INDIVIDUAL EXPERIENCE AS A FACTOR IN THE NAVIGATION OF MANX SHEARWATERS

G. V. T. MATTHEWS

FOR probing into some aspects of bird navigation, such as the parts played by learning and by individual variation, it becomes necessary to use the same birds repeatedly on homing flights. Pigeons have been used in this way (e.g., Matthews, 1952b; 1963) but, despite intense artificial selection over the last century, they are inferior in navigational ability to wild, long-distance migrants. Wild birds, however, are liable to desert their nests if subject to repeated disturbance during the nesting season; finding the same bird in succeeding years is often difficult; and the smaller species are in any case short-lived.

Leaving aside birds repeatedly retrapped in winter after being displaced short distances, the literature has little to offer on the study of individual navigation. Watson and Lashley (1915) record repeated sorties of 3 Noddy Terns (*Anous stolidus*) and 1 Sooty Tern (*Sterna fuscata*); Rüppell (1935) of 20 Starlings (*Sturnus vulgaris*); Wojtusiak and Ferens (1938) of 15 Swallows (*Hirundo rustica*); Lack and Lockley (1938) of 2 Manx Shearwaters (*Puffinus puffinus* = *Procellaria puffinus* of European literature); Griffin (1943) of 7 Herring Gulls (*Larus argentatus*); Matthews (1952a) of 4 Lesser Black-backed Gulls (*L. fuscus*) and 1 Herring Gull; Spaepen and Dachy (1953) of 7 Swifts (*Apus apus*); and Sargent (1962) of 19 Bank Swallows (*Riparia riparia*). Nothing very conclusive derived from the results of these studies. In most cases the birds were released at the same place both times. In 22 cases the second return was then faster, but in 22 cases it was slower or the bird failed to home. The Bank Swallows, which were released at different points, "generally showed better homing success than those released for the first time" (Sargent, 1962: 237).

The Manx Shearwater (*Puffinus puffinus puffinus*), besides being an accomplished navigator, is a long-lived bird which returns to the same, easily accessible nesting burrow year after year. Homing experiments were therefore carried out with this species from a colony on Skokholm Island (51° 42′ N, 05° 17′ W) in four successive breeding seasons, May to July. The general and experimental results have already been reported (Matthews, 1953b; 1955a, b); this paper presents and interprets the data obtained from repeated releases of individual birds.

TECHNIQUE

The methods of locating, excavating, and marking the nesting burrows, and of transport, have been detailed in the earlier papers. All releases,

TABLE 1

RELEASE POINTS USED IN THE EXPERIMENTS*

Release point	*Position of Skokholm with reference to release point*		*Symbol in Figure 1*
	Bearing	*Distance (miles)*	
Reading	274°	180	R
London	273°	215	L
Cambridge	262°	235	C
Llandovery	254°	65	Ll
Tenbury	252°	100	T
Birmingham	252°	155	B
Manchester	232°	170	M
Haydon	211°	265	H
Weather ship	150°	415	W
Kildare	146°	115	K
Dunmanway	087°	160	D

* See also Figure 1.

except one from a weather ship in the open sea (56° 40′ N, 10° 42′ W), were at points well inland where Manx Shearwaters do not penetrate except as storm-blown strays. The release points are listed in Table 1 and illustrated in Figure 1. The latter also indicates those coasts of southwest Britain with which the Skokholm population would be expected (from banding returns) to become familiar in the course of feeding and migratory journeys. They migrate down the coast of western France to northern Spain and then across the Atlantic to winter off Brazil and Argentina.

Every bird used was a known breeder in the current season, being taken off the egg or (rarely) chick. Only one trip was enforced in each season and only one bird of each pair was used. These precautions were to keep desertions minimal. The remarkable ability of the egg to withstand chilling (Matthews, 1954), and the capacity of the adult for remaining many days on the nest without feeding, were valuable in this respect.

Each bird was released singly and observed until out of sight with binoculars, its vanishing point being noted and approximated to one of 16 points on the compass. The nest burrow was checked two or three times a night (the birds only return during the summer darkness) until the tenth night; thereafter irregular checks were made.

