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Fog response of tenebrionid beetles in the Namib Desert

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Fog is an important water source for a number of tenebrionid beetles from the Namib Desert dunes. The response to fog of six species was shown to vary, however, the response of two species was found to be correlated with the water balance of the individual adult beetle, the characteristics of a fog and the climate occurring between fogs.

Introduction

Behavioural and ecological aspects of the use of fog as a water source for the long-lived adult tenebrionid beetles of the Namib Desert dunes have recently been described (Hamilton & Seely, 1976; Seely & Hamilton, 1976; Seely, 1979). However, response of these beetles to irregular fogs was observed to be unpredictable and showed no obvious relation to weather conditions between fogs or to characteristics of a fog. For this reason, an attempt was made to elucidate the factors controlling fog response in several dune tenebrionids.

A study site was selected near Gobabeb (23°34′S, 15°03′E) 56 km inland from the Atlantic coast in the central Namib Desert where advective, precipitating fogs occur 34 days per year and yield 27·7 mm of precipitation per year (n = 12 years). Fog precipitation has been recorded, on occasion, anytime between 2100 h and 1230 h and lasts for a mean duration of 3·1 ± 2·5 h (n = 171 events in 5 years). Non-precipitating fogs and dew have been recorded an additional 56 days of the year (n = 4·6 years). Precipitating fog has been recorded in every month of the year, but only from August to December inclusive has it been present in each of the 12 years for which data are available. Ninety-six days is the longest period on record without fog precipitation (n = 12 years) and 36 days is the longest period without dew or fog of any sort (n = 4·6 years).

Materials and methods

Observations were made every day in September 1977 from 2400 h until sunrise whether or not fog was present. From 1 October for the following 11 months, every time humidity reached 100 per cent a census of fog-responding beetles was made within half an hour and repeated at 2-hourly intervals until the fog lifted. A 600 m census route was established on a dune of medium height (approximately 30 m) which included the four main dune habitats: slipface; vegetationless dune slope; vegetated dune base; and lightly vegetated interdune valley with a gravel substrate. Thirteen numbered poles were erected at intervals to mark the borders of the habitats and divide the route into sections (I–XIII) which facilitated recording and location of the route on dark, foggy nights.

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Using an incandescent light source and tape recorder, observations were made for 3 m on each side of the route. Adult beetles that were on the surface engaged in fog-water uptake behaviour, were easy to see against a background of lightly vegetated or bare sand and because of their lethargic movements. They did not react to the observer. The following observations were recorded: number of individuals of each species; location with respect to the census line; habitat occupied; and activity. A count of the minimum number of beetles on the surface was used for analyses. For example, if in Section VI three beetles of one species were seen at 0400 h and 12 beetles at 0600 h, it was assumed that the initial three were included in the 12. Validity of this approach, based on little or no turnover of individuals during a fog, was confirmed using numbered individuals in a few fogs.

Measurements of temperature, humidity, wind and barometric pressure were made with a Lambrecht recording thermohygrograph and anemometer and a Short and Mason micro-barograph located at Gobabeb, 3·5 km away from the study area. Fog-water precipitation was measured using a wire-mesh cylinder (height, 20 cm; diameter, 9·5 cm) placed on a Lambrecht autographic rain gauge. One permanent gauge is located at Gobabeb and a second one was established approximately 150 m from the census dune beginning on 10 October 1977. Sand surface temperatures during fogs were measured with a standard mercury thermometer. 'Precipitating fogs' were defined as those which produced a recording on the chart of the fog gauge, although, precipitation was often registered during only part of the time that fog was visible. 'Non-precipitating fogs' were visible but did not produce a recorded value. Observations were made in precipitating and non-precipitating fogs.

Lepidochora discoidalis (Gebien) and *Onymacris unguicularis* (Haag) were most commonly observed in fogs and results pertain primarily to these two species. In addition, *L. porti* (Koch), *L. kahani* (Koch), *Zophosis* (*Cardiosis*) *fairmairei* (Péringuey), *Zophosis* (*Gyrosis*) *moralesi* (Koch) and *Z.* (*G.*) *orbicularis* (Deyrolle) were also included in some analyses. Nomenclature follows Koch (1962) and Penrith (1975, 1977, 1980).

