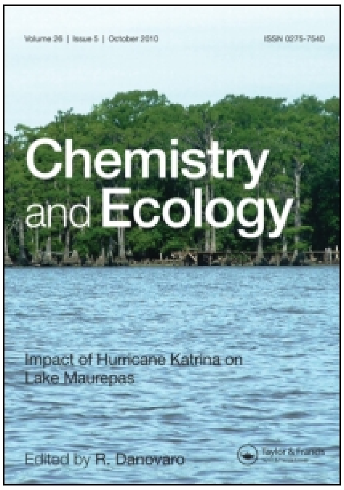

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S. Gambineri[a]; C. Rossano[a]; V. Durier[b]; L. Fanini[a]; C. Rivault[b]; F. Scapini[a]
[a] Dipartimento di Biologia Evoluzioistica "Leo Pardi", Università degli Studi di Firenze, Firenze, Italy [b] Ethologie-Evolution-Ecologie, UMR 6552, CNRS, University of Rennes 1, France

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Orientation of littoral amphipods in two sandy beaches of Brittany (France) with wide tidal excursions

S. Gambineri[a]*, C. Rossano[a], V. Durier[b], L. Fanini[a], C. Rivault[b] and F. Scapini[a]

[a]*Dipartimento di Biologia Evoluzioistica "Leo Pardi", Università degli Studi di Firenze, Firenze, Italy;* [b]*Ethologie-Evolution-Ecologie, UMR 6552, CNRS, University of Rennes 1, France*

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Sandhoppers orient towards the shoreline using a sun compass when they are subject to dry conditions. In this study we analysed the orientation of populations from two sandy beaches with wide tidal excursions (Brittany, France): at Damgan (sea to the South) and at Le Verger (sea to the North). At Le Verger beach *Talitrus saltator* was found together with *Deshayesorchestia deshayesii* (former *Talorchestia deshayesii*). The results of the experiments on sun and landscape orientation showed that the Damgan *T. saltator* oriented better with ebbing tides than with rising tides, while the Le Verger *T. saltator* showed the opposite trend as a response to tides. This is probably related to the differing risk of being swept away by tides at the two localities. *D. deshayesii* was found to be more scattered in orientation than *T. saltator*, probably because it is a recent colonizer of that beach.

Keywords: *Talitrus saltator*; *Deshayesorchestia deshayesii* (former *Talorchestia deshayesii*); orientation; tide; landscape vision; sandy beaches

1. Introduction

On sandy beaches the ability to recover the optimal zone is of paramount importance for those animals that move across the beach to feed and avoid stressful conditions [1]. The morphodynamics of the beaches influences population dynamics and the diversity of macrofauna [2]. Dissipative beaches (*sensu* [3]) favour reproduction more than reflective beaches and host a higher diversity of macrofauna. This trend may not be confirmed in the case of supralittoral and intertidal populations as the zones they occupy differ in harshness [4]. On reflective beaches supratidal populations easily avoid the risk of being swept away, simply by keeping themselves in a safe zone. Behavioural adaptations allow for the colonisation of morphodynamically changing beaches [5]. *Talitrus saltator* (Montagu, 1808; Crustacea, Amphipoda) and *Deshayesorchestia deshayesii* (Audoin, 1826; Crustacea, Amphipoda; former *Talorchestia deshayesii*, [6]; but see Davolos & Maclean [7], Dias & Hassall [8], Lastra et al. [9], Spicer & Janas [10] for the genus' name of the Atlantic and Baltic populations) are semi-terrestrial and live close to the shoreline on sandy beaches of the Mediterranean Sea and the Atlantic Ocean. These species have developed an orientation based on

*Corresponding author. Email: sigam71@libero.it

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sun compass to maintain the wet zone on the beach and recover it when displaced high up on the beach away from the sea. In the latter case they orient to the theoretical escape direction seawards (TED) following a trajectory perpendicular to the shoreline [11–13]. The sun compass is genetically fixed in those populations where the shoreline has not changed in the long term (centuries), while on highly dynamic, eroded or accreting shorelines (changing in the medium term of years or decades) talitrids tend to be scattered or refer to local landscape features [14,15]. Scattering can depend on genetic variation or plasticity. A genetic variation was also shown in populations from stable beaches, accounting for the possibility of changes in behavioural adaptation in case of shoreline changes [16]. A learning capability, based on a calibration of sun compass to local landscape references, was observed by Ugolini & Macchi [17]. This ability would allow displaced individuals to colonise rapidly changing shorelines or new shores. An orientation to landscape features was first demonstrated by Williamson [18] and analysed with respect to sun compass by Hartwick [19] and Ugolini *et al.* [20]. In both the latter cases, populations responded differently to landscape features, depending on their prominence landwards and on a capability of using the sun compass that differed among populations.

There are few studies concerning the orientation of *Deshayesorchestia deshayesii*. Nardi *et al.* [21] showed that the responses of *D. deshayesii* (called *Talorchestia deshayesii* in their paper) from Baltic shores to several stimuli (sun, artificial and natural landscape), were similar to those of *T. saltator*.

The present study analysed the influence of tides on the orientation of talitrid amphipods from Atlantic beaches with reference to sun and landscape vision. The orientation of populations from Brittany's sandy beaches was tested for the first time. We also wanted to confirm that on stable beaches, like those of Brittany, amphipods orient towards the TED. Moreover, we compared the orientation capability of *T. saltator* and *D. deshayesii*, living together on the same beach (therefore subject to the same environmental conditions), for similarities and/or differences.

2. Material and methods

Orientation experiments were carried out in June 2006 on two beaches of Brittany (France) with high tidal excursions: (1) Damgan (N 47° 31′ 04″, W 2° 35′; near Port Navalo; direction of the sea measured at the site where the experiments were conducted, TED = 342°); (2) Le Verger (N 48° 41′ 44″, W 1° 52′ 41″; near Saint Malo; TED: 342°). These coasts are stable and practically unchanged throughout a long period.

We carried out two series of experiments at Damgan and two series at Le Verger. We chose the dates for the experiments on each beach so as to have alternatively rising tide in the morning and ebbing tide in the afternoon and vice versa. We carried out experiments with ebbing tide during the morning and rising tide during the afternoon at Damgan on 16 June 2006 and at Le Verger on 27 June 2007; then we repeated the experiments with rising tide in the morning and ebbing tide in the afternoon at Damgan on 22 June 2006 and at Le Verger on 20 June 2007 (Figure 1). The tide forecast was calculated using the free WXTide32 software at the places nearest to our study sites: Port Navalo for Damgan and Saint Malo for Le Verger.

Every experimental series was repeated twice: in the morning at 9:00 (solar time; France time was 11:00) and in the afternoon at 15:00 (solar time; France time was 17:00). We collected all the samples needed for the experiments randomly. In each series 8 samples of 10 individuals were tested successively. Every two releases, a white cardboard was placed around the arena's circumference to screen off the landscape (see below). The orientation of individuals tested in small groups can be considered independent [22]. The analysis performed using SPLM accounts for environmental changes among tests.

