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RESEARCH ARTICLE

Felicita Scapini · Lorenzo Chelazzi · Isabella Colombini
Mario Fallaci · Lucia Fanini

Orientation of sandhoppers at different points along a dynamic shoreline in southern Tuscany

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Abstract Orientation experiments were carried out on *Talitrus saltator* (Crustacea Amphipoda) at four points along 3 km on a dynamic sandy beach inside the Maremma Regional Park (Grosseto, Italy) to highlight behavioural variation related to distance from a river mouth, to erosion or accretion of shoreline, and to human trampling on the beach. Tests were performed using circular transparent Plexiglas arenas, contemporaneously at the four points. Replicates were made in 2 different months (September 2002 and May 2003), on 2–3 successive days, in the morning and afternoon. The distributions of the angles of orientation were compared for the different points and seasons, and multiple regression analysis was performed to test the effects of environmental and intrinsic variables on orientation. Sandhoppers showed the highest scatter at the eroded shoreline, intermediate scatter at the accreting beach most distant from the river mouth, and consistent orientation seaward at the least disturbed point. Orientation of sandhoppers was significantly affected by season, global radiation, time of day, distance from the river mouth, and human trampling. Sex and air humidity were of minor significance in the multiple regression model. The results, on the one hand, confirm plasticity in orientation of sandhoppers living on a dynamic shoreline, and on the other hand, show that variation in orientation could potentially be used as a bioindicator of shoreline changes.

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F. Scapini (✉) · I. Colombini · L. Fanini
Dipartimento di Biologia Animale e Genetica,
Università di Firenze, Via Romana 17, 50125 Florence, Italy
E-mail: scapini@dbag.unifi.it
Fax: +39-55-222565

L. Chelazzi · M. Fallaci
Istituto per lo Studio degli Ecosistemi, Sezione di Firenze, 50125 Florence, Italy

Introduction

This article describes the sun orientation behaviour of the sandhopper *Talitrus saltator* (Crustacea: Amphipoda), collected at sites with different geophysical characteristics, on a single beach in Tuscany, Italy, and considers the potential of such behaviour patterns as indicators of sand-beach dynamics. This amphipod lives on sandy beaches above high tide marks, where it is more concentrated near the water's edge in summer and dispersed higher on the beach up the dune in winter (Fallaci et al. 2003). It performs regular migrations across the beach at night to feed on detritus and returns after dawn to the shoreline, where it burrows in the wet sand (Scapini et al. 1992). When disturbed during the day, or when the sand dries out, it regains the wet zone seawards, orientating visually with respect to landscape at night and to the sun after sunrise (Scapini et al. 1997). Previous research conducted on different beaches in Italy, the United Kingdom, and Tunisia had shown that talitrid populations orient significantly seawards on stable shorelines and are more scattered on eroded beaches, and on beaches affected by construction and human frequentation (Scapini et al. 1995; Borgioli et al. 1999a; ElGtari et al. 2000).

Conventional methods of monitoring change in sand-beach features, unless carried out continuously, only show snapshots of such changes. Yet sand-beach animals have continuous experience of environmental factors at the site at which they live, and the behavioural and physiological adaptations of key animal species are potential bioindicators of changes in shorelines. Behavioural adaptation in particular could provide a means of estimating environmental change over a time scale equal to the life-span of the species, or that of a few generations, if it is inherited. However, these bio-assays need to be validated. Changes in animal behaviour under natural conditions may be affected by several factors, both external and internal (Borgioli et al. 1999a, 1999b). One way to avoid such variation is by the use of laboratory experiments, but laboratory conditions often affect behaviour in an uncontrolled and undesirable way. In particular, captivity per se has been shown to influence the sun orientation of sandhoppers (Scapini 1986; Scapini et al. 1988). An alternative strategy is to analyse behavioural variation under natural conditions with replicates, using multi-factorial analysis, as suggested by Underwood and Chapman (1985). Presnell et al. (1998) and Marchetti and Scapini (2003) have developed multiple regression models for angular data. These models were used to test the contemporaneous effects of several environmental variables on orientation of two sympatric species of sandhoppers on a Tunisian beach, highlighting differences in orientation between *Talitrus saltator* and *Talorchestia brito* (Scapini et al. 2002). In that study, the influence of environmental factors such as sun azimuth and landscape vision on orientation, and of air temperature, humidity and season as motivators of behaviour, was confirmed under natural conditions. The objective of the current study was to highlight biological differences at different points along the same beach, with a view to investigating the relationship between sand-beach dynamics, human trampling, and variation in orientation behaviour of sandhoppers.

