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A STUDY OF THE HOMING HABIT OF THE LIMPET

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Littoral prosobranchs of the genus *Patella* are generally thought to have a home, often a scar caused by the shell wearing away the rock, to which they return after feeding excursions. Stephenson (1936) observed the South African species *P. granularis* return from up to 5 ft away, an impressive performance for an animal with an apparently simple nervous system. Such an observation raises the question of whether this is normal limpet behaviour, and if so what mechanism is involved. Homing has been observed by several authors, either by direct observation of single individuals or by the return of marked limpets seen to be away from home.

Observations on individual limpets (Roberts 1847; Davis 1885; Thorpe 1963) report the precision involved, and indicate that random searching is not involved. Morgan (1894) and Russel (1907) also report homing in British *Patella*, Russel stating that 'this fact (homing) may be taken as well established', and concluding that limpets over 15 mm long have a definite fixed position to which they return after feeding. Stephenson (1936) observed homing in five species of *Patella* in S. Africa including small *P. cochlear* returning to homes on the back of a larger individual, i.e. a moving home. Hewatt (1940) reported homing in the American species *Acmaea scabra* (Reeve).

Evidence that homing is not normal behaviour in *Acmaea* is given by Villee & Groody (1940) who observed 223 individuals of five species, of which only 29 out of 102 seen to leave base returned. Homing does not appear to be as common in *Patella* as supposed. Orton (1929) considers that limpets do not home in some circumstances; for example, if on smooth wet surfaces. Lewis (1954) found no evidence for homing on a smooth concrete breakwater at Aberystwyth. This indicates that homing is probably normal behaviour in most situations, but does not occur on surfaces where a limpet's shell would fit the substrate anywhere. This agrees with the idea that homing is an adaptation to avoid desiccation and displacement on uneven substrates.

The external conditions under which homing does occur are important in imposing limits on the information available; for example, polarized light is only available by day. There is little agreement as to when homing occurs. Russel (1907) reviewed the situation and although finding little agreement among the authors states that limpets more than 20 mm long only move when covered by the tide. The only author to record movement at night is Stephenson (1936). It is not clear whether other limpets are limited in the time at which they move, but visual information seems unlikely to be important in S. African *Patella*.

The form of the path taken by a moving limpet indicates that limpets do not wander randomly or home by chance (Davis 1885; Morgan 1894; Thorpe 1963). Fischer (1898) and Stephenson (1936) both report that the out and return paths of homing limpets are not necessarily the same; therefore, a limpet is not following some trail laid down on the outward journey. Hewatt (1940) found that all the *A. scabra* he observed followed their outward path home.

The existence of a kinaesthetic memory, i.e. computation of position by reference to previous movements, was postulated by Pieron (1909) on the basis that limpets homed more successfully after making the whole journey themselves than when displaced. Failure to home after displacement could also be explained by the limpet having been displaced further than it usually moved, if homing using a topographic memory, or by damage caused by removal from the rock. The ability to home at all after displacement is strong evidence against a kinaesthetic memory. Morgan (1894) found that 18 out of 21 limpets returned from 45 cm but only five out of 36 from 60 cm. Changing the surface topography of the rock, either by chipping away the surface or by building it up, varied in its effect upon the homing ability depending on the magnitude of the change (Bohn 1909; Pieron 1909; Hewatt 1940). This suggests that information from the substrate can only be altered to a limited extent before homing is prevented. Altering the shape of the edge of the shell does not prevent homing or scar recognition but may cause a limpet to change its home (Pieron 1909; Hewatt 1940).

By changing the position of a rock it is possible

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to change the direction of all information except that available from the rock or the limpet. This has been done by Bohn (1909) with the result that a limpet moved to a new home with the same position in space as its original home. A similar experiment by Hewatt (1940) indicated that *Acmaea* was not affected by moving the rock.

Davis (1885) removed the cephalic tentacles from *Patella* without preventing homing. He also washed the space between limpet and home in order to remove any possible chemical cues, but with no effect.

No satisfactory theory of homing emerges for *Patella*. The homing of *A. scabra* may be explained by the simple following of the outward trail, but this seems unlikely in *Patella*. There is also evidence against surface topography navigation, kinaesthetic memory, and the use of the sun or polarized light. Most of the studies cited have recorded observations on small numbers of individuals, with little indication of the proportion of animals in the population that were showing the observed behaviour.

