



Orientation of *Phalerisida maculata* Kulzer (Coleoptera, Tenebrionidae) in sandy beaches of the Chilean coast Orientation of *Phalerisida maculata* in sandy beaches

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Abstract

The orientation stimuli of adult individuals of the beetle *Phalerisida maculata* Kulzer (Coleoptera, Tenebrionidae) over the beach surface, were studied at two sandy beaches of the Chilean coast approximately 1300 km apart, Apolillado (ca. 29° S) and Playa Universitaria de Mehuín (ca. 39° S). *Phalerisida maculata* did not orient by astronomic cues such as the sun and moon, nor by the terrestrial magnetic field. Both populations showed positive scototaxis, and oriented downward on slopes with dry sediments, and upwards on slopes with wet sediments. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Some coleopteran insects, talitrid amphipods and oniscoidean isopods, are typical organisms which burrow at upper shore levels of sandy beaches (see review by McLachlan and Jaramillo, 1995). When active over the beach surface, they move away from their burrowing zones, to which they return in response to various stimuli which guide the individuals in a direction perpendicular to the coastline (Scapini, 1988; Scapini

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et al., 1992; Scapini and Mezzetti, 1993). Reported stimuli for such orientational behaviour include astronomical cues (sun and moon) for the amphipods *Talitrus saltator* and *Orchestoidea corniculata* in sandy beaches of Italy (Papi and Pardi, 1953) and California respectively (Enright, 1961) and for the coleopterans *Eurynebria complanata* on beaches of the Mediterranean and Atlantic seas (Colombini et al., 1994), and *Paederus rubrothoracicus* and *Stenus bipunctatus* on the estuarine beaches of Arno River in Italy (Ercolini and Scapini, 1976). The magnetic cues have been demonstrated on *Talitrus saltator* from the Tyrrhenian and Ligurian seas (Italy) (Scapini and Quochi, 1992). Arendse (1978) also mentioned this cue as important for the orientation of the coleopteran *Tenebrio molitor*. Scapini et al. (1988) found that direction and intensity of wind as well as different light wavelengths act as positive cues in the orientation of the amphipods *Talitrus saltator* and *Orchestia mediterranea* in sandy beaches with different orientation. Landscape has been found to have a significant role in the orientation of different populations of *Talitrus saltator* from the Mediterranean sea (Ugolini et al., 1986) and British beaches (Williamson, 1951; Edwards and Naylor, 1987); also in *Orchestoidea corniculata* from southern California (Craig, 1973), and in some populations of *Eurynebria complanata* from the coast of Italy and France (Colombini et al., 1994). Orientation to slope and water content of the sediments has been found in *Talitrus saltator* from a beach of central Italy (Ercolini and Scapini, 1974), in *Orchestoidea corniculata* in California (Craig, 1973), on the freshwater amphipod *Orchestia cavimana* from the Arno River (Scapini and Bartolozzi, 1983) and in the isopod *Tylos punctatus* from a beach of Baja California (Mexico) (Hamner et al., 1968). It has been also shown that behavioural timing cues may vary according to locality (Naylor, 1989). In the intertidal midge *Clunio marinus*, for example, low latitude populations utilize moonlight cues, whereas that is not so in populations of the same species in high latitudes where, because of weather conditions, moonlight is an unreliable synchronizer (Neumann, 1978).

Phalerisida maculata Kulzer, 1954, is a tenebrionid coleopteran that lives in the upper shore levels of Chilean sandy beaches from about 18 to 41° S (Jaramillo, 1987; Jaramillo et al., 1998), where the food of this species consists of algal fragments and other organic material stranded on the beach surface (Peña, 1996). Jaramillo et al. (2000) analyzed the diurnal and nocturnal activity of *P. maculata* during summer periods in northern (ca. 29° S) and southern Chile (ca. 39° S), and found that the adults are active only at night, whereas the larvae are also active during the day. During this beach surface activity, the insects move away from their burrowing zone, to which return when the period of locomotor activity comes to an end. The objective of this study was to evaluate the role of different stimuli on the zonal recovery of the adult individuals of *P. maculata* in the same area where the studies of locomotor activity were carried out by Jaramillo et al. (2000). Thus, we studied the response of *P. maculata* in two sites of the Chilean coast to evaluate possible differences in orientation stimuli related to latitude and differences in climatic conditions, since the lower latitude site could be expected to exhibit less cloud cover and hence more reliable exposure to the sun and moon as potential astronomical cues. The beaches were very similar in terms of beach categorization and aspect (see below).