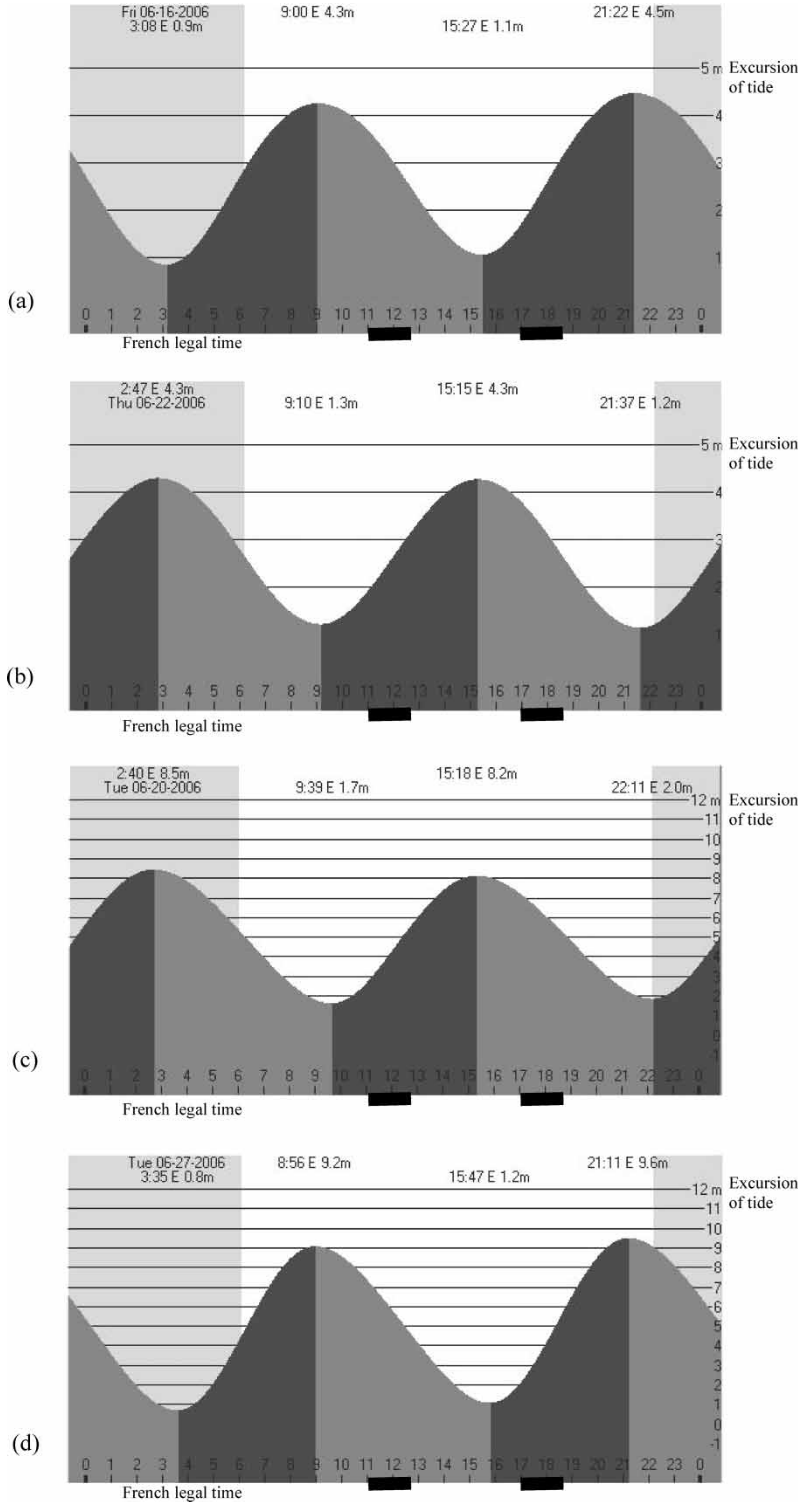

Figure 1. Tide progression during the days of the experiments: (a) Damgan: 16 June 2006; (b) Damgan: 22 June 2006; (c) Le Verger: 20 June 2006; (d) Le Verger: 27 June 2006. The bars indicate the times of the experiments (morning: 11:00 – 12:30; afternoon: 17:00 – 18:30).

The experiments were performed on the beach, using a Plexiglas arena with a 40 cm diameter, having 72 pitfall traps of 5° each at its rim; a cylindrical screen of transparent Plexiglas covered the entire device. The arena was positioned horizontally on a tripod at 1 m above the beach surface; pitfall trap 72 was oriented to the North. The animals were placed in the centre of the arena by means of a transparent Plexiglas tube with a 3 cm diameter inserted vertically through the cover of the arena; after 1 minute the tube was removed and the animals were free to hop or run in the chosen direction. At each release we registered the following variables: time of the release, traps where the animals had fallen, air temperature (°C; measured by means of a electronic thermo-hygrometer), air humidity (%; electronic thermo-hygrometer), sky cloudiness (0 – 8; visual appreciation), sun vision (visible, covered, shape, not visible; visual appreciation). At each experimental session a profile of the beach was drawn during low tide from the waterline to the base of the dune, using standard topographic methodology.

We tested a total of 307 individuals at Damgan (306 *T. saltator* and 1 *D. deshayesii*), and 316 individuals at Le Verger (267 *T. saltator* and 49 *D. deshayesii*). All individuals tested were kept in separate tubes filled with 75% alcohol for later morphometric measurement (cephalic length and number of segments of the second antennae) and to determine species and sex. The samples are preserved at the Dipartimento di Biologia Evoluzionistica, University of Florence, Italy.

The circular distributions of the angles of orientation were analysed using S-Plus 6 Insightful with a library developed *ad hoc* [23, 25]. For each circular distribution of angles, we calculated: the mean vector, the confidence interval of the mean direction, and performed the Rayleigh test for uniformity. When the distributions were clearly bimodal and axial, we used the method of doubling the angles and calculated orientation axes (second trigonometric moment [24]). A probability density function of each distribution was calculated using the kernel method and drawn double plotted to highlight all the peaks of the circular distributions [24]. The effect of variables on orientation was analysed using multiple regression models adapted to angular data (SPLM, Spherical Projected Linear Models). A multiple regression analysis was recommended when the data were obtained under natural (changing) conditions [26]. In such conditions several factors may influence orientation simultaneously and must be taken into consideration. Marchetti and Scapini [25] developed SPLM analysis for angular data. The variables and factors used are the following: place (Damgan or Le Verger), species (only Le Verger: *T. saltator* or *D. deshayesii*), morning/afternoon, sun azimuth (morning: range 105°–130°; afternoon: range 248°–265°), landscape vision (yes or no), tide (rising or ebbing), air temperature (range 20°C–37°C), air humidity (range 18%–67%), sun vision (visible, covered, shape or not visible), sky cloudiness (range 2–8), sex and age (male, female or juvenile), cephalic length (range 0.56 mm–2.04 mm), number of articles of second antennae (range 8–37). Additive baseline models were developed considering all the variables and factors that may influence orientation and the possible interactions of factors. Various models were compared, and the best model (maximum likelihood with the least number of parameters) was chosen using the Akaike Information Criterion (AIC). From the best model, the effects of single variables were estimated using the Likelihood Ratio Test (LRT), by comparing the best model with nested models not containing the variable tested.

