HOMING EXPERIMENTS WITH HERRING GULLS AND COMMON TERNS[1]

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INTRODUCTION

THE homing experiments described below were undertaken to obtain quantitative data bearing on the various theories advanced to account for the sensory basis of homing in birds. Herring Gulls and Common Terns were selected because both nest in large colonies and because extensive banding has traced their migration routes. Of 176 gulls which were carried as far as 872 miles, 162 or 93% are known definitely to have returned. The terns did not home so well, and only 34 (42.5%) returned out of 80 carried 94 to 456 miles.

Both species were released in familiar territory and in areas which almost certainly offered no previously perceived landmarks. A few were recaptured after a successful return flight and were shipped again to the same release point. The results of these experiments indicate how much use the birds may make of landmarks already known to them before the artificial transportation. A comparison of homing speeds from different release points permits certain conclusions about the effects of coastlines and river systems. Eight gulls were traced over a part of their return route, by observation from the ground and from airplanes. These definitely traced return routes throw some light on the behavior of the birds while they are orienting themselves. Certain important correlations were found between the birds' ability and atmospheric conditions. In a final section these data are discussed briefly with reference to the various theories of the sensory basis of homing. These theories have been reviewed in detail elsewhere (Griffin, in press).

These homing experiments were conducted during 1939, 1940, and 1941 with Common Terns (*Sterna hirundo*) and Herring Gulls (*Larus argentatus*) at a breeding colony on Penikese Island in Buzzard's Bay, Massachusetts. On one part of this island 300 to

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400 pairs of Herring Gulls nest on level grassy ground which made it possible to set traps over the nests. On another area there is a large colony of Common Terns estimated to contain 7,000 to 10,000 nesting pairs, and also a much smaller number of Roseate Terns.

Professor K. S. Lashley has contributed indispensable encouragement and advice throughout the experiments. The expenses have been defrayed in part through the generosity of Mr. Henry S. Shaw, the Society of Fellows of Harvard University, and Professor Alexander Forbes. The Woods Hole Oceanographic Institute very kindly provided a boat for transportation between Penikese and the mainland during 1941, and I am also indebted to this Institute for many other facilities and conveniences. Special thanks are due Mr. J. A. Hagar and the Massachusetts Division of Fisheries and Game for helpful cooperation and advice, and for permission to work at Penikese, which is a state sanctuary.

While birds are being released, someone should always be watching at the colony for returns, and in my case this was possible only because of a sort of wholesale cooperation from many of my friends. Invaluable assistance was rendered in watching for returns or in releasing birds by Malcolm Miller, Hermann Rahn, Joseph Riley, David E. Davis, Howard Vogel, Margaret Robinson, Robert Galambos, Robert B. Holden, Darcy Gilmour, G. Edgar Folk, Francis Friedman, V. C. Wynne-Edwards, Harold B. Hitchcock, Max F. Day, N. Nash, G. Bramhall, J. Warriner, G. F. Snell, D. G. Mayer, and Mary Sears. Douglas H. Robinson and Henry M. Parker deserve special acknowledgement, for they spent long periods on Penikese watching for returns while I was ashore releasing birds or attempting to trace their return routes. I am also greatly indebted to Professor Alexander Forbes for following gulls with his airplane so that I could attempt to trace their return route, and to Terris Moore and Norris Rakestraw for flying planes in similar attempts. Lastly, Mr. F. C. Lincoln and the U. S. Fish and Wildlife Service together with the Canadian National Parks Bureau granted all possible cooperation in issuing permits for this work. In addition the Fish and Wildlife Service permitted me to examine the recovery records of banded gulls and terns.

METHODS

Trapping.—Birds were trapped over nests, in most cases with complete clutches of eggs, and only one bird of each pair was taken. For terns, I used the simple "up-wind drop trap" described by Austin (1934). For Herring Gulls two types of traps were used: a funnel type, and in 1941 a more successful spring door type (Fig. 1). Both were made of 2″ mesh hexagonal netting, and staked to the ground over the bird's nest, or held in place by rocks. The funnel type was 2′ wide, 5′ long, and about 18″ high, with the netting bent in at the ends to form funnels tapering from the full width of the trap to an opening just wide enough to admit the gull. This opening should be at least 1′ high. Such a trap is best left for 3 or 4 days with the funnels bent open to the full width of the trap, so that the gulls can walk freely in and out. Then when the birds are to be trapped, the funnels are bent in to the "set" position, and the colony left undisturbed for about an hour. At the end of this time we would rush into the colony with as much noise as possible, and

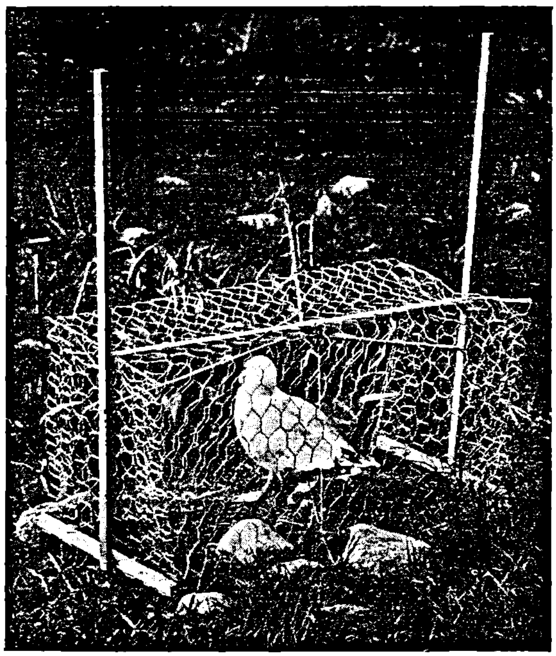


FIG. 1. Herring gull in spring door trap (note trigger rod extending across trap just above eggs).

transfer the gulls to cloth bags. It was necessary to work fast, and to keep the gulls frightened, or they would find their way out through the funnel openings.

The spring door traps (Fig. 1) were about 5′ x 2′ x 2′, with the 2′ square end openings covered by a wire netting gate, hinged at the top, and held closed by an ordinary screen door spring. Wooden rods fastened vertically along the center lines of the gates and extending three feet above the hinges held the gates open when swung up until the rods lay along the top of the trap. A simple trigger mechanism of heavy wire held the wooden rods to the top of the trap until a gull attempted to incubate. When the gull disturbed the trigger rod (extending across the trap 4″ above the eggs) the gates closed. Additional wooden strips across the bottoms of the gates and along the center of the top were necessary to prevent the wire from bending.

Herring Gulls are not trapped easily, and the netting should be as inconspicuous as possible. Eighteen gauge wire is satisfactory for the funnel traps, and 16 gauge for the spring door type. They can be bent to fit fairly rough terrain, and by turning out a few inches of netting at the bottoms they can be weighted down with rocks. The birds will not hurt themselves against the netting if undisturbed—in fact, they usually settle on the eggs again within five minutes. But when alarmed and struggling to escape they are likely to cut their wrists and feet, or break the wing feathers if not removed within a very few minutes.

Shipping.—All birds were shipped in wooden boxes with ventilation provided through covered openings which would permit no landmarks to be seen on the trip away from Penikese. No food was given since in all but the three longest shipments the transportation time was less than 36 hours. In the worst case gulls survived 57 hours with neither food nor water, although it is of course desirable to give them an opportunity to drink. No ill effects could be detected after shipment except that the birds were sometimes tired, and the outer primaries and the tail feathers were usually soiled and the barbs separated. This gave them a bedraggled appearance, but did not prevent rapid and powerful flight. In carrying gulls by airplane, cloth bags were used in some cases (shipments 4, 5, 9, and 10); but the birds were apt to become excessively hot, and a few even died from this cause. Shipments 6, 7, and 11 were made by plane in small metal boxes essentially like the regular wooden ones, but covered by wet towelling to cool them by evaporation.

