# Learning in Zonal Orientation of Sandhoppers

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## INTRODUCTION

It has long been known that amphipods living on sandy shores use a sky compass (the sun or moon) to find their way back to the damp belt of the splash zone (Pardi and Papi, 1952, 1953; Papi and Pardi, 1953). It has also been proved that the mechanism governing solar orientation in mediterranean sandhoppers is innate, and that these sandhoppers inherit the ability to assume a specific escape direction perpendicular to their own particular shore (Pardi et al., 1958; Pardi, 1960; see also Pardi and Ercolini, 1986 for a review).

More recently, different populations of sandhoppers living along a continuous stretch of a curved sandy coastline several kilometres long were studied to analyse the precision of their astronomical orientation (Scapini et al., 1985). Results confirm that the sandhoppers inherit the escape direction relative to their own population. Individuals born in the laboratory from adults collected from different points along the same coastal arc showed significantly different orientation, and their mean direction satisfactorily agreed with the expected theoretical escape direction (TED) of the sea facing the point where their parents were collected.

However, very few studies have been carried out to investigate whether sandhoppers can adjust their inherited orientation if the sea-land axis changes abruptly in space or time (Ugolini et al., 1984a; Ugolini and Scapini, 1987), and whether they can learn a new, ecologically efficient escape direction to suit the new conditions on their home beach or on another they might reach through active or passive displacement.

## 1. MODIFICATION IN ORIENTATION ON THE HOME BEACH

It has often been noticed (Pardi, 1960; Scapini et al., 1985; Scapini, 1986a; Ugolini and Scapini, 1987), that on their home beach sandhoppers can improve their seaward orientation, probably with the help of previous experience they have gained on their daily excursions up and down the Y axis at dusk and dawn, (Geppetti and Tongiorgi, 1967a;b).

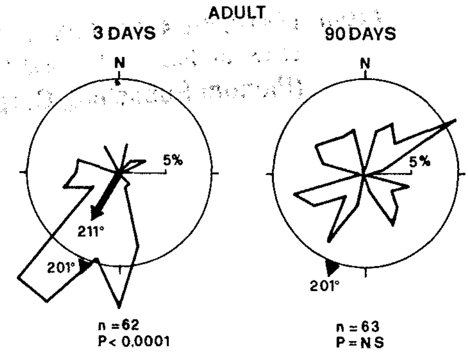


Fig. 1. Effect of captivity (3-90 days) on solar orientation. Black triangles outside the distributions represent TED; arrows, mean vectors (circle radius corresponds to mean vector length=1); n, sample size; P, probability level for V test (see Batschelet, 1981). (From Scapini; 1986 redrawn).

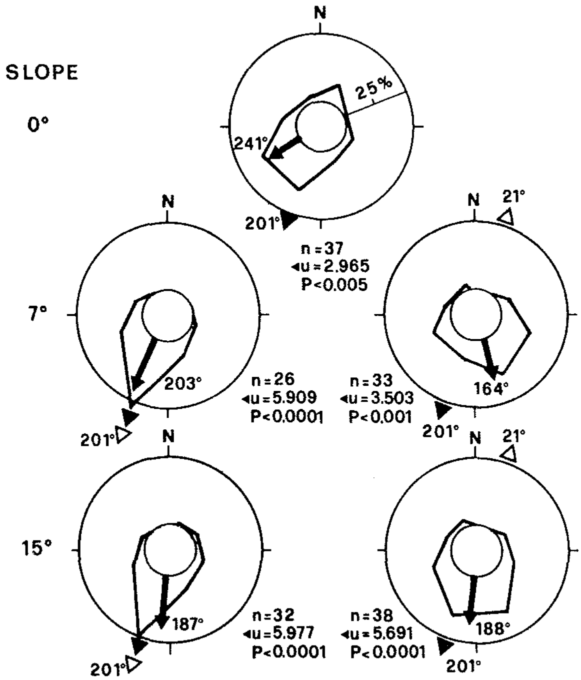


Fig. 2. Influence of ground slope on solar orientation. Dry substratum. Top distribution, controls (slope=0°); left, concordant stimuli; right discordant stimuli. Black triangles, TED for solar orientation; white triangles, TED for slope orientation. The V test (u) has been calculated assuming as expected direction the TED for solar orientation. For further explanations see Fig. 1. (From Ercolini and Scapini, 1974 redrawn).

