HOMING IN *PATELLA* SP.

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In 1964 Jelle Atema and Rob C. Peters studied homing behavior of the limpet (*Patella* sp.) at Dale Fort Field Centre (South West Wales) during a two weeks field practical, as was compulsory for students with a major in Comparative Physiology at Sven Dijkgraaf's laboratory. Aim of this practical was to have the students experience more biodiversity than was possible in the lab, and to demonstrate where the origin of scientific questions could be found. The enthusiasm of these two students resulted in a short paper, submitted to the scientific periodical *Experientia*. *Experientia* considered the manuscript did not contain enough new facts about *Patella's* homing behavior, and did not accept it for publication. *Stichting De Traditie* recovered the original manuscript to illustrate the broad scientific basis of the study of biology in the Netherlands in the 'sixties'. The reader is invited to compare the biological study programs of 2018 with those of 1964, to discover what is gained and lost by half a century of science management. Picture above: Jelle Atema (L) en Rob C. Peters (R) in Wales, 1964.

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Original ms 1964, summary, comments 2018, references, Acknowledgement

Feeding behavior and "homing" in the gastropod *Patella*

During a short stay at the Dale Fort Field Centre in South-Wales (U.K.[1]) the behavior and orientation of the limpet, *Patella* spec.[2], a prosobranch gastropod, was studied (28 August to 8 September, 1964). The animals live on the rocks and stones of the tidal zone. To feed, they crawl slowly about scraping off the film of algae. After this, each individual returns to its own specific resting place, its "home". The limpet settles upon its[3] home in much the same way a bird adjusts itself in its nest so that with passing time the shell edge and the surface of the home area on the rock fit perfectly. In order to study the feeding behavior of a number of limpets and to investigate the sensory basis of their homing, the shell of each animal and the rock near its home were marked with a specific signal consisting of dots of nail polish. This enabled us to follow the limpets individually.

Feeding behavior. On the basis of the location of the homes with respect to the tidal zones we distinguish three groups of animals: (1) those with their homes close to the low tide level (these animals get dry only during spring tide); (2) those with their homes between the low and high tide levels (these animals undergo all the changes of the tide every day); (3) those with their homes close to the high tide level (these animals get submerged only during spring tide).

Animals of the first group could not be observed for obvious (technical) reasons. Among the limpets belonging to the second group we distinguish two sub-groups: (a) those which live in pools persisting during ebb; and (b) those which live outside the pools. (a) Limpets living in pools grazed twice a day during ebb. It was observed that some individuals predominantly moved about during the night, others during the day. During the night ebb the activity was greater than during the day ebb. Animals active during the night left their pools sometimes for several hours, but mostly moved not farther away than a few decimeters. Some limpets chose the same

1 Original text: “England”
2 *Patella vulgata, P. intermedia, and P. aspera.*
3 Some linguistic corrections were made: e.g. “his” was replaced by “its”.

direction every time they left their homes, without, however, always pursuing exactly the same course. Before the flood reached the pool again, most limpets were either at home or on their way home. About 1 to 3 hours after the tide had receded from the pool, another period of activity began. (b) Limpets living outside the pools almost all crawled about upon the rocks during the night ebb. During the day ebb, generally those who had their homes in the shadow crawled about. During damp weather (fog) there was much more activity than during dry weather. Animals of this sub-group traveled over long distances (up to two meters). They were almost all back at home before high tide. A few did the last distance under water. About 1 to 5 hours after emergence from the water by the falling tide the limpets began to creep again.

Animals of the third group, getting submerged only during the spring tide, were found in and under the splash zone. In their active period, which lasted in our case about one week, they behaved as has been described for the limpets of sub-group 2b. They moved distances up to one meter. Apparently they do not move during the long dry periods, which last about 3 weeks. Their faeces were stored under their shell. So it seems that they are more or less sealed off from the external world during this time. The foregoing data show that *Patella* was not at rest during the ebb tide as is often assumed[4]. On the contrary, our limpets were creeping and feeding during ebb, when there was no danger of drying out or of being carried away by the water, whereas they stayed at home during the flood-tide.

