

Orientation and migration in *Talitrus saltator*

Orientación y migración en *Talitrus saltator*

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ABSTRACT

Talitrus saltator, a beach dwelling crustacean amphipod, has been for long the subject of orientation studies, as it shows orientation perpendicular to the shoreline in response to stressful factors of environmental dryness or submersion. Sun orientation permits zonal recovery in case of abrupt displacement from their burrows during the day, and is inherited with genetic differences among populations from differently oriented shores. Moreover, other orientation mechanisms are used in addition to or instead of the sun compass to maintain zonation. A learning capability has also been shown, which can modify the orientation after individual experience. Rhythmic components in the orientational responses have been demonstrated, which would be related to daily migrations in nature. In the laboratory under constant conditions, sandhoppers show rhythmic changes in their responses to simple visual stimuli and differences have been shown among populations from Mediterranean and Atlantic shores. A study is also presented aimed at answering the still open question of whether and how sandhoppers are oriented in nature during the foraging movements, which they perform at night under suitable meteorological conditions. Spontaneously active sandhoppers were captured with pit-fall cross traps positioned on the eulittoral and shortly after tested in orientation arenas. Changes in sandhopper orientation resulted during the night, which were related to their zonation and activity. The orientational cues were visual, to both sky and landscape factors. On the whole, the results throw new light on the ecological meaning of sandhoppers orientation and the conditions in which learning of direction finding may occur in nature.

Key words: *Talitrus saltator*, ethoecology, orientation, rhythms, genetics.

RESUMEN

Talitrus saltator, crustáceo anfípodo cuya residencia habitual son las playas de arena, ha sido por largo tiempo objeto de estudios de orientación debido a que se orienta perpendicularmente a la orilla del mar en respuesta a factores de estrés tales como desecación del ambiente o inmersión por efecto del oleaje. Durante el día la orientación solar le permite efectuar la recuperación zonal en el caso de un repentino traslado del área habitual de enterramiento. Este mecanismo de orientación se hereda y presenta diferencias genéticas entre poblaciones provenientes de playas con distintas orientaciones. Se presentan además otros mecanismos de orientación en adición o en vez de la orientación solar para mantener la zonación. También se ha comprobado una capacidad de aprendizaje que puede modificar la orientación como consecuencia de la experiencia individual. Se ha demostrado la existencia de componentes rítmicos en las respuestas de orientación que podrían relacionarse con las migraciones diarias recurrentes en la playa. Bajo condiciones constantes de laboratorio, los anfípodos muestran cambios rítmicos en sus respuestas a estímulos visuales simples, habiéndose demostrado diferencias entre poblaciones costeras del Mediterráneo y del Atlántico. El presente es un estudio que aspira a dar una respuesta a la pregunta aún abierta sobre la posibilidad y modo de orientación de los anfípodos durante su búsqueda de alimento, actividad que efectúan de noche cuando las condiciones meteorológicas son apropiadas. Se capturaron anfípodos con trampas ubicadas a ras de la arena para luego ser estudiados en cámaras de orientación. Los cambios de orientación que los talitridos manifestaron durante la noche se relacionaron con la zonación y el estado de actividad. Las referencias para la orientación fueron visuales, cielo y paisaje. En síntesis, los resultados entregan nuevos antecedentes sobre el significado ecológico de la orientación de los anfípodos talitridos y de las condiciones en las cuales el aprendizaje para recuperar una dirección podría darse en la naturaleza.

Palabras clave: *Talitrus saltator*; etoecología, orientación, ritmos, genética.

INTRODUCTION

The sandhopper *Talitrus saltator* (Montagu) is a sandy-beach dweller very common on Mediterranean and European Atlantic coasts. Its life style is roughly the same during its entire life cycle; it develops without larval

stage and juveniles are released from the brood-pouch of the female at an adult-like autonomous stage. Their typical habitat is the eulittoral above the high tide marks, with slight differences in the zonation of activity between adults and juveniles, being juveniles more active at water's edge. The research

done on this species has revealed many interesting points that make it a case-study, particularly for orientation and the genetic determination of orientation. We shall here present a brief review of this research considering the many aspects of eco-ethology of the species, highlighting new findings that await further clarification, namely the timing and plasticity of orientation behaviour. A field study and laboratory tests were performed in order to investigate how and to what extent the behaviour of sandhoppers is plastic, i.e. susceptible to both short term modifications by changing external conditions and/or internal factors, and to long term ones as far as endogenous inheritable information is concerned. This latter would be the basis of populations' adaptation and diversity.

MATERIAL AND METHODS

The experiments reported in the paper have been conducted on talitrid amphipods of the species *Talitrus saltator* (Montagu) from Mediterranean (Italy, Fig. 1) and eastern Atlantic (France, Wales) populations. To test the orientation of sandhoppers the following methods have been used: 1) releases in a glass bowl, 40 cm in diameter, according to Pardi & Papi (1953), in which the sandhopper directional choices have been photographically recorded from underneath at given intervals of time, when they hopped and crawled in the bowl; 2) releases from the centre of a circular arena, 40 cm in diameter, and captures with pit-fall traps positioned at its rim, underlying 5° each. This method was first introduced by Hartwick (1976) and modified by Scapini & Pardi (1979) to test sandhoppers singly; 3) releases on sand and recording of the path of each sandhopper by using the marks of the hops.