Our work was mostly done during June and July 1967 and 1968 on the western side of Saye Bay, Alderney, where the rock consisted of granite and dolerite, both boulders and parent rock being used. Some work was also done at Port Erin harbour, Isle of Man, in September 1967. The animals studied were *Patella vulgata* Linn., *P. depressa* Pennant, and *P. aspersa* Bean, all of which showed homing behaviour.

Observations

Methods

Marking Limpets. Limpets were marked with small plastic numbers of Dymo tape stuck on the shell with Araldite. The same number was stuck on to the rock next to the limpet in its home position. This method was most suitable when both rock and limpet were dry, and proved ineffective underwater. A white dot was painted on the apex of the limpet's shell to make it more conspicuous at night.

Marking the Plot. Most of the limpets observed were in small groups, from three to 39, on flat rocks. These were known as plots. An identification letter and three triangulation points were painted on the rock with white nitrocellulose lacquer, so that the points and limpets were co-planar. Originally these points were placed as far apart as possible, to give greatest accuracy of plotting, but later it was found more convenient to use a 25-cm equilateral triangle of reference points.

Triangulation. With the distances between the triangulation points known the position of any limpet could be recorded by measuring the distances between its apex and the triangulation points. Taking a series of such measurements at known time intervals provided a permanent record of the path taken by a limpet.

Photography. By taking a series of photographs of a moving limpet at known time intervals, a permanent record of both the path and orientation of the limpet was obtained.

Following. The path of a moving limpet was drawn directly on the rock with a crayon, chalk or chinagraph pencil. A photograph was taken of the completed record. There was a tendency for limpets moving over such drawn-in paths to remove the tracing, and possibly to follow it. Thus these results were not satisfactory.

Results

Observations were made whenever possible, and this covered most situations except high tide at night. Limpets were observed moving home at up to 1·5 cm/min, and this contrasted with their slower grazing speed. The excursions were not always limited to the planes of their homes, and homing around a right angle did not disorientate them. The track home was very often a straight line, especially when they moved rapidly.

When two limpets met, both lifted their shells where they touched, even when one was stationary. This was apparently a regular feature of limpet behaviour. Once this occurred when a limpet was nearly home, and after separating, it continued past its scar before turning and homing, perhaps being disorientated by its encounter.

On arriving at its home a limpet may be in any orientation. In order to be truly home, it must rotate to that unique position in which the shell fits the rock exactly. This is a slow movement and may be in a clockwise or anticlockwise direction. The shell seldom touched the rock until the correct orientation was reached, so there was probably no trial-and-error fitting of shell to rock, although the mantle tentacles could have been doing this.

It would seem valid to divide the limpet's homing process into two parts:

(i) The journey back to the home position.

(ii) The final orientation to home.

This distinction is based on behaviour only (see Fig. 1). In every case of successful homing the limpet homed, then orientated itself. There is no evidence that a limpet adjusts its course so as to reach home in the right orientation.

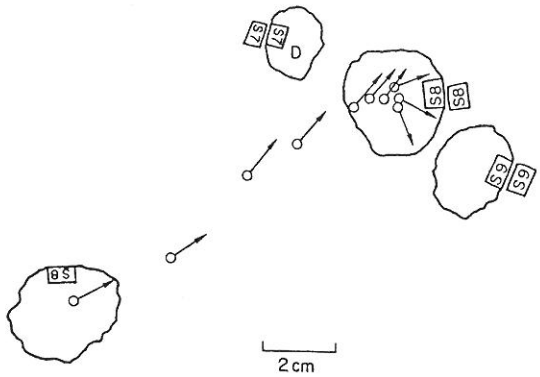


Fig. 1. The path and orientation of a limpet *Patella vulgata* returning to home, at 08.30 BST drawn by tracing projections of a series of still photographs, taken at 1 min intervals, and showing its rotation to its final position.

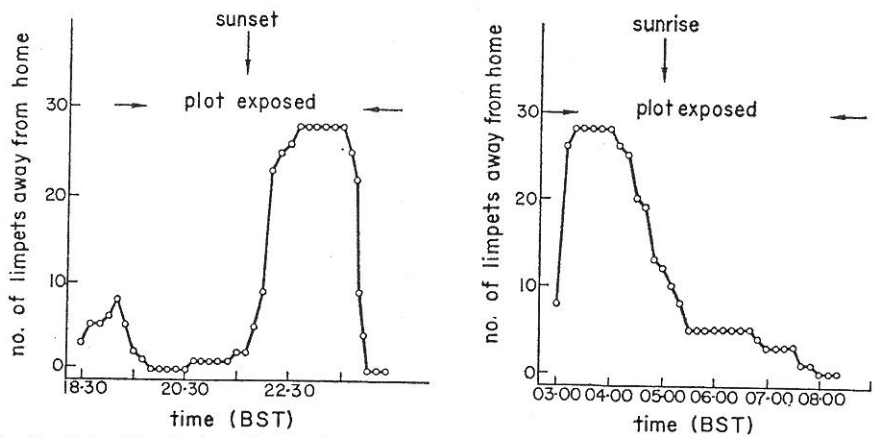
Occurrence of homing. 174 limpets were observed over a period of fourteen days, and 156 of these were observed away from home at least once, some as many as eight times. 469 excursions were observed during this period, of which 468 resulted in successful homing. It is believed that these limpets comprise a representative sample of the total population of Saye Bay, since they were not chosen on any behavioural basis, but only according to the accessability of the situation and the flatness of the rock. It is therefore, considered that homing is a consistent feature of limpet behaviour in this population at this time.