Table 1. Mean vector length and difference (in absolute value) between TED and mean angle for expert adults and their laboratory born offsprings (inexpert). S, Scapini; U, Ugolini. See text for further explanations.

| | MEAN VECTOR LENGTH | | $\lvert\Delta\alpha\rvert$ | | REFERENCE |
|---|---|---|---|---|---|
| TED | Expert | Inexpert | Expert | Inexpert | |
| 90 | 0.725 | 0.475 | 18 | 33 | S et al. 1987 |
| 160 | 0.844 | 0.586 | 6 | 7 | S 1986b |
| 160 | 0.769 | 0.639 | 2 | 7 | S et al. 1985 |
| 160 | 0.692 | 0.617 | 4 | 10 | U unpubbl. |
| 185 | 0.502 | 0.371 | 5 | 17 | S et al. 1985 |
| 200 | 0.750 | 0.478 | 16 | 3 | S et al. 1985 |
| 201 | 0.747 | 0.677 | 9 | 13 | S et al. 1985 |
| 201 | 0.640 | 0.490 | 10 | 18 | S 1986b |
| 211 | 0.513 | 0.406 | 1 | 16 | S et al. 1985 |
| 245 | 0.533 | 0.407 | 14 | 23 | S et al. 1985 |
| 245 | 0.499 | 0.355 | 17 | 21 | U & S 1987 |
| 260 | 0.557 | 0.210 | 5 | 34 | U & S 1987 |
| 264 | 0.625 | 0.400 | 17 | 9 | S et al. 1987 |
| 264 | 0.657 | 0.389 | 9 | 15 | U & S 1987 |
| 265 | 0.448 | 0.153 | 4 | 16 | U unpubbl. |
| 268 | 0.763 | 0.407 | 12 | 27 | U & S 1987 |
| 268 | 0.581 | 0.413 | 32 | 64 | U unpubbl. |
| 280 | 0.162 | 0.607 | 11 | 40 | S et al. 1985 |
| 280 | 0.661 | 0.361 | 10 | 16 | U & S 1987 |
| 285 | 0.622 | 0.144 | 2 | 8 | S 1986b |
| 285 | 0.650 | 0.376 | 29 | 5 | S et al. 1985 |
| 335 | 0.494 | 0.311 | 36 | 70 | S et al. 1985 |

Results from a number of experiments carried in Florence (and therefore considerably far from the sea) from 1979 to 1986 were compared. The experiments consisted in releasing the sandhoppers in a circular arena (20cm in radius) fitted with a screen to hide the landscape from view and shield them from the wind. The resultant mean vector length and angles of distribution were considered for experienced adult sandhoppers and for their offspring born in the laboratory (Tab. 1). 14 different populations from beaches relatively constant in direction were tested in a total of 22 experiments. The experienced adults proved to be far better clustered round their TED than their inexperienced young in 21 experiments out of 22 ($P<0.001$, $\chi^2$ test) and their mean angles were nearer their TED than those of their offspring in 19 experiments ($P<0.001$, $\chi^2$ test). Since the mechanism behind solar orientation in sandhoppers does not seem to develop with age (Scapini, 1986b), the difference in orientation can only be explained by experience. Previous experiments demonstrated how the length of time spent in captivity can also affect orientation in sandhoppers (Ercolini, 1964; Scapini, 1986a). After 3 months captivity in tanks containing uniformly damp sand and under a LD cycle in phase with and corresponding to the natural cycle, sandhoppers proved to be far more dispersed on release than freshly collected specimens (Fig. 1).

## 2. MODIFICATION IN ORIENTATION BASED ON LOCAL, NON-CELESTIAL FACTORS

The sandhoppers may be able to adjust their orientation by referring to local cues typical of their own collecting point, as well as by aid of previous experience from their daily excursions.

