

STUDIES IN THE BIOLOGY OF TALITRIDAE (CRUSTACEA, AMPHIPODA): VISUAL ORIENTA- TION IN *TALITRUS SALTATOR*

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(Text-figs. 1-4)

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ORIENTATION BETWEEN TIDEMARKS

The nocturnal migrations of *Talitrus* over the sand surface cover considerable distances, frequently taking specimens well below mid-tide level. In spite of this, by day the species occupies burrows in a broad, but fairly well-defined, zone in the region of high-water mark. The nocturnal distribution of the animals can be attributed to a somewhat random search for food, but the question arises (worded anthropomorphically), how do the animals find their way back to the high-water region? Perhaps in an attempt to answer this question, Verwey (1929) states briefly that *Talitrus* orientates on the beach by mnemotaxis to the wind, sun and direction of the sea, and by menotaxis (compass reaction). Mnemotaxis, or orientation by memory images, has been entirely eliminated from the modern classification of orientation reactions (Fraenkel & Gunn, 1940), so that Verwey's contribution is reduced to a statement without evidence that *Talitrus* orientates by means of a compass reaction to an unknown stimulus, and no other author mentions the orientation of *Talitrus* on the beach.

When, by day, specimens of *Talitrus* are taken from their burrows and released on firm sand between tidemarks, they will, either immediately or after a period of up to 3 min. apparently random wandering, take up a straight course towards high-water mark. Typical examples are shown in Fig. 1a, which, like other figures in this section, was drawn from freehand records of the animals' paths. Distances were gauged by pacing. Progress is made both by walking and jumping. When an animal jumps it usually turns in the air, and is seldom still pointing towards high-water mark on alighting, but it

immediately aligns its body with its former course before continuing. Small deviations are made towards pebbles or other objects projecting from the sand. Pebbles are not detected beyond half a metre, but the animal moves towards larger objects at greater distances, including the observer at up to 3 m. (In practice, therefore, the animals were observed from beyond this range.) Unless the *Talitrus* burrows, it soon continues on a course parallel to that previously followed. It burrows on encountering a piece of sand where the surface is broken, as at a worm-cast or a foot-print, or, eventually, on reaching the less tightly packed sand at high-water mark. A specimen has been observed to follow a straight course over 80 m. in length to high-water mark.

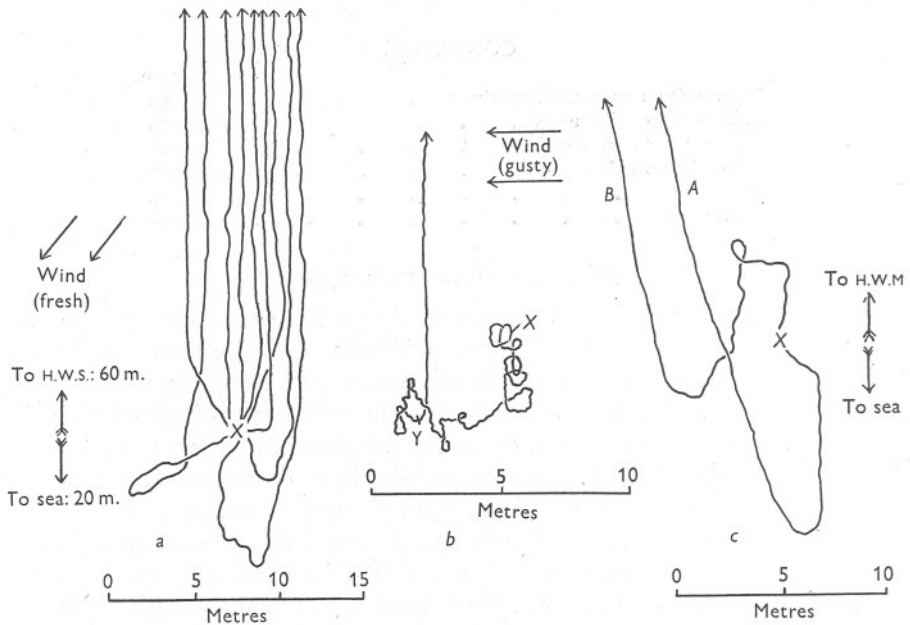


Fig. 1. *a*, tracks of nine *Talitrus saltator* released singly at X on a sandy beach; *b*, track of a specimen released at X with eyes painted (eyes cleaned at Y); *c*, tracks of (A) a normal adult male *Talitrus* released at X and (B) a similar adult male with right eye painted, released at same point.