Identification and Timing.—Birds were banded and also marked with quick-drying enamel paint in definite positions on both sides of the head, so that every individual had a characteristic pattern which could be recognized with binoculars or telescope. The colors used were red, green, and black on white areas, and white on the black crown of the terns. Blinds were located in central parts of the gull and tern colonies, from which could easily be seen the nests of all birds used in these experiments. The paint marks could be read with certainty on gulls at 200–300 yards, and on terns at 75–100 yards, provided that they were standing still. Flying birds could very seldom be identified, and it would often be necessary to observe a standing one for 4 or 5 minutes until it presented a clear view of the marked areas.

Usually the eggs of gulls would be destroyed by other gulls if the transported birds did not return within two or three days. In spite of this loss of eggs or nest, the bird would return to the territory it had established around the nest, and would often stand there for long periods during several days. For this reason it was possible to check the return time of gulls with considerable accuracy and assurance that they were seen soon after they reached the island.

Terns on the other hand were never seen molesting each other's eggs, but usually the untrapped mate would incubate for only two or three days unless the transported bird returned. When a tern arrived at its nest and found that the eggs had been deserted, it usually remained only a minute or two, and often never reappeared. This necessitated constant attention throughout the daylight hours, and may well have resulted in failure to record one or two returns.

I was unable to devise a method of determining age or sex of most of the gulls used, except that all were in the adult plumage. Both sexes seem to share incubation approximately equally, however, and certainly the results show that both home well. Work of this type would be improved, however, if age and sex were known, for some of the variability in homing performance might be thus explained.

The nests were watched as nearly continuously during the daylight hours as practicable. Usually at least 8–10 hours a day were spent in the tern blind when birds might be returning. The gulls were easier to spot since they remained for much longer periods near the nests, and an average of five hours per day was spent in the gull blind. The majority of returns were secured during the early morning and in the evening; at these times many more gulls are present at a breeding colony, and the watch was kept more constantly then.

Obviously the recorded times are maximal; any bird may have returned sooner. Conversely, the percentages recorded are minimal. Except as noted below, however, I am confident that 9 out of 10 gulls were recorded within an hour or two of their first arrival. It seems unlikely that many of the gulls escaped observation entirely after actually returning to Penikese, since none of those recorded season following their return to Penikese, but none of those recorded as "d.n.r." (did not return) have been retaken in later seasons. However, one tern, No. 326, was found dead on Penikese the season following its release at Rochester, N. Y. It had never been observed at Penikese until found in 1941 by another bander.

Observation after release.—When possible the birds were watched with binoculars or telescope after their release, but frequently they would all land on the nearest water, so that individuals in the group could no longer be recognized at a distance. Time did not permit a long wait for such birds to begin their return flight.

Ten attempts were made to follow gulls with a small airplane, because this method promised to yield very interesting data if homing gulls could be followed for any great distance. The safest and most practicable procedure was to circle about 2,000 feet above the bird. A Herring Gull is easily visible at this distance without using glasses, and the bird stands out clearly against all types of ground except white sand or a reflection of sunlight off water. Overcast days are therefore best for airplane observations.

When the plane is 2,000 feet above him, the gull gives no visible evidence of alarm or abnormal behavior. However, with a 145 h.p. Cessna monoplane at 1,000 feet, one gull became alarmed and would turn back every time that the plane flew across its path.

It is desirable to have a plane which will fly as slowly as possible, both to reduce gasoline consumption and thus increase flying time, and also to spare the observer from the somewhat unpleasant effects of prolonged flying at high speeds in small circles. The popular two place cabin planes are the best available because they can be flown at only 50 to 60 m.p.h. When flying in a straight line a Herring Gull averages about 30 miles per hour, and with these small planes one circle need be made only about every five minutes to keep the bird under observation. A "tandem" plane is preferable to a "coupe" because both pilot and observer have a good view on both sides. Autogiros would be still better, but they are scarce and expensive and usually have an insufficient fuel capacity for long flights.

Even my limited experience demonstrated both the difficulties and promise of airplane observation. More flexible planes with better visibility and longer flying time are needed for best results, but much can be done with the light planes obtainable at present. Days with high solid clouds are best, unless the aircraft can fly as slowly as the bird and thus avoid the necessity of circling and passing through a part of the circle where glare from water will render the bird invisible. Mufflers would no doubt permit a closer approach without frightening the bird. There is an indefinable feeling in watching a bird from the air that one is in the bird's own medium and can understand its problems and behavior far better than would ever be possible from the ground.

EXPERIMENTAL RESULTS

For all the transported terns, the time from release to first subsequent observation at Penikese Island is shown in Table 1.[1] Similar data for the Herring Gulls is presented in Fig. 2. Each gull's speed of return is shown graphically in the right hand portion of Fig. 2 by a solid dot.

In Fig. 2 I have attempted to summarize the weather conditions occurring while the birds of each experimental group were returning to Penikese. The complete data would consist of several hundred detailed weather maps, so that an extreme form of condensation has been necessary. Under the headings "Winds," "Convection," "Visibility," and "General" are entered symbols summarizing the weather for the entire period during which the birds in question were returning. The symbols range from + + + (Highly Favorable) to − − − (Very Unfavorable). Winds are considered favorable when strong and blowing from release point towards home. Convection is entered as favorable when cumulus clouds and unstable lapse rates[2] indicate the presence of updrafts. Cool temperatures, unlimited visibility, and fair weather are also considered favorable conditions. Gulls may be quite sensitive to heat as shown by the death of three which became too hot during transportation. Prevalent cloud types are listed in the last column, using the conventional abbreviations. The shipments are arranged in Fig. 2 according to approximate distance of shipment, and within distance groups according to average speed of return. This arrangement brings out any correlation between weather conditions and speed of return.

TABLE 1. HOMING OF COMMON TERNS

(d.n.r.=did not return. m.=miles. hrs. i.c.=hours in captivity.)

In computing average speeds, Nos. 79, 138, and 199 are neglected since they seemed weak or injured when released.

Shipment No.	*Place and time of release*	*Bird No.*	*Total time*	*Speed (miles per day)*
35	New Haven, Conn.	961	7 hrs.	350 (14.6 m.p.h.)
	102 m. West	963	10 hrs.	244 (10.2 m.p.h.)
	June 19, 1941	965	20 hrs.	122 (5.1 m.p.h.)
	9:45 a.m.	964	21 hrs.	117 (5.1 m.p.h.)
	22 hrs. i.c.	962	79 hrs.	31

[1]The shipments and individual birds are numbered for reference. The left-hand column contains the place and date of release (Eastern Standard Time), the distance and direction from Penikese to the release point, and the number of hours in captivity (abbreviated "*hrs. i.c.*"). The times given are total, including darkness. They are in hours up to 96 hours, and in days and hours for longer intervals, as they seem easiest to visualize in this form. A day is, of course, always 24 hours, beginning at the actual time of release. Speed of return is total time divided by the shortest distance (great circle) between home and release point, expressed in miles per day. In cases where the total time was less than 24 hours, the time is given in miles per hour as well. The tables would be misleading otherwise; for a bird such as No. 961, while flying 102 miles in 7 hours, traveled at the rate of 350 miles per day, whereas it might very well have been unable to maintain the same speed for 24 hours.

[2]Lapse rate is the rate of decrease of air temperature with altitude.

