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Behavioural adaptations of two sympatric sandhoppers living on a mesotidal European Atlantic sandy beach

Filipa Bessa [a, *], João Carlos Marques [a], Felicita Scapini [b]

[a] IMAR-CMA Marine and Environmental Research Centre, Department of Life Sciences, University of Coimbra, 3004-517 Coimbra, Portugal
[b] Dipartimento di Biologia, Università di Firenze, Via Romana, 17, 50125 Florence, Italy

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ABSTRACT

Behavioural adaptations of supralittoral species on sandy beaches are expressed as responses to environmental changes and constitute a key factor in their survival and evolution. Two sympatric talitrid amphipods (*Talitrus saltator* and *Britorchestia brito*) from a mesotidal exposed sandy beach on the European Atlantic coast (Portugal) were compared as regards orientation and littoral zonation patterns under natural conditions. Orientation experiments were carried out during spring and summer 2011 and 2012 at Quiaios beach, a highly dynamic exposed sandy beach. Multiple regression models were fitted to the angular data and the environmental effects on orientation were investigated for each species. Both talitrids were shown to be well orientated towards the shoreline and finely adapted to the mesotidal environment but a different use of local cues and climatic features between the two species was apparent. *T. saltator* showed a lower precision in the orientation performance (with a bimodal distribution sea- and land-wards), with less dependence on the sun cues and higher dependence on climatic features. In addition, the zonation of *T. saltator* was across the land–sea axis during both seasons. For *B. brito* the landscape vision, sun visibility and the tidal range enhanced the orientation to the shoreline. On this mesotidal Atlantic beach, *T. saltator* appeared to have a more flexible orientation with respect to *B. brito*, which appeared to be more dependent on the conditions offered by the intertidal zone, a behaviour confirmed by its restricted zonation below the high tide mark. Consequently, *T. saltator* showed a more flexible behaviour that may be considered an important evolutionary adaptation to dynamic and mesotidal sandy beaches.

1. Introduction

Exposed sandy beaches are extremely dynamic habitats, in which resident faunal patterns are well correlated with the physical environmental features, such as sediment properties, beach slope and intertidal swash climate (McLachlan and Brown, 2006). This concept has been widely tested and proposed as a general paradigm of sandy beach ecology (Defeo and McLachlan, 2005, 2011; McLachlan and Brown, 2006).

Sandy beaches are subject to periodic and predictable fluctuations (night–day, seasons and tides) and sandy beach macrofauna are finely adapted to the beach conditions, exhibiting specific adaptations including mobility, activity rhythms, changes in zonation and orientation (Defeo and Gomez, 2005; McLachlan and Brown, 2006). Consequently, measurements of behavioural traits may constitute a suitable indicator of species responses to environmental variations, since behaviour is correlated with the physiological changes exhibited by the animals under different environmental constraints (Scapini, 2006).

For decades, crustaceans were one of the most studied invertebrate taxa in behavioural research on sandy beaches (Pardi and Papi, 1953; Hazlett, 1995; Scapini, 2006). In Italy, Pardi and Papi (1953) demonstrated for the first time the ability of talitrid amphipods to use the sun compass to orient and maintain the optimal direction towards the safe zone near the shoreline. This behaviour was suggested as an important factor in their success in the supralittoral zone of exposed sandy beaches. Talitrids use behavioural strategies to avoid dehydration and submersion, performing nocturnal migrations to feed on stranded debris and recovering the wet sand stretch at the drift line (Scapini et al., 1992). Through "zonal recovery" talitrids tend to reach the optimal beach zone by orientating perpendicular to the shoreline both sea- or land-wards when they have been displaced by environmental fluctuations (e.g., higher temperatures caused by insolation) or other stressful

* Corresponding author.
E-mail address: afbessa@uc.pt (F. Bessa).

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conditions (e.g., predators, human trampling) (for a review see Scapini, 2006).

The sun compass represents the most reliable mechanism used by sandhoppers on a beach to perform a zonal recovery during the day, however, landscape vision, beach slope, habitat dynamics (e.g., tidal changes) and seasonality of climatic conditions, may influence the orientation performance of talitrids on sandy beaches (Scapini et al., 1997, 2006; Fanini and Scapini, 2008). In addition, beach morphology and ecology were also found important in determining the talitrid zonation along the beach (Colombini et al., 2002).

Scapini (2006) postulated that sandy–beach talitrids inherit a set of possible behavioural responses, of which selective pressures will act on the survival of individuals adopting the most suitable behaviour in the particular conditions they live. Thus, in these species inherited behavioural traits are coupled with a learning ability to modify the responses according to particular conditions. In addition, the need to cope with a highly variable physical environment, sandhoppers need to adjust their behaviour also to avoid intra- and inter-specific competition for space and food (Colombini et al., 2002; Lastra et al., 2010). Since niche partitioning increases resource exploitation by diverse species, differences in time and space zonation in supralittoral species are the strategy used to allow the coexistence of sympatric species (Fallaci et al., 1999; Bouslama et al., 2009; Lastra et al., 2010). Moreover, individuals often vary in their degree of behavioural adaptation, and species in which behavioural patterns are more flexible, have individuals more responsive to the variation of environmental stimuli (Brown, 1996). In addition, it is widely recognised that physiological capacities and tolerance of talitrid species with respect to specific abiotic factors (e.g., salinity, temperature) may limit their abundance and geographic distribution, but also their behavioural performances (Spicer and Gaston, 1999; Scapini, 2006).

