below the surface with jaws agape. When the prey was close enough, the larva stretched out the head and prothorax in the direction of the prey and grasped it (Fig. 3).

(ii) Active pursuit followed by grasping.

When the prey was crawling at a greater distance from the predator, the antlion emerged from sand, walking forwards on the sand surface, and then it pursued the prey and grasped it (Fig. 4). In contrast to other non-pit-builders, *Synclisis* larvae moved on sand surface forwards. Video recordings clearly demonstrated that, initially, the antlion larvae were buried deeper in the substrate, consequently, vision can be safely excluded.

In another species, the pit-building antlion *Myrmeleon hyalinus*, the larvae responded to artificial vibrations with a few behavioural patterns: sand tossing, climbing up the slope of the pit, and approaching the vibrating tip of the mini-vibrator. Common European pit-building antlion species *Euroleon nostras* responded to vibrational stimuli with sand tossing and approaching the vibrating tip of the mini-vibrator.

Transmission of vibrational signals deep into sand

To get insight into the signal transmission, artificial signals were first tested. When pure sine wave signals were applied, their amplitude was reduced during transmission deep into sand (Fig. 5). Damping depended on the frequency, sand particle size and depth of substrate and the results will be discussed in a separate paper.

Substrate borne vibrations produced by small arthropods, travelled in all directions, both on sand surface and deep into substrate (Fig. 6). Power spectrum revealed that the prey signals close to sand surface, at a depth of 1 cm were relatively broadband, with a frequency range up to 4 kHz. Deeper in the substrate, at the depth of 3 cm, the upper part of the frequency range was cut off at 3.5 kHz, while at 6 cm depth at 3 kHz respectively (Fig. 7). Similar results were obtained by all three prey species tested in the experiment. Attenuation depended on sand structure; finer sands highly attenuated vibrational signals. In finer sands, higher attenuation was noted than in coarser sands, amplitudes of the signal in finer sands are up to one order of magnitude less than in

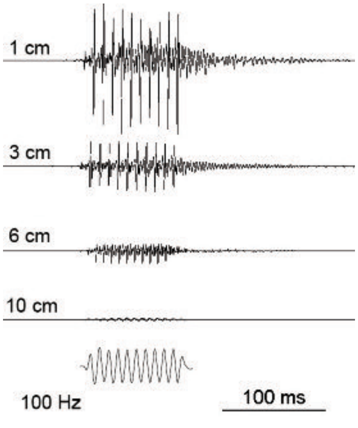

Fig. 5: Attenuation of the artificial vibrational signal (100 Hz) in coarse sand with mean particle size of 1650 μm, measured with an accelerometer at four different depths

Fig. 6: Oscillogram of the vibrational signal produced by a walking mealworm beetle (*Tenebrio molitor*), when the accelerometer was buried 1 cm deep into substrate. In this experiment, coarse sand with particle sizes 1000–2200 µm was used.

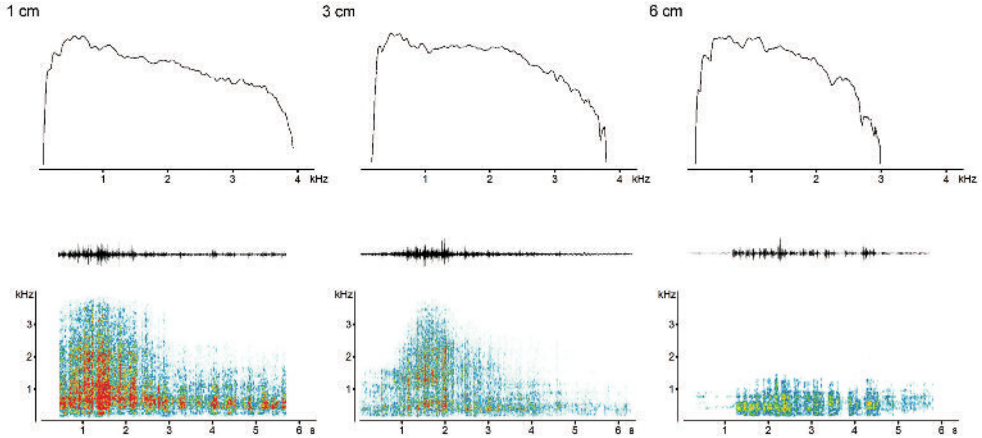

Fig. 7: Sonograms (*lower row*), oscillograms (*middle*) and power spectra (*top row*) of the vibrational signal produced by a walking *Tenebrio molitor*, when the accelerometer was buried 1 cm, 3 cm and 6 cm deep into substrate respectively. Medium sand, with particle sizes 540–1000 µm, was used.

coarser one. While fine sands filter higher frequencies, signals of low frequency are still conducted in distances of biological importance for the predatory behaviour.

Discussion

Non-pit-building antlion species are insufficiently known regarding their predatory behaviour and only a few papers describing it exist (for review, see Klokočovnik and Devetak 2014). Nevertheless, the larval behaviour in *Synclisis baetica* (included in the tribe Acanthaclisini) is described in a number of papers (e.g. Principi 1947, Krivokhatsky 2011, Badano and Pantaleoni 2014, Klokočovnik et al. 2016) and this species is surely one of the better known European non-pit-builder, being extensively studied (for review – see Badano and Pantaleoni 2014). Non-pit-builders are buried in sand but only occasionally move on sand surface. Most larvae (e.g. members of the tribes Palparini, Dendroleontini, Nemoleontini, Myrmecaelurini, Nesoleontini and Acanthaclisini) are able to move both forward and backward (Badano and Pantaleoni 2014), but only Myrmeleontini move exclusively backward and this character supports the monophyly of the tribe (Badano et al. 2017). In our study, we found that at least two predatory strategies exist in *Synclisis baetica*. Indeed, in contrast to pit-builders and to most non-pit-builders, the larva of *Synclisis* is able to move on sand surface both forward and backward. Moreover, it is also a quick runner able to pursue the prey.

It has been known for a long time that pit-building antlions rely on vibrational clues to detect prey (for review see Devetak 2014). In the present study, we demonstrated that even non-pit-builders detect substrate vibrations in sand. Propagation of vibrational signals is important in predator-prey interactions on sand surface, thus it is a well explored topic (e.g. Brownell 1977, Devetak et al. 2007, Fertin and Casas 2007, Devetak 2014, Martinez et al. 2018). Here, we present measurements of the vibrational signals in deep sand for the first time.

Signals produced by insect prey crawling on sand, travel on sand surface and penetrate deep into the medium. The vibrations propagating deep into the substrate behave in similar manner to surface waves (Devetak et al. 2007). However, both types of signals travelling through medium are attenuated, as a result of geometric spreading and frictional losses. Vibrations in fine sand are attenuated more strongly than in coarse sand, thus the predator detects its prey at a relatively short distance. Although the most efficient signal propagation seems to be in coarse sand, it contains too large particles thus it is inconvenient for antlions. Predators make a compromise between fine and coarse sand, choosing medium sand.

Acknowledgements

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