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NOTES ON THE OYSTERCATCHER (*HÆMATOPUS OSTRALEGUS*), WITH REFERENCE TO ITS HABIT OF FEEDING UPON THE MUSSEL (*MYTILUS EDULIS*).

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To say that the Oystercatcher eats Mussels is to assert a commonplace. Yet little seems to be known regarding the methods by which the shells are opened and are deprived of their contents. Apart from the question of expediency, the absence of information on this subject may be attributed to the difficulties inseparable from close observation of birds that are wary and not easy to approach. Oystercatchers avoid those places which permit an observer to approach unseen, they act with great rapidity, their methods are varied within wide limits, and it is only by the exercise of much patience that results of any value are obtained. The present account is based partly on observations of the birds themselves, and partly on an examination of the empty shells which are scattered over the feeding-places.

Oystercatchers are creatures of regular habit; their timetable is regulated by the ebb and flow of the tides, which they follow with more or less precision. Speaking generally, it may be said that the Mussel-scalps extend across the shore from a line distant about one hour from the high-water mark to a line corresponding with the low-water mark of neap tides. The

Oystercatchers spend the time of high-water resting near the high-water mark. They fly over to the scalps exposed by the ebb, and occupy themselves with the uncovered shell-fish; as the scalps become dry the birds turn their attention to the edges of the banks, the adjacent sand or mud, and the pools in quest of hidden Mussels. The period of slack water is devoted to repose, or is spent in other ways, and during the rise and flow of the tide over the scalps the Oystercatchers renew the search, until they are carried literally off their feet by the flood, when they betake themselves once more to the high-water mark. There is reason to believe that they are able to search effectively in the dark, and they are certainly active on moonlit nights.

The preceding paragraph shows that the Mussels must be surrounded by a certain amount of moisture if they are to meet the requirements of the Oystercatchers. With one exception, to which reference will be made, the Mussels which lie on the surface of the scalps are left alone when once they have become dry, and attention is concentrated on those which are covered by seaweed or by water, and on those which are buried in sand or mud.

The attitude of rest is one in which the valves of the Mussel are separated slightly along the free border, due to the tension of the elastic ligament; the tight closure of the valves is caused by the contraction of the adductor muscles, and its maintenance implies continuous exertion. The attitude of rest is possible only when the shells are under water or in moist situations; otherwise the delicate internal structures would shrivel. As soon as the shells become dry the Mussels must close their valves. Hence it is found that in the one case the shells are gaping slightly, in the other they are tightly closed. The former are liable to destruction by the Oystercatchers; the latter, with one exception, as far as can be discovered, are invulnerable. It is essential that the moisture should be saline. Heavy rainstorms interfere with the search of the Oystercatchers by flooding the scalps with fresh water, which has the same effect as the drying of the shells.

Inspection of any scalps on which Oystercatchers have been feeding shows a litter of emptied shells. Some still lie in position on the scalps, others remain at the bottom of conical

excavations in the sand or mud, and many have been carried to bare patches of rock to be cleared of their contents.

Careful examination furnishes an important clue to the position the shells occupied during life, and therefrom to the manner in which they were opened. It will be seen that of the shells in which the valves are still united many have the dorsal borders uppermost, and a lesser number the ventral borders; and of the shells in which the valves have fallen apart, some have the ventral borders adjacent and others the dorsal borders. The position of these shells should be compared with that of the unopened Mussels on the banks. The majority rest with the dorsal borders uppermost, and are fixed securely to the ground by strands which emerge between the ventral borders of the valves. In few instances is the converse true. Occasionally they lie in a vertical position, the posterior ends being superior.