Materials and methods

Study site

The study site is located inside the Maremma Regional Park (Grosseto, Tuscany, Italy) and is an almost straight beach, extending about 6 km eastwards from the mouth of the Ombrone River (42°39′25′N, 11°0′51′E) on its left side; the site offers an example of dynamic shoreline, with two major impacts. One is an erosion gradient from the river mouth to about 4 km and accretion in the rest of the beach, and the other is the impact of trampling by visitors related to the main accesses to the beach.

Four transects were chosen along the beach, which differed in their erosion/accretion dynamics, at about 3,000, 4,000, 5,000, and 6,000 m from the river mouth, which was taken as reference point 0. Nearer to the river mouth no talitrids could be found. The dune was severely eroded at point 3,000, well developed at 4,000, had an accreting foredune at 5,000, and was of new formation backed by marshes at 6,000. Different landscapes backed the beach at the different points: prominent dune (3,000, 4,000), low dune and cliff (5,000), very low dune and mountains (6,000). Moreover, the width of the beach at the different points varied, offering more or less compressed gradients across the beach. In each season, profiles of the beach were constructed at the experimental points; sand penetrability was measured each day, and sand samples were collected for laboratory analysis of granulometry, sand moisture, salinity pH, and organic content. Usual ecological methods were used in these analyses (Colombini et al. 2002). Meteorological variables such as air humidity, temperature, atmospheric pressure, and global sky radiation were recorded during the experiments with an electronic weather station positioned on the dune between points 4,000 and 5,000.

The impact of tourists and direct trampling was estimated from the available data on the visitors to the Maremma Park, who can reach the study sites by walking from the nearest car parking area (located at about 2,000 m from the river mouth) or from the route to Collelungo at 5,000 m. We used the numbers of visitors in March–September 2002 and October 2002–May 2003, which presumably had impacted the sandhopper populations in September 2002 and May 2003, respectively. Three levels of "trampling", low, medium, and high, were estimated from these data, assuming a Gaussian distribution of trampling with the mean value at the access to the beach (Caffyn et al. 2002).

Biometrics

Sandhoppers of the species *Talitrus saltator* (Montagu) were collected using pitfall traps positioned above water edge at each point (3,000, 4,000, 5,000, 6,000) the night before each test. Adults thus caught were taken out of the traps early in the morning and kept in containers filled with moist sand prior to testing. At point 3,000 in May the captures were not sufficient to perform the orientation experiments and extra captures were made by removing the sand by hand. At each station the abundance of the sandhopper population was estimated using two transects of pitfall traps from the dune to the shoreline, which were kept active for 48 h in September and 72 h in May (L. Chelazzi et al., unpublished). Other samplings were made at the same points on the beach to perform genetic analyses of the sub-populations (V. Ketmaier, unpublished).

All care was taken to ensure exactly the same experimental conditions at all points. Four trained teams used identical orientation arenas at the same time of day, to avoid introducing uncontrolled variables (Scapini and Pardi 1979; Borgioli et al. 1999a, 1999b). The arenas, one at each point, were positioned horizontally on the beach, 1 m above the beach surface to hide the experimenters from the sandhoppers' view. They had a diameter of 40 cm and had 72 pitfall traps at the circumference, each subtending 5°. Sandhoppers were inserted via a transparent tube through the transparent cover and positioned on the floor (covered with white paper) of the arena, at its centre. After 1 min, during which they were allowed to observe their surroundings, the tube was lifted and the animals released. They were then trapped at the circumference of the arena, and their angles of orientation with respect to the north were registered. At each site, 40 individuals were tested in each experimental session. These were released in four groups of 10 animals every 15 min, and the 1-h sessions were repeated in the morning starting at 09:00 and in the afternoon of the same day starting at 15:00, on consecutive days within the same month, 18 and 19 September 2002 and 19, 20, and 21 May 2003.