36	Gardner, Mass. 95 m. N.W. June 19, 1941 8:40 a.m. 22 hrs. i.c.	960 959 957 956 958	10 hrs. 11 hrs. 21 hrs. 80 hrs. d.n.r.	228 (9.5 m.p.h.) 207 (8.6 m.p.h.) 109 (4.5 m.p.h.) 28 —
37	Newburyport, Mass. 94 m. North June 19, 1941 9:17 a.m. 23 hrs. i.c.	952 954 951 955 953	24 hrs. 26 hrs. 32 hrs. 32 hrs. d.n.r.	94 87 71 71 —
38	Atlantic City, N. J. 234 m. S.W. June 17, 1941 12 noon 27 hrs. i.c.	937 936 940 938 939	42 hrs. 55 hrs. 67 hrs. d.n.r. d.n.r.	134 102 84 — —
39	Burlington, Vt. (Lake Champlain, near S. Hero) 242 m. N.W. x N. June 17, 1941 5:00 p.m. 30 hrs. i.c.	942 941 943 944 950	40 hrs. d.n.r. d.n.r. d.n.r. d.n.r.	145 — — — —
40	Belfast, Maine (Penobscot Bay, near Bucksport) 228 m. N.E. June 17, 1941 12:50 p.m. 26 hrs. i.c.	945 946 949 947 948	65 hrs. 65 hrs. 16 d., 7 hrs. d.n.r. d.n.r.	84 84 14? (Indentification uncertain) — —
41	Cape Charles, Va. 404 m. S.W. June 20, 1940 4:38 p.m. 29–31 hrs. i.c.	306 302 408 304 305 409 413 301 303	37 hrs. 51 hrs. 51 hrs. 51 hrs. 63 hrs. 7 d., 21 hrs. d.n.r. d.n.r. d.n.r.	262 190 190 190 154 51? (Identification uncertain) — — —
42	Rochester, N. Y. 384 m. W. x N. June 21, 1940 3:00–4:00 p.m. 50–54 hrs. i.c.	327 324 322 326 also eight birds	38 hrs. 4 d., 20 hrs. 5 d., 0 hrs. 13 months d.n.r.	243 79 77 1 (found dead) —
43	Eastport, Maine 312 m. N.E. June 21, 1940 3:15 p.m. 50–54 hrs. i.c.	314 312 313 also six birds	49 hrs. 5 d., 0 hrs. 6 d., 2 hrs. d.n.r.	153? (identification uncertain) 62 51 —

44	Shediac Bay, N. B. (Gulf of St. Lawrence) 456 m. N.E. June 10, 1941 12:05 p.m. 28–30 hrs. i.c.	five birds	none returned	—
45	Shediac Bay, N. B. June 29, 1941 2:20 p.m. 30 hrs. i.c.	410	87 hrs.	126
		also four birds	d.n.r.	—
46	College Bridge, N. B. (Upper Bay of Fundy, near Sackville) 445 m. N.E. June 10, 1941 2:20 p.m. 30 hrs. i.c.	932	45 hrs.	238
		933	77 hrs.	138
		931	d.n.r.	—
		934	d.n.r.	—
		935	d.n.r.	—
47	Sackville, N. B. 445 m. N.E. June 29, 1941 3:40 p.m. 31 hrs. i.c.	412	77 hrs.	139
		also four birds	d.n.r.	—

In Table 5 are presented data on certain special homing experiments with Herring Gulls which are discussed below under "Miscellaneous Observations."

The location of the various release points is shown in Figs. 3 and 4. Some are omitted from Fig. 4 to prevent crowding, and these are listed in Tables 1 and 5 and Fig. 2 as "near" some release point shown on the map.

The percentage of returns of Herring Gulls (93% of 176 shipped 15 to 872 miles) was exceptionally high compared with the results of homing experiments with other birds. Goethe (1937) also reported almost 100% returns with European Herring Gulls. Terns were not nearly as good homers, approaching 100% only at 100 mile releases. Of 80 shipped 94 to 456 miles, 42.5% returned.

There are great variations in the homing speed of different gulls from the same point on the same day, and striking differences in the average speed of return of groups released at the same point on different days. Terns were not tested as thoroughly as gulls, but they too showed great variability in homing speed. Pigeon fanciers find similar differences in homing speed on different days, and Rüppell (1935) has noted cases of the same sort with starlings.

WEATHER CONDITIONS

The relationship between bird flight and atmospheric conditions is an interesting study in itself, and it has an important bearing on the homing problem. For the ornithological aspects of this subject the reader is referred to Woodcock (1940a; 1940b) and Aymar (1935). Excellent discussions of the meteorological background can be found in Petterssen (1940) and Barringer (1938).

It is obvious that severe storms or very strong adverse winds would slow the homing of gulls and terns, regardless of the sensory basis of their orientation. Such storms were encountered after the release of groups 12, 15, 26, 27, 33, 44 and 46. As might be expected these groups showed a longer homing time than others sent to the same release point.

Less violent weather conditions also have a great effect on the flight of Herring Gulls as Woodcock (1940) has recently shown so clearly. Gulls prefer soaring to flapping flight and they are reluctant to travel long distances in air which is devoid of rising currents. Woodcock has shown, for instance, that Herring Gulls fly far out to sea from the New England coast only in winter when convection currents result from the meeting of cold air and warmer water. In my homing experiments the gulls tended to take off more readily after release and to cover more ground on days when rising currents of air were available.

Gulls have been observed to soar by means of thermal updrafts (caused by heating of air near the ground); obstruction updrafts (produced when a horizontal wind is deflected upwards by hills or buildings); and finally by means of velocity gradients in a horizontal wind produced in the first few hundred feet of air by friction at the surface (dynamic soaring). The first class is probably the most useful, for under favorable conditions thermal updrafts may be very powerful and widespread. An example of the power developed is the common heat thunderstorm, usually occurring in the afternoon of a hot day, when part of this convection energy is released as lightning. This source of power enables both soaring birds and glider pilots to make long journeys "riding the updrafts."

Atmospheric conditions adapted to one of the three types of soaring are the rule rather than the exception, for any wind will produce some updrafts. The worst condition is one with little wind, warm air and clouds which prevent solar heating of the ground. Stable air, which cools slowly as one ascends, is also unlikely to contain thermal updrafts and is thus bad for soaring.

A study of Fig. 2 shows that many of the differences in the homing times of gulls can be accounted for by weather conditions. The most rapid returns of gulls all occurred when there were strong winds blowing in the general direction of home with strong convection (groups 3, 6, 14, 16, 24, and 29). Hot stable air seemed to make gulls reluctant to take off after release, and when generally stable conditions prevailed gulls had to flap the entire distance or wait for better weather. Such stable air was prevalent after the release of groups 10, 20, and 28.

Some of the conclusions to be drawn from Table 3 in the section on "returns from familiar and unfamiliar territory" must be modified by consideration of weather. The Chicago-Savannah comparison, for instance, is not as critical as it appears, since the latter group had much more favorable winds and convection, although subject to greater heat. Gulls of group 25 did poorly despite good weather, but they were either kept abnormally long in captivity or else were weak and in poor condition. Some but not all of the differences in first and second returns from the same release point could be due to weather, as stated below in the section dealing with these second shipments.

On the other hand, Table 2 (terns) is not greatly affected by weather considerations. The birds at each distance were released at approximately the same time, and the weather was generally good for all nine groups. If anything, the inland and northeast coastal groups were favored, so that the differences shown in the table clearly cannot be ascribed to the weather. Terns are not soaring birds and they are probably far less dependent on updrafts than the gulls. Furthermore, the comparisons between groups 44 and 45 vs. 46 and 47; 26 vs. 27; and 20 and 21 vs. 17, 18, 19, and 22 remain significant because the differences in homing time are not those to be expected from the weather situation.

It is clear that data on homing and migration speeds, at least of soaring birds, cannot be safely compared unless the atmospheric conditions are taken into account.

