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Effective use of the desert dune environment as illustrated by the Namib tenebrionids

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Summary :

The sand dunes of the Namib desert support a varied fauna with tenebrionid beetles forming the most conspicious element. These beetles are substrate specific, and hence restricted to the dune field. Dune sand has advantages as a life support medium as the temperature below a certain depth remains almost constant throughout the year, humidity is relatively high and constant and animals can move easily through this lightly compacted substrate. As a consequence some of the dune animals spend their entire lives below the sand surface.

On the dune surface the temperatures fluctuate between approximately 70° C and 1° C and humidities may range from 100 % to less than 10 %. Adult tenebrionid beetles must occupy this environment, as drinking, feeding and reproductive behaviour are surface activities. A number of these tenebrionids are relatively K-selected, living for several years in the adult form, and are capable of reproduction throughout the year when conditions are suitable. Energy, mainly in the form of wind-blown detritus and water in the form of fog, must be regularly obtained for reproduction to occur. A variety of physiological and behavioural adaptations allow these tenebrionids to obtain food and water on the surface. A combination of field and laboratory techniques has been used to investigate these adaptations to the abiotic constraints of this desert environment.

Key words : « bet-hedging », Namib desert, sand dunes, tenebrionids.

I. Introduction

Despite their superficially hostile appearance, the sand dunes of the Namib desert provide a suitable habitat for a relatively great variety of animals, of which tenebrionid beetles are a major component (Fig. 1) (KOCH, 1961; LAWRENCE, 1959). The tenebrionid fauna which is restricted to the vegetationless parts of the Namib dunes is apparently richer than that of any similar ecosystem (SEELY, 1978). These beetles are psammophytic diggers (MEDVEDEV, 1965) and, together with many other dune animals including reptiles and mammals, move easily through the lightly compacted sand. Below about 30 cm, temperature and humidity in the sand are relatively constant at values agreeable to life while on the surface they are much more extreme. At rainfall below 300-500 mm per year the water holding capacity of sand is greater than that of other soil types thus, in the sand below the range of capillarity, at about 30 cm (NOY-MEIR, 1973), the humidity remains relatively high for long periods, although probably varying somewhat more than temperature. As a result conditions within the sand are very suitable for life and, in fact, a few Namib dune species spend their entire lives below the sand surface. Most other species, including the adult tenebrionid beetles, spend well over half of each day beneath the sand. The question thus arises, why not remain permanently in this more favourable environment ?

The relatively simple answer is that for most species food, water and mates are only to be found on the surface of the sand. Most of these animals, however, are nocturnally active and thus avoid the most adverse desert conditions. Many adult tenebrionids, by contrast, are diurnal species which are on the surface during the more stressful periods of the day searching for the resources necessary to maintain fitness. Energy is available to these beetles mainly as plant and animal detritus (KOCH, 1962) which comes from the sparse vegetation of the dunes and inter-dune valleys and is distributed across the sand by wind. Once on the dune it may be buried under the

