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RAPID COMMUNICATION

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The orientation of the sandhopper *Talitrus saltator* during a partial solar eclipse

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Abstract To acquire more information about the identification and use of the sun and other celestial cues in the sea–land orientation of the sandhopper *Talitrus saltator*, we carried out releases in a confined environment during a partial solar eclipse and at sunset. The sandhoppers were unable to identify the sun (86% covered) during the eclipse nor to use other celestial compass factors of orientation. This was probably due to the low level of light intensity (close to the minimum level for orientation recorded at sunset) and to the variations in intensity and pattern of skylight polarization.

Keywords Celestial orientation · Solar eclipse · Solar orientation · Sunset orientation · *Talitrus saltator*

Introduction

Solar eclipses have influenced many aspects of our life, from the study of physical principles to artistic expressions (for examples of the latter see Olson and Pasachoff 2002). They also affect some aspects of animal behaviour, like the stratal orientation (vertical migrations) of some planktonic organisms (e.g. see Giroud and Balvay 1999) and many other kinds of activity, even though the literature on this topic is not very substantial (Sanborn and Phillips 1992; Briceno and Ramirez 1993; Ortega Rubio et al. 1994; Uetz et al. 1994; Jennings et al. 1998; Spoelstra et al. 2000; Tramer 2000; Rutter et al. 2002). Regarding the astronomical orientation of animals, we have not been able to find any study dealing with the effect of a solar eclipse on visual compass mechanisms.

The ability of the sandhopper *Talitrus saltator* to use celestial and astronomical cues to return to the band of wet sand on the beach following the shortest path, i.e. the sea–land (= *Y*) axis, has been studied for many years (Pardi and Papi 1952). This zonal recovery is mainly based on the ability to chronometrically compensate for the apparent movement of the sun and moon to maintain (theoretically unaltered) the sea–land direction of orientation throughout the day (for reviews see Pardi and Ercolini 1986, Ugolini 2003; for recent findings on moon orientation see Ugolini et al. 1999a, b, 2003).

The old topic of the use and identification of astronomical and celestial orienting cues in sandhoppers (Terracini Debenedetti 1958–1962; see also Pardi and Ercolini 1986) has recently been examined from a new perspective (Ugolini et al. 1998, 2001). Sandhoppers tested under an artificial sun and sky (for methodological details see Ugolini et al. 1998) exhibit sun compass orientation similar to that recorded under natural conditions only when the artificial sun and sky are both illuminated and in the absence of a meaningful pattern of linearly polarized light. However, under natural conditions *T. saltator* is also able to maintain the correct *Y* axis direction when only the blue sky is visible (Pardi and Papi 1953, Ugolini et al. 1993); this is probably due to the use of the skylight polarization pattern. Experiments on the effects of spectral filtering on solar and sky orientation indicated that the sandhoppers perceived at least one orienting cue in the blue-UV range (Ugolini et al. 1993, 1996).

We decided to carry out tests of astronomical orientation during the partial solar eclipse of 11 August 1999, and at sunset to acquire more information about the identification and use of the sun and other celestial cues in the sea–land (*Y* -axis) orientation of *T. saltator*.

