HOMING EXPERIMENTS WITH LEACH'S PETRELS

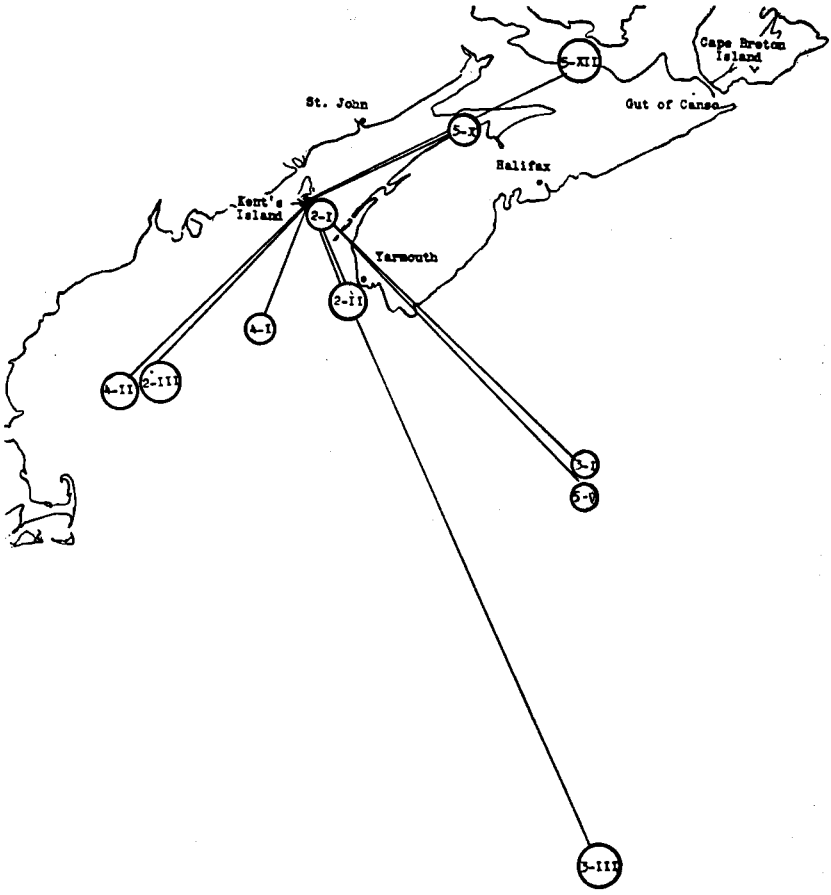
BY DONALD R. GRIFFIN

MOST of the homing experiments upon which are based our theories about birds' homing instincts have been conducted with land birds released on land (Casamajor, 1926; Exner, 1895; Kluijver, 1935; Rüppell, 1935, 1936, 1937; Thauziés, 1898, 1904, 1913; Wodzicki and Wojtusiak, 1934; and Wodzicki, Puchalski and Liche, 1938). Such experiments are inevitably open to the criticism that one never knows just how much territory a migratory bird has covered during its wanderings previous to the homing experiments. Consequently it is always possible that such land birds have been released within sight of landmarks already familiar to them or that after wandering a short time at random they may frequently encounter such familiar landmarks. Such returns from familiar territory do not tax the bird's powers of orientation as much as homing experiments where the birds are released at sea. The classic experiments of Watson and Lashley (1915) were free from this objection because some of the birds returned when released more than 150 miles from land, a distance at which no visual landmarks could possibly have been available. It seemed desirable therefore to repeat with seabirds released at sea some of the more recent types of homing experiment in which the transported birds are treated in various ways to test the possibility that specific senses may be used in homing (Rüppell, 1935; Kluijver, 1935).