The main object of the program was to study the individual navigational performances in unknown areas. Accordingly, second and subsequent releases were made at different places and, as far as possible, in different directions. Inevitably plans could not always be carried through.

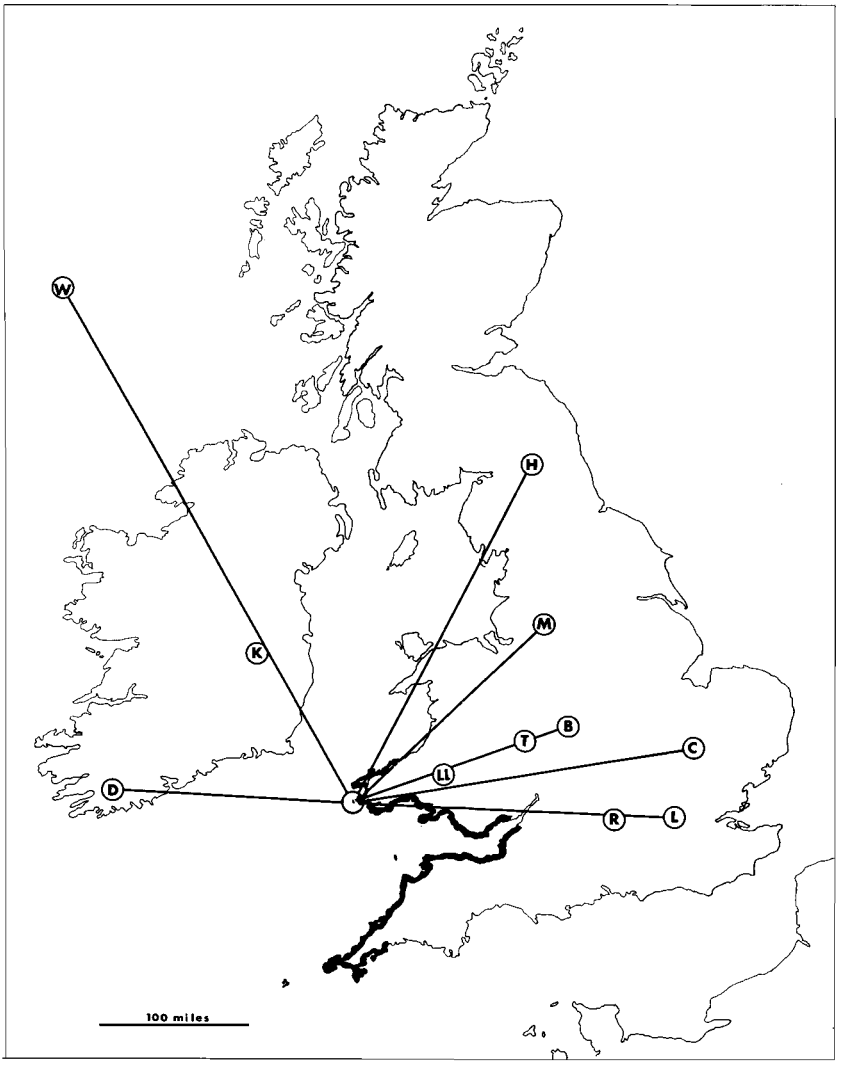

Figure 1. The location of release points. The distances, bearings, and names are listed in Table 1.

Chosen homers might not be incubating when the time came to load a shipment; the small boat from the harbor seven miles away might be prevented from sailing by the weather; the intended liberater might be unable to carry out his task; the Irish authorities might (and did) ban a crack consignment of homers on the grounds that the shearwaters were four-footed animals liable to foot-and-mouth restrictions.

