The effect of wind on foraging activity of the tenebrionid beetle *Lepidochora discoidalis* in the sand dunes of the Namib Desert

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The foraging activity of the tenebrionid beetle, *Lepidochora discoidalis*, was studied in the sand dunes of the Namib Desert. The surface activity of this beetle species was found to be correlated both with time of day and wind speed. Higher numbers were observed on the dune surface between 17:00–19:00 h when wind speeds were consistently higher than 9 m/s. Noise and vibrations in the dune sand were found to be highly dependent on wind speed. Wind blowing at speeds higher than 5 m/s lifts the surface sand grains and generates vibrations in the sand. The peak frequency of these vibrations is in the range of 700–1000 Hz. The vibrational amplitude at the peak frequency is on average 40 dB higher at those wind speeds when the beetles are active compared to lower wind speeds. The results indicate that wind is an important cue for these beetles and can be perceived by buried beetles through substrate vibrations.

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Ability to perceive and make use of wind has been studied in only a few animal species. In some environments wind is a consistent feature and animals, particularly invertebrates, have optimised their use of this feature. The Namib Desert is a case in point, where the wind is not only consistent within a particular season, it is also a reasonably reliable component of the daily weather pattern (Tyson & Seely 1980). At least 33 species of Namib tenebrionids are restricted to sand dunes (Seely & Griffin 1986) and may be affected by wind (Seely 1983). It has been pointed out that beetles emerging from the relatively protected environment of the dune sand are subjected to desiccation stress and that this feature is enhanced if they are exposed to wind (Seely & Mitchell 1987). The search for mates and food seems to be the prime reason why beetles expose themselves to these additional environmental stresses (Seely 1983). The dunes where these beetles are found are largely vegetation-free and the beetles seem to rely almost completely on the detritus buried in the sand for food (Seely 1978). Wind blowing over the surface of the dunes liberates this detritus. It would be to the beetles' advantage to be able to respond to the noise generated by the wind to begin feeding as the buried plant and animal remains are blown free of the sand. There is some evidence that increase in numbers of the beetle, *Zophosis fairmairei* (Peringuey), foraging on the dune slip face could be correlated with increased wind speed (McClain in Seely 1983).

The question arises as to whether beetles buried in the sand up to a depth of 100 mm (Seely, Mitchell & Louw 1985) can perceive wind blowing on the surface. In a previous laboratory study (Hanrahan & Kirchner 1994) we showed that wind blowing over a sand surface generates not only audible sound, but also substrate vibration induced by the movement of the sand grains. The beetles can sense these vibrations. Of the species studied, those living on the dunes, being more exposed to wind, showed significantly greater sensitivity to substrate vibration than those species occuring in the more protected river beds (Hanrahan & Kirchner 1994). The work reported previously was carried out under laboratory conditions. The aim of the current field study was to correlate behavioural activity of beetles living in the sand with the local wind pattern and vibrations in the sand caused by wind.

Materials and methods

The observations were carried out on Kahani Dune near the Desert Ecological Research Station of Namibia, Gobabeb, Namibia (23°34'; 15°03'E) on an east-facing slipface which varied in height because of the curvature of the dune, but was no more than about 20 m at the highest point. This complex dune (Lancaster 1982; Livingstone 1989) is part of the linear dune system south of Gobabeb. The site lacked vegetation and had a sharp and sinuous crest. The same site is being used for a long term pit-trapping experiment (Seely & Henschel unpublished) providing data on tenebrionid beetle abundance.

A number of beetle species are known to occur on the dunes but *Lepidochora discoidalis* was chosen as the most suitable for this study for several reasons. *L. discoidalis* was found to be one of the tenebrionid beetles most sensitive to substrate vibrations in our previous study (Hanrahan & Kirchner 1994). It is crepuscular (Louw & Hamilton 1972) and is therefore known to emerge at the time of day when there is most likely to be a breeze blowing across the dunes (Lindesay & Tyson 1990). Holm & Scholtz (1980) suggested that *L. discoidalis* surface activity is wind dependent.

We counted beetles emerging from the sand surface on this dune. Preliminary observations indicated that the foraging activity of this species at this time of the year was limited to the period from about 17:00 h to sunset. Continuous observations were therefore made each day from 2–10 April, 1996, from 16:00 to 19:00 h, when adequate light was no longer available. Observations were made from the crest of the dune down to the dune plinth, where the slipface ended. Beetle numbers were recorded by two observers, one on the dune crest and one at the foot of the dune. All beetle species that emerged were recorded. Observations were made every 15 min by scanning the site with binoculars.

Wind speed, wind direction, sand and air temperatures and humidity of the air were automatically recorded on site every 5 s using a portable Davies Weather Station. Air temperature and humidity were measured at a height of 1 m above ground and sand temperature was measured 5 cm below the sand surface.

Vibrations of the sand caused by the wind were recorded using two Brüel & Kjaer accelerometers type 4381, one connected to a B&K 2639 pre-amplifier attached to a B&K 5935 microphone supply, the other to a B&K 2635 charge amplifier, and a Sony TCD-D8 DAT-recorder. Recordings were made at different wind speeds at a depth of 10 cm below the sand surface.