Orientation tests were performed on the beach 1) with all cues available, 2) by excluding single cues (landscape vision, beach slope) and 3) by putting cues in opposition, after transferring sandhoppers to a differently oriented shore. Laboratory experiments have been carried out in controlled conditions, in order to test orientation to a single cue (sun, black boundary at the horizon, artificial

directional light, substrate slope, earth's magnetic field) or to two cues in opposition. Tests have been repeated at different times of day.

The genetics of sun orientation has been studied by testing the inexperienced progenies of different populations, reared in the laboratory under artificial light conditions; the learning capability by comparing the orientation of individuals from the same population which had had different experiences (in the rearing containers or in previous tests).

The genetic structure of natural populations has been analyzed with isoenzyme electrophoresis and a dendrogram has been calculated based on UPGMA clustering of genetic distance coefficients (Nei).

Spontaneous activity and migration in nature, its timing and zonation have been studied from the captures of sandhoppers in cross pit-fall traps positioned along a transect in the eulittoral zone of the beach. The traps have been controlled hourly throughout a 24 hour cycle, or every 2 hours for a period of 72 consecutive hours and repeating the survey each month for one year. Climatic and microclimatic conditions have been registered simultaneously.

Statistical analysis of the circular distributions has been performed according to Batschelet (1981). Linear simple and multiple regression analyses have been applied to the data (Statgraphics 5.0, 1991 STSC Inc.).

RESULTS

Orientation in sandhoppers

When a sandhopper is transferred from its burrow to arid conditions, it runs or hops seawards, while, when immersed in seawater or released on a water saturated substrate, it crawls or runs landwards (Scapini 1979). This behaviour has been defined as zonal recovery. Sandhoppers have at their disposal an abundance of mechanisms to maintain zonation by orienting along the sea-land axis, as reviewed by Pardi & Scapini (1987). The importance of astronomical cues, such as the sun and moon azimuths and the pattern of polarization of the light of the sky, were first

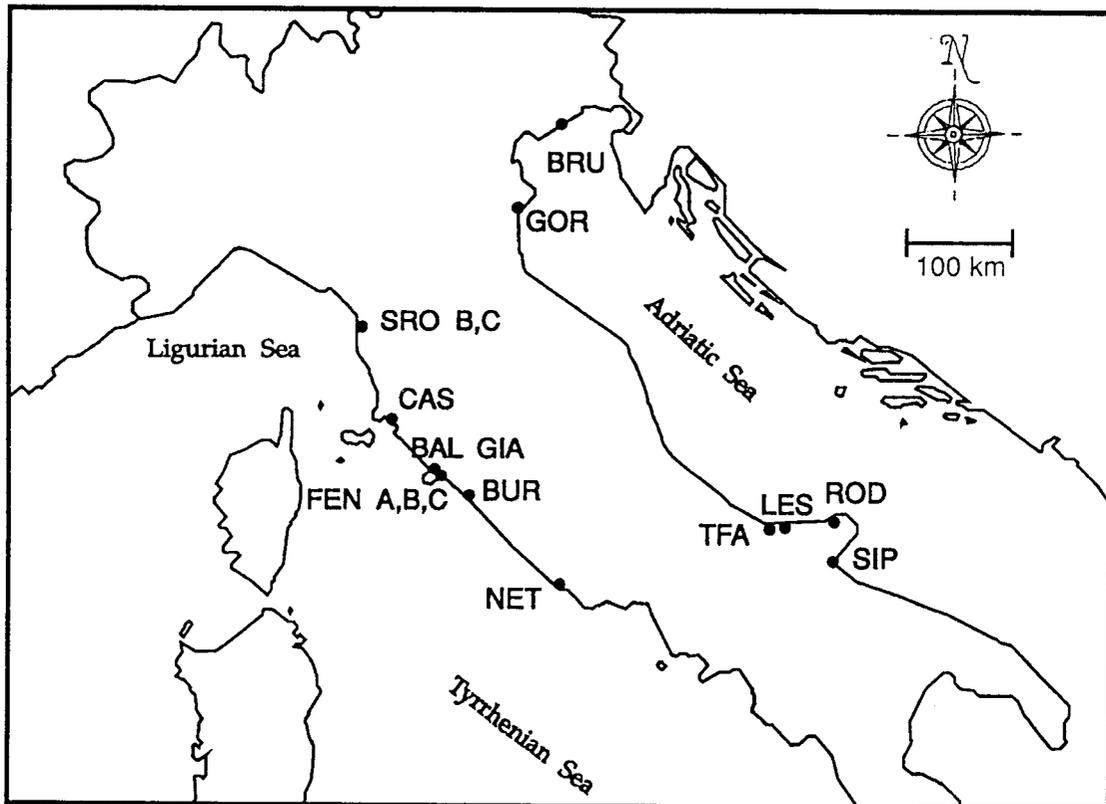


Fig. 1: Localities on the Italian coasts where the *Talitrus saltator* populations mentioned in the following figures were caught. SRO-San Rossore (Pisa); CAS-Castiglione della Pescaia, BAL-Bocca d'Albegna, GIA-Giannella, FEN-Feniglia, BUR-Burano (Grosseto); NET-Nettuno (Latina); BRU-Brussa (Venezia); GOR-Goro (Ferrara); TFA-Torre Fantine, LES-Lesina, ROD-Rodi Garganico, SIP-Siponto (Foggia). At SRO and FEN, two or three points were sampled.