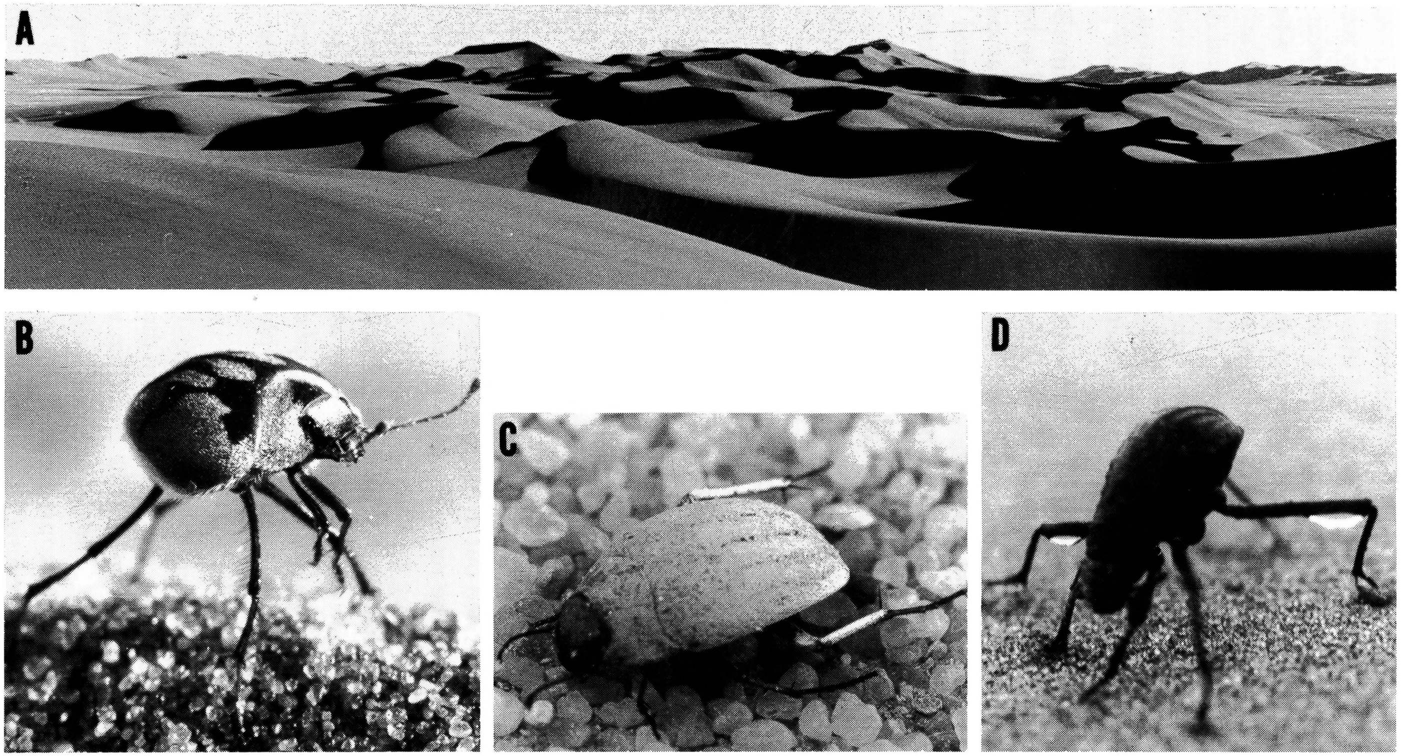

Figure 1 The vegetationless Namib dune environment (A) with examples of three of the adaptions contributing to overall fitness of the dune tenebrionids, (B) stiling by *Zophosis fairmairei*, (C) the waxy layer of *Zophosis mniszechi* and (D) fog basking by *Onymacris unguicularis*.

sand, stored for a period and then released when the wind changes direction, to be blown again across the sand surface. Because of these interactions between wind and sand, energy in the form of detritus constitutes a relatively predictable aspect of the environment as it is available throughout the year and during those years when primary production is exceptionally low. The biomass of detritus available in the Namib dune ecosystem was estimated as 0.4 $g.m^{-2}$ after a dry period lasting several decades and as 2.7 $g.m^{-2}$ following 100 mm of rain. Although total energy is not considered to be a limiting factor for the omnivorous tenebrionids, the low protein content of the vegetation available may be, especially during dry periods (SEELY & LOUW, 1980).

Water is probably the single most important limiting factor for the animals of the Namib (SEELY & LOUW, 1980) and the occurrence of fog is considered to be a primary factor contributing to the faunal richness of the dunes. Fog only dampens the surface of the sand but does not penetrate very far and is rapidly evaporated by the sun. Water from fog is therefore available only on the surface of the dune sand.

The tenebrionid beetles of the Namib dunes are relatively easy to observe against the lightly vegetated sand surface because of their colour and size and are present in large numbers. They thus provide suitable material for integrated field and laboratory studies of the behavioural and physiological adaptations related to life on the surface of this sand sea. The purpose of this paper is to describe the suite of adaptations used by an assortment of Namib dune tenebrionid beetles which allow them to : 1) extend time spent in the moderate abiotic conditions encountered below the sand surface and 2) efficiently forage for resources in the more extreme surface environment.

