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Zoology Department, University of the Witwatersrand, Johannesburg, and Theodor-Boveri-Institut für Biowissenschaften der Universität Würzburg

Acoustic Orientation and Communication in Desert Tenebrionid Beetles in Sand Dunes

SHIRLEY A. HANRAHAN & WOLFGANG H. KIRCHNER

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Abstract

Acoustic orientation and communication were studied in five species of tenebrionid beetles found in the Namib Desert in Namibia. The thresholds of their sense of vibration were studied in behavioural experiments. High sensitivity to substrate sound was found in those species restricted to living in sand dunes. Wind blowing over the surface of the sand was found to induce substrate noise perceivable to beetles buried in the sand. One species studied responded to this noise by coming to the surface. Detritus, a major food source, is freed from the sand by wind and concentrated at dune slipfaces. The noise generated by the wind is an important signal to the buried beetles that food is available. It is possible for beetles on the surface of the sand to perceive noises made by buried conspecifics and for buried beetles to perceive others walking on the sand surface.

Corresponding author: S. A. HANRAHAN, Department of Zoology, University of the Witwatersrand, WITS 2050, South Africa.

Introduction

Acoustic orientation and communication has mainly been reported in air, in water and on solid and water surfaces. Substrate vibrations, however, are not only transmitted on surfaces, but also within solid media. The subject of vibratory communication and orientation within solids has not been extensively studied. The ability of desert scorpions to locate prey in sand has been studied in some detail by BROWNELL (1977) and BROWNELL & FARLEY (1979), who also analysed some of the features of vibration transmission in sand. Ant-Lion larvae detect vibrations made by prey (DEVETAK 1985) and vibrational communication has been studied by MARKL (1983).

A diverse endemic tenebrionid fauna is present in the Namib Desert with 17

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species restricted to dunes and therefore to a sandy habitat (KOCH 1961, 1962). Few of these beetles are nocturnal and most species regularly bury themselves in the sand to avoid harsh surface conditions. They are found up to 100 mm below the sand surface (SEELY 1978; SEELY et al. 1985). Burrows are not made in the loose sand and therefore this behaviour isolates the beetles from potential mates, food sources and events on the surface (SEELY 1983). Apart from their normal daily activity patterns, when relatively few individuals emerge from the sand, beetles have been observed to come to the surface in large numbers in response to wind which releases buried detritus on which they feed (LOUW & HAMILTON 1972; HOLM & SCHOLTZ 1980; MCCLAIN cited in SEELY 1983). Wind is a consistent climatic feature in the Namib Desert environment (TYSON & SEELY 1980; LANCASTER et al. 1984). Only dune habitats are exposed to this strong and regular wind. Beetles living in sand in dry river beds with substantial vegetation where surface detritus is abundant seldom feel the effects of strong winds (HANRAHAN & SEELY 1990).

Beetles may also respond to vibrations made by other beetles. In a study on *Onymacris laeviceps*, HAUFFE et al. (1988) observed buried solitary males emerging from the sand when courting couples ran past on the surface and they suggested that the males were responding to vibrational stimuli. *Onymacris plana* males on the surface can accurately locate females buried in the sand both in laboratory and field conditions. It is possible that they use acoustic signals.

Little is known about the sense of vibration in beetles. In a physiological study by AUTRUM & SCHNEIDER (1948) the threshold of the sense of vibration in *Carabus hortensis* was found to be quite high: around 10 m/s^2. A number of insects of orders other than Coleoptera were found to be quite sensitive to vibrations of the substratum. The highest physiological sensitivities have been reported in the cockroach, *Periplaneta americana* (AUTRUM & SCHNEIDER 1948), which has been found to respond to vibrations of less than 10 pm amplitude. On the behavioural level, the thresholds are generally higher, e.g., about 150 nm in honeybees (MICHELSEN et al. 1986).

The purpose of the present study was to determine whether wind generates substrate-borne vibrations that can be perceived by beetles buried in the sand, whether it is possible for beetles buried in the sand to perceive noises made on the surface, e.g., by beetles running on the surface, and whether it is possible for beetles on the surface to perceive noises made by those buried in the sand.