Each individual tested for orientation was preserved in a tube of 75% alcohol to allow further observations and measurements in the laboratory. We determined sex by the presence of oostegites and of setae on the oostegyte in females and by the presence of a penis in males. A few juveniles were present in the samples of May, and they were discarded from the analysis. We measured the length of the cephalon (Marques et al. 2003) and counted the number of segments on the right and left second antennae (Williams 1978). From the latter figures we calculated an asymmetry index, comparing the number of articles of the right and left antenna (Scapini et al. 1999):

log (number of tagma of the right antenna/
number of tagma of the left antenna)

We analysed the morphological factors to ascertain whether intrinsic factors may have influenced the orientation of the samples. In previous articles differences in orientation linked to intrinsic characteristics of the sandhoppers had been highlighted (Borgioli et al. 1999a, 1999b).

Statistical analysis

For each point and each season, we analysed the angular distributions using the statistics of circular distributions. We calculated the mean vectors (mean directions and mean vector lengths) and sample circular dispersion and estimated density curves with the kernel method (Fisher 1993; Marchetti and Scapini 2003).

To estimate the contemporaneous effects of environmental variables and factors, we compared multiple linear regression models adapted to angular data. We considered the angles of orientation as response variable, and the environmental (geophysical, meteorological, and linked to human trampling) and intrinsic (biometric and sex) variables as influencing factors. We started with an additive model including all variables and factors: season, distance from the river mouth, trampling, day, time of day, air humidity, air temperature, atmospheric pressure, global radiation, sex of the animal, cephalic length, and asymmetry index of the antennae. Environmental factors, such as substrate granulometry, pH and organic matter content, beach slope and width, resulted correlated with distance and were thus included in this factor. The time of day also included the variation of sun azimuth. The cephalic length was correlated with the number of tagma of the antennae as both are indices of age. Factors related to the population, such as abundance and genetic variation, were also correlated with distance and were included in this factor. Then simpler nested models were compared using the Akaike information criterion, and the best model was chosen, which had the highest likelihood penalized with the number of parameters (Scapini et al. 2002; Marchetti and Scapini 2003). The effects of single factors and variables were then estimated by comparing the best model with a simpler one not containing the factor or variable. The difference between the likelihood of the two nested models gave the probability levels for the factor or variable under test.

Results

Data regarding the beach profiles, which changed from the erosion zone (3,000 and 4,000) to the accretion zone (5,000 and 6,000) and also varied between the two seasons, are shown in Table 1. Changes were most marked at point 4,000 where the beach became 10 m shorter and steeper between the two experimental sessions. The accretion of beach width at 5,000 and 6,000 was of about 4 m. The mean slope slightly decreased at 5,000 and increased at 6,000. Substrate features were correlated with the distance from the river mouth. Substrate data have been analysed in depth (L. Chelazzi et al., in preparation). The orientation of the shoreline and corresponding TEDs (theoretical escape directions seawards, perpendicular to the seashore) changed slightly from 200 to 220°, from point 3,000 to 6,000, and small changes were observed between the two experimental sessions (September 2002 and May 2003) (Table 1). The abundance of sandhoppers at the four sites increased with distance in

Table 1 Beach characteristics in the two seasons, at the four study sites at different distances from the river mouth

