THE COVERING REACTION OF SEA-URCHINS

I. A PRELIMINARY ACCOUNT OF COVERING IN THE TROPICAL ECHINOID *LYTECHINUS VARIEGATUS* (LAMARCK), AND ITS RELATION TO LIGHT

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INTRODUCTION

It has long been known that several species of littoral sea-urchins clothe themselves with fragments from their surroundings. The reaction has been interpreted as a means of concealment by Schmidt (see Brehm, 1884), MacBride (1909), Boone (1925), as a defence against desiccation and temperature extremes (Orton, 1929), or as a reaction to strong light (von Uexküll, 1899; Dubois, 1914; Lindahl & Runnström, 1929; Mortensen, 1943 b).

*Lytechinus variegatus* (Lamarck), a common littoral sea-urchin in the Caribbean, shows this habit strikingly (Field, 1892; Boone, 1925; Clark, 1933; Mortensen, 1943 a), for in Jamaica large numbers are found almost completely concealed.

Such a clear manifestation of covering is obviously suitable for determining how it is performed and factors which influence it. A summary of the main findings has already been published (Millott, 1955).

THE MECHANISM OF COVERING

(a) Taking up cover

This is performed primarily by the tube feet. Most commonly those below the ambitus extend until they reach loose objects to which the terminal sucker adheres, and each tube foot then contracts so as to pull the material firmly against the tips of the primary spines which are then moved aborally (Fig. 1). The spines, acting on the crowbar principle, lever the material upwards aided by their roughened surfaces and the action of tube feet situated more aborally, so as to bring it in contact with the tips of neighbouring spines which lever it nearer the periproct. On reaching the aboral surface it is held there by the underlying tube feet, and by repetition of this process an extensive covering may be assembled.

The process resembles that described by Schmidt (see Brehm, 1884), as occurring in *Toxopneustes lividus* Agass.,* and contrary to the statements of Clark (1933), the pedicellariae take no part in seizing or holding the fragments.

* The account of the habit of this species, attributed to O. Schmidt, appears in the French edition of Brehm, *Les Merveilles de la Nature, Les Vers, Les Mollusques etc.* (ed. de Rochebrune, Paris, 1884), under the description of the species ' *Toxopneustes lividus* Agass.' In a reference to this account, Dubois (1914) designates the species ' *Strongylocentrotus lividus* Brdt.' These appear to be the species described in Mortensen's monograph (3, 3, pt. 2, p. 157), as *Paracentrotus lividus* (Lamarck).
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Such behaviour may be elaborated when the urchin is subjected to directional or uneven illumination or when the pieces to be used for covering offer considerable resistance.

In the former case, the covering may be placed so as to shade the brightly illuminated areas of the surface, and when the urchin is turned, so that the covering no longer does this, either more covering is taken up or the existing covering is moved by co-ordinated action of the tube feet and spines until it regains its original position with reference to the light source. This behaviour recalls that described by Dubois (1914), as occurring in *Strongylocentrotus lividus* Brandt, and by von Uexküll (1899) in *Sphaerechinus*.

![Diagram showing a mode of action of the tube feet and spines, employed by *Lytechinus* in seizing and assembling as cover an empty gastropod shell (p. 508). The actions of two tube feet and one spine only are shown in successive stages I–III. Crossed arrows show the direction of movement of the shell; dotted arrows, the direction of the pull exerted by the tube feet; solid arrows, the direction of spine movement. I, extended tube feet are applied to the shell; II, the shell has been drawn to the test by the tube feet and bears against a primary spine; III, the spine is moved aborally and the shell levered upwards. Additional tube feet are extended as indicated by the dotted lines, the shell being held off the surface of the test by subjacent spines (not shown).](image)

The orientation of covering appears very striking where an urchin is crossed by a narrow band of light (Fig. 2). Four stones taken up in three ambulacra were moved approximately along the routes shown so as to become placed along the band of light. Here the co-operation between the tube feet and spines in different ambulacra and interambulacra is noteworthy.

The number of feet used in assembling pieces of covering is roughly in direct proportion to the resistance offered by such fragments. Again, when a covering piece is heavy, or firmly wedged in the substratum, urchins may use greater force by moving their bodies against it, with the subambital spines held stiffly erect. Thus partly raised or loosened, the object is then lifted as previously described. Alternatively, whilst anchored by the oral tube feet, urchins may bring the tips of the subambital spines to bear against the surrounding stones, which are then loosened by a vigorous sideways movement of the spines.

