

Context-dependent orientation cues in a supratidal amphipod

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Most mobile animals rely on orientation cues for either long-distance migration or to move shorter distances on a daily basis. Supratidal amphipods in the northern Gulf of Mexico regularly use orientation cues in both water and on dry sand to return to their home in seagrass wrack. I manipulated the presence of visual and magnetic cues in both water and sand. Visual cues were important for orientation in water, but magnetic cues were important on dry sand. The use of orientation cues by amphipods is context-dependent and suggests that some cues may be more reliable in different environments.

Keywords: amphipod; *Orchestia sp.*; navigation; cues; magnetic; solar; visual

Introduction

All animals disperse in at least one phase of their life cycle, requiring some ability to orient themselves in space. Orientation cues can be as simple as gravity or light, or can require complex organs that sense the global magnetic fields to navigate precisely during long migrations (Wiltshko and Wiltshko 2005). The use of orientation cues varies widely among taxa, including light, sound, solar, lunar, stellar, magnetic, chemical, olfactory, or tactical signals (Wehner 1998). Such cues have been studied primarily in long-migrating large animals, such as birds and sea turtles, where orientation is clearly important for completing the life cycle (Bingman and Cheng 2005). However, any free-living animal requires the ability to orient itself on a regular basis. Small crustaceans have served as a model system in the study of orientation cues on much smaller scales (e.g., Scapini 2006).

Inter- and supratidal organisms face additional challenges associated with orientation in that they must regularly orient in both aquatic and terrestrial environments. Many organisms switch habitats to feed during tidal changes, or must orient towards the shore upon being accidentally swept into the water. Orientation over short distances is crucial for survival in these environments. As different orientation cues may be more advantageous in different environments, redundant cues may be advantageous to many organisms (Walsh et al. 2010). For example, magnetic cues can become less reliable as animals experience water loss (Arendse and

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Barendregt 1981), indicating that the usefulness of this orientation cue could be dependent on environmental conditions.

Talitrid amphipods are an important member, both in abundance and ecology, of the inter- and supratidal community on many sandy beaches. Orientation cues have been well studied in supratidal Talitrid amphipods, particularly in the Mediterranean intertidal and mid-Atlantic Bight, (Scapini 2006; Forward et al. 2010; Pelletier et al. 2011). Amphipods in this family use several different cues to navigate between the shoreline and the dune (reviewed in Scapini 2006), including a sun compass (Scapini et al. 2002), lunar cues (Craig 1973), beach slope (Ugolini et al. 1986; Walsh et al. 2010), light (Ercolini et al. 1983), and magnetic fields (Arendse 1978). Redundancy of cues may also aid in orientation toward different habitats, as landscape and solar cues act in conjunction to guide *Talitrus* (Ugolini et al. 1986; Walsh et al. 2010).

In northern Florida, beach-dwelling amphipods within the family Talitridae, also known as beach hoppers, are important detritivores in the intertidal community. *Orchestia* sp. spends much of its life within seagrass wrack on the shoreline. *Orchestia* frequently ventures from the wrack and experiences two significant risks of mortality if they are unable to navigate back to the wrack line. Beach hoppers that are swept into the water are likely to be consumed by fish predators unless they are able to quickly orient and swim back towards the shore. On the other hand, the sand above the wrack line is much hotter and drier than the moist environment within the seagrass wrack, making beach hoppers vulnerable to desiccation unless they are able to navigate back towards the water (Pelletier et al. 2011). *Orchestia*'s remarkable ability to quickly return to the wrack line from either sand or water suggests that its ability to orient is finely tuned.

I examined the ability of *Orchestia* to use multiple orientation cues in different habitats. Visual and solar cues were manipulated simultaneously, in addition to magnetic cues. All cues were manipulated in both water and on dry sand at the shoreline and above the wrack line to determine whether some cues were more advantageous in different contexts.

