

SHORT COMMUNICATION

Optic flow and sea–land orientation in the sandhopper *Talitrus saltator*

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ABSTRACT

The problem sandhoppers face when they find themselves on the dry sand is to reach as quickly as possible the belt of moist sand near the water. In the present study, I ask whether, alongside many other orienting factors, sandhoppers use the optic flow they experience to maintain their bearing relative to the sea–land axis. Adult individuals of *Talitrus saltator* were released in a transparent Plexiglas bowl, horizontally placed between four walls with a pattern of vertical black and white stripes. The orientation of one pair of opposite walls was south–north, orthogonal to the sea–land axis of the home beach, whilst the second pair of walls was oriented east–west. The black and white striped pattern of opposite walls could be moved in pairs and in the same direction (speed=4.8 cm s⁻¹). The results demonstrate that the optic flow sandhoppers experience when moving on the sea–land axis of their home beach influences their direction of travel and could help sandhoppers in maintaining a straight path to reach favourable ground by the shortest route.

KEY WORDS: Orientation, Optic flow, *Talitrus saltator*

INTRODUCTION

The apparent motion of the landscape is one of the cues used by many species of arthropods for course control and odometry, for homing and during foraging (e.g. Wehner, 1981; Wolf, 2011). An extensive literature on mainly flies, bees and ants addresses the use of image motion in these tasks (e.g. Esch and Burns, 1995; Ronacher and Wehner, 1995; Srinivasan et al., 1997; Srinivasan et al., 2000; Esch et al., 2001). While many studies on crustaceans have addressed the physiological and behavioural aspects of optokinetic responses (Nalbach and Nalbach, 1987; Nalbach et al., 1989a; Barnes and Nalbach, 1993; Blanke et al., 1997; Barnes et al., 2002; Zeil and Hemmi, 2006), the visual ecology of sandhoppers has scarcely been considered (Ugolini et al., 1986; Ugolini et al., 2006; Forward et al., 2009; Walsh et al., 2010). All of these arthropod groups, however, are faced with different ecological conditions, which suggests that they may rely on different cues for orientation depending on the information content of their habitat (see Nalbach et al., 1989b; Nalbach, 1990). This is particularly true in the case of sandhoppers, which are known to use to a number of orienting cues when escaping predators and when moving up and down the beach to reach damp sand, in which they remain during the day to prevent dehydration (Pardi and Ercolini, 1986; Ugolini, 1996). The redundancy of orientation systems in sandhoppers appears to be important for determining and moving along the *y*-axis (sea–land) direction. Sandhopper *y*-axis orientation is based on bi-

directional movements without the need for place memory: sandhoppers do not have a ‘home’ and are not central place foragers. These bi-directional movements are mainly guided by local cues, such as the surrounding panorama (Williamson, 1951; Williamson, 1954; Craig, 1973; Hartwick, 1976; Edwards and Naylor, 1987; Ugolini et al., 1986; Ugolini and Cannicci, 1991), and by compass cues, such as the sun, the moon and the geomagnetic field (Ugolini, 2001; Ugolini et al., 2002; Ugolini et al., 2003), whereby the directional choice of sandhoppers also makes use of the spectral differences between the landward and the seaward part of the panorama (Ugolini et al., 2006).

Here I ask whether, in addition to these known directional cues, sandhoppers *Talitrus saltator* (Montagu) also use the optic flow they experience to maintain their bearing relative to the sea–land axis.

RESULTS AND DISCUSSION

Sandhoppers tested under the sun and blue sky whilst the black and white stripes were stationary show a good seaward orientation (Fig. 1A). When the stripes were in motion from west to east, concordant with the optic flow that the sandhoppers should theoretically see in the field whilst orientating toward the sea by the sun compass, the sandhoppers show a better concentration around the expected seaward direction (Fig. 1B); when the patterns moved in the opposite direction (creating a conflict with the direction indicated by the sun compass), the distribution is far more dispersed and not significantly different from uniformity (Fig. 1C), although there is a slightly tendency for sandhoppers to head in the direction of pattern movements (black triangle in Fig. 1C).

