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Behavioural plasticity as a key factor in the survival and evolution of the macrofauna on exposed sandy beaches

Plasticidad conductual como un factor clave en la sobrevivencia y evolución de la macrofauna de playas arenosas expuestas

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ABSTRACT

Behavioural patterns evident in members of the sandy-beach macrofauna, including tidal rhythms and orientational responses, are not inflexible but become modified according to physical circumstances. Both long-term and short-term flexibility in behaviour is apparent. The former often results in behavioural differences between populations and is relatively easy to study compared with short-term modifications, which are generally encountered by accident and are thus poorly documented.As survival on exposed sandy shores is only possible for animals that can react appropriately to changes in conditions, and particularly to dramatic, unpredictable perturbations such as beach erosion during storms, it is suggested that behavioural flexibility is a key factor which has been rigorously selected for in the evolution of the sandy beach macrofauna. The question is also raised as to whether synchrony of behaviour is a further genetically-facilitated attribute which has played a role in this evolution.

Key words: sandy beaches, behaviour, plasticity.

RESUMEN

Patrones conductuales evidentes en miembros de la macrofauna de playas arenosas, incluyendo ritmos mareales y respuestas de orientación no son inflexibles sino que se modifican según las circunstancias. Cambios de largo y corto plazo son aparentes. Los primeros (resultando en diferencias conductuales entre poblaciones) son relativamente fáciles de estudiar, pero los segundos se encuentran sólo por accidente y por lo tanto son pobremente documentados. Como la sobrevivencia en playas arenosas expuestas es sólo posible para animales que pueden reaccionar apropiadamente a los cambios en las condiciones, y particularmente a perturbaciones dramáticas e impredecibles, tales como erosión de la playa durante temporales, se sugiere que la flexibilidad conductual es un atributo clave, el cual ha sido rigurosamente seleccionado durante la evolución de la macrofauna de playas arenosas expuestas. Se plantea también si la sincronización de la conducta es un atributo determinado genéticamente que ha jugado un rol en esa evolución.

Palabras claves: playas arenosas, conducta, plasticidad.

INTRODUCTION

Although excellent work has been done, the overall picture of the ecophysiology of the macrofauna of exposed sandy beaches has not changed radically since the review of this topic published a little over a decade ago (Brown 1983). A single development has, however, changed the way in which the present writer thinks about life on exposed sands. This aspect is the plasticity of behaviour of the macrofauna and its significance both to the ecosystem as a whole and to the survival and evolution of individual species and populations.

The Oxford English Dictionary offers a number of definitions of the term "plasticity"; the one that concerns us here is "adaptability to circumstances", although we might take note of another definition - "the capability of being moulded." Behavioural plasticity is no more than hinted at in Brown (1983) and other reviewers do not seem to have taken it up at all (see Brown & McLachlan 1990). This is not altogether surprising, as examples of such flexibility are generally embedded in

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publications dealing mainly with other issues, although a notable exception is the series of recent papers by Scapini and her coworkers on populations of the talitrid amphipod *Talitrus saltator* (Scapini et al. 1988, 1993, 1995, Scapini & Fasinella 1990, Scapini & Ciuti 1993, Mezzetti et al. 1994). In addition, the series contains a more general paper on heredity and learning in animal orientation, which is extremely relevant (Scapini 1988). It is also worth noting that three papers in the present volume on sandy shores all mention behavioural plasticity of one kind or another (Colombini & Chelazzi 1996, Scapini & Fallaci 1996, Naylor & Rejeki 1996).

LONG-TERM PLASTICITY

Reviewing the scattered literature, it becomes apparent that it is not only convenient but essential to divide behavioural plasticity into two catagories - long term, involving changes which may develop slowly but then persist for lengthy or unlimited periods, and short term, in which the animal's response has to be virtually immediate, although the changed behaviour may not be evident for long. Long-term changes generally result from adaptation to a new environment and thus often lead to different populations of a species displaying differences in behaviour pattern. Their persistence makes them easier to study than short-term changes affecting a single population and there are many instances of such plasticity in a literature going back to the 1930s, although often the earlier authors were confused by their discoveries, expecting all populations of a species to display identical behaviours.

Among well-documented examples of long-term plasticity are differences in the behaviour and orientational responses of talitrids between Mediterranean and Atlantic shores in Europe, associated largely with differences in tidal range (Naylor 1988, Mezzetti et al. 1994). Similar differences are predicted for the isopod *Tylos europeaus* as well (Brown & Odendaal 1994). Indeed, it was while writing the review of *Tylos* cited above that the wide-spread manifestation of behavioural plasticity was brought home to the present writer. For example, *Tylos granuliferus* (= *T. granulatus* Miers) is, like other members of the genus, a burrower; but on coarse sands in parts of Japan it no longer burrows but hides during the day between pebbles and under debris (Imafuku 1976), a mode of life associated with other behavioural differences as well. Its circadian rhythm appears to dominate completely any tidal rhythm of activity and responses to beach slope seem to be minimal.