2. Material and methods

2.1. Area description

The study sites were Playa Apolillado (Apolillado hereafter) (29° 10' S, 71° 29' W) and Playa Universitaria de Mehuín (Mehuín hereafter) (39° 26' S, 73° 13' W) (Fig. 1a), about 1300 km apart. Apolillado is located closely to Martin's (1923) warm zone where the mean temperature for the warmest month varies from about 15 to 22°C, and for the coldest month from 10 to 13°C. Brattstrom and Johanssen (1983) state that the annual rainfall increases from about 110 mm at 30 °S to 760 mm at 37°S and still higher further south. According to Brattstrom and Johanssen (1983), Mehuín (ca. 39°S) lies within the rainy zone (38–56°S) of Martin (1923). The mean annual temperature at the latitude of Mehuín (ca. 39°S) is about 12.5°C. These climatic characteristics are graphically displayed by Walter's climatic diagrams (Fig. 1b). In this representation, the abscissa represents the months of the year, while the two ordinate axes represent temperature (°C) and rainfall (mm) (upper graph in Fig. 1b). Aridity (dotted area) is indicated when the curve of rainfall is located below the curve of temperature. With the exception of periods exceeding 100 mm rainfall which are black, humid periods are conventionally represented by vertical lines (di Castri and Hajek, 1976). While, Apolillado is typical of the warm zone delimited by Brattstrom and Johanssen (1983) where the arid period occurs during most of the year, Mehuín is typical of the rainy zone where there is an excess of rainfall during at least half of the year (Fig. 1b). The above description may be supplemented by the analysis of unpublished sand temperature data collected across the intertidal zone of both study sites (Fig. 1c). However, the following comparison must be viewed with caution since the data compared come from different years. Winter data collected during July show little difference between Apolillado and Mehuín (maximum of 13°C at the first site versus 11.3°C at the second). However, during spring (November), sand temperatures reach higher values at Apolillado (up to 32–33°C) than at Mehuín (up to 28.5°C). In the present comparison, late summer temperatures (March) were higher at Mehuín.

Unpublished data (Table 1) show that both beaches are quite similar in morphodynamic characteristics. According to Dean's parameter (Ω) parameter estimated for each beach (unpublished data source)

Table 1

Beach face slopes, wave characteristics, mean grain size of sands and Dean's (Ω) parameter estimated for each beach (unpublished data source)

	Apolillado		Mehuín	
	11/96	03/97	11/92	02/93
1/slope	1/21	1/21	1/20	1/31
Wave height (cm)	218.0	158.0	300.0	160.0
Wave period (s)	16.0	13.0	13.0	14.0
Mean grain size (μm)	229.0	187.0	300.0	250.0
Ω	4.7	6.0	5.6	3.5