In addition to the direct observation of fog response, four complementary field/laboratory experiments were carried out concurrently.

(1) Monthly field collections of 20 *L. discoidalis* and 10 *O. unguicularis* were made for 2 years within 10 km of the census dune. These individual beetles were dried in an oven at 70 °C until constant weight was attained (approximately 3 days) and the percentage water content was determined gravimetrically.

(2) Rates of water loss were determined in the laboratory under low humidity conditions by maintaining 20 individuals of *L. discoidalis* and 17 of *O. unguicularis* over silica gel in a desiccator at room temperature (20 ± 4 °C) and weighing the beetles at 2-day intervals. The humidity in the desiccator measured less than 10 per cent (Hygrodynamics Mini-Reader).

(3) Twenty *L. discoidalis* were collected in the field in the evening, individually labelled on the pronotum with plastic discs and then released where originally collected. The number of individuals on the surface during subsequent morning fogs was noted.

(4) Individuals of *O. unguicularis* (n = 49) were desiccated over silica gel at room temperature for 24 days. A control group (n = 46) was provided with oats and lettuce (96 per cent water) during the final 10 days of the same period. These beetles were then placed in an enclosure on a dune and a record was made of the number responding to fog the following morning.

Results

Daily observations during September from 2400 h to sunrise confirmed the almost complete absence of surface activity for these adult tenebrionids in the absence of fog or dew (Seely, 1979). From October to the end of the following August, the alarm system was set off by 100 per cent humidity 66 times. On 39 of these days fog-water precipitation was recorded near the census dune. Fog response activity was observed on 97 per cent of those days with fog precipitation and on 76 per cent of the foggy days without recorded precipitation. Although *O. unguicularis* and *L. discoidalis* were to be found on the sand surface during both precipitating and non-precipitating fogs (Fig. 1), the response to precipitating fogs were significantly greater (Table 1).