In the tightly closed shell the edges of the valves are in perfect apposition, with the exception of the middle portion of the ventral border. There a long and narrow fissure with rounded edges is present. This fissure is the weak point in the Mussel's armour, and it is seldom exposed on the open beds. Shells so placed are sought for eagerly by the Oystercatchers, and form the exception to the rule that dried and therefore tightly closed Mussels are left alone. When Oystercatchers are seen at work on dry Mussel-scalps it may be taken for granted that they are searching for these Mussels, and I have found repeatedly in these cases that only those Mussels were opened of which the ventral borders were uppermost. While the Mussels vary in size within wide limits, those which are attacked by the Oystercatchers agree closely in dimension with one another. One and a quarter inches to one and five-eighths inches in length by half an inch to three-quarters of an inch in breadth denote the normal variation. I have not seen Mussels of larger size than one and five-eighths inches by seven-eighths of an inch opened, and it would appear that Mussels smaller than one inch by half an inch are taken only when larger sizes are not available.

We have now to consider the way in which suitable Mussels are discovered, the manner in which they are opened, and how their contents are removed. Difficulties arise at once by reason of the variety of methods in use, the variable effect of these

methods on the shells, and the readiness with which the Oystercatchers adapt the methods to overcome varying and often unforeseen circumstances. I have thought it best to classify the shells according to the places at which they are opened, to describe the principal methods and their results in each class, and to mention some of the exceptions as they come under notice.

I. *Mussels opened through the dorsal borders.*

These form approximately seventy-eight per cent. of the shells opened by Oystercatchers. Bearing in mind that the Mussels in which the dorsal borders are present are the normal inhabitants of the banks, that they are available only when a sufficiency of moisture permits a separation of the valves, the reader will understand that the Oystercatchers must search for the gaping shells, and the birds are to be seen at these times walking sedately over the banks, their heads directed forwards, and their bills in a position ready to strike. Each Mussel is approached in the line of its major axis, and is submitted to a careful inspection, usually from the front, though why this should be I have not been able to decide.

If the Mussel meet with approval the Oystercatcher strikes a sharp blow with the point of its bill on the summit of the dorsal border, apparently to find out whether or not the bill will pass between the edges of the valves. Frequently this does not happen, and the bird continues the search. When the result of the tap is favourable the bill is pushed down into the Mussel before the valves have time to close by a number of jerks with great rapidity and force, until the deepest part of the much compressed bill comes to lie lengthwise between the margins of the valves. Usually further action is necessary, and it must follow soon after the introduction of the bill; but in a few instances the bird raises its head, looks about, and then proceeds leisurely to clear out the contents.

When this happens it is probable that the shell has been thinner than usual, and the stroke has not been delivered fairly between the valves; in consequence a small fragment of one valve is driven in before the point of the bill, and through the hole thus formed the Oystercatcher is able to extract the con-

tents. Occasionally empty shells are found which exhibit the depression of a fragment at the margin of one valve.

The simplest procedure is to shake or lever the bill violently from side to side, and is sometimes successful in separating the valves, as the Mussels are fixed securely to the ground. The two methods most in use may be employed independently one after another, or may follow the method just described, as circumstances require.

One method is as follows: The bill, sunk vertically between and in line with the valves, forms a pivot of a movement of the Oystercatcher to one side of the Mussel. As the Oystercatcher walks slowly round the bill turns through quarter of a circle and comes to lie with its greatest depth across the fissure, causing a marked separation of the valves. The same effect may be produced without moving the feet, by rotating the head to one side on a vertical axis. The other method is equally simple: The Oystercatcher lowers its head almost to the ground on one side of the Mussel, and the point of the bill, being well inside the shell, presses on the opposite valve which is separated widely from its fellow. This may have to be repeated several times. It is curious that, as far as observation goes, the Oystercatcher walks round or lowers its head to its own left side, and the left valve suffers more often than the right, because the bird approaches the Mussel more often from the front than from behind.

Now and again another and less simple method of opening the shells is seen. It may be employed from the first, or after other ways have been tried and have been found wanting. I have seen a group of Oystercatchers use it to the virtual exclusion of other methods for several days, and then apparently it was abandoned for months. This method requires that the bivalve be approached from behind. The bill is pushed downwards between the valves and behind the ligament, and perhaps, after ineffectual attempts to open the shell by lateral and rotary levering, the bill is drawn slowly and firmly backwards and downwards between the valves, until the head almost touches the ground behind the Mussel, and the bill, instead of being at right angles to the long axis of the Mussel, lies parallel to it between the margins of the valves at the posterior end. From

this position the bill is pushed in firmly until the point seems to reach the anterior end of the Mussel, when snapping motions of the mandibles occur, and are followed by gradual separation of the valves. It is plain that this method cannot be applied to Mussels buried in sand.