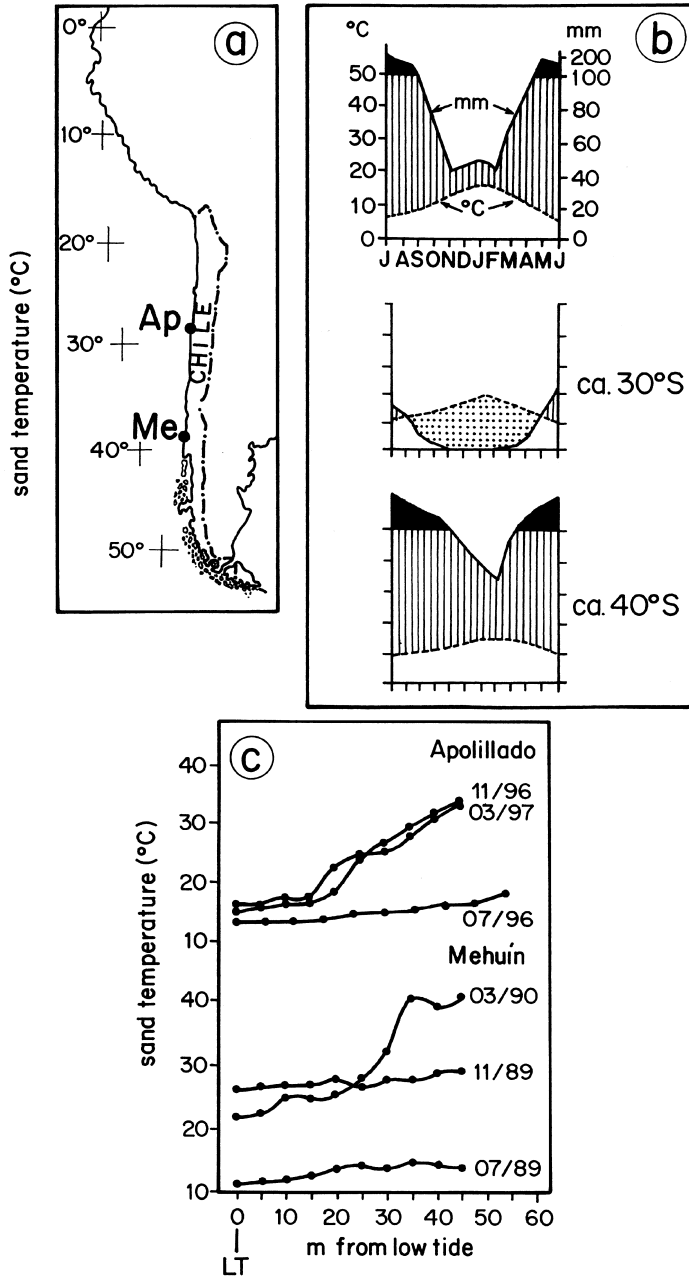


Fig. 1. a) Location of Apolillado (Ap) and Mehuín (Me) on the Chilean coast. b) Walter's climatic diagrams (temperature and rainfall) of two selected coastal localities, La Serena (ca. 30° S) and Punta Galera (ca. 40° S) closely located to the study sites (figures taken from di Castri and Hajek, 1976). The scales of this representation are shown in the inserted diagram on the upper side of Fig. 1b, c) across shore variability in sand temperature at Apolillado and Mehuín (unpublished data).

type of beaches), both beaches can be classified as intermediate (sensu Short and Wright, 1983).

2.2. Collection and maintenance of experimental animals

Experimental individuals were collected by using pitfall traps set in the intertidal zone during the night. For the majority of the experiments, insects were maintained for periods lasting 5–6 days in plastic trays filled with damp sand and kept in a constant temperature room with simulation of the natural photoperiod. These animals were fed ad libitum with the algae *Macrocystis pyrifera* (Linnaeus) C. Agardh. For some experiments (orientation to astronomic cues, see below) the collected animals were used immediately after collection. Each tested animal was used only once; i.e. after only once run the insects were returned to the beach.

2.3. Experiments

Experiments were carried out with adults in response to astronomical cues (sun and moon), earth's magnetic field, artificial landscape (scototaxis to a black strip), and slope (with differing water contents of substrate).

To evaluate the effect of sun and moon on the direction of *P. maculata*, 20 beetles were placed individually in a glass arena (26 cm diameter and 8 cm high in the centre), the base of which was divided in $36 \times 10^\circ$ sectors (Craig, 1971) (Fig. 2a). The glass container was placed on a flat surface with total exposure to the sky, and with no objects nearby to create shadows. An opaque cardboard cylinder of 5 cm height was placed around the arena, to eliminate a view of the surrounding landscape. Individual insects were placed at the centre of the container, their position being registered every 5 s until 20 records for each individual were obtained. The experiment was repeated at two different times during the day and night, to determine the direction of orientation in relation to different positions of the sun and moon. These experiments were carried out on the home beach, immediately after collection.

To study the role of the earth's magnetic field, experiments were carried out in a modified circular arena based upon the design of Scapini and Pardi (1979). The arena had two circular surfaces, one 15 cm above the other, the upper one of 40 cm of diameter and the lower one of 50 cm (Fig. 2b). Adults of *P. maculata* (about 100 beetles) were placed individually at the centre of the upper surface, over which they could move freely until reaching the edges. When falling to the lower disk the beetles were caught in one or other of 36 plastic jars (3 cm diameter and 5 cm height) arranged around the periphery. The arena was placed horizontally in a dark room, without sediment on the upper surface, and it was assumed that the only stimulus available for the individual was the earth's magnetic field, following Arendse (1978). The experiments were carried out at night (00:00–03:00 h.).

To evaluate the scototactic response of *P. maculata*, experiments were carried out in a wooden arena surrounded by a cardboard cylinder 40 cm high, painted with 180° white and black arcs (Fig. 2c). During the experiments, the position of the dark arc was varied with respect to the cardinal points. For each experiment, about 100 individuals were

