DETECTION OF SUBSTRATE VIBRATIONS IN
THE ANTLION LARVA, MYRMELEON FORMICARIUS
(NEUROPTERA: MYRMELEONIDAE)*

ZAZNAVANJE VIBRACIJ PODLAGE PRI LARVI VULKCA
MYRMELEON FORMICARIUS (NEUROPTERA:
MYRMELEONIDAE)

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PRI LARBI VULKCA MYRMELEON FORMICARIUS (NEUROPTE-
slov., 31 ref., 9 slik, 3 tabele).
Slave Klavore 6, YU 62000 Maribor.

Larva vulkca Myrmeleon formicarius zazna svoje žrteve na razdalji nekaj centime-
trov na osnovi vibracij peščenega substrata. Žival reagira na bližajoči se plen z razpi-
ranjem čeljusti in ali z lučanjem peska. Larva je izredno občutljiva na rahle tresljaje
podlaje (pražna vrednost amplitudne je pri frekvenci 500 Hz pod 50 nm, pražna vred-
nost pospeška pri frekvencah 20 in 200 Hz pod 0,1 ms⁻²). Za taktilne dražljaje je to-
raks najobčutljivejši del telesa.

ABSTRACT — DEVETAK, D.: DETECTION OF SUBSTRATE VIBRA-
TIONS IN THE ANTLION LARVA, MYRMELEON FORMICARIUS
(Engl., 31 ref., 9 figs., 3 tab.). Slave Klavore 6, YU 62000 Maribor, Yugoslavia.

Antlion larva, Myrmeleon formicarius, detects its victims while still a few centi-
metre away by sensing the vibrations they generate in the sand. The animal reacts to
the approaching prey by opening its mandibles and/or by sand tossing. The larva is
extremely sensitive to small disturbances of the substrate (the threshold amplitude
lies at the frequency of 500 Hz below 50 nm, the threshold acceleration at the fre-
cuencies of 20 and 200 Hz below 0.1 ms⁻²). For tactile stimulation the thorax is the
most sensitive part of the body.

* This paper is dedicated to Mr. Herbert Höltel, the great authority on palaeartic
Myrmeleonidae, on the occasion of his 60th birthday.
INTRODUCTION

The larva of the common European antlion, *Myrmeleon formicarius* L., digs a conical pit in the sand and loose soil and then waits for prey at the bottom of the pit. Often only the antennae and the mandibles of the larva are visible. This sessile predator feeds on small arthropods which slide into the trap. Predatory behaviour of the myrmeleonid larvae is described by many authors (in *Myrmeleon formicarius*: REDTENBACHER 1884, DOFLEIN 1916, EGLIN 1939, in other pit-making antlion species: RABAUD 1927, RICHARD 1952, NIEBOER 1960, PLETT 1964, 1975, GRIFFITHS 1980, KOCH 1981, 1983, KOCH and BONGERS 1981, etc.). When a victim falls into the pit the larva attempts to capture it and insert its mandibles. If the larva doesn’t succeed in capturing the prey during its first attempt and/or if the prey evades the larva and starts to climb out of the pit, the antlion tosses sand with violent flicks of its head, thereby causing miniature landslides carrying the prey back to the antlion’s mandibles.

During the predatory behaviour mechanical and visual stimuli are of great importance. According to the authors describing antlion’s behaviour (RABAUD 1927, RICHARD 1952, NIEBOER 1960, PLETT 1964, 1975, KOCH 1981, 1983, KOCH and BONGERS 1981) when locating a prey the larva responds to substrate vibrations. Sand throwing at the potential prey is an automatic reaction to vibrations from the prey moving near the pit. Tactile stimuli are important during the direct contact between the predator and the prey.

The objective of this study has been to investigate the antlion’s behaviour when substrate vibrations play an important rôle in prey detection.

MATERIALS AND METHODS

Experimental animals

All the antlion larvae used were collected in NE Slovenia. Most of the experiments were carried out on the 2nd instar larvae. For a microscopic study the 3rd instar larval larvae were used. Instars were identified by the measurement of the head capsule size (see also EGLIN 1939, BONGERS and KOCH 1981, FURUNISHI and MASAKI 1982). Workers of ant species *Lasius niger* (L.), *Lasius fuliginosus* (Latr.), *Formica rufa* L. and an isopode *Trachelipus sp.* were used in arena experiments.