Leach's Petrels (*Oceanodroma l. leucorhoa*) nesting on the outer sea islands of the Bay of Fundy were selected for these experiments because they are colonial, thus permitting the capture of large numbers at one time, and because they nest in burrows. This latter habit facilitates the recapture of transported birds. The majority of the work was done at the Bowdoin Scientific Station on Kent's Island, near Grand Manan Island, New Brunswick. The director, W. A. O. Gross, and the entire staff were extremely helpful and cooperative at all times. Special acknowledgment is due, however, to Frederick Greeley, Douglas Robinson and Samuel Lacy, for without their assistance in many unexciting and routine tasks these experiments could not have been conducted. I am also indebted to the Canadian National Steamships, Ltd., the Eastern Steamship Lines, and to Captain Henry Russell of Grand Harbor, New Brunswick, for carrying birds to sea in their ships. Professor K. S. Lashley has provided constant guidance and encouragement. The expenses of the summer's work were met by a grant from the Hodgson Fund.

Leach's Petrel is a highly specialized seabird which normally lays one egg a year in a burrow which it digs in the soil of some small island off the North

Atlantic coast. These habits, in addition to the bird's relative helplessness on land, render it very subject to destruction by predators. Apparently it nested even on the mainland until the advent of man, but domestic cats and dogs restricted it to sparsely inhabited islands. Even the Herring Gull will



TEXT-FIG. 1.—Homing experiments with Leach's Petrel.

often attack petrels near land during the daytime, and it is perhaps for this reason that the birds come to their nests after dark only. Petrels are never normally seen in daylight within about three miles of land, except, of course, for those that spend the day incubating their eggs below ground.

Fog is very prevalent in the Bay of Fundy and the petrels must normally find their way to land under conditions of darkness and fog where vision can

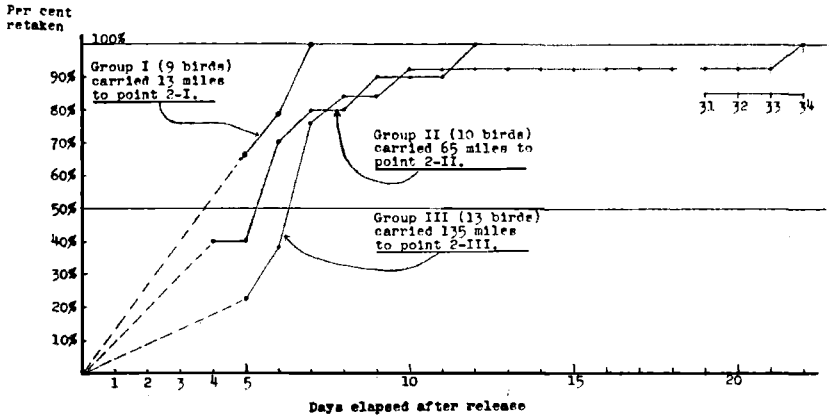
hardly play a part. Each bird spends three or four days at sea, and then returns to relieve its mate who has been incubating for that period. These visits to the nest are apparently made irrespective of the weather. All observers agree that the petrels are if anything more active on foggy nights, and my daily checks of many burrows disclosed no significant correlation between the weather and the number of burrows at which a shift of birds occurred.

Petrels have some disadvantages as experimental animals. I could not feed them successfully in captivity, although they would take small shrimps if these were forced down their throats. They have a tendency to desert their nests if too much disturbed, especially in the latter half of the incubation period, and their natural three- or four-day incubation cycle makes their exact homing time variable and hard to determine. For example, when a group of birds are caught for a homing experiment, some have just returned from a trip at sea, while others may have been incubating for three days. Possibly the latter birds when transported might remain at sea three or four days even though capable of returning sooner. Birds taken just after they have relieved their mate will probably have a strong incentive to return, but the absence of both parents may kill the egg. This may cause a desertion of the nest, rebuilding of the burrow, acquisition of new mate or all three. Time was not available to check each burrow daily for several days before an experiment to determine the birds' individual cycle and to enable selection of the birds at the most favorable point in that cycle. All these factors make for lack of uniformity in return speeds, and it seems clearest to compile the results of the homing experiments in the form of a curve, such as Wodzicki and Wojtusiak (1934) used, in which the time elasped after release is plotted against the total percentage of birds which had returned. These percentages are of course *cumulative*—the curve never goes down—and the end point is a horizontal line. If a fairly large number of birds is used in each experiment, comparison of the curves should disclose any significant difference present in the birds' homing behavior.

