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ORIGINAL ARTICLE

The moon orientation of the equatorial sandhopper *Talorchestia martensii* Weber

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Abstract
The difficulties to use the moon as a compass cue are well known: in the same lunar month, the moon never rises at the same hour, it does not show the same shape, and it is not always visible at night. At the equator, the use of the moon as an orienting cue is even more difficult than in the temperate latitudes. In addition to the difficulties listed above, it should be added (1) the relevant variation in its hourly azimuthal speed when the moon approaches the zenith, (2) the zenithal culmination (i.e., no angle on the horizontal plane), and (3) its changes in the culmination (from North to South and vice versa). Here, I present some experiments carried out using the equatorial sandhopper *Talorchestia martensii* during the zenithal culmination of the moon to clarify its use as an orienting cue taking into account the already demonstrated use of the magnetic field in the orientation of this species. Experiments were carried out in confined environment, with the magnetic sNorth deflected to East, in nights of zenithal culmination of the full moon. The results indicate that the moon is used together with the magnetic field by *T. martensii* when the azimuthal variation of the moon is ≤10°/h and its zenithal distance is >10°. However, when the moon's azimuthal variation is >10°/h and its zenithal distance is ≤10°, the moon is no longer used as an orientating cue. The sole compass reference is now the magnetic field. Therefore, equatorial sandhoppers use the same relationship between orienting mechanisms to overcome the difficulties with astronomical orientation to the sun or the moon.

Significant statement
At the equator, the use of the moon as an orienting cue is difficult. Sandhoppers use the moon and the magnetic field only when the moon is far from the zenith; otherwise, they use the magnetic compass alone.

Keywords Orientation · Amphipods · *Talorchestia martensii* · Moon · Magnetic field · Equator

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Introduction

It is well known that sandhoppers are crepuscular–nocturnal animals and their use of the moon as a compass cue to orientate along the sea–land axis of the beach has been discussed in the past (Papi and Pardi 1953, 1959, 1963; Papi 1960; Enright 1961, 1972; Craig 1971). Quite recently, this capacity has been confirmed (Ugolini et al. 1999a, 2012). Despite the difficulties to use the moon as compass cue (in the same lunar month, the moon never rises at the same hour, it does not have the same shape, it is not always visible at night), the sandhopper *T. saltator* uses the moon as a compass reference chronometrically compensated. Moreover, this capacity seems to be innate (Ugolini et al. 2003, 2005); the chronometric mechanism of moon's azimuthal variation is separated from the mechanism of sun compensation (Ugolini et al. 1999a), and it is operating even when the moon is not visible (new moon phase) (Ugolini et al. 2007).

In the 1960s, Pardi and Ercolini carried out a series of experiments to test the use of the sun and moon as orientation cues at equatorial latitudes by the sandhopper *Talorchestia martensii* (Pardi and Ercolini 1965, 1966). Some years later, new experiments were carried out to shed light on the capacity to use the sun as an orientation cue despite (1) its changes in culmination twice per year. In fact, the sun crosses the equator (with zenithal culmination) twice per year at equinoxes (March and September). Therefore, an observer on the equator line will see the sun apparently traveling from East to West passing from North for 6 months, or South for the next 6 months, (2) its change in azimuthal speed (mainly in the central hours of the day), and (3) its zenithal culmination. The equatorial sandhopper *T. martensii* does not use the sun compass when the azimuthal speed of the sun is greater than 15°/h, and its zenithal distance is less than 10° (Ercolini 1964a; Ugolini 2001, 2002). During these periods of particular difficulty to use the sun as a compass reference, the natural magnetic field prevails as a compass cue along with local orienting factors, like the vision of the landscape (Pardi et al. 1988; Ugolini and Pardi 1992; Ugolini et al. 1999b; Ugolini 2001, 2002; Ugolini and Ciofini 2015).

At the equator, the use of the moon as an orienting cue is far more difficult. In addition to the difficulties mentioned above, the other difficulties arise (1) the relevant variation in its hourly azimuthal speed when the moon approaches the zenith, (2) the zenithal culmination (i.e., no angle on the horizontal plane), and (3) its frequent changes in the culmination (from North to South and vice versa). These characteristics are similar to those shown by the sun; however, whilst the sun culminates in the zenith twice a year, and changes its culmination every 6 months, in the year 2013 (the year of the experiments reported in the present paper), the moon at night (i.e., when it is visible by the sandhoppers and its illuminated fraction is >45 %) changed culmination 20 times, and in the sole month of February of the same year, its zenithal distance has been 9 times less than 10° on nine separate nights.