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Materials and methods

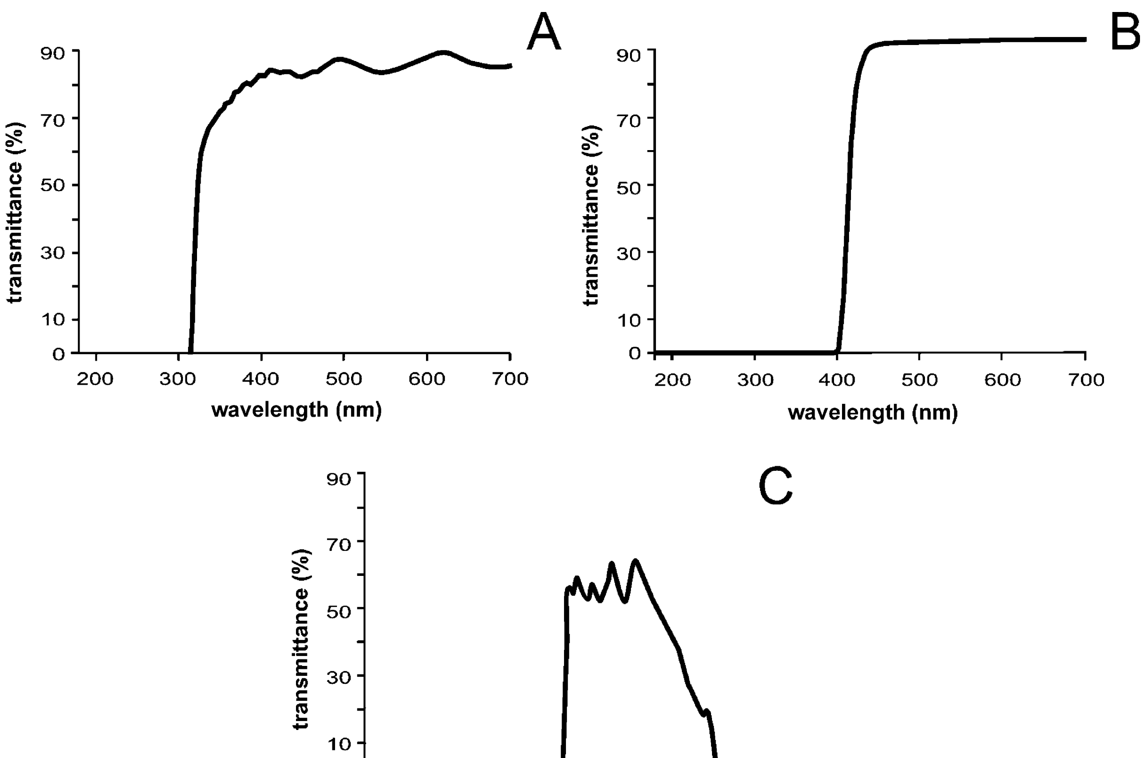
We used adult individuals of the sandhopper *T. saltator* collected no more than 30 days earlier on a beach of southern Tuscany (near Albegna) with a seaward direction of 268°. The sandhoppers were kept in the laboratory in plastic containers with wet sand and dry fish food. Artificial illumination was provided by neon tubes and the light:dark cycle corresponded in phase and duration to the natural one.

Group releases of 9–12 individuals at a time were carried out using a device described previously (Ugolini and Macchi 1988). In brief, it consisted of a transparent Plexiglas bowl (diameter 18 cm) set on a transparent Plexiglas plate placed horizontally on a tripod. A cylindrical white Plexiglas screen (10 cm high) around the bowl prevented the sandhoppers from viewing the surrounding landscape but allowed vision of the sun and sky (115° from the centre of the bowl). We set up two devices: one with the bowl covered by an acetate sheet that did not alter the spectral composition of the skylight (Fig. 1a) and prevented the sandhoppers from jumping out of the bowl; the other device was equipped with a UV-blocking filter (CR39, Fig. 1b) placed horizontally over the circular screen. Each group of individuals was dehydrated for about 5 min before the release to provide a motivation for seaward orientation. Dehydration was obtained keeping the sandhoppers under the sun in white opaque plastic containers. Each individual was tested only once and a single direction per individual was recorded 1 min after the release by means of a videocamera underneath the bowl. The experiment lasted from 10:30 to 12:16 local time on 11 August 1999; the maximum of the partial solar eclipse was at 11:39:15 (sun's area eclipsed = 0.860)

Radiometric measurements of the sun and the zenithal part of the sky were performed throughout the experiment with an optical power meter (Graseby model 370, Fig. 2) equipped with a silicon photodetector (Fig. 2). Two fixed filters (Shott BG1 h and CVI SWP600) are located inside the cylindrical head, in front of the photodetector, in order to eliminate wavelengths longer than 600 nm and shorter than 405 nm (Fig. 1c) to which the sensitivity of the sandhopper's eye is very low (Ugolini et al. 1996).