This orientation has been confirmed in several dozen specimens of *Talitrus* on five different sandy beaches in Northumberland. Courses usually run at right angles to high-water mark, but occasionally, though straight, they are at a slight angle to the normal. All animals released at the same point follow approximately parallel courses.

A compass reaction to the sun or wind could only take place if the animal reached its inter-tidal position by following a certain course, and returned on a reciprocal bearing. The behaviour of *Talitrus* was shown not to be an example of this type of orientation by carrying animals from their place of

capture to their release point in a covered container. Such animals orientated in the normal way. Animals collected from different points along the beach, or which had been kept in captivity for several days, all followed parallel courses from the same release point, showing that the reaction is not homing behaviour. The orientation was found to be uninfluenced by the position of the sun in the sky, or by overcast conditions, or by the direction of the wind. Strong winds would at times blow animals some distance along the beach, but on regaining their feet they would take up a course parallel to that previously followed.

That the animals did not make use of the slope of the beach was shown by releasing specimens on a raised sandbank and on an undulating surface; tracks were always towards high-water mark whether leading downhill, level or uphill. There was in no case any gradient or discontinuity of salinity, moisture or humidity that the animals could have followed, and the orientation appeared too rapid and too accurate to be due to any of these factors.

It was noticed that orientating animals always held the antennae outstretched sideways with the tips on the sand. From this it was thought possible that these appendages were acting as receptors to some directional stimulus, perhaps vibrations from the sea, but the orientation was clearly shown by animals whose antennae had been amputated.

The possibility of a visual orientation was tested by using animals whose eyes were painted with a mixture of glue and indian ink. Such specimens showed no trace of a directional orientation (Fig. 1*b*). This not only showed that the orientation was visual, but confirmed the inability of the animals to make use of the slope of the beach. Previous observations that the orientation was independent of the position of the sun showed that it was not a simple light reaction; it therefore appeared that form-vision was involved. The fact that the orientation was not destroyed in unilaterally blinded specimens (Fig. 1*c*) confirms that a light-balance between the two eyes is not involved. If such had been the case, unilateral blinding would have led to circus movements. Fig. 1*c* also gives an example of tracks which are not perpendicular to high-water mark.

Animals released from such a position that their direct route to high-water mark was barred by water, showed a normal orientation until within about 2 m. of the water, when they turned and ceased to follow a straight path (Fig. 2). This suggests that, although water can be detected at short range, the tracks of the animals towards high-water mark cannot be the result of orientation away from the sea. This is confirmed by watching orientating animals, which, when walking, follow a straight course without turning the body, yet the position of the eyes makes it quite impossible for them to see the sea.

The fact that all tracks from the same release point tend to run parallel all the way to high-water mark suggests that orientation is to some distant object, beyond high-water mark. Considering the range at which *Talitrus* detects

objects on the beach (such as pebbles and man) the only suitable objects, large enough to be detected, which are normally present are sand dunes or other features composing the skyline. Orientation to the highest point on the skyline does not explain all observed cases, nor has any feature yet been detected which can be regarded as directing the orientation.

It seems, at first sight, improbable that form-vision plays an important part in directing the reactions of a nocturnal animal, yet there are very few summer nights when a silhouette of the sand dunes against the sky is not visible to man from the beach, and *Talitrus* may have better night vision than man. Some evidence for infra-red vision in *Talitrus* is provided by the fact that several

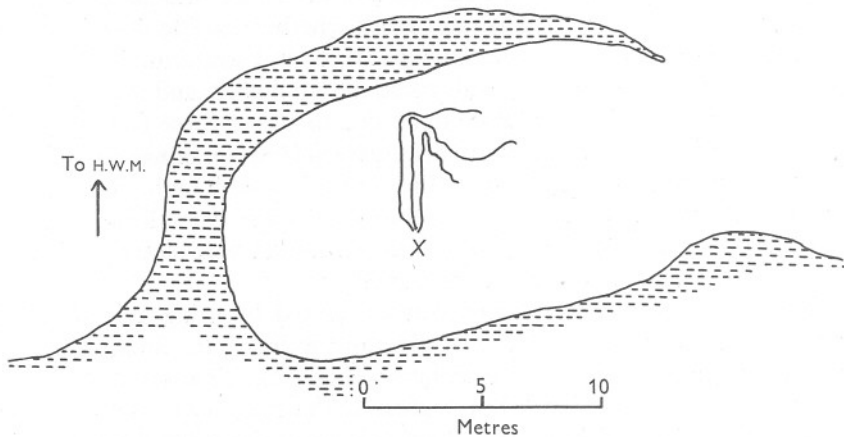


Fig. 2. Tracks of three *Talitrus saltator* released on a sandbank almost surrounded by water.

specimens showed the normal inter-tidal orientation in a fog which limited human vision to about 200 m., and the peaks of the nearest sand dunes were about 250 m. from the release point. Even if *Talitrus* is unable to use this orientation at night, it could still be of great importance, for the general return to the high-water region probably takes place at dawn.