Here, I present some experiments carried out during the zenithal culmination of the moon to clarify its use as an orienting cue by equatorial sandhoppers taking into account its possible relationships with the magnetic compass.

Materials and methods

Adults of *T. martensii* were collected on a beach of Djibouti City (sea—land axis of their home beach = 60° towards sea—240° towards land) not more than 1 week before the tests. Sandhoppers were kept in white plastic containers with damp sand, in natural conditions of temperature and photoperiod. Food (universal dried food for fish, SERA Vipan, placed on blotting paper) was constantly available.

Experiments were conducted near Obock (Djibouti, 43°17′ E, 11°57′ N) in February 21–27, 2013, moon's illuminated fraction: 78–100 %, North and South culmination. Therefore, the releases were carried out in the periods in which the moon rises from East and set on West culminating North (= North culmination, anticlockwise path), and in the period in which the moon rises from East and set on West culminating South (= South culmination, clockwise path)

Experimental set-up

The experiments were carried out with an apparatus (see Ugolini 2001) consisting of a transparent Plexiglas bowl (diameter 14 cm), into which the individuals were released one at a time or in group of 8–10 individuals. Individual releases were preferred to avoid the formation of heaps registered in sun compass experiments during some particular astronomical conditions (e.g., the zenithal culmination of the sun) (Ercolini 1964a, b; Ugolini 2001, 2002). However, in certain cases (e.g., deflection of the moon's azimuth by a mirror), I tested groups of sandhoppers to reach a statistically sufficient sample size in a short time. The bowl was covered by a sheet of acetate to prevent sandhoppers to jump out. Releases were performed in dry conditions. A circular white Plexiglas screen (2-cm high) placed around the bowl prevented the animal from viewing the surrounding landscape but allowed it to see the moon and the sky. The bowl and the screen were set on a transparent plate, equipped with a transparent plastic goniometer, placed horizontally on a tripod. The angles the amphipods have taken along the periphery of the bowl were recorded by a videocamera placed under the transparent plate. Experiments were carried out under natural conditions of geomagnetic field or deflecting by 90° clockwise and anticlockwise its horizontal component, i.e., deflecting the magnetic North on East or West. This was achieved by placing the bowl between a pair of Helmholtz coils (diameter 65 cm, distance 35 cm). The artificial magnetic field was regulated by an electronic device. Each individual release continued until ten directions were recorded. Whilst the sandhopper in the bowl was jumping or crowling, directions were taken at intervals of 3–5 s, about 30 s after the introduction of the sandhopper. In case of group releases, only one direction for each animal was recorded after 1’ from the introduction. To minimize observer bias, blinded methods were use when all behavioral data were recorded. For a more detailed explanation of the device see Ugolini (2001).

Data elaboration and statistics

Taking into account the period in which it has been demonstrated, the difficulty to use the sun as a compass cue (Ugolini and Pardi 1992; Ugolini 2001, 2002), for both conditions of moon culmination (North and South), I divided the experiments into two periods on the basis of the theoretical difficulty of using the moon compass (see also Ugolini 2001): (1) determination time period; (2) double indetermination time period.

In the determination time period, the sandhoppers should theoretically be able to determine the angle they must assume with respect to the moon (not necessarily time compensated) to orientate according to the sea–land axis of their home beach. As it is for the sun, in this period, the moon moves a little from the East or from the West (azimuthal variation ≤10°/h). The double indetermination time period is characterized by (1) a first factor of indetermination caused by the azimuthal speed of the moon (>10°/h, azimuthal indetermination zone) and (2) by an additional factor represented by the zenithal distance of the moon (zenithal indetermination zone 10°–0°). Because of the difficulty to get a sufficient number of data for a robust statistical analysis, it was not possible to divide the double indetermination time period in two periods as I made for sun experiments (azimuthal indetermination period and zenithal indetermination period; Ugolini 2001, 2002).