The one excursion that did not result in homing was interesting in that the 'errant' limpet came to rest on the scar of another limpet, which then took up a position about 2·5 cm from home. Both limpets remained stationary, until 61 hr after the situation was first observed, the obstructing limpet moved away. The other limpet then moved accurately to its home position.

Timing of homing. Limpets were seen to home both at night and during the day, and at all states of the tide, although no observations were made at high tide at night. Of 468 recorded homings, 309 occurred during darkness (i.e. between 22.00 and 05.00 hours BST). The remaining 159 occurred in daylight. Sixteen instances of homing under water were observed and 10 limpets were actually observed leaving home under water. They can home in the dark, in conditions varying from a clear moonlit night to a thick fog, and during the day, either in clear or overcast conditions. Thus there appear to be no limitations to the natural conditions under which a limpet can home. The timings of their excursions, however, fall into a pattern.

P. aspersa normally lives under water in rock pools or very low down on the shore. This species did not move according to a very rigid schedule but there was a tendency for those individuals on exposed rock to move more at high tide than when uncovered. *P. vulgata* and *P. depressa* moved when covered by the tide only if they were high up on the shore. Neither of these species were seen moving at high tide on the middle and lower shore. These observations contrast with those made at Port Erin in September 1967 where *P. vulgata* moved mainly at high tide at all levels of the shore.

To investigate the timing of movements records were made on a plot of 30 marked *P.*



Figs 2 a & b. The timing of excursions and its relationship to tidal events, sunset and sunrise.

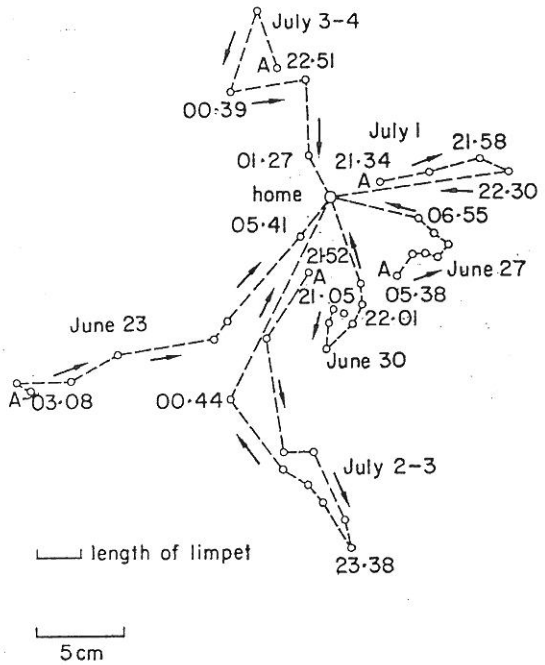


Fig. 3. The tracks of the same limpet on the dates and times shown (1967), returning home from a different direction each time. The position of the limpet was only known exactly (by triangulation) at the points shown 'o'. Times (BST) are indicated as convenient.

vulgata on two occasions when tidal effects could be separated from diurnal effects. It can be seen from the resulting graphs (Figs 2a and 2b) that the limpets moved before tidal events could affect them. This suggests that an endogenous rhythm is involved and that these movements are not made merely in response to stimuli from the ascending and descending water.

It is also clear that light intensity has an effect, forays tending to begin shortly after sunset and end shortly before sunrise, within the limits set by tidal exposure.

Stephenson (1936) suggests that humidity plays an important role in determining the time at which limpets' excursions occur. As night time humidity was uniformly high, it could not be involved in the determination of the movements recorded in Fig. 2. Humidity may have an effect on day time movements, but as few excursions began in daylight no further work was attempted in this field.