Localidades de la costa italiana donde se recolectaron poblaciones de *Talitrus saltator*. SRO-San Rossore (Pisa); CAS-Castiglione della Pescaia, BAL-Bocca d'Albegna, GIA-Giannella, FEN-Feniglia, BUR-Burano (Grosseto); NET-Nettuno (Latina); BRU-Brussa (Venezia); GOR-Goro (Ferrara); TFA-Torre Fantine, LES-Lesina, ROD-Rodi Garganico, SIP-Siponto (Foggia). En SRO y FEN se muestrearon dos o tres puntos.

demonstrated by Pardi & Papi (1953). However, also landscape cues, such as the dune boundary (Williamson 1951; 1954; Karlbrink 1969; Ugolini et al. 1986), the differences in the sky's radiance over land and sea resulting in different colour composition (Ercolini et al. 1983), the earth's magnetic field (van den Bercken et al. 1969; Arendse 1978), and the slope of the beach (Craig 1973 for *Orchestoidea corniculata*; Ercolini & Scapini 1974, for *T. saltator*) may direct the course of sandhoppers also in overcast conditions. The wind may also direct sandhoppers as they show anemonegative taxis (Papi & Pardi 1953; Scapini et al. 1988). When the sun is visible these references favour a more precise orientation towards the sea or the

land, according to the dryness/moisture of the substrate. With experiments of displacement of individuals to beaches differently oriented from the original one, it was demonstrated that astronomic orientation generally prevails over local cues (Pardi & Papi 1953; Ercolini et al. 1983). However, different populations behave differently in this context, some of them being more tied to local cues than to astronomical ones (Ugolini et al. 1986). When sandhoppers are tested on a beach differently oriented from their home beach, they may refer to local cues (landscape vision) (Fig. 2 B) or still to the astronomical reference (sun) as on the home beach (Fig. 2 D). According to Hartwick (1976), *Orchestoidea corniculata* from

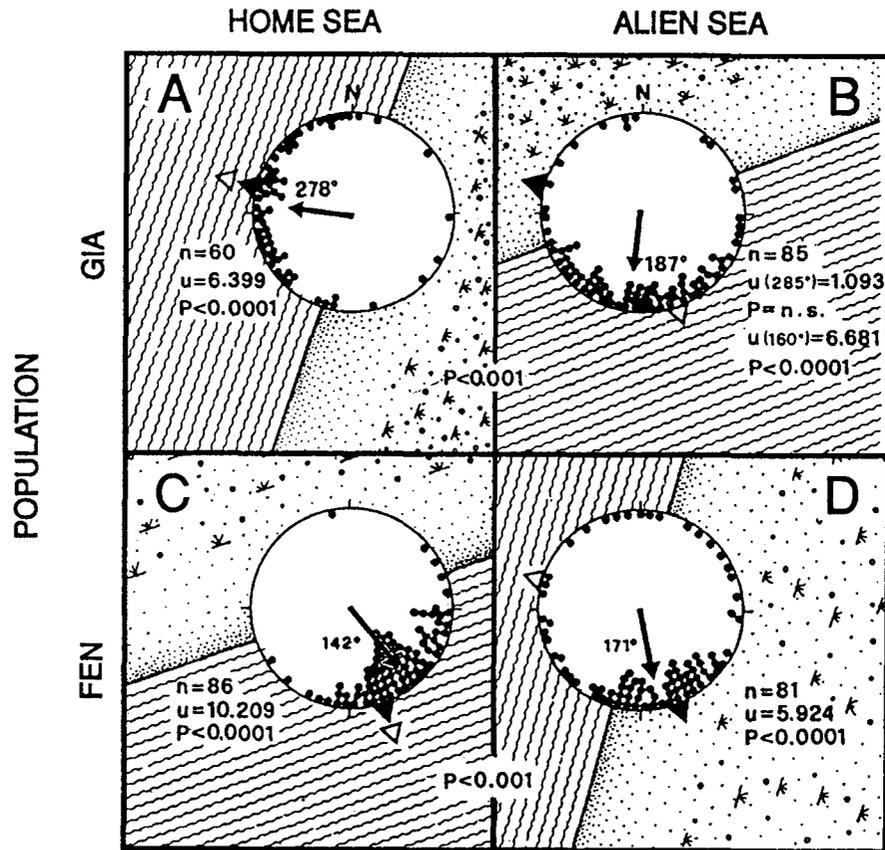


Fig. 2: Experiment of displacement to a differently oriented shore of *Talitrus saltator* from the GIA-shore with the sea at 285° and the FEN-shore with the sea at 160°. Tests in orientation chamber with view of sun, sky and landscape. A: GIA-population tested at GIA-beach; B: GIA-population tested at FEN-beach; C: FEN-population tested at FEN-beach; D: FEN-population tested at GIA-beach. Points, orientation angles of individuals; arrows, mean vectors of the populations; black triangles, home sea direction; white triangles, direction of the sea at the release site; u, V test with its probability; comparisons between distributions, Watson's U-square test. The tests were carried out on May 31 and June 30, 1978. (Ugolini et al. 1986, modified)