For the analysis of individual distributions, I used the methods of circular statistics (Batschelet, 1981). It is known that *T. martensii* often orients both towards land or sea to escape from stressful conditions (e.g., low relative humidity, high temperature). In both directions, in fact, these amphipods find suitable conditions of humidity: obviously towards the water, but also towards land under the stranded materials during the tides. However, it is known that in case of bi-, tri-, or tetramodal distributions, the method of multiplying the angles by 2, 3, or 4 usually does not provide a sufficiently accurate description of the data. Therefore, after testing the uniformity of each individual distribution, using the Rao's test ($p < 0.05$ at least), I followed the procedure already used in similar experiments carried out under the sun (see Ugolini 2001). The uni- or pluri-modality of the individual distributions was determined by a computer, by multiplying the data by an index that varied from 1 (unimodal distribution) to 4. If the length of the mean resultant vector increased when the angles were multiplied by an index >1, the distribution was considered non-unimodal and automatically open in the points of greatest separation between the directions taken by the sandhopper. The mean angles of the groups of directions thus formed were calculated separately. Of course, there is a frequent and large disparity in the size of the clusters of directions of the non-unimodal individual distributions. Therefore, in the analysis of the second-order distributions, I did not consider the length of the mean resultant vectors, but only the mean angles (e.g., see Fig. 2). For completeness, and graphical reasons, however, within each second-order distribution, the mean resultant vectors of the statistically significant individual distributions were reported. The mean angles of individual distributions not statistically significant were omitted.

To evaluate whether the second-order distributions differed from uniformity, I used the method already published (Ugolini 2001). Each distribution was divided into four quadrants, two corresponding to the sea–land axis and two to the axis parallel to the shore of the home beach. I attributed 1 point to each individual distribution and 0.5, 0.33, and 0.25 points to each mean angle of the bi-, tri-, and tetramodal individual distributions, respectively. The frequencies belonging to each symmetric couples of quadrants, appropriately cumulated, were compared with the *G* test or Binomial test (Zar 1984). The same tests were also used to compare two distributions.

To provide a measure of the possible difficulty of orientation of *T. martensii* in the different experimental conditions, I considered the frequency of the non-significant individual distributions (out of the total number of individuals released in each condition).

Results

Releases in the determination time period

Group releases made in North (Fig. 1a, c) and South (Fig. 1b, d) culmination, under natural magnetic field, in which the moon azimuth was deflected by 90° anticlockwise (Fig. 1c) or clockwise (Fig. 1d) by a mirror show evident differences with respect to their control releases (Fig. 1a, b). Whilst the controls tested in North culmination (Fig. 1a) were well directed towards the seaward direction, the experimentals subjected to deflection of the moon's azimuth by a mirror showed a deflection in the seaward (and landward) mean angle with only 28° of difference with respect to the new expected direction (Fig. 1c).

Similar tests made in South culmination showed that controls were bimodal in accordance with the sea–land axis (Fig. 1b), even the experimentals were bimodal: one mode was in agreement with the new expected direction for the deflection of the moon's azimuth, whilst the second was still directed in accordance with the seaward direction of their home beach (Fig. 1d).

Distributions obtained by individual releases in North (Fig. 2a, c) and South culmination (Fig. 2b, d) under the natural magnetic field (Fig. 2a, b) or with the magnetic North deflected to the East (Fig. 2c, d) showed that sandhoppers tested under natural conditions were well directed along the sea–land axis of their beach (Fig. 2a, $G = 13.013$, $df = 1$, $p = 0.000309$; Fig. 2b, $G = 14.509$, $df = 1$, $p = 0.000139$, *G* test), whilst the two distributions obtained deflecting the magnetic North on East are not different from uniformity (Fig. 2c, $G = 0.630$, $df = 1$, $p = 0.427355$; Fig. 2d, $G = 0.673$, $df = 1$, $p = 0.412008$, *G* test).

Comparisons between distributions showed no statistically significant difference between North and South culmination tests made under natural magnetic field (Fig. 2a vs b, $G_1 = 0.594$, $p = 0.440876$, *G* test) and made under deflected magnetic North on East (Fig. 2c vs d, $G_1 = 0.042$, $p = 0.83762$, *G* test). The comparison between distributions obtained under natural and artificially deflected magnetic North, in North, or