Form of path. All the movements of which there was sufficient information (at least four or five clearly separate points) were plotted from the triangulation results, and upon analysing these, three observations were made:

(1) An individual limpet does not necessarily follow the same path on different excursions (Fig. 3). Of the 39 individuals tracked more than once, only five showed any evidence of making the same journey on different days. There is thus no question of the animal carrying out a regular programme of movements that always return to the place from where it started.

(2) Limpets in the same area did not all start moving at the same time, or in the same direction, nor did they make journeys of similar length or duration (Fig. 4). The limpets were not, therefore, all reacting in the same way to external stimuli such as the direction of illumination.

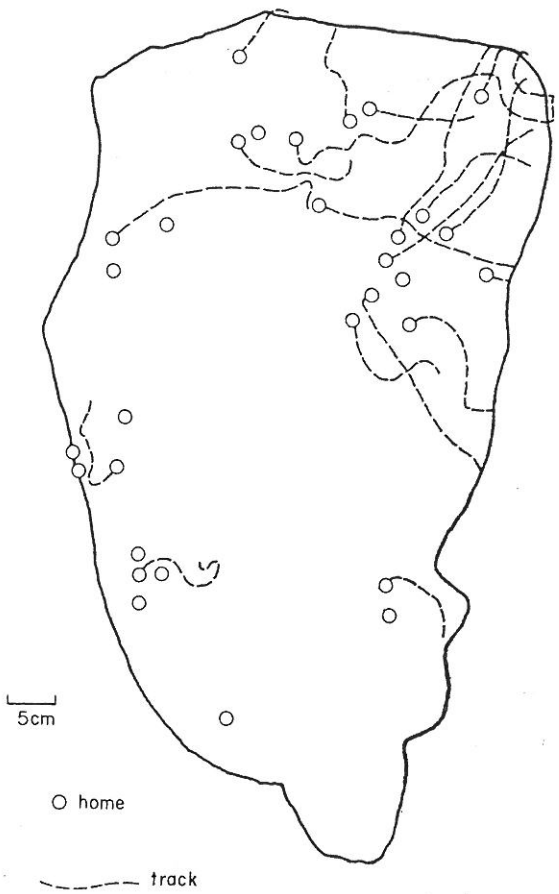


Fig. 4. The tracks of all limpets on a single plot on a single night between 03.30 and 05.00 BST showing paths crossing and the lack of a common direction. These tracks were obtained by triangulation.

(3) An individual limpet does not necessarily follow its outward path home (Fig. 5). In five plots, from 23 tracks long enough to be useful there were 19 examples of out-and-return paths possibly using the same route (e.g. that shown in Fig. 6), and four examples where they were definitely different. It is more significant that limpets can home without following their outward path, than that they frequently do, as this is strong evidence that a limpet does not home by following a chemical trail laid down on the outward journey.

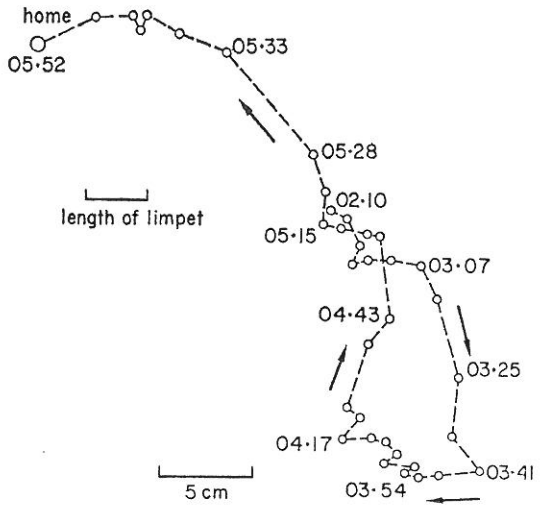


Fig. 5. Return track obtained by triangulation between 02.10 and 05.52 BST showing that a limpet need not necessarily follow its outward trail in order to home.

Limpets were not affected by the process of measuring their positions. On some occasions a limpet was accidentally touched, whereupon it clamped down and remained stationary for some time, but later resumed movement and homed successfully. At night unshielded torches seemed to affect the limpets, causing premature homing, but this was not noticed when a red light was used. The limpets were illuminated only when measurements were being made.

The serial photographs showed similar results to those of triangulation. The out-and-return trace in Fig. 6 is reconstructed from 29 serial photographs. This shows the orientation of the shell as anteriorly pointing arrows, but these are not absolutely accurate, being drawn from the peak of the shell to the leading edge, and thus subject to the changing parallax between the two. They are accurate enough to show that a limpet makes no great variation of orientation from the direction of travel. This supports the view expressed by Thorpe (1963) that the animal is 'properly oriented through its journey'.