Breeding

The larvae were kept in small plastic containers (volume 0.2 l) partially filled with sand. To prevent canibalism they were partitioned separately (see also SIMBERLOFF et al. 1978, BONGERS and KOCH 1981 etc.). Sand from natural habitats was sieved (the grain diameter ≤ 500 μm). Feeding was daily: first instar larvae and young second instar larvae were fed on *Lasius niger* and *L. emarginatus*, second and third instar larvae with larger ant species — *L. fuliginosus* and *Formica rufa*. In this way adequate relative sizes of predator and prey were achieved (see also WILSON 1974, GRIFFITHS 1980 a, b). On the experiment day the antlions were not fed. Temperature and humidity were controlled during the experiments (the room temperature being 19—24°C, the relative humidity 60—75 %).

Arena experiments

Reactions of the larvae to the presence of prey were observed in plastic trays (60 mm high, 120 mm in diameter; 90 mm high, 230 mm in diameter; filled with 3 cm sand). Most of
the experiments were conducted on the second instar larvae.

The larva reacts to the presence of prey in the tray — in „arena“ by tossing sand, more or less accurately towards the potential victim. The eyes of the antlion larvae were covered with opaque paint (Karbon) to exclude visual information. The position of the antlion larva in the centre of the pit preying on its victim is shown in fig. 4A. Only the head with the antennae and the mandibles are visible, other parts of the body being hidden in the sand. The position of the prey from which the sand tossing is released was determined by a transparent stencil, divided into 8 sectors (see also KOCH and BONGERS 1981). The stencil was superimposed over the tray so that the centre of the stencil was above the centre of the antlion pit. The victim was placed on the ground and its relative position when the sand tossing occurred was recorded. The distance from the pit centre to the prey (distance d, Fig. 1) was calculated by measuring the distance from the prey to the pit edge (a) and the pit diameter (2d).

\[ d = \sqrt{(a + b)^2 + c^2} \]

*Fig. 1. Relations between predator and its prey: A, a potential victim; B, the predator; a, the distance from the prey to the pit edge; b, the pit radius; c, the pit depth; d, the distance from the prey to the pit centre (the antlion)*

According to the equation \( b \approx c \) the distance \( d \) was calculated

*Measurements of substrate vibrations*

Vibratory signals were synthesized with a function generator Philips (PM 5168), a burst generator Philips (PM 5183) and an amplifier Philips (PM 5175). Pure sine wave signals were mediated to the sand surface with a vibrator Brüel & Kjaer (type 4810 minishaker) and its additional piece (a metal rod — 4 mm diameter, 60 mm length). The distal part of the rod was sunk into the substrate approximately 1 cm. Sand with grain diameter \( \leq 500 \mu m \) was in the styrofoam box (dimensions 40 x 35 x 20 cm) with inner surfaces coated with a soft textile. The intensity level of vibrational signals was measured by an accelerometer Brüel & Kjaer (type 4338), a pick-up preamplifier B & K (type 2625) and a measuring amplifier B & K (type 2606). The accelerometer was placed on the substrate with its sensitive axis perpendicular to the substrate surface. The intensity level of signals was recorded at different distances from the source of the vibration.

Acceleration produced by the moving animals (potential prey) was thus recorded: accelerometer was submerged to different depths (distance x, Table 3) in the sand so that its sensitive axis was perpendicular to the surface of the substrate. The rest of the set-up was the same as in the registration of the synthetic vibratory signals.

*Mechanical stimulation*

Antlion larvae were stimulated by means of a loudspeaker visaton (type DTW 7, 8 Ω, 40/120 W). The ventral side of the animal was glued to the membrane of the loudspeaker
with a wax-colophonium mixture, so the head, the prothorax, the first and the second pairs (or only the first pair) of the legs were freely movable. Vibratory signals were generated by a laboratory-made sine wave oscillator and amplified by a laboratory-made amplifier. Observations were made of reactions to sinusoidal vibratory stimuli with the duration of 500 ms, varying their frequency and amplitude. The time interval between stimuli was 20 to 30 seconds. To reduce noise from the surroundings the loudspeaker was placed on a concrete plate (75 x 50 x 4 cm, 37 kg) supported by a spongy-rubber layer. In these experiments the whole animal was made to vibrate.

