Behavioural Processes 113 (2015) 13–23

Contents lists available at ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

Sandhopper orientation under natural conditions: Comparing individual tracks

Simone Gambineri*, Felicita Scapini

Department of Biology, University of Florence; Via Romana, 17, 50125 Florence, Italy

ARTICLE INFO

Article history:
Received 22 September 2014
Received in revised form 2 December 2014
Accepted 26 December 2014
Available online 30 December 2014

Regional terms:
Europe
Mediterranean
Italy
Tuscany
San Rossore beach: 43°42′46″ N, 10°16′41″E

Keywords:
Talitrus saltator
Orientation behavior
Orientation track
Track classification
Experience of natural conditions
Wind direction

ABSTRACT

The analysis of animal movements may help to understand orientation strategies. While there have been many studies on sandhoppers' orientation mechanisms through the analysis of their orientation angles, no attempts have been made to analyze individual tracks under (varying) natural conditions. The species *Talitrus saltator* (Montagu, 1808) has the ability to recover the optimal zone of the beach at or below the drift-line and burrow into moist sand when released in the upper beach during the day. On dry sand sandhoppers typically jump and leave tracks; we measured the tracks in relation to the starting point. For each track we calculated: the mean angle of direction, distance covered from the starting point, number of jumps, number of effective turnings, rectilinearity and efficiency (how well the track was directed to the goal). We proposed a classification of the tracks based on both rectilinearity and efficiency. Freshly collected adult individuals from the population of San Rossore beach (Pisa, Italy) were compared to laboratory-born ones so as to highlight eventual differences related to experience. Most of the wild individuals made tracks with high rectilinearity and efficiency. This good orientation suggests that these individuals had developed experience of their beach rapidly recovering the optimal zone. Laboratory-born individuals showed a higher scatter in orientation and winding tracks. The factors that influenced the individuals during their movements could also be inferred by the track course. In addition to the sun azimuth (sun compass), wind direction appeared to be a major factor influencing orientation. The individuals released with onshore winds were more efficiently oriented seawards than those released with winds from other directions.

1. Introduction

1.1. Why study animal tracks?

Orientation tracks of animals are generally studied to analyze the geometry of trajectories (Benhamou, 2004; Knaden and Wehner, 2005), understand orientation strategies (Bonadonna et al., 2005; Gurarie et al., 2009), or see what can happen in the event of damage to a body structure involved in orientation (Kraus-Epley and Moore, 2002). The study of tracks may be complex because tracks have both temporal (time series) and spatial (linear and circular) components. *Talitrus saltator* (Montagu, 1808) (Crustacea, Amphipoda) sandhoppers move by jumping, therefore making irregularly broken tracks unlike running, swimming or flying animals, which move in a continuous way, allowing for analyses of regular divisions of the path course (Bonadonna et al., 2005). Generally, orientation experiments on sandhoppers have been performed in a circular arena to analyze only the first response of the individuals to the orientation cues (Scapini, 1988; Scapini et al., 2005; Gambineri et al., 2008). Pardi and Papi (1953) described these amphipods' tracks recorded, but did not perform an analysis of them. In further sandhopper orientation studies, the analysis was limited to the final direction of the track, without considering the total course from the starting point (Scapini, 1995; Borgioli et al., 1999a). However, when the behavior of single individuals is analyzed, this is important to understand their response to various cues, the effect of experience as well as behavioral plasticity (Scapini et al., 1988). The purpose of this study was to make the first ever analysis of the entire track made by *T. saltator* when released under natural conditions, tackling the problem from a qualitative and quantitative point of view, considering the peculiar characteristics (jumping behavior on an unsuitable dry substrate) and needs (a wet substrate to burrow into) of the animals studied. We propose here a track classification for comparing the orientation of

* Corresponding author. Tel. +39 0552755150.
E-mail address: simone.gambineri@unifi.it (S. Gambineri).

http://dx.doi.org/10.1016/j.beproc.2014.12.007
0376-6357/© 2015 Published by Elsevier B.V.

different individuals relating the type of track to the meteorological conditions during the release and the individual experience.