Materials and Methods

All beetles used in this study were collected near the Desert Ecological Research Station at Gobabeb, Namibia (23°34′S, 15°3′E). Three dune-dwelling species were used: *Onymacris plana plana* (Peringuey), *Zophosis orbicularis* (Deyrolle) and *Lepidochora discoidalis* (Gebien). Two species living in the Kuiseb River bed were also studied: *Onymacris rugatipennis* (Haag) and *Physodesmia globosa* (Haag).

The beetles were studied in the laboratory in Würzburg, Germany. They were housed in plastic containers filled with Namib-Desert sand to a depth of 5 cm. They were kept under natural daylight at 28 °C. Infra-red light was used to heat the surface of the sand to about 40 °C for several h a day. They were fed on oats and fresh lettuce.

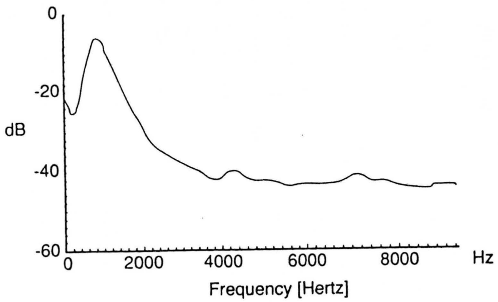

Fig. 1: Vibrations generated by wind. The substrate borne noise generated by air currents on the sand surface was recorded using a B&K accelerometer at a depth of 20 cm in dry sand at a wind speed of 20 m/s. 0 dB corresponds to 1 m/s^2. The noise is generated by saltating sand grains on the surface layer of the sand.

Vibrations were recorded in the sand using Bruel & Kjaër accelerometers type 4375 and 4381, connected to either a B&K 2639 pre-amplifier attached to a B&K 5935 microphone supply or a B&K 2635 charge amplifier, and a Sony TCD-D3 DAT-recorder. Calibrations were made using a B&K 4294 vibrational calibrator. Recorded vibrations were analysed using a CED 1401 FFT-spectrum analyser connected to an AT personal computer. Graphs of the temporal structure of signals were made using a Philips PM 3305 digital oscilloscope connected to a HP 7470 plotter.

Wind, generated in the laboratory using compressed air, was calibrated with an anemometer. Artificial vibrations were generated with B&K 4810 vibration exciters. Substrate-borne vibrations were generated using a vibration exciter connected by a 10-cm long, 5-mm thick aluminium rod to a 1-mm thick, 3-cm diameter copper plate buried in the sand. Brief pulses of vibration were generated using a Philips PM5134 function generator directly connected to the vibration exciter. Another vibration exciter placed below an arena 10 cm in diameter, 6 cm in height, was used to study the sense of vibration. Pulses of various frequencies and amplitudes and of 1 s duration were generated using a Philips 5133 function generator and a HP 6825A power amplifier. The vibrational stimuli were alternated with sham stimuli, which did not vibrate the arena. Stimuli were applied when the beetles were still. Any movements of legs and/or antennae observed during the stimulus or sham stimulus, or within 1 s after the stimuli were recorded. The individual beetles were tested at each of the combinations of frequency and amplitude 20—30 times. A χ^2-test was used to decide whether the response rate to the vibrational stimulus was significantly higher than the response to the sham stimulus ($p < 0.01$). The threshold of the sense of vibration of each of the individuals at each of the frequencies tested was defined as the lowest amplitude at which a significant response rate was found. The threshold amplitude for the samples of 4—7 beetles are the mean values of these individual thresholds ± S E. All vibrational amplitudes are given as root mean square (RMS) acceleration values.

Results

Wind blowing on the surface induces substrate sound in the sand. An air stream of 20 m/s blowing across loose sand generates noise of about 1 m/s^2 (RMS) acceleration at the peak frequency of about 1 kHz in a depth of 20 cm below the surface (Fig. 1). This noise is generated by the movement of sand grains in the surface layer. The attenuation of substrate sound with distance travelled is relatively small. With 2 accelerometers, 50 cm apart from each other, an attenuation of the noise at 20 dB was found. The propagation velocity was determined using short pulses of artificial vibrations. It was found to be about 100 m/s.