In the second part of the experiments local regions of the body of the larva were stimulated. A styrofoam column (5 x 5 x 7 mm) was glued to the membrane of the loudspeaker with an insect pin (dimension 1) inserted in. The distal 5 mm of the pin were free. The larva glued to a micromanipulator was stimulated with the tip of the pin. Amplitudes of the vibrating membrane were determined under the microscope at high voltage levels and extrapolated for low values of voltage.

Microscopy

Larval morphology was studied under the light microscope and scanning electron microscope Cambridge Stereoscan (S 600).

RESULTS

Responses to the presence of the prey

Antlion larvae feed on a variety of animals (Table 1; see also REDTENBACHER 1884, DOFLEIN 1916, EGLIN 1939, KOCH 1981, KOCH and BONGERS 1981, etc.). In the investigated area (surroundings of Maribor; Boč) ants represent approximately one half of the prey they capture.

Table 1 — The prey spectrum of M. formicarius in the surroundings of Maribor and Boč

<table>
<thead>
<tr>
<th>Oligochaeta: Lumbricidae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acarina: Trombidium sp.</td>
</tr>
<tr>
<td>Araneae gen. sp.</td>
</tr>
<tr>
<td>Isopoda: Trachelipus sp., gen. sp.</td>
</tr>
<tr>
<td>Myriapoda: Iulus sp., Lithobius sp.</td>
</tr>
<tr>
<td>Thysanura gen. sp.</td>
</tr>
<tr>
<td>Collembola gen. sp.</td>
</tr>
<tr>
<td>Blattaria: Ectobius sp.</td>
</tr>
<tr>
<td>Dermaptera: Forficula sp.</td>
</tr>
<tr>
<td>Heteroptera gen. sp.</td>
</tr>
<tr>
<td>Homoptera: Cicadina, Aphidina</td>
</tr>
<tr>
<td>Coleoptera: Staphylinidae, Cantharidae, (larvae)</td>
</tr>
<tr>
<td>Diptera gen. sp.</td>
</tr>
<tr>
<td>Lepidoptera gen. sp. (larvae)</td>
</tr>
</tbody>
</table>

The antlion reacts to an approaching prey by opening its mandibles and/or by tossing sand more or less accurately towards its victim. The larva detects a potential prey without
seeing it. Animals react with sand tossing only in 15 to about 50%. When an animal falls into the pit the antlion tries to grasp it. Snapping is a normal response during the direct contact between predator and prey. It is released by tactile and probably visual stimuli. Mandible opening, sand tossing and snapping / grasping are elements of appetitive behaviour (see also Plett 1962, Koch 1983).

![Fig. 2. Mandible opening: A, resting position; B, reaction to vibrations or tactile stimuli](image)

![Fig. 3. Responses to mechanical stimulation (vibrations, tactile stimuli): A, resting position; B, head movements in dorsoventral direction; C, snapping (after photographs)](image)

Antlion detects its prey by sensing substrate vibrations caused by the prey's movements in the sand. Sand tossing was released in different distances from the middle of the pit to the prey (distance $a + b$ in Fig. 1) depending on the different prey species. Distance $d$ correlates well with the weight of the prey. Correlation coefficient between mean fresh weight of the prey and mean distance $d$ is +0.71 (the coefficient is significant, $P < 0.01$). The second instar larvae reacted to the ant species Lasius niger from a distance ($d$) of more than 3 cm, to Lasius fuliginosus from a distance of more than 5 cm, to Formica rufa from a distance of more than 6 cm, to the isopode Trachelipus sp. from a distance of more than 7 cm.

**Conduction of substrate disturbance in sand**

Sand strongly attenuates mechanical vibrations. Sinusoidal signal with frequency of
100 Hz and acceleration of 39.2 ms\(^{-2}\) was attenuated by increasing the distance from the source of vibration as shown in Fig. 5. The intensity levels of the signals produced by moving animals on the sand surface are summarized in Table 3. Acceleration range in the distance of 1 cm from the animal was between 0.01 to 0.001 ms\(^{-2}\).