Light floating or suspended objects such as dead leaves (or in the laboratory cover-glasses) may be seized by the aboral tube feet, pulled down on the neighbouring spines, held as covering here, or after being moved over the surface of the urchin, as described above.

The number of tube feet used varies considerably. One aboral tube foot is sufficient to seize a floating $\frac{1}{8}$ in. cover-glass and pull it below the meniscus, but usually when the floating object has been captured, the tube feet concerned are supplemented by others which adhere to it and assist in pulling it below the surface.
Since tube feet extend to capture the floating pieces, we may seek to find the type of stimulus involved.

That tactile stimuli are not significantly involved, and that a change in light intensity is important is shown by moving clear and enamelled cover-glasses over the brightly illuminated aboral surface of naked urchins. Enamelled ones elicit extension of tube feet from the areas they shade, whereas the clear ones do not. Again, cover-slips enamelled with a simple pattern are usually seized by tube feet extended from the areas shaded by the pattern as shown in Fig. 3.

We may now ask whether the process previously described as occurring in continuous illumination may not have been due to shading, since urchins move about among stones, shells, etc., big enough to cast shadows on some part of their surface. That this is not so is shown by using lights mounted directly above urchins on a dull black background. Tube feet are extended and attached to shells, etc., despite the fact that the latter cast no shadow on the urchin. Again, where covering is moved over the surface, the shadows cast by it could be a factor bringing about extension of successive tube feet, but since clear cover-slips can be carried over the surface of the test and positioned in the same way as opaque objects, shadow cannot always be important.

The covering process is thus affected by light, but in one case by continuous bright light and in the other by a change in intensity. To what extent the two processes are distinct is not yet clear. Where urchins transferred from shade to bright

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**Fig. 2.** Diagram showing the placing of cover over localized, brightly illuminated, areas of the surface (p. 509). Four stones, each shaded by a distinctive convention (lines, dots, circles, or solid black), are moved into a narrow band of sunlight (stippled) crossing the aboral surface of an urchin, approximately over the routes shown by successive outlines and arrows, drawn with the corresponding conventions. The interambulacra are distinguished by cross-line shading. The urchin endeavoured to take up stones from area \(A\), but failed. No material suitable for cover was available in area \(B\). \(P\) = periproct.
light take up covering they tend to do so initially when their surface is brightly and evenly illuminated, using the mechanism described on p. 508. Later, all tube feet exposed to light and not involved in holding the covering (see below) may be withdrawn, but by shading they can sometimes be induced to re-extend and take up covering.

Stimuli of other kinds may interfere with the extension of the tube feet. Thus touching a spine brings about instant withdrawal of any neighbouring tube feet extending into shadows, but if the tube feet are already attached by their suckers, they will not free themselves unless the spines are tapped vigorously and repeatedly. Again, the general behavioural state is important, for during active locomotion urchins usually cannot be induced to take up covering.

It now remains to discover how the covering is held in place.

![Diagram](image-url)

**Fig. 3**. The effect of a shadow cast on the surface of *Lytechinus* (drawn without spines and pedicellariae) which seizes a ½ in. cover-glass (C), floating on the overlying surface film (F) of sea water, contained in a shallow dish with one side marked A. Note the three tube feet extended from the area covered by the shadow (S), cast by the opaque (enamelled) margin of the cover-slip, to which their suckers adhere (p. 510).

(b) **Holding cover**

Covering is maintained by prolonged contraction of tube feet which are assisted to varying degrees by the spines. This raises the question whether the same tube feet are involved the whole of the time. No satisfactory means was devised to answer this when opaque fragments were held, but it was possible to see what happened when the covering was transparent. When clear cover-glasses were placed over a part of the urchin's surface which had just been shaded, they were seized and retained as cover, even when the shaded areas were re-illuminated by two 50 c.p. lamps placed about 1 ft. away.

In one such experiment the cover-slip was initially held against the tips of the subjacent spines by the pull of nine tube feet originating from the aboral region of...
one ambulacrum. Later they were supplemented (see below) and their suckers were disposed roughly in three groups A, B and C (Fig. 4). The cover-slip was held in this position for 17 hr., and though it was not possible to observe the tube feet all the time, continuous periods of observation of up to 1½ hr. were possible.