Distance from river mouth (m)	Season	Beach profile data: Beach mean slope (%)	Beach width (m)	Orientation (°)	Population abundance (number of captures in the transects)	Trampling level
3,000	September	10.2	14	200	5	High
	May	9.8	13	205	9	Low
4,000	September	2.9	32	205	419	Low
	May	3.8	22	205	218	Low
5,000	September	2.2	30	213	1704	Medium
	May	1.8	34	210	599	Medium
6,000	September	0.6	38	220	6133	Low
	May	1.6	42	215	1365	Low

both seasons. Therefore an effect of abundance on orientation could not be separated from that of distance. The data on the macrofauna community are analysed elsewhere (L. Chelazzi et al., in preparation). Also genetic variation of the sandhopper sub-populations was correlated with distance (V. Ketmaier, in preparation). Trampling was high at point 3,000, medium at point 5,000, and low at points 4,000 and 6,000. The data on visitors showed a clear seasonal variation at point 3,000, with 150,000 entrance tickets sold from May to September and only a few in the other months, and the visitors coming to the entrance at point 5,000 were 25,287 and 20,775 in April–September and October–April, respectively. The meteorological variables varied with the season and the day. In Fig. 1 we plot the mean values and variation of air temperature and humidity, atmospheric pressure and global radiation, at the times of the experiments. Air humidity was significantly lower in May on the first (Fig. 1: day 3) and third (Fig. 1: day 5) day (compare the confidence intervals of the means). On these days global radiation was also significantly higher than in September. The scatter of values on the second day of the May experiment (Fig. 1: day 4) derived from a sudden and temporary rain fall during this day.

Intrinsic factors, such as cephalic length and antennal asymmetry, did not vary significantly between samples. The protocol required the use of adult individuals only and juveniles were discarded from the samples. The sex ratio at the four sites was male biased, particularly at point 3,000 compared to the other points (Pearson $\chi^2 = 55.037$; $P < 0.0001$, $df = 3$).

The orientations of the samples tested at points 3,000, 4,000, 5,000, and 6,000, in the two seasons (September and May) are shown in Fig. 2. The mean angles of orientation relative to the sun changed during the day and were maintained approximately in a seawards direction (south–southwest) at each experimental point, but the mean angles of orientation also changed with location along the beach (Table 2), becoming more westwards orientated from the point at 3,000 to that at 6,000, in both seasons, except for 6,000 in May. The trend of change of mean orientation roughly corresponded to change of TED (the direction perpendicular to the shoreline). The mean resultant lengths, which are indexes of concentration, were high at 5,000 in both seasons, and at 4,000 in May; were low at 3,000 in both seasons, and at 4,000 in September, and were intermediate at 6,000 in both seasons. The circular dispersions of the samples varied conversely, from 0.681 (5,000 in September) to 3.984 (3,000 in May). Comparing the orientation at each point in the two seasons, the greatest variability and greatest deviation from TED was observed at 3,000 and the highest concentration seawards at 5,000 consistently in both seasons; at 5,000 small seasonal variation appeared, whereas at 4,000 considerable decrease of concentration was observed between September and May (the circular dispersion decreased by a factor of about 5), while the mean orientation did not vary considerably; on the other hand, a change of mean orientation of 54° was observed at 6,000 between September and May. The density curves were smoother in May than in September, and at point 5,000 compared with the other points; some secondary peaks were observed particularly at 3,000, and a bimodality appeared at 6,000 in May, reflecting a change of orientation from the morning to