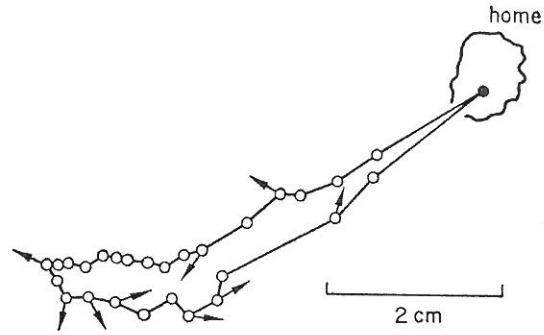


Fig. 6. An out and return track of *P. vulgata* reconstructed from photographs showing position and orientation at 5 min intervals.

The smoothness of movement extends to the behaviour when orientating on the scar, as shown in Fig. 1 which is reconstructed from 20 serial photographs. No trial-by-error fitting of shell to rock prior to attainment of the correct orientation is evident.

Experiments

Reorientation

Four limpets were labelled on a small rock, and were observed to home regularly to the positions at which they had been labelled. When all four were away from home at low tide, the rock was turned on a horizontal axis through 180 degrees. A similar experiment was conducted at Port Erin in September 1967, but using a larger sample and turning the rock when the limpets were home.

One limpet died as the rock was turned on to it. The other three, however, returned to their marked homes. The results at Port Erin were less satisfactory. Out of 23 limpets on the eight rocks turned over, there were eight instances of homing, one limpet homing twice. But there were also three instances of limpets apparently taking up new positions after the rock was moved. However, even before the rock was moved, two limpets were observed to adopt new homes. The behaviour of those which moved after reorientation, but did not home, could therefore be attributed to the normal mobility of the limpets at this place and time.

The ability of limpets to home after the reorientation of the rock severely limits the sources of information they could be using. The information must be some property of the rock,

i.e. topographic or chemical, or of the past behaviour of the limpet, i.e. a kinaesthetic memory.

Path Experiments

Displacement. Previous displacement experiments have suffered firstly from damage to limpets caused by their removal from rock, and secondly from a lack of recorded tracks both before and after displacement. We attempted to overcome the first fault by persuading the limpets to walk on to something held in their paths, thus removing themselves from the rock. Despite extensive trials with various materials it proved impossible to make this system work and in the end crude, violent removal was employed. The animals were knocked off with a single sharp tap to the base of the shell from a flattened piece of wood. Sixteen limpets were treated thus, ten of which were then displaced for distances 5 and 7·5 cm and six of which were replaced in the position from which they were removed. The latter served as a control group for any possible damage caused by violence.

The second fault was easier to rectify and tracks were recorded using triangulation, both before and after the removal of both experimental and control animals. Homing of limpets is apparently unaffected by dislodgement and replacement, though their arrival at home was in all cases delayed.

Figure 3 shows two records of movements before and after displacement. If a kinaesthetic memory were involved in homing, the track after displacement should be parallel to that before and should terminate after covering a distance equivalent to the untravelled portion of the original homeward path. No limpets showed anything approximating to this behaviour and all homed successfully, eight within 2 hr and two after one tide.

Damage. Areas of rock between 12 feeding limpets and their scars were damaged with a geological hammer. The depth of the damage was such that the surface was transformed from quite smooth to very rough. After the damage had been completed the rock was washed with sea water to remove dust. The paths of four other limpets close to the experimental ones were left undamaged as a control in case the vibration of the rock might have upset them. Of all these limpets including the controls, only one failed to home successfully. One limpet was observed while making its journey and appeared not to be