The acceptance angle of the sensor was limited to 2° by a baffle (Fig. 2b). A V-shaped support (not indicated in Fig. 2) was fixed on a tripod and used to hold the detector aligned toward the zenith. A similar support was aimed at the sun. The same sensor head could easily be moved from zenith alignment to sun alignment and back (see Fig. 2). The radiometer was connected to a portable PC (Fig. 2) that acquired data through a PB-IB interface. Radiometric measurements were repeated with and without a CR39 filter in front of the sensor (Fig. 2); a complete set of four

Fig. 1 Transmittance diagrams of the acetate sheet (**a**), CR39 filter (**b**), and of the filters package (Shott BG1 h plus CVI SWP600) placed on the sensor head (**c**)



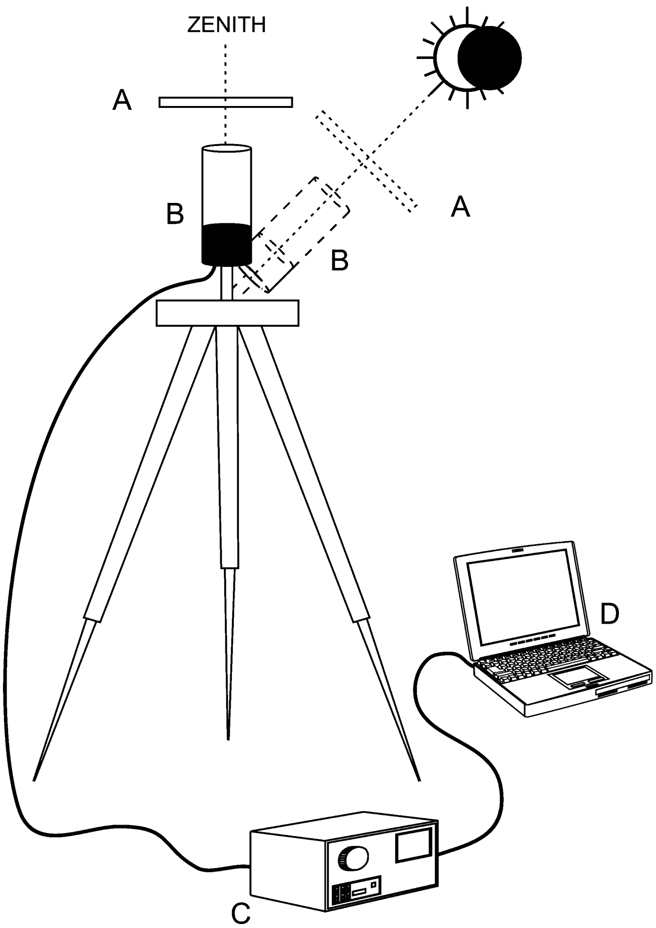


Fig. 2 Device used for radiometric measurements during the eclipse. *A* CR39 filter; *B* sensor head equipped with a silicon filtered photo-detector assembled in a cylinder, in the two measurement positions; *C* radiometer; *D* computer

measurements (sun; sun + CR39; zenith; zenith + CR39) was performed every 5 min. The acquisition time of each measurement was also stored.

Some releases were performed at sunset (July 1999), under a clear sky and with the acetate filter on the bowl, to determine the minimum sky intensity for sandhopper orientation. The releases were performed in the same apparatus described for the eclipse releases but with a 3-cm-high screen to block the landscape (instead of 10 cm high). The sky intensity was measured with the Graseby 370 radiometer and filters described above. The acceptance angle of the sensor was 104°.