II. Materials and methods

Field studies were carried out in the dunes near Gobabeb (23°34'S, 15°03'E) and laboratory experiments in the research station nearby. In order to determine 1) the effects of food quality on egg production and therefore fitness, 2) the rate of lipid deposition with optimal diet, 3) the effects of desiccation on foraging activities and 4) the effect of wind on surface activity, three species of tenebrionid beetles, *Onymacris plana* (Péringuey), *O. unguicularis* (Haag) and *Zophosis (Cardiosis) fairmairei* (Péringuey), belonging to the tribes Adesmiini and Zophosini were used. Nomenclature follows PENRITH (1979, 1980).

For determination of the effect of food quality on egg production in *Onymacris plana* 60 females and 20 males were collected from the dunes and placed into four glass terraria. A heater in a lower corner of the terrarium was covered by foam rubber and then a layer of approximately 5 cm of sand. This arrangement assured a temperature gradient within the sand from approximately 40 to 20° C for 18 hours of the day. Two of the terraria, each containing 15 females and 5 males, were provided with fresh flowers of the nara, *Acanthosicyos horrida* each day and two with leafy stalks of the grass *Eragrostis spinosa* bearing flowers and seeds. In the field *O. plana* are found to be particularly numerous at nara plants, although they occur throughout the dune field, hence the selection of food types. Each morning the sand was sieved and the eggs counted. At the end of the 32 days' experimental period half of the surviving females were dissected and the eggs within the oviducts counted. The water content of the remaining females was determined gravimetrically. To determine the water content of a field population, 10 *O. plana* were collected monthly for two years, weighed, dried and reweighed in the laboratory.

The rate of lipid deposition was also determined using *O. plana*. Twelve individuals were collected from the field and six were immediately frozen. The experimental group was fed for eight days on what was thought to be an optimal diet of nara flowers, lettuce, oats and detritus. These individuals were also frozen and the lipids of both groups were later extracted using the method of FOLCH, LEIS & SLOAME-STANLEY (1957) as described by COUTCHIÉ & CROWE (1979).

Field studies were carried out on vegetationless slipfaces where detritus accumulates. The effect of the state of dehydration on the surface foraging period was investigated using *Onymacris unguicularis*, the most conspicuous diurnal foraging species regularly responding to fog. For each of six experimental days one male and female were desiccated for ten days prior to field observations and one male and one female were given water *ad libitum*. All were painted distinctive colours for ease of recognition. All four beetles were then placed in a small enclosure on the slipface late in the day where they soon buried in. Early the next morning the enclosure was removed and the area closely observed until they emerged for foraging. Their behaviour was noted until they buried below the surface for the night. These individuals were weighed before the period of desiccation, before being placed in the field and after the day's observation when they were dried and their water content calculated. On the same day observations were made at ten minute intervals of the number of naturally occurring *O. unguicularis* foraging on the same slipface. Qualitative observations of detritus movement and accumulation were made concomitantly. Temperature determinations of the surface and at depth below the sand were made using a YSI telethermometer. Ambient conditions were measured with a Lambrecht sling psychrometer. Wind values were obtained using a Lambrecht autographic anemometer at Gobabeb about 3.5 km distant from the study site, to give an approximate indication of the wind prevailing at the study site.

The effect of the wind on surface activity was investigated using *Zophosis fairmairei*. The number present on one slipface was counted at half hourly intervals during their afternoon foraging period for three days. Surface temperatures were measured with a Lambrecht triple depth thermometer. Wind speeds were obtained from Gobabeb, about 6 km distant from this study site.