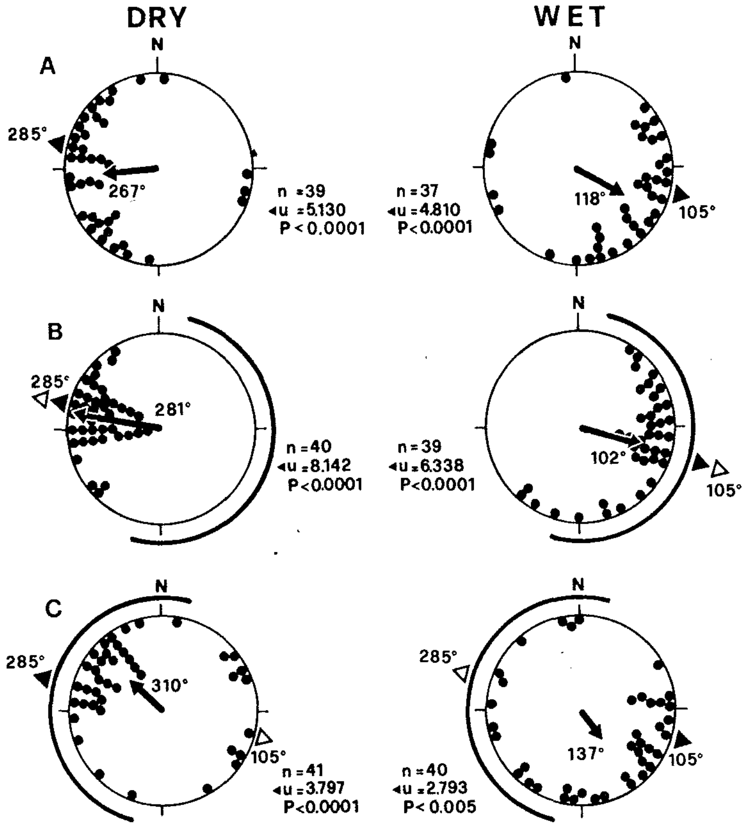


Fig. 3. Influence of sight of artificial landscape (semicircles outside the distributions) on solar orientation. Left, experiments on dry substratum; right, experiments on wet substratum. A, controls; B, concordant stimuli; C, discordant stimuli; white triangles, TED for landscape orientation. For further explanations see Fig. 1.

2.1. Slope (Fig. 2)

In the absence of any other orientating stimuli, sandhoppers will use the slope of the substratum to find their way back to their desired spot, as Craig (1973) proved in *Orchestoidea corniculata*, and Ercolini and Scapini (1974) in *Talitrus saltator*.

Dehydrated sandhoppers tested in the dark will always head for the lower end of a tilted box, but will opt for the higher end if the substratum is wet. In the circular arena under the sun, they show a marked improvement in orientation if the arena slopes towards the TED (Fig. 2 left). If the arena slopes in the opposite direction to the TED (Fig. 2 right) their orientation is worse, although they are still directed towards the sea.