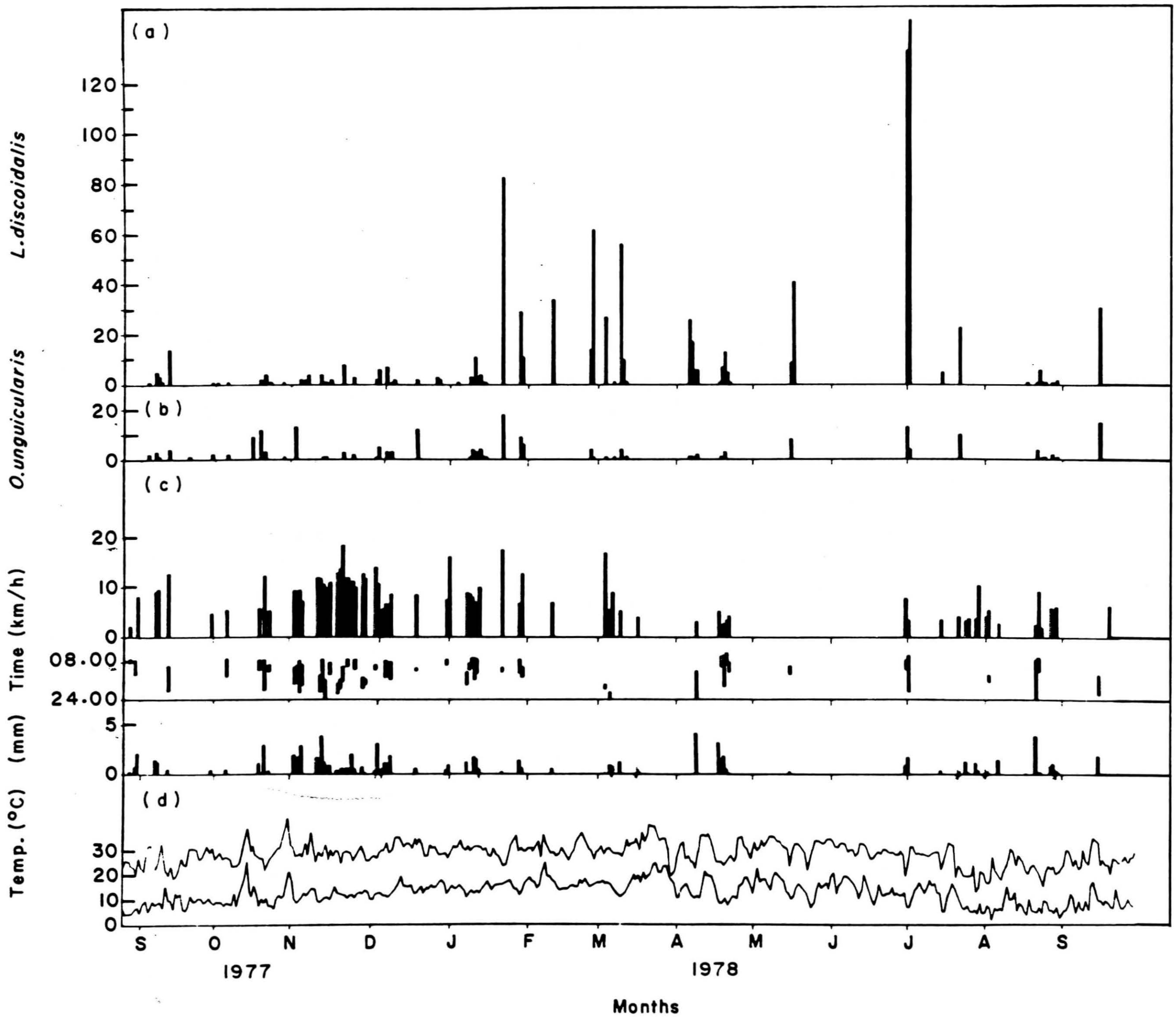

Figure 1. The upper two histograms present daily total numbers of (a) *Lepidochora* species and (b) *Onymacris unguicularis* responding to fog. The central three histograms, (c) give maximum wind speed at Gobabeb during fog-water precipitation (km/h) and the time (h) and amount (mm) of fog-water precipitation at the Dune Gauge. The lower graph, (d) presents daily maximum and minimum temperature values (°C) at Gobabeb during 1977 and 1978.

Significant correlations were found between *O. unguicularis* and *L. discoidalis* and some of the fog characteristics and weather parameters when the data were used from each day ($n = 66$) that 100 per cent humidity was registered and beetles responded (Table 2). A significant correlation (Spearman's Rank Correlation Coefficient) was found between one or both species and the following: (1) number of individuals of the other species also active;

Table 1. *Mean minimum number of* L. discoidalis *and* O. unguicularis *present during fogs where precipitation was or was not recorded at the study site* (t-*test for two means*)

	Precipitation recorded (n = 39 days)	Precipitation not recorded (n = 27 days)	Significance
L. discoidalis	15·2	10·8	$P < 0{\cdot}001$
O. unguicularis	4·0	1·4	$P < 0{\cdot}02$

(2) amount of fog-water precipitation; (3) rate of fog-water precipitation; (4) duration of fog-water precipitation; (5) sand-surface temperature during fog; (6) number of days since the previous fog; (7) mean maximum temperature since the previous fog; (8) mean minimum temperature since the previous fog; and (9) mean relative humidity (at 1400 h for *O. unguicularis* and at 2000 h for *L. discoidalis*) since the previous fog.

However, no relationship was found between the number of *L. discoidalis* or *O. unguicularis* actively collecting fog-water and: (1) maximum wind velocity during a fog; (2) barometric pressure at the start of fog-water precipitation; or (3) change of barometric pressure for 3 h preceding fog-water precipitation. Moreover, the number of beetles responding to each fog was not uniformly distributed between the months of the year for any of the six most frequently observed species (χ^2, $P < 0{\cdot}005$) (Figs 2, 3), nor was there an obvious trend to be observed in the daily records (Fig. 1). For four of the species surface foraging activity seasons were also observed in the same area and for these species there was no correlation (Spearman's Rank Correlation Coefficient) between the monthly pattern of fog response and that of foraging activity (Fig. 3).