III. Results

The effect of food quality on egg production in *O. plana* was measured for 32 days during which time the number of eggs laid per day by the 30 females feeding on nara flowers (15.0 ± s.e. 1.7) was significantly greater than the number laid by the 30 females feeding on grass (5.2 ± s.e. 0.8) ($t = 5.2218$, $p < 0.001$, $n = 32$ days). Moreover, at the conclusion of the experiment a significantly greater number of eggs was found in the oviducts of those which had been feeding on nara (2.7 ± s.e. 0.4, $n = 14$) than in those which had been feeding on grass (0.9 ± s.e. 0.3, $n = 14$) ($t = 3.5602$, $p < 0.01$). In contrast, those which had been feeding on grass had a higher water content (61.56 % ± s.e. 1.20, $n = 15$) than those feeding on nara (57.84 % ± s.e. 0.60 %, $n = 14$) ($t = 2.8102$, $p < 0.01$). Although water balance is known to affect egg production in the dune species, the values obtained suggest that water balance was not the determining factor in this case. The water contents measured for the above beetles were well within the range of mean monthly values found in a field population of *O. plana* over a period of two years (56.87 % ± s.e. 0.80 %; range 48.11 % - 68.15 %).

Lipid deposition was measured in another group of *O. plana* where it was found that, after eight days on an optimal diet, the total lipids, as a per cent of soft body weight, had increased significantly from 14.28 % ± s.e. 1.56 % ($n = 6$) to 45.11 % ± s.e. 6.12 % ($n = 6$) ($t = 4.88$, $p < 0.001$).

The effect of the state of dehydration on the surface foraging activity of *O. unguicularis* is presented for one of the experimental days in Fig. 2. Similar values were observed for the other five days. Total time on the surface was greater for the desiccated individuals (251 minutes, nos. 1 and 2) than for the hydrated beetles (209 minutes, nos. 3 and 4). However, the mean surface temperature during foraging was significantly greater for the two hydrated individuals (49.01° C ± 2.77° C) than for the desiccated ones (38.61° C ± 7.26° C) ($t = 6.3940$, $p < 0.001$). Moreover the activity of the non-desiccated individuals occured with the main peak of activity of the resident population of that dune slipface.

The contraints imposed by temperature on surface activity are also illustrated in Fig. 2. Fog response is apparently not temperature limited and individuals of *O. unguicularis* have been recorded out in the fog when surface temperatures were as low as 3.2° C. Foraging activity of this species takes place mainly between 20° C and 50° C surface temperature. Maximum air temperature for the day at 1 cm above the ground was 36.5° C.

Observations of the effect of wind on foraging activity were carried out using *Zophosis fairmairei* on three afternoons with similar surface temperatures but varying wind speeds (Fig. 3). On days 1 and 3 the number of beetles active on the surface paralleled the variation in wind speed while on the day 2 no clear trend appeared.

IV. Discussion

DOYEN & TSCHINKEL (1974) point out that relative to most insects many tenebrionids are probably K-selected. The life history patterns of the Namib dune tenebrionids show some of the traits associated with being K-selected. For example, adults live for several years, are relatively large and reproduce repeatedly throughout

