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Predation of Limpets and Dogwhelks by Oystercatchers

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LIMPETS *Patella spp.* are commonly taken by Oystercatchers *Haematopus ostralegus,* and the methods of attack have been described by Dewar (1919). Dogwhelks *Nucella lapillus* are less commonly taken, and Dewar (1910) considered that, owing to the low success rate of attempts to break dogwhelk shells, and the small quantity of food eventually obtained, dogwhelks did not constitute an economical prey. However, Gudmundsson (in Dare 1966) regarded dogwhelks as an important food of Oystercatchers in Iceland.

Small numbers of Oystercatchers visit rocky shores in Yorkshire, chiefly during the winter, and their diet consists mainly of *Patella vulgata, P. aspera* and *Nucella lapillus.* Mussels *Mytilus edulis* are taken in small numbers. Periwinkles *Littorina littorea* and dogwhelk shells inhabited by hermit crabs *Eupagurus spp.* were occasionally turned over by Oystercatchers, but they were never seen to be attacked.

This investigation was initially undertaken to describe the methods used by Oystercatchers in attacking dogwhelks (preliminary observations revealed that the technique was different from that described by Dewar (1910)), and to discover what was responsible for the preference for *Patella aspera* over *P. vulgata* where the two species of limpet coexisted. The study was concentrated on an exposed reef at North Cheek, Robin Hood's Bay, Yorkshire, but supplementary data on size selection were gathered from three other localities in Robin Hood's Bay, and also from Filey Brigg (fig. 1).

METHODS

Direct observations of feeding birds showed that limpets and dogwhelks which had been attacked were almost invariably left upside down. Collections of their shells were made on 20-minute searches of the reef at North Cheek, at least six searches being made at low tide each month. (From searches of the reef on ebb tides, before the Oystercatchers arrived, it was found that all shells from the previous day had been washed off the open rock.) All shells collected were measured to nearest millimetre with vernier calipers, and samples of the populations, from quarter-metre square quadrats thrown at random in areas where predated animals were found, were similarly measured. In dogwhelks shell height, and in limpets shell length, were the parameters used.

In addition, predated limpets were recorded as damaged or undamaged, and, if damaged, the positions of chips in the margins of the shells were noted to discover at which point the attacks were directed.

In an attempt to explain the high failure rate of attacks on dogwhelks, the opercular widths were measured to the nearest 0.1 mm., and the time taken for snails to withdraw into their shells after disturbance was obtained using a stop watch. Because of a possible relation between predation and castration by larvae of the trematode parasite *Parorchis acanthus*, dogwhelk shells were broken and the gonads were examined for infection.

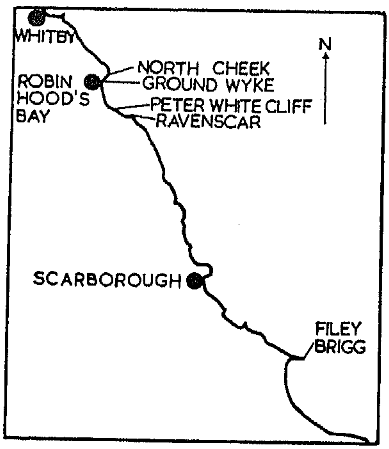

FIGURE 1. Sketch map of part of the Yorkshire coast, showing where samples were taken.

PREDATION OF LIMPETS

Oystercatchers did not attack every limpet encountered as they walked across the rocks, and they ignored even some of the largest individuals. Limpets were attacked essentially in the manner described by Dewar (1913). A thrust at the margin of the shell with the closed bill usually resulted in *Patella vulgata* being knocked off the rock, but the shells of *P. aspera* frequently broke, and the Oystercatcher then inserted the closed bill into the fracture and levered the limpet off the rock. Once a limpet had been dislodged,