The attached tube feet remained in the same three groups, but all the tube feet did not adhere permanently, some in each group were periodically withdrawn and replaced by others so that the total number of tube feet involved varied from 9 to 27. An idea of the total rate of change can be obtained from Table 1, and the rate of change in each group is shown in Table 2. Some tube feet remained attached to the cover-slip for 1½ hr., while others beneath it took no part.

Though the effective tube feet were subjected to abnormal conditions in being continuously and brightly illuminated, it is significant that opaque cover-slips were held by the same urchins alongside the clear ones. No difference in the way of holding the two types was observed, though we have no comparable details of the distribution and behaviour of the tube feet below the opaque cover-slips, because any attempt at lifting the cover to inspect such tube feet always resulted in some of them becoming detached.

Table 1. Total number of tube feet used in holding one ½ in. cover-slip between periproct and ambitus

(Time to nearest half minute)

<table>
<thead>
<tr>
<th>Time</th>
<th>No. of tube feet in use</th>
<th>Time</th>
<th>No. of tube feet in use</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.36 p.m.</td>
<td>9</td>
<td>4.51 p.m.</td>
<td>19</td>
</tr>
<tr>
<td>4.37</td>
<td>8</td>
<td>4.52</td>
<td>19</td>
</tr>
<tr>
<td>4.39</td>
<td>11</td>
<td>4.53</td>
<td>21</td>
</tr>
<tr>
<td>4.41 ½</td>
<td>13</td>
<td>4.54</td>
<td>20</td>
</tr>
<tr>
<td>4.45 ½</td>
<td>14</td>
<td>4.54 ½</td>
<td>19</td>
</tr>
<tr>
<td>4.46</td>
<td>12</td>
<td>4.55</td>
<td>22</td>
</tr>
<tr>
<td>4.48</td>
<td>13</td>
<td>4.57</td>
<td>23</td>
</tr>
<tr>
<td>4.49</td>
<td>14</td>
<td>4.58</td>
<td>22</td>
</tr>
</tbody>
</table>

THE EFFECT OF LIGHT

Taxic responses and the responses of various organs to changes in intensity show that *Lytechinus* is affected by light.

The effect of light on certain tube feet has already been mentioned, but since these are primarily important in covering, their responses have received special attention and will now be described more fully.
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(1) Responses of the tube feet

In most cases reactions were studied in the laboratory using young urchins and, as the light source, overhead tungsten lamps or 50 c.p. spot-lamps. The use of spot-lamps eliminates significant heating effects, for the urchins were invariably several inches below the surface of the water, and under such conditions two beams were found to raise the temperature of the water by but 1° C. in 45 min. Most experiments were of much shorter duration.

Table 2. Rate of change of tube feet in the groups A, B and C (see Fig. 4)

(Note: Owing to difficulties in observing and recording simultaneous changes in three groups, the following figures must be regarded as minimal. Time to nearest half minute.)

<table>
<thead>
<tr>
<th>Time</th>
<th>Group</th>
<th>Change in no. of holding tube feet</th>
<th>Time</th>
<th>Group</th>
<th>Change in no. of holding tube feet</th>
</tr>
</thead>
<tbody>
<tr>
<td>6.03</td>
<td>B</td>
<td>-1</td>
<td>6.33°5</td>
<td>B</td>
<td>+1</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>+1</td>
<td>6.34</td>
<td>A</td>
<td>-1</td>
</tr>
<tr>
<td>6.05</td>
<td>A</td>
<td>-1</td>
<td>6.34°5</td>
<td>A</td>
<td>+1</td>
</tr>
<tr>
<td>6.08</td>
<td>A</td>
<td>+1</td>
<td>6.36°5</td>
<td>A</td>
<td>+1</td>
</tr>
<tr>
<td>6.09</td>
<td>A</td>
<td>-1</td>
<td>6.37</td>
<td>C</td>
<td>-1</td>
</tr>
<tr>
<td>6.10°5</td>
<td>A</td>
<td>+2</td>
<td>6.42</td>
<td>A</td>
<td>-1</td>
</tr>
<tr>
<td>6.13°5</td>
<td>A</td>
<td>-1</td>
<td>6.44</td>
<td>A</td>
<td>+1</td>
</tr>
<tr>
<td>6.15</td>
<td>C</td>
<td>-1</td>
<td>6.45</td>
<td>C</td>
<td>-2</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>+1</td>
<td>6.45°5</td>
<td>B</td>
<td>-1</td>
</tr>
<tr>
<td></td>
<td>A</td>
<td>+1</td>
<td>6.48</td>
<td>A</td>
<td>+2</td>
</tr>
<tr>
<td>6.16</td>
<td>C</td>
<td>+1</td>
<td>6.49°5</td>
<td>C</td>
<td>-1</td>
</tr>
<tr>
<td>6.19°5</td>
<td>A</td>
<td>+1°*</td>
<td>6.50</td>
<td>A</td>
<td>-1</td>
</tr>
<tr>
<td>6.20</td>
<td>A</td>
<td>-1°*</td>
<td></td>
<td>B</td>
<td>-1</td>
</tr>
<tr>
<td>6.24</td>
<td>A</td>
<td>+1</td>
<td></td>
<td>B</td>
<td>+1</td>
</tr>
<tr>
<td>6.25</td>
<td>A</td>
<td>-2</td>
<td>6.51</td>
<td>A</td>
<td>-1</td>
</tr>
<tr>
<td>6.27°5</td>
<td>A</td>
<td>+1</td>
<td>6.52</td>
<td>B</td>
<td>-2</td>
</tr>
<tr>
<td>6.29°5</td>
<td>A</td>
<td>-1</td>
<td>6.52°5</td>
<td>C</td>
<td>+2</td>
</tr>
<tr>
<td>6.30°5</td>
<td>B</td>
<td>+1</td>
<td>6.53</td>
<td>A</td>
<td>+1</td>
</tr>
<tr>
<td>6.31</td>
<td>B</td>
<td>+1</td>
<td></td>
<td>C</td>
<td>-1</td>
</tr>
<tr>
<td>6.33</td>
<td>C</td>
<td>-1</td>
<td>6.55</td>
<td>C</td>
<td>-1</td>
</tr>
</tbody>
</table>