3. Results

3.1. *Profiles of the beaches*

In June 2006, Damgan beach (Figure 2a) had a wide intertidal zone (147 m) and a limited width (42 m). The slope of the intertidal zone was not remarkable, and there were some rocks emerging from the sand. The slope of the supratidal beach was steeper (2°–7°). The tidal excursion was about 3 m (Figure 1a,1b).

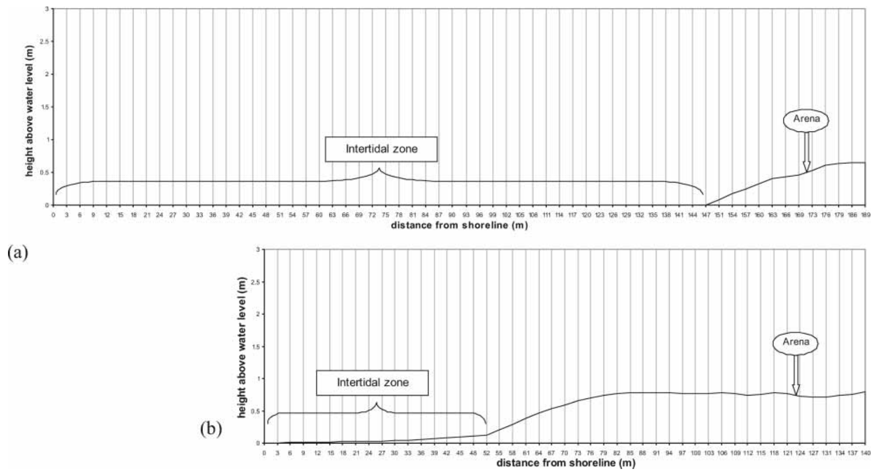

Figure 2. Profile of Damgan beach on 16 June 2006 (a; total length = 189 m; intertidal zone = 147 m; supratidal beach = 52 m; position of arena at 172 m) and Le Verger beach on 20 June 2006 (b; total length = 140 m; intertidal zone = 52 m; supratidal beach = 88 m; position of arena at 123 m).

In June 2006, Le Verger beach (Figure 2b) had a narrow intertidal zone (52 m), and a wide supratidal zone (88 m). The intertidal zone had slopes of 0°–2°, while the supratidal beach had slopes of 3°–10°. The tidal excursion was about 7 m (Figure 1c,1d).

Both beaches were stable throughout the period of the experiments. The profiles drawn on the same beach on the two days of experiments did not differ significantly.

3.2. *Populations*

The samples of the two populations were composed of adults of both sexes and juveniles (Figure 3). Only in Le Verger did we find a sufficient number of *D. deshayesii* for the analysis (Figure 3).

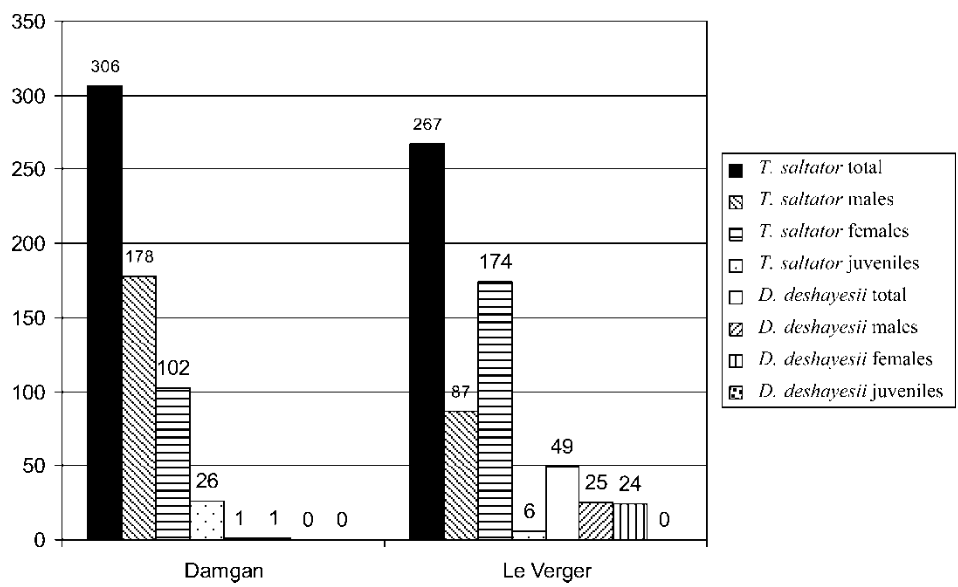

Figure 3. Population structure of the samples of talitrids used in the experiments of orientation at Damgan and Le Verger beaches.

Regarding *T. saltator*, in Damgan we found a higher number of males, while in Le Verger we found a higher number of females. The age-sex structure of the samples probably did not reflect the population structure of the sites as we tended to select large individuals for the experiments.

3.3. *Orientation*

On the whole, both in Damgan (Figure 4a) and Le Verger (Figure 4b), the samples of *T. saltator* were unimodally oriented towards the respective TEDs; the Damgan samples were better oriented (the mean vector length was higher) than those at Le Verger. The samples of *D. deshayesii* (Figure 4c) were more scattered, even if they tended to direct towards the TED. For all three distributions the Rayleigh test of uniformity proved significant.

Starting from a baseline additive model with all the variables and factors (M1, Table 1) we calculated several different models with a smaller number of variables which were compared using the AIC; the best model was found to be M2 (Table 1), including only species as an intrinsic factor, plus locality, tide, time of the day and meteorological variables.