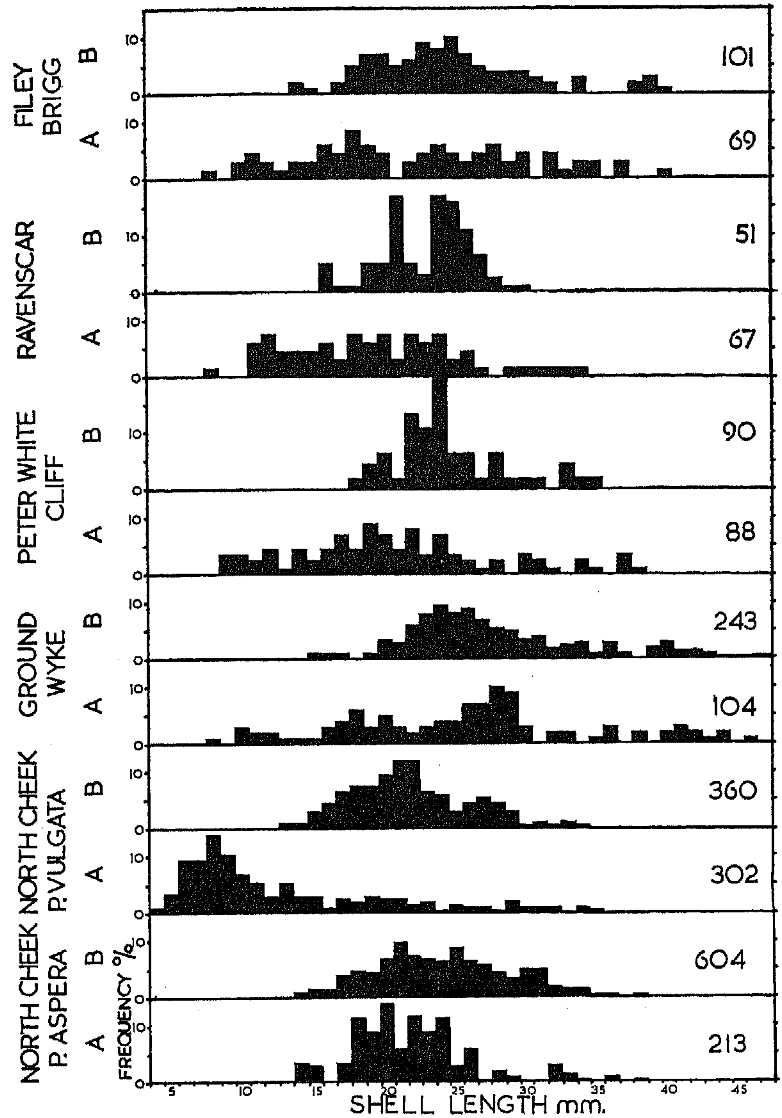

FIGURE 2. The shell length frequency distributions of six limpet populations (A), and of limpets taken by Oystercatchers (B) from these populations. The size of each sample is given at the right of each histogram.

it was carried a short distance to a site where it could be supported while the Oystercatcher cut round the adductor muscle.

The size frequency distributions of five populations of *P. vulgata*, and one of *P. aspera*, were obtained, together with the size distributions of limpets taken from these populations by Oystercatchers (fig. 2). The presence of a large number of small *P. vulgata* at North Cheek, forming a distinct mode, suggests that these were first year animals. If this is so the limpets found in the other populations were probably at least two years old, and had had little recruitment during the past year.

Comparison of the populations and of the limpets taken from these populations (fig. 2) shows that size selection was limited to the avoidance of the small size categories, and a tendency to take the largest available limpets. This was the conclusion reached by Norton-Griffiths (1967) in his study of Oystercatcher predation of mussels, but part of the selection of larger mussels was due to their clumped distribution, with the largest individuals occupying the outside positions. There appeared to be no distributional peculiarities in the limpet populations studied here, and the predation of large limpets presumably gave the Oystercatchers optimum return for the amount of energy expended.

Their main food at North Cheek, particularly during the spring, was *P. aspera*, which was abundant in the low shore and in mid shore pools, while *P. vulgata* was widely distributed in the mid and upper shores.

During the collection of samples of the populations it was found that, in levering off the limpets with a scalpel, shells of *P. aspera* frequently broke, while those of *P. vulgata* rarely broke or chipped, and appeared to be stronger. *P. aspera* may therefore have been easier for the Oystercatchers to remove from the rock, despite the fact that many shells were camouflaged against their background by being covered with the calcareous red algae *Corallina sp.* and *Lithothamnion sp.*, and also with mussels. Table I, showing the proportions of limpets taken by Oystercatchers which had broken, chipped or intact shells, reveals that those of *P. aspera* were more susceptible to breakage than those of *P. vulgata* when subjected to Oystercatcher attacks.

TABLE I—THE NUMBER OF LIMPETS DAMAGED DURING OYSTERCATCHER ATTACKS
Figures in brackets are percentages.