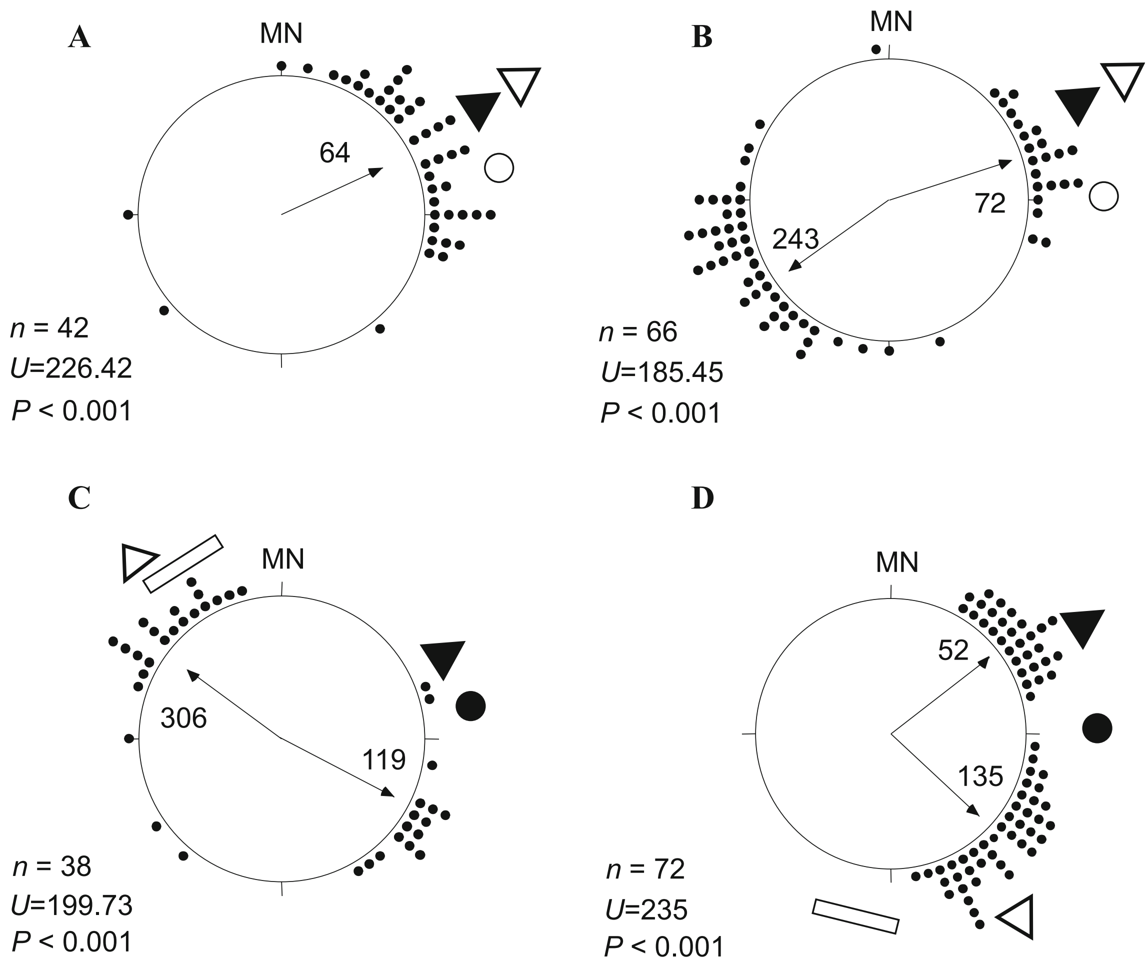

Fig. 1 Mirror experiments. Group releases. Releases were made in North (**a**, **c**) and South (**b**, **d**) culmination of the moon during the determination time period (moon zenithal distance >10°, azimuthal speed <15°/h). **a**, **b** Releases under natural moon and magnetic field (the *open circle* out of the distributions indicate the moon's azimuth at the moment of the release). **c**, **d** Releases under the natural magnetic field and the azimuth of the moon deflected by a mirror (*white bar*), the natural moon being screened out (*black circle*). Each distribution is also reported: *black dots*, directions of sandhoppers; *black triangle*, seaward direction based on the magnetic compass; and *white triangle*, seaward direction based on the moon compass. *MN* magnetic north. Inside each distribution, reported are the mean angle and the mean vector (the radius of the distribution corresponds to the maximum length = 1). *n*, sample size; *U*, Rao's test value; *p*, probability level

South culmination reaches the statistical significance in both cases (Fig. 2a vs c, $G = 9.858$, $df = 1$, $p = 0.001691$, G test; Fig. 2b vs d, $G = 4.707$, $df = 1$, $p = 0.03004$, G test). No comparison between frequencies of statistically significant individual distributions out of the total of released individuals (Fig. 4a) reached the statistical significance ($p \geq 0.233239$ in any cases, G test)