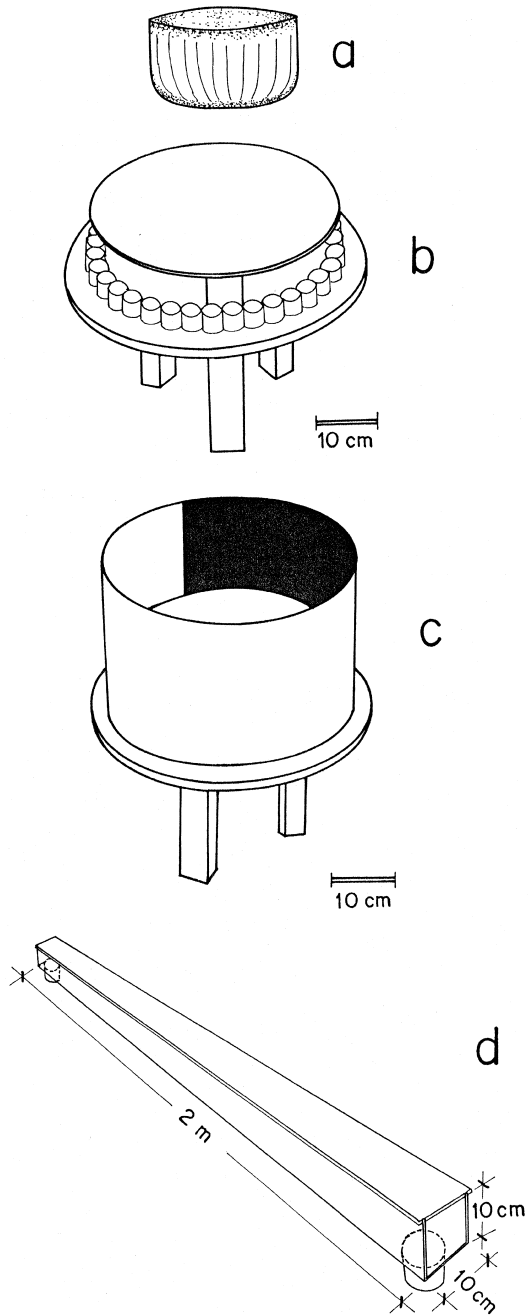


Fig. 2. Experimental arenas used in this study. (a) glass arena used to evaluate orientation to astronomical stimuli, (b) wooden arena used to analyze the role of earth magnetic field, (c) wooden arena used to study the role of an artificial landscape, (d) wooden corridor used in testing the response to slopes and water content of sediments.

observed for 15–20 min. The experiments were carried out at night (00:00–03:00 h.) in a dark room with dim red illumination from above.

To test the influence of beach slope with differing sediment water content, on the direction of *P. maculata*, a wooden corridor was used (2 m length, 10 cm width and 10 cm height) (Fig. 2d). The experiments were carried out in the laboratory under dark conditions. Different slopes, with dry sediment and wet sediments were used. Dry sediments refer to those collected from the zone above the drift line (mean water content: 2–3%, EJ unpublished data), while wet sediments refer to those collected from the middle of the retention zone (mean water content: 10–12%, EJ unpublished data). Fifty individuals were used in each experiment. The numbers of beetles aggregated at each end of the corridor were counted after 45 min, numbers buried or still walking (no more than 10%) being ignored. The experiments were carried out at night (00:00–04:00 h.) in a dark room. Experiments were carried out with slopes of 0, 1, 3, 5, 7 and 10°, first with dry sediment in the experimental corridor and then with wet sediment.

2.4. Statistical analysis

Statistical analysis of circular distributions in the arena experiments followed Zar (1996). To test for orientation to the sun and moon, using data from the glass bowl apparatus, the mean angle and vector length for each individual was determined from the 20 recorded directions, then the second order mean angle and vector length was calculated from these data for the all individuals in the experiment, using circular statistical techniques described by Zar (1996). For earth's magnetic field and scototaxis, the average angle (a) was calculated and the dispersion of the data (r) around this angle (based on the frequency allocation obtained by the Rayleigh test (z)) was used to calculate the probability that the studied population presented a circular uniform distribution. The χ^2 test was used (Siegel, 1956) for analysis of results obtained using the experimental corridor.

3. Results

Fig. 3 illustrates the escape directions of *P. maculata* in relation to two positions of the sun and moon at each locality studied. In all cases the escape directions were random, indicating no fixed angle orientation to either the sun or the moon, and no time-compensated escape direction irrespective of the positions of the sun and moon.

Fig. 4 presents the pooled escape direction for all *P. maculata* tested for orientation to the earth's magnetic field at the two study localities. The results obtained with both beetle populations, exhibit uniform circular distributions ($P > 0.05$), indicating no significant effect of the earth magnetic field on orientation.

Escape directions of *P. maculata* in response to scototactic cues are illustrated in Fig. 5. Irrespective of the position of the black 180° arc of the cardboard at both localities, the individuals showed a statistically significant scototactic response towards the black boundary in each of its four positions at each locality.