	P. aspera	*P. vulgata*
Broken	230 (38.1)	44 (12.2)
Chipped	117 (19.4)	23 (6.4)
Intact	257 (42.5)	293 (81.7)
Total	604	360

P. aspera had a significantly higher proportion of damaged shells than *P. vulgata* ($X^2=19.9$, $p<0.001$).

The ease with which *P. aspera* shells were damaged resulted in the point at which the bird first struck the shell frequently showing as a chip or fracture. It is thought that shells which had their centres missing were broken while the bird was cutting round the adductor muscle, rather than during the initial dislodgment of the limpet, since Oystercatchers were never seen to attack the centre of a shell. Where chips and fractures, indicating the site of attack, were clearly visible, their positions were recorded and the distribution of attacks is shown in fig. 3. Dewar (1913) stated that no particular part of the shell margin was preferentially attacked, but fig. 3 shows that at North Cheek most of the attacks were directed at the anterior end of the shell, and that this end the right-hand section received more attacks than the left.

In order to explain this in terms of the birds' behaviour, Oystercatchers were watched at close range while feeding in the low shore at North Cheek on *P. aspera*, and at Peter White Cliff, where only *P. vulgata* was present. The majority (*P. aspera*—78.7%; *P. vulgata* —86.3%) of attacks were delivered with the head turned so that the bill pointed down and slightly to the right.

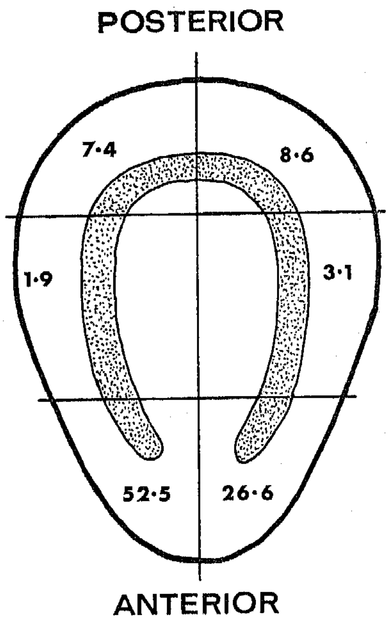

FIGURE 3. The distribution of Oystercatcher attacks on shells of *Patella aspera*. Comparing anterior and posterior: $X^2=67.6$, $p<0.001$: comparing anterior right and left: $X^2=8.6$, $p<0.01$. The stippled area represents the position of the adductor muscle.

The adductor muscle of a limpet is horseshoe-shaped, with the open end of the horseshoe at the anterior (fig. 3), so that this end probably has the weakest hold on the substrate. If so, Oystercatcher attacks delivered here are more likely to be successful than attacks elsewhere on the shell margin. The observed distribution of attacks on *P. aspera* shells is the distribution of successful attacks, but whether this is a reflection of the distribution of all attacks is not known. This would involve recognition of the anterior of a limpet by Oystercatchers, which would be possible if the birds watched grazing limpets, when their heads move from side to side in an arc (see Lewis 1964, plate 38). However, limpets are frequently attacked when they are on bare rock, and not feeding. In this situation the anterior of *P. aspera* could be identified by its more pointed appearance, but the oval shell of *P. vulgata* would render this identification more difficult. It would also be difficult with *P. aspera* when the shells are covered with *Corallina* and mussels, but shells like this are only found in pools where the grazing movements would be apparent.

TABLE II—SUCCESS OF OYSTERCATCHER ATTACKS ON TWO SPECIES OF LIMPETS ON OPEN ROCK AND IN POOLS AT ROBIN HOOD'S BAY, YORKSHIRE

Species of limpet	*Locality*	*Situation*	*No. of attacks*	*No. successful*	*% successful*
P. aspera	North Cheek	Rock	78	57	73.1
P. aspera	North Cheek	Pool	97	97	100.0
P. vulgata	Peter White Cliff	Rock	30	9	30.0
P. vulgata	Peter White Cliff	Pool	71	31	43.7

The success of attacks on *P. aspera* was significantly greater than on *P. vulgata* on both rock and in pools ($X^2=18.0$, $p<0.001$; $X^2=22.1$, $p<0.001$ respectively). In *P. aspera*, the difference between the success of attacks on rock and in pools was significant ($X^2=4.22$, $p<0.05$), but in *P. vulgata* the difference was not significant.

Measurement of the success rates of Oystercatcher attacks (Table II) showed that limpets on bare rock were more difficult to dislodge than limpets in pools. On bare rock limpets clamp their shells down more firmly than in pools, where the absence of desiccation means that the shell need only be pulled down during disturbance. Table II also shows that in both situations *P. aspera* was easier to dislodge than *P. vulgata*, this perhaps being a reflection of the bird's difficulty in locating the anterior end of the shell of the latter species, and also of its harder shell.