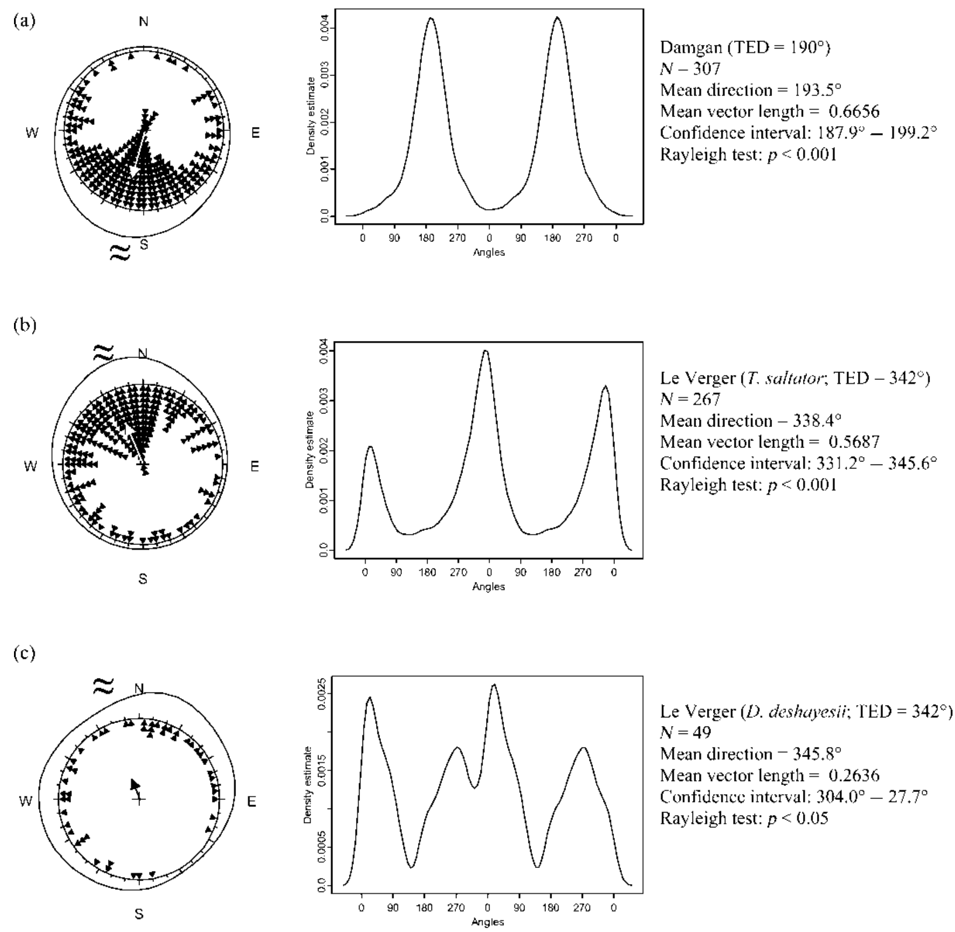

Figure 4. Distribution of orientation angles of (a) all the samples of *Talitrus saltator* at Damgan; (b) all the samples of *Talitrus saltator* at Le Verger; (c) all the samples of *Deshayesorchestia deshayesii* at Le Verger. Probability density estimates with kernel method double plotted; the symbol '≈' shows the direction of the sea; arrows, mean vectors.

Table 1. SPLM (Spherically Projected Linear Models) fitted to the data. The symbol '×' indicates the interactions between factors; the asterisks above the factors show the result of the Likelihood Ratio Test for that factor (*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$); AIC: Akaike Information Criterion.

Model	Dependent variable	Independent variables and factors	–2 log likelihood	AIC	Number of parameters	Degrees of freedom
M1: baseline additive model with all the variables that could influence orientation	angle	species + locality + morning/afternoon + azimuth + landscape + tide +air temperature + air humidity + sun + sky cloudiness + sex + cephalic length + number of articles of the second antennae	1705.5728	1773.5728	34	589
M2: best model	angle	species*** + locality*** + morning/afternoon*** + tide** + air temperature** + sun*** +sky cloudiness*	1717.1336	1757.1336	20	603
M3: baseline model with the interaction of locality	angle	locality × (morning/afternoon + azimuth + landscape + tide + air temperature + air humidity + sky cloudiness + sex + cephalic length + number of articles of second antennae) + species	1629.7625	1729.7625	50	573
M4: best model	angle	locality*** × (azimuth*** + landscape*** + tide*** + sex**) + number of articles of second antennae***	1652.1130	1704.1130	26	597
M5: baseline additive model for Damgan	angle	morning/afternoon + azimuth + landscape + tide + air temperature + air humidity + sun + sky cloudiness + sex +cephalic length + number of articles of second antennae	709.5751	769.5751	30	277
M6: best model	angle	morning/afternoon*** + landscape*** + tide*** + air temperature*	725.6321	745.6321	10	297
M7: baseline additive model for Le Verger	angle	species + morning/afternoon + azimuth + landscape + tide + air temperature + air humidity + sun + sky cloudiness + sex + cephalic length + number of articles of second antennae	906.7733	966.7733	30	286
M8: best model	angle	species* + landscape* + sun*** + sex**	920.5151	948.5151	14	302
M9: baseline model with the interaction of species with other factors for Le Verger	angle	species × (morning/afternoon + azimuth + landscape + tide + air temperature + air humidity + sky cloudiness + cephalic length + number of articles of second antennae) + sex	898.6543	986.6543	44	272
M10: best model	angle	species** × (sky cloudiness**) + landscape** + sex**	920.4620	948.4620	14	302
M11: baseline additive model for *T. saltator* of Le Verger	angle	morning/afternoon + azimuth + landscape + tide + air temperature + air humidity + sun + sky cloudiness + sex + cephalic length + number of articles of second antennae	730.3503	786.3503	28	239
M12: best model	angle	landscape** + sun* + sex**	748.2339	772.2339	12	255
M13: baseline additive model for *T. deshayesii* of Le Verger	angle	morning/afternoon + azimuth + landscape + tide + air temperature + air humidity + sky cloudiness + sex + cephalic length + number of articles of second antennae	153.9047	197.9047	22	27
M14: best model	angle	sky cloudiness* + sex + number of articles of second antennae	163.2272	179.2272	8	41

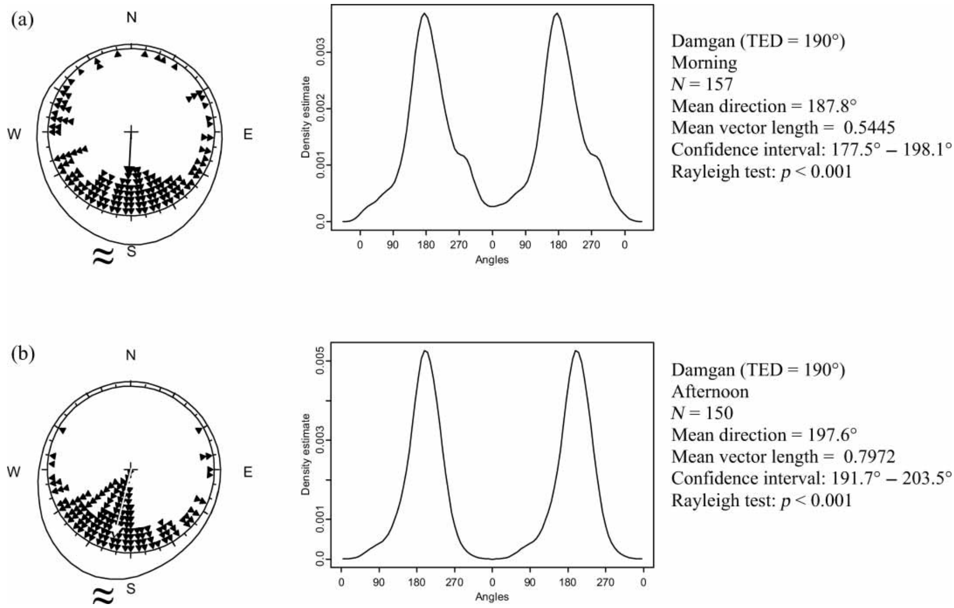

Figure 5. Distribution of orientation angles of *Talitrus saltator* at Damgan during (a) the morning; and (b) the afternoon. Probability density estimates with kernel method double plotted; the symbol '≈' shows the direction of the sea; arrows, mean vectors.