Experimentos de desplazamiento de *Talitrus saltator* desde las playas de origen de GIA con el mar a 285° y FEN con el mar a 160° a una playa de diferente orientación. Pruebas en cámara de orientación con vista del sol, cielo y paisaje. A: población de GIA estudiada en la playa GIA; B: población de GIA estudiada en la playa FEN; C: población de FEN estudiada en la playa FEN; D: población de FEN estudiada en la playa GIA. Puntos: ángulos de orientación de los individuos; flechas: vectores medios de las poblaciones; triángulos negros: dirección del mar en el sitio de origen de los anfípodos; triángulos blancos: dirección del mar donde se liberaron los talitridos; u, test V con sus probabilidades, comparaciones entre distribuciones, test U^2 de Watson. Los experimentos se realizaron entre el 31 de mayo y 30 de junio de 1978 (modificado de Ugolini et al. 1986).

Californian populations show a plasticity in the use of these orientation mechanisms. They are oriented to landscape cues instead of the sun, in dependence of the conspicuousness of landmarks on the horizon. An alternative hypothesis, which is dealt with in following section, would be to assume genetic differences between populations,

which would explain the divergent results in orientation tests between populations.

Genetic control of orientation

Sun orientation in sandhoppers is probably favoured by high selection pressure. In fact, rapid return to the wet zone of the beach has

survival value in cases of active or passive displacement to dry sand, particularly when the sun is shining. The most important feature of astronomical cues is that they are reliable only if the animals reside continuously in a particular place. Individuals caught in the wild and tested away from the seashore display a sun orientation with an escape direction that well matches the land-sea direction of their home locality. This capability is inherited, as laboratory-born juveniles which had had no experience of the natural environment, show a mean orientation significantly correlated with that of their parents (Fig. 3). Genetic differences in directional choices among natural populations have been demonstrated also within small geographical distances, which are related to different orientation of the shorelines (Pardi 1960; Scapini & Pardi 1979; Scapini et al. 1985; Scapini & Fasinelia 1990).

Indeed, a low dispersal rate along the coastlines is suggested both by ecological data and by genetic evidence. On one particular beach (BUR) the spontaneous movements of sandhoppers were registered throughout one year. It was found that about 85% of the migration was along the land-sea axis, while only a minor drift occurred along the seashore also when geographic barriers were absent (Scapini et al. 1992).

Genetic analysis carried out with isoenzyme electrophoresis on various natural populations sampled along the Italian coasts (Fig. 1) indicates that the gene flow among populations is relatively low (De Mattheais et al. 1994). Measurable differences exist among some Tyrrhenian populations even with small geographic distances, while two population groups of *Talitrus saltator*, one living on the Ligurian-Tyrrhenian shores and the other on the Adriatic, diverge at a genetic distance of 0.4 (Fig. 4).

Genetic heterogeneity was also shown to exist within natural populations when the orientation performances of the progenies of different pairs were compared (Scapini & Buiatti 1985; Scapini et al. 1989). The variances within each family were smaller than those among the various families. The intra-population heterogeneity would favour long term adaptation to a changing environment.

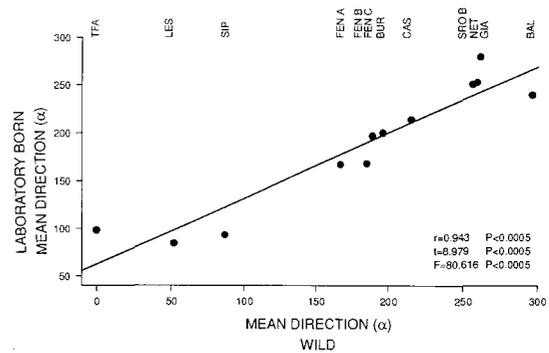


Fig. 3: Sun orientation of *Talitrus saltator* from various Italian populations tested in Florence (about 100 Km inland). For each population about 90 wild individuals, caught on the shores shown in Fig. 1, and 90 laboratory-born juveniles were tested. The mean directions of wild (horizontal axis) and laboratory-born (vertical axis) sampled from the same population were compared and a linear correlation was calculated. The tests were carried out in the years 1979-1990. (Scapini et al. 1995, modified).

Orientación solar de diferentes poblaciones italianas de *Talitrus saltator* estudiadas en Florencia (cerca de 100 km del mar). Para cada población se estudió un número aproximado de 90 individuos capturados en terreno (Fig. 1) y 90 individuos nacidos en condiciones de laboratorio. Se compararon las direcciones medias de los individuos capturados en la naturaleza (eje horizontal) con las de los nacidos en laboratorio (eje vertical) y se calculó la correlación lineal. Los experimentos se llevaron a cabo durante los años 1979-1990 (modificado de Scapini et al. 1995).