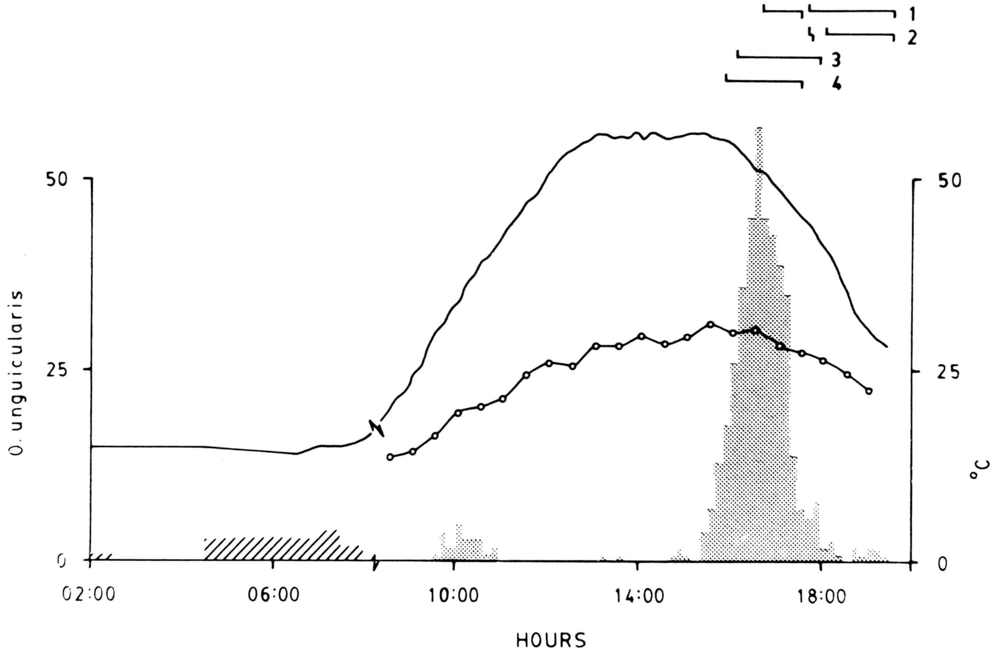

Figure 2 A composite diagram of fog response on 4 December 1977 (indicated by the histogram between 02 h 00 and 08 h 00) and foraging activity on 9 December 1977 (indicated by the histogram between 08 h 00 and 20 h 00). The length and position of the horizontal lines located above the main afternoon activity peak indicate the time spent on the surface by : 1) desiccated male, 2) desiccated female, 3) hydrated male, 4) hydrated female. The upper curve represents sand surface temperature and the lower curve ambient temperature.

the year unconstrained by periods of dormancy. However, another possible explanation for the observed trends of reproduction is termed « bet-hedging ». Adaptations leading to a pattern of « bet-hedging » include iteroparity, smaller reproductive effort, longer life, fewer young per brood and more broods (STEARNS, 1976), a pattern well suited to the fluctuating desert environment. Moreover, « bet-hedging », in contrast to r- and K-selection, assumes that schedules of fecundity and juvenile mortality may vary with time (STEARNS, 1976), a reasonable assumption in a desert environment (CRAWFORD, 1981).

Namib tenebrionids are capable of reproducing throughout the year (SEELY, 1981). One to many large eggs (e.g. 7.0 x 2.0 mm in *O. plana)* may be laid in a day. However, egg production may be reduced at any time by a scarcity of food or water or, as shown here, even by an apparent nutrient deficiency. Egg production is also limited by cold temperatures. But to successfully « bet-hedge », the best adaptation would be to continually produce a small number of eggs throughout the year taking

