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THE RELATION OF THE OYSTERCATCHER TO ITS NATURAL ENVIRONMENT.

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I.—Introduction.

The effective relation of an animal to its environment largely depends upon characters that are structural, physiological, and psychological. The more specialized these characters are, the more rigidly limited is the nature of the environment to which the animal is able to respond. The Oystercatcher is structurally specialized for a particular mode of feeding. Physiologically, it appears to need large quantities of bulky, soft food, such as shell-fish in winter, large earthworms and larvæ inland in summer, as it does not remain long in localities where these are not available. Psychologically, the individual behaviour is mostly stereotyped, and there is little evidence, short of the experimental, of any capacity for adjustment to environments which do not fulfil the special conditions of existence. Specialization secures the Oystercatcher from active competition with neighbouring forms, especially for food, but it necessarily results in the distribution of the species being discontinuous and dependent upon the simultaneous recurrence of complex and little variable environmental conditions.

1. *Areas under Observation and Method of Inquiry.*—The present communication reports the results of enquiries made on the south shore of the Firth of Forth during the winters 1906–1914 inclusive; on Loch Tummel, the lower portion of the River Tummel,

the River Gairy below the village of Blair and in Glen Fender, all of which are in North Perthshire, during the summers 1909 to 1914 inclusive. The former represent the winter environment; the latter a summer environment of the Oystercatcher, no data being here included from the coastal breeding stations. Observations of a less continuous character were made in other localities as a means of control. No attempt was made to work out the local distribution in either the summer or the winter area, or to obtain experimental control of any environmental factors.*

On the Firth of Forth localities were noted where Oystercatchers were found to occur. By repeated observations it was ascertained whether the places were in permanent winter occupation or not. In the former case, the number of occupants was periodically estimated, and the environmental conditions were, as far as possible, discovered. *Mytilus edulis* was accepted as the chief food supply of the Oystercatcher. Where the birds were occasional visitors to important stations of *Mytilus*, or did not occur at all, the stations were regarded as potential Oystercatcher stations, and their conditions found. Two chief types of habitats were recognized on the sea-beach. These were compared intensively, in order to determine which might be the more favourable to the Oystercatcher.

In the summer environment three habitats were separated. The number of pairs per linear measure of loch, river, and hill-stream was used to determine the most favourable habitat. The conditions of all likely or occupied breeding-stations under observation were noted and compared to find those common to all the stations, those present only in the more favourable stations, and those awanting at potential stations. The results derived from the individual stations were then aggregated for the several habitats, and the conditions of the most suitable habitat discovered.

II.—The Winter Environment.

1. *General Considerations.*—The northern shore of the Firth of Forth, below the Forth Bridge, generally descends steeply into

* Valuable information on the areas under observation was obtained from the 'Memoirs of the Geological Survey of Scotland,' Nos. 32, 33, and 55; Appendix III. to the 'Weekly Weather Report' for 1906; the Admiralty Charts and Manual.

the sea, and the breadth of the littoral zone is small. The abruptness of the gradient is due to the passage of the deep north channel (the old river-bed) close by the northern shore. The exposure eastwards of Kinghorn to easterly and south-easterly storms is severe, and the beach is mostly rocky and sea-worn. The southern shore, on the other hand, descends gently into the bed of a shallow sea, and the depth of the littoral zone is, in most places, considerable. The greater part of the coastline is sheltered from storms. To the east of Weak Law, however, the shore falls more rapidly towards the sea; the littoral zone becomes narrower, and the rocks more and more sea-worn, as the exposure to the effect of storms and the depth of the adjacent waters increase. The distribution of the Oystercatchers is evidently affected by the general features of the coastline, for they are relatively scarce along the northern shore, plentiful on the south coast westward of Weak Law, and less numerous eastward on the open coast.

Geologically, the south coast shows an ascending series of rocks from east to west. Beginning in the Old Red Sandstone period, a change occurs in the vicinity of Weak Law to the Carboniferous series, which persists to and beyond the western end of the area. The sedimentary rocks have little importance in the present connection. The abundance of durable volcanic lavas and intrusions has a considerable indirect effect on the Oystercatcher population; the non-columnar form of analcite basalt being especially favourable to the formation of *Mytilus* settlements.

The average temperature for the whole year at Leith (5·5 metres above M. S. L.) is 8·83° ± 3·72° C. The monthly means are 6·16° ± 3·00° in November, 4·11° ± 2·83° in December, and 3·89° ± 2·95° in January (1871–1905).

The mean rainfall at Leith is 0·60 metre; the number of wet days, 179 (1871–1905).

The prevailing winds are westerly.

The ordinary spring tide rises 3·7 metres at Dunbar, 4·6 metres at Prestonpans, 5 metres at Leith, and 5·8 metres at the Forth Bridge. The increase in rise of tide from east to west causes the foreshore to be deeper for equal gradients in the higher reaches of the estuary. Full seas occur in late autumn

and early spring, when the available feeding-grounds are greatly enlarged at low water. The vertical range of the low-water line is much greater than that of the high-water line, so that the advantage gained in the lower zones of the beach during spring tides is more than lost during neaps. For the same reason, the diminution of tidal range in passing from spring to neap tides is not directly proportional to the loss in height of the tide, but diminishes at a greater rate. The tidal range during neap tides is, therefore, a factor of importance in controlling the numbers of a settlement. The area under observation was too small to allow of a comparative study of the effects of locally different tidal ranges. The occurrence of the fortnightly succession of highest tides between the hours of one and five has, in the daytime, an important bearing on the welfare of the Oystercatcher in relation to human activities.

All three divisions of a sea-beach recognized by Pearse in Massachusetts * occur in irregular sequence on the south side of the Forth. They are the rock-beach, sand-beach, and the mud-flat. The first and last are habitats of *Mytilus*; the second is of minor importance to the economy of the Oystercatcher. As the division was found to be a natural one, the rock-beach and the mud-flat will be taken, for comparison, as the two locally typical habitats of the Oystercatcher. Along the sixty odd kilometres of coastline from the Forth Bridge to Belhaven, Dunbar, there were found seven permanent winter settlements of the Oystercatcher. Of these, one is a purely mud-flat station, two are mud-flat, rock-beach stations, while the remaining four are confined to rock-beaches only. In addition, two large *Mytilus* stations, not permanently occupied by Oystercatchers, were under observation. In the next section an account is given of the general features of the stations examined, in order to afford some idea of the nature of the ground in this locality.

2. *Mud-flat Habitat.*—Estuary of the East Lothian Tyne. The river flows into a small estuary locked from the North Sea by a long sandbar. The substratum consists of sand in the outer and marginal parts of the estuary, and of a fairly firm mud in the centre of the area, through which the channel flows. Weed is not common. There is a plentiful supply of Mussels of

* 'Rev. Knowledge,' 1915, p. 59 (no reference given).

good size on the mud. The central area slopes more steeply downwards where it borders the channel so that, when the tide is out, the birds can feed without being readily seen from the land. The feeding area is more than 150 metres from the grass. The central portion of the sandbar does not cover at high water, when it is used as a refuge. There is a moderate stock of Oystercatchers.

3. *Rock-beach, Mud-flat Habitat.*—A. *Aberlady Station.* Aberlady Bay is a large sandy and muddy flat, intersected by the channel of the Peffer Burn. The bay may be divided into three transverse zones. The highest zone is rarely visited by Oystercatchers. The middle zone, west of the channel, is a mud-flat. The mud is tenacious and does not shift readily. The greater part of the area is covered with Mussels of a good size, and is more than 150 metres from the nearest danger point. Eastward of the channel the conditions are, at first, similar to those of the western part of the middle zone, but they soon change to a sand-beach, which extends to the eastern high-water mark. The lower zone is composed mainly of sand-flats, which become extensive as the bay widens towards its outlet. In the middle zone, with the exception of the steep borders of the channel, the substratum lies mostly above mean-water level. In Gosford Bay is a large smoothly contoured area of volcanic rock. *Mytilus* is abundant here and of fair size. The mud in the lower part of the bay is apt to shift and bury the lower lying Mussels. East of these rocks a sandy bay is a factor of some importance. The rocks at the east and west ends of Gosford Bay are loaded with *Fucus*. At the east end of Longniddry Bay is a stretch of low-lying volcanic rocks, well provided with Mussels. These rocks, though lying rather near the high-water mark, are covered early by the incoming tide. The volcanic rocks east of Gullane Point have considerable supplies of Mussels. These rocks alternate with sand-beaches. They lie close in to the shore generally, and through their conformation are easily approached. One part extends far out into the sea, but the non-tidal portion runs nearly as far, and is well adapted for stalking. The area is visited irregularly by Oystercatchers. The refuge for this station is nearly five kilometres distant (Eyebroughty). The resident stock is, perhaps, the largest in the Forth. The birds

have a special tidal range of movement. Beginning at low water at the western-most feeding-place, they move eastward by stages, according to the tide, each of the three main feeding-places being adjusted to a certain state of the tide, and end towards high water at the eastern-most part of their range—on the refuge of Eyebroughty. The sequence is reversed on the ebb.

B. *Drum Flats Station.* The two previous examples of the mud-flat habitat are enclosed in small estuaries, debouching in the one case into the North Sea, in the other, into the estuary of the Forth. The Drum Flats, now to be described, border the Forth itself, and form on the southern shore the lowermost part of the continuous mud-beaches of the upper estuary. The mud is light and shifting in places, more tenacious in others. Weed is luxuriant. Bordering the channel of the River Almond the mud is firmer, and large areas afford an abundant and good supply of Mussels. The feeding area lies more than 150 metres from the land. A large stock is resident in winter. A range of tidal volcanic rocks lying to the west of Granton Harbour and well off shore is covered with Mussels in the absence of weed, and is much visited by the settlement. Cramond Island, lying at the mouth of the Almond Channel and close to the principal feeding area, is inhabited. The Oystercatchers do not resort to it. The refuge is on the Islet of Inchmickrey, lying on the middle bank of the Firth of Forth. The exposure is not severe.