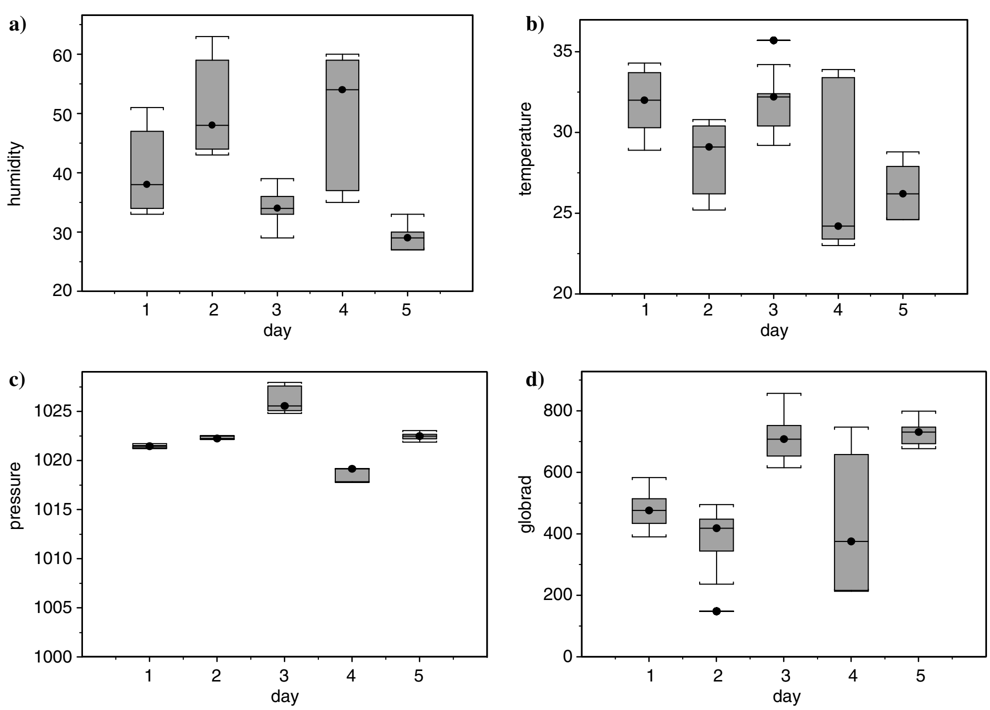

Fig. 1 Variation of (**a**) air humidity, (**b**) air temperature, (**c**) atmospheric pressure, and (**d**) solar global radiation (*globrad*) during the experimental sessions. On the *x*-axis, *1* and *2* are 18 and 19 September 2002, respectively; *3*, *4*, and *5* are 19, 20, and 21 May 2003, respectively