"Homing". Some preliminary experiments were carried out in order to clear up in which way *Patella* manages to find again its home after a feeding period and before the flood comes up. *A priori*, orientation might be based upon visual, gravitational, chemical or tactile stimuli — or on a combination of these. For the experiments animals were chosen that had their homes on large but movable (by two men) stones. By turning the stone while they were away from home, though still on the stone, orientation to incident light and to gravity were tested. Orientation to chemical stimuli (marks on the rocks, trails of mucous) was roughly checked by means of scrubbing the route of their course with soap and water while they were away. Orientation on the basis of tactile stimuli was tested by damaging the surface of the stone by creating a circular groove of a few centimeters wide with a diameter of about 20 centimeters, around their home, again while they were away. Combinations of these three methods including turning of the stone together with scrubbing and the application of a groove were also tried. However, in nearly all cases the limpets still found their way home. Unless one would assume that *Patella* recognizes its home visually - which seems rather improbable with regard to the structure of its simple eyes - another assumption seems inevitable, *i.e.* that the limpet, besides knowing from experience the characteristics of the next-door environment of its home, has a kinaesthetic sense by which it records its locomotory movements. In this way the animal could permanently be aware of its position with regard to its home. As to the knowledge of the rock surface we observed that *Patella*, when creeping, contacts the ground with its tentacles. When we took an animal from the rock and put it on a smooth aluminum plate, it followed minute scratches on the plate. All limpets that were taken from their home during ebb and put on the rock at a distance of about 20 centimeters, in arbitrary directions, were back at home before high tide. In similar experiments with animals that were taken on their feeding way during ebb, about 75% returned to their home. Further experiments are needed to solve this orientation problem in the limpet.

4 See for example Barrett & Yonge 1964, p. 128.

Zusammenfassung.

Das Verhalten der Schnecke *Patella* in der Brandungszone einer englischen Felsküste wurde beobachtet. Die Tiere krochen während der Ebbe nahrungsammelnd auf den Felsen herum, begaben sich aber vor Eintritt des Hochwassers zurück zu ihrem fixen Ruheplatz (ihrem "Home") und verharrten dort bis zur nächsten Ebbe. Weder Umdrehen des bewohnten Felsblocks (zur Änderung der Licht- und Schwerkraftrichtung) während die Bewohner auf Futtersuche unterwegs waren, noch

Schrubben der Oberfläche (zur Entfernung etwaiger chemischer Reizmarken) oder Anbringen eines kunstlichen Grabens im Felsen rings um das Heim (zur Störung taktiler Orientierung), noch auch die Kombination all dieser Eingriffe verhinderte die zeitgerechte Heimkehr der Tiere an den Ruheplatz. Es wird daher - neben erfahrungsbedingter Kenntnis der nächsten Umgebung des Heims – raumliches Orientierungsvermogen auf kinästhetischer Grundlage angenommen.

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In retrospect it is surprising that our manuscript did not give figures of the number of *Patellas* studied. This is the more surprising as the Dutch version of the field trip report does give more detailed information. Apparently we – the students – did not realize the importance of such data. The Dutch version of the field report mentions about a hundred *Patellas* in all, but does not specify how many animals were tested more than once (Atema & Peters 1964). The overall outcome, however, is that the strongest interference with homing is caused by displacement during grazing, and by interfering with the gravity stimulus. See the results section of the original field trip report hereafter (translated by J.A. from Atema & Peters 1964):

Experiments

1. Gravity Sense. During ebb tide we rotated 3 rocks, each with 10-15 *Patellas* that were 5-20 cm away from home. The rocks were about 40x40x40 cm. Directly after the subsequent flood, all but 3 *Patellas* appeared to be home. We repeated this experiment twice.
2. Light Sense. See 1 above.
3. Chemical Sense. During ebb tide, when they were up to 1 m away from home, we soaped and scrubbed 5 home areas of about 20 *Patellas*. By the subsequent flood they were all home. We repeated this experiment 3x.
4. Touch Sense. During ebb tide, when the snails were as much as 2 m away from home, we hacked in the rock surface around the home site of 3-10 *Patellas* a circular groove of about 3 cm wide. We did this in 2 places. By the next flood they were all home.
5. Combination of 1-4. During ebb tide we rotated, scrubbed and hacked a rock with about 12 *Patellas* that were 5-20 cm away from home. By the next flood only one snail was not home.
6. General direction sense. (a) During ebb we took 7 *Patellas* from their home and displaced them about 20 cm in random directions. By the next high tide they were all home. (b) During ebb tide we displaced 20 moving *Patellas* by 10-30 cm in random directions. By the next flood 75% of displaced snails were home. (c) During ebb we picked up and placed 4 moving *Patellas* each onto its own home 5-20 cm away. One *Patella* moved away from its home and settled permanently 10 cm away.