When the patterns moved from south to north (Fig. 1D), most individuals ($n=56/83$, 67%) moved towards the south. Therefore, the direction of movement of sandhoppers can be modified by laterally placed moving patterns. The distribution is clearly bimodal, indicating that some individuals actually head in the direction of pattern movement, possibly attempting to minimize the image motion they experienced. Interestingly, the larger mode is deflected towards the west, a compromise direction between the direction of pattern motion and the *y*-axis direction of the sandhoppers’ home beach, indicated by the sun compass. The results thus clearly demonstrate that the image motion sandhoppers experience when moving on the sea–land axis of the beach influences their direction of travel.

The problem sandhoppers face when they find themselves on dry sand is to reach as quickly as possible areas of the beach where the sand is moist. They need to be able to identify the seaward direction and maintain a straight path to reach favourable ground by the shortest route. In the field, the optic flow could be due to direct vision of stranded material and the inhomogeneities of the sandy beach surface, which is often characterized by areas of light and shadow. Monitoring the direction of image motion along the sea–land axis may help them to keep to a straight line, to monitor their progress and to correct displacements by wind with respect to

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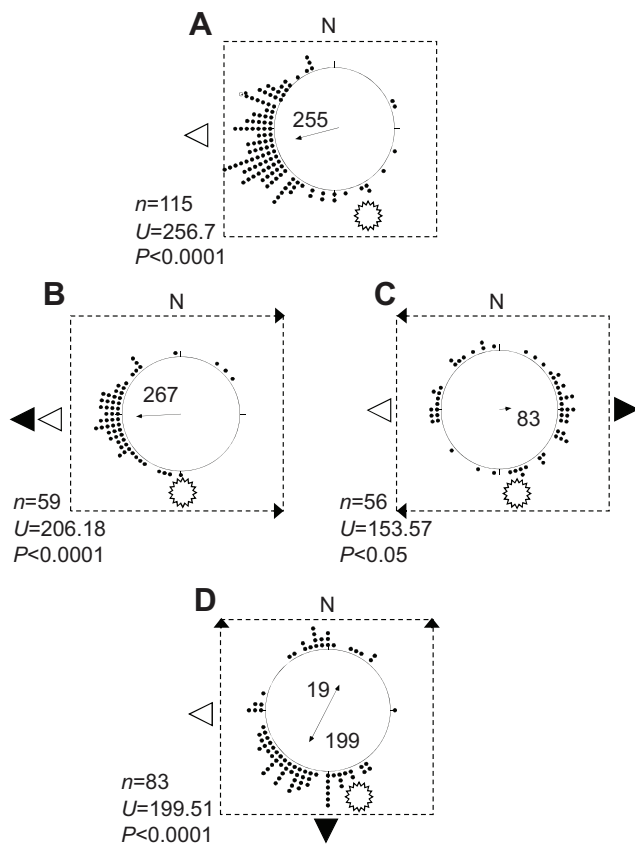


Fig. 1. Influence of artificial optic flow on sea–land orientation of *Talitrus saltator*. (A) Control releases: the bowl is surrounded by four stationary walls with black and white vertical stripes. (B–D) Two out of four walls in motion: the arrows outside the distributions indicate the direction of the stripes' movement. (B) The stripes' movement is concordant with the direction of the apparent movement of landscape a sandhopper should see during its seaward crawling. (C) The stripes' movement is opposite to the previously described condition. (D) The stripes' movement is orthogonal to the sea–land axis of the beach and could facilitate a photopositive choice. The arrows and the numbers inside each distribution represent the mean vector (length varies between 0 and 1=radius of the circle) and the mean angle, respectively. Black circles indicate individual directions. N, magnetic north (=0 deg); white triangle, expected (seaward) direction based on solar orientation; black triangle, expected direction based on optic flow vision. The sun azimuth is represented outside each distribution. *n*, Sample size; *U*, Rao's test value.

the direction indicated by the sun compass. Note that the other orienting cues sandhoppers have been shown to rely on, such as the sun and the landscape panorama (for reviews, see Pardi and Ercolini, 1986; Ugolini, 2003), cannot be used to monitor progress and to compensate for displacements.

MATERIALS AND METHODS

I used adult individuals of *Talitrus saltator* collected on a beach near Grosseto (Albegna, southern Tuscany), with the seaward side 268 deg relative to north.

