Day-time spatial orientation of *Pachyphaleria capensis* (Laporte), an endemic tenebrionid beetle of the South West African coast.

by

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ABSTRACT

The orientation behaviour of *Pachyphaleria capensis* (Laporte), a psammo-halophilic tenebrionid beetle of southwestern Africa, was investigated. Skototaxis and pilotage are the main mechanisms adopted by the beetle to escape solar radiation. A negative phototactic response results in a non-chronometrical solar orientation. On overcast or foggy days the day-time response tends to occur in a north-south direction.

CONTENTS

1 INTRODUCTION

Pachyphaleria capensis (Laporte) is a psammo-halophilic (salty-sand loving) tenebrionid beetle found along the coast of southwestern Africa, from Terrace Bay (19° 56'S, 13° 02'E) to the cape Peninsula (pers. comm. Dr. M.-L. Penrith). Distribution is restricted to within 10-50 m of the shore-line, and may be related to the susceptibility of *P. capensis* to dehydration and the beetles' inability to float or swim.

In summer activity occurs in the early morning, evening and at night. During the day, large aggregations of juveniles and adults occur buried into the damp subsurface soil layers or taking refuge under debris.

The tenebrionid beetle *Phaleria provincialis* (Fauv) occurs in a similar habitat on the shores of the Mediterranean. It displays landward or seaward movements that always occur perpendicular to the shore-line. The direction followed is apparently determined using the position of the sun and/or the angle of skylight polarisation (Pardi 1956). Using an artificial light source, Pardi (1958) demonstrated that *P. provincialis* accommodates for movements of the sun. The orientation mechanism used can therefore be described as chronometrical solar orientation. At night *P. provincialis* exhibits sun-night orientation similar to that shown in *Talitrus* (Pardi, 1953-1954), orientating as if retracing the suns' daytime path.

P. capensis has not been extensively studied and the phenomenon of spatial orientation has never been investigated. The purpose of this investigation was to examine the mechanisms influencing the day-time spatial orientation of *P. capensis* and to compare this species with *P. provincialis* on the basis of ecological criteria.

2 MATERIALS AND METHODS

The research was conducted in the Namib Desert of southwestern Africa during February and March of 1983.

Field observations were conducted at two coastal locations near Walvis Bay and Swakopmund. The shorelines at these experimental sites had E-W and N-S orientations and an inland escape direction (IED) of 170° and 90° respectively. Field and laboratory observations were also carried out at the Desert Ecological Research Unit (DERU) at Gobabeb, roughly 56 km from the Atlantic Ocean.

Preliminary observations involved the release of specimens on shores from which they had been collected. Quantitative tests were also conducted in which specimens were released at different distances from the sea and on beaches that had different orientations to the original ones. Mirrors were also used according to the technique of Santschi (1911). Further quantitative laboratory observations involved the use of artificial light sources.

Field observations and tests were conducted under various climatic conditions viz. on clear, overcast and foggy days. The Namib Desert coast is characterised by fog. Often moving in from midnight onwards, it may persist till 10.00 am or longer. The quantitative tests were conducted using a circular masonite arena (radius = 40 cm) which was divided into 16 sectors. A minimum of 50 individuals were used for each experiment. Following the release of individuals into the centre of the arena, the exit sector selected by each individual was recorded. The response of individuals when given an option of 2 directions, at 180° to each other, was also tested by placing individuals in a transparent plexiglass corridor, open at both ends.

The results were analysed using circular statistics (Batschelet, 1981) and regression analysis.

Time refers to South African Standard Time which is 2 h ahead of Greenwich mean time.

3 RESULTS

Preliminary Observations:

Earlier observations on specimens released on clear days showed that *P. capensis* buried or, in the case of a hard superficial sand layer, escaped to protected areas such as under kelp, debris etc.

The path selected by a group of 30 individuals, which had been released near the water-edge in the centre of a square area lacking debris but with a natural slope tending seawards, was investigated on a clear day. The course taken by the individuals was slow and winding. During their course individuals stopped several times. All indications suggested that the paths were directed inland.

Quantitative Tests:

(a) Tests for skototaxis

To establish the skototactic tendencies of *P. capensis*, tests were conducted using an arena sunk 20 cm below the level of the surrounding sand such that a shadow in a N-E-S hemicircle was cast (Table Ia). As revealed by Fig. 1, *P. capensis* congregated in the shaded half of the arena.