* Same tube foot.

Tube feet respond to continuous light and to changes in intensity. To the former they react variably, not only in different individuals but also in the same individual at different times. Thus tube feet may be unresponsive, withdrawn, extended without attachment or extended and attached to surrounding objects. Sometimes they withdraw immediately after a light beam is projected on to them, at other times they require more prolonged illumination from the same light source before withdrawing. Where tube feet appear unresponsive they may be induced to withdraw more quickly by increasing the light intensity; thus in one experiment 15 sec. illumination from one 50 c.p. lamp was required, but only 5 sec. from two such lamps placed at the same distance.

Responses both to increases and to decreases in intensity are more constant; the responses to shadows are the most constant and striking. In either case tube feet are quickly withdrawn and then, after a varying interval, slowly extended. If they
touch anything suitable they adhere and by contraction attempt to pull it on to the surface of the urchin, otherwise they wave or circle actively for 60–90 sec. before withdrawing again. Such reactions can be obtained repeatedly, and, further, follow too rapidly after the changes in intensity to be due to temperature changes.

Deep shadows are not essential. Thus when urchins were illuminated by two convergent beams focused on to the same area, cutting off one was sufficient to cause extension, despite the fact that the change in intensity at the surface of the urchin, as measured by a Weston ‘Master II’ exposure meter, was only from 20 to 13 units. Similarly, small colour filters (Ilford yellow-green no. 605, red no. 608 and violet no. 601) placed between the urchin and the light brought about extension.

During active locomotion, it is difficult to elicit any reaction in the tube feet by changing the light intensity; further, they appear relatively insensitive to contact stimuli and do not readily attach themselves, though sometimes the tube feet of the leading ambulacra only are so affected. When locomotion ceases the tube feet regain responsiveness in 13–17 min. Responses to increases in intensity sometimes appear some 10 min. before those to decreases.

When a narrow beam, projected on to one ambulacrum, is interrupted, the tube feet extend in neighbouring ambulacra, but in smaller numbers and less rapidly. Since the beam was narrow, the change in intensity in the neighbouring ambulacra was clearly less than in the illuminated one, and it was therefore suspected that there might be a relation between the speed of extension of the tube feet and the degree of change of intensity. The following experiments show that this is so.