Experiment 1.—On June 25, 1938, seven petrels were taken to a point about twenty-five miles northwest of Kent's Island and released a mile or so from the mainland in a thick fog (visibility less than one hundred yards). Two were evidently somewhat confused, for they flew to a height of about a hundred feet and circled until lost to view. The rest flew off in various directions, none more than five feet off the water while still in sight (petrels never normally fly far above the water's surface). The fog did not lift until about twenty-four hours later. One bird returned during the first night, and two others the second night after release. All but one of the remaining birds were taken from burrows where no eggs were present, and

later experience showed clearly that petrels would practically always desert their burrows if they were caught and banded before the eggs were laid. This experiment suggested that fog may delay the birds when released twenty-five miles from their home island, but that at least one was able to return under those conditions before the fog lifted.

Experiment 2.—Thirty-two incubating birds were caught between 9 p. m. and 1 a. m. on the night of June 29 to 30 and carried by Diesel cargo vessel, bus and steamer to points 2-I, 2-II and 2-III on the map (Text-fig. 1). All of these birds were released in good condition, the weather conditions were favorable, and the birds left the ship in a great variety of directions on all three occasions. The results from these three groups of petrels are shown in Text-figure 2, a return curve of the type described above.



TEXT-FIG. 2.—Results of Experiment 2, including incubating birds only.

Subsequent experience showed that the first week of July is the most favorable time for homing experiments with Leach's Petrels in this region. Most burrows have eggs, and in the early stages of incubation the eggs are more resistant to temporary absence of the parents. This means that the transported birds are less likely on returning to find the eggs dead and then leave the burrow before they can be captured—a difficulty which was encountered later in the summer. I was unable to return to the island until four days after the birds of Experiment 2 were released, so that the earlier parts of the curves are uncertain. The results of Experiment 4 suggest, however, that the broken lines resulting from extrapolation are essentially correct.

Experiment 2 shows that practically 100% of the birds can find their way home from as far as 135 miles when released at sea where the nearest land

would be visible only at a height of about 730 feet.[1] The surprising point is that most of the birds released only thirteen miles from their nests did not return for five to seven days. This delay must have been due to factors other than difficulties of orientation; probably the petrels' three- to four-day incubation cycle delayed some of the birds' return. The most significant figure for the time of return is perhaps the *difference* between experimental and control curves. If judged by this standard 80% of the birds in groups II and III covered about sixty to seventy miles per day.

The fact that these speeds were not dependent on the distance transported indicates that random wandering was not the method by which the birds found their way home, for in that case the speed should decrease with greater distance since the birds must cover a greater *area* in their aimless flight. The speeds and distances are so small, in this case, however, that random wandering of group III might not show in the results. Largely to check this point birds were carried to greater distances in the next experiment.

Experiment 3.—Seventy-nine incubating birds were caught on July 10 and carried to East Ferry (near Tiverton), Nova Scotia, in the Bowdoin Scientific Station's cruiser. From there they were carried to Halifax by automobile and given to Mr. R. F. Leslie, chief officer of the S. S. *Colbourne* sailing from Halifax for the West Indies. These birds were released on July 12 and 13 as follows:

Group I (twenty birds), cage rotated on a phonograph turntable at about 25 r. p. m. for ten minutes at a time, about six times during the trip to Halifax. It was thought that this treatment should prevent any memory by the bird of the direction in which it was carried based on sensations from the inner ear. Group I was released at point 3-I on the map (Text-fig. 1), 170 statute miles from the nearest land and 280 miles from Kent's Island. (This bird would have to fly to a height of 11,000 feet before it could see land.) Visibility at time of release about one mile—weather moderate.

Group II (twenty birds) untreated, released at same time as group I.