**Table 2 — Fresh weight of four prey species and the distance from the pit centre to the prey (d)**

<table>
<thead>
<tr>
<th>The prey species</th>
<th>Fresh weight (mg)</th>
<th>Calculated distance d (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean value ± standard deviation</td>
<td>mean value ± standard deviation</td>
</tr>
<tr>
<td></td>
<td>(N = number of individuals)</td>
<td>(N = number of reactions)</td>
</tr>
<tr>
<td>Lasius niger</td>
<td>1.6 ± 0.2 (N = 101)</td>
<td>21.8 ± 10.5 (N = 9)</td>
</tr>
<tr>
<td>Lasius fuliginosus</td>
<td>3.9 ± 0.2 (N = 109)</td>
<td>37.2 ± 8.7 (N = 21)</td>
</tr>
<tr>
<td>Formica rufa</td>
<td>8.3 ± 2.1 (N = 103)</td>
<td>38.2 ± 11.9 (N = 21)</td>
</tr>
<tr>
<td>Trachelipus sp.</td>
<td>50.0 ± 3.3 (N = 20)</td>
<td>45.0 ± 14.3 (N = 21)</td>
</tr>
</tbody>
</table>

**Table 3 — Acceleration of the signals produced by the moving animals on the sand surface (ms\(^{-2}\) x 10\(^{-3}\))**

<table>
<thead>
<tr>
<th>Animal species</th>
<th>Distance (x) from the animal to the accelerometer (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>3</td>
</tr>
<tr>
<td>Cetonia aurata</td>
<td>4.9—14.7</td>
</tr>
<tr>
<td>Trachelipus sp.</td>
<td>cca 10</td>
</tr>
<tr>
<td>Formica rufa</td>
<td>4.9—6.9</td>
</tr>
<tr>
<td>Lasius fuliginosus</td>
<td>cca 4</td>
</tr>
<tr>
<td>Lasius niger</td>
<td>cca 1.6</td>
</tr>
</tbody>
</table>

**Responses to synthetic vibratory and tactile stimuli**

Very different behaviour patterns were registered as reactions to vibratory stimuli: mandible opening; head movements in dorsoventral direction; snapping; antennal or leg movements (Figs. 2 and 3). The threshold values of stimuli were determined for two kinds of reactions: mandible opening, and head movements in dorsoventral direction (Fig. 6). Between 200 Hz and 300 Hz the threshold value for both reactions was at the amplitude of about 60 nm, at 500 Hz it was below 50 nm. The threshold acceleration values were below 0.1 ms\(^{-2}\) or between 1 and 0.1 ms\(^{-2}\) (for the frequencies up to 700 Hz; Fig. 6). Changing the number of reactions per 5 stimuli at different frequency/intensity combinations is shown in Fig. 7. After cutting off all the legs, sensitivity of the larvae did not change significantly (Fig. 8).

Reactions to tactile stimuli were the same as to vibratory stimuli. The number of reac-
Fig. 4. Sand tossing released by four different prey species: A, Lasius niger; B, Lasius fuliginosus; C, Formica rufa; D, Trachetis sp. Orientation of the preying larva is shown in A. Triangles (in A): reactions of the first instar larvae; circles: reactions of the second instar larvae.

Fig. 5. Attenuation of the sinusoidal signal with the frequency of 100 Hz and the acceleration of 39.2 m/s².
tions per 5 stimuli at the frequencies of 50 Hz and 200 Hz was recorded. The head and the dorsal parts of the first three abdominal segments (median and mediolateral part of each abdominal segment and scoli, i.e. lateral tubercles with tufts of long bristles) were less sensitive — at the frequency of 200 Hz the threshold amplitudes were at values below 600 nm. More sensitive were the dorsal parts of pro-, meso- and metathorax (scoli, median and mediolateral parts of meso- and metathorax) — at the frequency of 200 Hz the threshold amplitudes were at values below 60 nm.

**Fig. 6.** Threshold curves for mandible opening (filled circles) and for head movements in dorsoventral direction (open circles) as reactions to vibrations

**Fig. 7.** Suprathreshold response magnitudes at different frequency/intensity combinations of vibratory stimuli. Response: mandible opening. The number of responses per 5 stimuli is represented by the height of the bars
DISCUSSION

Many arthropods use vibration in solids or water as a channel for the conduction of information (for review see MARKL 1969, 1973, 1983; KALMRING and KÜHNE 1983, GOGALIA 1985). Sand has certain properties that favour conduction of low-frequency waves (BROWNELL 1977). A well investigated example of sand-dwelling animals which use substrate vibrations for orientation and detection of prey, is sand scorpion, Paruroctonus mesaeensis (BROWNELL and FARLEY 1979 a, b, c). The scorpion detects both longitudinal (compressional) waves and surface (Rayleigh) waves.