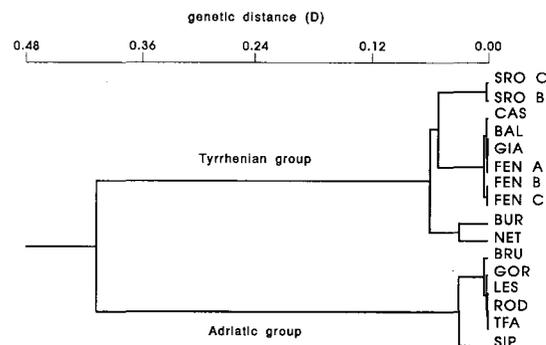


Fig. 4: Dendrogram of *Talitrus saltator* populations based on UPGMA clustering of genetic distance coefficients (Nei) calculated from an allozymic study on 19 loci. The localities are shown in Fig. 1. (De Mattheais et al. 1994, modified).

Dendrograma de poblaciones de *Talitrus saltator* basado en el agrupamiento UPGMA de coeficientes de distancia genética (Nei) calculados en estudio alozímico de 19 locus. Las poblaciones son las mismas indicadas en la Fig. 1. (Modificado de De Mattheais et al. 1994).

Flexibility of orientation

On the other hand, a merely inherited sun orientation without control and/or compensation mechanisms would be too rigid a behaviour and not really adaptive in a highly variable environment such as a sandy shore (Hazlett 1988). Sandy beaches are subjected to periodic and aperiodic actions by wind, waves and currents, which may well change the direction of shorelines even on a relatively short time scale in relation to the lifespan and generation rate of sandhoppers (McLachlan 1988). Both from laboratory rearing and a survey in the field, evidence has been found that *T. saltator* on the Mediterranean coast can survive more than one year, with a maximum of two years, while three months are needed to develop to the adult stage (Scapini, unpublished data). Thus, in the course of their life sandhoppers may well be obliged to change their inborn sun orientation according to local changes in the shoreline direction, as well as in case of accidental displacement to a differently oriented shore. Evidence that learning a new direction occurs in nature can be seen in sandhoppers living on a lagoon shore almost opposite to the seashore: adults collected in the field and tested with the vision of the sun, oriented according to the lagoon shore, while their laboratory-born offspring directed seawards (Ugolini & Scapini 1988). A modification of orientation was obtained by rearing sandhoppers from the seashore in enclosures positioned on the lagoon-shore opposite to it (Ugolini et al. 1988). Scapini et al. (1988) succeeded in training individual adult sandhoppers to orient in a direction different from the inborn one (Fig. 5).

Other orientation mechanisms, response to slope, to a black/white boundary above the horizon and magnetic compass, have been shown to be inborn, but also subjected to modification according to experience. In some populations a magnetic compass is present in laboratory-born individuals while it disappears in experienced wild-caught individuals (Scapini & Quochi 1992). The scototactic response towards a black shape is also more evident in young individuals than in adult ones, and the response can be modified by rearing sandhoppers in containers that

present a black/white boundary on the horizon (Scapini et al. 1993).

Migration in nature, its timing and control

The timing of spontaneous movements on the beach, their zonation and the climatic conditions in which movements occur have been studied on a beach-dune system of the Tuscan coast (Scapini et al. 1992). It has been shown that sandhoppers emerge spontaneously after sunset and burrow into the sand again during the first hours of the day (Fig. 6). A similar rhythm of activity has been shown to be endogenous in the laboratory under constant conditions on Atlantic sandhoppers by Bregazzi & Naylor (1972) and Williams (1983). But in nature there were seasonal differences in this rhythm as well as differences between adult and young individuals (Fig. 6, A, B). Moreover, limited activity during the day was in some condi-

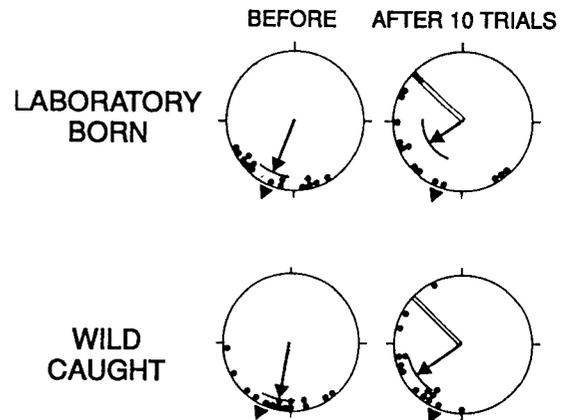


Fig. 5: Sun orientation of *Talitrus saltator* before and after 10 training trials within a tube oriented at 120° from the home sea direction. CAS population tested in Florence. Points, directions chosen by the individuals in the test arena; arrows, mean vectors of the samples with their confidence limits for $P = 0.05$; triangles, home sea direction; double lines inside the circles, tube position during the training. (Scapini et al. 1988, modified).

Orientación solar de *Talitrus saltator*, antes y después de 10 pruebas de adiestramiento dentro de un tubo orientado en 120° con respecto a la posición del mar en el lugar de origen (población CAS estudiada en Florencia). Puntos: direcciones elegidas por los individuos en la arena experimental; flechas: vectores medios de las muestras con sus límites de confianza para $P = 0.05$; triángulos: dirección del mar en el lugar de origen; líneas dobles dentro de los círculos: posición del tubo durante el adiestramiento. (Modificado de Scapini et al. 1988).

