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Dedicated to Professor Dr. H. Engel

Some remarks on ecological problems in *Patella vulgata* L.

A. PUNT

ABSTRACT

Some ecological observations on *Patella vulgata* L. are recorded.

1. Homing is a very normal behaviour, older animals being more attached to a specific "home" than younger ones.

2. Orientation on the way back is still obscure. It looks as if no chemical, visual or tactile stimuli are involved.

3. There is a correlation between the position of the limpets on their homes and the angle of inclination of the rock surface. On vertical rocks the limpets sit head down.

4. Some remarks on temperature measurements in the animal during the dry period are added.

5. There is some evidence that the animals most exposed to the dry period in the tidal rhythm have the most conical shells.

During several excursions with students under the direction of my colleague Engel and myself to marine-biological laboratories (Ambleteuse, Roscoff, Banyuls, Menai-Bridge etc.) one of the subjects of field-studies was the behaviour of *Patella*. *Patellas* living in the tidal zone on rocky shores habitually wander around in search of food when submerged by the sea. As soon as the water recedes they go back to a specific, and nearly always exactly the same, place on the rock, the "home" of the limpet, where they stay, firmly attached to the stone to overcome the dry period.

Like so many biological phenomena this well-known behaviour is said to have been mentioned already by Aristoteles. It was described by J. R. A. Davis (1885), C. Lloyd Morgan (1890), and J. R. Ainsworth Davis (1895). Several investigators tackled the problem of how *Patella* could find its way back towards its home, what landmarks were used and what sense-organs were involved, but up till now no satisfactory explanation could be brought forward (H. Piéron, 1909; A. J. Southward — J. M. Dodd, 1956; Edelstam

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& Palmer, 1957). Yet I think some remarks and new points evolved from the above students' observations are worth mentioning.

HOMING

The homing was studied intensively, and films in time-lapse technique were made. The animals were marked with water-proof paint ("Fluorart", Winsor & Co. Ltd., London), and the same markings were painted on the rock near the homes.

The constancy in keeping the same home was proved. Even when, at low tide, the limpets had been removed from their homes and replaced on the rock at a small distance, a high percentage, (i.e. 90%), of them were refound on their own homes and in exactly the right position after the tidal submersion.

After displacement over more than 25 cm, however, this percentage fell to about 50%, though homing over more than 60 cm was regularly observed.

It turned out that large and older limpets showed a more pronounced homing behaviour than young ones (Van Bree, 1959).

Though spontaneous homing was occasionally observed, and the ability of forced homing was obvious in the above experiments, we did not know whether all the animals, when submerged, left their homes and went around on the rock.

To get an answer to this question an interesting experiment was made by Dr. I. Kristensen at Menai-Bridge. Large lumps of rock, containing *Patellas* on their homes were fixed with rope under a floating pontoon-bridge, just below the surface, so that the animals remained submerged, but could be observed at any moment of the tidal cycle. It turned out that all the animals (14) left their homes one to two hours after the flood had set in. They went around, covering distances of up to 64 cm. They homed when the hour of low tide drew near although of course they could not observe any difference in water level.

Evidently the behavior was influenced by an internal clock. After observation during several tidal cycles we established that 79% of the limpets returned exactly to their homes. In the meantime they had made excursions of different types. Some of them always returned to their homes by the way they had gone. Other animals however, made the same round-trip every flood-period, following another way in coming back than going out, and still others made different trips in different directions during every "submersion" (Kristensen, not published).

We also tackled the problem of what beacons and sense organs, if any, are involved in the homing behaviour.

A. CHEMICAL STIMULI

Although from the above experiments it was already evident that in homing the animal did not necessarily follow a specific trail made by itself on its outgoing excursion, we made the following experiment.

Limpets were removed from their homes. Beginning at the spot of the home a smear of limpet-mucus was made on the rock. The limpet was put on the end of this trail. Subsequent homing was evident, but the artificial trail was not followed at all.