The inter-tidal orientations of other talitrids have not been studied in the same detail as those of *Talitrus*, but a few observations have been made on *Talorchestia deshayesii*, *Orchestia gammarella* and *O. mediterranea*.

Talorchestia deshayesii appears to show similar reactions to *Talitrus*, but, owing to its small size and the necessity of standing at least 3 m. away from the specimen, it is soon lost to view, and when jumping it is influenced much more by the wind than is *Talitrus*.

The reactions of the species of *Orchestia* on a rocky beach would be likely to have important bearings on their natural behaviour, but the abundance of cover among rocks makes the observance of such reactions very difficult. Bate & Westwood (1863) state that when *O. mediterranea* is disturbed it always

jumps towards the sea, but I am unable to confirm this. As far as can be observed, both this species and *O. gammarella* scatter in all directions.

Observations have been made on a number of *O. gammarella* released on sand. Specimens released within about 100 m. of rocks made straight towards the rocks. Of specimens released well away from the rocks, one consistently made straight towards the sea in several tests. This reaction was destroyed by painting the eyes. Other specimens followed courses away from the sea, which, though fairly straight, did not run parallel.

While further observations are necessary before forming any conclusions about the visual orientation of *O. mediterranea* and *O. gammarella* in nature, it seems that *Talitrus*, and probably also *Talorchestia deshayesii*, makes use of some feature of the skyline in returning to high-water mark from between tidemarks.

LABORATORY EXPERIMENTS

Having obtained strong evidence that *Talitrus* makes use of form-vision in nature, laboratory experiments were designed to investigate the ability of the animals to distinguish between different shapes, and, if possible, to obtain further information about their visual responses.

Before proceeding further, some explanation of the use of the term 'telo-taxis' is necessary. It has been described by Fraenkel & Gunn (1940) as 'orientation to a source of stimulus, as if it were a goal', and implies the direct attainment of orientation without a balance of intensities of stimulation. The difference between this type of reaction and balance reactions (tropo-taxis and klino-taxis) is seen when two sources of stimulation are present; an animal orientating by a balance reaction will then make between the two (assuming a positive reaction), while an animal orientating by telo-taxis will make towards one and ignore the other, though if the two sources are of similar intensity it may frequently switch its orientation from one to the other, giving a zig-zag path. Such a zig-zag path is associated with telo-taxis alone.

Fraenkel & Gunn 'restrict the term "taxis" to a reaction in which the stimulus is undifferentiated and does not involve form-vision', and, as an extension of this rule, apply the term 'telo-taxis' to certain reactions to light only. Cases in which animals react to shapes by the same orientation (e.g. *Carcinus*, *Eupagurus*) are excluded from the category on the grounds that 'the reaction is . . . rather too complex to be called a taxis'. Although form-vision is a more complex process than the detection of light, the orientation, in examples such as *Carcinus* and *Eupagurus*, is no more complex than photo-telo-taxis; in fact, if the stimulus were unknown, the two could not be differentiated. Telo-taxis is the description of a particular type of orientation, and as such it must include all examples of this type of orientation, whatever the stimulus. Certainly more complex forms of orientation should be excluded from telo-taxis, but it is not a description of stimuli. For these reasons I have used the term 'telo-

taxis' in the following pages to refer to *any* reaction in which 'orientation in the direction of the source of stimulation occurs without balance' as if to a goal (Fraenkel & Gunn, 1940).

Apparatus and Method

For investigating the visual orientation of *Talitrus*, apparatus was used as shown in Fig. 3. An animal placed on a horizontal blackboard, measuring 6×4 ft. (1.85×1.23 m.), could see a vertical white screen or the projections thrown upon it at one end of the board, but was screened from direct light from the projector. The figures for the projections were painted in indian ink