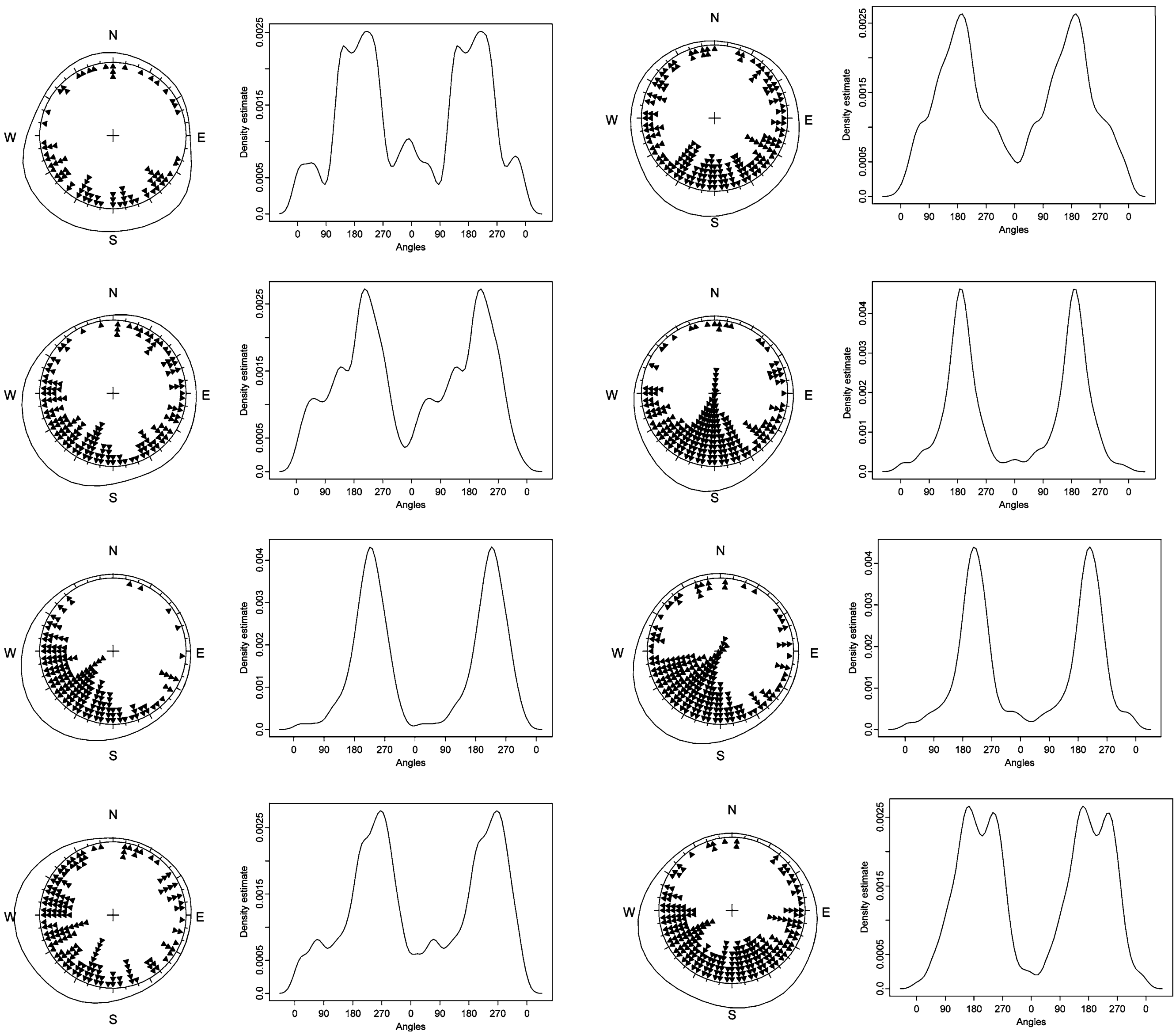

Fig. 2 Orientation of *Talitrus saltator* in the four sites (from *top* to *bottom*: 3,000, 4,000, 5,000, 6,000 m from the river mouth) on the beach at Maremma Regional Park, in September 2002 (*left*) and May 2003 (*right*). Shown are the individual angles, in the *circles*, and the density curves (calculated with the kernel method and reported twice to show circularity). Summary statistics of the orientation distributions are reported in Table 2

the afternoon, in keeping with sun azimuth change (Fig. 2).

Several variables and factors could explain the observed differences in orientation. To analyse the effects of those factors simultaneously, multiple regression analysis was performed on the data, using linear regression models adapted to angular data (SPLM, Scapini et al. 2002; Marchetti and Scapini 2003). Starting from an additive model including all the variables and factors that could affect orientation angles, the following best model was chosen according to the Akaike information criterion (AIC):

$$\text{Distance from river} + \text{Season} + \text{Time of day} + \text{Sex} + \text{Global radiation} + \text{Air humidity} + \text{Trampling Likelihood} = 4076.0849;$$
$$\text{AIC} = 4108.0849;\ \text{df} = 1368$$

We discarded the models including non-informative factors. Air temperature, atmospheric pressure, cephalic length, and the asymmetry index of the antennae did not improve significantly the likelihood of the model, suggesting that the variation of the orientation of the samples did not depend on these variables. The day replicates resulted in not being included in the model. The chosen model above was then compared with simpler nested models excluding one factor or variable at a time, to estimate its influence on orientation (Table 3). Season (two levels: September and May) was found to be the most influencing factor, followed by global radiation and time of day (two levels: morning and after-

Table 2 *Talitrus saltator*. Summary statistics of orientation distributions in the two seasons, at different distances from the river mouth with varying beach profiles. *TED* theoretical escape direction

Distance from river mouth (m)	Season	TED (°)	Mean angle (°)	Mean resultant length	Circular dispersion	Sample size
3,000	September	200	198.5	0.3549	3.313	82
	May	205	179.6	0.3409	3.984	191
4,000	September	205	201.1	0.3208	3.939	163
	May	205	189.5	0.6493	0.738	250
5,000	September	213	226.0	0.6974	0.681	166
	May	210	214.5	0.6464	0.743	231
6,000	September	220	247.1	0.3862	2.802	166
	May	215	192.8	0.4784	2.100	245

Table 3 *T. saltator*. Comparison of the chosen model and nested simpler models to estimate the significance of each factor