We calculated Pearson's correlation coefficients between time of day, temperature, humidity, and number of beetles seen on the surface at 15-min intervals. After transforming the number of beetles observed in order to obtain homogenous variances, we performed a linear regression analysis (Unistat 3.0). The sound recordings were analysed in the laboratory using a Hewlett Packard 35670A signal analyser and a desktop computer.

Results and discussion

Although the observation period chosen was near to the equinox, the dune still retained its summer form (Livingstone 1990). The dune was strongly concavely curved at the observation site so that the effect of the wind was to erode the west slope, depositing sand on the east slope and concentrating detritus on the east face, several meters up from the dune base. The wind was deflected northwards parallel to the dune crest with eddies tumbling detritus across the slip face and concentrating the loose material into distinct patches. There was a rich supply of detritus blowing over the slipface surface. Wind direction was generally consistent on particular afternoons and ranged from south-south-west to north-west. There were no hot dry east winds. This was to be expected for this time of the year with the east winds becoming more common from May onwards (Lancaster 1982; Livingstone 1989, 1990).

Lindesay & Tyson (1990) showed that these sea breezes which are most frequent at the equinoxes build up after 14:00 h and seldom last beyond 20:00 h. Their observations were made in midsummer but our results fitted this general pattern. The wind speeds varied from 2.7 m/s to 12.0 m/s. Particular afternoons were characterized by relatively consistent wind speeds. We observed that the wind lifted the surface sand grains at speeds of 5 m/s and more, agreeing with the figure quoted by Bagnold (1941). When wind speeds were higher than 5 m/s sand was eroded from the west dune slope. The adjacent convex slipface set up irregularites so that wind eddies blew across the study slipface in small whirlwinds in the reverse direction.

Air temperature ranged from 19°C to 42°C, humidity from 14% to 35%. No fog occurred during the study period. Soil temperature declined from 36–42°C at the first observations to 23–28°C at dusk.

A number of beetle species are known to occur on Kahani dune. Only three species were seen on this site during the period of observation, namely, *Lepidochora discoidalis* (Gebien), *Onymacris unguicularis* (Haag) and *Zophosis fairmairei* (Peringuey). *L. discoidalis* was observed almost every day but numbers were relatively low in spite of strong winds. *O. unguicularis* was seen on two occasions and *Z. fairmairei* was seen on a number of occasions but few individuals were visible at each observation time. No beetles were observed on the adjacent convex dune surfaces. Pit-trapping data from Holm & Scholtz (1980) show that *L. discoidalis* can be expected in fair numbers from March to August. The absolute numbers of beetles we recorded were lower than expected. However, the total beetle population has been declining steadily since the last wet period in the 1970's according to observations by Seely & Henschel (unpublished data). Figure 1 contains data from their pit-trapping records of the months of April in a number of years after the last high rainfall event and one of our data sets for comparison. Pit trapping has all kinds of limitations as a method for recording abundance, but, given the reservations one may have, the trend seems very distinctive for *Z. fairmairei*. Results for *L. discoidalis* do not show such a marked decline. The analysis was therefore restricted to the activity of *L. discoidalis*. Large concentrated populations of *L. discoidalis* have been observed emerging from the slipface under very windy conditions (Hanrahan pers. obs.). We cannot assume that the beetles were not present and we have to allow for the possibility that our observations were not made under optimal conditions for emergence.

A distinctive temporal pattern of emergence of *L. discoidalis* was seen. A few *L. discoidalis* emerged shortly after 17:00 h, but the numbers rose substantially to peak between 18:00–19:00 h. After a short foraging period the beetles buried themselves in the sand (Figure 2). At the same time the number of beetles seemed to be highly dependent on the prevailing wind speed (Figure 3). The two parameters, wind speed and time of day, were not significantly correlated with each other ($r = -0.1$, $n = 108$, $t = 1.2$, n.s.) during the observation period, and were therefore used in a linear regression

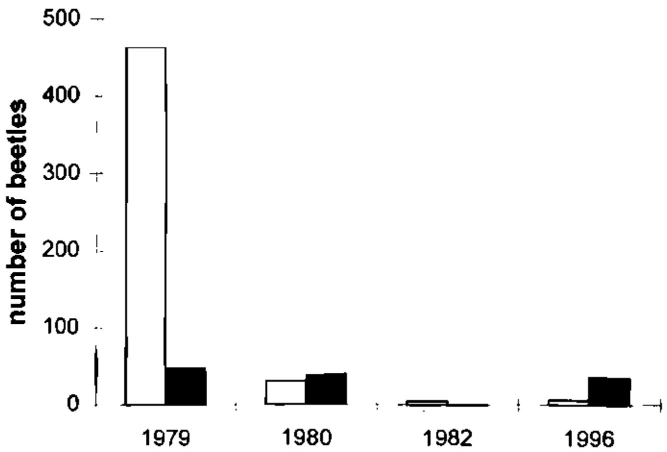

Figure 1 Number of *L. discoidalis* (black bars) and *Z. fairmairei* (clear bars) at Kahani Dune on single days in April. Data from 1979–1982 are from a long-term pit-trapping study (Seely & Henschel unpublished), 1996 data from the present study. Data were collected at roughly the same time of the day in all 4 years, and the day of the highest beetle activity was selected from the available data sets.