FIGURE 1: A test with the arena in partial shade. (N-E-S hemicircle shaded). The black dots represent the specimens and the arrow the mean escape direction. The values of the polar coordinates of the mean vector are indicated. Inland is represented by a dark area.

(b) Tests near the water-edge

To determine whether substrate slope influences orientation, tests were conducted on clear days (Fig. 2) with the arena having been placed in a horizontal position (Table Ib) and on an inland facing slope (Table Ic). The direction of the mean vector followed shifted 29° when individuals were then placed on a slope.

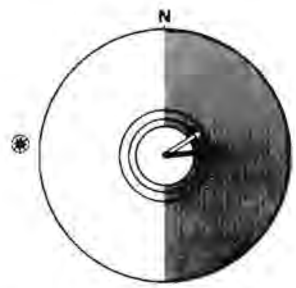

FIGURE 2: The mean vectors of tests carried out near the sea, with the arena placed in a horizontal (black arrow) and on inclined (white arrow) position. The circles correspond, from inside to outside to 5%, 1% and 0.1% levels of significance respectively. Inland is represented by the shaded area. The external symbol represents the sun.

The orientation reactions of individuals placed on a beach of different orientation to that of the original were also investigated. In this instance two groups of 50 individuals collected on the beach at Walvis Bay were tested at Swakopmund. In one test the arena was placed directly on the ground (Table In; Fig. 3a), while in another test (Table Io, Fig. 3b) the arena was placed at a height of 1 m to prevent the animals from obtaining visual cues from the environment.

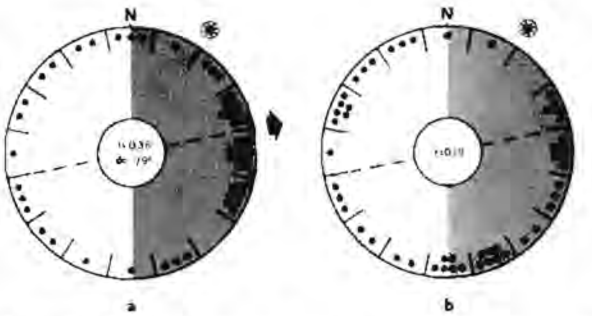

FIGURE 3: Tests carried out on a beach other than the original one. The dotted line is indicative of the shoreline of the place of origin (IED = 170°). The dark area represents the local inland (IED = 90°). Specimens were permitted (a) or not permitted (b) to see the environment. For symbols see Figs. 1 and 2.

(c) Tests far from the sea

Individuals, placed in the arena when it was situated at a distance of 100 m from the sea and prevented from obtaining cues from their environment, were tested at three times (Table Im,p,q).

Other time test experiments without visual cues, were performed at Gobabeb using specimens that had been collected at Walvis Bay and kept in an insectary containing damp sand (Table Ih,i,j). To establish the relationship between the sun azimuth and the mean escape direction, analysis by regression was performed (Fig. 4). The correlation coefficient is high (r = 0.98) and the regression line y = -167° + x is of great interest since its angular coefficient coincides with the value of the bisecting line of the first quadrant. The *Chi* square test ($x^2 = 2.7; 0.50 \le P \le 0.75$)