TABLE 2

DISTRIBUTION OF VANISHING POINTS OF SHEARWATERS RELEASED UNDER DIFFERENT CONDITIONS*

*Class***	*Conditions*	*Compass point deviation from home bearing*									*Number of sorties*	*Per cent of total deviating ±3 points or less*
		±0	*±1*	*±2*	*±3*	*±4*	*±5*	*±6*	*±7*	*±8*		
A	Sun	13	20	15	10	5	5	6	6	1	81	72
	Cloud	2	9	16	7	11	4	8	11	6	75	45
B	Sun	8	15	8	11	11	1	6	7	4	71	59
	Cloud	3	8	11	5	9	12	12	5	6		38

* Figures in all columns but that on the right represent absolute numbers.

** A, birds released either under clear or under cloudy skies; B, individual birds released both under clear *and* under cloudy skies.

RESULTS

In all, 144 individual Manx Shearwaters were released more than once at a distance from home, giving a total of 343 sorties; 94 made two, 45 three, and 5 made four sorties. In the appendix are given details of the dates and weather conditions at the times of the 36 experiments in which the present birds were released. Only six sorties were made from a place at which the birds had been previously released, and these have been excluded from the general analysis. Full details of each individual sortie are deposited at the Edward Grey Institute, Oxford, England.

Initial orientation.—A completely random dispersion will result in 7/16, i.e., 44 per cent, of the vanishing bearings falling within ± 3 compass points of the home direction; for a significant homeward tendency (at 5 per cent; i.e., 95 per cent confidence level) the proportion must exceed, for example, 55 per cent of 80 bearings, 60 per cent of 40 bearings, etc. Such homeward tendencies in shearwaters have been demonstrated (Matthews, 1953b) when skies were clear or lightly clouded. With heavy broken cloud, and especially with overcast, no tendency, other than to drift downwind, was observed. The present analysis supports and extends these conclusions, and only results falling within 95 per cent confidence limits are stressed.

In Table 2, A, the comparison is made between 81 sun and 75 cloud releases when the same birds were *not* used in both conditions. The definite homeward tendency of the birds released in sunny conditions contrasts with the random scatter of those released with heavy cloud or overcast. The second comparison (Table 2, B) concerns 71 birds released alternately in sunny *and* in cloudy conditions or vice versa. The homeward tendency in the sunny sorties is not quite so marked but is still quite significant; the cloud sorties again cannot be distinguished from a random scatter. This excludes the possibility that differences such as in the first

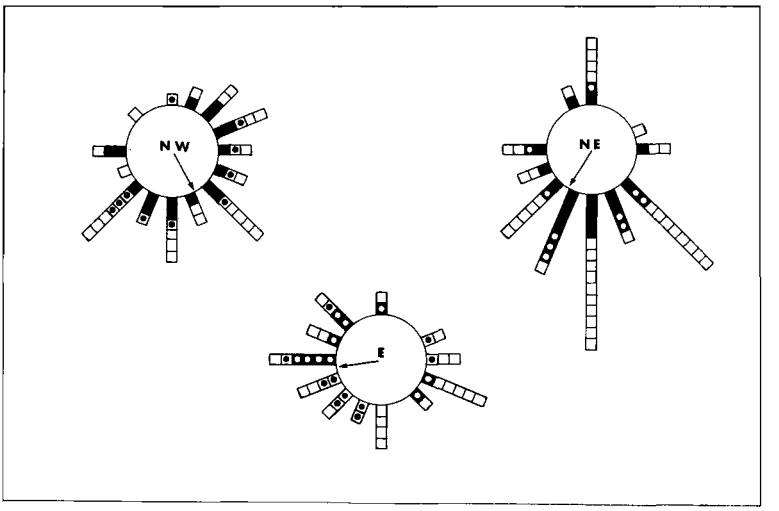

Figure 2. The homeward tendency of vanishing points for Manx Shearwaters released in sunny conditions at points different in direction from home, with particular reference to changes in the orientation of individuals. Key: black squares, birds released both to NW and NE; white circles on black, birds released both to NE and E; black circles on white, birds released both to E and NW; white squares, birds released at points of similar bearing from home (but *not* at the same place) each time, or which were released in cloud the other time, or for which the paired orientation data are lacking.

comparison are due to the use of different individuals. The *same* individuals are apparently able to orient in one set of conditions but not in the other. The suggestion that some type of sun orientation must be concerned is strengthened.