Urchins were illuminated by three lamps arranged to shine directly on to one ambulacrum in which the tube feet were withdrawn. An opaque object was moved into the light path, and the time required for the tube feet to touch it was determined, first with one lamp, then with two and finally with all three. Since the background lighting was dim and the shading object opaque, throwing a shadow

<table>
<thead>
<tr>
<th>Expt. no.</th>
<th>Intensity of illumination expressed as an approximate scale reading of the photometer</th>
<th>Average time of contact of the first four tube feet in six successive trials (expressed in seconds)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>300</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>800</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>1200</td>
<td>20</td>
</tr>
<tr>
<td>2</td>
<td>300</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>800</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>1400</td>
<td>11</td>
</tr>
<tr>
<td>3</td>
<td>200</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>400</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>700</td>
<td>17</td>
</tr>
<tr>
<td>4</td>
<td>200</td>
<td>23</td>
</tr>
<tr>
<td></td>
<td>800</td>
<td>14</td>
</tr>
<tr>
<td></td>
<td>1200</td>
<td>10</td>
</tr>
</tbody>
</table>

In experiments where temperatures were taken, the heating effects due to the spotlamps were found to be negligible, amounting to 1° C. in 90 min.
larger than the ambulacrum, it is safe to assume that the degree of intensity change increased with the number of lamps and roughly in the same measure as the intensity of the light they produced. The light intensity at the surface of the urchin was measured roughly by means of a Weston 'Master II' exposure meter. The shading object was held just beyond the tips of the longest spines projecting from either side of the ambulacrum, and so its distance from the test was approximately constant for each urchin. The average time required for the first four tube feet to touch it was determined in six successive trials. The results are shown in Table 3.

The rate of extension of the tube feet therefore increases with the degree of intensity change.

There is a noteworthy difference in the reactions to shadows shown by the tube feet of *Lytechinus* and those of *Diadema*. In the latter, which does not cover, the reaction is simpler; the extended tube feet are usually flexed towards the substratum and then quickly recover (Millott, 1954).

**Table 3.** Percentage of population showing degree of covering indicated in the left-hand column

(Note: in this and succeeding tables, urchins in which the aboral surface was largely concealed, are referred to as 'fully covered'.)

<table>
<thead>
<tr>
<th></th>
<th>Shaded zone</th>
<th>Sunlit zone</th>
</tr>
</thead>
<tbody>
<tr>
<td>Without cover</td>
<td>13</td>
<td>nil</td>
</tr>
<tr>
<td>Partly covered</td>
<td>67</td>
<td>13</td>
</tr>
<tr>
<td>Fully covered</td>
<td>20</td>
<td>87</td>
</tr>
</tbody>
</table>

(2) **Covering responses to diurnal changes in light intensity**

The extent to which urchins cover at various times throughout the day in their normal environment was determined. In view of the suggestions already made by previous workers (p. 508), it was essential to make observations in a locality where the urchins were never exposed to air nor subjected to considerable temperature change.

Such a locality exists in Jamaica, as a gully, through which passes a constant stream of sea water, the flow being such that the temperature in the mid-morning sunlight of December in the centre of the open stream was 27·5° C. and half a degree higher at the edges, while in the shade, that of both centre and edges was 27·5° C.

Some 3 hr. after sunrise, when about three-quarters of the gully was shaded from the sun, about 94% of the urchin population carried some covering, but there was a significant difference in the extent of the cover carried by urchins in the sunlit and shaded zones (Table 4). One hour later the shaded portion of the gully was smaller and there were fewer naked urchins. In both shade and sunlight there was a greater proportion fully covered (Table 5).

With the fall in intensity at sundown, urchins shed covering (Table 6). Two hours after sundown the proportion of naked urchins living where the gully had previously
been exposed to the setting sun had increased over twofold, whereas in the part that had been shaded it remained about the same.

Table 5. *Percentage of population showing degree of covering indicated in the left-hand column*

<table>
<thead>
<tr>
<th></th>
<th>Shaded zone</th>
<th>Sunlit zone</th>
</tr>
</thead>
<tbody>
<tr>
<td>Without cover</td>
<td>7</td>
<td>nil</td>
</tr>
<tr>
<td>Partly covered</td>
<td>63</td>
<td>5</td>
</tr>
<tr>
<td>Fully covered</td>
<td>30</td>
<td>95</td>
</tr>
</tbody>
</table>

Table 6. *Percentage of population showing degree of covering indicated in the left-hand column*

<table>
<thead>
<tr>
<th></th>
<th>Shaded zone</th>
<th>Zone illuminated by setting sun</th>
</tr>
</thead>
<tbody>
<tr>
<td>Without cover</td>
<td>37</td>
<td>15</td>
</tr>
<tr>
<td>Partly covered</td>
<td>47</td>
<td>68</td>
</tr>
<tr>
<td>Fully covered</td>
<td>16</td>
<td>17</td>
</tr>
</tbody>
</table>

Thus covering is influenced by light intensity, though a surprisingly large proportion (about 60%) of the urchins retained some covering in darkness.