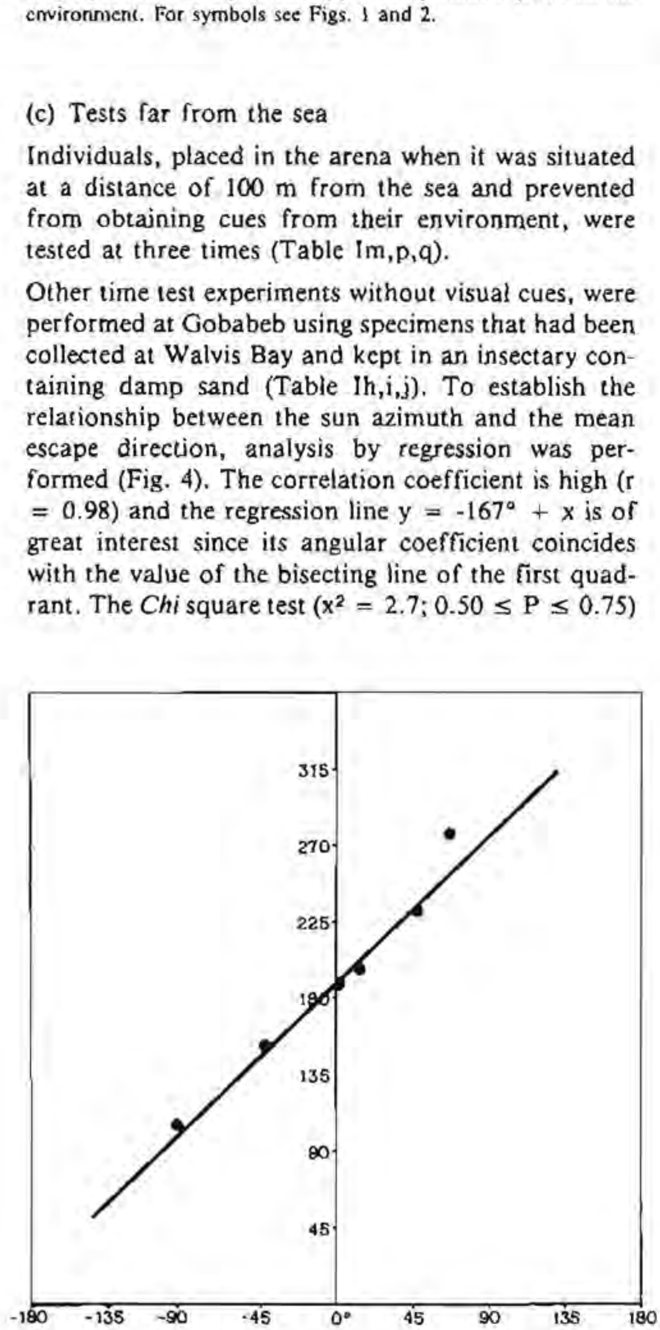

FIGURE 4: Tests carried out far from the sea. The abscissa corresponds to the sun azimuth value and the ordinate the mean escape direction. The dots correspond, in increasing order, to the tests j, q, p, i, m, h (Table I).

confirmed the goodness of fit of the regression line with the observed data.

Tests conducted to verify that the sun influences *P. capensis'* orientation revealed that a disorientated response prevailed on partially sunny days. (Table If, Fig. 5a).

Using the Santschi technique, i.e. blocking the sun but allowing it to reflect at a 180° angle, individuals were shown to have a well orientated response (Table Ik; Fig. 5b).

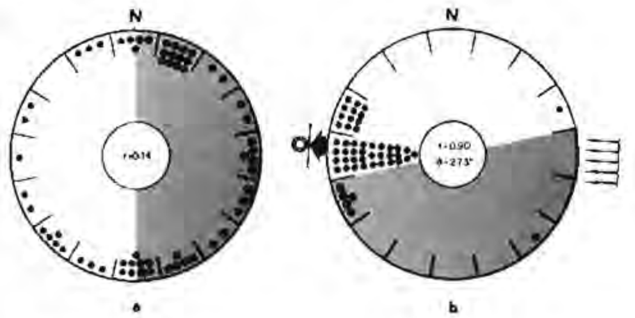

FIGURE 5: Tests with the sun intermittently visible (a) and blocked but using a mirror (b) (Santschi's technique). For an explanation of the other symbols see Figs. 1 and 2.

(d) Tests with a darkened sun

These tests were conducted on foggy mornings using the usual arena (Table Id, e, r, Fig. 6a) and using the plexiglass corridor orientated along different compass directions. Of 60 individuals released centrally into the N-S orientated corridor (Walvis Bay, March 10, 09h15) 41 were found to move northwards while 19 were observed to move southwards ($x^2 = 8.07$; $P<0.01$). Then with the corridor orientated in an E-W direction, the results were different, with 31 individuals moving eastwards and 29 westwards.

The results of other tests conducted in the arena on an overcast afternoon and at sunset at Gobabeb are presented in Table Ig, Fig. 6b and Table 2, Fig. 6b respectively.