4. *Rock-beach Habitat.*—Of the four stations of rock-beach habitat coming under observation, one (Eyebroughty) will be described in some detail, and only the factors by which the others differ from the Eyebroughty station will be mentioned. In the Eyebroughty station a long tidal reef, lying to the west of Eyebroughty, and about 450 metres from the mainland, provides quantities of *Mytilus*, for the most part of small size. The settlement feeds here a good deal, but the foothold is only moderately good, and in storms the reef is wave-swept. Near Cheese Bay there are two large bosses of volcanic rock lying well off the land. They are crowded with *Mytilus* of small size, and are visited daily. At the east end of Redhouse Bay there is a flat, low-lying rock forming a horn to the bay. The outer part carries a moderate stock of small Mussels. Part of the

ground is under 150 metres from cover. Here the birds are irregular visitors, mostly in the mornings and in bad weather, if tides are suitable. West of Weak Law is a bed of shale abundantly supplied with shell-fish of various kinds and suitable size. It lies more than 150 metres from cover. The rocks at Weak Law are poor in *Mytilus*, but rather rich in *Modiolus* and *Patella*. They run well out to sea. Approach, however, is easy owing to the lie and nature of the rocks. They are seldom visited. Further east lies a great mass of lava, portions of which are permanently cut off from the main mass by water. *Mytilus* is abundant but small. The birds visit these rocks frequently, and are here difficult to approach. The western part of Fidra Brig (lava) provides quantities of *Mytilus* and *Modiolus*. The rock is hummocky, and the feeding area is not too far from the mainland. The birds visit occasionally and can be stalked with comparative ease. Eyebroughty Brig lies more than 360 metres from the mainland, opposite the central portion of the shore area. It is used as a refuge. The stock of birds is small.

The Seacliff settlement is small. The features are similar to those found at Eyebroughty, but the depth of foreshore is less, and there is a severe exposure to storms. In some places the *Mytilus* stations are within 150 metres of the grass. A long volcanic reef, dry at high water, lies well off shore, is used as a refuge, and probably also as a feeding-ground.

The Lamb station is peculiar in that the islet forms both the refuge and the principal feeding-ground. Supplies are also drawn from the Longskellies and from skerries off North Berwick. The exposure is fairly severe. The feeding-grounds are difficult of access. The stock is small.

The small Cuthill settlement lives in unusual surroundings. A low-lying, slabby rock centres a small bay of gravelly sand, and lies about 180 metres from the coast road. A small harbour, a tile-works, a coal-pit, and a number of miners' rows partially surround the locality, which is in itself rather difficult of access, and therefore not much disturbed. The rock has a good supply of *Mytilus*. A volcanic dyke, dry at high water, lies off shore, and is used as a refuge and a *Mytilus* feeding-ground.

Two large *Mytilus* stations of rock-beach habitat occur at

Redhouse and at Seafield. Neither has a resident stock of Oystercatchers, and visits are irregular, occurring mostly in the early morning. At the former station the rocks descend abruptly to a sand-beach, and have little breadth. The larger sizes of Mussels preponderate, but lie well within 150 metres of the grass. In the latter, the eastward rocks have a similar character. Towards the west the rock-beach is prolonged out to sea by a succession of more or less isolated reefs carrying plenty of Mussels. The foreshore here is much disturbed. Neither of these areas has a refuge within ordinary range.

III.—Discussion of the Winter Environment.

Summing up the conditions common to all the occupied stations of the rock-beach and mud-flat habitats on the south shore of the Firth of Forth, we have the following:—A body of seawater; *Mytilus* in sufficient quantity, of a suitable size, in accessible situations, and at or more than 150 metres from the nearest danger point; a place of refuge which can be resorted to for safety during the period of high water, and at other times when the feeding-grounds are disturbed.

Resort to a place of refuge at certain times is a local adjustment to human interference. In the early part of the winter, when disturbance is infrequent, the birds rarely leave Aberlady Bay during diurnal high water, and if they do, it is with manifest reluctance. At high water they collect at one part of the shore, which is a constant for the purpose, and takes the place of the refuge as the headquarters within the territory. As the winter advances, the birds are more liable to be driven from the high-water mark. They then proceed to the refuge. Later still, in the daytime they "anticipate" disturbance by not coming in to the high-water mark at all during spring tides, and proceed to the refuge one or two hours before the time of high water. But throughout the whole winter, during the diurnal high water of neap tides, and the nocturnal high water of all tides, the birds remain at the headquarters in the bay. In the former instance, the low gradient of the beach enables the birds to remain on the high-water line beyond the range of gunfire. In little disturbed localities, permanently occupied winter stations occur which have no special refuges. The Oystercatchers which feed

on the Mussel-bank at the mouth of the River Awe, or the Mussel-scalps on lonely parts of the coast of Northumberland, have no distinctive refuge. They pass the time of diurnal high water on a constant part of the high-water mark. When disturbed, they proceed to little-frequented fields in the vicinity.

Oystercatchers show a decided preference for Mussels about 3·5 cm. in length. Why, has not been determined. Probably Mussels ranging closely about this size provide food in due proportion to the amount of labour required to get it. When the Mussels are larger, too much energy is needed to open them; when they are smaller, too many have to be opened, and the more fragile shell is apt to be crushed into the body of the mollusc. In this condition they are commonly refused.

The situation of the feeding-ground at or more than 150 metres from the nearest danger point is also an adjustment, probably local, to human intervention. In the Firth of Forth large areas of Mussel-scalp, providing an abundance of food, lie too near the shore line owing to steepness of the gradient. These areas are seldom visited. When they occur near to or within a permanent winter station, they are visited only at night or in the early morning.

To most of the permanent stations in the Firth there are attached areas of wet sandy beach, generally lying close to the feeding-grounds. These areas are much used, especially after a spell of feeding, for the purpose of crowding together, preening and resting, and, in fine weather, for the sunning reaction. The presence of such an area is, however, not essential, for the condition is absent from the Lamb territory. The habit is not protective during the resting periods. The birds are very conspicuous while on the sand, whereas on the rocks or on mud, crowded with Mussels, they are often hard to distinguish. Crowding together appears to form an essential part of the habit. Owing to the irregularities of rocky areas and of mud-banks, dotted with clumps of Mussels, crowding can rarely be possible in these localities. A smooth expanse of sand is better adapted to the purpose. It is also possible the soft wet sand is a necessary condition of the response.

Along the Forth the Oystercatcher has few enemies, and even the depredations of man—the most important destructive

agent—have no apparent effect in the course of the season on the general mass of the birds. Comparative immunity is due to the wildness of the birds and to their extreme sensitiveness to the existence of potential dangers. Man, however, is himself an important condition of the environment. He has modified the local habits of the birds by leading to the establishment of refuges, and by limiting the number and size of the available feeding-grounds. The Peregrine is able to produce little more than a momentary commotion in the ranks of the Oystercatcher: no attack has been seen. The Sparrow-Hawk and the Kestrel are ignored. The Great Black-backed Gull is treated with some respect. The two species have not been seen very close together. No attack has come under observation. Throughout the winter the number of Oystercatchers in the area is not appreciably diminished, though there must always be the loss of a few.

The activities of the Oystercatcher are controlled in winter by the rhythm of the tides. The birds are slavish followers of the tideline. For about four hours during each period of high water the main supplies of food are inaccessible. As a consequence, the periods of rest and activity are determined by the tidal rhythm. There is also a rhythm of longer wave length dependent on the fortnightly oscillation of the tides. This rhythm is never manifest in early winter, but gradually appears in consequence of human interference. It shows itself by day, as a "reflex anticipation" of the greater height of the high water of spring tides. It is not due simply to the tide carrying the birds above the high-water mark of neap tides, for restlessness and the departure to the refuge occur long before the neap high-water mark is reached by the tide. The basis of the reaction is evidently complex.

It is doubtful if a true tidal habit, diurnal or bi-weekly, is ever established. No observations on this matter are possible on the shore. I have so far seen no sign of a tidal rhythm in the habits of the birds when they begin to move up the rivers where they breed. Diurnal rhythm is obscured in the winter environment of the Oystercatcher, the activities of the birds being regulated by the movement of the tides. Search for food continues after dark, and is evidently carried on much as in

daylight. The accumulation of excrement on the high-water mark of the night tide, when the latter reaches its highest point hours after darkness sets in, is sufficient evidence of night feeding, for the process of digestion and excretion in the Oystercatcher is extremely rapid. Darkness, however, has a restraining influence on nocturnal flight; for, whenever high water occurs in Aberlady Bay near the time of sunset, the birds, if disturbed, show unwillingness to fly to the refuge on Eyebroughty, and remain over the bay, prosecuting an aimless flight until the tide ebbs far enough to enable them to alight out of range. Further, by night the birds remain, so far as known, in the central parts of the feeding-grounds. They extend their feeding excursions to the more distant parts of their territory only in bright moonlight.

In winter the influence of variations in climatic conditions is mainly an indirect one, for the Oystercatcher is remarkably hardy, no extremes of temperature or humidity likely to occur in the Forth area seeming to have any harmful effect. Torrential rain inhibits all except compulsory movements, until the need of satisfying hunger becomes paramount. Really hard weather increases the food activities, at the same time suppressing all motor signs of the pleasure state. The appearance of the birds, however, never suggests a condition of "physiological misery." With the coming of the new year, moderately cold weather, if associated with bright sunshine, is favourable to early nuptial developments, while the mild weather of autumn brings out "autumnal genital activities."