Releases in the double indetermination time period

Whilst the distribution testing individual amphipods under natural conditions and north culmination did not reach the full statistical significance (Fig. 3a, $G = 3.308$, $df = 1$, $p = 0.068943$), the correspondent distribution obtained during South culmination was statistically different from uniformity (Fig. 3b, $p = 0.019$, Binomial test). In both cases, the majority of the mean angles of individual significant distributions were concentrated in the sea–land quadrants. These results indicate that *T. martensii* orients by the magnetic and moon compasses. The two distributions obtained deflecting the magnetic North on East, even though based on small sample size due to the high number of not significant individual distributions, reached the full statistical significance (Fig. 3c, $p = 0.007$; Fig. 3d, $p = 0.019$, Binomial test). The mean angles of individual releases concentrated in the sea–land quadrants as indicated by the magnetic reference. In fact, similar to what was found in the determination time period, the comparison between distributions obtained under natural and artificially deflected magnetic North, within North, or South culmination reached the statistical significance in both cases (Fig. 3a vs c, $p = 0.008$, Fisher's test; Fig. 3b vs d, $p = 0.007$, Fisher's test).

Even in double indetermination time period, the comparisons between the frequencies of statistically significant individual distributions out of the total of released individuals

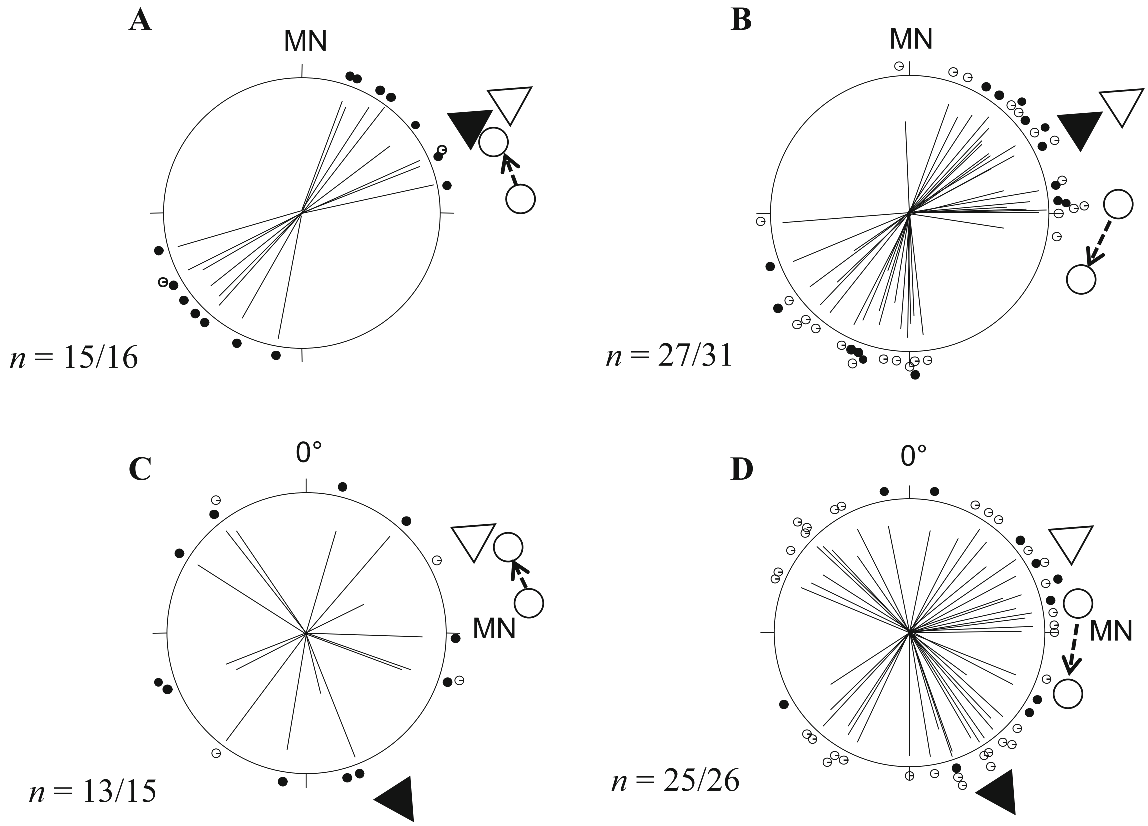

Fig. 2 Individual releases in the determination time period (moon zenithal distance >10°, azimuthal speed <15°/h). **a**, **c** Releases during North culmination. **b**, **d** Releases in South culmination. **a**, **b** Releases under natural conditions of the magnetic field and the moon. **c**, **d** Releases with the magnetic North deflected on East. *Black dots*, mean angles of individual significant unimodal distributions; *open dots*, mean angles of individual significant not unimodal distributions. The individual mean vectors are also reported (*thin lines* inside each distribution). The *open circles* with the *dashed arrows* outside the distributions indicate the moon's azimuthal variation during the experiments. *n*, number of individual significant distributions out of the total number of individual distributions. For further explanations, see Fig. 1

(Fig. 4b) did not reach the statistical significance ($p = 0.396144$, *G* test).