Unlike today, literature search in 1964 had to be done by hand and on foot; not by computer and through the internet. It took time; lots of time. That, and the pressure to continue with our regular major programs instead of elaborating the *Patella* manuscript after the field work trip, must have been the cause for the absence of more references than just Barrett's guide to the sea shore (Barrett & Yonge 1964). On the other hand, profesor Dijkgraaf - who submitted the ms on our behalf - did not have any objections, although he felt somewhat embarrassed by the rejection afterwards. We did not know at the time that our neighbors from Amsterdam University had made a similar field trip to the Ambleteuse coast with professor Punt, and to Wales Menai Strait in 1958 and 1959 respectively (Kristensen & Parma 1968). The results of these earlier studies and of later, more sophisticated work, corresponded remarkably well with our field trip findings of 1964. Whereas most of the later studies deal with grazing behavior in general, timing, population density (*e.g.* Blackmore 1969, Chelazzi *et al*. 1990, Chelazzi 1992, Funke 1968, Jenkins & Hartnoll 2001, Papi ed. 1992, Santina *et al.* 1994, Salvini-Plawen 1971), only a few tackle the homing enigma more in depth. If we compare our observations of 1964 with later published work, we feel most comfortable with the papers of Blackford-Cook (1969), Cook *et al.* (1969), Gray & Williams (2010), Hartnoll & Wright (1977), Ng *et al.* (2013), and Williams *et al.* (1999). These authors describe a homing frame which matches our observations of 1964.

*Grazing***:** what we experienced as a discrepancy between our 1964 observations and publications on homing and grazing, turned out to be just one of the six sides of the 'orientation cube'. Limpets graze at high tide during daytime, and show nocturnal activity at ebb depending on geography (Blackford-Cook 1969, Gray & Naylor 1996, Gray & Williams 2010, Hartnoll & Wright 1977, Santina *et al.* 1994). The timing of grazing is, among other things, controlled by endogenous clocks and exogenous factors like water spraying and light conditions (Gray & Williams 2010, Santina & Naylor 1993). Our findings that switching on a torch at night induced a grazing limpet to return to its home, and that the limpets at the *Pelvetia canaliculata* zone only began to graze at spring tide, match these later, more elaborate, experiments nicely.

Homing: Without disrespect to other researchers, we consider the papers of Blackford-Cook (1969) and Williams *et al.* (1999) most revealing with respect to the neural mechanisms underlying homing behavior. Blackford-Cook concludes that distant cues are not relevant for homing, neither mucous trails (*cf.* also Hutchingson *et al*. 2007 , Ng *et al.* 2013), or dead reckoning. What seems to be essential for homing is knowledge of the terrain, in other words the internal presence of a 'cognitive map' (*cf.* O' Keefe & Nadel 1978). Whereas no specific cue could be found on which the homing faculty would depend, the slope of the rocks in combination with the light conditions (Williams *et al.* 1999) seemed to play an essential part.
In absence of a specific homing-controlling stimulus, we still wonder how exactly limpets find their homes. How should we interpret, for instance, Professor Punt's finding that limpets could home after having their tentacles removed, or after having their mantles damaged. Why has damaging of the shell rim such a deteriorating effect on the homing capacity (Kristensen & Parma 1968)? What does it mean that limpets rest at their homes with their heads downward. (Williams *et al.* 1999)? May we consider this as proof of the existence of a gravity-based bi-sensor system (Schöne 1984)? These facts in combination with the findings of Williams *et al.* (1999) on the effect of rock slopes suggests the shell may play an key part in orientation. After all it is no simple thing to carry a solid and rigid piece of carbonate on one's back all the time.

The future: For future experiments we would suggest to have a closer look at the part played by the shell in regulating the activity and in forming an internal map of the surroundings. During activity and grazing, the dynamically changing load of the shell might very well contribute to the construction of an internal map. And since sensitivity to the magnetic field of the earth has been demonstrated in several gastropods (Prato *et al.* 1996), one might investigate possible influences of the earth magnetic field on orientation and homing as well.

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