Climatic control is exercised mainly over the available food supply. The Oystercatcher cannot open a Mussel when it is tightly closed, unless the byssal cleft can be reached, or the Mussel is small enough to be crushed. The former possibility rarely occurs; the latter seems to be dictated by necessity and not by preference. Extremes of temperature and moisture (bright sunshine, heavy rain, dry winds, hard frost) lead to an early and firm closure of the shell-valves of *Mytilus* soon after the Mussels emerge from the tide. The search for Mussels is then greatly restricted. The climatic aspect of the problem is important, for, so far from being a rare occurrence, weather conditions affect the food supply on almost every tide.

(To be continued.)

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(Continued from p. 291.)

IV.—The Summer Environment.

1. *General Considerations.*—The area which came under observation as a nesting habitat consisted of Loch Tummel; that portion of the valley of the River Tummel extending from Faskally to the junction of Tummel and Tay at Ballinluig; the Vale of Atholl between the villages of Blair and Killiecrankie; and the lower part of Glen Fender. Only the south shore and the foot of Loch Tummel were systematically observed.

The rocks of the area belong to the metamorphic series, and consist mainly of sedimentary limestones and schists, together with numerous igneous sills scattered all through the various schists.

The area forms part of a "land of ridges and broad valleys," the weather conditions being of the Atlantic type. From Loch Tummel to the junction of the Tummel and the Garry, the gradient is steep, and there are hardly any deposits of alluvium. At the junction is a series of terraces, covered with gravel and cut out of a thick deposit of boulder clay. Similar conditions prevail as far as Pitlochry. From this point to Ballinluig the gradient is slight, and the river has denuded the bottom of the ancient glacial lake, forming a large plain of alluvium. Between Blair and Killiecrankie the slope is considerable, but less than in higher parts of the Garry. Here large alluvial terraces have been formed. The hill-streams are mostly torrential in character, and deposit little alluvium. The lower portion of Strath Tummel is well wooded, while natural birch is general up to about 300 metres. The distribution of the human population is determined by the boulder clay deposits which favour arable

cultivation, and maintain a larger number of persons. Between Blair and Killiecrankie the drifts are a mixture of moraines and boulder clay. This area is occupied by numerous farms. On the north side of Loch Tummel there is an important deposit of boulder clay, which is largely farmed. The left bank of the Tummel below Faskally has large deposits of boulder clay, and is the chief area of arable cultivation in the valley. The alluvial plains of the Tummel lie more as pasture than under cultivation. Elsewhere there is a cold inferior soil suitable only for sheep pasture.

The meteorological data available come from Ochtertyre, Central Perthshire (90 metres above M. S. L.). The mean annual temperature is 8·16° ± 4·06° C.; the average rainfall for the year being 1·05 metres on 192 days (1871–1905). The mean monthly temperature and rainfall for April, May, and June are here given in the form of a table for Leith (sea-beach habitat) and Ochtertyre (*quasi* river valley habitat), for the sake of comparison.

Table 1, showing Average Monthly Temperature and Rainfall for April, May, and June at Leith and Ochtertyre (1871–1905).

Temperature.	April.	May.	June.
Ochtertyre...	7·13° ± 4·56°	10·05° ± 5·11°	13·44° ± 5·11°
Leith	7·31° ± 4·16°	10·05° ± 4·28°	13·28° ± 4·34°
Rainfall.			
Ochtertyre...	0·058 m.	0·060 m.	0·076 m.
Leith	0·036 m.	0·042 m.	0·049 m.

The breeding stations within the area examined fall into three distinct habitats—a hill-stream, a river valley, and a lake beach habitat. The Fender Burn is representative of the first, the Rivers Garry and Tummel of the second, and Loch Tummel of the third. A strong similarity exists among all the stations of each habitat, variability of the factors being much less pronounced than in the winter environment.

2. *Hill-stream Habitat.*—A general survey of the whole area made in 1909 showed that Oystercatchers do not nest along the

hill-streams in this locality. The occupation of Glen Fender appears to be due to a circumstance not forming an integral part of the environment of a hill-stream. The breeding territories extend along the glen for a distance of two kilometres from the top of the terminal gorge at 230 metres up to the 305 metres contour line. Within this course the stream is of small size and flows with a moderate gradient. Areas of shingle are few in number, and possibly too small to be serviceable for nesting purposes. The south bank, lying between the stream and the public road, has an average breadth of 450 metres, and lies mostly below the 305 metres line. It is a terrace, a steep slope joining the upper and lower levels. More than twelve years ago the south bank was densely wooded. The trees were felled, and the roots left in the ground to bleach. As grass grew, sheep were turned down. The conditions have remained unaltered to the present time. The ground is permanently wet in places. There is a moderate supply of Earthworms, and a fairly abundant supply of tipulid and coleopterous larvæ. The northern slopes of the glen have a thick deposit of boulder clay, and are cultivated below the 305 metres level. The arable land forms the general or distant feeding-ground, and provides a large part of the Earthworms required to feed the young. The rest of the glen is under heather and grass. Three pairs are cantoned along the south bank, which forms the local feeding-ground. The nesting-sites have not been seen. The tree-stumps are used as watchtowers, and for the sunning reaction. The roots, now of a light grey colour, form an important element in the crouching response of the chicks. The terraced nature of the ground is used successfully by both young and old in evading detection. The area is little disturbed.

3. *Lake-beach Habitat.*—Loch Tummel is a deep rock basin, 4·4 kilometres long. The shore descends steeply into the water, and is marked by a narrow fringe of angular boulders, resting on the mud substratum. At the east end, or foot, of the loch there is a storm-beach of light grey shingle, grading northwards into a fine sand-beach, and running upwards into the true lake margin of angular boulders. The storm-beach has a breadth of about 45 metres. A strip of uneven grass-grown ground, with a few trees, separates the beach from an alluvial plain which is

under cultivation. On the south shore of the loch, the Lochan a Chait, Frenich, and Cragan Dubh Burns have deposited cones of alluvium, in that order from east to west. The cones are margined by light grey shingle on the east and north aspects. Towards the west the shingle thins out into a scanty fine gravel, resting on the mud substratum. The shingle rarely exceeds 25 metres in breadth, and mostly is much narrower. The eastern cone forms an old enclosed pasture, and shows very well terracing into two levels. The large Frenich cone is under arable cultivation, which, however, leaves a broad strip of turf thinly planted with trees along its water margin. The western cone is very small, and consists entirely of natural turf, thinly sown with alders. Small sand-beaches are intercalated in the shingle at places. The water is fairly deep on the east side of the cones, shallow on the west, where mud-banks are forming which expose at low water, and become then, like the mud shore, more or less grass-grown. The true lake margin is not evident on the beaches of the cones. The hillside behind the southern shore shows heather and rock grading into natural birch and alder wood towards the west. The north bank of the loch is largely under arable cultivation. Within the area examined, nesting is confined to the storm-beach and the beaches of the alluvial cones. The ground behind the storm-beach and the turfed portions of the alluvial cones form the local feeding-grounds. The arable land at Frenich, Duntanlich, and on the north side of the loch form the general or distant feeding-grounds. From these, large quantities of Earthworms are brought to the young. The local feeding-grounds provide tipulid and coleopterous larvæ in plenty. The true lake margin has a large invertebrate population, but the beaches of the alluvial cones are deficient in this respect. The open spaces in the woods also contribute supplies. The whole of the breeding territories and local feeding-grounds lie considerably below the 152 metres contour line. A large sand-bank at the head of the loch, and a boulder area on the north shore, near the exit of the loch, are used every year by the birds that have failed to breed as places of assembly for bathing, sunning, and other activities.

4. *River-valley Habitat.*—A. *The River Garry.* The river in the four kilometres of its course between Blair and Killiecrankie

falls about 15 metres from an elevation of about 120 metres at the former place, and describes two major curves bordering extensive alluvial plains. The beds of shingle are fairly large, and composed of a light grey, water-worn stone of moderate size. The Strath is well farmed and populous. The river side is easy of access to the public. The resident stock has been much harassed and rarely succeeds in breeding on the shingle. The birds have taken to nesting away from the river on naked moraines, other collections of stones, and, in at least one instance, on the ballast of the railway track.* All the breeding territories and local feeding-grounds lie below the 152 metres contour line.

B. *The River Tummel.* Between Faskally and Ballinluig the Tummel is a pool, rapids river of considerable size. Above Pitlochry it flows through a narrow glen, ending in a rocky gorge. At Faskally there are broad river terraces, fringed by a bank of shingle, composed of light grey stones of moderate size, and rising at least one metre above summer water-level. The Faskally terraces show two main levels, an upper and a lower, and are in pasture. At Clunie there is a crescentic band of shingle backed by a steep wooded slope. From Pitlochry to Ballinluig the gradient is gentle (about 1 in 400), and the river has formed "a large flat of alluvium." The plain has been cut by the river into cones. These are fringed with light grey shingle, which spreads out into larger areas, or banks below the cones, the size of the areas increasing from above downwards, and culminating in the relatively vast area of shingle running alongside Logierait Wood, on the right bank of the river. The cones are entirely in pasture, or the basal portions are cultivated. The hill slopes on the left bank, being covered largely with boulder clay and having a south-western exposure, are mainly under cultivation. The slopes on the right bank are little farmed, being mostly in natural grass, or, as in the lower reaches, densely planted with wood.