Comparisons between determination time period and double indetermination time period

The comparison between the frequencies of statistically not significant individual distributions out of the total of released individuals in the determination time period vs double indetermination time period (Fig. 4a vs b) shows a statistically significant greater number of individual not significant distributions in double indetermination time period. ($p \leq 0.039974$ at least, *G* test)

Discussion

Results presented here indicate that at the equator, *T. martensii* uses the moon as an orienting cue only when its azimuthal variation is modest (<15°/h about) and its zenithal distance is >10°. These findings correspond to those found for the use of the sun and moon by sandhoppers at similar latitudes (Ercolini 1964a, b; Pardi and Ercolini 1965, 1966; Ugolini 2001, 2002). However, whilst at the equator, the sun is used as a compass cue chronometrically compensated in a certain period of the day and of the year (Ercolini 1964a, b; Pardi et al. 1988; Ugolini 2001), differently from the experiments carried out at temperate latitudes (Ercolini 1964b; Ugolini et al. 1999b; Ugolini et al. 2003); for the equatorial moon, my experiments did not allow to affirm the existence of a chronometric moon compass in *T. martensii*. Therefore, it is not possible to affirm its capacity of differential compensation of the moon's azimuthal variations (Pardi and Ercolini 1965) during the nights of zenithal culmination at least.

In the determination time period, as shown by the experiments of moon's azimuth deflection by a mirror (Fig. 1), and by the releases with the magnetic North deflected on East (Fig. 2), *T. martensii* does use the moon along with the magnetic compass. In fact, the distribution obtained releasing sandhoppers under the deflected moon's azimuth (North culmination, Fig. 1d) shows that 42 % ($n = 30/72$) of animals concentrated around the direction expected for the use of the magnetic compass, whilst the other 58 % are concentrated around the direction expected for the use of the moon