The results of experiments testing whether *P. maculata* moved up and down sloping

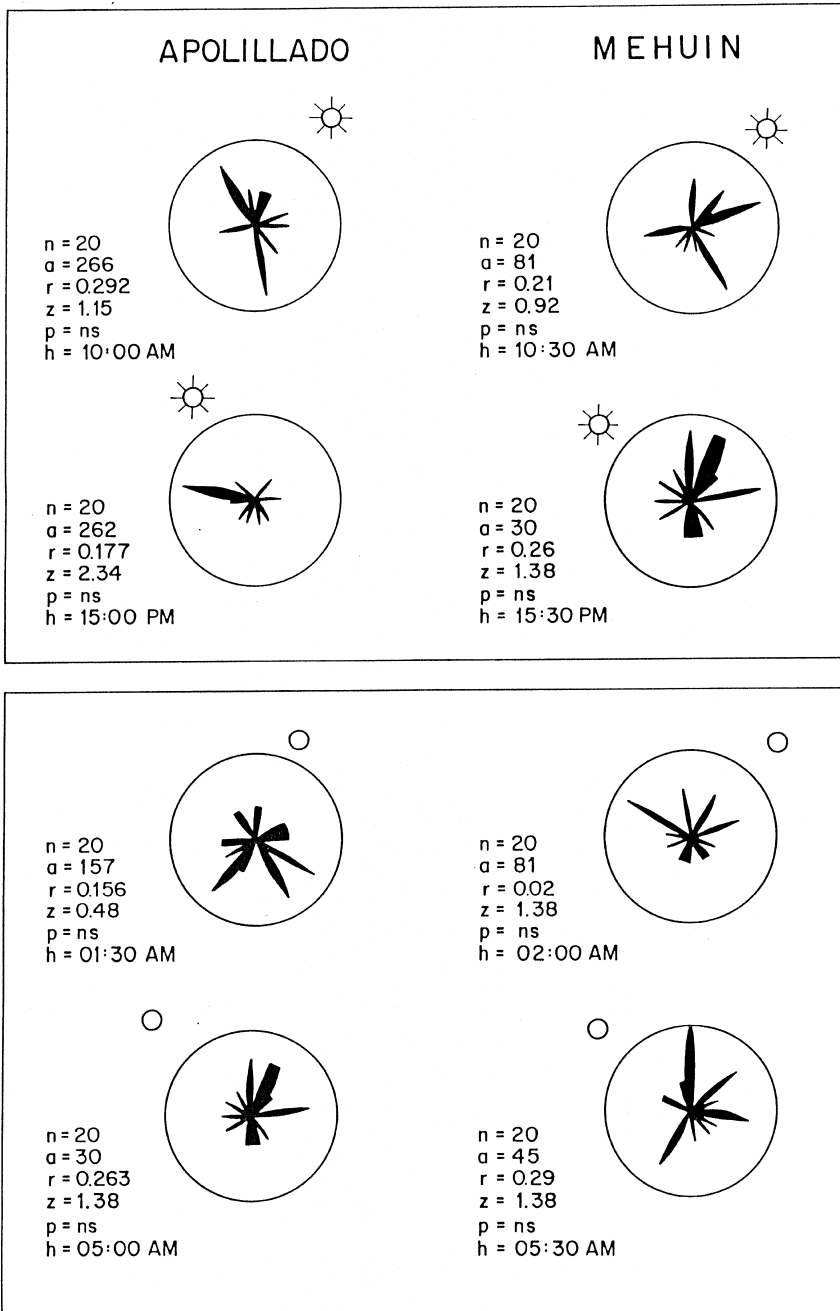


Fig. 3. Testing orientation of *P. maculata* in arenas on the shore of Apolillado and Mehuín with respect to the position of the sun (upper box) and moon (lower box). n : number of individuals tested, α : average angle, r : resulting vector, z : Rayleigh's test, $P = ns$ or $P > 0.05$. The position of the north is in the upper centre of the perimeter of each arena, while the sea was located at the left side of each arena.

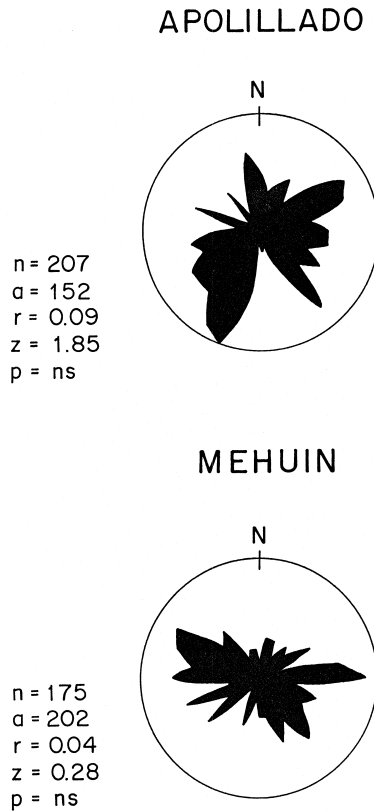


Fig. 4. Testing orientation of *P. maculata* of Apolillado and Mehuín with respect to the earth's magnetic field. N, position of the magnetic north; *n*, number of individuals tested; *a*, average angle; *r*, resulting vector; *z*, Rayleigh's test; *P* = ns or *P* > 0.05.