Nine stations in all were recognized and kept under observation between Faskally and Ballinluig. They have not, however, an equal value for population, the numbers varying from one

* This happened above Blair.

pair to ten or more pairs in each station. Denoted by the nearest place-name on the map, they are, from above downwards, Faskally, Clunie, Pitlochry, Black Spout, Dunavourd, Haugh, Moulinearn, Logierait Wood, and Ballinluig. (Ballinluig Island is here included in the Logierait station.)

Faskally has already been described. It is quite a typically favourable river station, having a fairly large and high shingle-bed, well secured from intrusion; a terraced local feeding-ground in pasture; and general or distant feeding-grounds which, however, are rather far away. The Clunie area is much disturbed, and is backed directly by a steep, wooded bank. No young birds have been seen here. The Pitlochry station is the first of the large areas, the extensive and high bank of shingle being centred by a small grassy island with a few pine trees. The cone is beautifully terraced, and is in pasture. It now forms a public park. No birds breed here. The Black Spout and Dunavourd areas are similar to Faskally in all respects, except that general feeding-grounds are not far away. Dunavourd ceased to be occupied when the pasture of the local feeding-ground was ploughed. The Haugh station, though very large, has a simple composition. There is an extensive and high bank of shingle containing a grassy island. The alluvial flat has considerable extent, is obscurely terraced. Most of it is pasture, but portions farthest from the river are under cultivation. The area is much disturbed by the human population. Moulinearn and Logierait are large stations with diverse features. A more intensive examination will probably break them up into several distinctive areas. The upper part of the Moulinearn margin is composed of large stones having more an appearance of moraine than of river shingle. It grades into a belt of true shingle, which spreads out into a large area of shingle below the alluvial cone. The latter is mainly in pasture, distinctly terraced, and marked with clumps of whins, shallow irregular mud-pits and sand-bunkers. The basal part is cultivated, and there is a back-water with wide, muddy margins. The Logierait area measures over 1600 metres in length by 400 metres in breadth. The upper part is a terraced alluvial cone in pasture with a shingle fringe of considerable size. At the extreme north-western corner, what appears to be morainic material, similar to that found at

Moulinearn, is occupied by a small settlement. Below the alluvial cone the shingle forms a broad belt, backed by the steep wooded slope of Logierait, and margined by three wooded islands. These islands form local feeding-grounds. The uppermost is a dense, natural wood, with wet sand-gullies and pot-holes gouged out of the substratum by the winter floods. The lower islands are flat, grass-grown and artificially wooded. The Ballinluig area presents a sequence of appearances very similar to that of Moulinearn. It also contains a plateau planted with pines and having a turf layer on a clay substratum. This station is of moderate size, and is subject to considerable disturbance.

The whole of the breeding territories and local feeding-grounds lie between 60 and 105 metres above sea-level. The 76 metres contour line crosses the river at the upper part of the Haugh area.

Nesting is mostly confined to the shingle. At Moulinearn and Ballinluig, however, more nests are seen on mud and turf, due in the former place probably to carting of stones, and in the latter to other human interference. Nesting far from the river is rare. One instance came under notice. Towards the end of June a chick, a few days old, was seen on the hillside above Dunfallandy House. The chick must have belonged to a second, or possibly a third, laying.

The shingle shows few living invertebrate forms. At the time of the hatch, and possibly at other times, large quantities of Stonefly nymphs are to be found under stones at the water margin. These nymphs are fed extensively to the young during the early days. The local feeding-grounds, where in pasture and open to examination, are rich in tipulid and coleopterous larvæ. The bulk of the worms comes from the arable land. Only the upper Logierait wooded island was examined. The substratum is sandy. Where the sand was dry, the nature of the food supply observed to be got by the birds could not be determined. The wet sand of the gullies and pot-holes contained an abundance of worms of sand and silt bottom formation.

(To be continued.)

THE RELATION OF THE OYSTERCATCHER TO ITS NATURAL ENVIRONMENT.

By J. M. Dewar, M.D.

(Continued from p. 346.)

V.—Discussion of the Summer Environment.

The conditions common to most of the stations of the summer habitats are the following: a body of fresh water, a breeding area of water-worn shingle, composed of light grey stones of medium or small size, the area being adjacent to water, raised above the level of summer floods, and fairly well-preserved from human intrusion; a local feeding-ground to which there is easy access for the young on foot, rich in tipulid and coleopterous larvæ, and with at least a moderate supply of large earthworms; a more distant feeding-ground of cultivated land, accessible to the adults, and richly stocked with large earthworms.

The first condition is an essential requirement and is used in many ways, of which the act of drinking is only one. Both the adults and the young bathe in the water, and stand in it by the hour. A large still body of water, or a narrow deep or quickly flowing stream, safeguards one border of the breeding area from intrusion, and favours the detection of approaching danger. The young in danger frequently crouch in shallow water among stones, and in the last resort swim boldly out on the open lake or across narrow and not too rapid streams. In the river settlements especially, a portion of the food supply for the young is got from the shallow waterside.

Shingle does not form a necessary condition of the breeding area. It is absent from North Holland where the birds nest commonly on areas of grey mud, as do most of the birds in the Moulinearn Settlement, while at Ballinluig nesting on turf under trees is common. On shingle, however, the eggs and young are incomparably harder to find than on any other substratum used

in this locality. At Moulinearn and Ballinluig the young are led to the shingle soon after they leave the nest, and thenceforth the shingle forms both their refuge and resting place. The eggs laid on mud or turf are not better protected by their surroundings than they would be on shingle, but in disturbed areas they have a better chance of escaping human observation which, by tradition or personal experience, tends to be concentrated on the shingle. The young get the benefit of the shingle even in disturbed areas, because, unlike the eggs, they can occupy positions likely to evade detection on the approach of danger. And in all the stations examined, with the exception of those in the hill-stream habitat and in the aberrant area of the Garry, the shingle forms the headquarters of the young. In wet weather, however, the shingle looks almost black. The eggs and young then show up more distinctly. But the deficiency has less importance than it seems to have. The adults, which stand out conspicuously from the dry light grey shingle, assimilate more or less completely to the shade of the wet stones, and during wet weather the parents are covering either the eggs or the young. After a short exposure to rain the wetting of the outer down changes its hue from light greyish to drab. The young then approach in shade that of the wet stones.

Evidently the essential requirement of a breeding territory is an open area of sufficient extent, and approximating in colour appearance to that of the eggs and young. These conditions are best fulfilled by shingle devoid of vegetation. The bareness of the normal breeding territory has, however, a wider significance. After the young are hatched, and for several weeks to come, they are prevented by the parents from going among wet grass when the temperature is low. The combination of moisture and low temperature occurs regularly in the early morning, and occasionally through the daytime as well. The chicks are compelled to remain on the shingle where, though the stones may be wet, the chicks at least remain dry. The proceeding must have attached to it a pronounced biological advantage, for I have repeatedly seen hungry chicks which have already learnt the association of the position of the feeding-ground with the act of being fed, trying to entice the adults to follow or lead them on to the wet grass to be fed. A second result of the bareness

of the nesting area is the poverty it shows of animal food. The normal hatching of the chicks coincides with the presence of large numbers of Stonefly nymphs under the stones at the water's edge. These nymphs are fed extensively to the young soon after they leave the nest. Beyond this the breeding area contributes little or nothing to the feeding of the young, and the need is insistent for an additional area capable of supplying the food required. In all the occupied areas the shingle or mud stands high enough to be above the probable level of spring and summer floods. It matters little for the young, but it may be serious enough for the eggs. Evidence is not awanting to show that the nesting activities in relation to water level are adjusted to the normal breeding time only. When a second laying becomes necessary, adjustment is not so accurate.

On the shingle nesting and the rearing of young are confined to those parts where the stones are not larger than the eggs. The stones may, however, be much smaller—little more indeed than fine gravel—without preventing nests being formed and eggs laid. But wherever the stones are considerably larger than the eggs nesting does not occur, unless there are islets of smaller stones amongst the larger. These islets are used occasionally, even though little larger in area than the nest itself. But the protection afforded to the nest by the substratum is inadequate, for the nest, together with the clutch, break the monotony of the general surface, and are fairly easily found. Though the young, in the act of crouching, may respond to a larger boulder by moving up against it, they invariably rest on shingle not larger and often smaller than themselves, and the bulk of their activities, within the breeding territory, is confined to areas of shingle whose components are of medium or small size.

On the River Lyon a pair of Oystercatchers breed successfully on a small shingle island near Chesthill. The island is wholly devoid of vegetation, and completely isolated by turbulent rapids. The history of the settlement was not worked out. But the difficulty of evoking the crouching reponse of the young from the mainland, and the comparative indifference of the adults to one's presence, render it unlikely that the young are not born and bred on the island. Thus a local feeding-ground, accessible to the young, is not a necessary condition of the

summer environment. In all the other stations, with the exception of Clunie, where eggs have not been known to hatch, a local feeding-ground is present, and may, therefore, be regarded as having great ecological value.

The most valuable conditions of the local feeding-ground are the presence of a large stock of tipulid and beetle larvæ, and comparative freedom from human intrusion. The conditions are best fulfilled by fenced-in old pastures. Ground of this nature is attached to most of the breeding areas. On the Orchy, however, it is absent, and the grassy river-bank takes its place. The great value of an area of old turf is made evident by the history of the Dunavourd territory, where the breeding territory ceased to be occupied whenever the old pasture was ploughed. Occasionally arable land forms the local feeding-ground. In the middle Logerait settlement, and on a shingle island in the River Lyon near Chesthill, wooded islands are the only available local feeding-grounds. The upper island at Logerait and the island at Chesthill are apparently of natural origin, and provide a different food supply for the young from that occurring in the normal feeding-ground. The fauna of the ground strata of the naturally wooded islands appears to be that of the flood-plain forest association.