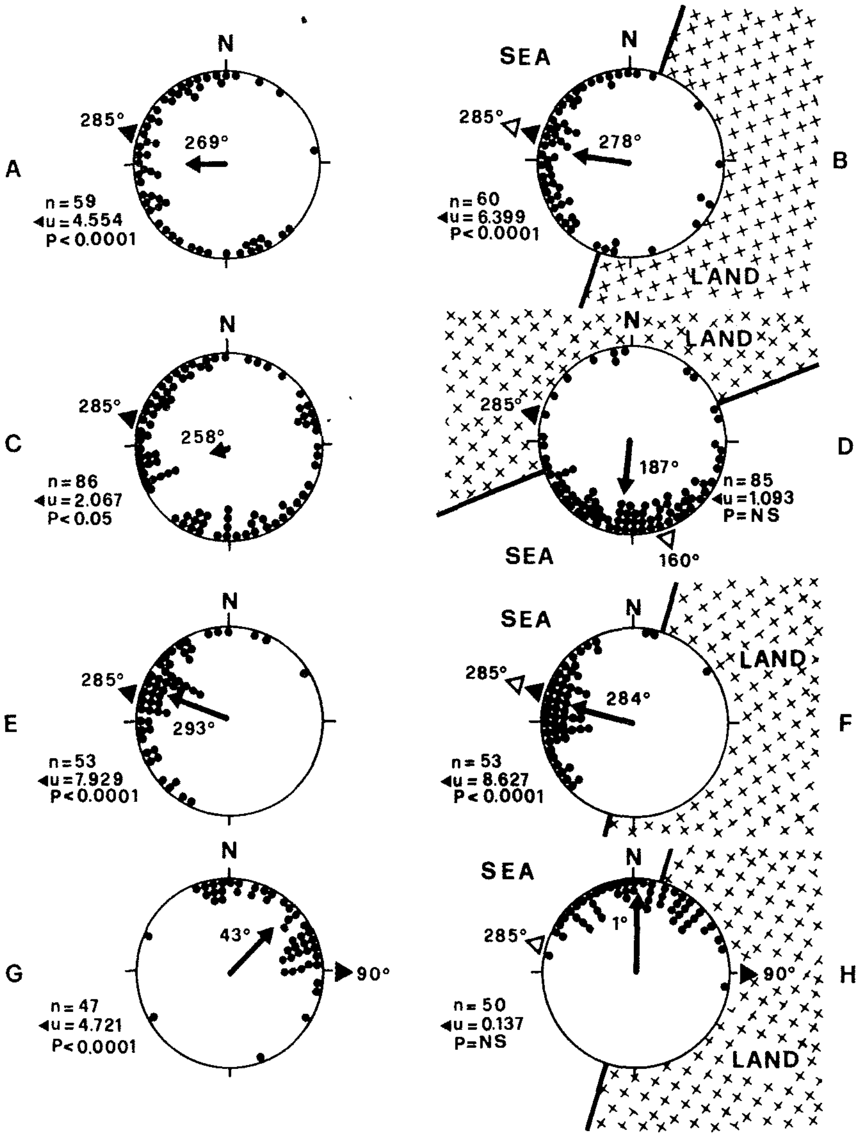


Fig. 4. Influence of sight of natural landscape on solar orientation. A and B, experiments on home beach in arena with and without screen, respectively. C and D, experiments on differently orientated beach, with and without screen, respectively. E-H, experiments on home beach using controls (E,F) and clock-shifted individuals (G,H), with screen (E,G) and without screen (F,H). For further explanations see Fig. 1. (From Ugolini et al., 1986 redrawn).

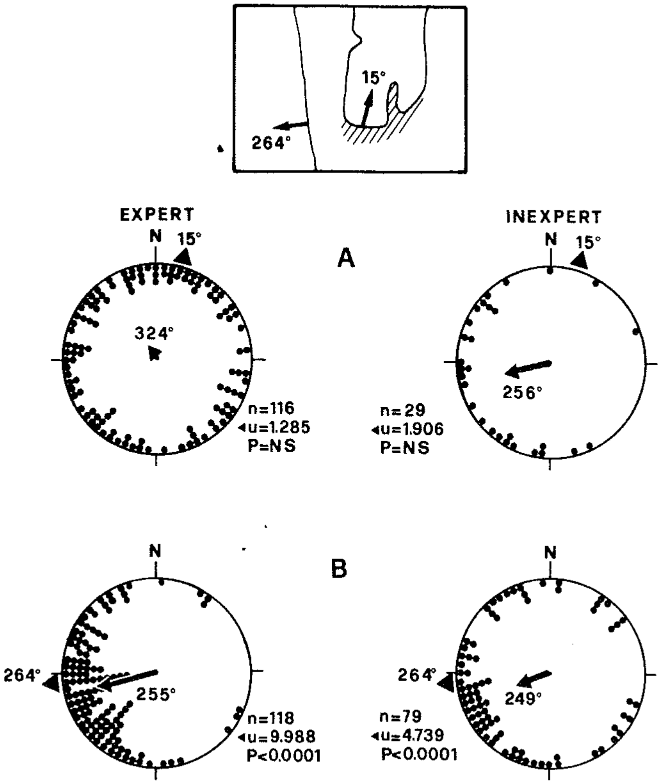


Fig. 5. Solar orientation in experienced adults and inexperienced young, tested in the arena away from the sea. TED=15°. A, individuals from the lagoon; B, individuals from the seashore. A schema of the locality of collecting is also given. For further explanations see Fig. 1. (From Ugolini and Scapini, 1987 redrawn).

## 2.2. Landscape (Figs. 3,4)

It has been proved (Williamson, 1954; Hartwick, 1976; Pardi and Scapini, 1979; Scapini and Ugolini, 1981; Ugolini et al., 1984b; 1986; Edwards and Naylor, 1987) that the view of the landscape has a profound effect on orientation in sandhoppers, both on precision and on the number of individuals clustered around their TED. This applies equally well to the natural landscape as to an artificial one constructed out of black cardboard shapes occupying 180 of the horizon round the arena used in the experiments (Ugolini et al., 1986). If the sun and the landscape convey the same directional information, the sandhoppers show a marked improvement in orientation - towards the sea on a dry substrate (Fig. 3B left), towards the land on a wet one (Fig. 3B right). If the two stimuli conflict each other (with the artificial landscape placed in the hemicycle of the sea), orientation in the sandhoppers deteriorates (Fig. 3C).