When the empty shells are examined it is found that, with the exception of those opened by the last method, one valve in each is fractured—that the fracture extends in most cases from a point on the dorsal border of the valve, one-eighth of an inch from the posterior end of the ligament, along a curved course following one of the lines of growth to the anterior end of the shell, and passes above the insertion of the anterior adductor muscle.

The upper and anterior fragment of the valve is raised by the passive contraction of the ligament, and its posterior free end is twisted outwards. Less frequently the fracture turns backwards instead of forwards, separating an upper and posterior portion from the rest of the valve. Occasionally the fracture extends transversely across the valve, isolating the posterior portion, and more rarely from the ventral border transversely across the valve to a point about a quarter of an inch below the posterior end of the ligament, and then horizontally to the anterior end.

In this case the lower and anterior portion of the valve is separated, the posterior portion united to the upper and anterior portion remains with the other valve, and from posterior end of the ligament is twisted markedly outwards.

It is noteworthy that the edges of the valves seldom show where the bill has been introduced. In the only example I have seen the margins of the valves a little behind the posterior end of the ligament were ground away, so that when the valves were brought together an elliptical hole was formed, which admitted the deepest part of a bill lengthwise.

It can be shown experimentally that the fracture starts at the place where pressure is applied, and when the lever is rotated between the valves it begins at that edge of the lever towards which pressure is directed. On a few occasions these processes were verified by observing the Oystercatchers at work, and afterwards by examining the particular shells they had opened.

II. *Mussels opened through the ventral borders.*

These amount to nine per cent. of the empty shells. Mussels in which the ventral borders are directed upwards are vulnerable at all times, and while the relative percentage is low the actual percentage may be as high as a hundred. When they are exposed to view on the banks they require no tentative inspection or tapping, and are opened at once. Oystercatchers can be seen to sight them from a distance, and to run eagerly to open them. The valves are separated in the ways which have been described, and whenever close inspection is possible the bill is seen to enter nearer the posterior than the anterior end of the fissure. The method whereby the bill, after being introduced, is lowered from the vertical to the horizontal position, and then pushed home to the anterior end of the shell, I have seen in use once with a shell of this class. It was employed after an ineffectual attempt had been made to separate the valves by a vigorous shaking of the bill sidewise. The snapping motions of the mandibles in the anterior end of the shell were followed by the gradual and wide separation of the valves, which were seen plainly to fall away from one another on to the sand.

Damage to the margins of the valves occurs seldom or never, and a considerable proportion of these Mussels is opened without fracture of the valves. When fracture does occur the right valve usually suffers, and the commonest form is a simple transverse fracture extending from the point on the margin of the valve where the bill was introduced to the dorsal border. Frequently a large quadrilateral fragment is separated from the valve opposite the posterior half of the fissure, and from the lower angles of the gap thus formed lines of fracture may travel to the dorsal border and to the anterior end.

More Mussels are opened by way of the ventral borders when buried than when exposed to view. Those Mussels are covered by a film of sand or mud, frequently as much as one inch in depth, and are found by a process of tapping the surface with the point of the bill. At first the ground is tapped here and there in tentative fashion. Sometimes a single tap leads directly to the Mussel; more often numerous taps are made in a small area until one is made in the right place, when the bill sinks quickly

into the sand and the Mussel is opened in one or more of the ways which have been described.