Antlion larva, Myrmeleon formicarius, detects its victim from a distance of a few centimetres (ant species, Formica rufa, from a distance of about 6 cm, an isopode, Trachelipus sp., at about 7 cm; Table 2). A closely related antlion species, Euroleon nostras, detects a large milkweed bug, Oncopeltus fasciatus, weighing about 40 mg, from a distance of about 8 cm (Koch 1981, KOCH and BONGERS 1981). Detection of substrate vibrations in antlions is probably important in conspecific communication (McCLURE 1976): it is quite likely that larvae are able to detect the pit-digging activities of neighboring larvae.

Removal of all the legs in M. formicarius demonstrates that the critical vibrreceptors are not positioned in them (Fig. 8). For tactile stimulation the most sensitive region of the body is the thorax. The whole body of the antlion larva is covered with a few types of bristles and hairs (see also LOZINSKI 1910, DOFLEIN 1916, STITZ 1931, GAUMONT 1976, etc.), the dominant ones being long bristles, short bristles and feathered hairs (»Langborsten«, »Kurzborsten« and »Fiederhaare« sensu DOFLEIN 1916) (Fig. 9). The functions of these structures and other mechanoreceptors in antlion larva have not been examined till now.
tions per 5 stimuli at the frequencies of 50 Hz and 200 Hz was recorded. The head and the dorsal parts of the first three abdominal segments (median and mediolateral part of each abdominal segment and scoli, i.e. lateral tubercles with tufts of long bristles) were less sensitive — at the frequency of 200 Hz the threshold amplitudes were at values below 600 nm. More sensitive were the dorsal parts of pro-, meso- and metathorax (scoli, median and mediolateral parts of meso- and metathorax) — at the frequency of 200 Hz the threshold amplitudes were at values below 60 nm.

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Fig. 9. A scanning electron micrograph of the median part of the pronotum: short bistles (left) an feathered hairs (right). The horizontal bar in the lower right part of the photograph represents 40 μm.

Acknowledgements

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Raziskovali smo odzive larv volkca Myrmeleon formicarius na prisotnost plena in na umetne vibracijske in taktilne dražljaje. Vibroreceptija ima pri volkcih (Myrmeleonidae) ključni pomen pri zaznavanju plena.

1. Blizajoči se plen ropar zazna na osnovi vibracij in nanje reagira z razširjanjem čeljsti in z lučanjem peska proti žrtvi (slike 2, 3, 4). Z lučanjem peska reagira na plen, ki je oddaljen več kot 6 cm (mravlja Formica rufa) oz. več kot 7 cm (izopod Trachelipus sp.) (tabela 2). Korelacija med srednjo vrednostjo tež plena in srednjo vrednostjo razdalje, na kateri volkec zazna plen, je zelo visoka (koeficient korelacije, r = + 0,71; P < 0,01), kar kaže na zelo občutljiv sistem recepcije.

2. Štiri vrste plena (Trachelipus sp., Formica rufa, Lasius fuliginosus, L. niger) med hojo povzročajo vibracije, ki imajo v pesku v globini 1 cm vrednosti pospeškov od okrog
10^{-2} \text{ ms}^{-2} \text{ do manj kot } 5 \times 10^{-3} \text{ ms}^{-2} \text{ (tabela 3). Pesek je snov, ki močno duši vibracijske signale (slika 5).}

3. Volkec že reagira na sinusne vibracije z razširjanjem čelasti oz. z premikanjem glave v dorzoentralni smeri v območju od 20 do 200 Hz pri pospeških z vrednostmi pod 0,1 oz. pod 1 ms⁻², pri 500 Hz reagira na vibracije z amplitudo, manjšo od 50 nm (slika 6). Občutljivost živali na sinusne vibracije se po odstranitvi vseh treh parov nog bistveno ne spremeni (slika 8).

4. Pri apliciranju taktilnih dražljajev na izbrane dele telesa se izkažejo najobčutljivejši trije torakalni segmenti, manj sta občutljiva glava in abdomen. Toraks je pri volkcu, prežičem na dnu lijaka, dotikom žrtev bolj izpostavljen kot abdomen.

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