The statistical analysis of the circular distributions was performed with the procedure reported by Batschelet (1981). We calculated the mean resultant vector for each distribution. The V test was used to assess whether the distribution differed from uniformity ($P < 0.05$ at least). For each distribution, the "goodness of seaward orientation" (YSc) was calculated with the same formula of the "homeward component" (see Batschelet 1981): $\mathrm{YSc} = r \cos(\alpha - YS)$, where r is the mean vector length, α is the mean angle, YS is the expected seaward direction of Y axis orientation. The parameter YSc ranges from 1 (perfect orientation) to −1 (opposite orientation) passing through zero (uniform distribution).

Results and discussion

Figure 3 shows the results of the radiometric measurements. The intensity level varied markedly in both the zenithal sky (Fig. 3a) and sun (Fig. 3b) recordings because of the passage of some thin clouds. The measured curves with and without the CR39 filter are very similar, probably due to the presence of the filters added to the sensor.

Figure 3c clearly shows that the YSc of the unfiltered and CR39 filtered individuals decreased dramatically in correspondence to the maximum of the eclipse. The sandhoppers' orientation ability remained practically constant for zenithal sky intensities of 0.0366 μW cm^{-2} or greater and for sun intensities of 12.1 μW cm^{-2} or greater (Fig. 3c). The minimum YSc corresponds to zenithal sky and sun intensities of 0.0216 and 7.51 μW cm^{-2}, respectively. There is also no appreciable difference in the YSc between filtered and unfiltered releases.

Therefore, the sandhoppers were unable to identify the sun (86% covered) during the eclipse or to use other celestial compass factors of orientation. Nevertheless, the sunset experiments (Fig. 3d) showed that *T. saltator* can detect and use a celestial orienting factor (probably skylight polarization) as a compass reference, albeit only for sky an intensity greater than 0.002–0.0025 μW cm^{-2}. In the experiments performed during the eclipse, this threshold value corresponded to about 12% of the maximum sky intensity. Similarly, during the experiments at sunset, the sandhoppers showed good orientation at sky intensities greater than 16% of the maximum.

We believe that the celestial factor involved in the sandhoppers' sunset orientation is skylight polarization. Although trials dealing with the use of skylight polarization by sandhoppers in the early 1950s were only preliminary investigations (Pardi and Papi 1953), other indirect experiments (spectral filtering tests without the use of a polarizing filter) have suggested that sandhoppers can use skylight polarization perceived in the UV-blue band to orient themselves in the sea–land direction of their home beach (Ugolini et al. 1993, 1996, 2002).

Therefore, we can argue that there are two main reasons why the sandhoppers were unable to use skylight polarization as an orienting factor during the maximum of the partial eclipse: (1) the level of light intensity was too low. The good correspondence between the two minimum values of sky intensity (during the eclipse and at sunset) at which the sandhoppers did not detect any compass information from the blue sky is noteworthy. The 4% difference between the two thresholds of orientation recorded in the sunset and eclipse experiments is probably not relevant considering the difference in the acceptance angle of the sensors used