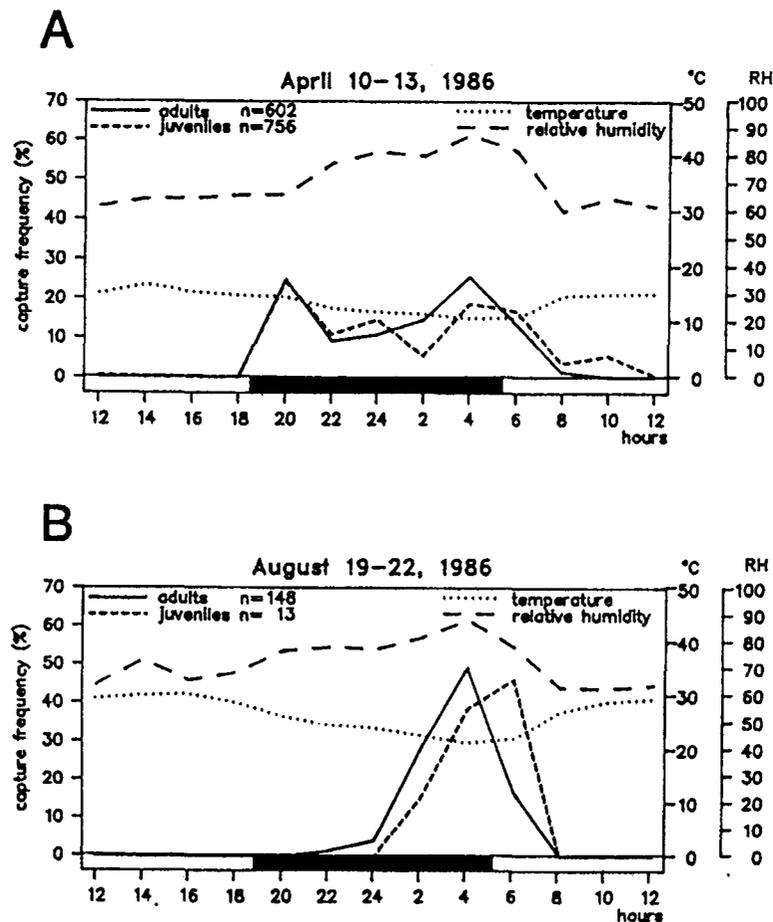


Fig. 6: Surface activity along the day of adult (continuous lines) and juveniles (broken lines) *Talitrus saltator* on the BUR beach, from capture rates with pit-fall traps. Air temperature and relative humidity are reported. n: total number of sandhoppers in the traps. (Scapini et al. 1992, modified).

Actividad diurna en superficie de adultos (líneas continuas) y juveniles (líneas discontinuas) de *Talitrus saltator* en la playa BUR. Estimaciones obtenidas de capturas con uso de trampas colocadas a ras del suelo. Se grafica también la temperatura y humedad relativa. n: número total de anfípodos en las trampas (Modificado de Scapini et al. 1992).

tions apparent on the Mediterranean, while on the Atlantic and Baltic it has been excluded for the adults (Karlbrink 1969) but not for the juveniles (Rüppel 1967).

A multiple regression analysis of surface activity with various climatic and microclimatic parameters reveals that in nature activity is modulated by external conditions. The surface activity of adult sandhoppers turned out to be significantly correlated with air and sand temperature and humidity, air pressure, wind or rain. The picture changes at different times of the year as might be expected. For example, high air temperature

was an inhibiting factor in summer and autumn, while it favoured activity in spring; air humidity and rain generally favoured activity, while air pressure was positively correlated with activity in winter but negatively in summer. Moreover, the activity of young sandhoppers of a size up to 5 mm seems to be more linked to relative air humidity and to wind speed than it is in adults.

Orientation of spontaneous activity

Another question was whether the spontaneous movements of the animals were also oriented during active migrations. In general

landward migration occurred in the early hours of the night, later and in daylight becoming seaward (Scapini et al. 1992). The landward migration might be seen as a passive flux or drift, conditions at the water's edge being limiting; in fact sandhoppers do retreat from water (Scapini 1979). However, this might also be an active orientation directed by environmental cues.

Aiming at understanding if sandhoppers' spontaneous movements are oriented and which orienting factors, astronomical and/or landscape cues, are actually used by the animals, we tested sandhoppers in two circular arenas positioned on the sand, one of which screened the view of the landscape, while both permitted a complete view of the sky. The sandhoppers were captured when spontaneously moving as was previously described, and were tested immediately afterwards. On a clear night with a full moon a seaward orientation was apparent in both the arenas (Fig. 7 A, B), thus confirming the results of Pardi & Pardi (1953, 1959) on moon orientation. In fact even the sandhoppers which could not see the landscape were oriented seawards. The present results are interesting because, unlike previous tests of Pardi and co-workers, the sandhoppers here were not subjected to high temperature or dehydrating conditions prior to the test in order to enhance their response compelling them to search for optimal humidity. Here the environmental conditions in the arenas were "basal" ones, that favoured night migration. At 3.00 and 4.00 in the unscreened arena (Fig. 7 A) and at 3.00 in the screened one (Fig. 7 B), no orientation was apparent, the external conditions being almost identical throughout the night. This is in accordance with the results obtained by analysing the capture rates in the cross-pit-fall traps (Fig. 7 C) in which at 1.00 and 3.00 sandhoppers were apparently not oriented. The question is still open as to why on that particular night no landward migration took place. In any case, this is being investigated during different weather conditions and moon phases.