It is probable, as Macgillivray* suggested in the case of the Dunlin, that "they discover the object of their search rather by the kind of resistance which it yields than by touch like that of the human skin." Sand overlying smooth rock is equable to the touch, and I have noticed that the tapping instrument meets with greater resistance over the presenting border of a Mussel than elsewhere, but I have not been able to distinguish a Mussel from inanimate objects. Possibly the movement which the Mussel makes in closing its valves and drawing them more nearly to the rock is transmitted to the bill through the sand; the high proportion of hidden Mussels opened through the ventral borders, together with the circumstance that the relative frequency of the several positions assumed by the Mussel is not influenced by the presence or absence of overlying sand and mud, leads me to believe that it is so, and the movement which apprises the Oystercatcher of the presence of its prey often defeats the end in view, unless the ventral border of the Mussel is open to attack.

At these times delicate imprints made by the point of the bill are seen on the sand or mud around the scalps. Usually at wide and unequal intervals, in places they are crowded together, and there may be a few shallow probings, some of which are bridged by septa of sand or mud, showing that the mandibles are slightly separated. In several places these clear imprints are obliterated by footmarks, often deeper than usual; in the centre of each place there is a deep conical pit surrounded by ejected material, and the empty shell lies at the bottom, or it is found near by.

The Oystercatcher removes the Mussel from its anchorage under the sand or on the open banks from choice, or as the result of the undesirable attention of others, and to avoid the prolonged submersion of the head under water which extraction of the contents sometimes requires. A fine distinction is drawn between the shells of the two classes. Those which present the ventral borders are opened up before being detached from their foundations, while those in which the dorsal borders are present

may have the valves separated slightly when the Mussels are in position, and the opening up completed at leisure after detachment. The reason is to be found in the characters of the two borders. Along the dorsal border the valves meet at an acute angle and rest insecurely on the ground, while on the other side they meet at an open angle, and are flat-bottomed like a barge.

The Oystercatcher empties a shell at the bottom of a deep hole in the sand as easily as one on the open ground.

After the shell has been opened the separation is effected by introducing the upper mandible within the shell, and by gripping a valve—usually the damaged one—between the mandibles, a few vigorous shakes and a pull in the upward direction being sufficient to detach the shell.

III. *Mussels opened through the posterior ends.*

Forming about thirteen per cent. of the shell remains, the valves of these Mussels are never fractured, and at most show some comminution of the thin posterior edges. The fragments remain attached to each other, and are not driven inside the shell.

It is, therefore, likely that the valves are separated to some extent before the bill is introduced. This can be the only route to the interior of the buried shells, the long axes of which are vertical, but in the case of Mussels placed horizontally on the banks it is not easy to understand why the posterior end of each should be chosen.

The method is simple enough. The point of the bill is inserted quickly between the valves and pushed home by a number of forcible jerks. Vigorous shaking of the bill sidewise follows, and is sufficient to open the shell. When the Mussel lies horizontally the Oystercatcher approaches from behind with its head lowered nearly to the ground, and the point of the bill directed forwards.

A feature which the shell opened at the posterior end exhibits more frequently, and to a greater degree than the shell opened by any of the other routes, is a partial rotation of one valve on the other, about a point situated near the middle of the ligament.

* 'History of British Birds,' vol. iv. p. 212.

Among the litter of empty shells the presence of a variable number of unopened shells is of daily occurrence.

Some are quite uninjured, the margins of the valves are in perfect apposition, and are tightly closed. More commonly the valves of each Mussel are rotated partially on one another, so that the margins overlap, and a portion of the mantle is nipped between the edge of one valve and the inside of the other. When the valves are not shut firmly this rotation is produced easily by applying pressure to the valves in opposite directions; the Mussel makes no attempt to readjust the relative position of the valves, and slowly adducts them in their altered relation. As might be inferred from what has been stated, the right valve is as a rule lower posteriorly than the left, and the dorsal border is uppermost as the shell lies on the ground.

Shells which measure not more than an inch nor less than half an inch in length are searched for, and opened in the same way as the larger specimens, but the introduction of the bill and the subsequent manœuvres require less force, and are performed more rapidly. Frequently, however, the Oystercatcher approaches with the bill opened widely, and pushes the upper mandible between the valves; simultaneous rotation of the head to one side on a vertical axis and approach of the lower to the upper mandible follow, so that the upper mandible rotates into a transverse position within the fissure, and the posterior portion of one valve is crushed and twisted outwards in the firm grip of the bill.