The third area of a favourable station—the general or distant feeding-ground—has, as its chief functions, the feeding of the adults and the supply of large earthworms for the young. For the latter purpose cultivated land is best adapted. Cultivated land adjoins all the breeding areas of the Tummel, Garry and Fender. Under certain conditions (*e.g.* drought) the young receive very little food from farm land. Arable soil is practically absent from Upper Glenlyon, and from Glenorchy above the Bridge of Orchy. It is, therefore, not essential. But the distribution of the birds shows that, wherever the unproductive hillside takes the place of cultivated land, a much larger area is required to support the same number of birds. The occurrence of cultivated land in the environment is, of course, a secondary condition. It is possible the distribution of the boulder clay, and especially its presence on south-western exposures, favoured the settlement of the earthworm, and thus effected a primitive control over the distribution of the Oystercatcher population,

and cultivation, by still further favouring the earthworm, only confirmed the process.

Summing up the essential conditions of the breeding habitat, we have: a sheet or stream of water; a nesting area to which the eggs, and more especially the young, have a protective resemblance; a general feeding-ground accessible for the adults and providing a large supply of earthworms; comparative immunity from enemies in the breeding territory. A local feeding-ground is of so general occurrence, that it may be regarded as approaching the essential. The requirements here are accessibility for the young, a large stock of tipulid and coleopterous larvæ, and a certain freedom from disturbance.

In summer enemies have a greater influence than in winter. Most injury is wrought before the end of incubation. So much is this the case that, if only the young can be hatched, they have a very good chance of reaching the stage of flight. Most destruction is caused by man. He takes the eggs, while youths, as I have observed, stone the young. The adult birds do not suffer in themselves through the agency of man. On the contrary, they benefit, as I have shown. In nesting areas, to which sheep and cattle have access, the eggs may be trodden upon. On one occasion I witnessed the actual event: on another I found a nest containing crushed and flattened eggs, to account for whose state cattle were the most likely explanation. The young do not appear to suffer from these animals. But they may come to grief from the chance step of a human being, as then the adult birds do not interrupt the special means which serve as stimuli for the crouching reaction. Without disturbing the crouching response in the least degree, I have abraded the skin of a chick which I failed to see in time to avoid the accident. The Buzzard causes a good deal of commotion, but has not been seen to attack the young. The Sparrowhawk, Kestrel, and Merlin produce little effect. The Lesser Black-backed Gull, as it sails over the breeding area, has a profound influence upon the situation. The young Oystercatchers crouch at once in response to the warning call of the adults, which, thereafter, stand absolutely still in dumb watchfulness. No attack has been observed. The Black-headed Gull, which often tries to snatch away the young of the Ringed Plover and Lapwing, has been observed to threaten only the very young Oystercatcher. The effect of ground vermin is not known. But no eggs or young under observation have disappeared without the disappearance being accounted for, at least as well, in other ways.

In the breeding season, so far as one is able to judge, the succession of day and night is a factor, but not an important one, in regulating the activities of the birds. The diurnal cycle is rather complex, but it may be summed up as a periodic alternation of rest and activity, the latter being of two kinds—nuptial or social, and food activities. It should, however, be understood that these periods are not simply periods of rest and activity. All that can be said is that in one period the resting phase predominates, in the next the active phase, and so on alternately. The period of greatest darkness lasts from about 11 p.m. to 1 a.m. Contrary to what one might expect, it is not a period of rest but is rather a period of the wildest activity, and that apparently not of food-getting, but nuptial. Activity continues till 4 a.m., but it passes gradually into food-getting for both adults and young. After 4 a.m. the sun begins to diffuse an appreciable warmth. Activities lessen, and a quiescent period appears which lasts till 10 a.m. During the earlier part of this period most of the "apparent" sleep is obtained. Ten a.m. till 2 p.m. is a fairly active period, devoted mostly to food-getting. From 2 p.m. till about 6 p.m. the birds are mostly resting except for occasional and short-lived storms of either kind of activity. After 6 p.m. the birds are really active, at first in getting food for themselves and the young, and then, by degrees, the feeding activity is interrupted by the nuptial activities which later work up into the fully developed midnight orgy. Such is in general outline the diurnal rhythm of the Oystercatcher at an inland breeding station. Exceptional features, of course, occur at any hour and place, and very frequently the normal rhythm is entirely upset. On very dark nights all activities, so far as one can then determine, are suspended for the hour or so of greatest darkness. On very clear nights many birds (? barren) leave the breeding areas and make extended journeys into the hills, where they are not seen in the daytime.

It will be observed that the two periods of rest coincide, the

one with the period in which the warmth of the sun is first beginning to be felt after the cold of the early morning, and the other with the period in which the heat of the sun is most fully developed, and that the two chief periods of food-activity, that is morning and evening, coincide with the periods of greatest activity in the earthworm. It is probable that the periods of rest have become rhythmic habits, at least during the breeding season, for they appear even when the weather is cold and wet.

In the breeding quarters the variations of temperature, occurring in May and June, have no apparent effect on food-supply; any disturbance that takes place being due more probably to the other climatic conditions commonly associated with temperature extremes. In hot weather the adults may become dull and listless, but the condition does not last long owing to the frequent recurrence of food—and other activities. The chill of night has evidently no more than a bracing effect on the birds. One instance of "physiological misery" has come under notice. An adult, after a spell of food-getting for the young in the early morning, bathed about 4 a.m., and then went to "apparent" sleep. The rigor which followed lasted a considerable time. The young bear wide variations of temperature with equanimity. During the first two days of life they are very sensitive to cold, and are covered almost continuously. Thereafter, they have to rub along on all sorts of days without additional warmth, except during the coldest part of the night. They seem indifferent to hot sunshine, and I have not seen them shelter under the wings of the parent when the sun is particularly hot, as young Lapwings do in similar conditions.

In summer no injurious effect of excessive moisture on adults or young was discovered. Both are extremely hardy, and they then enjoy an abundance of food, especially of earthworms. Drought reduces the supply of these both for the adults and the young. Worms may even be unobtainable. If worms cannot be got, efforts are rarely made to bring other food from the distant feeding grounds, and prodigious exertions are evoked to supply the wants from the feeding area attached to the nesting quarters. The sun-baked ground is hammered and pickaxed with the powerful bills, the parents working feverishly, and for long periods at a time, to supply the necessary quantity of food

for the young. Occasionally, young have been seen to manifest signs of more than passing hunger owing to the drought-induced dearth of earthworms and the difficulty of getting other supplies. But in no observed instance have the young appeared to suffer permanently in consequence of the shortage.

VI.—The Choice of a Nesting-Site.

In the choice of a nesting-site which is placed near a body of water, an important factor must be the relation existing between the position of the nest and the level of the water at the time of building, and any possible rise in the level of the water during the subsequent period of laying and incubation. In the river-valley habitat the nests are formed on the highest part of the banks of shingle, and in the case of the semilunar beds, which form on the convexities of the alluvial cones, the nests are laid on the longitudinal ridge which has formed in the shingle, a short distance from the grass bank. In the lake-shore habitat, as represented by Loch Tummel, the problem does not appear to be so simple. The beach of the alluvial cones has, for the most part, an even gradient from the water-edge up to the grass. The nests, as a rule, are formed on, or about, the highest winter water-mark. But in places the mark is not evident, and apparently is not detected by the birds. In other parts the high-level mark reaches up over the grass. Where this happens, the nests are formed on the shingle within a half to one metre of the bank. It is probable that, in the choice of a nesting-site in this locality, the adjustment of the bird to the environment is more perfect at the normal period of laying than it is at a later time. This may be put in another way by saying that the normal period of laying occurs at a time when the level of the loch is already low and still falling. At a later period the loch is either at bottom level or has actually begun to rise. At the former period the choice of a nesting-site is stereotyped, appropriate to the local conditions, and successful. At the later period the birds respond with the stereotyped reaction to conditions which are essentially, though not obviously, different from the normal, and which day by day may depart still further from the normal.

(To be continued.)

THE RELATION OF THE OYSTERCATCHER TO ITS NATURAL ENVIRONMENT.

By J. M. Dewar, M.D.

(Continued from p. 383.)

In North Perthshire the average monthly rainfall shows a progressive increase in amount through April, May, and June, the first being the driest month of the year. In April and May the rainfall tends to be evenly distributed over each month, and the water is largely absorbed by the soil. In June the greater rainfall is apt to be concentrated into torrential downpours, and most of the water runs directly off the land into the streams. The loch faithfully registers the increase and the changed character of the rainfall. In April and May the level is falling. Towards the end of May the loch is at bottom level. With the entry of June it begins to rise more or less quickly, according as the rainfall is above or below the average, and is, or is not, torrential in character. The fall and subsequent rise of the loch were well marked in May and June, 1912, the first half of June being excessively wet. At the time of the first laying in the beginning of May, 1912, the level of the loch was 0·6 metre below the winter high-water mark. The level fell another 0·3 metre in the course of May. From June 10th to 17th the water rose 0·7 metre. From this date the level of the loch fell irregularly. Data were obtained for four pairs in as many territories. In one instance the first laying was unknown. In the other three instances both the first and second layings were under observation. The first layings took place in the beginning of May, and all came to grief from various causes. The second layings occurred in the end of May and beginning of June. The relation of the seven nests to the level of the water, and the subsequent histories of the second layings, proved highly interesting. The results are given in the form of a table which is subjoined. The measurements are distances, no means being available to measure the heights of the nests above water-level. The fall of the loch was determined on two posts by the water-marks visible in the end of May. The subsequent rise was anticipated by marking the posts from the observed lowest water-level.