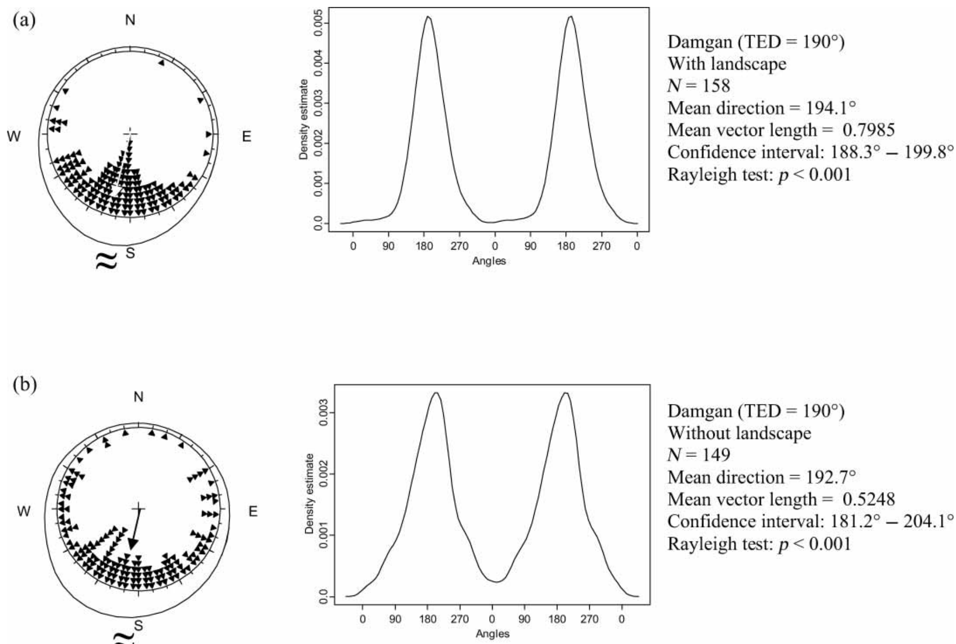

Figure 6. Distribution of orientation angles of *Talitrus saltator* at Damgan when (a) they could see the landscape; and (b) they could not see the landscape. Probability density estimates with kernel method double plotted; the symbol '≈' shows the direction of the sea; arrows, mean vectors.

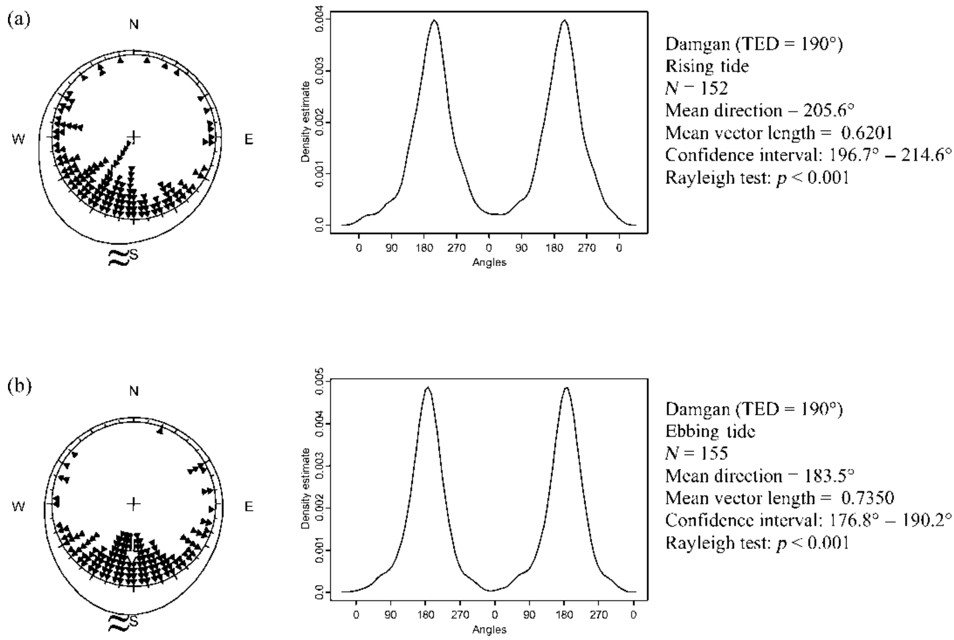

Figure 7. Distribution of orientation angles of *Talitrus saltator* at Damgan with (a) rising tide; and (b) ebbing tide. Probability density estimates with kernel method double plotted; the symbol '≈' shows the direction of the sea; arrows, mean vectors.

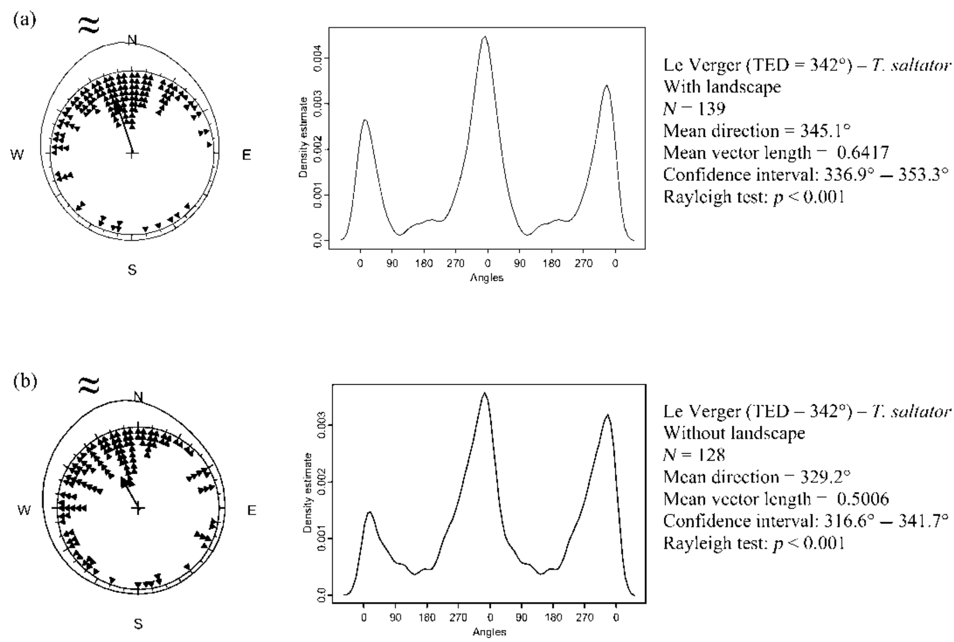

Figure 8. Distribution of orientation angles of *Talitrus saltator* at Le Verger when (a) they could see the landscape and (b) they could not see the landscape. Probability density estimates with kernel method double plotted; the symbol '≈' shows the direction of the sea; arrows, mean vectors.