RETURNS FROM FAMILIAR AND UNFAMILIAR TERRITORY

Two hundred records of Common Terns banded in Massachusetts and recovered outside the state were obtained from the U. S. Fish and Wildlife Service. 191, or 95.5%, were from points southwest along the Atlantic coast, from the West Indies, or from South and Central America. Five, or 2.5%, were from northeast along the coast, in Maine or the Maritime Provinces; and only four, or 2%, were inland on the Great Lakes or in Quebec. Similar figures for 526 Herring Gull recoveries (birds banded in Maine and Massachusetts) were 94.6% southwest along the coast; 3.8% northeast coastal; and 1.6% inland in the Mississippi Valley or the Great Lakes. Gross (1940) reports that of 773 recoveries of banded Herring Gulls from Kent's Island, N. B. only nine, or 1.2%, were from inland points (Great Lakes, upper New York State, or the upper St. Lawrence Valley).

Thus it seems likely that release points more than 100 miles northeast along the coast were probably outside the territory familiar to the terns, and points 100–400 miles inland almost certainly so, while any area southwest along the coast had undoubtedly been visited on previous migratory flights. Herring Gulls are frequently seen along inland waterways, and, in contrast to the terns, those released 100–250 miles inland may not have been very far from familiar territory. The occasional inland excursions of gulls may be of short duration, so that practically no

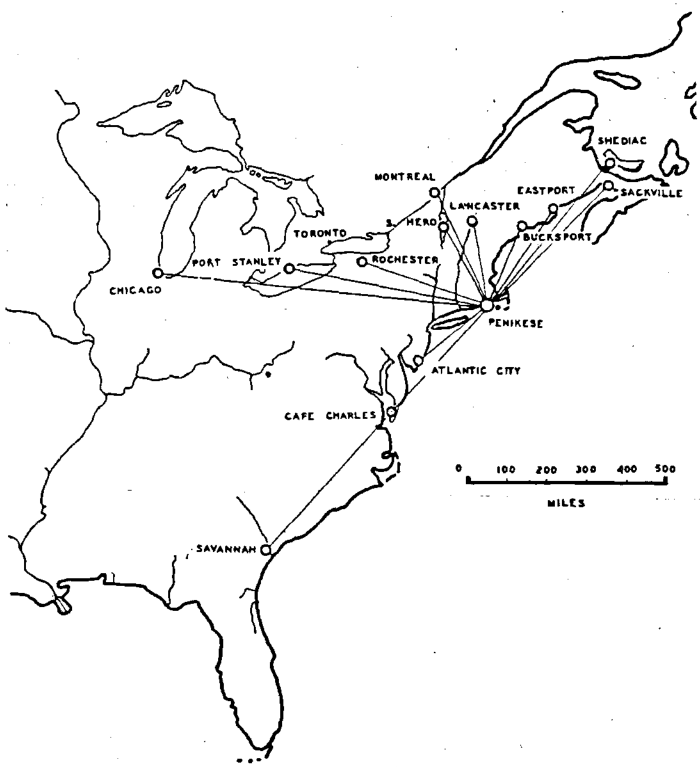


FIG. 3. Release points of gulls and terns.

banded ones are recovered; yet they may be sufficient to acquaint the birds with considerable inland geography. However, points over 500 miles inland, such as Port Stanley and Chicago, were almost certainly in unfamiliar territory, while of course all the southwest coastal regions must have been visited on previous migrations.

The per cent returns and the average homing speed (miles per day) from these three classes of release point are summarized in Tables 2 and 3. The speeds are averages of those birds which did return.

TABLE 2. HOMING OF COMMON TERNS FROM FAMILIAR AND UNFAMILIAR TERRITORY

Distance shipped	*Southwest coastal (known)*	*Northeast coastal (probably unknown)*	*Inland (unknown)*
94–102 miles	100% 171 m./d.	80% 81 m./d.	80% 144 m./d.
228–242 miles	60% 107 m./d.	40% 84 m./d.	20% 145 m./d.
312–404 miles	56% 199 m./d.	22% 57 m./d.	25% 133 m./d.

TABLE 3. HOMING OF HERRING GULLS FROM VARIOUS DIRECTIONS

Distance shipped	*Southwest coastal (known)*	*Northeast coastal (probably unknown)*	*Inland (probably unknown)*
94–104 miles	100% 68 m./d.	100% 210 m./d.	96% 143 m./d.
234–302 miles	100% 84 m./d.	100% 118 m./d.	92% 83 m./d.
445–540 miles	—	87% 52 m./d.	60% 57 m./d.
870–872 miles	80% 120 m./d.	—	67% 58 m./d.

There is a marked tendency for terns to home faster and in higher percentages from what the banding evidence suggests are familiar regions. These differences were not due to weather conditions, for the weather was generally good in all cases, the wind direction favoring the inland and southwest coastal groups at 100 miles, but favoring the birds from unknown territory in the longer shipments.

The gulls, on the other hand, show a much less clear trend for better returns from familiar territory (Table 3). Some of those shipped 100–250 miles may have made use of experience gained on previous inland flights. Or variability caused by weather conditions or other factors may mask any trend which might appear in a sufficiently large series of homing experiments. The birds released at Port Stanley had been in captivity 57 hours owing to delays at customs and express agencies, and their relatively poor showing may be from this cause rather than because they were in unfamiliar territory. The gulls shipped to Chicago and Savannah show the most striking contrast; in fact, the Savannah group returned faster than those released only about half the distance northeast along a coast which was perhaps unfamiliar. (Compare shipments 29 and 26.) But this comparison is not as conclusive as it seems, for the Chicago and New Brunswick birds had definitely adverse weather conditions, while almost every aspect of the winds and weather were ideal for those released at Savannah. As shown above many of the other differences in homing of these gulls can be similarly explained.

Thus the data from shipments of terns fit quite well the theory of exploration by radial scattering from the release point (Claparède, 1903). The per cent returning falls off sharply once the birds are carried far into unknown territory, even though it be along the coast where food and a suitable environment are available. The generally low percentages of returns recorded may be partly due to the technical difficulties discussed on page 7; but the relative difference between familiar and unfamiliar territory can scarcely be due to a failure to observe the birds at their nests. Yet on the other hand, there is little decrease in the speed of those birds which do return. With gulls there is only a slight trend towards better homing from familiar territory, and what difference there is might well be due to a familiarity with local atmospheric conditions or food resources, rather than because their orientation depends upon recognition of familiar landmarks. The same reasoning can less easily be applied to the terns, for in their case the differences in homing performance are more striking. To be sure, their feeding habits are so specialized that knowledge of local conditions may assume greater importance than with gulls, but the difference in homing performance from southwest and northeast coastal points seems too striking to explain on this basis.

Second Shipments of the Same Bird

During 1940 and 1941 we captured several gulls which had already been shipped to a distance once during the previous season and had returned within a few days. Nine of these were carried again to the same release point, or another not far distant. Four others were released at quite different points. The results are summarized in Table 4.[1]

[1] I have not included in Table 4 one gull shipped twice to Lake Champlain whose homing time was 26 hours the first year and 71 hours the second year because it was very weak and in bad condition when released on the second occasion. Nor have I included two additional birds (Nos. 159 and 161) shipped 8 and 14 days respectively after their first shipment, in both cases to Penobscot Bay. These two returned at exactly the same time from their first shipment, their nests being 50 feet apart. No. 161 was shipped again 8 days after its first trip, along with 162, which was back promptly in 26 hours. But No. 161 was very slow, and when it did come back it was again at exactly the same time as 159 returned from a second shipment. Evidently the two had met somewhere along the way. After they were back No. 159 on at least one occasion was clearly seen seeding the young of 161 which had hatched in their absence. Clearly some unusual social relationfhip was involved, and homing may well have been delayed by other factors than sensory difficulties.