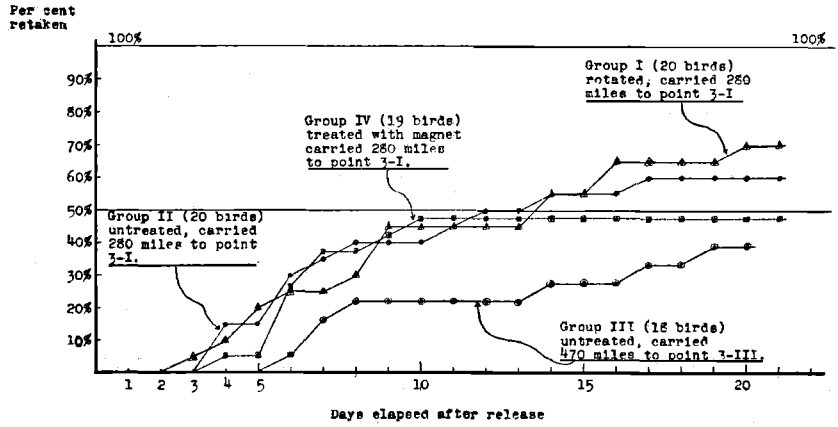
Group III (twenty birds) untreated, released at noon, July 13, at point 3-III on map, about 360 miles from nearest land and 470 miles from Kent's Island. This point is approximately at the center of the Gulf Stream. The weather was squally at the time of the release with a thirty m. p. h. wind and occasional heavy rain. Two birds were found dead in the cage when the rest were released. They had been in captivity for nearly three days without food, although water was provided to all the transported birds by placing a small sponge saturated with fresh water in each compartment.

[1] The formula for the distance, d, at which an object h feet above sea level is visible to an observer h' feet above sea level is approximately $d = 1.317\ (\sqrt{h} + \sqrt{h'})$ miles.

Here the height of the nearest land is not more than 500 feet and $d = 65$ miles; thus: $65 = 1.317\ (\sqrt{500} + \sqrt{h'})$, or $h' = 730$ feet.

According to Mr. Leslie's report "50% were fairly active although appearing much weaker than birds in groups I, II, and IV. The sudden rise in air temperature entering the Gulf Stream has a depressing effect on humans and this no doubt would be felt by the birds."

Group IV (nineteen birds). These were released at the same time as group I and were handled in the same manner except that before leaving Kent's Island each bird was held for about thirty seconds in the field of a powerful electromagnet (field strength throughout bird's head at least 500 gauss). This treatment, it was thought, might disclose whether any of the magnetic theories of homing could be applied to the petrel. It seems likely



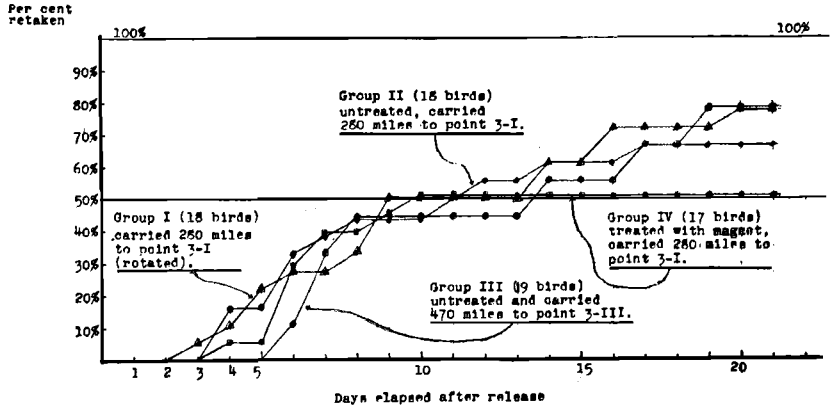
TEXT-FIG. 3.—Results of Experiment 3. Curve A, returns plotted as percentages of total birds released alive.

that any magnetic receptor sufficiently delicate to satisfy the postulates of Viguier (1882), Thauziés (1898), Casamajor (1926) and Stresemann (1935) would be seriously injured by such a treatment and that if magnetic senses were involved in the homing of the petrel this group treated with a magnet might show a delayed homing. This experiment held only a bare possibility of confirming the magnetic theories; negative results would not necessarily disprove them.