PREDATION OF DOGWHELKS

Dogwhelks were taken only during the autumn and spring. At these times, at North Cheek, dogwhelks were moving into and emerging from aggregations in clefts and pools, in which they overwintered (Feare 1970). Direct observation showed that dogwhelks in these winter aggregations were not attacked; nor were those in aggregations on the open shore, but dogwhelks distributed singly on the open shore were attacked. On each day that observations were made, only one or two Oystercatchers fed on dogwhelks, the remainder concentrating on limpets.

When a dogwhelk had been selected, the bird turned it over with the bill and immediately pecked at the opercular opening of the shell, without carrying its prey to a site where the shell could be supported. This behaviour contrasted sharply with attacks on limpets, and with the attacks on dogwhelks described by Dewar (1910), in which the birds attempted to break the shells. In Robin Hood's Bay, only the head, foot and operculum were taken, the gonad and digestive gland remaining in the undamaged shell. Only adult dogwhelks were taken, and the shell height of these dogwhelks was 21.1 ± 2.0 mm., while that of the adult population was 20.3 ± 1.6 mm.

Dewar (1910) found that when Oystercatchers attempted to break dogwhelk shells, only 21% of the attacks were successful, but at North Cheek 61% of the attacks were successful. Inability to break the shells accounted for Dewar's high failure rate, but other factors were involved at North Cheek. Although comparison of an Oystercatcher bill with the dimensions of the opercular apertures of dogwhelk shells suggested that the width of the aperture might be limiting, no significant difference was found between the aperture widths of successfully and unsuccessfully attacked dogwhelks ($t = 0.842$; $p = 0.4$ for samples of 46 and 79 respectively).

The rapidity with which an Oystercatcher attacked a dogwhelk after turning it over, without carrying it to a site which would support the shell, suggested that the critical factor in the success of attacks might be the time taken for a dogwhelk to withdraw into its shell after disturbance.

Measurement of this time for a sample of 111 dogwhelks in April 1967, when the air temperature was 14C°, gave a mean figure of 14.0 seconds, but a range of 1 to 35 seconds. In relation to animal responses in food collection this range is probably large, and slower dogwhelks would undoubtedly be more susceptible to predation. The reaction times of dogwhelks infected with *Parorchis acanthus* were not significantly different from those of 'normal' dogwhelks ($t = 0.184$; $p > 0.8$ for samples of 31 and 80 respectively), and infected dogwhelks were not, therefore, selected due to their having slower reaction times.

As stated above, only dogwhelks which were distributed singly on the open shore were attacked; those in aggregations were not touched. In September 1966, when 57% of the adult dogwhelks were already aggregated in clefts and pools, it was known that only 1% of these were infected by *Parorchis acanthus*, but 13% of the dogwhelks taken by Oystercatchers were found to be infected. Table III shows the rates of infection of dogwhelks from the three situations on the shore in which dogwhelks were found in the autumn. The infection rate in the situation exploited by Oystercatchers was the same as that in the dogwhelks taken by Oystercatchers, and they were not, therefore, selecting infected dogwhelks. *P. acanthus* castrates its host, and tends to produce growth and behavioural

TABLE III—PROPORTIONS OF DOGWHELKS INFECTED WITH *Parorchis acanthus* IN DIFFERENT SITUATIONS ON THE SHORE AT NORTH CHEEK, AND IN THOSE TAKEN BY OYSTERCATCHERS, IN SEPTEMBER 1966

Situation	*Infection rate %*	*Sample size*
Aggregations in clefts	1.0	100
Singly on open shore	12.7	55
Aggregated with immatures on open shore	48.0	50
Taken by Oystercatchers	13.0	100

abnormalities (Feare 1970), the result of the latter being to make infected adults go into winter aggregations later than uninfected adults. They are therefore made more available to Oystercatchers, which are one of the final hosts of this trematode (Fretter and Graham 1962), and the alteration of dogwhelk behaviour described above, increasing their susceptibility to predation, is of survival value to the parasite.

DISCUSSION

Attacks directed at particular points on prey shells have been recorded for cockles (Drinnan 1957) and mussels (Dewar 1908, 1913), but Dewar (1913) found that, in *Patella vulgata*, no point on the shell margin was particularly susceptible to attack. Insufficient data for *P. vulgata* were obtained in the present study owing to the small proportion of shells which were damaged. However, the anterior end of *P. aspera* can be recognised visually, and this end received the majority of successful Oystercatcher attacks, probably because attacks directed at this end are most likely to be successful owing to the shape of the adductor muscle (fig. 3). It seems unlikley, however, that a limpet will be more easily dislodged if the right anterior section, rather than the left, is attacked, but experimental evidence is required to back this statement.