We then calculated a model in which the locality was in interaction with the other variables (M3, Table 1); the species factor was excluded from the interaction because in Damgan we did not have a sufficient number of *D. deshayesii* for the analysis. The best model for the interaction of locality was M4 (Table 1), which included azimuth, landscape and tide as well as some intrinsic factors.

The comparison between the M2 and M4 models by LRT shows the importance of the interaction ($p < 0.001$), so we analysed the populations of the two localities separately.

First, we analysed the Damgan population starting with the baseline additive model (M5, Table 1). The best model was M6 (Table 1), including tide, time of day, landscape and a meteorological variable.

The comparison of the distributions with reference to the morning/afternoon factor (Figure 5) shows that in the morning sandhoppers were more scattered than in the afternoon. However, in the afternoon the confidence interval did not include the TED. The comparison of the distributions with reference to the landscape factor (Figure 6) shows that talitrids were better oriented when

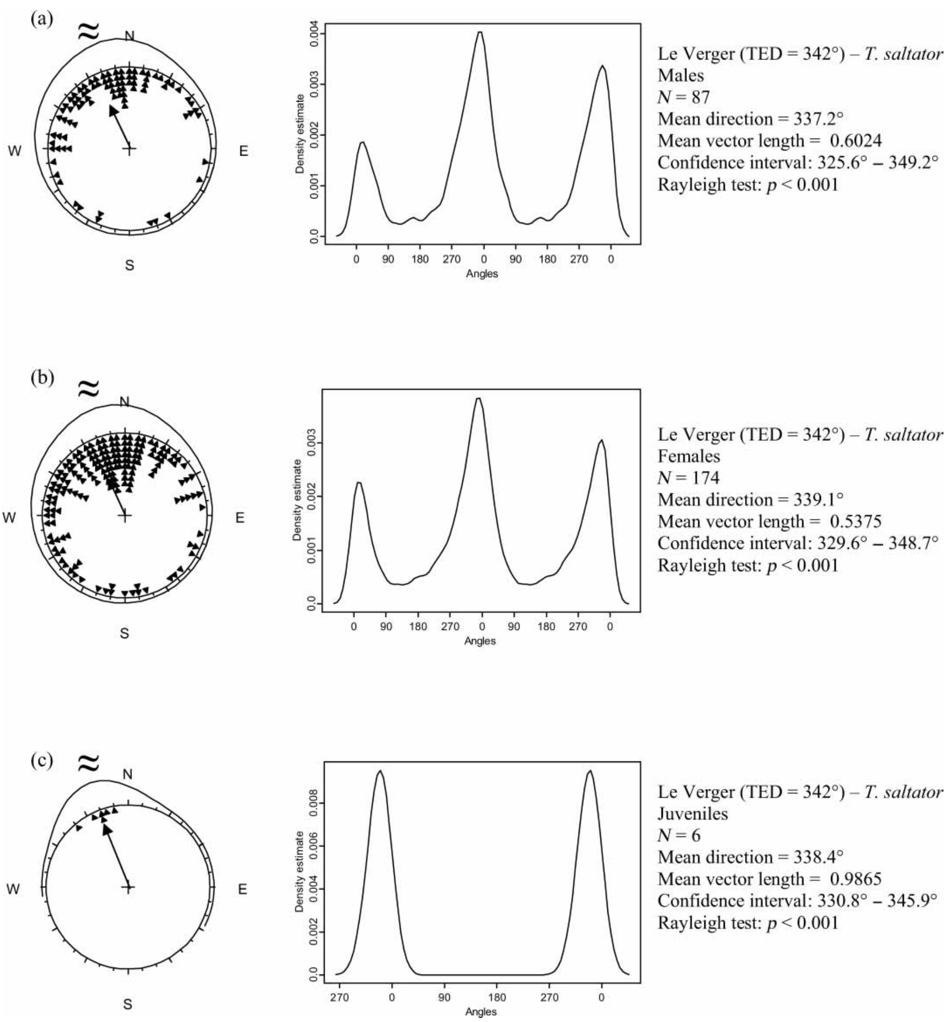

Figure 9. Distribution of orientation angles of *Talitrus saltator* at Le Verger of (a) males, (b) females and (c) juveniles. Probability density estimates with kernel method double plotted; the symbol '≈' shows the direction of the sea; arrows, mean vectors.

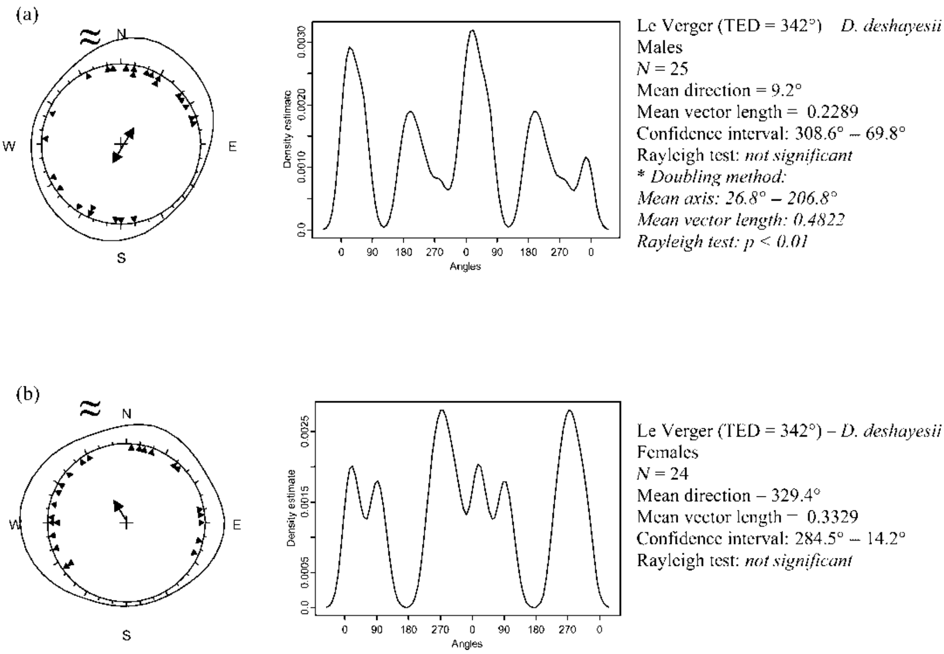

Figure 10. Distribution of orientation angles of *Deshayesorchestia deshayesii* at Le Verger of (a) males and (b) females. Probability density estimates with kernel method double plotted; the symbol '≈' shows the direction of the sea; arrows, mean vectors.