Factor excluded	Difference of likelihood	Difference of degrees of freedom	*P*-value
Season	83.5146	2	< 0.001
Global radiation	76.5633	2	< 0.001
Time of day	73.5241	2	< 0.001
Trampling	46.0543	2	< 0.001
Distance from river	21.4614	2	< 0.001
Air humidity	8.2214	2	< 0.10
Sex	6.4290	2	< 0.25

noon). Global radiation reflected seasonal differences, as in May the sun was higher on the horizon than in September, but also differences in sky cloudiness during the experiments (Fig. 1d). The level of trampling, which may significantly affect sandhoppers' abundance and population structure, was significantly reflected in orientation. The distance from river mouth was a highly significant factor. This factor included substrate variables correlated with distance. Air humidity and sex were important in the multiple regression model but influenced variation of orientation only slightly.

The effect of the difference between males and females was analysed more accurately as the multiple regression model included sex as a factor, but sex alone did not explain the observed variation in orientation (Table 4). The summary statistics for male and female orientation at the four points are shown in Table 4, where sex ratios are also reported. The mean angles of orientation were consistently slightly bigger (more westwards oriented) in females than in males, with the exception of point 3,000; the mean resultant lengths were consistently higher for females than males, and circular dispersion was smaller for the latter, showing in general a higher scatter of males.

Discussion and conclusions

The results indicate that there is considerable variation in the sun compass orientation within a single population of *Talitrus saltator* dwelling on an extended sandy beach, and that this is correlated with beach dynamics and tourist frequentation. The correlation observed over a distance of a few kilometres is consistent with earlier observations by Scapini et al. (1985, 1995), Borgioli et al. (1999a), and ElGtari et al. (2000) on solar orientation in *T. saltator* from stable and unstable beaches in Italy, the United Kingdom, and Tunisia and supports the sug-

Table 4 *T. saltator*. Variation of sex ratio with distance and effect of factor sex on orientation

Distance from river mouth	Sex	Sex ratio	Orientation: summary statistics			
(m)			*N* (°)	Mean angle	Mean resultant length	Circular dispersion
3,000	Males	4.06	191	184.0	0.3639	3.278
	Females		47	189.1	0.2854	5.832
4,000	Males	1.13	196	188.8	0.4727	1.796
	Females		174	194.3	0.5046	1.344
5,000	Males	1.17	184	216.1	0.6356	0.847
	Females		157	223.2	0.6942	0.593
6,000	Males	1.23	214	212.2	0.3837	3.119
	Females		174	213.1	0.4134	2.692

gestion that such variation may serve as a bioindicator of sand-beach dynamics and human impact.

In the natural state, differences in orientation behaviour may be attributed to both intrinsic and extrinsic factors, and the results presented above suggest the position of the sampling site along the beach may be an important environmental influence. Greatest difference among the distributions was found in scatter (circular dispersion), although significant variation is also shown in mean angle, which tends to follow the change of shoreline direction (Table 2). The highest scatter was observed in the samples from the eroded part of the beach, point 3,000, which had the highest density of trampling by tourists during the summer. The results at point 4,000 were less consistent. Trampling was here not relevant as this point is far from any access. This part of the beach has been subjected to erosion only recently; an erosion of 10 m of the beach was observed within the time span of the present research (from September 2002 to May 2003). Older cartography shows that this point was in a state of dynamic equilibrium (E. Pranzini, personal communication). The beach at point 5,000 showed slight accretion and has a well-developed foredune. Sandhoppers at that point showed a good and consistent adaptation to the orientation of shoreline during both seasons, as may be seen from the smooth frequency curves obtained (Fig. 2). The level of trampling by tourists at this point was medium and relatively constant throughout the year. The beach at point 6,000 is also accreting, but it is evident that it is a beach of new formation, with a low foredune, backed by marshes. At this point sandhoppers were abundant and scarcely affected by tourist activity (Table 1). However, the distribution of orientation angles shows relatively high levels of scatter and polymodal distribution in their orientation patterns (Table 2, Fig. 2). The latter can be explained in terms of a recent colonisation by sandhoppers from other points coming together on this beach of recent development. The presence of marshes behind the low dune, and the possibility of finding wet sand in other directions than the seashore, could also account for the relative high scatter observed. The theoretical escape direction seawards, perpendicular to the seashore, changed slightly from 200 to 220°, from point 3,000 to 6,000, and the small changes observed between the two seasons (September 2002 and May 2003) are also consistent with a tendency of the shoreline to become straight. Accordingly, the mean directions at the different points gradually changed from 179.6° (3,000 in May) to 247.1° (6,000 in September; Table 2).