Two experiments were carried out to test how sandhoppers react when the natural landscape seems to contradict solar information: 1) sandhoppers were released on their home beach, in the screened arena with the landscape hidden from view (Fig. 4A) and in the unscreened arena

(Fig. 4B): view of the landscape improves orientation. A second batch from the same population was released at exactly the same time under the same conditions on a strange shore with a different geographical orientation (Figs. 4C,D): whilst the controls are still orientated in the direction of their home beach TED (Fig 4C), the experimentals in the unscreened arena turn towards the TED of the alien shore (Fig. 4D).

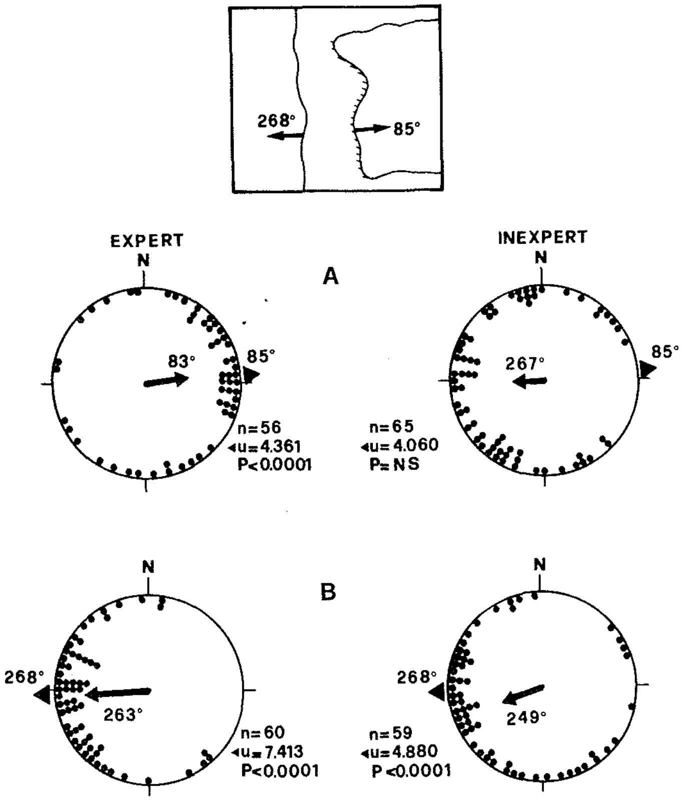


Fig. 6. Solar orientation in experienced adults and inexperienced young, tested in the arena away from the sea. TED=85°. For further explanations see Fig. 5.

2) Controls and experimentals (clock-shifted back 9 hours) were released on their home beach in the screened and unscreened arena. The controls in the screened arena are well clustered around their TED (Fig. 4E) but orientation improved in the arena without a screen (Fig. 4F). The mean vector of the experimental screened sandhoppers points towards the TED (Fig.4G), whilst without the screen points halfway between the TED and the direction indicated by the landscape (Fig. 4H).

Even when T. saltator is heading seawards it can still to see the dune and the retrodunal vegetation on account of its wide visual field (146 for each eye, Beugnon et al. 1987).

## 3. MODIFICATION IN ORIENTATION AFTER NATURAL DISPLACEMENT TO A DIFFERENT BEACH

After active displacement (daily migrations in search for food, Geppetti and Tongiorgi, 1967a;b), or passive displacement (e.g. caused by sea storms or currents), some individuals may find themselves on a differently orientated beach from the first. In these circumstances, it is of vital importance for the individual to adapt its own orientation to the new sea-land axis. To investigate this possibility, a series of experiments was carried out in the summer of 1985 and 1986 on two populations of sandhoppers living on the banks of lagoons behind the sand dunes. The populations living on the seashore immediately in front of the dunes, where the lagoon population probably originally came from, were taken as controls. Releases were made 1) in the screened arena at the collecting points, 2) away from the sea (in Florence), and 3) directly onto the sand at the collecting points.