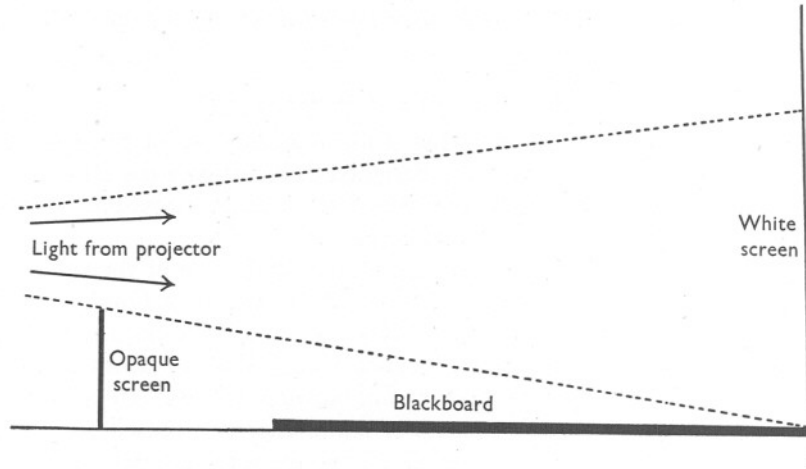


Fig. 3. Arrangement of apparatus for studying visual orientation in *Talitrus saltator*.

on blank lantern slides. Specimens were released from under an inverted jar so that the experimenter could not influence the direction in which they faced at the time of release. As the animal crawled on the board the observer marked its track with chalk. As long as the hand and chalk were kept behind the specimen it showed no reaction to them.

Orchestia and *Talorchestia* are much less suitable than *Talitrus* for use with this apparatus. Being smaller, they are less easy to see and less easy to handle, and they show effects of desiccation more quickly. They also jump a great deal more than *Talitrus* so that their courses cannot be plotted as accurately. Experiments were therefore confined to *Talitrus*. Adult specimens of both sexes were used.

In Fig. 4 the projection on the vertical screen is shown directly above the tracks of the specimen on the horizontal blackboard. All tracks in the same figure refer to the same specimen, released at different points (marked *X*). In general, different figures refer to different specimens.

Results and Discussion

When first removed from beneath the sand in laboratory cultures, specimens of *Talitrus* usually show a photo-negative reaction, but, if kept in the light, the orientation changes to photo-positive within 10 min. Such photo-positive animals were used in the following experiments. When confronted with an illuminated, white screen (Fig. 4*a*) they made towards it, but followed no very direct path, nor did the tracks end near any particular point on the screen. A similar, rather inaccurate, photo-positive reaction was shown when much of the screen was darkened so as to give a black-white, vertical boundary (Fig. 4*b*), and when the projection was a white square (Fig. 4*c*). In these three cases the animals orientate towards the light, and there is no suggestion of form-vision.

The reaction to a large, illuminated rectangle (Fig. 4*d*) shows quite a different orientation from the inaccurate photo-positive behaviour already seen. The tracks are more direct, and most of them are towards one or other of the upright boundaries of the rectangle, sometimes changing from one to the other to give the zig-zag path which characterizes telo-taxis. The sources of stimulus for the telo-tactic reaction are not light sources, but the vertical dark-light boundaries. The reaction cannot be explained except as a case of form-vision though the shape of an upright line is as simple a form as can be imagined. Three of the seven tracks (and part of one of the other four) are not in the direction of these objects, but only in the general direction of the screen. In these cases the specimen is showing the photo-positive behaviour seen in Fig. 4*a-c*.

Telo-taxis to a vertical dark-light boundary is even more clearly shown to the projection of two light squares (Fig. 4*e*). Here none of the reactions are to light; they are all to the shape of the upright edges. The fact that most of the tracks end at the edge of the right-hand square was probably the result of this square being slightly the more brightly illuminated.

Orientation to a more complex shape is seen in Fig. 4*f, g*. In both cases the animals make towards the foot of an incline. With several different specimens it was found that with the single slope (Fig. 4*f*) the majority of the tracks led directly to the foot of the incline when the angle a was between 15° and 70° , but beyond these limits the tracks were not precisely directed, but were examples of the inaccurate photo-positive orientation illustrated in Fig. 4*a-c*. Similarly, with the projection shown in Fig. 4*g*, well-directed responses were obtained when $a_1 = a_2 = 15^\circ$ or bigger, but only occasional tracks led to the foot of the slopes when $a_1 = a_2 = 10^\circ$.

Comparison of Fig. 4*h, i* shows that the directed orientation to a downward taper is not given to an upward taper.