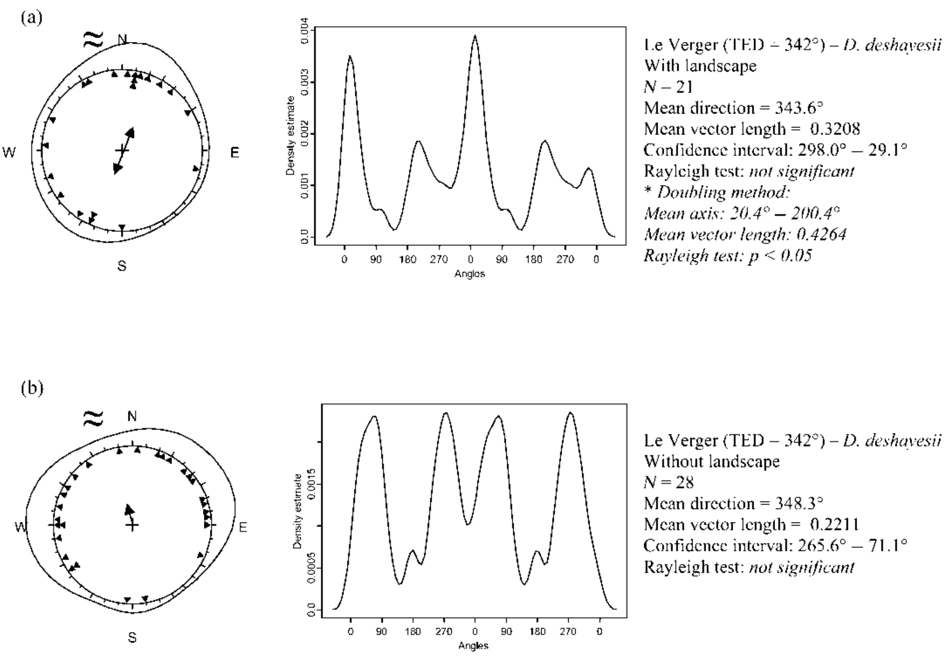

Figure 11. Distribution of orientation angles of *Deshayesorchestia deshayesii* at Le Verger when (a) they could see the landscape and (b) they could not see the landscape. Probability density estimates with kernel method double plotted; the symbol '≈' shows the direction of the sea; arrows, mean vectors.

they could see the landscape. The comparison of the distributions with reference to the tide factor (Figure 7) shows that talitrids were better oriented with an ebbing tide, while with a rising tide the confidence interval did not include the TED. The Rayleigh tests for both these distributions were highly significant ($p < 0.001$).

For the Le Verger population, we calculated a baseline additive model M7 and selected the best additive model M8 (Table 1).

Since in Le Verger there were two species, we calculated a model with the species factor in interaction with the other variables (M9, Table 1); the sun factor was excluded from the model because its information was included in other factors. The best model with interaction was M10 (Table 1), which included species, landscape vision, sex and a meteorological factor, but did not include tide as a factor.

The comparison between the models using AIC showed that model M10 was slightly better than M8. Therefore, we analysed the two species separately.

First, we analysed the Le Verger *T. saltator* population starting from the baseline additive model (M11, Table 1). The best model was M12 (Table 1), including landscape, sun vision and sex, but not tide.

The comparison of the distributions with reference to the landscape factor (Figure 8) showed that talitrids were better oriented when they could see the landscape; without the landscape vision the confidence interval did not include the TED. The comparison of the distributions with reference to the sex factor (Figure 9) showed that *T. saltator* males were better oriented than the females. The few juveniles tested were very well oriented (mean vector length = 0.9865). The Rayleigh test for all these distributions was highly significant ($p < 0.001$).

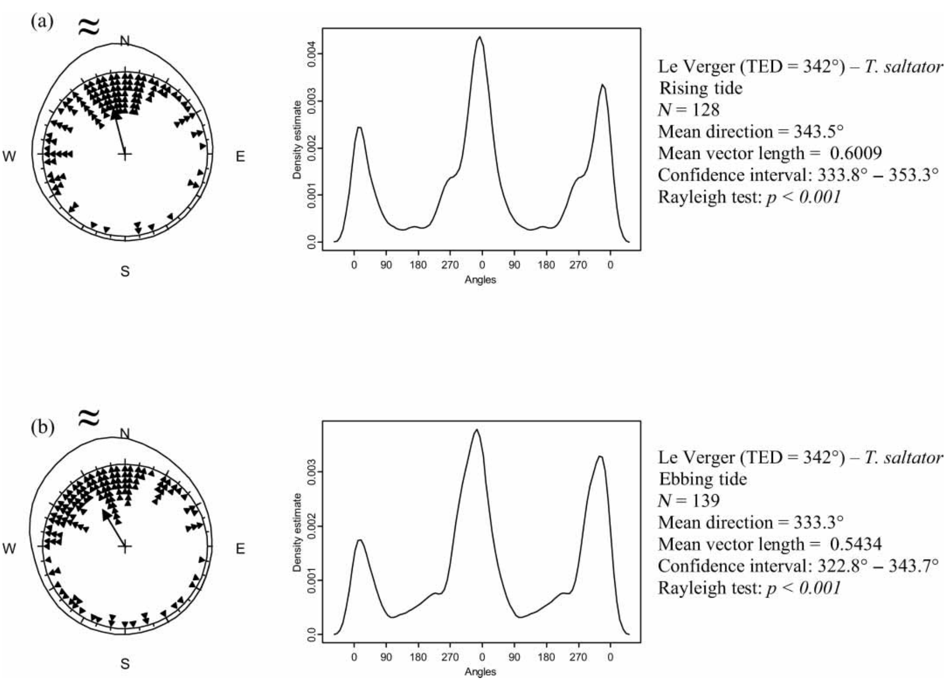

Figure 12. Distribution of orientation angles of *Talitrus saltator* at Le Verger with (a) rising tide and (b) ebbing tide. Probability density estimates with kernel method double plotted. The symbol '≈' shows the direction of the sea; arrows, mean vectors.