Methods

Experiments were conducted on the shoreline in front of the Florida State University Coastal and Marine Laboratory in St. Teresa, Florida. Throughout the summer and fall, the high tide line of this sandy beach is rife with seagrass wrack that is home to hundreds of beach hoppers (*Orchestia* sp.) per m² (pers. obs.). Clear plastic circular trays (30 cm diameter) were used as trial arenas in the field. In each of 112 trials, I added approximately 25 freshly collected beach hoppers to each tray and allowed the animals to acclimate for 1 min, after which I counted the number of individuals in the shoreward and the seaward halves of the tray and calculated the proportion of individuals moving towards shore. Although some random movement of beach hoppers in the tray was possible, if beach hoppers were orienting shoreward, I expected to find a greater number of beach hoppers in the shoreward side of the tray, relative to the seaward side of the tray. I considered a random distribution of beach hoppers between the two sides as an evidence for a lack of orientation in either direction.

All trials were conducted on two warm, sunny days in June 2008 at low tide. I manipulated four variables in a fully factorial design: tidal zone, substrate, light cues, and magnetic cues. Trays were placed in one of two tidal zones: either on the

sand at the water's edge or on dry sand in the supratidal. Although the beach slope was similar in all trials, I leveled the trays to account for any minor differences in slope. I manipulated the substrate by filling trays with either water or dry sand collected from the supratidal area. Visual and solar cues were manipulated simultaneously by removing light. Trays were placed inside of a covered bucket placed inside a black garbage bag. This manipulation placed the beach hoppers in darkness and impaired their ability to use light-based cues. Additionally, magnetic cues were disrupted by taping a small magnet (~ 0.1 Tesla) to the bottom of the plastic tray, with the negative pole closest to the dish and the positive pole closest to the ground. The strength of the magnet was several orders of magnitude stronger than the earth's magnetic field and was intended to disrupt that field and impair use of it for orientation by the beach hoppers.

Visual and magnetic cues, as well as substrate type and tidal zone, were manipulated in a fully factorial design. Each treatment combination was implemented once at each of seven locations on the same shoreline, separated by at least 50 m ($N=112$; 2 magnet treatments \times 2 visual treatments \times 2 substrate types \times 2 zones \times 7 locations), with each location serving as a statistical replicate ($n=7$).

The effect of each treatment on the proportion of individuals moving towards shore was analyzed using a four-way analysis of variance, with all factors fixed. Data were arcsine-square-root transformed to meet the assumptions of parametric tests. Statistical analyses were conducted in SAS version 9.1 (SAS Institute Inc, Cary, NC, USA).

Results

In most trials, beach hoppers tended to display one of the three behaviors: clustering in a small area headed directly towards shore, clustering in a small area headed towards the sea, or moving in circles around the tray (resulting in a random distribution of individuals). Substrate had a significant effect on the proportion of individuals moving towards shore (Table 1). In water, beach hoppers tended to move towards shore, but on dry sand, beach hoppers tended to move towards the sea (Figure 1). Tidal zone did not have any significant effect on which direction beach hoppers moved, nor were there any significant interactions between tidal zone and other factors in the model (Table 1).

Visual and magnetic cues both had significant effects on the orientation behavior of beach hoppers, but these effects were dependent on substrate type (Table 1). When on dry sand, the removal of visual cues had little effect on the orientation of beach hoppers, as most still moved towards the sea (Figure 1). In water though, the lack of visual cues resulted in a more random distribution of beach hoppers (Figure 1). When magnetic cues were removed, beach hoppers on dry sand showed more random distribution. Beach hoppers in water still moved primarily towards shore, despite lack of visual cues (Figure 1). When both visual and magnetic cues were removed, amphipods on both substrate types showed more random distribution (Figure 1).

Discussion

Talitrid amphipods in the northern Gulf of Mexico often need to orient towards their home in the seagrass wrack in the supratidal, either after foraging away from the

Table 1. Results of a 4-way ANOVA comparing the effects of tidal zone (upshore, above the wrack line, or downshore, near the water line), substrate (sand or water), visual cues (present/absent), and magnetic cues (present/absent) on the proportion of beach hoppers moving towards shore.