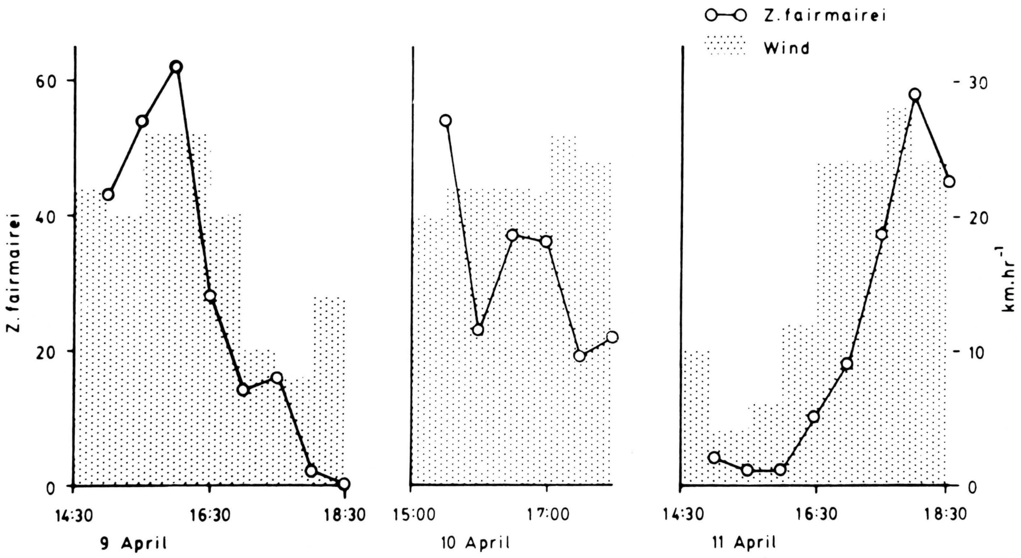

Figure 3 Wind speed (stippled area) and *Zophosis fairmairei* activity measured on three successive days in April 1981 with varied wind regimes. Surface temperatures between 14 h 30 and 18 h 30 were similar on all three days decreasing from 55° C to 31° C on the 9th, from 50° C to 31° C on the 10 th and from 55° C to 37° C on the 11th (unpublished data, E. McCLAIN).

advantage of any propitious, but unpredictable period of increased nutrients for larval development. In the Namib dune beetles studied, there exists a suite of physiological and behavioural adaptations which apparently favour continual production of a small number of eggs. Although there are many inter-related adaptations acting in concert, the water balance of the adult beetles appears to be the focal point around which they revolve (Fig. 4). Water balance directly influences all surface activities which, in turn, affect water balance and egg production.

Water loss rates for Namib dune tenebrionids are among the lowest measured (EDNEY, 1971). A number of these species can also secrete a waxy layer on the integument (Fig. 1) which appears to contribute to a further reduction of water loss as well as to thermoregulation when these species are on the surface. This waxy layer is renewable, as it disappears in high humidity, *i.e.* fog, and is also continuously worn away by abrasion from sand grains (McCLAIN, 1981). Beneath the surface, water loss would be reduced even further because of the favourable humidity levels (EDNEY, 1971) and, in addition, the moderate temperature would promote continuation of enzymatic activity associated with metabolism, in particular the developmental stages of the eggs. Adaptations which lead to efficient procurement of resources on the dune surface and thus increase time beneath the sand, also contribute to overall fitness and to the success of « bet-hedging ».

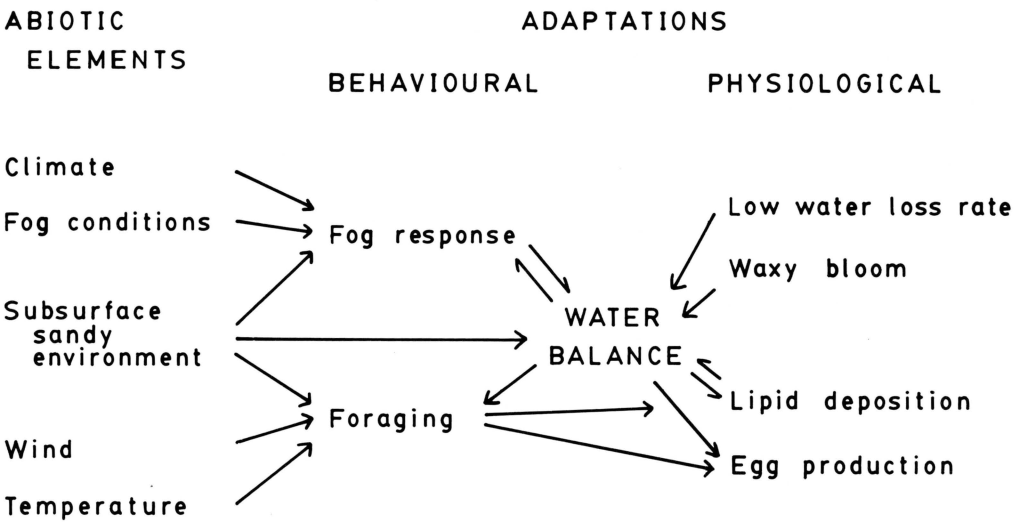

Figure 4 Some major influences of abiotic elements in the Namib environment on the behaviour and physiology of the dune tenebrionids and the interacting adaptations of these beetles which lead to maximum fitness.