Neither the rotation nor the treatment with a magnet had any noticeable effect on the return curves of groups I and IV as compared to the untreated birds of group II. There is no reason to infer from the group III curve (Text-fig. 3) (even if uncorrected for the poor condition in which the birds were released) that the speed of return depends on the distance transported as it should if the birds were merely wandering at random until they found some familiar landmark. This is probably the case even if the return time

is taken as the difference between the actual time and that taken by the birds of Experiments 2 and 4 which were released at or near the home island.

Undoubtedly the longer time without food left the birds of Experiment 3 in poorer condition at the beginning of their return trip than those of Experiment 2. It would have been desirable to remedy this situation by faster transportation, but this was impossible. However, a truer picture of the results can be obtained by a simple quantitative treatment of the source of uncertainty, namely, the poor condition of the birds of group III. According to Mr. Leslie's report 50% of these birds were in poor condition while "90% of the birds of groups I, II and IV were active and flew away immediately in northwest direction (approximately toward their home).



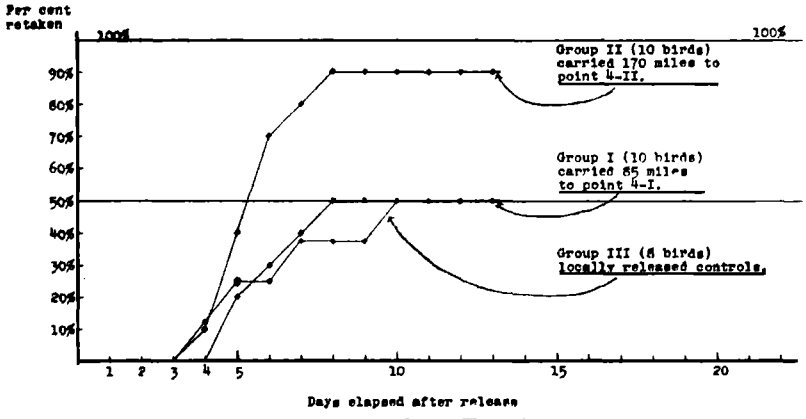
TEXT-FIG. 4.—Results of Experiment 3. Curve B, returns plotted as percentages of birds estimated to have been released in good condition.

Three or four were making short flights and appeared to have difficulty in rising from the sea."

I have therefore plotted the returns from Experiment 3 in a separate curve (Text-fig. 4, return curve 3b), assuming that only 90% of groups I, II and IV survived and that only 50% of group III were able to make the return journey. Subsequent experience gained in Experiment 5, in which birds were observed after two or three days in captivity suggested that this estimate was reasonable. Inspection of Text-figure 4 shows that if the above assumptions are valid there was little difference between the percentages returning from the various groups.

Experiment 4.—Thirty birds were caught from burrows containing eggs on the night of July 20 and carried by fishing boat, automobile and steamer to points 4-I and 4-II on the map. The former is 85 miles from Kent's Island and 65 miles from the nearest land; the latter is 172 miles from the

island and 65 miles from the nearest land. Group III was released on Kent's Island as controls. I remained on Kent's Island to check the burrows from the beginning, which had not been possible in Experiment 2. The two transported groups were kept in captivity for 48 and 53 hours due to an accidental delay. The control birds (group III) were held for three days so that I could observe for myself how that period in captivity affected the birds and judge its probable influence on the birds of Experiment 3, group III. Another reason for the long period in captivity for the controls was that their eggs would remain unincubated for more nearly as long as those of the transported birds, and no difference in the percentage retaken should result from that cause.



TEXT-FIG. 5.—Results of Experiment 4.