TABLE 4. HERRING GULLS TRANSPORTED TWICE TO THE SAME RELEASE POINT

Bird No.	*Release point*	*Interval between shipments*	*First release*		*Second release*	
			Homing time	*Speed (miles per day)*	*Homing time*	*Speed (miles per day)*
95	Lake Champlain	1 year	10 days	29	29 hours	199
100	Lake Champlain	1 year	4½ days	52	48 hours	120
110	Lake Champlain	1 year	6 days	40	18 hours	120
150	Newburyport, Mass.	24 days	9 hours	250	30 hours	118
151	Newburyport, Mass.	15 days	10 hours	225	8 hours	282
162	Penobscot Bay, Me.	8 days	29 hours	200	26 hours	216

The three cases where birds were shipped about 250 miles in two different years seem to be very interesting (Nos. 95, 100, and 110). All were quite slow on their first trip and a year later they showed a very marked improvement. This is just what one would expect if they had deviated considerably from the true course in exploring for familiar landmarks, but profited by the experience when shipped to the same region the following season. These three cases are of course too few to rely upon.

The weather may have had some effect, for Nos. 95 and 110 had better conditions for the second trip, but No. 100 did not, and the improvement of 95 and 110 was much greater than the usual difference between birds released in good as opposed to mediocre weather. Nos. 150, 151, 159, 161, and 162 all had better weather for their second trip than that encountered after the first release. Nos. 150, 151, and 162 showed no important difference between first and second shipments, but the interval between shipments was so short that the homing performance may have been impaired for this reason.

Of the four birds shipped the second time to a different release point some were slower and some faster on the second shipment. Apparently this correlated with the weather conditions, and the details do not seem worth reproducing. The lack of any clear trend indicates that a second trip *per se* did not have any effect.

EFFECTS OF TOPOGRAPHY AND GEOGRAPHY

Shipments 26, 27, 44, 45, 46, and 47 were designed to test the birds' tendency to follow a coastline. Gulls and terns were released on both sides of the isthmus connecting Nova Scotia to New Brunswick. The total distance differed by only 4%, yet in one case the birds were in the Bay of Fundy, one coast line of which would lead them home directly, while in the other case they were released in the Gulf of St. Lawrence, where one coastline would never lead them home while the other would do so only with a detour of several hundred miles.

The results showed a definite difference in homing performance. With terns both speed and per cent returns were less from the Gulf of St. Lawrence. Three out of ten returned from the Bay of Fundy, while only one out of ten came back from the Gulf of St. Lawrence. With gulls the homing varied in the same way. In neither case was the difference as large as one would expect if the coastlines were followed blindly. The first two gulls to return from the Gulf of St. Lawrence probably flew directly across the isthmus, for their homing time is approximately that of the first birds back from the Bay of Fundy. But others were so slow that they could have flown around Nova Scotia, while perhaps the slower birds of the Bay of Fundy group flew down the Nova Scotia side of the bay and then turned back. This suggests the possibility that birds released along an unfamiliar stretch of coast might remain near it, flying in either direction for some time and turning back if they found nothing familiar. About half should take the right direction if they did this, while the others might be able to realize their mistake after flying two or three hundred miles and still be able to return in time to constitute the slower returns from actual coastal release points.

A comparison of the birds released at Lancaster, Charlotte, South Hero, Mt. Johnson, and Montreal is also interesting. (Shipments 17, 18, 19, 20, 21, and 22). All were released along watercourses, but on very different ones which would vary widely in their usefulness as guide-lines for an exploring bird. At Lancaster the only river is the Connecticut which dwindles to a very small size within 50 miles to the north, but flows straight south to Long Island Sound with which the gulls were probably familiar. Lake Champlain is drained by the Richelieu River, flowing north; but Lake George and the Hudson valley might look equally attractive to a lost gull. Montreal, however, is on a large river which would have led the gulls far astray if followed in either direction. The returns show a slight deterioration in homing performance as we go from Lancaster and Lake Champlain on the one hand to Mt. Johnson and Montreal on the other. The Mt. Johnson results might be explained by the weather, but the Montreal release was on the same day with the same conditions as the Lancaster and the first South Hero shipments.

BEHAVIOR AFTER RELEASE

There is only one way to establish with certainty whether birds in unknown territory fly straight home rather than by exploring

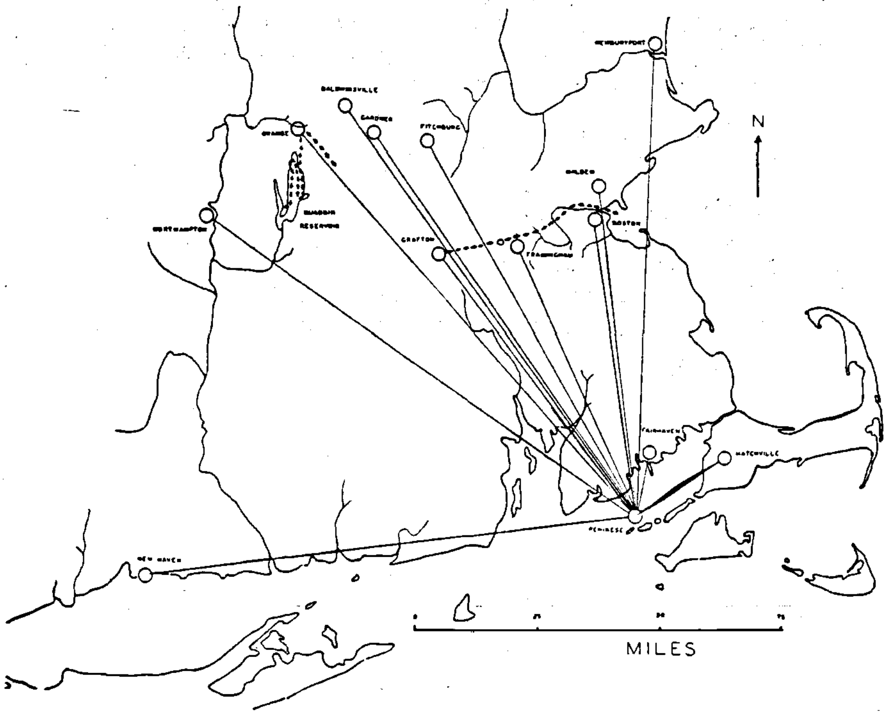


FIG. 4. Release points of gulls and terns, together with actual return routes of three gulls traced by direct observation from airplanes (cases 4, 5, and 6).

at random. The return route must be observed directly, either by recoveries en route or by following the birds. As described above, it is easy to observe the initial direction taken by a bird immediately after its release. But unless special methods are used it is seldom possible to trace them for more than about a mile. Twenty-five Herring Gulls were thus observed near the point of release. As with some other species (Rüppell 1935), there was no marked tendency to start home in the correct direction.

To analyse the results of these observations further, I have computed the coefficient of correlation between the speed of the bird's return and the deviation of its initial course from the true course home. If the birds tended consistently to continue their initial course for long distances, those returning first should be the ones showing the least deviation from the true direction of home, and the correlation between deviation and speed should be high and negative. Actually the coefficient of correlation for 25 gulls between deviation (compass points) and speed of return (miles per day) was +0.772, and the coefficient between deviation and order of return was −0.286. This indicates that if anything the birds which started in the wrong direction were the first to return.

However, the direction of the first mile or two of flight may be determined by local topography, a search for food or water, or merely a desire to depart as rapidly as possible from the observer. There is almost always much circling and changing of direction at this time, although there was no indication of any one definite pattern of behavior on release, some birds flying off immediately in a straight line, others circling and still others landing on the ground or water at the first opportunity and remaining there for long periods. Of course, birds in poor condition would often be slow to take off, and on hot overcast days when the air was very stable and had little "lift" the gulls were noticeably reluctant to fly at all. This is merely a special case of the dependence of gulls on updrafts which has been noted by Woodcock (1940).

By methods described above it was possible to observe a few Herring Gulls for longer distances, in one case for 37.5 miles of the return flight. Most of the gulls discussed below are included in the 25 whose initial direction was found not be to correlated with speed of return. Except for Case 3, the birds may not have been far from familiar territory. This is particularly important in considering Cases 4, 5, and 6.