substrates of wet or dry sand (see Materials and methods) are illustrated in Fig. 6. On dry sand, beetles from Apolillado and Mehuin showed no significant orientation on slopes less than 3°. However, on steeper slopes, up to the maximum of 10° tested, all beetles from both areas moved significantly in a downward direction. In contrast, the opposite was found when wet sediments were used; on slopes equal and greater than 1° (Apolillado) and equal and greater than 3° (Mehuín), *P. maculata* moved significantly in an upward direction.

4. Discussion

The results of this study, show that of the four stimuli tested to evaluate their role in the orientation of *P. maculata*, only a 180° black arc (artificial landscape) and slope together with water content of sediments, were effective.

The negative results of the experiments carried out with astronomical stimuli (sun and

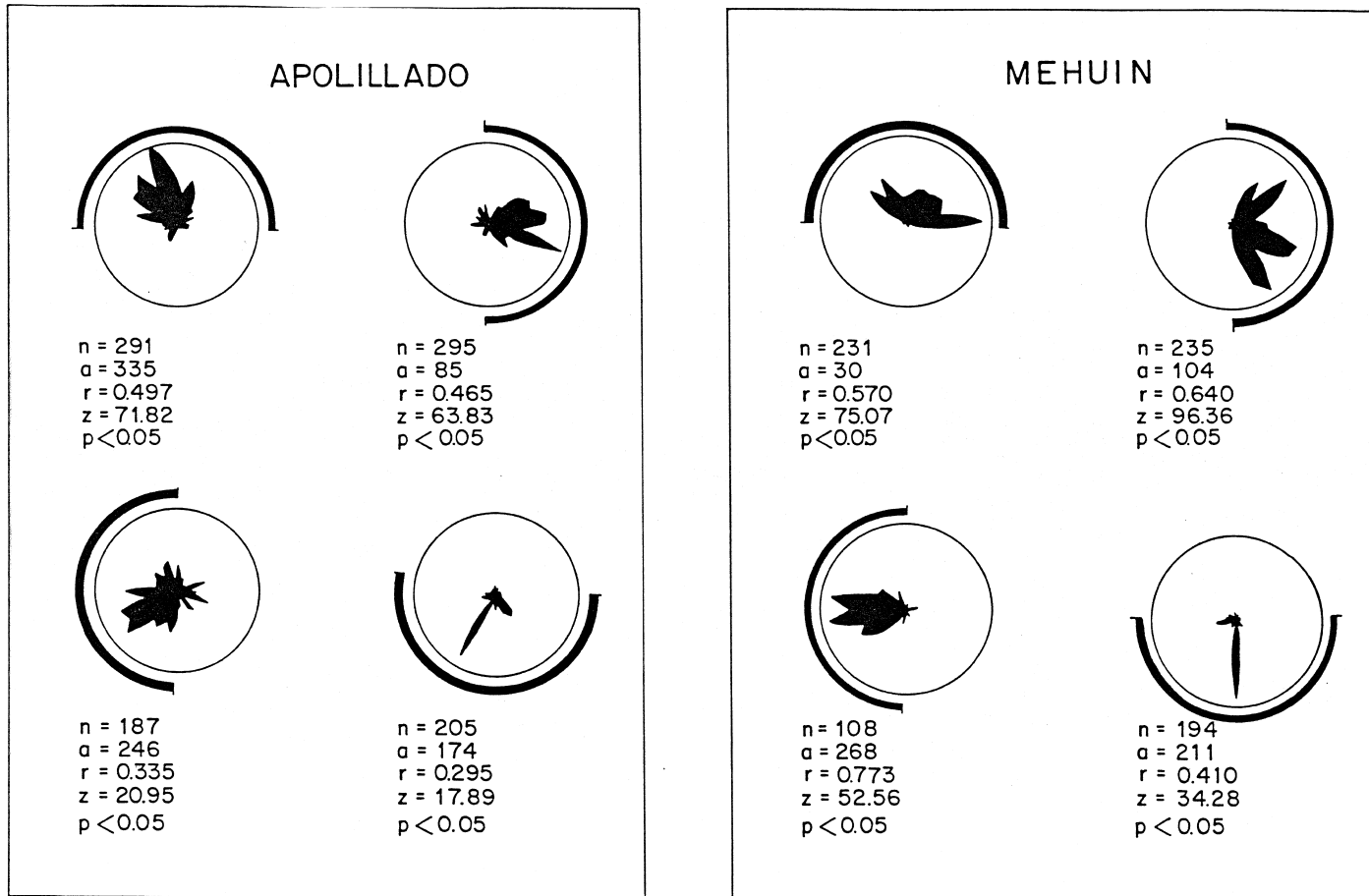


Fig. 5. Orientation of adults of *P. maculata* of Apolillado and Mehuín with respect to artificial landscape. The external line shows the position of the dark part of the landscape during testing. *n*, number of individuals tested; *a*, average angle; *r*, resulting vector; *z*, Rayleigh's test, $P = \text{ns}$ or $P > 0.05$. The position of the north is in the upper centre of the perimeter of each arena, while the sea was located at the left side of each arena.

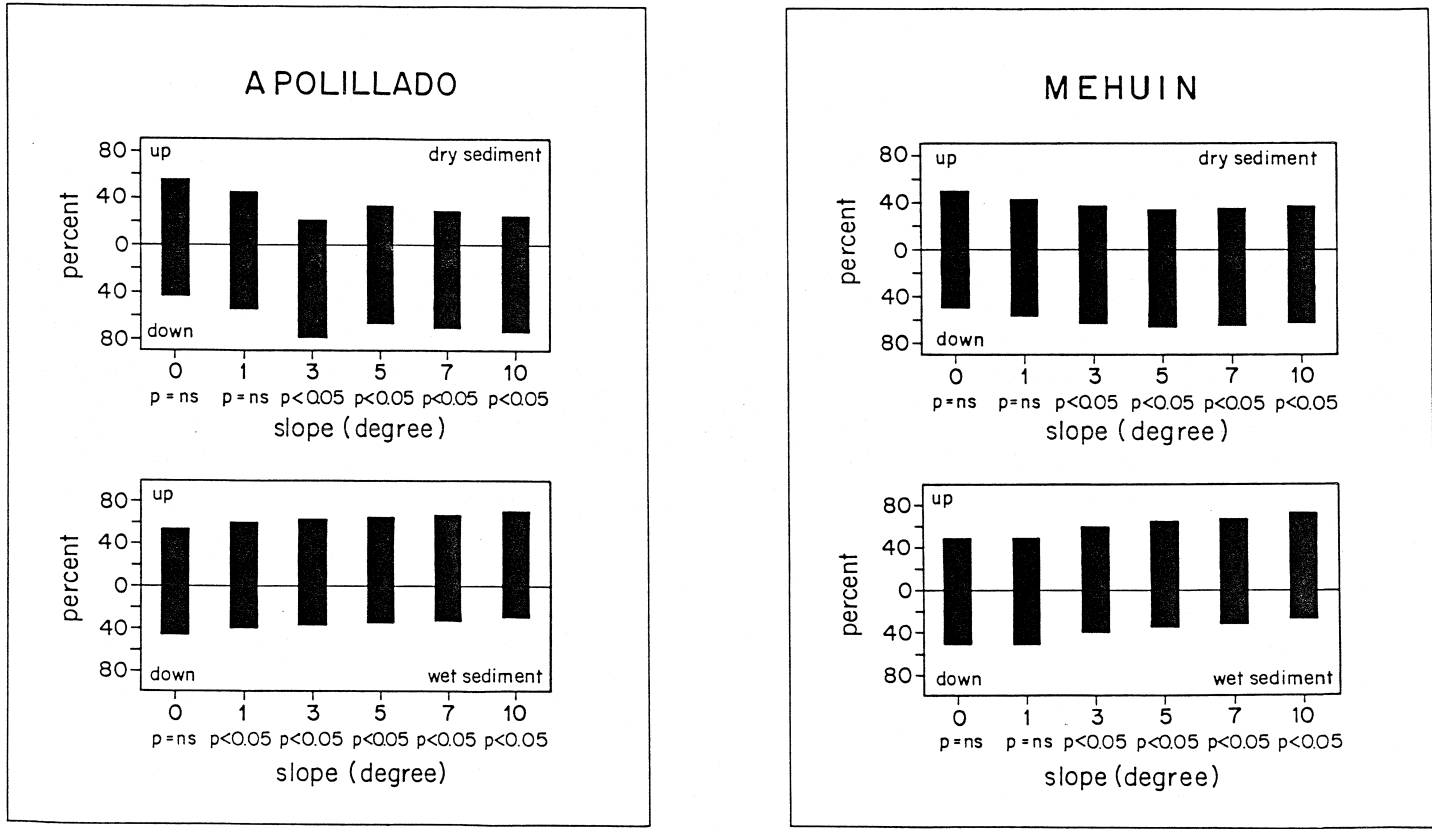


Fig. 6. Testing orientation of adults of *P. maculata* of Apollillado and Mehuin with respect to slope and water content of the sediment. The experimental procedure is described in the text and the distributions on each slope at the end of the each test are compared by the χ^2 square test.