The actual results (Text-fig. 5) were paradoxical. The birds from group II (carried 170 miles) returned more rapidly and in greater numbers than the locally released controls. This must have been because of the poor condition of the latter, but this fact confirms the results of Experiment 2 in showing no dependence of speed of return on distance transported.

It is interesting to compare the curves for Experiment 3, group III, released 470 miles from Kent's Island and group III of Experiment 4; for both groups were kept without food for approximately the same time (three days). The difference in time of return and percentage returning is very slight, and suggests that the low percentage retaken from the release at 470 miles was due to factors other than the birds' powers of orientation.

Experiment 5.—Seventy-two birds were caught on August 3, 4 and 7, on Little Wood Island. All were taken from burrows containing eggs, although at this date many petrels have young and the eggs of others are nearly ready to hatch. These birds were treated as follows:

Group I (twenty birds) kept in captivity forty-eight hours and released locally in good condition.

Group V (seven birds) untreated, released at point 5-V on map after about three days in captivity. This long period in captivity was caused by the fact that the ship was nearly twenty-four hours behind schedule in reaching Halifax.

Group VII (seven birds) released at same time as group V but treated before transportation with electromagnet (field strength about 9700 gauss).[1]

Group VIII (ten birds) locally released controls for group VII, treated with magnet but released on Kent's Island forty-eight hours after capture, about three miles from their nests.

Group IX (five birds) released at same time as group V but rotated on phonograph almost continuously during trip as far as Windsor, Nova Scotia. Up to that point the cage was spinning all but about 5% of the time.

Group X (five birds) untreated, released about twenty-four hours after capture at point 5-X on map in the upper Bay of Fundy; birds in good condition.

Group XI (five birds) released at same time as group X but treated before transportation with electromagnet as described under group VII.

Group XII (five birds) untreated, released in fair condition about forty-eight hours after capture at John Bay (point 5-XII on map) on the southern shore of the Gulf of St. Lawrence.

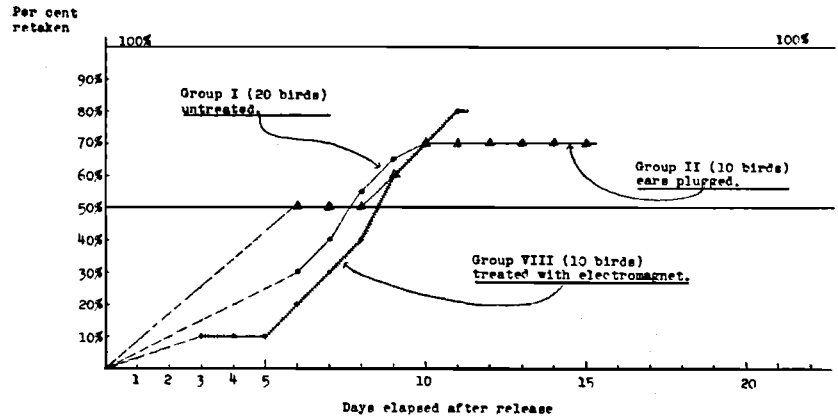
Group XIII (three birds) released at same time as group XII, but 'magnetized' as group VII had been with a magnetic field of 9700 gauss.

Group XIV (three birds) released at same time as group XII, but rotated just as group IX had been.