Among the supralittoral species on temperate sandy shores, we focused the abundant sympatric talitrids *Talitrus saltator*(Montagu 1808), which are widely distributed throughout the northern temperate zone (European Atlantic coast and Mediterranean Sea) (Marques et al., 2003; Scapini, 2006) and *Britorchestia brito* (Lowry and Bopiah, 2012) (formerly *Talorchestia brito*; Stebbing 1891), which often occurs in sympatry with the former species on Atlantic beaches though rarely on Mediterranean ones (Vader, 1970; Scapini et al., 2002; Gonçalves et al., 2003; Lastra et al., 2010; Fanini et al., 2012).

The ecological relationships between environmental features and behavioural adaptations of *Talitrus saltator* have been widely studied, especially on the Mediterranean coasts (Scapini et al., 2005; Scapini, 2006; Fanini et al., 2007; Colombini et al., 2013; Scapini, 2013). In contrast, on the European Atlantic coast, research studies where mainly focused on the ecology and dynamics of *T. saltator* populations (Williams, 1978; Anastácio et al., 2003; Marques et al., 2003; Gonçalves et al., 2009) with behavioural studies being performed only on the British and French coasts (Williams, 1995; Scapini, 1997; Fallaci et al., 1999; Scapini et al., 1999; Gambineri et al., 2008; Rossano et al., 2009). For *Britorchestia brito*, population dynamics was also studied on the Portuguese Atlantic coast (Gonçalves et al., 2003), but the behavioural adaptations of both species to this coastal environment were never recorded.

The overall outcomes from the behavioural studies are in accordance with the fact that behavioural responses of talitrids may vary according to the habitat and physical conditions (exposure and tidal ranges) from specific environmental contexts. In fact, the orientation of *Talitrus saltator* and *Britorchestia brito* in sympatry recorded by Scapini et al. (2002) on a microtidal Mediterranean beach in northern Tunisia and by Fanini et al. (2012) in a microtidal Atlantic coast in north-western Morocco revealed a different use of sun and local cues in the individual behavioural performance of these species. In addition, comparing populations from Mediterranean and Atlantic European beaches, the latter are expected to orient mainly on terrestrial visual cues (Williamson, 1951; Edwards and Naylor, 1987), while the former tend to rely more on sun orientation (Pardi and Ercolini, 1986; Scapini et al., 2002, 2005).

Therefore, we predict that sympatric talitrids living in the highly dynamic conditions offered by mesotidal sandy beaches in the European Atlantic coast might need to adopt specific mechanisms of spatial and temporal variations in their behavioural strategies to cohabit in this environment and avoid potential inter-specific competition. It was hypothesised that these sympatric talitrids may differently use environmental cues as compared with populations on microtidal Mediterranean beaches. In addition, we tested the hypothesis that a better orientation is expected for the species that is zonated more seawards and is less tolerant to temperature fluctuations (Colombini et al., 2002), and that a higher behavioural flexibility is expected for the more robust and resistant species (Morrit, 1987). The aim of this study was therefore to compare the behavioural adaptations of two sympatric sandhoppers (*Talitrus saltator* and *Britorchestia brito*) inhabiting a dynamic mesotidal Atlantic sandy shore, namely, the orientation performance and zonation patterns. The comparison between the adaptations of these two sympatric talitrid species from both mesotidal and microtidal beaches from the Atlantic and Mediterranean coasts were also evaluated.

2. Methods

2.1. Study site

Field studies were carried out at Quiaios beach (40°12′21″ N, 8°53′48″ W) on the European Atlantic coast in Portugal (Fig. 1). This relatively undisturbed beach has a mean width of about 100 m and is backed by small dunes of about 2 m height (Gonçalves et al., 2009). According to the McLachlan (1980) scheme, Quiaios is classified as a very exposed beach (exposure rate: 16). This coastal area, located in the central region of Portugal presents a warm temperate Atlantic-Mediterranean climate and semi-diurnal tides with maximum amplitude of about 3.5 m (Gonçalves et al., 2009). The investigated area is characterized by a maritime climate with mild winters and cool summers. The thermal amplitude is low and advection fog is frequent throughout the year, even during summer mornings (Danielsen, 2008).

Previous studies performed at Quiaios beach showed that the macrofauna community diversity inhabiting this area was relatively scarce (about 14 species) and that crustaceans were the most abundant taxon. Among them, the dominant species were the talitrid amphipods *Talitrus saltator* and *Britorchestia brito* and the oniscoidean isopod *Tylos europaeus* (Gonçalves et al., 2009; Bessa et al., 2014).

2.2. Orientation experiments

The orientation of the two sympatric talitrids *Talitrus saltator* and *Britorchestia brito* were tested at Quiaios beach during spring (May) and summer (July) 2011 and during the same months in 2012 (four experimental sessions in total). The highest temperatures in this temperate Atlantic area are reached during the spring-summer seasons (Gonçalves et al., 2009), and high temperatures are suitable to test orientation capabilities in these species (Scapini, 2006). The arena experiments during the day simulate the natural situation of talitrids that may emerge from the sand under stressful conditions such as predators or waves during the high tides, and permit to evaluate their zonal recovery abilities.

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