In the study year the period with a higher incidence of fog extended from October to January inclusive. When the three unusual days (see below) were eliminated and the periods with more or less fog were compared, the response of *O. unguicularis* was not significantly different for the two-halves of the year while the response of *L. discoidalis* was significantly greater during that part of the year with less fog (Table 3).

Three foggy days in the year showed an unusually high response rate greatly affecting the January and July totals. On 22 January, when only 0·2 mm of fog-water precipitation was recorded, 10 per cent of all *L. discoidalis* and 12 per cent of the *O. unguicularis* active in

Table 2. *Correlation coefficients (Spearman's Rank Correlation Coefficient) and significance of response of* O. unguicularis *and* L. discoidalis *with eight factors (see text) characterizing fog or weather conditions between fog events*

	O. unguicularis	Significance	*L. discoidalis*	Significance
O. unguicularis	—	—	+0·3262	0·02
L. discoidalis	+0·3262	0·02	—	—
Amount	+0·3980	0·05	−0·1594	NS
Rate	+0·4760	0·01	−0·1792	NS
Duration	+0·3062	0·05	+0·1298	NS
Sand temperature	+0·3709	0·05	+0·2501	(0·1)
Days	+0·4451	0·01	+0·1537	NS
$T_{max.}$	+0·2908	(0·1)	+0·1080	NS
$T_{min.}$	+0·3598	0·05	+0·3427	0·05
R.H.	−0·2297	(0·1)	+0·0618	NS

NS, not significant.

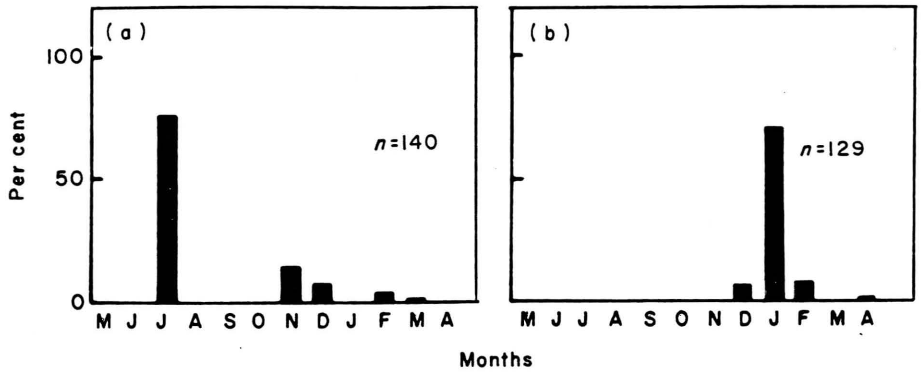

Figure 2. Fog response of (a) *Z.* (*G.*) *moralesi* and (b) *Z.* (*G.*) *orbicularis* during one year (per cent by month).

fogs during the year were on the surface. This same morning *Z.* (*C.*) *fairmairei* (72 per cent), *Z.* (*G.*) *moralesi* (10 per cent) and *Z.* (*G.*) orbicularis (36 per cent) were also present in unusually high numbers. On 22 January, despite the small amount of recorded fog-water precipitation, the fog was unusual, lasting until after 0900 h at which time the visibility was still approximately 30 m. On 1 and 2 July when 0·95 mm and 1·65 mm of precipitation were recorded, there was also a high proportion of the year's total number of beetles responding: *L. discoidalis* (33 per cent), *O. unguicularis* (11 per cent) and *Z.* (*G.*) *moralesi* (39 per cent). The fog on 1 July was the first fog for 45 days during which time desiccating 'east winds' had dominated the weather.

During the 2 years in which the water content of field-captured *L. discoidalis* and *O. unguicularis* was being measured, values for the two species were similar (Table 4) and varied little throughout the year (Fig. 4) although *L. discoidalis* exhibited a slightly greater range.