Rhythms of orientation with respect to visual stimuli

The above results stress the importance of rhythmic changes in the orientational re-

sponse, which favour zonal recovery or drift at the appropriate time. Edwards & Naylor (1987) tested an Atlantic population of *Talitrus saltator* under constant laboratory conditions for its response to black/white boundary on the horizon, and obtained a

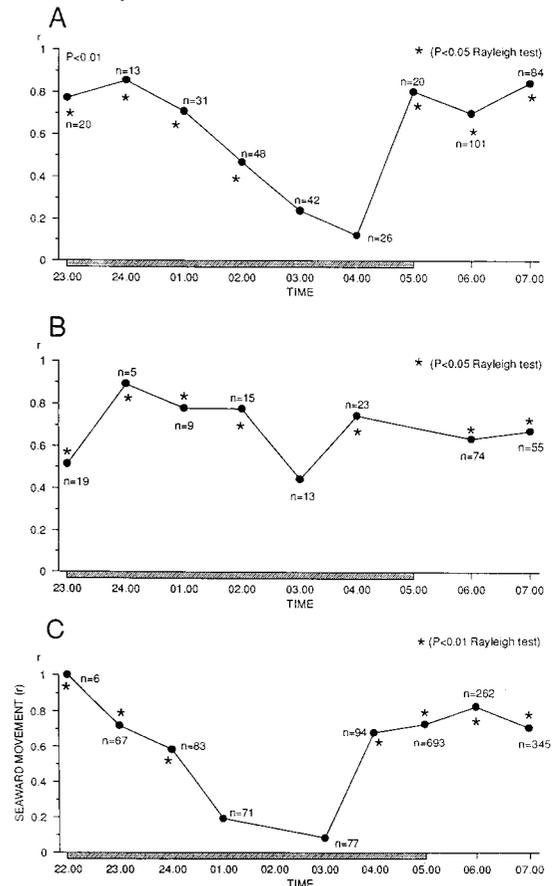


Fig. 7: Variation of the orientation index (mean vector length, r , which is a measure of the concentration around the mean) of *Talitrus saltator* on the BUR beach tested immediately after capture in an unscreened arena that permitted view of the landscape (A), in a screened arena, with only the vision of the sky (B), and during the spontaneous movements as calculated from the capture rates in the four cross-traps (C). n: number of individuals in each hourly distribution. The tests were carried out on a full moon night the April 26/27, 1994.

Variación del índice de orientación (longitud del vector medio r : medida de la concentración de datos en torno al valor medio) de *Talitrus saltator* en la playa BUR. Estudio realizado inmediatamente después de la captura, en arena no cubierta, lo que permitía vista del paisaje (A), en arena cubierta con vista sólo del cielo (B), y durante los movimientos espontáneos calculados a partir de las frecuencias de captura de cuatro trampas cruzadas (C). n: número de individuos en cada distribución horaria. Las pruebas se realizaron durante noche de luna llena del 26/27 abril, 1994.

clear orientation toward the boundary during the day with scattering at night. By way of contrast, a response away from the boundary at night, with scattering during the day, was obtained with a Mediterranean population (Fig. 8; Mezzetti et al. 1994).

A rhythmic responsiveness of Mediterranean sandhoppers was also shown in the laboratory with respect to a directional light, with one peak at night when a blue light was used, and two peaks at dawn and at sunset with a yellow light (Fig. 9 A). A similar drop of response around the middle of the night was apparent in nature with the full moon, as stressed above (Fig. 7). Again, this behaviour contrasts with the orientation of a French Atlantic population (Fig. 9 B), which was photopositive at night and photonegative during the day (Mezzetti et al. 1994).

These differences in behaviour among populations can be explained by the different ecological pressures, as was stressed by Mezzetti et al. (1994), who compared Atlantic and Mediterranean populations subjected to different tidal regimes. On the Mediterranean coasts the highest risk apparently is dehydration, thus a rapid seaward zonal recovery has a higher survival value, while on the Atlantic tidal shores the risk of being washed away favours landward orientation at dawn from the feeding zone between high and low tide marks.

DISCUSSION

On the whole we have here a picture of a very plastic behaviour, which can be finely modulated on the individual level as the environment changes. Moreover, adaptive modifications can be fixed in the gene-pool on a population level, as demonstrated by both the behavioural (orientation and rhythms of responsiveness) and molecular (isoenzymes) differences recorded among the populations.

We can now propose a model which suggests how differences could rapidly emerge and be fixed as heritable mechanisms in populations living on beaches subjected to different ecological pressures. As we have already pointed out, sandhoppers in nature integrate and opportunistically respond to a

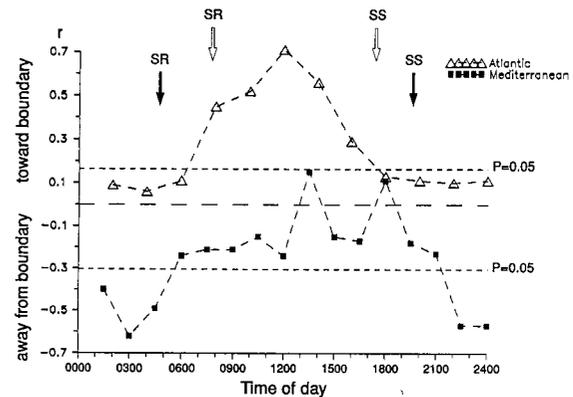


Fig. 8: Rhythm of orientation of *Talitrus saltator* from a British Atlantic, Newborough Anglesey, (triangles) and the Mediterranean BUR (squares) populations with respect to a black/white boundary on the horizon. Tests were conducted in the laboratory under continuous light conditions. SR: subjective sunrise; SS: subjective sunset; P: probability levels for the Rayleigh test. Each symbol represents the mean vector length of one sample. (Mezzetti et al. 1994, modified).