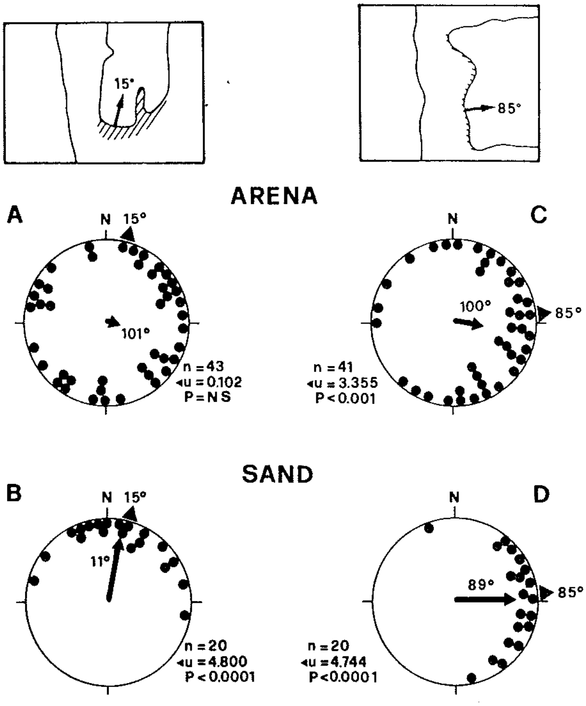


Fig. 7. Solar orientation in adults from the lagoons. A and C, tests in screened arena; B and D, releases on sand at collecting points. For further explanations see Fig. 1.

The experienced adults from the banks of the lagoon (TED=15°) near the River Serchio Estuary (Province of Pisa) (Fig. 5A left) are dispersed, but the sandhoppers from the sea shore immediately in front of the lagoon are well clustered round their TED (=264°) (Fig. 5B). The inexpert young born in the laboratory from both populations (Fig. 5 right) are clustered round the TED corresponding to the seashore. However, it must be stressed that this lagoon has a wide damp belt (approximately 5m wide along the Y axis) (Fig. 5 top) and that its banks are not stable throughout the year. A survey in November, 1986

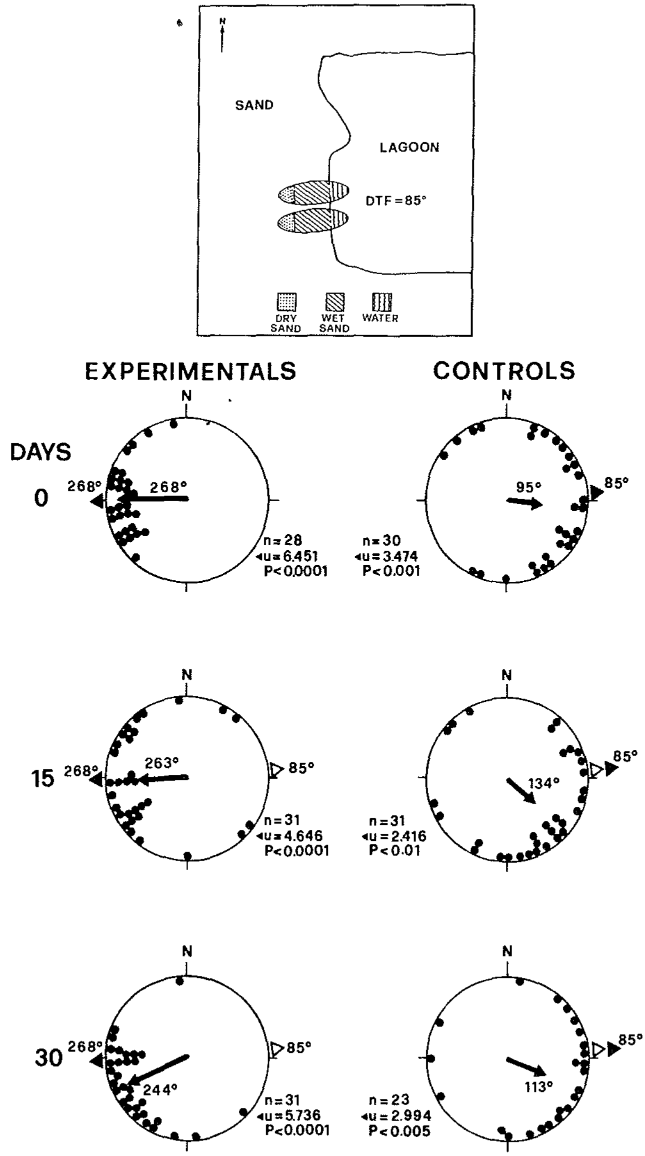


Fig. 8. Learning of new TED in adults. Experimentals, individuals collected on the seashore; controls, individuals collected on the lagoon banks. Left, length of time spent in the tanks on the lagoon shore. White triangles, new TED. The V test is calculated referring to the TED of home beach. Top, schematic representation of the tanks on the bank of the lagoon with TED=85°. For further explanations see text and Fig. 1.

found that the River Serchio had completely destroyed the banks of the lagoon at that point.