Case 1.—At Charlotte, Vt., on May 16, 1940, nine gulls were released on an overcast day with low clouds and occasional rain showers. The wind was southeast and fresh to strong. The birds were followed with a 50-power telescope from the top of a 900 foot hill (Mt. Philo) which rises steeply from the surrounding plain about two miles west of the release point. Eight birds landed on Lake Champlain about a mile east of the point where they were set free. One, however, started directly southeast—almost exactly in the direction of its home. Yet this bird made the poorest homing record of the group. No sign of it was seen until 39 days after its release when a bird with worn paint marks was observed which might have been the one in question. The paint was too badly worn, however, to permit certain identification, so that it is questionable whether this gull returned at all.

Case 2.—Ten birds were released May 26, 1940, at the foot of a 750 foot hill (Mt. Johnson) near the Richelieu River, about half way from Lake Champlain to the St. Lawrence. The wind was southeast and moderate. The birds' home lay 291 miles to the southeast. The birds were watched from the hilltop with binoculars and telescope and the behavior of those which could be traced for any distance was as follows:

No. 41—Circled constantly but drifted gradually north and was lost about five miles due north of the release point. This bird returned in 79 hours, the fastest of the group.

No. 43—Flew north with much circling and was lost seven miles north of the release point; homing time 91 hours, the third bird to return.

No. 44—Circled near release point, found an updraft and rose within a few minutes to 4,000 or 5,000 feet. Return time, 7 days, 21 hours, the eighth bird to return.

The remaining Mt. Johnson birds either rested on the ground until the observers left or were lost before they had flown more than a mile. None flew south while under observation.

Case 3.—One of the five gulls of group 25 released May 31, 1940, at Port Stanley, Ontario, was observed by Mr. and Mrs. J. M. Spiers at Toronto, Ontario, from June 9 to June 12. This bird returned to Penikese on the 16th, and at Toronto it was not very far off the true course home. Evidently the final 460 miles from Toronto to Penikese were accomplished in four days, whereas the gull may have used nine days to cover 115 miles from Port Stanley to Toronto.

Case 4.—On June 28, 1940, gull No. 140 was released at 3:55 p.m. from an airport near Grafton, Massachusetts—67 miles N.W. of Penikese. It was followed by Dr. Norris Rakestraw of the Woods Hole Oceanographic Institute in a Piper "Cub" tandem plane with Dr. Mary Sears as observer. The wind was W.S.W. less than 10 m.p.h. on the ground. The gull was unable to soar, but flew off with a steady flapping flight, N.W. for five minutes, south, then east, southeast with occasional circling, and then east for twenty minutes. During this period there was much changing of direction, but the bird's next course was easterly. At 4:30 p.m., it landed for seven minutes on a reservoir near Ashland, Mass., then rose and headed east again for about seven minutes when it evidently found a weak updraft. For at this point it rose to about 1,000 feet although it had previously never exceeded 200–300 feet. At all times, however, the flight was flapping and not soaring. When it had risen to about 1,000 feet, Boston was clearly visible from the plane and apparently the gull could see it also, for after this point there was very little deviation from a straight easterly course. The bird was followed all the way to Boston harbor, but was unfortunately lost there. At 6:15 p.m. of the following day this gull returned to Penikese, although there had been strong S.W. winds, rain, and generally nasty weather most of the day. This gull's course, as far as it was traced, is shown in Fig. 4.

Case 5.—On May 23, 1941, seven gulls were released at Orange, Mass., and observed from a 90 h.p. Rearwin airplane with Dr. Norris Rakestraw again flying and the writer observing. In the early morning it was clear and calm, but gradually a N.N.W. wind sprang up and cumulus clouds began to form at about 4,000 feet. At 9:45 a.m. when the first bird was released the ground wind was 15–25 m.p.h. and gusty. Cumulus clouds had by then covered about half the sky; and by 11:00 there was an almost solid overcast; at 11:45 there was one brief shower. The temperature was about 60° and there were strong updrafts. The wind velocity increased throughout the day and by 2:00 p.m. it was at least 50 m.p.h. at 2,000 feet. The visibility, excellent at the beginning of the observations, became steadily poorer, and at 2:00 p.m. was 5 miles to the west and 8–9 miles in other directions.

Five of the birds were lost before they had flown more than a mile; their initial directions were included in the correlation calculations on page 20. The strong thermal updrafts enabled all birds to soar well and they wheeled in circles with very little flapping, often gaining altitude rapidly without much effort.

No. 403, released at 10:30 a.m., flew strongly and with considerable circling S.S.E. to a pond about two miles from the airport where it had been released. It sat on a stump in the middle of the pond splashing and preening from 10:40 to 11:20 when it flew off, soaring and circling to the S.E. (downwind). At Petersham (about twelve miles from the release point) it evidently found an updraft of unusual intensity, for it circled steadily over one area and rose until our plane was forced to within 500 feet of the solid cloud base. The plane was not equipped with blind-flying instruments and could not safely (or legally) climb much farther. The gull continued to rise until it could no longer be observed because the wing of a high wing monoplane greatly restricts visibility at one's own altitude when the plane is circling.

When last seen this bird was 10 to 12 miles from the airport, at least 2,500 feet above the ground, and climbing rapidly so that it must soon have approached the clouds.

At 12:50 p.m., No. 171 was followed as it circled to the southeast from the airport, rising with little flapping, and when 2 or 3 miles from the airport it began the same rapid climb in a strong thermal updraft. At 1:05, it was lost at about 2,500 feet after the same frantic chase in steep climbing turns.

As shown in Fig. 2, this group of gulls (shipment No. 3) returned with remarkable speed. The weather conditions were ideal, and if the birds had merely drifted downwind while soaring the N.W. wind would have brought them to the coast quite near to Penikese. Since the wind was certainly 40 to 50 m.p.h. at altitudes to which two gulls were observed to climb, these returns may not represent any better orientation than that displayed by other groups.

Case 6.—On July 18, 1941, another successful attempt was made to follow gulls released at the Orange airport with the writer flying an 85 h.p. Rearwin two place tandem airplane and George Scott observing. The weather was ideal for the purpose, temperature about 70° or 75° F., wind gentle S. to S.W. and a high broken overcast at more than 5,000 feet. The visibility was about ten miles. No. 367, released at 10:00 a.m., alighted on a sandy patch and was lost, but when No. 369 was released, at 10:10, it flew to the south and was soon joined by the first bird. These gulls flew mostly by flapping, with an occasional short period of gliding flight; there were apparently no updrafts capable of supporting prolonged soaring.

These two gulls remained within a few hundred feet of each other and flew to the south with some circling. They turned S.W. as they approached Quabbin reservoir, a large artificial lake (as yet only partially filled) lying about five miles south of the airport. At 11:25, both gulls landed on a wooded island in this lake and then moved to the middle of one of its arms a few minutes later. After five or ten minutes more, one of them flew north almost to the end of the lake and then back to where they had separated. The other had disappeared by this time, and the one just back from the north end of the reservoir began to explore its southern branches. At 11:55 it was over the S.W. section of the lake heading S.W. or W. as though preparing to fly over the land. The Connecticut River lay about 15 miles to the west, but it would not have been visible to the gull, for even at 2,600 feet we could not see it and the gull was within 300 feet of the lake.

At this time we lost sight of the gull because an army training plane appeared and flew for some minutes so close to us that we had to cease circling and following the gull to avoid collision. When this exasperating disturbance ended we searched the entire vicinity but failed to find either gull again.

Fig. 4 shows the relative positions of Penikese, Grafton, and Orange and the routes followed by these birds while they were under observation. These maps of return routes are tantalizing in their inadequacy; but they show how much will be learned when more such work is done. The method of airplane observation is quite practicable under the right conditions; and it offers the best method to test critically the exploration hypothesis. Unfortunately it is slow and expensive; but after the present war light planes and helicopters should be developed further and the method can then no doubt be extended.