After capture, sandhoppers were transferred to the laboratory and kept in Plexiglas boxes containing wet sand. They were kept at ambient temperature and under a light:dark cycle in phase with and of duration corresponding to the natural one. Food (universal dried food for fish, Sera Vipan) was provided *ad libitum*.

Releases were made outdoors in Florence from 11:30 to 13:00 h in June 2012, with full view of the sun and blue sky. Groups of four to six individuals were released in a transparent Plexiglas bowl (diameter 10 cm),

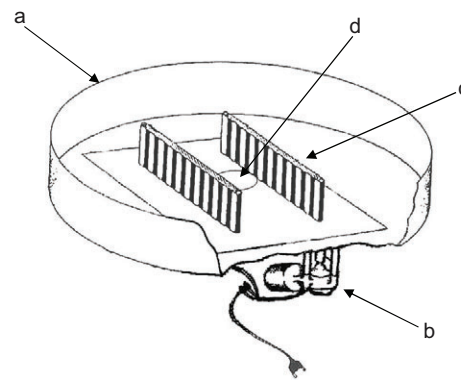


Fig. 2. Device used to produce an artificial optic flow (modified from Ugolini, 1987). (a) Screen for the natural landscape; (b) electric motor for moving the walls with the black and white stripes; (c) walls with black and white vertical stripes used for the artificial optic flow, (only two of the four walls are represented). During the experiments, the Plexiglas bowl with sandhoppers was placed between the walls, on the transparent plate (d).

horizontally placed between four walls that were 18 cm apart and 5 cm high (Fig. 2). The four walls had a pattern of vertical black and white stripes that were 5 cm high and 2 cm wide. The orientation of one pair of opposite walls was south (178 deg)–north (358 deg), orthogonal to the sea–land axis of the home beach, whilst the second pair of walls was oriented east (88 deg)–west (268 deg). A white Plexiglas screen (20 cm high, diameter 80 cm) surrounded the apparatus and prevented the view of the landmark panorama. This apparatus has been used previously, with slight modifications, to test the homing ability of paper wasps (Ugolini, 1987). The black and white striped pattern of opposite walls could be moved in pairs and in the same direction by an electric motor at a speed of 4.8 cm s^{-1} . This speed was selected because is similar to the speed of a crawling sandhopper recorded in artificial (laboratory) conditions ($n=20$, mean= 5.2 cm s^{-1} , s.d.= 1.535). To determine the sandhoppers' speed, I released 20 adult individuals one at a time in the centre of a circular arena (diameter 30 cm), on a wet substratum to decrease the chance of a jump. I recorded the time taken by each sandhopper from release until it reached the edge of the arena. The bowl containing the sandhoppers was covered with an aluminium net to prevent the animals from escaping and was placed on a goniometer on a horizontal transparent Perspex plate. The directions of sandhoppers were recorded from below with a video camera. Each sandhopper was tested only once and only one direction for each individual was recorded when they had reached the edge of the bowl. Once released in the transparent bowl, the majority of sandhoppers reached the bottom edge of the bowl, and arranged themselves in a radial direction relative to the center of the bowl, with the head facing outwards. In this position they are unable to move forward because of the wall of the bowl and alternate jumps with periods of crawling on site. Therefore, the landscape the sandhoppers see during the experiment can be still or moving at the programmed speed without (or with a very reduced) influence of the self-induced optic flow.

As controls, sandhoppers were released in the presence of stationary striped patterns. Tests were performed under the following three conditions: (1) with striped patterns moving from west to east, coinciding with the apparent motion of the landscape a sandhopper would experience when moving in a seaward direction at its home beach, as indicated by the sun compass; (2) with striped patterns moving in the opposite direction, i.e. coincident with the optic flow direction experienced during landward orientation (i.e. opposite to the seaward direction given by the sun compass); and (3) with striped patterns moving from south to north, coincident with the theoretical self-induced optic flow direction for a photopositive choice based on the sun's disk vision, i.e. roughly perpendicular to the direction indicated by the sun compass.

Directions were analysed using circular distributions and statistics (see Batschelet, 1981). For each distribution, the mean vector length and the mean direction were calculated. Rao's test was used to test for non-uniformity of distributions (with significance defined as $P<0.05$).

Bimodality was assessed using the procedure of doubling the angles (Batschelet, 1981).

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Competing interests

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