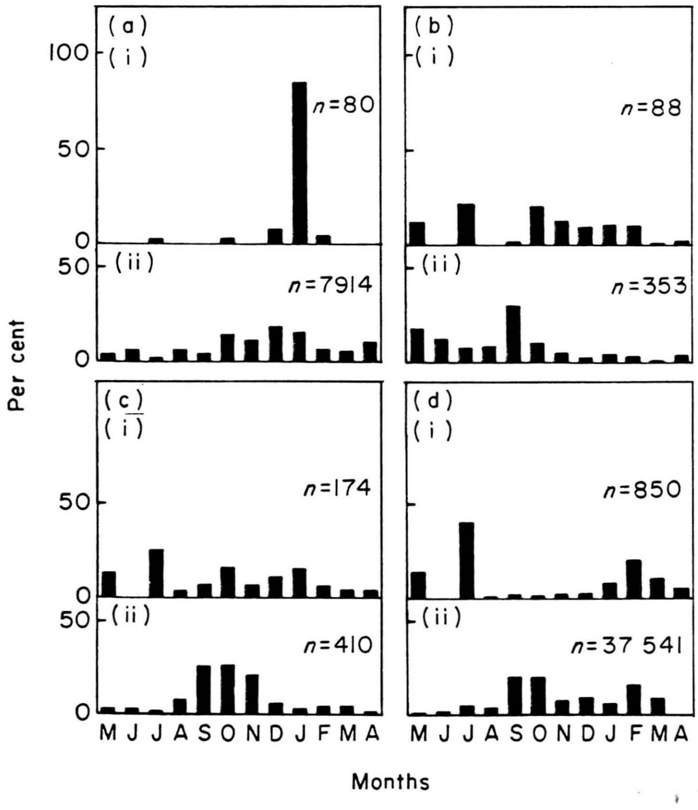

Figure 3. Fog response (i) and foraging activity (ii) of (a) *Z.* (*C.*) *fairmairei*; (b) *L. kahani*; (c) *O. unguicularis* and (d) *L. discoidalis* (per cent by month).

Table 3. *Mean minimum number of* L. discoidalis *and* O. unguicularis *active on the surface on census days during the period with more fog (34 fogs yielding 34·1 mm precipitation in 110-day period) and during the period with less fog (39 fogs yielding 19·4 mm precipitation in 247-day period)* (t-*test for two means)*

	More fog	Less fog	Significance
L. discoidalis	3·5	13·6	$P < 0.01$
O. unguicularis	2·8	1·6	NS

NS, not significant.

Under desiccating conditions in the laboratory, 10 of 20 *L. discoidalis* were still alive after 34 days while eight of 17 *O. unguicularis* were alive after 78 days. The rates of weight loss (presumed water loss) also varied, that for *L. discoidalis* being 1·06 ± 0·5 per cent of initial weight per day and that for *O. unguicularis* being 0·38 ± 0·03 per cent per day. Using *O. plana* rather than *O. unguicularis*, Hadley & Louw (1980) also found a much lower rate of water loss per unit body mass for *L. discoidalis* than for the much larger *O. plana*.

When 20 field-caught *L. discoidalis* were weighed, numbered and immediately returned to the field the same evening, a mean number of 8·2 ± 2·4 of these beetles responded to precipitating fog the following morning ($n = 5$ foggy days).

Onymacris nymacris unguicularis, some of which had been desiccated and others provided with food and water previous to observation, were released into an enclosure on a sand dune. Of those beetles ($n = 46$) which had been desiccated, 83 per cent were observed fog basking the following morning in a light fog. None of those beetles ($n = 49$) which had not been desiccated but provided with food and water responded to the fog, all remaining beneath the sand surface until they began foraging later in the day.