moon) conflict with those reported for some other high shore, sandy beach organisms (Papi and Pardi, 1953; Pardi, 1954; Papi, 1960; Enright, 1961; Herrnkind, 1972; Ercolini and Scapini, 1976; Colombini et al., 1994.) However, present findings are similar to those found with the amphipods *Orchestoidea corniculata* from Californian beaches (Craig, 1971), *Orchestia cavimana* from river shores in Italy (Scapini and Bartolozzi, 1983), *Orchestoidea tuberculata* from Chilean beaches (Kennedy, 1997), the isopod *Tylos punctatus* from Californian beaches (Hamner et al., 1968) and the coleopterans *Heterocercus fenestratus* (Scapini et al., 1993) and *Stenus bipunctatus* in Italy (Ercolini and Scapini, 1976). Indeed, for nocturnal species, several authors have questioned the role of sun as a directional stimulus (Hamner et al., 1968; Herrnkind, 1983) and have pointed out the weather-related unreliability of moonlight cues, particularly in high latitudes (Neumann, 1978; Naylor, 1989). In addition, Scapini et al. (1996), have emphasized for talitrid amphipods on steep beach slopes and dunefields that landscape orientation mechanisms may override astronomical cues.

Following reports of magnetic field orientation in the sandhopper *Talitrus saltator* by Arendse (1978, 1980) and Arendse and Kruyswijk (1981), several investigations have sought unsuccessfully for evidence of such orientation mechanisms in talitrids, namely in *Talitrus saltator* (Naylor, 1989), *Talorchestia deshayesei* (Scapini and Quochi, 1992) and *Talorchestia martensii* (Scapini and Ercolini, 1973). The conflict in these observations remains to be resolved (Scapini and Quochi, 1992), but present data for another high shore invertebrate suggest that perception of the earth's magnetic field is not involved in orientation behaviour of this species.

The two studied populations of *P. maculata* showed statistically significant scototaxis towards a black arc of an artificial arena irrespective of the compass orientation of that arc. This conforms with reports by other workers of such orientation in a number of sand-beach organisms. It is possible, as has been previously suggested that the response to the black arc is related to response to the relatively higher landscape at the back of the beach. The importance of landscape as a directional cue in the orientation of sandy beaches organisms was initially emphasized by Williamson (1951, 1954) who studied the amphipod *Talitrus saltator*. Later, similar findings were reported in the amphipods *Orchestoidea corniculata* (Hartwick, 1976) and in *Talitrus saltator* (Scapini and Pardi, 1979; Ugolini et al., 1986) and the insect *Eurynebria complanata* (Colombini et al., 1994). However, Edwards and Naylor (1987) having confirmed that *Talitrus saltator* was indeed responsive to dark areas of artificial landscapes by day, found the amphipod to be indifferent to such landscapes at night. Those authors suggested that phasic changes in orientational responses are involved in daily up-and-down shore migrations of this species, as was further confirmed by Mezzetti et al. (1994).

Consistent movement down-slope on dry sand and up-slope on wet sand in both populations of *P. maculata* studied here is similar to that found in the amphipods *Orchestoidea californiana* (Craig, 1971), *Talitrus saltator* (Ercolini and Scapini, 1974; Scapini et al., 1996), *Orchestia cavimana* (Scapini and Bartolozzi, 1983) and *Orchestoidea tuberculata* (Kennedy, 1997). The explanation for this type of behaviour is that this stimulus allows the individual to determine the direction of its burrowing sites from the inclination of the substrate and the water content of the sediment.

In conclusion, the results show that of the possible cues studied, only the scototactic

response and beach slope were important in the orientational behaviour of the two populations of *P. maculata* studied. Astronomical cues were not important, even though the two beaches studied were 1300 km apart in a north–south direction and would be expected to experience differences in the predictability of exposure to the sun and moon. Both beaches were, however, in localities with pronounced beach slopes and where dunes or cliffs offered pronounced landscape cues upshore. As suggested by Scapini et al. (1996) orientation to landscape and beachslope may be enhanced by learning in such localities, contrasting with the greater emphasis on astronomical cues in localities where local topography is relatively featureless.

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