B. VISUAL STIMULI

In order to find out whether the direction of incident light was of any influence the following experiments were made.

1. Lumps of rock covered with *Patellas* were turned round in the horizontal plane (90° and 180°). The limpets were removed from their homes and replaced on the rock at distances from 10 to 30 cm, in order to get forced homing in the next tidal submersion. No difference could be found in the percentage of successful homings (e.g. 91% after 10 cm displacement).

2. In another experiment the lump of rock on which the limpets were in the act of moving to their homes was turned round. Though the data are rather few this observation yielded very interesting results. 12 out of 21 homing limpets turned round and went in the wrong direction, but 10 of them for a few minutes only. These animals made a correctional movement and made straight for their homes. The two other limpets were found at their homes after the next tidal submersion. Seven animals stopped their march home at the turning of the stone, but they too were back after the next period of high water. The remaining two limpets were not disturbed at all by the rotation of the rock, and did not stop the homing movement. From these observations it is evident that distant visual beacons are only of minor importance.

3. With a small thermocauter the eye spots at the base of the antennae were destroyed. No difference in homing behaviour could be observed.

C. TACTILE STIMULI

Is there any evidence that tactile stimuli make orientation possible?

1. Ainsworth Davis (1885) already extirpated the tentacles without finding any difference in homing ability. We repeated this experiment several times with the same result.

2. With very fine scissors we removed all pallial tentacles as well. Even then homing occurred with nearly the same success.

3. We altered the direct surroundings of the homes by removing all barnacles and small ridges by knocking off particles of rock. The limpets were placed at a certain distance from their homes. In comparison with blank experiments in which the surroundings of the homes were left unaltered and in which the same number of limpets were displaced over the same distance no significant difference in homing could be observed.

D. GRAVITATION

Though it looks as if in homing the influence of gravitation (as assumed

by Bohn, 1909) is not very probable the following observations may be of interest.

A correlation could be found between the situation of resting *Patellas* on their homes and the inclination of the surface. On perpendicular rocks 73% of the limpets sat head down on their homes. The next table gives the data from over 200 observations.

Angle of inclination	% head downwards	% head indifferent	% head upwards
20°	41	48	11
40°	56	37	7
70°	68	32	0
90°	73	25	2

It will be rather difficult to exclude experimentally the sense organ which is supposed to be involved in this phenomenon. The otocyst is situated near the pleural connectives and as a consequence is very difficult to remove.

SOME PHYSIOLOGICAL REMARKS

Staying over the period of low tide on the drying rocks must be a physiological stress for the limpet.

In this period its temperature may rise considerably. This was proved by drilling a small hole in the top of the shell and inserting a micro thermistor into the nuchal cavity. Temperature could be measured electrically using a portable wheatstone-bridge. Although these experiments were made on relatively cool days temperatures of 8° C above the temperature of the seawater were found. Temperatures within the animals were even higher than ambient air temperature (e.g. 21° C and 17° C) due to absorbed radiant heat.

On really hot days these differences will be even greater.

We observed that the shells of the animals found highest on the rocks were more conical than those at a lower level, which are, of course, submerged for a longer time.

This could mean that the more conical the shell, the larger can be the nuchal cavity in the top of the shell, in which the animal can store water to overcome the dry period.

From measurements of 200 limpets, in which the height of the shell was compared with its length and width — thus giving a relative height index — it was found that in one place at the channel coast of France (Audresselles) this index $\left(\frac{\text{length} \times \text{width}}{\text{height}}\right)$ was 62.3 in animals from the *Fucus platycarpus* zone (high on the rocks) and 85.9 in animals from the *Laminaria* zone.

In other places, however, no such striking difference was found. Although it is not probable that different species are concerned, we have to bear this explanation in mind and further investigations have to be made.

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Professor Dr. A. PUNT
Laboratory of Animal Physiology
University of Amsterdam — The Netherlands