On tidal beaches, *Tylos* typically crawls down the slope after emerging from its burrows, moving up again as the tide rises, but the population of *T. latreillei* (? *T. europeaus*) studied by Geppetti & Tongiorgi (1967) on a Mediterranean beach, moved up the slope on emergence and down after feeding. This is true also of Mediterranean talitrids (Scapini et al. 1992). The reversed behaviour is understandable in view of the fact that the available food on these beaches tends to lie well above high water mark but it is the fact that the orientational reponses can be reversed that is of interest. Some populations of *Tylos capensis* in the Eastern Cape Province of South Africa have gone even further by totally abandoning their position just above high water mark and moving into the dune slacks on a permanent basis (McLachlan & Sieben 1991). This, too, is associated with food availability. The usual tidal rhythm of emergence is suppressed in these populations, although the nocturnal response remains.

The talitrid amphipod *Talorchestia capensis* in these areas has also given up intertidal excursions in favour of residence among the dunes (McLachlan 1986, Matthewson 1991), although elsewhere populations of the same species migrate up and down the intertidal slope.

It is not only the semiterrestrial macrofauna that shows such adaptability; aquatic psammophiles also change their behaviour in reponse to changed circumstances. An example is that of the surfing whelk *Bullia digitalis*, a scavenger which normally swash-rides up and down the beach with the tides (Brown 1982). On some very exposed beaches, the whole *Bullia* population is often to be found off-shore, in the surf zone and beyond (Brown 1971), remaining below tide marks until conditions on the intertidal beach again become suitable for exploitation. It was long assumed that these on- and offshore movements were passive and brought about by changes in water current patterns. However, in view of the fact that surfing *Bullia* have now been shown to have very precise control over their movements (Odendaal et al. 1992, Heine & Brown, in prep.), it is probable that these migrations are dictated by the animals themselves and provide an instance of behavioural flexibility. *Bullia rhodostoma* provides a somewhat different example. Along the south coast of South Africa it surfs high up the shore, generally occupying a zone above that of *B. digitalis* (McLachlan et al. 1979), and often venturing well above the swash zone to feed on stranded animal matter. For many years it was thought to be absent from the west coast but in fact it does occur there in small numbers (Brown, unpublished), no longer high on the shore but subtidally, well below the zone of *B. digitalis*, although it again becomes intertidal in the mouth of Saldanha Bay (Brown 1977).

SHORT-TERM PLASTICITY

Much less well documented are abrupt, short-term changes in behaviour initiated by often dramatic, unpredictable environmental perturbations. This topic has been poorly researched because, as Stephen Jay Gould (1991) has said, "one cannot set out deliberately to find the unexpected." Furthermore, when one does encounter, by chance, some unexpected behavioural reponse, one is likely to be ill-equipped to study it before it ceases. Another factor that militates against good documentation of short-term responses is that they are often associated with storms, when the researcher is unlikely to be on the beach. In fact the present writer has been unable to trace a single paper dealing specifically with a short-term aberrant response on sandy shores; such phenomena are simply mentioned in passing in a literature mainly devoted to more easily quantifiable topics.

Storms, with their high levels of wave action and erosion of the beach, present one of the greatest hazards to sandy-beach communities, often accounting for greater mortality than predation (Brown & McLachlan 1990). One might therefore expect that macrofaunal species capable of colonising exposed beaches would show associated responses subtending survival, and this proves to be the case. For example, the talitrid amphipod *Talorchestia capensis*, on Cape Peninsula beaches, appears able to detect an approaching storm and migrates in its thousands, up the beach and beyond, into the dunes, into seaside cottages and across roads (Muir 1977, Brown unpublished). This may even happen during the day, the amphipods not only temporarily abandoning their normal responses to wet and dry sand and to slope but also suppressing their photonegative habit.

Moving up the slope or digging deeper into the sand (see Brown 1983) are not the only ways of avoiding being swept out to sea. A remarkable example of a different response is reported by Yuasa (1973), who observed the migration of large numbers of *Tylos granuliferus* onto a breakwater, during the day, allegedly to escape typhoon waves. Such a response involves the animals moving towards the source of danger rather than away from it, in order to invade a man-made structure, the presence of which must have been learnt by that particular population. A similar phenomenon was described by Tongiorgi (1969) for *T. europaeus* on a Mediterranean beach.