Despite their inadequacy, a few tentative generalizations can be made from the data presented above. Evidently a gull released inland tends to search for strong updrafts and to climb on them if possible to at least 3,000 feet (Cases 3, 4, and 5). This will give greater visibility if the air is clear, or if the bird is going to drift with the wind, it would be carried much faster at higher altitudes. If updrafts are available the birds may drift downwind while riding on them (Cases 2 and 5). They frequently fly to a large body of water and rest there to preen and drink or feed (Cases 1, 4, 5, and 6). The direction of flight up to three miles from the release point is in no way related to the true direction of home. Of seven birds followed for more than three miles only two (Case 2) took a completely wrong direction. Those followed farthest (Cases 3, 4, 5, and 6) were making relatively small deviations from a true course home (45°, 75°, 0°, and 45° respectively). But it should be recalled that in Cases 4, 5, and 6 the birds may have found familiar landmarks. Many more observations like those presented above will be needed to give a final answer to the question raised by Hodge (1894) and Claparède (1903): Do birds fly straight home or do they explore at random?

Miscellaneous Observations

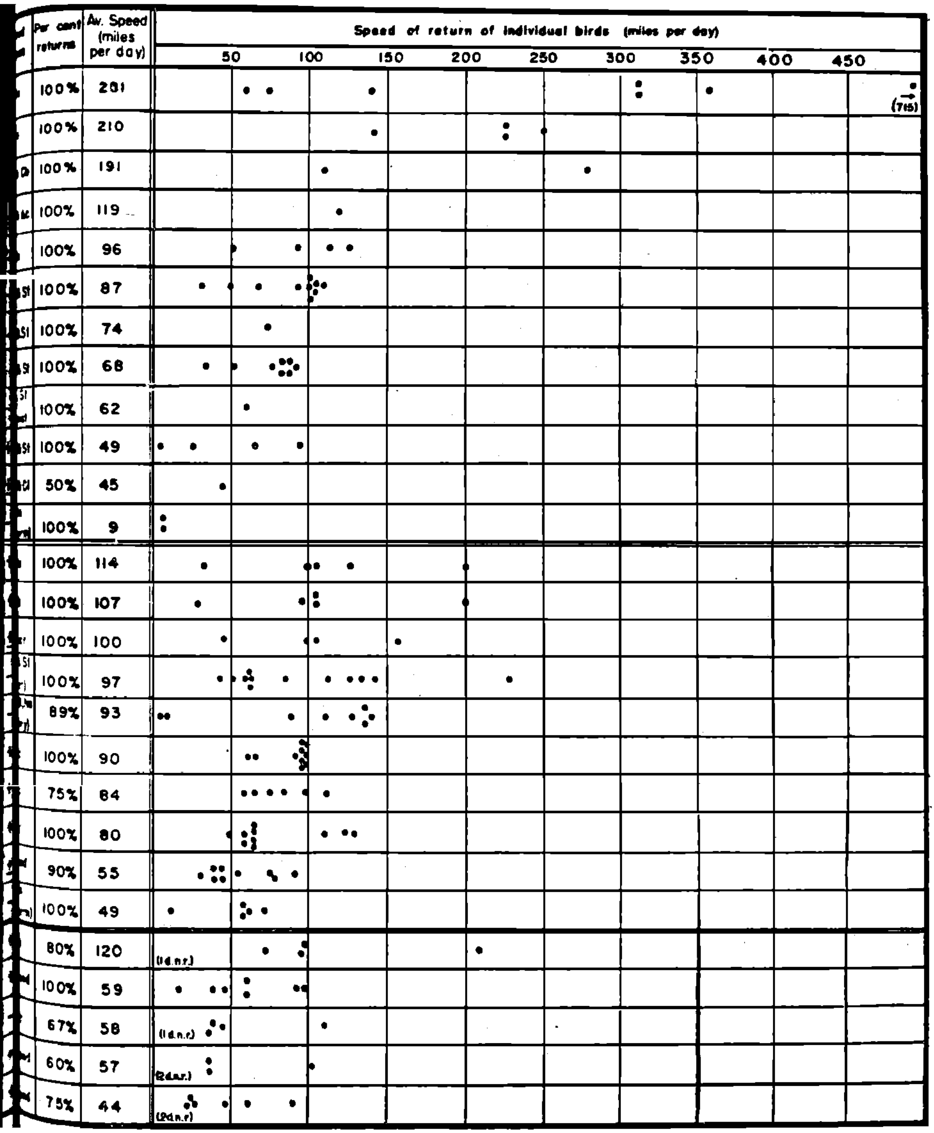
On May 26, 1940, four gulls were carried to South Hero, Vt., and kept in constant rotation from New Bedford, Mass., to Keene, N. H., when the mechanical rotating device (mounted on a trailer) ceased functioning. The birds (group 34) showed no ill effects of the treatment, and behaved normally on release, as shown in Table 2. They were distinctly slower (67, 60, 52, and 36 miles per

TABLE 2. MISCELLANEOUS HOMING EXPERIMENTS WITH HERRING GULLS
(Same abbreviations as Table 1)

Shipment No.	*Place and time of release*	*Bird No.*	*Total time*	*Speed (miles per day)*
30	Fairhaven, Mass.	129	6 hrs.	60 (2.5 m.p.h.)
	15 m. N.N.E.	133	22 hrs.	16 (0.7 m.p.h.)
	June 7, 1940	131	25 hrs.	14
	10:20 a.m.	132	5 d., 3 hrs.	3
	4 hrs. i.c.	130	6 d., 8 hrs.	2
31	Hatchville, Mass.			
	22 m. N.E.	154	17 hrs.	31 (1.3 m.p.h.)
	May 17, 1941	156	17 hrs.	31 (1.3 m.p.h.)
	3:30 p.m.	155	26 hrs.	20
	7 hrs. i.c.			
32	Woods Hole, Mass.	197	9 hrs.	40 (1.7 m.p.h.)
	15 m. E.N.E.	200	78 hrs.	5
	June 8, 1941	198	4 d., 6 hrs.	4
	9:45 a.m.	301	4 d., 6 hrs.	4
	25 hrs. i.c.	199	8 d., 2 hrs.	2 (weak)

Group No.	Place of release	Date & time of release	Number of birds	Distance shipped (miles)	Direction shipped	Winds	Convection
3	Orange	May 24, 1941 - 10 a.m.-2 p.m.	7	104	N. W.	+++	++
14	Newburyport	May 15, 1941 8 p.m.	4	94	N.	+++	++
6	Orange	July 12, 1941 10 a.m.	2	104	N.W.	++	++
5	Orange	July 5, 1941	1	104	N.W.	--	++
2	Northampton	June 15, 1940	4	106	N.W. x W.	+	+
8	Baldwinsville	May 21, 1939	10	101	N.W. x N.	+	--
11	Framingham	July 11, 1941	1	62	N.N.W.	--	±
1	New Haven	May 21, 1939	9	100	W.	-	--
10	Grafton	June 28, 1940	1	67	N.W.	--	±
13	Malden	June 5, 1940	4	67	N.	+	++
7	Orange	July 18, 1941	2	104	N.W.	--	±
12	Boston	May 22, 1940	2	63	N. x W.	++	---
16	Atlantic City	June 17, 1941 12 noon	5	234	S.W.	++	+++
24	Bucksport	May 22, 1941 5 a.m.	5	241	N.N.E.	++	+
23	Bucksport	May 15, 1941 5 a.m.	4	241	N.N.E.	--	±
19	South Hero	June 2, 1940 5 p.m.	12	247	N.W. x N.	++	+
17	Charlotte (Lake Champlain, 20 m. S. of S. Hero)	May 16, 1940 2 p.m.	9	230	N.W. x N.	+	+
22	Lancaster	June 1, 1939 9 a.m.	10	214	N. x W.	++	++
21	Montreal	June 1, 1939 7 p.m.	8	302	N.N.W.	+	+
18	South Hero	June 1, 1939 3 p.m.	10	247	N.W. x N.	+	+
20	Mt. Johnson (near Montreal)	May 26, 1940 1 p.m.	10	291	N.N.W.	-	-
15	Atlantic City	June 3, 1941 3 p.m.	5	234	S.W.	--	--
29	Savannah	June 4, 1941 3 p.m.	5	870	S.W.	++	++
26	College Bridge (near Sackville)	June 10, 1941 2 p.m.	7	445	N.E.	±	+
28	Chicago	May 31, 1941 4 p.m.	6	872	W.	-	--
25	Port Stanley	May 31, 1940 4 p.m.	5	540	W. x N.	+	±
27	Shediac Bay	June 10, 1941 12 noon	8	456	N.E.	±	+

Fig. 2 - HOMING



R HERRING GULLS.