Table 2, Showing Positions of First and Second Nests of each Pair Relative to Water-Level: Loch Tummel, 1912.

Nest A^1 (unknown)	A^2 Below winter H.W.M. 0·9 m. Above water-level, time of laying ... ... 6·4 m.
Nest B^1 Above winter H.W.M. 1·2 m. Above water-level, time of laying ... ... 6·7 m.	B^2 Below winter H.W.M. 2·1 m. Above water-level, time of laying ... ... 6·1 m.
Nest C^1 Above winter H.W.M. ? Above water-level, time of laying ... ... 6·4 m.	C^2 Above winter H.W.M. ? Above water-level, time of laying ... ... 6·4 m.
Nest D^1 On winter H.W.M. Above water-level, time of laying ... ... 6·85 m.	D^2 On winter H.W.M. Above water-level, time of laying ... ... 10 m.

Remarks.—At A^2 the winter high water-mark passed along the grass bank slightly above the shingle. On June 15th, 1912, the bird was flushed from the nest, which contained a pool of water. The margin of the loch was not far from the rim of the nest, the height of which was subsequently fixed at 0·74 m. above water-level at the time of laying. This bird converted the nest hollow into a platform 0·03 m. higher than its surroundings, and continued to incubate. The danger was past after the 17th, and the bird continued to sit. At B^1 and B^2 the position of the winter high water-mark was fixed with difficulty, there being no drift. The second nest was 3·35 m. further down the shore than the first, but the two nests were both situated at similar distances from the water-levels at the respective times of laying. The height of B^2 was later fixed at 0·66 m.; that of B^1 was +0·9 m. above bottom level. On June 17th, 1912, B^2 was drowned out and deserted, being 0·05 m. under water. At C^1 and C^2 the position of the winter high water-mark could not be determined, but judging from collateral evidence both nests were considered to be much above that level. Both nests were equidistant from the water-levels at the time of laying. C^2 escaped the highest flood-level of June 17th with a good margin, the calculated height above bottom level

being 0·96 m. At D^1 and D^2 the winter high water-line was marked by a large quantity of small flood rubbish. Both nests were laid on this line, D^1 slightly above, D^2 slightly below, its centre. D^2 was in no danger, being 0·9 m. above bottom level.

It is evident from the history of these nests that, in any further observations on the choice of nesting site, distance from the water will have to be considered along with height above water. The D^1, D^2 nests lead one to expect that flood rubbish, when it is present, controls the tendency to follow the descent of the level of the water. The main point, however, which it is desired to bring out has already been stated, and may here be repeated, that the stereotyped behaviour appropriate to the normal laying period, when the rainfall is small and fairly uniform and the level of the loch is sinking, is not so successful in controlling the situation in the different environmental conditions of a later abnormal laying period when the rainfull has increased and the level of the loch is rising.

VII.—The Law of Territory.

Each settlement on the south shore of the Forth has an habitual range which it rarely exceeds. Individual settlements have not been known to trespass on each other's feeding-grounds for the purpose of feeding. It is remarkable that from winter to winter the position and total areas of the several territories show no change, and that the occupants of each territory have a similar routine of activities year after year. It has not been found possible to point to any general or specific variation of behaviour, relative to the environment, by comparing the observations of one year with those of another (1906–1914). All the settlements under observation in the Firth of Forth have, in each case, a refuge which is also the headquarters of the station. In places where the refuge is not resorted to at every high water (neap tides, nocturnal high water) and in localities where no refuge is available or necessary, a certain part of the beach, on the high water-mark, is constantly used in preference to other parts as a resting place during high water, and therefore may be regarded as the headquarters. In the Forth the territories are well-defined owing to the intervention of broad bands of neutral shore having little food value. The more

intimate nature of the probable inter-relations of the settlements of a district has been observed in the Aberlady district. The Aberlady, Eyebroughty and Lamb stocks have never been known to visit each other's feeding-grounds for food. The Aberlady and Eyebroughty stocks share Eyebroughty, as a refuge. On one occasion a shooting party was landed on Eyebroughty towards the time of high water, the boat which brought them being sailed about in the vicinity. The Eyebroughty settlement anticipated the boat's arrival by proceeding towards the Lamb, on which they were observed through field-glasses to alight, and where they evidently remained. The Aberlady Bay waders arrived shortly after at Eyebroughty, and were unable to land. They did not proceed to the Lamb, but flew round and round high over Eyebroughty for nearly two hours, until the ebb of the tide allowed them to return and alight safely in Aberlady Bay. After Christmas, when the first signs of nuptial activities begin to appear, visits are exchanged between the Aberlady and Eyebroughty settlements, and between the latter and the Lamb settlement; but, so far as known, never between Aberlady and the Lamb.

As a possible indication of the need of controlling the food-supply for the welfare of the settlement, by maintaining territorial rights, there may be cited the results of a periodical examination of the sizes of shells opened by the Oystercatchers at the Eyebroughty station in the course of winters 1908–1909, 1911, and 1912. The results suggest that, in this area at least, the food-supply is subjected to a considerable strain in meeting the needs of the settlement.

In the Eyebroughty area the average and largest sizes of the mussels showed a continuous fall in the course of the winter 1908–9.

Table 3, Showing Seasonal Diminution in Size of Opened Shells of Mytilus from "Mussel-Rocks," Eyebroughty: Winter 1908–9.

Date.	Number.	Average.	Largest Shell.
Oct. 29th, 1908	10	3·1×1·4 cm.	3·7 cm. long
Nov. 16th, 1908	23	2·25×1·0 cm.	2·8 cm. long
Jan. 4th, 1909	....	...	2·5 cm. long
Jan. 26th, 1909	....	...	1·9 cm. long

A considerable proportion of the food-supply at Eyebroughty is derived from the oil-shales in the bay west of Weak Law. The collections made here in the course of the winters 1911 and 1912 show a steady seasonal fall in the sizes of *Tapes* and *Modiolus*, and confirm the results for *Mytilus* in the same area.

Table 4, Showing the Seasonal Diminution in Sizes of Opened Shells of Modiolus and Tapes from "Shales," Eyebroughty: Winter 1911–1912.

	Modiolus.		Tapes.	
Date.	*No.*	*Average.*	*No.*	*Average.*
Nov. 30th, 1911	8	5·0×2·5 cm.	6	3·0×2·3 cm.
Dec. 11th, 1911	...	...	6	2·6×2·2 cm.
Dec. 26th, 1911	8	2·8×1·55 cm.	...	...
Dec. 27th, 1911	...	...	32	2·4×1·5 cm.
Nov. 18th, 1912	13	4·9×2·4 cm.	...	...
Nov. 28th, 1912	...	...	20	2·6×2·0 cm.
Dec. 12th, 1912	...	...	15	2·3×1·7 cm.
Dec. 17th, 1912	38	2·3×1·3 cm.	...	...

The Limpets are more abundant on the shales than are *Tapes* and *Modiolus*. Though they are largely fed upon, the Limpets show great recuperative powers. Grouped in the two fortnightly periods for November, 1912, the results do not show an appreciable change. When, however, separate returns are taken from a fortnightly feeding period, a gradual fall appears in the averages.

Table 5, Showing Seasonal Average Sizes of Limpets fed upon by Oystercatcher: "Shales," Eyebroughty, November, 1912.

Date.	Number.	Average.
November 15th, 1912	53	2·2 × 1·5 cm.
November 28th, 1912	66	2·0 × 1·5 cm.
November 12th, 1912	8	2·7 × 2·0 cm.
November 14th, 1912	24	2·3 × 1·4 cm.
November 18th, 1912	19	1·9 × 1·5 cm.

In the summer habitats each pair has an habitual range in a nesting area and in a local feeding-ground. The boundaries, where the range of one pair meets those of adjacent pairs, are elastic; depending, in part, on the presence or absence, at the moment, of the adjoining pairs. Each station, composed of the breeding area and the local feeding-ground, has a headquarters generally, but not always, situated on a small eminence between the two areas. At the headquarters the birds keep watch and issue challenges. All other birds of the species are driven from the breeding area and the local feeding-ground. The territorial arrangements show no change from year to year (1909–1914). The young at first do not have an habitual range. Where two territories adjoin, the young of one territory are apt to wander into the other until they are called back by their parents or driven away by the other pair. The general or distant (neutral) feeding-ground is apparently common property. All the birds of a district appear to be free of the arable land near the breeding territories, and mingle without signs of hostility. It is, however, probable that closer observation would show that each bird has an habitual range in the general feeding-ground, though there is no apparent tendency to exclude other birds from its range.

Thus the main requirement of the Law of Territory, enunciated by H. Eliot Howard, is fulfilled in the summer environment of the Oystercatcher. The law should be extended to apply to the birds in winter, as they then have territories, though no opportunity has come under notice of a territory needing to be defended against intruders. The mode of acquiring the winter territory is unknown. In summer, the method differs from that observed by Howard in British Warblers, as Seton Gordon records that the birds ascend the rivers in pairs. My own observations indicate pairing to take place on the sea-coast. The subsequent course of events nearer the breeding territories is not known. Howard's view that the possession of territories is a biological advantage both to the individual and the species, by securing an adequate, and no more than an adequate, supply of food, is borne out by the general evidence derived from the areas under observation, and by the results obtained at Eyebroughty.*

(To be concluded.)

* H. Eliot Howard, 'The British Warblers,' part iii., 1909; Part v., 1910; Part ix., 1914. Seton Gordon, 'Birds of the Loch and Mountain,' p. 97.