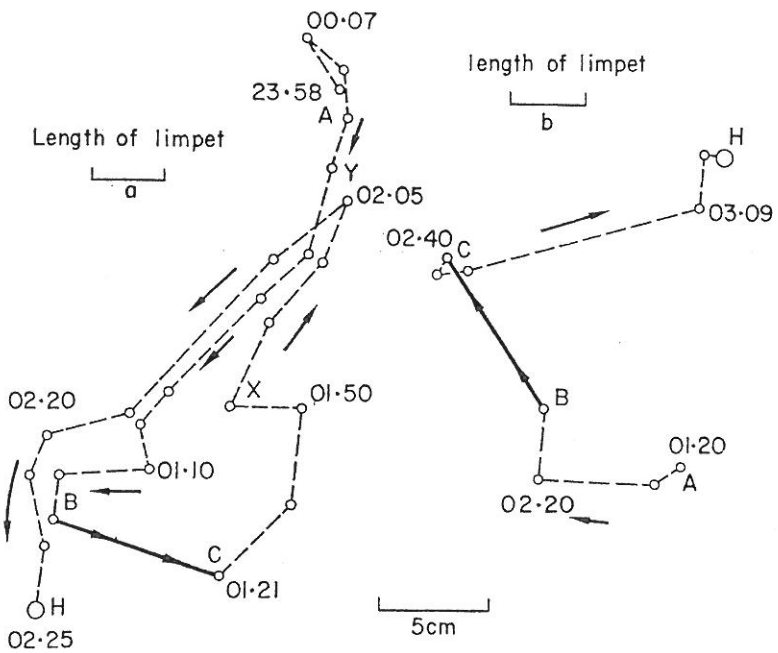


Fig. 7. Tracks obtained by triangulation and showing movements of two limpets before and after displacement. Tracks start at A and limpets are displaced from B to C. H is home. Note retraced path X – Y in (a).

affected by the rock damage. It changed neither direction nor speed on reaching the damaged portion of the rock and moved straight home.

Cleaning. Attempts were made to remove any chemical on the rock which may be used in homing.

The paths of four limpets were scrubbed with a strong detergent solution. The rocks were then washed with sea water. All these animals homed successfully.

Following this negative result a more drastic procedure was employed. The rock surface was cleaned using a foaming oven cleaner, consisting of 0·75 N NaOH with foaming and wetting agents. The results of these experiments are summarized in Table I.

Whilst the results of experiments 3 and 4 were encouraging, a *t*-test on the whole series (ignoring pilot experiments 1 and 2) gave a probability of 0·1 that experimental and control data are from the same universe. Thus these experiments do not give clear evidence in favour of a chemical trail theory of homing.

Obstruction. Plaster of Paris was placed between three limpets and their scars in an attempt to deprive them of both topographic and chemical information from the rock. All limpets skirted the obstacle and then homed (Fig. 8).

The role of plaster of Paris in this experiment was investigated by displacing limpets on to the plaster. In all three experiments conducted the limpets clamped down and did not move before being covered by the tide. This indicates that the plaster has a positive effect on the limpets rather than simply having the negative effect of concealing information and explains the difference in behaviour when trails are affected by chipping and by plaster. The clamping down observed could be a reaction to the dessication caused by the drying plaster.

Discussion of Trail Experiments

The results of chipping experiments suggests that neither chemical nor topographic senses are involved, unless either the surface of the rock was not completely removed or the limpets proceeded in a straight line over the damage area until information was picked up on the far side. Either or both of these could be the case, and so chipping experiments cannot rule out either chemical trail detection or topographic memory, though both are rendered less likely.

The observed ability to skirt large introduced obstacles and then home successfully also argues against simple chemical hypotheses as the limpet is forced off its course. By elimination, kinaesthetic memory is suggested, though the results of the displacement experiments appear to rule this out.

If kinaesthetic memory is ruled out then re-examination of the other two hypotheses is

Table I. Summary of Results Obtained from Experiments Designed to Remove Any Chemical on the Rock by Treatment with NaOH.

Experiment No.	Displaced	Washed	Replaced	Time between displacement and replacement	No. of limpets	Survived 24 hr	Moved within 24 hr of replacement	Homed
1 Control*	from home	by 2 tides	12 cm below home	24 hr	5	4	0	0
Expt	,, ,,				10	8	2	0
2 Control	whilst away	by 2 tides	,,	24 hr	8	8	3	0
Expt	,, ,,		,,		9	9	4	1
3 Control	,, ,,	doused 10 times with a bucket of sea water	at point of	30 min	10	10	10	8
Expt	,, ,,		displacement		8	6	6	2
4 Control	,, ,,	,,	,,	,,	7	4	4	4
Expt	,, ,,				10	7	6	1
5 Control	,, ,,	,,	,,	,,	6	6	6	2
Expt					8	7	4	2
6 Control	,, ,,	,,	,,	,,	6	5	4	2
Expt	,, ,,				9	3	6	1

*The only difference between the control and the experimental was that the latter was sprayed with oven cleaner.