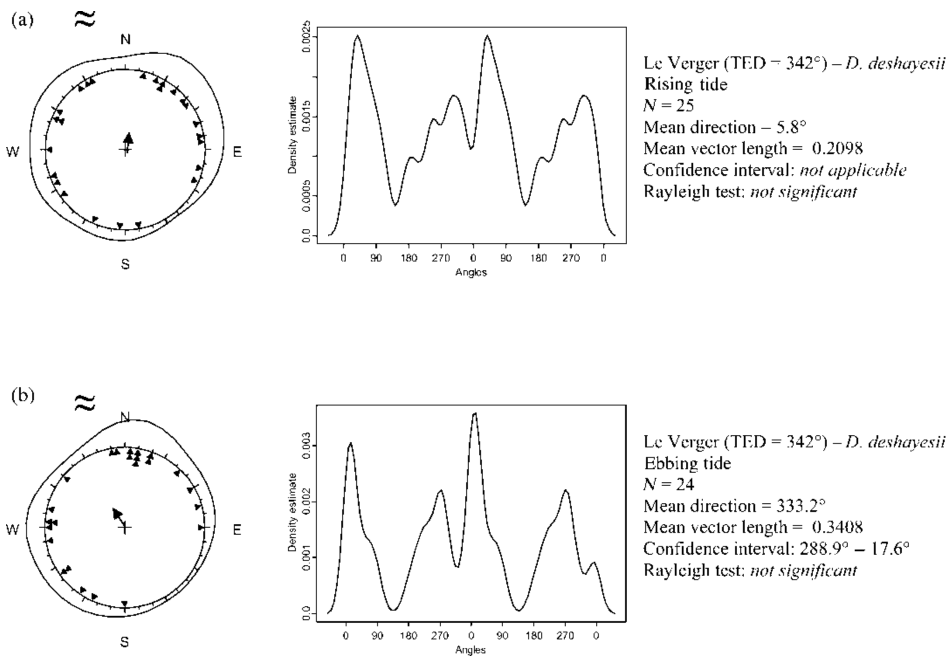

Figure 13. Distribution of orientation angles of *Deshayesorchestia deshayesii* at Le Verger with (a) rising tide and (b) ebbing tide. Probability density estimates with kernel method double plotted; the symbol '≈' shows the direction of the sea; arrows, mean vectors.

Then, we analysed the Le Verger *D. deshayesii* population starting from a baseline additive model (M13, Table 1). The best model was M14 (Table 1). In this model only the sky cloudiness factor was significant at $p < 0.05$; the two other intrinsic factors, though not significant for the LRT, were included in the model chosen because their elimination decreased the likelihood of the model.

The comparison of the distributions with reference to the sex factor (Figure 10) showed a scatter response for the females (Rayleigh test not significant), while the males had an axial orientation (axis: 26.8°–206.8°) different from the TED (Rayleigh test: $p < 0.01$ and confidence interval).

The distributions for *D. deshayesii* with reference to the landscape factor (Figure 11) showed that when the animals could not see the landscape, they were scattered (Rayleigh test not significant), while when they could see the landscape, they had an axial orientation (axis: 20.4°–200.4°) that was, however, different from the TED (Rayleigh test: $p < 0.05$ and confidence interval). The distributions for *T. saltator* with reference to the tide factor (Figure 12) showed a better orientation with a rising tide, while *D. deshayesii* (Figure 13) had a better orientation when it was ebbing, although this was not significant (Rayleigh test).

4. Discussion

This study analysed the escape reaction of samples of *T. saltator* and *D. deshayesii* released on a dry substrate in an experimental arena on the beach during the day. This situation is not normal for these crustaceans as during the day they tend to remain burrowed in the wet sand. However orientation in these conditions may have a survival value in case of passive displacement of the animals by a predator, e.g., when they are active on the surface as a consequence of the drying up of the sand. In these conditions, a prompt orientation seawards using a sun compass is expected

([27] for a review). In this study sandhoppers from Brittany's beaches were studied for the first time and sun orientation was confirmed in those populations. The aim of the experiments was to analyse eventual differences of orientation with rising or ebbing tides at two different times of the day (morning or afternoon). Moreover, we analysed eventual differences of orientation with and without landscape vision.

Regarding *T. saltator*, its orientation confirmed our expectation, both at Damgan and at Le Verger: the orientation of *T. saltator* was well defined and towards the TED on both beaches, as expected for stable shorelines [14].

On the basis of the analysis using multiple regression models, we showed that the landscape factor significantly influenced the orientation of *T. saltator* in both localities. The distributions (Figures 6 and 8) showed that when the animals could not see the landscape, they were more scattered than when landscape vision was not screened off. This means that these amphipods use the visual information of landscape to help sun compass.

We also showed that the orientation of the Damgan talitrids was influenced by the time of the day (i.e. morning or afternoon), by the tide (i.e. rising or ebbing) and by air temperature. The orientation of those of Le Verger was influenced by sun visibility (i.e. visible, covered, shape, not visible) and the sex.

The tide was not included in the Le Verger model, but the circular distributions (Figure 12) showed an opposite trend as a response to rising or ebbing tides as compared with the Damgan talitrids. In fact the Damgan talitrids were better oriented when the tide was ebbing, as if they tended to follow the water that moved away to search for a shelter against dehydration near the waterline; instead, when tide was rising, these talitrids were more scattered, as if they tended to escape from the advancing water to avoid being submerged. On the contrary, at Le Verger talitrids showed a better orientation when the tide was rising. This difference can be explained if we consider the dissimilarities of the two beaches and the different tidal excursion on these two coasts. The intertidal zone at Damgan beach is much a more extended (about 150 m) than Le Verger beach (about 50 m), while the tidal excursion is higher in Le Verger (Figures 1 and 2). The Le Verger talitrids have a more extended beach where they can disperse to search for food, and consequently maintain the seaward direction with higher precision.

D. deshayesii had a different behaviour with respect to our expectations: its orientation was not well defined, and a marked scattering was shown, even if on the whole the mean direction was towards the TED (Figure 4c). Besides, the best SPLM (Table 1) for this species shows that the factors influencing orientation were sky cloudiness (environmental), sex and the number of articles of the second antennae (intrinsic factors). The distributions with reference to the landscape factor (Figure 11) showed that landscape vision had an effect on orientation; in fact, bimodal orientation was observed when the samples of *Deshayesorchestia* could see the landscape. They were oriented along an axis at about 40° from the TED, directed towards a promontory present at one end of the beach. These animals appeared to move towards and away from this prominent landscape feature, instead of moving seawards, probably using a scototaxis. This could imply that *D. deshayesii* is a recently immigrated population to this beach and has not had enough time to fix the beach characteristics (namely shoreline direction) in its behaviour.

Regarding tides, which were non included in the best model for *Deshayesorchestia*, this species seems to orient tendentially like the Damgan *Talitrus* with ebbing tides. *Deshayesorchestia* is more subject to dehydration than *Talitrus*, and lives closer to the sea [28–29].

Sex was included as a factor in the best model for both species at Le Verger. In *T. saltator*, in contrast to our expectations [30], the males were better oriented than the females (Figure 9). During the day, the females of this population tend to remain burrowed landwards probably to protect juveniles, carried in their pouch from predators and dehydration.

In conclusion, we observed a well adapted orientation of talitrids on Brittany's beaches, and confirmed the validity of this behaviour as a beach stability indicator [31]. Moreover, we showed that tides influence the orientation of the two species tested. The effect was more evident in Damgan, where the supratidal zone is narrow and the intertidal zone extended. We also showed that *T. saltator* and *D. deshayesii* at Le Verger were differently oriented. Since *D. deshayesii* was more scattered, it seems logical to infer that it has colonised this beach for a shorter time than *T. saltator*.

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