This can also be shown in the laboratory where many urchins continue to cover in captivity, but their covering is not so extensive nor is it usually held for so long as in their natural surroundings, even when fragments normally employed as covering are used. Thus many urchins living in glass aquaria lighted by an east window begin to pick up cover about 1 hr. after sunrise, slowly shedding it in the fading light of the late afternoon.

The tendency to cover is most marked in the 3 hr. after sunrise, which suggests that the preceding sojourn in darkness may have increased responsiveness to light. This is confirmed by keeping urchins which have become unresponsive in darkened dishes for 4–16 hr., after which they often cover again.

(3) Covering responses to artificial light

Covering can sometimes be induced by one or more 50–100 W. tungsten filament lamps, either alone at night or added to sunlight at various times of the day. Heating effects can be discounted, for the aquaria were large and covering was completed about 5 min. after the light was switched on. Conversely, covered urchins transferred to darkness may shed their covering.

Differences between individuals are very great; some urchins could not be induced to cover in strong light, but moved into shade, while a few retained their covering in darkness for as long as 19 hr.

In general, however, the covering behaviour of urchins under experimental conditions agrees with that observed in their normal surroundings and shows the
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influence of light, though the range of variation would suggest that some urchins may become less sensitive to it in captivity. Again, the possible existence of an inherent physiological rhythm should not be overlooked, but the effect of light is sufficiently clear to show that if such a rhythm exists it is by no means the only factor involved.

This variation in behaviour toward light recalls that encountered in sea-urchins such as Arbacia (Holmes, 1912) and Diadema (Millott, 1954). In the latter, as in Lytechinus, sensitivity to light varies with body colour, though Diadema shows physiological colour change (Millott, 1952) which I have not seen in Lytechinus.

(4) The influence of body colour

The predominant colours of L. variegatus are green and white, varying in relative proportion as well as in the depth of the green colour, so that pale, dark and intermediate individuals can be distinguished.

Animals of all shades cover in their natural surroundings, and I found no difference in the extent of their covering. However, pale urchins stripped in the mid-morning sunlight tend to cover again more readily and quickly than dark ones similarly treated, so that in a sample containing both kinds the pale individuals picked up covering within 4 min., whereas the dark did not begin until some 9 min. later. Again, when the illumination of an indoor aquarium was increased by two overhead lamps (100 and 75 W.) all the pale urchins, together with a few dark ones, began to cover, while a greater number of dark ones remained uncovered. Usually, in well-lighted aquaria where urchins remain uncovered, there is a preponderance of dark individuals among them, and unless they are subjected to direct sunlight dark individuals carry less cover than pale ones.

The reason for this is obscure, but from purely physical considerations the green pigment would appear not to be involved directly in any photoreceptive process which leads to covering, otherwise the opposite would be expected. It could serve as a screening pigment, but if this were so, since light influences dark forms as well as pale, it would appear that the pigment is either insufficient or absent from some, at least, of the light-sensitive areas. The existence of such screening pigment has already been demonstrated in the skin of Diadema by Millott (1954). Much earlier von Uexküll (1897, 1900) suggested that the pigment in the skin ('Pigmenthülle') of echinoids such as Centrostephanus serves as a light screen, and he noted that species lacking such protection cover themselves with debris. In Lytechinus, however, the differences between dark and pale forms are not necessarily due solely to differences in the amount of green pigment. There is at least one reddish pigment and there may be others masked by the green.

(5) The effect of photosensitizing dyes

The importance of light in relation to covering is also shown by injecting photosensitizing dyes dissolved in sea water or coelomic fluid into the perivisceral coelom. The dyes used, rose bengal (tetrachloro (P) tetraiodo (R)-fluorescein), eosin Y (tetrabromo-fluorescein) and neutral red are known to photosensitize (Metzner,
1927; Welsh, 1934), and are marketed respectively by Messrs B.D.H., the National Aniline Division of the Allied Chemical and Dyeing Corp., N.Y. and G.T. Gurr (their ‘vital’ grade). Controls were set up in which similar amounts of sea water or coelomic fluid alone were injected. No attempt was made to standardize the amount of dye used. The injected urchins and the controls were kept in glass aquaria and provided with ample material with which to cover.