THE RELATION OF THE OYSTERCATCHER TO ITS NATURAL ENVIRONMENT.

By J. M. Dewar, M.D.

(Concluded from p. 431.)

VIII.—The Optimum Habitat in Winter.

On the south side of the Firth of Forth three areas carry large stocks of Oystercatchers. These areas are chiefly, or entirely, mud-flat habitats. The remaining four areas, coming under observation, are rock-beach habitats, and they carry small stocks. As it has not been possible to determine the total quantity of Mussels available in each area; and as periodic estimations of the numbers in each stock, excepting those of the small stocks, proved disappointingly variable, the direct method of comparing the numbers of the birds with the size of the *Mytilus* areas, where they feed, could not be used. Recourse was had to other means.

I have elsewhere * stated, from fairly extended observations, that the Oystercatcher is unable to open tightly-shut Mussels, unless it can reach the byssal cleft, or the Mussels are small enough to be crushed. The former possibility occurs infrequently, Mussels opened through the straight border forming only nine per cent. of the opened shells examined. The latter is apparently avoided, whenever possible, and the birds reject Mussel-flesh mixed with fragments of shell. Dryness of the surroundings brings about a tight closure of the shells, and follows shortly after the tide has receded from the scalps. The birds are then confined in their search to the tide-line, pools, under seaweed, and under mud near the scalps; a hunt for Mussels presenting the straight border, and the hammering of small Mussels being evidently the last resort. Mussels that become covered with mud are soon killed, and are never numerous; their presence under seaweed is accidental; while *Mytilus* is predominantly not a pool-dwelling form in the littoral zone. The principal search must, therefore, be confined to the margin of the tide.

From these considerations it is evident that the ultimate bearing capacity of a *Mytilus* station is directly determined by

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the quantity of Mussels available in the water margin during successive phases of the tide, and not by the total number of Mussels on the station; and that, other things being equal, the longer, that is, the more sinuous the contour lines, and the more shallow the gradients of the station—the greater the number of Oystercatchers a given area will support. These requirements are fulfilled better by the mud-flat than by the rock-beach habitat. In the former, the presence of banks and the extreme shallowness of the gradients cause a comparatively large area of the Mussel-scalp to be kept in a moist condition at all states of the tide within the *Mytilus* zone. As a result, the birds have not only a long contour line along which they can extend, but also, owing to the great breadth of shallow water, they can work over a greater area, and in several rows, or even in masses. In general, contrary conditions prevail on the rock-beach. The greater steepness of the gradients and the shortness of the contour lines narrow and reduce the length of the zone available at a given time, so that it is unusual to observe the birds in more than single file in the tide-line, after drying of the exposed Mussels. Other circumstances favour the mud-flat habitat. The Mussels run to larger sizes than on the rock-beach, and provide a greater proportion of those sizes most usually taken by the Oystercatcher. The exposure to the effect of storms is negligible on the mud-flat. Wave-action here does not interrupt the operations of the birds. The rock-beach has mostly a great, or severe, exposure to storms, and in bad weather, which in winter may last for days, wave-action interferes with search in the tide-line, and in some places may render whole feeding-grounds entirely inaccessible. Exposure of the rock-beach to severe wave-action is a necessity for the existence of *Mytilus*, for wherever the rocks occupy sheltered positions, the growth of weed is excessive and Mussels are absent. The mud-flat habitat is not drawn upon by Diving Ducks, which devour large quantities of Mussels on the rock-beach habitat; there being here a different time-distribution in the community, the Ducks operating towards high water and the Oystercatcher towards low water on the same feeding-grounds. Owing to the great area exposed on the ebb and the uniformity of the surface, the mud-flat is more favourable to the Oystercatcher in regard to human in-

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On these grounds the mud-flat is regarded as an optimum habitat of the Oystercatcher, on the south shore of the Firth of Forth, in so far as food activities are concerned. It is obvious, however, that a mud-flat will not form an optimum habitat in a district having a large human population, unless it has attached to it a place of refuge, available during high water and at other times, when the feeding-grounds are disturbed. There are other non-essential conditions of which one—the wet sand-beach—has been definitely recognized.

In more general terms, the conditions of an optimum habitat in winter are: (1) a body of sea-water; (2) edible Mussels in sufficient quantity and of a suitable size (mostly not under 2·5 cm. in length), stationed on an area which has shallow gradients and sinuous contour lines, and which is not exposed to severe wave-action; (3) areas of soft wet sand near to the feeding-grounds, attractive in connection with the crowding and other reactions. Wherever the presence of man makes itself felt, there fall to be added: (4) separation of the feeding-grounds from the nearest potential source of danger by a distance of, at least, 150 metres; and (5) a place of refuge which is not too far away, and affords a considerable amount of security during the period of high water, and in the event of human disturbance of the feeding-grounds.

In the Firth of Forth, the large human population of its banks is, on the whole, adverse to the Oystercatcher as a species. Extensive feeding-grounds exist on both shores, which are seldom visited, and which, as far as can be seen, would adequately support a larger stock of birds than that, at present, inhabiting the whole estuary. The destruction wrought each winter on the resident stocks is so slight as to be imperceptible in the mass. This fortunate circumstance is solely due to the fact that the territories, which are inhabited, provide the conditions which make it very difficult to bring the birds within range of the gun.

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The River Orchy is a fairly large river with large areas of light grey shingle. The glen is open and is occupied by a very small human population. The soil is inferior and suitable only for sheep-pasture. There is little cultivation. The birds, therefore, have to depend on the river banks and the hillside for their feeding-grounds. The supply of worms and larvæ is not so plentiful as it is on the Tummel.

The hill-stream habitat comes next in an ascending order. Its low grade value is probably due to elevation above sea-level (230–305 metres), which certainly restricts the area under cultivation, and probably affects the supply of worms and larvæ as well. The local feeding-ground comes within the normal range of the Curlew, and much of the area being marshy, there is also a large number of Snipe. Both of these birds compete with the Oystercatcher in the subterranean ground stratum of the local feeding-ground. The hill-stream habitat is peculiar in the sense that it owes its occupation by the Oystercatcher, not, it would appear, to the presence of the Fender Burn and other common elements of an occupied station, but to the large number of bleached tree-stumps scattered over the local feeding-ground. The young assimilate in colour to these stumps, which are frequently associated with the crouching response. The stumps also contribute to the food supply. The area has great breadth, and the shingle-beds in the burn course are small. The young are led much greater distances away from the shingle than is usual in other stations, and the reason which makes this possible appears to be, the tree-stumps afford protection to the young,

which especially as they grow older, seldom retreat to the shingle in the event of human or other intrusion. A later stage of the same kind of area is seen on the Cragan Dubh alluvial cone on the south side of Loch Tummel. Here the local feeding-ground on the cone is dotted over with mossy hillocks, under which, and completely covered by the vegetation, are very ancient stumps of trees. The station continues to be occupied yearly by a pair of birds, and young are usually reared, but the old tree-remains have no evident biological significance to either old or young of the Oystercatcher. The Cragan Dubh cone, though small, is a comparatively rich area, and the young do not need to be led far. The wide range of the young in the Fender area appears to be due to relative poverty of the food supply, and is undoubtedly rendered possible by the protective value of the tree-stumps. When these are covered over by vegetation at a future date, a change may be expected in the distribution or range of the birds.

Next in the sequence comes the lake-beach habitat, as represented by the south shore of Loch Tummel. The conditions here are, on the whole, favourable to the occupants and to the rearing of the young, but the size of the population is evidently controlled by two factors, of which one is the relative narrowness of the shingle beaches which are not greatly favourable, on that account, to the concealment of the eggs or the young, and the other is the limitation of the local feeding-grounds to the discontinuous alluvial cones, for suitable local feeding-grounds do not occur elsewhere.

The portions of the Garry and Tummel under observation have a higher population per kilometre than any of the other areas. In this respect they show a pronounced difference from the other representative of a river-valley habitat, already described. Using a salient and ecologically important feature, it is, therefore, proposed to distinguish a river-valley habitat, such as the Orchy, from a drift-river-valley habitat, of which the lower reaches of the Garry and Tummel are representatives. In these areas the drift, or boulder-clay, covers a large part of the ground, and is largely cultivated. With the drift, as of importance for the Oystercatcher, must be associated the large deposits of alluvium which determines the distribution and area of the

local feeding-grounds. The drift and the alluvium are more favourable to the existence of the animals on which the Oystercatcher feeds, than the poor soil of the denuded river-valley. Cultivation follows the distribution of the drift and further increases the food-supply. But cultivation means human occupation, which is generally destructive. Cultivation, therefore, operates in two opposite directions in controlling the ratio of Oystercatcher population. Cultivation tends to increase the numbers of the stock an area may carry, and, at the same time, it is constantly tending to reduce the stock by means of human interference. Evidently, a balance has been struck, as the Oystercatcher population shows little or no change from year to year. The ratio of stock on the Garry to that on the Tummel is about 1 : 2. The most evident differences between the two areas are the smaller size of the Garry and its shingle areas, and the larger agricultural population. The smaller shingle-beds on the Garry are less favourable to the safety of the eggs and young than is the case on the Tummel. But, even on the large shingle areas at Moulinearn and Ballinluig, there is seen a tendency to desert the shingle for the river-bank, and the connection between this phenomenon and human interference is well established. Nesting in unusual places is general in the Vale of Atholl, but it must be fairly successful, as no diminution in the local stock has been recognized. Here the abnormal behaviour is probably connected with the semi-public character of the shingle and the large human population, the Vale of Atholl being the most populous district in the area under observation. It would appear as if, under the present secondary conditions of the river-valley, a too large human population outweighs the advantages which drift, and cultivation by a moderate population, confer upon the Oystercatcher.