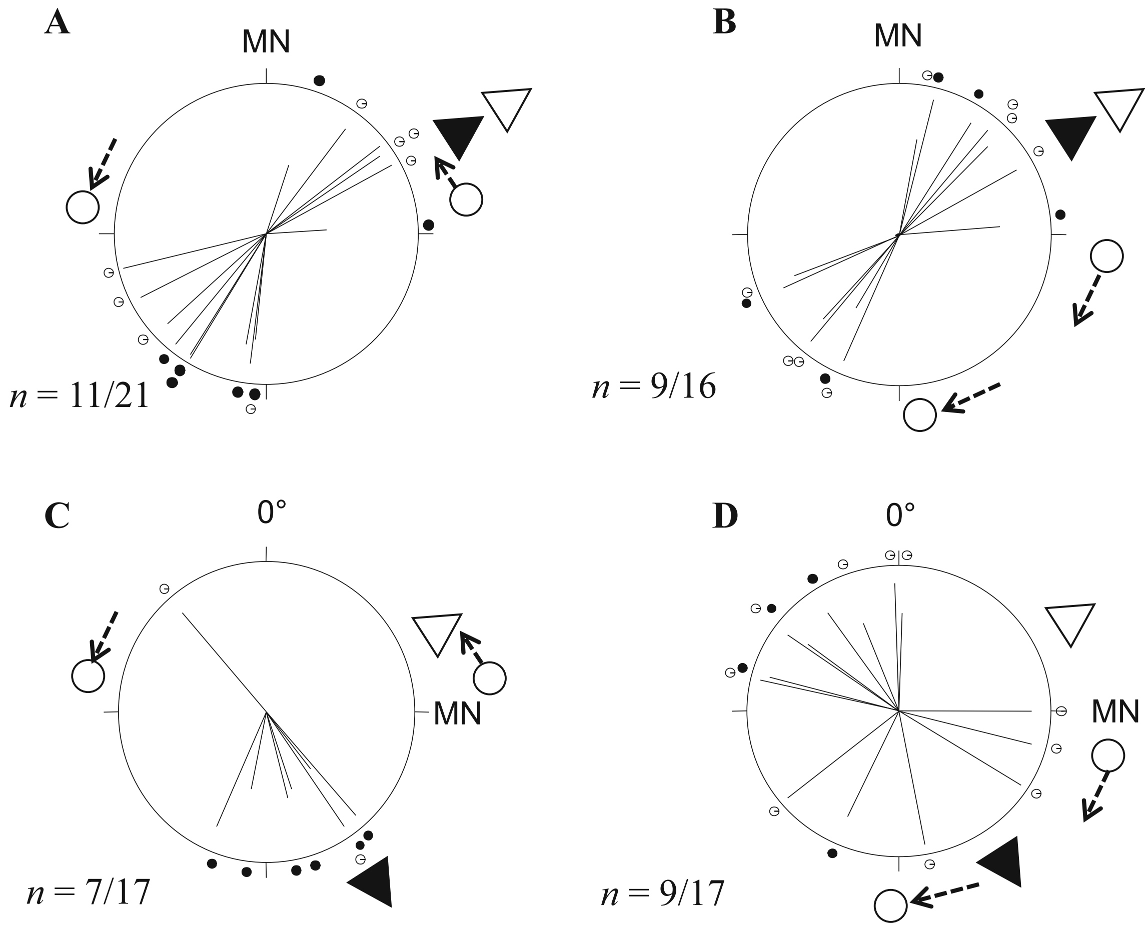

Fig. 3 Individual releases in the double indetermination time period (moon zenithal distance <10°, azimuthal speed >15°/h). **a**, **c** Releases during North culmination. **b**, **d** Releases in South culmination. **a**, **b** Releases under natural conditions of the magnetic field and the moon. **c**, **d** Releases with the magnetic North deflected on East. For further explanations see Figs. 1 and 2

compass. It is not the same for animals tested under the deflected moon's azimuth (North culmination, Fig. 1c): in this case, the moon compass directional information seems to override the magnetic reference. The dispersion of individual mean directions found in releases under magnetic North deflected on East (Fig. 2c, d) could also be interpreted as a conflict between two directional indications (provided by the moon and the magnetic field) 90° apart. I also would like to highlight that the distribution represented in Fig. 2d could also be interpreted as a tetramodal distribution. Perhaps, it is useful to remember that in equatorial sandhoppers tested under the sun or the moon, it is frequent to obtain bimodal distributions (e.g., see Ercolini 1964a, b; Pardi and Ercolini 1966; Pardi et al. 1988). It is probably due to the presence on the beach of two zones in which *T. martensii* can find suitable environmental conditions: the damp sand towards the sea, and (opposite) the line of stranded material towards land.

In the double indetermination time period (Fig. 3), even though the number of individual significant distributions is not high, there is a general tendency to orientate along the sea–land axis direction indicated by the magnetic compass (Fig. 3c, d). Moreover, in the double indetermination time period, no difference in the directional choice seems to exist depending on the culmination of the moon (North, Fig. 3a, or South, Fig. 3b).

However, the higher frequency of not significant individual distributions with respect to the determination time period is relevant. As outlined several times, in equatorial solar experiments, the magnetic field seems to be less easy to use than the solar reference for their orientation. This seems valid also for the moon and this could be the reason why in the double indetermination time period, when the moon is not a reliable compass cue, the frequency of not significant individual distributions increases. Moreover, in the double indetermination time period at night, the absence of not significant or tetramodal distributions in experiments with the magnetic North deflected on East (i.e., with conflicting directional information) shows that the magnetic compass is sufficient (and perhaps easier to use than the moon compass) to determine the correct direction of the sea–land axis of the home beach.

Unfortunately, it is not easy to compare the results presented here with those obtained by Pardi and Ercolini (1965) on