The results were striking. Urchins injected with dye began to cover about 2 hr. after injection, and when stripped of covering re-covered themselves immediately even in fading daylight, while the controls remained naked. About 1 hr. after sunrise the injected urchins showed abnormally great activity, their tube feet extending in all directions, those below the ambitus rapidly picking up covering while those of the controls were still inactive. Activity continued until the urchins were completely buried while the controls remained uncovered. Covering was extensive, whether the injected urchins were pale or dark, exposed or in the shade, and it was retained until after sundown; but they would not cover in darkness. The effect lasted up to 7 days depending on the amount of dye used; urchins could be resensitized by one or two subsequent injections, but too much dye proved toxic. The effect was sometimes observed in urchins which had been kept in aquaria for a number of days and which had ceased to cover.

Neutral red brought about an effect similar to that of rose bengal and eosin Y; safranin (water soluble, G.T. Gurr) and methylene blue (vital, G.T. Gurr), did not enhance the covering response, the former appearing toxic to the urchins.

The effective dyes when dissolved in sea water absorb extensively between 410 and 565 m\(\mu\) (Fig. 5). If this is roughly the same when the dyes become associated with the living matter, then in view of the photosensitizing effect of the dyes it follows that the naturally occurring pigments cannot effectively screen all the living matter from these wave lengths.

Among the dyes used that were likely to affect oxidation-reduction potential, neutral red was effective but not methylene blue. This may indicate that their possible effect on oxidation-reduction balance has little direct significance here, though they are poised at very different levels.

It is noteworthy that photosensitization could influence the relatively complex co-ordinated activity of covering, and thus the foregoing experiments strengthen previous indications that covering is influenced by light. They also show that the energy quanta normally available in the environment are adequate to excite the response and that pathways exist for the transfer of energy from mechanisms affected by such light to a co-ordinated system of effectors. Such mechanisms may or may not operate in the normal animal, for the use of such dyes may create artificial light-absorbing mechanisms. It is simplest to assume that the dye augments normal photoreceptive mechanisms, but it might have created others, for example, by making the effectors or intermediate elements such as nerves light-sensitive, as has already been shown possible by Lillie (1924), Lippay (1929) and Auger & Fessard (1933). The relation of such photosensitive processes to normal biological mechanisms is thus obscure (see also Blum, 1941; Blum & Kauzmann, 1954).
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Nevertheless, in *Lytechinus*, these dyes affect activities that are normally influenced by light such as withdrawal of tube feet and movements of pedicellariae, as well as the covering reaction, more obviously and regularly than the other activities that were observed. Again, many of the injected urchins survived in captivity as long as their controls.

![Graph showing comparative light absorption of dyes](image)

Fig. 5. Comparative light absorption, in the wavelength range 400–600 mμ, of the dyes used in the photosensitization experiments reported on pp. 517 and 518. For the purpose of comparison the dyes were dissolved in sea water and the concentration adjusted so that the maximum absorption in the visible range of the spectrum was approximately the same in each case.

The responses of the tube feet to light and more especially the responses to shadows are, in general, what would be expected in view of the tendency to cover during continuous bright light and after changes in intensity (p. 510). Their variability and the influence of other activities indicates that covering movements are integrated into general behaviour and are not merely the result of simple responses of the tube feet to light. A few simple experiments were performed to discover whether the central nervous system is involved.

SIGNIFICANCE OF THE NERVE RINGS

No detailed descriptions of the nervous system of *Lytechinus* are known, but from our knowledge of the disposition and working of the system in other echinoids (Romanes & Ewart, 1881; Romanes, 1885; Fredericq, 1876; Delage & Hérouard, 1903), we may suspect that a circum-oral and perhaps an aboral nerve ring are involved in the covering reaction.
In the first type of experiment the lantern with the peristome and surrounding test was excised, and the urchin was replaced in a sunlit area of its normal environment. It slowly covered itself with stones. An oral nerve ring is thus not essential. In the second, the periproct and surrounding regions of the test were removed before replacing in sunlight. Covering was taken up as usual, the pieces being moved aborally as far as the cut edge of the test and held there. An aboral nerve ring is thus not essential.

These experiments are insufficient to eliminate completely central nervous coordination of covering movements, for the radial nerve cords were still intact and, further, the capacity of mutilated urchins to orientate covering with respect to the light source, or to move pieces of covering over the various routes seen in the intact animal (p. 509), was not demonstrated. Further observations and experimental analysis are clearly required.