Sandhoppers from another small lagoon behind the dunes near Grosseto, South Tuscany, tested in Florence (Fig. 6A, left) showed a statistically significant clustering round the lagoon TED (=85°), whilst their laboratory born offspring were still orientated towards the sea (Fig. 6A, right). In the controls (TED=268°, Fig. 6B), both the adults and their laboratory born offspring showed a seaward orientation. The banks of this lagoon do not fluctuate with the seasons, and the damp belt is narrow (approximately 1m wide) (Fig. 6 top).

When the lagoon sandhoppers were released in the arena at the collecting points (Fig. 7A,C), results were similar to those of the previous experiments, but when they were released directly onto the sand (Fig. 7B,D), those with TED=15° pointed in a mean direction corresponding to the TED of the collecting point, whilst those with TED=85° improved their orientation.

## 4. THE ABILITY TO LEARN A NEW TED

Experiments were carried out in nature in the summer of 1986. The population of sandhoppers living by the lagoon with a TED=85° were used as controls, and the population from the sea shore in front of the dunes (TED=268°) as experimentals. Two lots (experimentals and controls) were put separately into white plexiglass tanks (140x40x30 cm). The tanks (Fig. 8 top) were placed on the banks of the lagoon with the long axis perpendicular to the shore, keeping to the natural slope of the ground; one end of the tank always contained water. The adults were tested in the screened arena before they were put into the tank, then again after they had been inside for approximately 15 and 30 days. The offspring born in the tanks were tested when they reached about one week of age.

The results (Fig. 8) show that adult sandhoppers do not alter their original orientation. After about one month in the tank, the difference between the mean angle and the TED was only 24° in the experimentals, and clustering remained practically the same (Fig. 8 left). The control adults showed a constant escape direction and clustering, in the direction of the water of the lagoon (Fig. 8 right).

When the sandhoppers were made to flee landwards in their typical escape reaction, by stirring the sand in the tank, and the number of individuals counted heading up the slope (towards the land behind the lagoon) and those heading down the slope (towards the land backing the sea = water in the lagoon), the experimentals which had only been in the tank for one hour were seen to move significantly downwards (i.e. in the direction of the land on the seashore), whilst the controls opted for the landward direction behind the lagoon (Fig. 9 top). The difference between experimentals and controls proved to be statistically significant. After 10 days in the tank, the experimentals behaved in more or less the same way as the controls and headed towards the land behind the lagoon (Fig. 9 centre). After about one month they still behaved in the same way (Fig. 9 bottom).

The young sandhoppers born in the tanks from the experimentals and tested in the arena, turned in a different mean direction from their parents, pointing towards the lagoon TED and not that of the seashore (Fig. 10 left). The offspring born in the tanks from lagoon-dwelling controls were also significantly clustered round the lagoon TED (Fig. 10 right), and not round the seashore TED as those born in the laboratory were (see Fig. 6A, right).

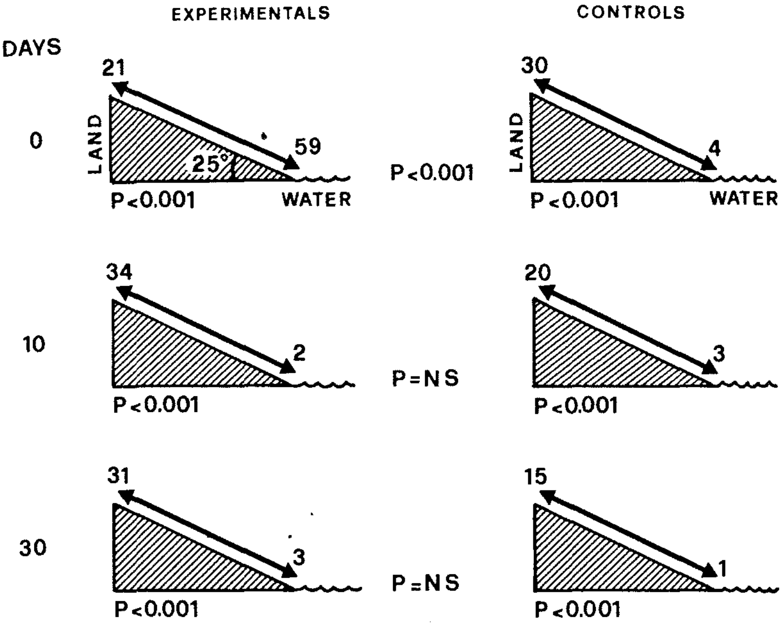


Fig. 9. Escape reaction in adults provoked by stirring the sand in the tanks. The numbers over the arrows represent the number of sandhoppers moving up (land) or down (water) in the tanks. Left, time spent in the tanks. Comparisons between frequencies were made with $X^2$ test (probability level, P, is also given). See text for further explanations.