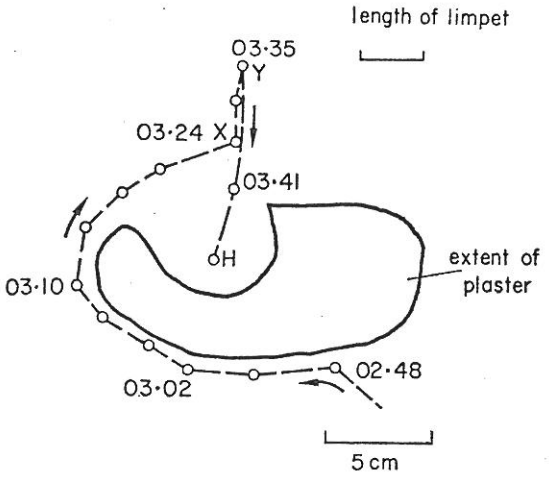


Fig. 8. A track obtained by triangulation and showing the movements made when confronted by a plaster obstacle on the rock. Track starts at A. Note that portion XY is retraced before homing. H is home.

necessary. Topographic memory is most unlikely on *a priori* grounds, as such a use of proprioceptive information is unknown in soft bodied animals (Wells 1965b). Simple retracing of the outward chemical trails is ruled out, by the observation that outgoing and return trails are not always the same. There is, however, no conclusive evidence against a more complex chemical homing theory. This proposes that a limpet may home either along its outward trail or along the trails of its previous excursions, when these are encountered. Such trails would have to be individual specific as they often cross and limpets seldom get lost. They must also be persistent and polarized. These properties are discussed later. Such a chemical theory, whilst presenting difficulties is consistent with the evidence to hand. Topographic and kinaesthetic theories are inconsistent not only with the evidence but also with the known limitations to soft bodied animals.

Scar Experiments

Damage. The rock scars of ten limpets were damaged as described for the path chipping experiment. All limpets returned to the damaged area around their homes, but none settled there. They moved to new positions that bore no constant relationship to their original home.

The scars of another three limpets were scrubbed with a stiff brush and strong detergent with no effect on home recognition.

Obstruction. The limits of five scars were marked whilst the limpets were at home. During the subsequent excursion the marked areas were completely covered with plaster of Paris. On their return the limpets examined these areas with their cephalic tentacles before moving away (Fig. 9).

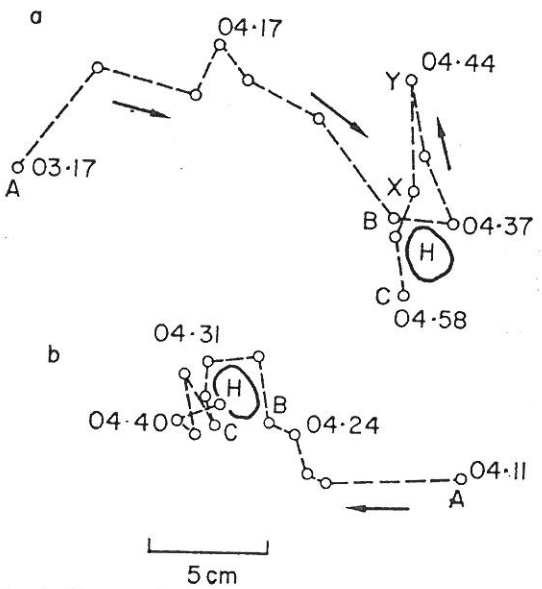


Fig. 9. Two tracks obtained by triangulation showing the movements made when the scar is completely covered by plaster. Tracks begin at A, the limpet reaches the plaster at B and finally settles at C. Note retraced path X – Y in (a).

Crossing over. It had been noticed during other experimental procedures that the scar of any limpet was accepted as home in preference to previously unoccupied rock. This observation was further investigated by exchanging the labelled populations of two plots (18 limpets in all) so that on each plot there were nine labelled 'foreign' limpets and nine labelled unoccupied scars. After one tide two scars were occupied by labelled limpets, and one by an unlabelled one. After a week eight labelled scars had been occupied in all. Furthermore all but one of the occupying limpets were in the same orientation as the previous tenants.

Discussion of Scar Experiments

In both the chipping and the obstruction experiments the behaviour of the limpet towards treatment of its scar is different from that observed when treatment is confined to the trail.

The repeated skirting of the animal round its scar indicates that there is locating information in this area. The experiment does not supply

evidence as to what this is but the wandering would neither be predicted nor explained by a kinaesthetic theory.

The results of the crossing over experiment cannot be chance, nor can they be a question of fit with the rock as some limpets obviously do not fit the scar that they come to occupy. In these cases new shell is laid down rapidly to perfect the seal with the rock.

An absence of other organisms may mark a limpet's scar but this would hardly account for the adoption of the correct orientation by the foreign limpets. This observation is most easily explained by postulating an orientated, individual specific chemical label on the scar. If specificity of response drops when the limpet is unable to find its own home, it will come to occupy a foreign scar.