Dewar (1908, 1913), Drinnan (1957, 1958), and Norton-Griffiths (1967) found that, in bivalves, there was a tendency for only one valve to be fractured during Oystercatcher attacks, and Dewar (1908) discovered that the left valve of mussels was more often damaged than the right valve, owing to the birds usually lowering their head to this side. In cockles, Drinnan (1957) found that left and right valves were fractured in a 1 : 1 ratio, and Heppleston (1968) found the same ratio in mussels, but at Pensarn (Caernarvonshire) 32% of attacked mussels bore damage to the left valve, and 45% bore damage to the right valve, while at Morpha the proportions were 52% and 36% respectively (Drinnan 1958). If, as Dewar (1908) claimed, damage to one or other valve was due to the Oystercatcher lowering its head to the left or right side, the Pensarn and Morpha Oystercatcher populations must have contained different proportions of left and right-handed birds. Dextralism and sinistralism have been recorded in parrots (Psittaciformes) (Friedman and Davis 1938) and in grey phalaropes *Phalaropus fulicarius* (Cooch 1965), and the thrusting of the bill to the right in Robin Hood's Bay showed that these Oystercatchers were predominantly dextral in their attacks on limpets.

SUMMARY

The predation of Oystercatchers on two species of limpet and on dogwhelks on the Yorkshire coast is described.

Limpets were dislodged by one or more thrusts with the bill at the margin of the shell, and then carried to sites where they could be supported while the bird cut out the meat. Oystercatchers took the largest available limpets and avoided the smaller ones. Attacks were directed mainly at the anterior of the shell, and the predominance of attacks at the right anterior of the shell was related to the feeding methods of the birds.

Dogwhelks were eaten as soon as they had been dislodged, but only the head, foot and operculum were taken. Failure of attacks on dogwhelks was probably due to the rapid withdrawal into the shell of some individuals, rather than to their having small shell openings. The trematode parasite *Parorchis acanthus* made infected dogwhelks more available to Oystercatchers.

Dextralism and sinistralism in Oystercatchers are discussed.

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REFERENCES

GOOCH, F. G. 1965. An example of sinistralism in red phalaropes (*Phalaropus fulicarius*). *Auk*, 82:276-277.

DARE, P. J. 1966. The breeding and wintering populations of the Oystercatcher (*Haematopus ostralegus*) in the British Isles. *Fish Invest., Lond. Ser.* II., 25:1-69.

DEWAR, J. M. 1910. A preliminary note on the manner in which the Oystercatcher (*Haematopus ostralegus*) attacks the purple shell (*Purpura lapillus*). *Zoologist*, 14:109-112.

DEWAR, J. M. 1913. Further observations on the feeding habits of the Oystercatcher (*Haematopus ostralegus*). *Zoologist*, 17:41-56.

DRINNAN, R. E. 1957. The winter feeding of the Oystercatcher (*Haematopus ostralegus*) on the edible cockle (*Cardium edule*). *J. Anim. Ecol.*, 26:441-469.

DRINNAN, R. E. 1958. The winter feeding of the Oystercatcher (*Haematopus ostralegus*) on the edible mussel (*Mytilus edulis*) in the Conway Estuary, North Wales. *Fish Invest., Lond. Ser. II*, 22:1-15.

FEARE, C. J. 1970. Aspects of the ecology of an exposed shore population of dogwhelks *Nucella lapillus* (L.) *Oecologia* (*Berl.*), 5:1-18.

FRETTER, V. & A. GRAHAM. 1962. *British Prosobranch Molluscs*. London.

FRIEDMANN, H. & D. E. DAVIS. 1938. 'Left-handedness' in parrots. *Auk*, 55:478-480.

HEPPLESTON, P. B. 1968. An ecological study of the Oystercatcher (*Haematopus ostralegus L.*) in coastal and inland habitats of North-east Scotland. Unpub. Ph.D. Thesis, University of Aberdeen.

LEWIS, J. R. 1964. *The ecology of rocky shores*. London.

NORTON-GRIFFITHS, M. 1967. Some ecological aspects of the feeding behaviour of the Oystercatcher (*Haematopus ostralegus*) on the edible mussel *Mytilus edulis*. *Ibis*, 109:412-424.

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