Effect	$F_{1,96}$	P
Location	0.060	0.807
Substrate	59.8	<0.001
Visual	31.3	<0.001
Magnetic	5.03	0.027
Loc*Sub	0.060	0.800
Loc*Vis	0.001	0.983
Loc*Mag	1.70	0.195
Sub*Vis	28.4	<0.001
Sub*Mag	7.63	0.007
Vis*Mag	0.190	0.665
Loc*Sub*Vis	0.360	0.550
Loc*Sub*Mag	0.250	0.618
Loc*Vis*Mag	0.370	0.545
Sub*Vis*Mag	0.750	0.390
Loc*Sub*Vis*Mag	0.060	0.810

Note: Bold values indicate significant effects.

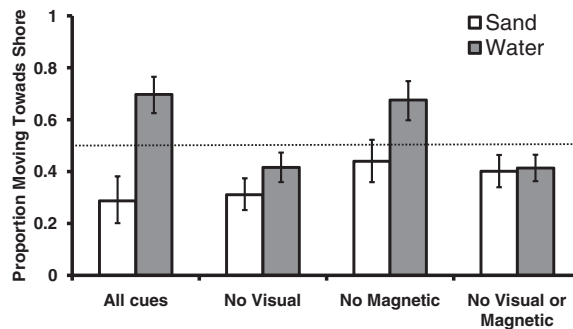


Figure 1. The orientation behavior of beach hoppers in response to the removal of different potential orientation cues. Data represent the proportion of beach hoppers moving towards shore (the remaining beach hoppers were moving seaward). Bars represent back-transformed means and 95% confidence intervals, pooled across upshore and downshore locations. Large values on the y-axis indicate beach hoppers moving toward shore, and away from the water. Smaller values indicate movement toward the water, and away from shore. The dotted line represents an equal number of beach hoppers moving in either direction. Confidence intervals that do not include the dotted line indicate movement that is significantly different from random.

wrack or upon disturbance by waves or wind. These beach hoppers display an impressive ability to navigate quickly back towards the wrack line from tens of meters away – beach hoppers removed from their natural habitat and placed in the water quickly swim towards shore and hop directly towards the wrack line (pers. obs.). Similarly, beach hoppers placed on dry sand above the wrack line navigate directly towards the water to reach the wrack line. In plastic trays in this experiment,

beach hoppers displayed the same substrate-dependent behavior, moving towards the shore in wet environments and towards the water in dry environments (Figure 1).

This ability to orient appears to be aided by both visual and magnetic cues (Figure 1). Visual cues are used by many animals for orientation and magnetic cues are more commonly used than once thought (Wiltshko and Wiltshko 2005; Lohmann et al. 2007). Life forms as divergent as bacteria (Blakemore 1975) and loggerhead sea turtles (Lohmann 1991) have been demonstrated to use geomagnetic cues for orientation. In that sense, the use of both visual and magnetic cues by beach hoppers may not be entirely different from the way in which many animals orient. Importantly though, here the use of different cues was context-dependent, as the beach hoppers in this study used visual cues in water and magnetic cues on dry sand. Beach hoppers only navigated poorly in the water when the visual cues were removed, but only navigated poorly in dry sand when the magnetic cues were removed.

Work with Mediterranean amphipods suggests that multiple cues can be used in conjunction with one another, or as redundant cues for navigation (Ugolini et al. 1986). Studies in a mid-Atlantic species (*Talorchestia longicornis*) suggest that different cues are used in a hierarchy, with amphipods preferring to use a sun compass over beach slope and landmarks as cues (Walsh et al. 2010). In this northern Florida system, on both substrate types, removing both cues appeared to have no further effect than the removal of a single cue, suggesting that use of one cue does not depend on the other, nor do cues appear to be redundant. Rather, the use of cues was substrate-dependent and implies that different cues are more advantageous, or can be more easily perceived, in different environments.

This study only manipulated two of the possible cues that beach hoppers may use for orientation. Also, note that the manipulation of light cues by placing amphipods inside of a covered bucket, actually manipulated several cues, including solar, wind, or detection of the slope of the landscape. Additionally, placement of a magnet on each tray may have physiological effects on beach hoppers unrelated to orientation, but this seems unlikely given that beach hoppers behaved normally in the water when a magnet was present. Further work in this north Florida system, as well as on other sandy beaches with similar species, could explore the exact cues that amphipods are using and determine experimentally the benefits of different cues in different environments.

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