Other important environmental factors affecting orientation include season and time of day effects. Except for point 5,000, the distributions and density curves were smoother in May than in September (Fig. 2), suggesting that the sandhopper populations were better adapted to the shoreline during May. This is most evident at point 4,000, where the population appears to be well adapted to the shoreline in May, but scattered in September. This may be related to the dynamics of shoreline as discussed above. The clear bimodality in May at point 6,000 indicates a change of orientation from the morning to the afternoon, following changes in sun azimuth. According to previous results, inexperienced sandhoppers, such as laboratory-born juveniles, show a tendency to orient seawards as the population of origin, but they also express a phototactic behaviour relative to the sun, which could be considered "basic" in the development of solar navigation and probably fundamental in the evolution of navigation behaviour (Campan 1997; Scapini 1999). The phototactic tendency observed at point 6,000 could be related to the fact that a behavioural adaptation to the shoreline is not fixed yet in this population. Another "basic" behaviour would be the orientation with respect to landscape dishomogeneities (Williamson 1951; Edwards and Naylor 1987). In this study, both points 5,000 and 6,000 presented cliffs and mountains in the landscape, which could offer orientation cues to the sandhoppers under natural conditions. It is likely that at 6,000, sandhoppers rely more on landscape than on the sun for their movements across the beach, and in the test conditions, in which landscape view was screened off, most individuals were disoriented or phototactic with respect to the sun. On the other hand, at point 5,000, sun compass (which implies compensation of azimuth differences) was efficiently used by sandhoppers.

Of the intrinsic factors investigated, only sex had an effect on the orientation of *T. saltator* (Table 3). Females were more concentrated than males in both seasons, and this result confirms that of Borgioli et al. (1999b) on Italian populations, although at Zouara on the Tunisian coast males were more concentrated than females during the autumn months and no effect of sex was observed in spring (Scapini et al. 2002). In the present study, the better concentration of females could be interpreted in terms of the need for gravid animals to recover the wet zone near the shoreline more promptly than males, which are more scattered on the beach. The higher scatter of males could also explain the biased sex ratio at point 3,000. At this point the population may be composed mainly of immigrant males coming from other points of the shoreline. Both these hypotheses need further evidence based on ad hoc observations.

In previous research on other beaches from the same coast in Tuscany, Feniglia, Giannella (both located south of the Maremma Park), and Castiglione (located north of the Maremma Park), differences of sun orientation between populations from points distant by a few kilometres on the same beach were observed in experiments under controlled conditions distant from the sea (Scapini et al.1985, 1995). The relationships of the mean direction and the orientation of the beaches were explained in terms of genetic adaptation to a shoreline. Preliminary genetic analyses on the Maremma populations tested for orientation have shown genetic differences between sampling points (V. Ketmaier, unpublished).

Overall, the results of the present study confirm the suggestion that behavioural adaptation of animals living on beaches is correlated to beach dynamics and frequentation by tourists. Behaviour can thus be used as a rapid bio-assay to assess stability or instability of shoreline over a short time. The present data also support the general hypothesis that the major adaptation of organisms living on beaches is plasticity (Brown 1996; Soares et al. 1999). Moreover, the present study shows a gradient of increasing behavioural adaptation of sandhoppers with increasing stability (equilibrium) of the shoreline. It will be interesting to monitor changes of behavioural adaptations related to shoreline changes in the same locality in the coming years. Unfortunately, the population at 3,000 m is rapidly disappearing (Table 1). The point at 6,000 m from the river mouth is apparently a new beach recently colonised by a nearby population, and we would predict an improvement of adaptation with time.

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