**DISCUSSION**

It is clear from the foregoing account that the covering habit of *Lytechinus* is related to light. The same has been maintained concerning covering in other urchins by von Uexküll (1899), Dubois (1914), Mortensen (1943a, b) and Cuénot (1948). In a brief reference to the habit in *Lytechinus variegatus*, Clark (1933) remains non-committal, but Boone (1925) rejects the significance of strong light, stating that individuals kept for several weeks in relatively dark indoor aquaria covered as thoroughly as those on open reefs. I cannot confirm Boone’s observations (p. 516), nor did I succeed in keeping *Lytechinus* healthy in indoor aquaria for more than 2 weeks, but the effect of light on covering in the natural surroundings (p. 515) is clear enough.

In *Lytechinus* both continuous bright light and changes in intensity can induce the covering response. This is noteworthy, since photic stimuli of both types are known to elicit responses of a different kind in other echinoids (Millott, 1954). Whether other environmental changes can induce covering in this species is unknown.

Such characteristic and well-defined behaviour is likely to be in some measure adaptive and to have a definite selective value. It should therefore be related to some particular environmental requirement, and since the habit is common in littoral urchins we should seek factors that operate particularly in shallow water.

Temperature extremes and desiccation can be eliminated, since *Lytechinus* is tropical or subtropical and has always been immersed in the situations where I have found it. The mechanical effect of wave action can be discounted, for not only is the habit commonly displayed where such action does not exist, but it is doubtful whether covering would afford real protection for the surface of the urchin; it might even be a disadvantage, for covered urchins when displaced (as they could be by waves) are top heavy so that righting is difficult.

Light is a significant factor in shallow water, especially where it is intense as in the tropics.
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Indirectly, it may make an animal conspicuous. Covering might prevent this and so has been interpreted as a means of advantageous concealment in *Lytechinus* (Boone, 1925). There is not sufficient evidence for this, for I have yet to find animals which prey upon this urchin; and though they may exist, predators with sufficient appreciation of form and pattern, as well as discrimination of intensity and colour, must be known before such views can be accepted. The same applies to concealment from potential victims, especially as it is by no means clear what the urchin feeds on; Boone describes a diet chiefly of 'small molluscs, crustaceans and worms', while Mortensen (1943 a) finds the food to consist of 'bottom material, with shells and bits of plants'.

In a brief reference to covering in this species, Mortensen (1913 a), expresses similar scepticism.

Light acting directly appears sometimes to be a nociceptive stimulus to *Lytechinus* (p. 513), suggesting that the animal has insufficient protection. An opaque covering acting as a light-shield would therefore confer an advantage, increasing the distribution range of the species by enabling individuals to seek food with impunity in shallow sunlit waters. The idea gains strength from the fact that there are vast numbers of this species in Kingston harbour, and like Field (1892) I have found that dredges rapidly become filled with them. It therefore seems reasonable to suppose that intraspecific competition, at least, is keen and that population pressure in slightly deeper waters is considerable.

The idea of covering acting as a light-screen in other echinoids has been advanced by Dubois (1914), Lindahl & Runnström (1929), and Mortensen (1943 a, p. 389, 1943 b, pp. 135 and 210).

In the instance of *Centrostephanus* von Uexküll (1897) goes further in suggesting that screening pigment might be a means of preserving photolabile visual pigment in the skin.

The same might apply to covering, but such an idea lacks sufficient evidence. Nevertheless, there are indications of photolabile pigments in echinoderms (von Uexküll, 1897; Crozier, 1915, 1920; Millott & Vevers, 1955), though carotenoids were found only in traces in the skin of *Lytechinus pictus* (Fox, 1953).

**SUMMARY**

1. *Lytechinus variegatus* (Lamarck) covers the parts of its skin that are exposed to light with fragments taken from its surroundings.

2. The covering is taken up by the tube feet, assisted by the spines, and held in place by the tube feet acting in relays. It may be orientated with respect to the light source. There are indications of adaptability of behaviour where the covering pieces offer resistance to being lifted.

3. Covering is related to light and to diurnal light changes, being assumed in strong light and rejected, after a varying interval of time, in darkness. Both continuous bright light and decreases in light intensity evoke covering. The tube feet react to the same stimuli and the speed of their extension is roughly proportional to the change of intensity.
4. The tendency to cover is increased after a sojourn in darkness and is greater in pale individuals than in dark ones.
5. Urchins can be photosensitized by injection of dyes so that they cover in dim light.
6. The prehension and holding of covering does not involve the oral and aboral nerve rings.
7. The relation of covering to light and environment favours the idea that it acts as a screen against strong light.

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REFERENCES

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