While storms are the most obvious erratic occurrences to impinge on the sandy-beach ecosystem, they are not the only unpredictable hazards the fauna may have to face. A striking instance was provided by Kensley (1974), while studying *Tylos granulatus* Krauss on a South African beach. The occurrence in question was a spill of crude oil from a tanker. A spring tide next day resulted in the beach being covered in oil up to extreme high water mark. The upper slope, under which *Tylos* lay buried, was covered in a particularly thick layer. Nearly the whole *Tylos* population stayed in their burrows that night. However, the following night a large proportion emerged through the oil, now partly weathered and hence less toxic (see Brown 1985). They moved up the shore instead of down and reburied themselves amongst the dunes, well above the level reached by the oil. There they remained, emerging at night to eat dune vegetation (which they normally reject) and avoiding all contact with the kelp which forms their staple diet but which was now contaminated with oil. After about three weeks they returned to their normal position just above high water mark and resumed their former behaviour. Through the ability to abandon their habitual life style and respond to the crisis in a highly appropriate manner, they had survived an event to which any less adaptable animal must have succumbed.

PLASTICITY, LEARNING ABILITY AND EVOLUTION

Reviews of sandy-beach ecophysiology invariably state that most members of the macrofauna of exposed beaches must, in order to survive, display a tidal rhythm of emergence from the sand, followed by the ability, once emerged, to orientate to the physical environment in such a way as to maintain overall position on the beach (Creutzberg 1975, Brown 1983, Brown & McLachlan 1990). What is not usually pointed out is that, over and above these two requirements, it is essential that the animal be able to modify both its tidal rhythm and its orientational responses to meet changing circumstances and particularly to survive crises such as increased wave action and erosion of the beach during storms. Clearly, the more exposed the beach, the more important does this ability become. As Scapini (1988) has pointed out, "stable, predictable environments tend to produce homogeneous behaviour while rapidly changing, unpredictable environments tend to induce learning and plasticity." This phenomenon is, of course, not limited to sandy beaches (e.g. see Ugolini & Pezzani 1995).

Scapini (personal communication) postulates that, as far as long-term flexibility is concerned, sandy-beach talitrid amphipods inherit a suite of possible orientational responses, from which they adopt the most appropriate for the conditions in which they find themselves, coupled with the ability to learn to modify the chosen responses according to circumstances. Over and above the ability to adapt behaviour to shore-line orientation, slope, tidal range and other features of the physical environment, most members of the macrofauna appear to have, in reserve, an escape response which overrides other orientational responses in times of short-term crisis, such as storms.

However, even the escape response can apparently be modified according to circumstances (as in the case of *Tylos* migrating onto breakwaters), so that even here learning ability and experience may play a major role.

If the three behavioural characteristics now seen to be essential for life on exposed sandy shores - tidal rhythms, appropriate orientation and plasticity of response - are necessary for survival, then all three must have been selected for during the course of evolution. We usually think of selection for a clearly defined characteristic or behaviour pattern but in the present case we have to conclude that behavioural flexibility it self has been a selected feature. The inheritance of such flexibility may, of course, be very complex and, although heterozygote advantage may be very relevant to it (Scapini & Fasinella 1990, Scapini et al. 1995) this cannot be the whole story. Certainly, if behavioural flexibility is a genetically facilitated, the actual changes in orientational behaviour must be largely learnt.

The idea that behavioural plasticity may be a key factor in evolution is not totally original. Hazlett (1988) developed the same concept, based on work on hermit crabs. He states that "the essential feature of behaviour is its flexibility in interfacing organisms with an environment which is variable in time and space" and that this plasticity must have been rigorously selected for in unpredictably harsh environments where the loss of such flexibility would preclude the animal from survival.

We might go one step beyond this and note that, just as behavioural plasticity becomes more marked the more exposed the beach, so apparently does synchrony of response within the population. For example, *Tylos* on sheltered beaches emerge over a period of time, individuals apparently paying little attention to what the others are doing; in contrast, *Tylos granulatus* on exposed South African west coast beaches virtually all come to the entrances to their burrows at the same time and then pause until one individual emerges, whereupon the others follow suit (Brown & Odendaal 1994). Reburrowing at the end of an activity period is also remarkably synchronous. Can it be suggested that synchrony is also genetically determined and has been selected for, or is it a learnt behaviour pattern?

However that may be, it is clear that insight into behavioural plasticity remains one of the major gaps in our knowledge of sandy-beach animals in general and one that needs to be filled if we are to achieve an understanding of life in such habitats. I appeal to biologists to report observations of "unusual" behaviour even if it has not been quantified or observed repeatedly. To the animal on the beach, our ability to quantify or to set up controlled experiments is of no significance at all and phenomena which we can at present only describe may, as in the case of behavioural plasticity, be of more importance to it than many features which lend themselves to quantification and statistical treatment.

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