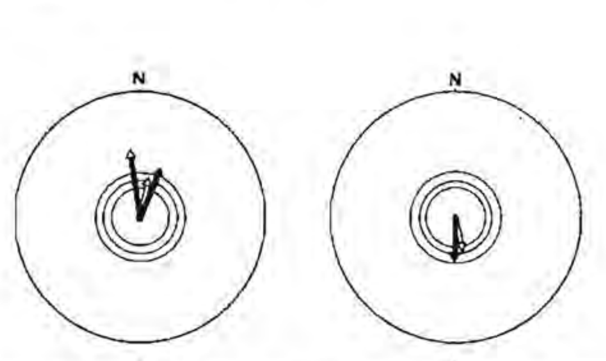

FIGURE 6: Tests with the sun darkened. (a) Foggy morning test carried out at Swakopmund Feb 8 (dark arrow), Feb 9 (lined arrow) and at Walvis Bay March 10 (white arrow). (b) Tests carried out on an overcast day in the afternoon (dark arrow) and after sunset (white arrow). The circles represent the levels of significance for n = 50.

TABLE 1: Open Air Quantitative Tests

	o.p.	t.p.	date	hr	n	ϑ	r
a	W	G	1 F	11.35-12.00	100	100°	0.75***
b	S	S	7 F	18.15-19.00	50	85°	0.47***
c	S	S	7 F	19.00-19.25	50	56°	0.31**
d	S	S	8 F	10.10-10.25	50	23°	0.44***
e	S	S	9 F	08.50-09.15	50	352°	0.53***
f	S	S	9 F	12.10-12.45	61	-	0.14
g	S	S	9 F	18.30-18.50	50	177°	0.35**
h	W	G	16F	08.32-08.50	50	277°	0.43***
i	W	G	16F	12.10-12.17	50	196°	0.35**
j	W	G	16F	19.20-19.45	50	105°	0.42***
k	W	G	3 M	19.00-19.10	50	273°	0.90***
l	W	G	3 M	19.10-19.20	50	174°	0.27*
m	W	W	8 M	09.30-10-10	150	233°	0.33***
n	W	S	9 M	11.02-11.12	50	79°	0.38**
o	W	S	9 M	11.15-11.30	50	-	0.19
p	W	W	9 M	12.36-13.18	150	189°	0.26***
q	W	W	9 M	15.48-16.38	150	151°	0.61***
r	W	W	10M	08.30-09.05	123	14°	0.31**

Table I: Specified are: o.p.-original place viz. place where the specimens were collected; t.p. test place viz. place where the experiments took place, W - Walvis Bay; S - Swakopmund; G - Gobabeb; F - February ; M - March; h - the starting and ending time of each test; n - the number of specimens tested; (v,r) - polar coordinates of the mean vector. When the length of the mean vector was not statistically significant, the value of the mean angle was omitted. Levels of significance (0.05, 0.01, 0.001) are indicated with one, two and three asterisks respectively.

(e) Indoor tests

Two time tests were conducted in a dark room using 100 individuals collected from Walvis Bay. The individuals were collected two days prior to the experiment and maintained under a natural photoperiod. In the first test (Table 2A) the light source (15W a.c.) was placed 2 m from the centre of the arena in an easterly position. Observations were made every 2 h for a 24 h period commencing from 1.00 pm. The length of the mean vectors was significant ($r \geqslant 0.21$) and the mean angle within a range spanning 29° ($250° \leq \delta \leq 279°$) (Fig. 7).

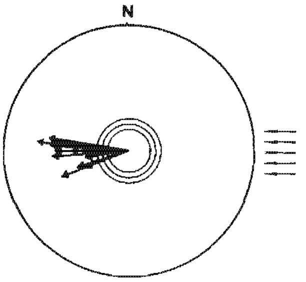

FIGURE 7: Tests with an artificial light source placed in an easterly position. The central arrows represent the mean vectors. The circles represent the levels of significance.