Water uptake from fog (e.g. Fig. 1) occurs only on the surface. Individuals in negative water balance must expend the energy necessary to obtain fog-water until they have attained a positive balance. Fog uptake behaviours of the various groups of species are fine-tuned to obtain the maximum amount of fog water in the minimum length of time possible (SEELY, 1979). Fog response, in some species more than others, is also influenced by abiotic factors including the weather occurring between fogs and the conditions of the fog itself. NICOLSON (1980) has shown that *O. plana* may be able to metabolize lipid material to assist with the maintenance of a positive water balance. Thus, the rapid deposition of lipid material would increase the time tenebrionids remain below the sand by contributing to water balance and lipid stores. Water balance also has a direct effect on the search for food and mates. Individuals in positive water balance are able to tolerate the hotter temperature and desiccating winds which occur during the early part of the main afternoon feeding period. Stilting behaviour, *i.e.* raising the body as high as possible above the surface level (Fig. 1) to catch the wind, also increases tolerance of elevated sand temperatures (see also HENWOOD, 1975). Because winds in excess of approximately 10 $km.h^{-1}$, or even less, continually replenish detritus accumulations, the early foragers, in positive water balance, have priority access to any potentially nutritious portions of food. This in turn would allow them to maintain reproductive condition and to lay down lipid reserves which further contribute to continued reproduction and water balance.

Thus, in addition to water balance, foraging activity is dependant on several inter-related abiotic factors, mainly sand surface temperatures and wind. Surface temperature has been suggested by many authors e.g. HOLM & EDNEY (1973), as a major factor affecting diurnal activity of adult tenebrionids. An example of the bimodal foraging activity, presumably dictated by sand surface temperatures and commonly observed in summer, is presented in Fig. 2. The strong facultative response to wind of the crepuscular to nocturnal dune slipface tenebrionid *Lepidochora discoidalis* is attributed, by LOUW & HAMILTON (1972), to both the cooling effect of wind and the transportation of detritus by the wind. A similar facultative response to wind by *Z.fairmairei* is illustrated in Fig. 3.

The characteristics of dune sand, in conjunction with the influence of the environment of fog and wind (see ROBINSON & SEELY, 1980), apparently provide an excellent life support medium for a number of substrate dependant Namib animals. The sand gives psammophytic diggers easy access to depths where equitable temperatures and humidity provide an 'incubation chamber' where metabolic rates are maintained and egg production can be supported continually. The favourable conditions beneath the sand also serve as a place of refuge when the physiological state of the beetle is not optimal and/or when the surface conditions are unsuitable for water uptake or foraging. The physiological state of the beetle allows effective use of prime foraging time and the beetles employ behavioural adaptations to fine-tune their surface foraging and water uptake activities to the prevailing abiotic conditions. In this way a combination of adaptations leads to the success of « bet-hedging », the efficient intake of resources' found only on the more extreme' sand surface and maximal use of the moderate subsurface environment.

Acknowledgements

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Discussion

WEIDEMANN, G. : (1) Can you say anything about developmental time in tenebrionid larvae ?
(2) Are there great fluctuations in tenebrionid abundance or not ?

SEELY, M.K. : (1) Developmental time may vary between 6 months and more than 15 months for one species.
(2) Yes.

HEYDEMANN, B. : Do you know anything about the desert adaptations of tenebrionid larvae ?

SEELY, M.K. : Experiments in progress are providing indications of the length of time required for larval development, and for the preferred temperature and humidity.

ANDERSON, J.M. : (1) Can you give some indications of the qualitative and quantitative variations in the detritus resources ?
(2) Is there any marine littoral insert in the margins of the desert during storms ?

SEELY, M.K. : (1) I can only provide you with the extreme values already mentioned with respect to quantitative variations.
(2) The marine detritus is not carried more than a few kilometers inland so far as I have observed.

WHITFORD, W.G. :(1) Have you made any measurements of egg production of beetles on high quantity food but constant humidity, *i.e.* 50 % or 100 % relative humidity ?
(2) What about use of insect carrion ? Is there much in the wind blown detritus ?

SEELY, M.K. : (1) Such measurements have not been made.
(2) Any insect carrion is immediately consumed although it does not constitute a large part of the detritus.

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