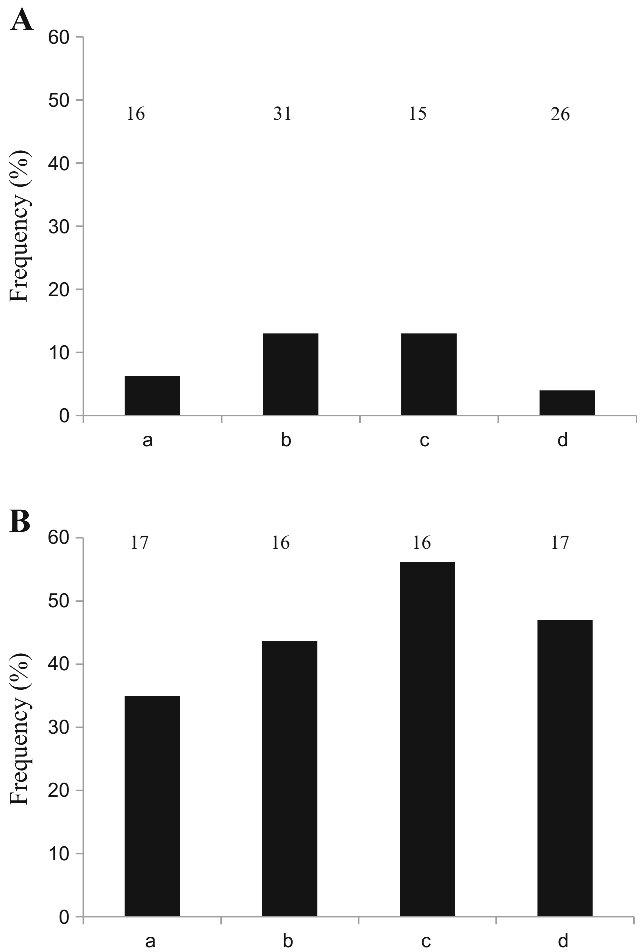

Fig. 4 Frequency of not significant individual distributions recorded in the determination time period (**a**) and in the double indetermination time period (**b**). **a**, **c** and **b**, **d** Correspond to the releases carried out in North and South culmination, respectively. **a**, **b** Natural condition of the moon and the magnetic field. **c**, **d** Natural condition of the moon with the magnetic North deflected on East. The *numbers* on the top of each bar are the total number of sandhoppers individually tested for each experimental condition

moon orientation capacity in the same species, because they always performed group releases in all astronomical conditions. These authors found some differences in orientation between experiments carried out during South or North culmination of the moon, whilst I did not find significant differences. Pardi and Ercolini (1965) also found a marked dispersion of the sandhoppers when the moon is near the zenith. My findings did not agree with the results of Pardi and Ercolini probably because testing individual sandhoppers prevents the formation of clusters' characteristic of the double indetermination time period. In practice, as already found in solar orientation tests (Ugolini 2001, 2002), individual releases force the sandhoppers to orient (i.e., to keep a direction) instead of hiding one under the other. In contrast to the use of solar compass (Ercolini 1964a, b; Pardi and Ercolini 1966), no relevant differences can be seen in the orientation capacity between North and South culmination of the moon, and this is in agreement with the use of the magnetic field as a compass cue.

In the determination time period, my results on moon orientation seems to be different from those I obtained in tests under the sun (Ugolini 2001). In fact whilst under the sun, the sandhoppers are able to maintain the correct orientation along the sea–land axis of their home beach even in the absence of the magnetic reference; in the case of moon orientation, it seems that both the moon and the magnetic field are used at the same time.

Finally, I would also like to underline that in the days in which the moon is near its zenith culmination, in the determination time period, the lunar azimuthal variation changes its direction: e.g., the moon initially moves clockwise then changes its azimuth moving anticlockwise. In my experiments, this variation is about 10° and it could be an additional problem for chronometric compensation of the moon's azimuthal variation. Therefore, in the determination time period, we can hypothesize the use of the moon in a photomenotactic and not chronometric way (i.e., maintaining a constant angle with the orienting cue). Ercolini (1964b) already hypothesized the use of the sun in a menotactic mode; however, for the moon orientation of *T. martensii*, Pardi and Ercolini in the 1965 proposed the existence of a compass system to compensate the azimuthal variations of the moon. Unfortunately, as occurred for the capacity to compensate the sun azimuth variations at the equator, they did not take into account the existence of a not chronometric compass reference: the natural magnetic field. In the same year, Merkel and Wiltschko (1965) demonstrated the existence of the magnetic compass.

Therefore, I can hypothesize an integrated use of the moon and the natural magnetic field in the determination time period (e.g., see the experiments by Baker 1987, on the moth *Agriotis exclamationis*); in the double indetermination time period, this integration seems absent. The integrated use of orienting cues is a quite common feature among many species of invertebrates and vertebrates; however, the most part of this kind of researches deals with biological models which have ecological problems of spatial orientation different from those of sandhoppers: for example to maintain a rectilinear route to reach a spatially not defined goal or to return to a punctiform goal by pluridirectional orientation. Since the zonal recovery of sandhoppers is typically unidirectional orientation, I do not think it is interesting to compare the different integrated systems of orientation in this paper.

In summary, in the days of zenithal culmination of the moon, the moon is used by *T. martensii* in the determination time period together with the magnetic field. In the double indetermination time period, the moon is no longer used as an orientating cue, the sole compass reference being the magnetic field, under these experimental conditions at least. Therefore, equatorial sandhoppers use the same relationship between orienting mechanisms to overcome the difficulties to use the sun and the moon.

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Compliance with ethical standards

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Conflict of interest The author declares that he has no conflict of interest.

Ethical approval N/A

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