1.2. Open questions in T. saltator orientation

T. saltator is a common dweller of Mediterranean and eastern Atlantic sandy beaches, where it performs its whole life cycle without dispersal stages. The species has the ability to recover the optimal zone of the beach in the supralittoral zone to avoid dehydration when dislodged from the burrowing sites during the day, orienting mainly with sun compass (Scapini et al., 1985), slope (Ercolini and Scapini, 1974) and landscape features (Ugolini et al., 1986). On Mediterranean beaches a spontaneous dislodgement of part of the population was observed near the waterline as a consequence of waves, tides, rainfall, or the action of predators, followed by a recovery seawards (Scapini, 1997). Theoretically, when individuals are displaced in the upper beach, they orient to the theoretical escape direction seawards (TED) following a trajectory nearly perpendicular to the shoreline (Pardi and Papi, 1953). The sun compass was shown to be genetically fixed in those populations where the shoreline had not changed in the long term (centuries), while on highly dynamic, eroded or accreting shorelines (changing in the medium term of years or decades) sandhoppers tend to scatter in various directions, or to orient on the basis of local landscape features (Scapini et al., 1995; Borgioli et al., 1999b; D'Elia et al., 2001). Scattering can depend on genetic variation or behavioral flexibility. Intra-population genetic variation was shown in populations from relatively stable beaches, thus making changes in behavioral adaptation possible when shorelines gradually change; however, under natural conditions the genetic variation can be "masked" by experience (Scapini and Buiatti, 1985; Scapini and Fasinella, 1990; Ketmaier et al., 2010). A learning capability, based on the calibration of sun compass to local landscape references, was observed in populations from highly dynamic beaches near river mouths (Ugolini and Macchi, 1988). This ability would allow displaced individuals to colonize new or rapidly changing shorelines. An orientation to landscape features was first demonstrated by Williamson (1951) and analyzed with respect to the sun compass by Hartwick (1976) and Ugolini et al. (1986). In both the latter cases, the populations responded differently to landscape features, depending on the prominence of visual cues landwards, or on a differing ability of the populations to use the sun compass. Scapini et al. (2005) showed that the precision of sun orientation is closely related to the morphodynamics of the beach in which sandhoppers live. Other orientation cues were also shown to be used by talitrids under natural conditions, e.g., beach slope (Ercolini and Scapini, 1974). The possible effect of wind direction on sandhopper orientation was excluded in previous experiments by using screened arenas, or was considered a disturbing factor (Borgioli et al., 1999a; D'Elia et al., 2001; Gambineri and Scapini, 2008). However, the regularity of winds on beaches with respect to the land-sea axis make wind a good candidate cue in addition to the more studied visual orientation cues. The wind may have two effects, by passively displacing jumping individuals and helping their course seawards (offshore winds), or acting as an orientation cue when it blows from the sea conveying sea odours (onshore winds). Winds blowing from other directions may act as disturbing factors requiring corrective turning during orientation.

The present study analyses sandhopper movements under natural conditions, to understand orientation strategies, in particular by comparing the tracks observed inexpert and inexpert individuals. The question of the influence of wind direction was approached in this study by comparing orientation with winds from various directions.

1.3. Hypotheses tested through the study of tracks under natural conditions

Based on the literature, the following hypotheses were formulated a-priori for this study:

1) the individual tracks of wild *T. saltator* are better oriented to the shoreline, i.e., are more efficient, than those of laboratory-born individuals of the same size;

The effect of wind direction on sandhopper orientation had not been previously tested and three hypotheses could be suggested:

2a) the wind is a disturbing factor and the animals correct their tracks with turnings when the wind is from a different direction with respect to the goal (the shoreline);

2b) the wind favors the movement while the animals are jumping and tracks are more rectilinear when the wind is blowing in the direction of the shoreline (offshore wind);

2c) the wind acts as an orienting cue as it conveys the odors from the sea; consequently sandhoppers are better directed to the sea with onshore winds.

To distinguish between the last three hypotheses, releases with winds blowing from different directions were necessary; thus the study was carried out in different seasons and times of day.

2. Materials and methods

2.1. Study site

Orientation experiments were carried out in spring–summer 2000 on an exposed beach located in the Natural Regional Park of Migliarino – San Rossore – Massaciuccoli (Pisa, Italy, N43°42′46″ E10°16′41″), where *T. saltator* sandhoppers are abundant. The orientation capabilities of this population and innateness of the sun compass were known from previous studies carried out both on the beach and far from it, offering a sound background to the study of the tracks (Scapini, 1979; Ugolini and Scapini, 1988; Borgioli et al., 1999a, b; Scapini et al., 1999; D'Elia et al., 2001; Gambineri and Scapini, 2008; Ugolini et al., 2009; Fanini et al., 2009; Ugolini et al., 2012a, b). San Rossore beach is located at a distance of about three km from the Arno River mouth and has been subject to strong erosion from the sea, necessitating mitigation measures to contrast the loss of sediment, such as filling it in with material of land origin (wood and gravel), groyne building and beach nourishment (Aminti, 1997; Cipriani et al., 2001; Fanini et al., 2007). All the orientation experiments were carried out on the same beach.

2.2. Orientation experiments

We tested a total of 300 individuals of the *T. saltator* species, 260 wild and 40 laboratory-born, singly and once in 16 experimental sessions from March to September: 10 during the day (around noon), 3 after dawn and 3 before sunset, so as to have different wind directions. In each session about 20 individuals were tested successively under the same conditions. The sand surface was cleaned between releases, thus preventing possible tactical and/or odor effects from the previous tracks. Wild adult individuals were captured on the beach on the same day as the experiment and kept in the shade for a maximum of two hours in a opaque white plastic container partially filled with moist sand, so that their motivation to orient seaward would not change with respect to individuals buried in the moist sand under natural conditions. To obtain the laboratory-born individuals for the experiments, in March we collected about 100 adult sandhoppers that were then transported to a laboratory in Florence, where they were reared in groups of about 20 individuals inside 26 × 15 × 17 cm containers, with the bottom covered by a 5 cm layer of wet sand from the collection site. The