Shells of half an inch by quarter of an inch and those of smaller size are torn from the rocks, one at a time, and are swallowed entire. Macgillivray,* speaking of the contents of the stomachs, states that the bivalve shells are generally, "when of small size, either entire or merely crushed"; and Professor Patten† has found "in several gizzards small bivalves with unbroken shells which measured 12 by 5 mm."

The greater part of the mollusc makes a few mouthfuls. Large pieces are torn away and transferred to within reach of the tongue by jerks of the head. At each projection of the head the bill, as it were, slides over the piece, and the return of the

* 'History of British Birds,' vol. iv. p. 156.

† 'Aquatic Birds of Great Britain and Ireland,' p. 249.

morsel is prevented by pressure of the mandibles and the reverted cusps on the palate.

When entrance has been gained through the middle part of a border, one end is cleared out first and then the other, the Mussel, if detached, being turned round by the Oystercatcher, and, if not, the Oystercatcher, after emptying the end farthest from itself, walks round to the opposite pole and clears out the other. When the chief part of the mollusc has been removed there remains material adhering to the inner surface of the valves, chiefly the mantle. To remove this material the bill is employed like a pair of scissors. It is laid flatly on the inner surface of a valve near one end, and as it is pushed forward it snips away the adherent flesh. After reaching the opposite end of the shell the bill is returned to one side of its starting point, and snips its way along a line adjacent and parallel to the preceding, and so on, until the adherent flesh has been removed from both valves. This skilful procedure is carried through rapidly without pause, and often without moving the shell. It is seldom seen towards the end of the feeding periods, and at these times shells are to be found in which portions of the mantle remain.

Consideration of the methods employed by the Oystercatcher leads to the conclusion that fracture and rotation of the valves are in no way essential to the complete exposure of the contents of the shells. This view is supported by the cases in which neither occurs, and by the position, relative to the Mussel, in which the bill is introduced. It will be seen that the bill is inserted in the posterior half of the commissure between the valves, and when the attack is made on the borders it is pushed down just in front of the posterior adductor muscle. In this position the bill separates the valves most widely where separation is most required. Observation proves that mere rotation of the bill between the valves is sufficient to rupture the fused portion of the mantle, and to impair the action of both muscles; they contract very slowly after slight extension. The wider separation, usually produced, tears the posterior muscle from its attachment to the valve, which forms the fulcrum of the lever, and the anterior adductor gives way in similar fashion whenever the valves are set farther apart.

The position in which the bill is introduced, the quickness with which the Oystercatchers remove the anterior and posterior parts of the molluscs, and the interesting cases in which the bill, after it has been sunk vertically between the borders, is borne down between the posterior margins, destroying on its way the posterior adductor, and is pushed on at once to cut through the anterior muscle, go far to prove that the Oystercatchers are acquainted with the position and relative importance of the two muscles, and fully realize the necessity for their early destruction.

The fractures, when they occur, depend primarily for their production on the relative strength of the shell, the adductor muscles, and the ligament; their situation and character are determined by the position in which the force is applied, the position of the muscles and the ligaments, and the direction of the lines of least strength in the shell.

In these notes I have attempted to describe the ways by which Oystercatchers deal with Mussels; I have shown how the Oystercatchers are limited to certain Mussels, how entrance to the shells is effected, how the valves are separated so as to prevent their adduction while the molluscs are being devoured; I have brought forward observations which seem to prove that the Oystercatchers, far from being actuated by blind impulse, on the contrary proceed deliberately to remove certain structures which hinder the achievement of their desires; and I may say with truth that we have in the Oystercatcher a living illustration of the principle of the lever, by means of which a comparatively feeble instrument is enabled to render the stoutest resistance of no avail.

It remains for me to point out that interest must centre largely on the manifold ways in which the bill is employed, and on the attempts which may be made to assemble its numerous modes of action in the order of their development in Time.