Owing to the erratic nesting behaviour in the Vale of Atholl no reasonably complete figures could be obtained for the ratio of families to nests, and hence no comparison of the breeding results in the Garry area with those on the Tummel is possible. The results obtained at Loch Tummel, however, show that the relatively moderate stock on the south shore of Loch Tummel, as compared with the relatively large stock carried by the lower part of the river Tummel, is not due to greater difficulties in rearing young.

In 1912, nine pairs on the south shore and the storm beach of Loch Tummel produced four families of altogether nine young. In 1914, eight pairs produced three families of 4 + X young (probably seven). On the river Tummel, in 1909, at Moulinearn, eleven pairs had five families of eleven young. On the Logierait, upper island station, in 1910, ten pairs had four families of eight young, and in 1912 eight pairs had three families of six young. The ratios of adults to young in the two habitats are, therefore, approximately similar, being about 2·2 : 1. These two habitats are equivalent in human population and in amount of human intrusion in the territories. But the ratio of stocks in the two areas is relatively high, being as 2·5 on the river to 1 on the loch. The control of the Oystercatcher population in the two areas must, therefore, be sought in the factors already given, namely, the size and distribution of the shingle areas, alluvium, and boulder-clay. These three factors are equivalent on the Garry and the Tummel, except in total area. The size of the total area, when continuous as it is on these rivers, ought not to affect the linear distribution of the birds. The cause of the lesser population per kilometre in the Vale of Atholl may, therefore, with a fair degree of probability, be referred to the greater human population.

Thus, on the basis of population ratio and other considerations already mentioned, the drift-river-valley may be regarded as an optimum habitat in summer, within the area placed under observation. In some, the prevailing conditions of an optimum habitat in summer are:—(1) A breeding area and refuge, of sufficient extent, close to a body of water, rising well above summer flood level, devoid of vegetation, assimilating in colour appearance to the eggs and more especially the young, and fairly secure from human and other enemies.

(2) A local feeding-ground of sufficient area, to which the young have access on foot, terraced to form two adjacent levels so that, when the birds are on one level, they cannot readily be seen by an enemy from the other, covered with old turf, rich in tipulid and coleopterous larvæ, together with at least a moderate supply of earthworms, and fenced in, or in other ways protected from disturbance; both the breeding area and the local feeding-ground being held as territories, and situated on that account not too near the habitual stations of "barren pairs."

(3) A distant or general feeding-ground resting on boulder-clay or alluvium, and preferably cultivated, to which the adults may resort for food, and from which they may bring a large supply of large earthworms to the young. Auxillary conditions which have some value are:

(4) The presence of a wet sand-beach in some part of the breeding territory; and

(5) An abundance of Stonefly nymphs, along the river margin, at the time when most of the young Oystercatchers escape from the eggs.

Resumé and Conclusion.

The general results of the inquiry point to the mud-flat in winter, and the drift-river-valley in summer as optimum habitats within the areas under observation. The presence of a large human population has a pronounced effect on the distribution and numbers of the Oystercatcher. The Law of Territory is shown to be valid for the Oystercatcher, both in winter and in summer. The arrangement and extent of the territories, and the general movements of the birds therein, remain the same year after year. The theory of the biological advantage, or necessity of conserving the food-supply for the exclusive use of the settlement, by the maintenance of territorial rights, is supported by observations made at one winter station, where the food-activities of the settlement were found to strain the reproductive powers of the shellfish of the area. In relation to climatic conditions certain activities, normally successful, become ill-regulated when they are elicited at an abnormal period. The intangible associational barriers of Grinnell prove to be fully applied to the Oystercatcher, both in winter and in summer. They are (1) kind of food-supply afforded; (2) presence of safe breeding-places, and (3) presence of places of temporary refuge for individuals, when hard pressed by predatory enemies.* The last condition, though long known, had not previously been given the formal position its importance deserves among the factors of distribution. In summer for the young, and in winter for the settlements of the Oystercatcher, places of refuge are an important factor controlling distribution in the areas under observation.

* Amer. Nat. 1914, vol. 48, p. 252.

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local feeding-grounds. The drift and the alluvium are more favourable to the existence of the animals on which the Oystercatcher feeds, than the poor soil of the denuded river-valley. Cultivation follows the distribution of the drift and further increases the food-supply. But cultivation means human occupation, which is generally destructive. Cultivation, therefore, operates in two opposite directions in controlling the ratio of Oystercatcher population. Cultivation tends to increase the numbers of the stock an area may carry, and, at the same time, it is constantly tending to reduce the stock by means of human interference. Evidently, a balance has been struck, as the Oystercatcher population shows little or no change from year to year. The ratio of stock on the Garry to that on the Tummel is about 1 : 2. The most evident differences between the two areas are the smaller size of the Garry and its shingle areas, and the larger agricultural population. The smaller shingle-beds on the Garry are less favourable to the safety of the eggs and young than is the case on the Tummel. But, even on the large shingle areas at Moulinearn and Ballinluig, there is seen a tendency to desert the shingle for the river-bank, and the connection between this phenomenon and human interference is well established. Nesting in unusual places is general in the Vale of Atholl, but it must be fairly successful, as no diminution in the local stock has been recognized. Here the abnormal behaviour is probably connected with the semi-public character of the shingle and the large human population, the Vale of Atholl being the most populous district in the area under observation. It would appear as if, under the present secondary conditions of the river-valley, a too large human population outweighs the advantages which drift, and cultivation by a moderate population, confer upon the Oystercatcher.

Owing to the erratic nesting behaviour in the Vale of Atholl no reasonably complete figures could be obtained for the ratio of families to nests, and hence no comparison of the breeding results in the Garry area with those on the Tummel is possible. The results obtained at Loch Tummel, however, show that the relatively moderate stock on the south shore of Loch Tummel, as compared with the relatively large stock carried by the lower part of the river Tummel, is not due to greater difficulties in rearing young.

In 1912, nine pairs on the south shore and the storm beach of Loch Tummel produced four families of altogether nine young. In 1914, eight pairs produced three families of 4 + X young (probably seven). On the river Tummel, in 1909, at Moulinearn, eleven pairs had five families of eleven young. On the Logierait, upper island station, in 1910, ten pairs had four families of eight young, and in 1912 eight pairs had three families of six young. The ratios of adults to young in the two habitats are, therefore, approximately similar, being about 2·2 : 1. These two habitats are equivalent in human population and in amount of human intrusion in the territories. But the ratio of stocks in the two areas is relatively high, being as 2·5 on the river to 1 on the loch. The control of the Oystercatcher population in the two areas must, therefore, be sought in the factors already given, namely, the size and distribution of the shingle areas, alluvium, and boulder-clay. These three factors are equivalent on the Garry and the Tummel, except in total area. The size of the total area, when continuous as it is on these rivers, ought not to affect the linear distribution of the birds. The cause of the lesser population per kilometre in the Vale of Atholl may, therefore, with a fair degree of probability, be referred to the greater human population.

Thus, on the basis of population ratio and other considerations already mentioned, the drift-river-valley may be regarded as an optimum habitat in summer, within the area placed under observation. In some, the prevailing conditions of an optimum habitat in summer are:—(1) A breeding area and refuge, of sufficient extent, close to a body of water, rising well above summer flood level, devoid of vegetation, assimilating in colour appearance to the eggs and more especially the young, and fairly secure from human and other enemies.

(2) A local feeding-ground of sufficient area, to which the young have access on foot, terraced to form two adjacent levels so that, when the birds are on one level, they cannot readily be seen by an enemy from the other, covered with old turf, rich in tipulid and coleopterous larvæ, together with at least a moderate supply of earthworms, and fenced in, or in other ways protected from disturbance; both the breeding area and the local feeding-ground being held as territories, and situated on that account not too near the habitual stations of "barren pairs."

(3) A distant or general feeding-ground resting on boulder-clay or alluvium, and preferably cultivated, to which the adults may resort for food, and from which they may bring a large supply of large earthworms to the young. Auxillary conditions which have some value are:

(4) The presence of a wet sand-beach in some part of the breeding territory; and

(5) An abundance of Stonefly nymphs, along the river margin, at the time when most of the young Oystercatchers escape from the eggs.

Resumé and Conclusion.

The general results of the inquiry point to the mud-flat in winter, and the drift-river-valley in summer as optimum habitats within the areas under observation. The presence of a large human population has a pronounced effect on the distribution and numbers of the Oystercatcher. The Law of Territory is shown to be valid for the Oystercatcher, both in winter and in summer. The arrangement and extent of the territories, and the general movements of the birds therein, remain the same year after year. The theory of the biological advantage, or necessity of conserving the food-supply for the exclusive use of the settlement, by the maintenance of territorial rights, is supported by observations made at one winter station, where the food-activities of the settlement were found to strain the reproductive powers of the shellfish of the area. In relation to climatic conditions certain activities, normally successful, become ill-regulated when they are elicited at an abnormal period. The intangible associational barriers of Grinnell prove to be fully applied to the Oystercatcher, both in winter and in summer. They are (1) kind of food-supply afforded; (2) presence of safe breeding-places, and (3) presence of places of temporary refuge for individuals, when hard pressed by predatory enemies.* The last condition, though long known, had not previously been given the formal position its importance deserves among the factors of distribution. In summer for the young, and in winter for the settlements of the Oystercatcher, places of refuge are an important factor controlling distribution in the areas under observation.

* Amer. Nat. 1914, vol. 48, p. 252.