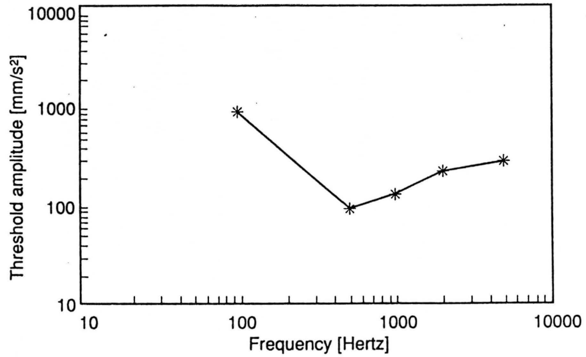

Fig. 2: Sense of vibrations. Behavioural thresholds of the sense of vibrations were determined in seven *Onymacris plana* males using artificial vibrations in a small arena. The threshold amplitude (in mm/s^2 RMS) of each individual is the lowest amplitude at which the response rate was statistically significant (χ^2-test, $p < 0.01$). The animals are most sensitive at 500—1000 Hz.

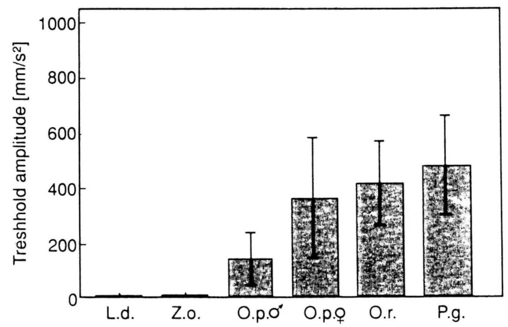

Fig. 3: Sense of vibrations. The behavioural threshold of response to vibrations is compared at 1 kHz between three species living in the sand dunes (*Lepidochora discoidalis*, n = 6; *Zophosis orbicularis*, n = 5; *Onymacris plana*, males: n = 10, females: n = 4) and two species, which live in the river bed (*Onymacris rugatipennis*, n = 7; *Physodesmia globosa*, n = 7. Means of the lowest amplitudes at which each of the individuals exhibited a statistically significant ($p < 0.01$) response ± SE.

Only *Lepidochora discoidalis* buried in the sand responded to the artificial wind by coming to the surface. Within 1 h, five out of nine beetles emerged, whereas, during 1 h in which no wind was applied, only one out of nine beetles appeared on the surface ($p < 0.05$, χ^2-test).

Sensitivity to vibration of the substrate was studied in behavioural experiments with five different species. In seven *Onymacris plana* males, vibrational sensitivity was measured in the frequency range from 20 Hz to 10 kHz. No response to vibrational frequencies lower than 100 Hz and higher than 5 kHz was observed. The highest sensitivity was found at 500—1000 Hz (Fig. 2). The threshold amplitude of 143 mm/s^2 ± 95 mm/s^2 (RMS) at 1 kHz corresponds to a (peak-to-peak) displacement amplitude of 10 nm. At 1 kHz, thresholds were also determined in female *O. plana* (n = 4, Fig. 3), which were found to be 2.5 times less sensitive to vibration than the males ($358\ mm/s^2 \pm 223\ mm/s^2$). Sensitivity to vibration varied among beetle species (Fig. 3). *Lepidochora discoidalis* and *Z. orbicularis*, both dune dwellers, as are *Onymacris plana*, were found to be even more sensitive ($3.2\ mm/s^2 \pm 0\ mm/s^2$ in n = 6 *L. discoidalis* and $10\ mm/s^2 \pm 0\ mm/s^2$ in n = 5 *Z. orbicularis*). The two beetle species that do not live in the dunes were found to be less sensitive to substrate vibration: *Onymacris rugatipennis* ($409\ mm/s^2 \pm 158\ mm/s^2$, n = 7), *Physodesmia globosa* ($466\ mm/s^2 \pm 189\ mm/s^2$, n = 7). The differences in the sensitivity between the dune beetles *L. discoidalis*, *Z. orbicularis* and male *O. plana* compared to the beetles from non-dune habitats and compared to female *O. plana* are statistically significant ($p < 0.01$, Mann Whitney U-test).