Again, using the projection of two squares shown in Fig. 4*e*, but with one coloured red and the other green, or red and blue, similar tracks were obtained to those using white light. While not revealing any colour preference on the

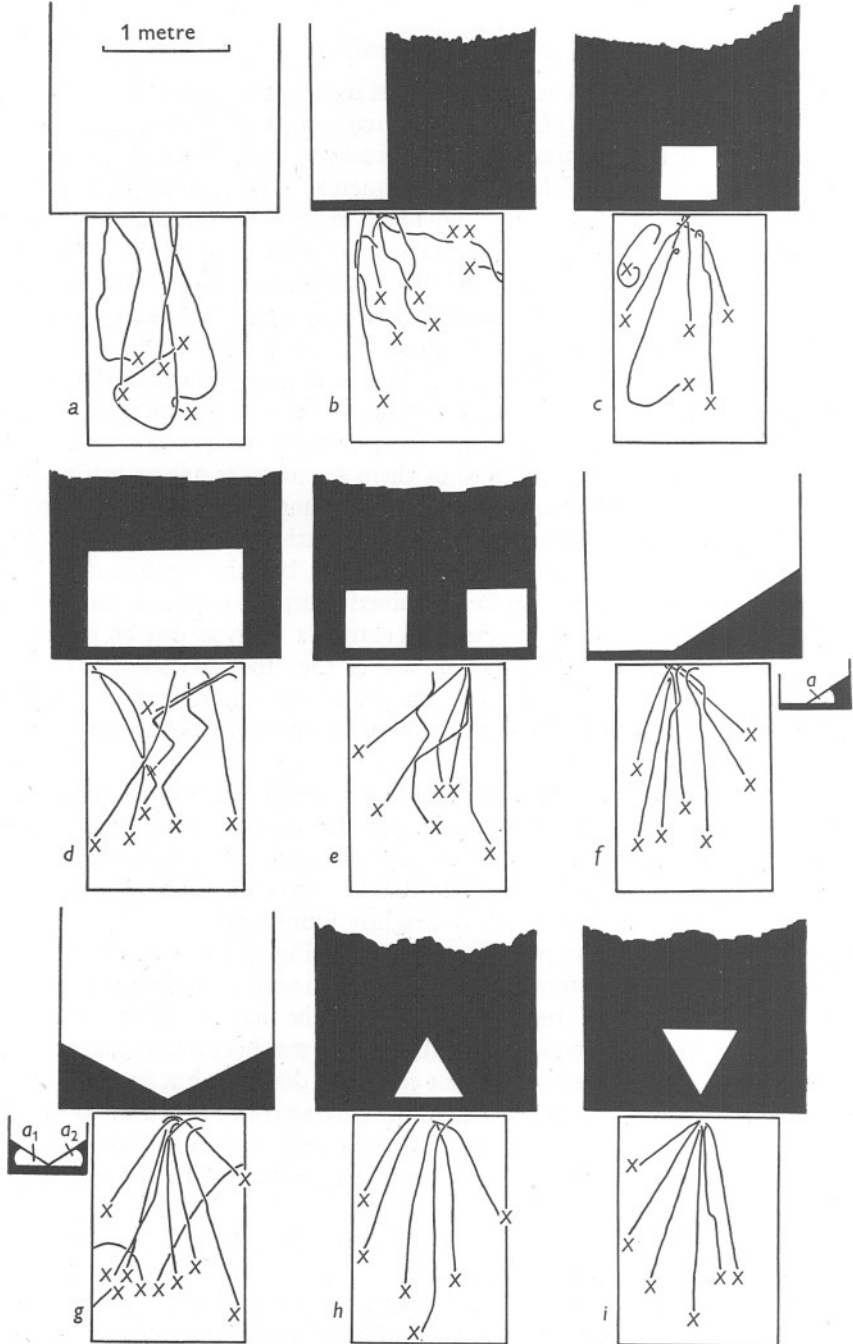


Fig. 4. Visual orientation in *Talitrus saltator*. The upper part of each figure shows projection on vertical white screen; the lower part shows tracks of specimens released at X on the horizontal board.

part of the animals, or demonstrating colour vision, it shows that all three colours are within their visual frequency range.

It has not been possible to link the laboratory behaviour of *Talitrus* to specific shapes with its orientation on the beach, but the laboratory experiments have confirmed beyond doubt the conclusion drawn from the beach experiments that *Talitrus* is capable of form-vision and shows a positive orientation to certain shapes.

I am indebted to Prof. A. D. Hobson for advice and encouragement in this work, which was carried out at King's College, Newcastle-upon-Tyne, under his supervision.

SUMMARY

Talitrus saltator placed on firm sand, between tidemarks, in daylight, usually follows a direct course to the high-water region.

The orientation is visual, and probably involves form-vision of distant objects.

Form-vision in *Talitrus* was demonstrated in the laboratory by its reaction to silhouettes. It makes towards the foot of an incline and sometimes towards a vertical, dark-light boundary.

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