Ritmo de orientación de *Talitrus saltator* en una población Atlántica Británica, Newborough Anglesey (triángulos) y una Mediterránea (playa BUR, cuadrados) en relación a un límite negro/blanco en el horizonte. Los experimentos se realizaron en el laboratorio bajo condiciones de luz continua. SR: amanecer subjetivo, SS: atardecer subjetivo; P: niveles de probabilidad para el test de Rayleigh. Cada símbolo representa la longitud del vector medio de una muestra (modificado de Mezzetti et al. 1994).

complex of environmental stimuli typical of a particular beach, which may change periodically and aperiodically. At birth a sandhopper has a set of simple behaviours at its disposal, such as biological clocks and different taxes: orientation to slope, earth's magnetic field, sun, moon, polarized light, dune contour, brightness of the sea. These innate responses have been experimentally demonstrated at least for some populations. Experience with one particular environment may induce an integrated response to the complex of environmental stimuli, different for different localities. For example, in one locality, with an obvious dune and a sloped beach, orientation to landscape and slope may become particularly important, together with a coupling of the circadian clock with the sun-sky polarization movement. Moon and magnetic orientation would be useless in such conditions and therefore inoperative. In contrast, in another environment, landscape

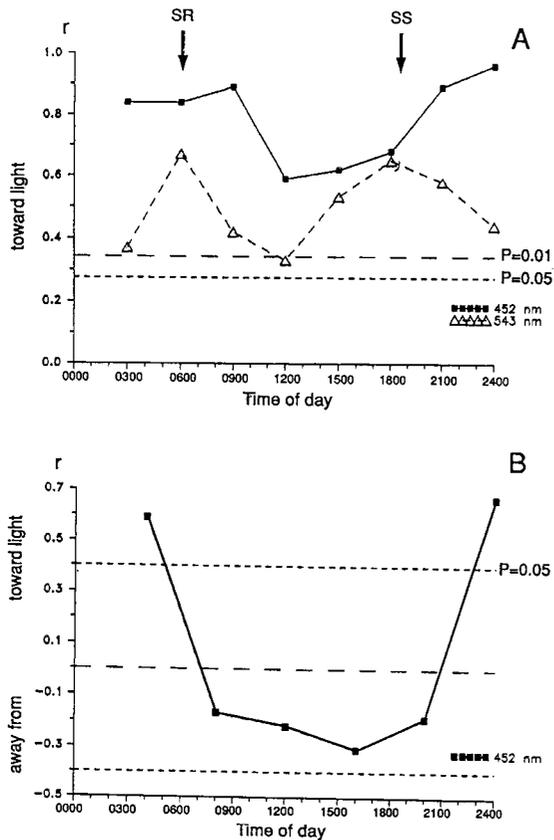


Fig. 9: Rhythm of orientation of *Talitrus saltator* from the Mediterranean BUR (A) and a French Atlantic, Gran Crohot, Bordeaux, (B) population with respect to a monochromatic blue (squares) and yellow (triangles) light. Tests were conducted in the laboratory under continuous light conditions. Each symbol represents the mean vector length (r) of one sample. SR: subjective sunrise; SS: subjective sunset; P: probability levels for the Rayleigh test. (Mezzetti et al. 1994, modified).

Ritmo de orientación de *Talitrus saltator* en una población Mediterránea, BUR (A) y una Atlántica Francesa, Gran Crohot, Bordeaux, (B) con respecto a luz monocromática azul (cuadrados) y amarilla (triángulos). Los experimentos se realizaron en el laboratorio bajo condiciones de luz continua. Cada símbolo indica la longitud del vector medio (r) de una muestra. SR: amanecer subjetivo, SS: atardecer subjetivo. P: niveles de probabilidad para el test de Rayleigh. (Modificado de Mezzetti et al. 1994).

and beach slope factors would be irrelevant and therefore the corresponding taxes would be turned off, while magnetic orientation would be adaptive and used together with or instead of astronomical factors. The latter was shown by Pardi et al. (1985) for the equatorial sandhopper *Talorchestia martensii* Weber.

The new generation would inherit all the simple behaviours and select among them the adaptive complex according to its experience. But, in particular cases regarding relatively stable beaches, it might also inherit a facilitation for coupling some adaptive taxes, in the form of regulatory genes. Previous research on the inheritance of the sun orientation directional tendency in Mediterranean sandhoppers has dealt with such a case.

The differences in timing of the orientational responses to different visual stimuli which were shown in Atlantic and Mediterranean populations might be inherited as well, but this still awaits evidence, remaining a working hypothesis that should and can be easily tested.

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