Male and female *O. plana* were separated for several days. Males were introduced into an arena in which females had buried themselves in the sand. Within minutes they were able to accurately locate and excavate the females. Isolated males also located and excavated other buried males. This was also observed in beetles which had experimentally been covered with a 5-cm sand layer. Using an accelerometer on the surface of the sand, no stridulation or other specific acoustic calling activity was noted in the laboratory in buried female *O. plana*. However, sounds of movement or chewing food made by females buried in the sand were clearly perceivable. The maximum amplitudes of these noises were about $250\ mm/s^2$ on the surface. Sounds of beetles running across the sand could be picked up clearly 5 cm below the surface with an accelerometer buried in the sand; the maximum amplitudes were about $150\ mm/s^2$.

Discussion

Wind blowing across the surface of loose sand induces substrate noise which is intense enough to be perceived by a sense of vibration in many species (MARKL 1973). The measurements of vibrational amplitudes in the sand in this study are conservative estimates of those which could be measured in the field, because wind in the laboratory was induced only locally above a small patch of sand. Field studies on noises induced by wind on dunes are needed. Given that the attenuation of the vibrations with distance was found to be relatively low, we can expect even higher amplitudes when wind blows homogenously across a large surface. The velocity of propagation of substrate sound in loose sand found in this study is relatively low compared to other media, in accordance with the theoretical predictions, and confirms earlier measurements by BROWNELL (1977).

Lepidochora discoidalis, the highly specialized dune species, emerged from the sand in the laboratory in response to the vibrations induced by wind. This is the first experimental evidence supporting the hypothesis of LOUW & HAMILTON (1972) and MCCLAIN (cited in SEELY 1983), that *L. discoidalis* can sense the wind blowing on the surface. Other species have been observed to be more active when the wind blows but field studies are needed to quantify this response. It can only

be assumed that the laboratory wind simulation was too crude to induce the same response in the other dune species.

These thresholds of the sense of vibration of the beetles are those of a behavioural response, not of sensory perception. Thus, it is possible that the beetles are even more sensitive to substrate vibrations than the sensitivity recorded in these experiments. However, the behavioural thresholds determined here for the dune-dwelling species are extremely low compared to other insects. On the behavioural level the desert beetles are more sensitive than Ant-Lion larvae to substrate vibrations. A higher sensitivity in behavioural experiments has, however, been found in scorpions (BROWNELL 1977). In physiological investigations of the sense of vibration in insects, a number of species have been found to be far more sensitive to vibrations than the beetles studied here (AUTRUM & SCHNEIDER 1948; MARKL 1973).

This high sensitivity makes it possible for the beetles to perceive noise induced by wind blowing on the surface, which is an important cue for foraging. The effects of wind on sand and on sand dunes have been analysed by BAGNOLD (1941). The turbulence caused at the air-sand interface is responsible for noises created within the sand and is also responsible for sorting particles according to mass. During windy periods, detritus is freed from the sand and collects on the dune slipface. Windy periods are therefore opportune times for the beetles to forage. The beetles studied were all dark in colour and are highly visible against the desert sand. Only some of the beetles emerged each day, males more frequently than females. By emerging in response to wind they optimised their foraging opportunities and minimized their risk of predation. Strong wind may also move substantial amounts of sand and beetles may come to the surface and rebury to maintain a mean burial depth.

The beetles' high sensitivity to vibration makes it possible for males to localize females submerged in the sand by listening to the noise they make eating food or moving in the sand. However, under laboratory conditions, the females never emitted any specific sound signals and the males did not need them to find the females. In addition to these cues, virgin females may also make specific calling signals which would make localization even easier for the males. Unfortunately, virgin females were not available in this study. This behaviour may well operate using olfactory rather than auditory cues. The fact that beetles buried in this experiment could be found just as easily implies that surface olfactory cues may be less important, but it does not rule them out. The problem warrants further study.

Thus, we conclude that the Namib-Desert Dune Beetles, living in an environment where vision and olfaction are of very limited use, have evolved a high sensitivity to substrate sound and make use of vibrational signals for their orientation and communication.

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