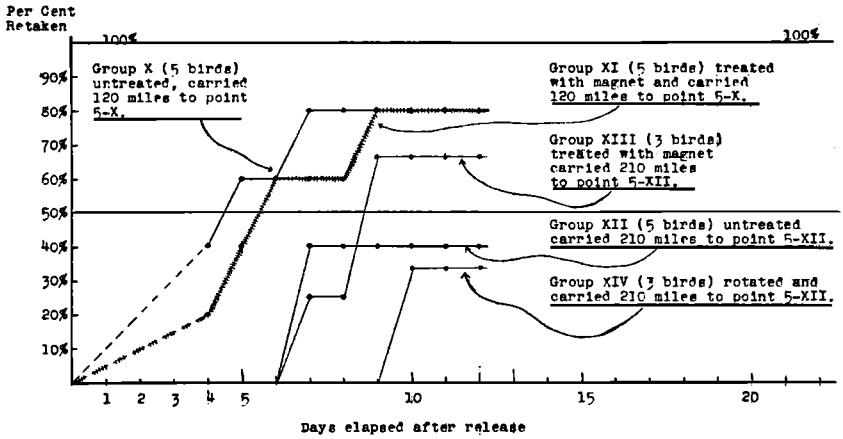
It is clear from the results of Experiment 5 (shown graphically in Text-figures 6 and 7) that conditions for the recording of returns were far less favorable than earlier in the summer when Experiments 2 and 3 were conducted. Many eggs had hatched before the parents returned and these parents often visited their nests almost every night but did not remain in the burrow. After about July 25, I found that the returns secured could be increased materially by inspecting all burrows at regular intervals throughout the night. This procedure had its dangers, however, as too much attention to the burrow with the inevitable disturbance occasioned by reaching into it may have caused desertions which would not otherwise have occurred. All of these factors reduced the percentages retaken in both Experiments 4 and 5. This fact is obvious on inspection of the percentages

[1] I am greatly indebted to the Harvard Engineering School for allowing me to use this electromagnet and to Mr. L. P. Winsor for measuring the flux density which was produced between its poles.

recorded for the locally released controls at different times during the summer (100% on July 1, 50% on July 23 and 70% to 80% on August 8). Therefore it is obvious that the returns from the experimental groups cannot be expected to be as high as those obtained in Experiments 2 and 3.



TEXT-FIG. 6.—Results of Experiment 5; locally released controls.



TEXT-FIG. 7.—Results of Experiment 5. Groups X, XI, XII, XIII, and XIV (birds carried north from Grand Manan Island into territory presumably unfamiliar to them).

The petrels released on August 10 south of Halifax (point 5-V) did not return as rapidly or in as high percentages as those of Experiment 3, that had been released at approximately the same point. The curves for these three groups showed no effect of the various treatments, and since they do not add anything to the results of Experiment 3 they are not reproduced.

The birds of groups X to XIV are of some interest because they were re-

leased in territory presumably unfamiliar to them. It is doubtful if Leach's Petrels nesting on Kent's Island or Little Wood Island had ever visited the upper reaches of the Bay of Fundy, and almost inconceivable that they had visited Northumberland Straits in the southern half of the Gulf of St. Lawrence. The returns from the upper Bay of Fundy showed a speed and percentage retaken comparable to Experiment 2; homing from that point presents no special theoretical problems since the birds would have only to follow the coast line in either direction until they came to familiar waters.

Groups XII, XIII, and XIV were carried to Northumberland Strait because of the large difference in distance between a straight course over Nova Scotia and the water route around Cape Breton Island. The shortest distance from point 5-XII to the home island is about 210 statute miles. Via the Gut of Canso the distance is about 500 miles and around Cape Breton it is about 710 miles. The average speed of return of these birds is shown in Table 1 in comparison with the homing speed of petrels in other homing experiments.

One is forced to conclude from this table either that the birds of groups XII and XIII (untreated and 'magnetized') averaged very much faster flights (while all the factors of birds' condition, and stage of the nesting season tended in the opposite direction) or that they flew over at least eighteen miles of land, a most extraordinary action for so strictly marine a bird as the petrel. This apparent straight-line flight over a new and strange environment points definitely toward a very strong ability for absolute orientation. Unfortunately, however, after the mortalities of the long trip, prolonged by the delay at Halifax in waiting for the steamer, there were only eight birds in these two groups in such condition that it seemed possible for them to survive. It is certainly dangerous to base any general conclusions on such small numbers of individuals.

The group that was carried to the Gulf of St. Lawrence and rotated during a part of the journey is especially interesting. Only three of these birds survived this trip, and only one was retaken at Little Wood Island. This bird required ten days for the trip. This case is not so clear-cut as the results from groups XII and XIII for in previous experiments a few of the first arrivals had attained the speed which this bird would have registered if it had flown around Nova Scotia. This uncertainty demonstrates very clearly the desirability of using large numbers of individuals in each group and of good experimental conditions. It is hoped that future homing experiments, benefiting from my experience, may satisfy these requirements.