Of significance here may be the existence of a red ring on some scars, roughly corresponding to the mantle space of the occupant. A red stain was also noticed under a limpet during the experiment in which individuals were displaced onto plaster.

Although this may be involved in scar recognition its obliteration in chipping and obstruction experiments did not prevent homing. The limpet thus does not depend for homing upon a chemical emanating from the scar area.

General Discussion

We have shown that homing is a general phenomenon in this limpet population at the time of study, and this may be correlated with the uneven substrate. Our observations restrict the source of information used for homing to that from the rock surface and from past movements. This is shown by (a) the ability to home being independent of periodically available sources of information, (b) the persistence of homing on reorientated rocks, and (c) the lack of correlation between the movements of individual limpets. This case may be contrasted with the mechanisms described for *Littorina* by Newell (1958). Here the movements show a common orientation either to gravity or the sun.

It has already been shown that the information used by limpets in homing must be a property of the rock or of the limpet itself. Consideration of the sense organs of the limpet further limits the information to topographic and chemical cues and kinaesthetic memory.

The results of the displacement experiments are inconsistent with the theory of kinaesthetic memory.

It is difficult to separate chemical and topographic cues as these are both rock surface properties. However, the results of the crossing over experiment cannot be explained by topographic memory which therefore cannot be involved in scar recognition. There are good a priori grounds for believing that topographic senses are not involved in homing. In *Octopus*, the only mollusc in which proprioceptive senses have been studied, (Wells 1965a), it has been shown that such information is used only as part of the effector system analogous in function to that from vertebrate muscle spindles (Pringle 1962).

Thus, the only tenable hypothesis appears to be that a chemical is used. The simplest chemical mechanism, of returning along the outward trail, does not always occur (Fig. 5) and would not account for the result of displacement experiments. A more complex theory is proposed, according to which the return home can be along any remaining trail of a previous excursion. These trails are persistent, individual-specific and polarized.

Persistence is best accounted for by suggesting that the homing component of the slime trail becomes adsorbed onto the rock and lasts longer than the remainder. An adsorbed protein trail could have enough variability to account for the necessary specificity. Adsorbed proteins are not unknown; one is involved in the settlement of barnacle larvae (Crisp & Meadows 1962). Polarity is difficult to account for. Portions X to Y of Figs 7a, 8 and 9a could show limpets striking trails and turning the wrong way along them. This part of the path is later retraced before homing. The distance retraced, it is suggested, is at least that needed to detect the polarization and ranges from 4 to 10 cm. A concentration gradient is perhaps the simplest hypothesis, though no evidence can be produced on this question.

Attempts to remove all chemicals from the rock gave unsatisfactory results, and therefore no claim can be made to have proved a chemical hypothesis for homing. Moreover, the hypothesis proposed makes great demands on the synthetic and perceptive abilities of the limpet. On the other hand, there are none of the grave objections encountered with all other theories and on these grounds alone it deserves further consideration. It has been shown that scar recognition is chemical, and it is likely that the mechanisms of homing and scar recognition are closely related. On the grounds of economy of hypothesis,

chemical homing is clearly indicated, but confirmation of this must await further field and laboratory work.

Summary

1. About 400 limpets were observed in June and July 1967 and 1968 at Saye Bay, Alderney, in the Channel Islands, in order to study their homing behaviour.

2. Movements of limpets were recorded using triangulation and photography. Homing was a regular feature of the behaviour of these limpets at all times and states of tide.

3. The movements of *P. vulgata* are governed by a timing sense by which they consistently return home before being covered by the tide.

4. The limpets did not use celestial information to navigate home, since they are capable of homing at any time of day, and in any weather, and even when the rock is reorientated. It is, therefore, concluded that the information available for homing is restricted to the rock and the past movements of the limpets.

5. Displacement experiments were conducted, the results from which were inconsistent with the idea of a kinaesthetic memory.

6. Experiments in which trails were damaged by rock chipping and by scrubbing with detergent failed to prevent homing. Limpets were also able to home after forced detours resulting from obstruction on their homeward trails. These results cast doubt on topographic memory and simple chemical trail-following as homing cues. Later experiments in which the rock surface was cleaned chemically gave inconclusive results, as homing ability was not significantly lowered.

7. Recognition of scars by limpets other than the occupant is demonstrated, and it is postulated that orientated chemical labelling is necessary.

8. Chemical hypotheses of homing, scar recognition, and orientation on to the scar are proposed and discussed.

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