Discussion

In the Namib Desert, fog as a water source for tenebrionid beetles is irregular and unpredictable in both timing and character. Nevertheless, the fog response of the two

Table 4. *Water content of* L. discoidalis *and* O. unguicularis *expressed as a percentage of the field weight. Values were obtained monthly for 2 years* (L. discoidalis, n = *20 per month;* O. unguicularis, n = *10 per month)*

	L. discoidalis (per cent)	*O. unguicularis* (per cent)
Two-year mean of monthly values	63·9 ± 1·0	61·9 ± 0·7
Highest monthly mean	73·8 ± 1·1	70·1 ± 2·0
Lowest monthly mean	53·0 ± 1·6	57·4 ± 0·8
Highest individual value	84·9	79·4
Lowest individual value	38·1	51·3

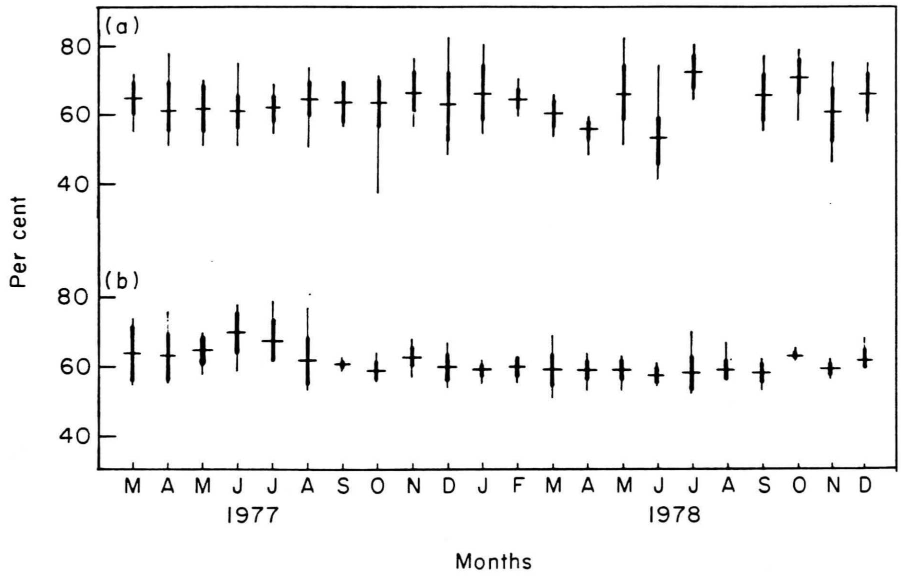

Figure 4. Monthly per cent water content of (a) *L. discoidalis* and (b) *O. unguicularis* collected from the dunes for two years.

most commonly observed species of tenebrionids, *O. unguicularis* and *L. discoidalis*, was found to be significantly correlated indicating some form of parallel control. However, the characteristics of a fog and, to a lesser extent, the weather conditions between fogs had more influence on *O. unguicularis* than on *L. discoidalis*. No correlation was found between fog or weather parameters and the other five tenebrionid species commonly observed.

The present study was conducted during a relatively wet year in the desert when humidity at 10 cm beneath the sand surface was recorded as varying between 25 and 46 per cent during the year (Robinson & Seely, 1980). Moisture content of the sand has been found to increase with depth to at least 40 cm (Seely, unpublished). The beetles under consideration all spend more than half of their daily cycle beneath the sand surface at depths greater than 20 cm. Hence any dehydrating influence of atmospheric conditions on the beetles during this study would have been less effective than during a drier period with lower sand moisture content.

The weather conditions did have some effect on internal water status was indicated by the water percentages measured on the field populations (Fig. 4). The lowest mean monthly water content values in the 2 years were obtained for *O. unguicularis* and *L. discoidalis* in late June 1978. In the latter half of May and the entire month of June no fog was recorded in the dunes and on 1 and 2 July very high fog response was recorded. Towards the end of July 1978 the moisture content of *L. discoidalis* reached its highest value during the 2 years of measurement, although *O. unguicularis* showed a less dramatic increase.

Several aspects of the physiology of these beetles could contribute to relative independence from climatic control of fog response. As Nicolson (1980) has shown for *O. plana*, these beetles may be able to metabolize lipid material to maintain positive water balance. The large amount of cuticular hydrocarbons found in Namib dune beetles (Hadley & Louw, 1980) may also contribute to low rates of water loss. Moreover, the measured rate of weight loss (presumed water loss) in dry air which has been found to be very low in these and similar species (for example, Edney, 1971; Hadley & Louw, 1980; this study), is reduced to an even lower rate at 90 per cent relative humidity (Edney, 1971).