33	Orange, Mass. 104 m. N.W. (anaesthetized en route) June 5, 1941 11 a.m. 24 hrs. i.c.	194 193 195 192	32 hrs. 44 hrs. 4 d., 8 hrs. 14 d., 9 hrs.	78 57 24 7
34	South Hero, Vt. (Lake Champlain) 247 m. N.W. x N. (rotated during transportation) May 26, 1940 4:00 p.m. 34 hrs. i.c.	50 99 100 102	88 hrs. 4 d., 2 hrs. 4 d., 19 hrs. 6 d., 21 hrs.	67 60 52 36

day) than others released at South Hero (shipments 18 and 19), but little if any slower than those released the same day at Mt. Johnson (shipment 20) about 40 miles to the north. In view of the distinct possibility that gulls home by exploration, no further attempts at rotation experiments were made, nor did I test the effects of rotation *per se.* The slight difference between the rotated birds and group 20 does not seem sufficient to offer any serious support to the kinesthetic theory.

One preliminary experiment with transportation under anaesthesia was also attempted (group 33—see Table 2). Abbott veterinary Nembutal (1 gram per ml.) was given in two equal intramuscular doses into each pectoral muscle. A total initial dose of 0.6 to 1.0 ml. was sufficient to anaesthetize two gulls completely so that all postural reflexes were lost, although the nictitating membrane responded when the cornea was touched. The birds had to be well wrapped, otherwise they became chilled (first symptom was cold feet, followed by violent shivering and death). To keep the birds unconscious extra doses of 0.5 ml. were necessary at 45 min. to 2 hour intervals. There was great individual variation, one bird dying after 1.2 ml., while others were still active after greater doses. To keep four birds unconscious during a five hour auto trip from Barnstable, Mass., to Orange required 1.5, 2.0, 2.1, and 2.7 ml. respectively.

Two of the birds (Nos. 193 and 195) recovered well and flew actively after less than an hour's rest. The others, Nos. 192 and 194, were noticeably weak when liberated. Unfortunately there was a steady rain and stormy winds on the day of release, so that the rather poor homing which resulted may have been due to this cause. The only comparable weather occurred after shipment No. 12 when even slower homing resulted. The details of this shipment under anaesthesia are given for the possible benefit of future workers; obviously the results themselves are of no significance.

One fact which I am totally unable to explain is the poor homing of birds released very close to home (see Table 2—shipments 30, 31, and 32). I can only point to similar phenomena noted in homing experiments with other birds (Loos, 1907; Goethe, 1937; Watson and Lashley, 1915; and Griffin, 1940a). Even bats home better when released at 10–50 miles than when set free very close to their homes (Griffin, 1940b). If this is a consistent effect it might conceivably offer a clue to the fundamental problems of homing.

With bats I have offered the explanation that the annoyance of trapping and handling was, in local releases, associated with the home, and thus homing was discouraged, while at greater distances such was not the case. A purely local release of four Herring Gulls resulted in the return within 3 or 4 hours of all four birds, so that this explanation does not seem as satisfactory as with bats.

DISCUSSION

Like most preliminary data, these homing experiments seem to raise more questions than they solve. No really valid comparisons of homing times from various release points are possible without several releases at each point on as many days. Only in this way could one obtain statistically significant results in which the effects of weather conditions and other variables could be neglected. So far I have not been able to operate with Herring Gulls on a sufficiently large scale to secure such data; and conclusions based on a single release at a given point are very dangerous regardless of the number of individuals involved.

It is clear that the gulls scattered in all directions for the first mile or two, and if they are able to select the correct direction without visual landmarks, the process of orientation requires considerable time. Very few gulls or terns came home at average speeds even approximating their known velocity of flight. The majority may have either deviated considerably from the true course home, as in exploring for known visual landmarks, or else they may have spent long periods resting or searching for food. Three gulls showed a marked improvement in homing speed when shipped a second time to the same release point, while with terns at least there was a clear drop in percentage (but not in speed) of returns as the distance of shipment was increased. These facts are consistent with the hypothesis that the birds may scatter in any direction from the release point and return only when they encounter by chance some part of the area with which they are already familiar. Evidence concerning the actual route followed is necessary to actually test such theories.

In addition to the records listed above under "Behavior after release" Rüppell (1937) records three cases in which starlings were recovered *en route* with deviations from the true course of 9°, 9°, and 20° and Gibault (1930) reports six cases in which untrained pigeons visited other lofts en route home from unknown territory, none registering more than about 60° deviation. These records indicate that an essentially straight course is followed, but there are some exceptions (Case 2 above) and more observations of the return route are needed before one can draw satisfactory conclusions. The use of airplanes and helicopters for the study of bird behavior is a practically untouched field, and it seems to offer great promise of solving not only this problem but many others as well.

SUMMARY

1. 176 herring gulls were released at distances from 15 to 872 miles from their nests on the coast of Massachusetts. 163 or 93% returned the same season that they were transported. Of 80 common terns carried 94 to 456 miles, 34 or 42.5% were definitely observed at their nests within the next few days.

2. The speed of return of herring gulls varied from 15 miles in 8 days to 104 miles in 3¼ hours. At distances of 60 to 300 miles practically all birds returned, most of them covering from 50 to 200 miles per day. At greater distances there were almost always some losses, but at 872 miles inland 4 out of 6 returned. In most cases the average speed of return was far below the gulls' known velocity of flight (25–30 m.p.h.), so that if they flew at all continuously they must have deviated extensively from the direct course home.

3. Those terns which did come back to Penikese averaged from 31 to 350 miles per day—most of them covering more than 100 miles per day.

4. Much of the variability in the gulls' homing seems to be correlated with weather conditions. Rapid homing is favored by unstable air with strong updrafts to permit soaring, moderate to fresh favorable winds, good visibility, and lack of violent winds or prolonged precipitation.

5. Returns from territory which the banding evidence indicates to be familiar to the birds were faster and losses fewer. This tendency was clearly marked with terns, but with gulls it was so confused by weather-induced variability that its existence can be questioned.

6. Three gulls homed very slowly in 1940 but when shipped to the same release points in 1941 they returned with remarkable speed. This could have been caused only in part by the weather conditions, and may well have been due to the learning of visual landmarks during the first return flight.

7. A slight deterioration in homing could be noted when birds were released on river systems or parts of the coastline where the

topography might tend to lead them astray; but the data are insufficient to constitute more than a suggestive tendency.

8. Twenty-five Herring Gulls were observed for the first two to 37 miles of their return routes, and they showed no correlation between the correctness of their initial direction and speed of return.

9. Two birds were observed to fly 5 and 7 miles in a direction directly opposite to that of their home. Five others were followed for 5 to 37 miles with an airplane and one was observed en route at 115 miles from the release point. When last seen these birds had deviated about 45°, 75°, 0°, 0°, 45°, and 45° from the true course home. The two showing no deviation were drifting downwind.

10. Homing was very slow when the birds were carred only 15–25 miles—a fact which is difficult to explain in view of the striking returns from much longer shipments.

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