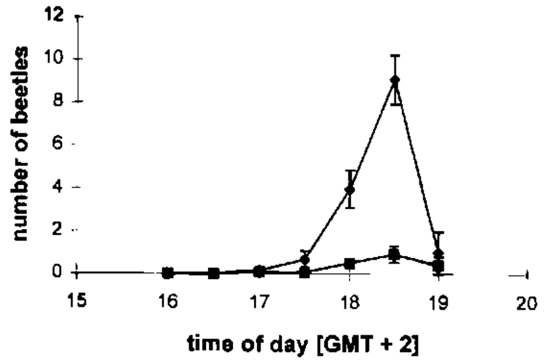

Figure 2 Numbers of *L. discoidalis* observed from 16:00–19:00 h. Circles = beetles observed on three days when wind speed was greater than 9 m/s. Squares = beetles observed on six days when wind speed was less than 7 m/s. Bars = standard error.

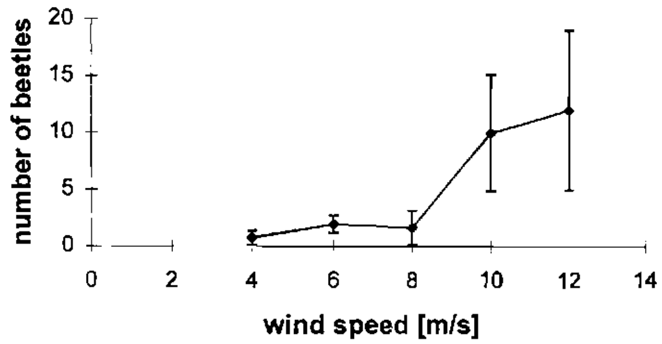

Figure 3 Mean numbers of beetles observed from 16:00–19:00 h at different wind speeds. Bars = standard error.

analysis, which revealed that both variables significantly contribute to the variance in the number of beetles seen at the surface ($F_{(2,105)}$= 27.6, $p << 0.001$). As temperature and relative humidity were significantly correlated with time of day we did not include these variables in the regression analysis. The effect of wind on the beetles' activity is further illustrated by the fact that 78% of all beetles were seen during three days on which the average wind speed was higher than 9 m/s and only 22% on six days on which the wind speed was less than 7 m/s.

The amplitude of vibrations of the sand was strongly influenced by wind. The spectral composition of the vibrations of the dune sand induced by the wind was found to be essentially similar to that measured with small quantities of sand and a compresssed air source under laboratory conditions in our previous laboratory study (Hanrahan & Kirchner 1994). The peak frequency was in the range of 700 to 1000 Hz. The vibrational amplitude at the peak frequency was on average more than 40 dB higher at high wind speeds, when the sand grains in the surface layer were rolling, compared to lower wind speeds (Figure 4).

One of the effects of the wind is to uncover material buried in the eroding dune face, particularly dead insects. For example numbers of dead *L. discoidalis* carapaces were observed blowing over the dune crest. Louw & Hamilton (1972) comment on the preference of *L. discoidalis* for animal remains. The second effect is to concentrate the detritus from a wide area of the dune. The lighter detritus particles are swirled about by the wind and the irregularities of the dune cause

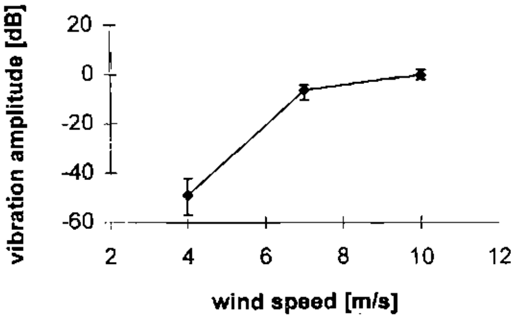

Figure 4 Relative amplitude of vibrations recorded at a depth of 10 cm below the sand surface at different wind speeds. Bars indicate the range.

whirlwinds to form which concentrate the detritus and therefore the food. The *L. discoidalis* could be seen following the detritus as it blew across the dune. This food source is readily available for only short times as the slightest disturbance causes a slipface avalanche and the detritus becomes buried. As the beetles are highly selective in what they eat from the detritus it is worth their while to cue into the wind as a signal that food is readily available.

The vibrational cues seem to play a very important role in the beetles' activity cycles and this particular species shows a high level of sensitivity (Hanrahan & Kirchner 1994). These cues are not the only ones and a very distinct temporal pattern of emergence from the sand is also seen (Louw & Hamilton 1972). However, it would appear that very few beetles respond on a particular day to temporal cues when there are no vibrational stimuli from the wind. The optimal conditions of mass emergence for foraging are still not defined and may be influenced by other factors such as humidity.

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