It is interesting to note that Dircksen (1932) released in the Baltic terns nesting on the coast of the North Sea and that in at least one case the speed of return was so high that a direct overland flight (perhaps following the Kiel Canal) seems more probable than a detour around Denmark. Further-

TABLE 1

HOMING SPEEDS OF LEACH'S PETRELS

Experiment number	*No. of birds released*	*Distance carried*	*Mean homing speed (miles per day)*	*Remarks*
2-II	10	65 miles	10.5	
2-III	13	135 miles	18.5	
3-I (rotated)	20	280 miles	28.5	
3-II	20	280 miles	30.8	
3-III	18	470 miles	42.3	
3-IV ("magnetized")	19	280 miles	41.2	
4-I	10	85 miles	13.0	
4-II	10	170 miles	29.3	
5-V	7	272 miles	36.0	
5-VII ("magnetized")	7	272 miles	32.5	
5-IX (rotated)	5	272 miles	36.0	
5-X	5	120 miles	24.0	
5-XI ("magnetized")	5	120 miles	20.0	
5-XII	5	210 miles	30.0	Assuming birds flew back on an air line.
5-XIII ("magnetized")	3	210 miles	26.3	
5-XIV (rotated)	3	210 miles	21.0	
5-XII	5	231 miles	33.0	Assuming birds flew the course requiring the shortest overland flight.
5-XIII ("magnetized")	3	231 miles	29.0	
5-XIV (rotated)	3	231 miles	23.1	
5-XII	5	500 miles	71.4	Assuming birds flew through Gut of Canso.
5-XIII ("magnetized")	3	500 miles	62.5	
5-XIV (rotated)	3	500 miles	50.0	
5-XII	5	710 miles	101.4	Assuming birds flew around Cape Breton Island.
5-XIII ("magnetized")	3	710 miles	88.7	
5-XIV (rotated)	3	710 miles	71.0	

more there is the remarkable fact that one of two Manx Shearwaters sent by Lack and Lockley (1938) from the coast of Wales to Venice, Italy, outside the known range of the species, returned to its nest in fourteen days. The overland distance in this case is 900 miles, requiring the strictly marine shearwater to cross the Alps, while the distance by water is 3700 miles. These results certainly indicate strongly a power of absolute orientation capable of guiding these three genera of birds over totally unfamiliar territory.

SUMMARY AND CONCLUSIONS

(1) Leach's Petrels lend themselves well to homing experiments, although they may not be the best bird for the purpose and are certainly not ideal. The first week in July is the best time to transport them from the outer sea islands in the Bay of Fundy, for they are least likely to desert their nests at that time. Since petrels cannot very conveniently be fed in

captivity they should be carried to the point of release within twenty-four or at most forty-eight hours.

(2) A large percentage of the birds returned from distances up to 360 miles from the nearest land and 470 miles from their nests.

(3) Several birds seem to have flown over at least eighteen miles of high wooded land rather than follow the coast line around Nova Scotia.

(4) Vision can probably be eliminated from consideration as a means by which the birds find their way home by the distance from land to which they were carried and because they were transported in covered cages.

(5) Memory of the direction transported as perceived by means of the inner-ear labyrinth seems not to be necessary, for homing was equally rapid and consistent after birds were rotated during part of the transportation. Further experiments with better apparatus enabling rotation of the birds throughout the trip would be necessary to establish this point with absolute certainty.

(6) Random wandering as a means of homing is made quite unlikely by the combination of results indicating that the speed of return is independent of the distance, and that the birds apparently return in a direct line, over land if necessary. Random wandering in the case of the birds released in Northumberland Strait would presumably have been confined to the water.

(7) The homing ability of the petrels was not affected by subjecting them for several seconds to a magnetic field many hundred times as intense as the earth's field.

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