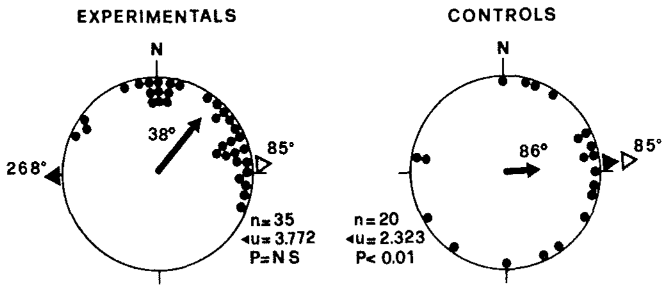


Fig. 10. Learning of new TED in young born in the tanks (about one week old). For further explanations see Figs. 1,9.

## CONCLUSIONS

Results lead to the conclusion that the sandhoppers can use local, non-celestial cues (landscape and slope of the substratum) to improve their solar orientation along the sea-land axis, regardless of any learning processes (Figs. 2, 3, 4 and 7). They also learn how to perfect their sun compass mechanism when they refer to these cues. In fact young sandhoppers born in the laboratory are significantly worse in their solar orientation than their experienced parents (Tab. 1), and experienced adults kept in captivity for a long time are more dispersed on release than freshly gathered specimens (Fig. 1).

Depending on local physical conditions, the sandhoppers can also drastically change their original orientation through the learning process.

On a wide damp belt (which decreases motivation to move rapidly up and down the y axis), or where the shore fluctuates in time and the sandhoppers are not always present, the sandhoppers learn not to rely on their sun compass (Fig. 5A, 7A), but to steer exclusively by local, non celestial cues (Fig. 7C). If the sandhoppers come from a narrow damp belt on a stable shore, they can learn to find their new flight direction with the aid of the sun compass (Fig. 6A).

As for their learning ability, first results seem to indicate that adult sandhoppers cannot learn to adjust their sun compass to new situations (Fig. 9). They learn to find their new, ecologically efficient flight direction by referring to local cues (Fig. 10). The ability to adjust the sun compass to the new direction of the sea seems to be a prerogative of young sandhoppers (Fig. 11).

The learning ability in young Talitrus may at first appear redundant with the fact that escape direction is genetically controlled, which should be sufficient in itself to guarantee a mean orientation in line with their own TED, even for populations living several kilometres apart on the same stretch of curved sandy coast line (Scapini et al., 1985). Local, non-celestial cues and compass references would be coadjutant factors in solar orientation, or could substitute the sun-compass if the need arises. However, it must be remembered that 1) the sun still remains the most important factor in orientation (see also Pardi and Ercolini, 1986), and since it is totally unaffected by local changes it can always be relied upon; and 2) the boundary line between water and the land is the least stable of all the ecotonal systems (see Hernkind, 1972; 1983; Vannini and Chelazzi, 1985). Therefore it is advantageous for the sandhoppers to be able to learn how to adapt the daily cycle of variation in their orientation angle even on their own home beach. Moreover, it has already been demonstrated that other riparian arthropods also have this capacity (wolf spiders, Papi et al., 1957; Tongiorgi, 1961; Papi and Tongiorgi, 1963; rove beetles, Ercolini and Badino, 1961; crickets, Beugnon, 1986), and it is probably shared with Dermaptera (Labidura riparia) and a fresh-water shrimp (Palaemonetes sp.) (Ugolini unpublished data). The learnt component in solar orientation is therefore probably more developed in animals living on shores where the coast line is subject to a sudden change in direction, and in rapidly moving animals which could often find themselves on differently orientated shores.

If future experiments prove that only young sandhoppers can adjust their sun compass to a new escape direction, then this ability would seem to be restricted to a limited period in the life of the sandhopper when it is least resistent to dehydration. Adult sandhoppers which actively or passively find themselves on a alien shore could still survive by referring to the landscape, ground slope, or some other orientating factor such as the earth's magnetic field (Arendse, 1980; Arendse and Kruyswijk, 1981) to maintain their zone. Their offsping, on the other hand, could learn to use their sun compass regardless of what their genetically inherited information tells them about the direction of their home shore.

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