The rates of water loss calculated from our data indicated a lower rate of weight loss than measured by Edney (1971). This could probably be attributed to the lower temperatures used during our desiccation procedure. However, the length of the period of desiccation was also of importance. When the rate of weight loss was calculated from our data after 5 days, the rate is twice that found for the longer periods (34 days for *L. discoidalis* and 78 days for *O. unguicularis*). Edney (1971) calculated his rates for a 5-day period. However, considering the observed intervals between precipitating fogs in the Namib we felt that the longer desiccation periods were warranted.

When the results derived from long term desiccation in the laboratory were combined with the moisture contents measured in the field population (Table 4), theoretical survival times in the absence of fog or any other water source could be calculated. At a rate of water loss of $1{\cdot}06 \pm 0{\cdot}50$ per cent/day an individual of *L. discoidalis* would remain within the population mean for 20 days and within the extreme field values for 44 days. For *O. unguicularis*, at a rate of $0{\cdot}38 \pm 0{\cdot}03$ per cent/day, an individual would remain within the mean range for 34 days and within the extreme range for 74 days. However, as more than half the daily cycle of these beetles is spent beneath the sand surface where the humidity is higher than on the surface, their survival periods could possibly be double those calculated above.

Thus, *O. unguicularis* was shown to lose moisture at a lower rate than *L. discoidalis* and calculations suggested longer survival for *O. unguicularis* in the absence of fog-water uptake. However, *O. unguicularis* exhibited a lesser range of body water content in the field. In addition, the results of our fog-response observations indicated that *O. unguicularis* was more strongly influenced by atmospheric conditions between fogs and by characteristics of the fog events. Several factors may help explain this apparent paradox.

Both species occupy the vegetationless slipfaces of the dunes and feed predominantly on wind-blown plant detritus. *Onymacris unguicularis*, the larger of the two species, is diurnally active, particularly in the afternoons when the wind has cooled the sand surface to approximately 50 °C. *Lepidochora discoidalis* becomes active only later when shadows occur on the slipface and they may remain active until well after dark. Therefore, *O. unguicularis* is exposed to higher temperatures and lower humidities than *L. discoidalis*, which would suggest a relatively higher rate of water loss for *O. unguicularis* under field conditions than was indicated by the laboratory experiments. Hence, consideration of activity patterns alone, would suggest that weather conditions between fogs would have a greater impact on the fog response of *O. unguicularis* than that of *L. discoidalis*.

Lepidochora discoidalis, by constructing fog trapping trenches (Seely & Hamilton, 1976), is able to take advantage of a wider variety of fog and dew conditions than is *O. unguicularis*. *Lepidochora* species are more active during the early portion of a fog event (Seely, 1979) and have often been found active well before precipitation occurs, as well as during non-precipitating fogs and dew. They disappear from the surface as the fog lifts. In contrast, *O. unguicularis* which uses fog-basking behaviour to obtain fog-water (Hamilton & Seely, 1976), is more restricted to that period during which condensing fog is present. Hence, the correlation between fog characteristics and *O. unguicularis* response, which was not observed for *L. discoidalis* response, was not entirely unexpected.

In addition, *L. discoidalis* occurs across the entire width (*c.* 140 km) of the central Namib Desert dune field where it can take advantage of fogs in the west and dew in the east. The range of *O. unguicularis* extends from the foggy coast inland only as far as the study site 56 km inland. If fog is the limiting factor on this inland margin of its range, a correlation between fog response and fog events and weather conditions between fogs would be predicted.

Throughout the Quaternary the Namib Desert had been arid, although during this time the degree of aridity has fluctuated (Tankard & Rogers, 1978). Currently some source of atmospheric moisture, either precipitating fog, non-precipitating fog or dew, is present at least 90 days of the year at the study site towards the center of the dune field. As the present study of fog response was carried out in a decidedly wetter year than average, it is probable that not all of the beetles were experiencing the usual conditions of water stress. It is, therefore, suggested that this entire complex of fog response behaviours associated with fog-water use is not organized for the maintenance of water homeostasis during these wetter periods, but that it may contribute to the survival of these dune tenebrionids during the drier decades and centuries experienced by the Namib desert.

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