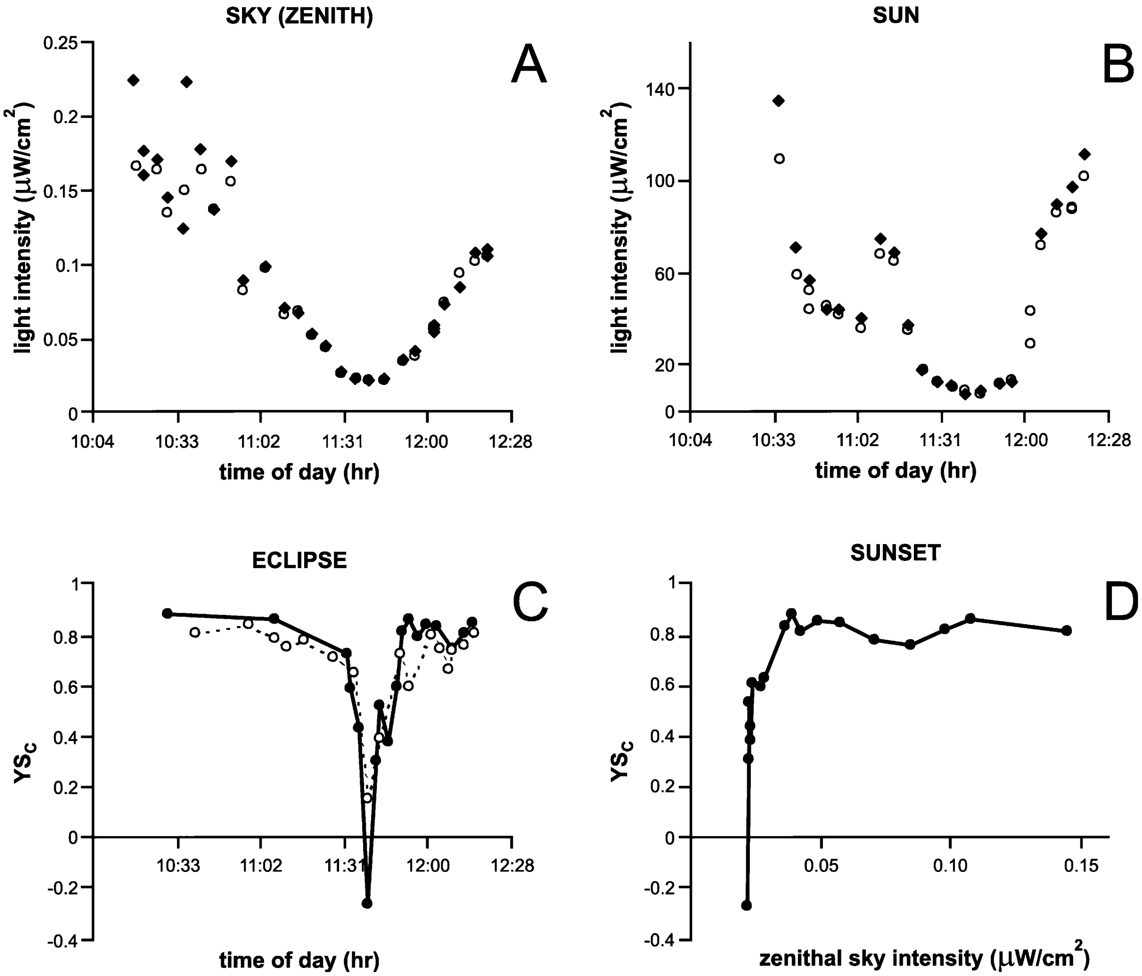


Fig. 3 Diagrams of the intensity of the zenithal sky (**a**) and the sun (**b**). The maximum of the partial eclipse was at 11:39:15, local time. *Black dots* measures carried out under natural conditions, *open dots* measures under the CR39 filter. **c** Goodness of orientation (seaward direction of the sea–land *Y* axis, YSc) during the eclipse. *Black dots* indicate the YSc of individuals tested under the acetate sheet; *open dots* YSc of sandhoppers tested under the CR39 filter. Each dot corresponds to one release of 9–12 sandhoppers. **d** Relationship between zenithal sky intensity and YSc of individuals tested under natural conditions (acetate sheet) at sunset

(104° and 2°, respectively). Therefore, the low level of sky intensity during the maximum of the partial eclipse could well explain the lack of difference in the YSc between the filtered and unfiltered tests (both show a YSc around 0), (2) during the eclipse, the skylight polarization underwent various changes in pattern and intensity that made it difficult to use as a compass reference (Piltschikoff 1906; Pomozi et al. 2000; Horváth et al. 2003).

Finally, we should note the absence of a marked difference between the filtered and unfiltered releases at the beginning (till about 11:17) and the end (from about 11:51) of the eclipse. However, the sun was still easily identifiable by the sandhoppers at those times and *T. saltator* is able to assume the expected direction of orientation even in the absence of sky polarization (Ugolini et al. 1998). Therefore, the effect of the UV spectral filtering on the perception of a celestial orienting factor was probably masked by solar orientation.

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