In the second test (Table 2B) the light (2W d.c.) was placed 1 m above the centre of the arena. Observations were made every 3 h from 7.00 am to 10.00 pm. In all tests the animals were disorientated, the length of the mean vectors never exceeding the value r = 0.15, which is not significant at the 5% level (n = 100, r (0.05) = 0.17)

TABLE 2: Indoor quantitative test.

	date	hr	ϑ	r
A	27,28F	13	274°	0.59***
		15	266°	0.59***
		17	250°	0.43***
		19	278°	0.61***
		21	276°	0.70***
		23	279°	0.64***
		01	275°	0.60***
		03	270°	0.53***
		05	254°	0.42***
		07	271°	0.26***
		09	270°	0.21**
		11	262°	0.38***
B	5 M	07	–	0.13
		10	–	0.13
		13	–	0.15
		16	–	0.14
		19	–	0.12
		22	–	0.08

Table II: Specified are: The date of the two series of tests; F - February; M - March; the time (h) of each test and the polar co-ordinates of the mean vector (v,r) are specified. Levels of significance (0.05; 0.01) are indicated with one, two and three asterisks respectively.
A: Tests with the light source in an easterly position.
B: Tests with the light source in a vertical position.

4 DISCUSSION

Some aspects of the orientation responses displayed by *P. capensis* have been clarified. The orientation behaviour appears to be a response to the environmental conditions which are associated with the South West African beaches.

Specimens used for the field tests were collected immediately prior to the experiment, thus excluding the possibility of conditioning due to captivity. Individuals treated in such a manner responded quickly and with apparent accuracy. Useful information has also been gained from the indoor tests.

In almost all tests the mean vectors were significant. Even the negative results have contributed to an understanding of the mechanisms controlling the orientation responses of this beetle. Individuals provided with a vertical light source were unable to orientate themselves. Also, the inability of beetles to locate the sun on overcast days accounts for their "lack of orientation" behaviour patterns. Animals tested near the sea, but which were prevented from using pilotage, were disorientated as they could not resort to heliotaxis.

It appears that *P. capensis* benefits from cues from the environment. Dark objects or shadows play an important role in determining the escape direction from stress sites. Thus, the skototactic behaviour is an important component of the orientation responses of *P. capensis.*

Pilotage and skototaxis are the main mechanisms used by the beetle when it has nearby cues. Tests in which the arena was placed horizontally or on an incline suggest that gravity does not influence the orientated responses.

In the absence of nearby cues the beetles respond by being negatively heliotactic. Tests carried out with individuals on the beach, either at their collection sites or further inland showed that the escape direction was opposite to the direction of sun azimuth.

The mirror and darkened sun tests confirm that the sun determines the orientated responses which *P. capensis* exhibits in the absence of nearby cues. Phototactic responses were substantiated with indoor tests, a lateral light source resulting in individuals moving in the direction opposite to the source of light and a vertical light source resulting in a disorientated response.

In some riparian arthropods, phototaxis is known to play a role in the mechanisms of orientation. In amphipods a positive heliotaxis accounts for a chronometrical solar orientation (Pardi 1957, 1960; Ercolini 1963, 1964a, 1964b). In staphylinids both astronomical orientation with compensation and negative heliotaxis occur (Ercolini and Scapini 1976). Unlike *P. provincialis* which exhibits chronometrical solar orientation lacking an associated phototactic response (Pardi 1956), *P. capensis* does not compensate for the motion of the sun and thus shows an associated phototactic behaviour pattern. This response was observed during the day-time in the field experiments and with an artificial light source both during the day- and night-time. Another interesting feature of the orientation behaviour of *P. capensis* is the tendency of the beetle to move in a north-south direction in the absence of the sun. The physiological basis for this response (non-sense orientation) is not yet understood.

5 CONCLUSION

Under natural conditions, when *P. capensis* is far from the sea, skototactic behaviour prevails. Beetles placed in an exposed position will bury or take refuge under debris or in sheltered areas. In the absence of sheltered areas they will move in a direction opposite to that of the sun.

Various mechanisms appear to influence the orientation responses of *P. capensis.* The phenomenon of several mechanisms contributing to the control of the orientation of organisms has been observed in riparian arthropods and has recently been investigated in the talitrids (Pardi and Ercolini 1984).

Comparisons between *P. provincialis* and *P. capensis* are of relevance as they are related species living in similar habitats i.e. a coastal psammic environment, both fill similar trophic niches (stranded organic debris) and have similar eco-ethological adaptations (twilight-night habits, gregariousness, ability to bury etc.).

For *P. capensis* a chronometrical solar orientation would be useless since it lives in a fog associated region. The flexibility of the orientated behaviour of this South West African species is advantageous since it enables the animal to select the most suitable direction from time to time.

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