The geographical relevance of the Manx Shearwaters' departure tendencies is more clearly demonstrated by grouping the vanishing points according to the direction of the release points from Skokholm. Table 1 shows that these fall into three groups, to the east (Skokholm bears 274°–252°), to the northeast (232° and 211°) and to the northwest (150° and 146°, there being no sunny release from Dunmanway). In Figure 2 the vanishing points are superimposed accordingly. The direction tendency shifts roughly according to the direction of the release point. The 37 cases in which two sunny sorties were made from different directions by the same bird are marked distinctively. These are shown to fly in a different direction on the subsequent release, generally in one more appropriate to the new home direction.

Figure 2 also demonstrates that there is no indication of a fixed "nonsense" orientation for the Skokholm shearwaters such as has been demon-

TABLE 3

DISTRIBUTION OF VANISHING POINTS IN RELATION TO PAST EXPERIENCE*

*Class***	*Experience*	*Compass point deviation from home bearing*									*Number of sorties*	*Per cent of total deviating ±3 points or less*
		±0	*±1*	*±2*	*±3*	*±4*	*±5*	*±6*	*±7*	*±8*		
A	Sun on first	6	7	8	5	–	2	3	2	1	34	76
	Sun on second	7	2	9	4	7	–	4	1	–		65
B	Sun on second (Cloud on first)	4	11	2	7	5	1	1	2	1	34	71
C	Inexperienced	–	16	7	6	2	2	3	1	–	37	78
	Experienced	4	16	3	6	7	1	–	3	1	41	71

* Figures in all columns but that on the right represent absolute numbers.

** A, individuals released in sun on two occasions; B, other birds released with sun on the second occasion but which had had cloud on the first; C, direct comparison of inexperienced and experienced birds released on the same day, with sun.

strated in terns, ducks, and probably some stocks of homing pigeons (Griffin and Goldsmith, 1955, 1956; Bellrose, 1958; Matthews, 1961, 1963). It was seen from the start of the experiments that release points in several directions were needed "to check that orientations were not due to some local peculiarity of topography or, say, a simple tendency to fly west when released inland" (Matthews, 1953b). Southerly release points were deliberately omitted since they would have had to be at relatively short distances and/or close to familiar coasts.

It is perhaps remarkable that any homeward tendency is apparent while the birds are still in sight of the liberater, within, on the average, three minutes after release. The whole process of capture, transportation, and release must be something of a traumatic experience, and one might expect the birds to concentrate first on putting as much distance between themselves and the liberater as possible, and on doing this in any direction. Repeated releases might then lead to less scatter, not so much from an improvement in the accuracy of the orientation process, as from a reduction in this period of random flight, so that orientation is more likely to be taken up within sight of the observer.

Two experiences of sunny conditions on release did *not* lead to an improvement of the initial orientation, as will be seen from Table 3. The second orientation was, moreover, no better than that for birds whose first release had been disorientated in cloudy conditions, i.e., the experience of orientating in sunny conditions did not lead to improvement at this stage of the bird's career (it already having had plenty of experience on migration and feeding flights). The lower part of Table 3 confirms the

TABLE 4

PERCENTAGE DISTRIBUTION OF HOMING TIMES OF SHEARWATERS IN RELATION TO EXPERIENCE

*Class**	*Release*	*Night of return*					*Number of sorties*
		1st–2nd	*3rd–4th*	*5th–10th*	*11th–20th*	*Later*	
A	First	20	18	28	11	23	100
	Second	43	31	11	9	6	
B	Second	31	38	14	12	5	42
	Third	60	26	6	–	–	

* A, birds returning on both first and second releases; B, birds returning on both second and third releases.

lack of improvement by comparing the orientation of inexperienced and experienced homers released on the same four sunny days (Haydon, 25-V-52, 22-VI-52, 30-V-54; and Kildare, 30-VI-53). Thus when released under identical conditions the experienced birds did *not* have an advantage over those being released for the first time.

Only 13 birds had their third release in sunny conditions, but they showed a remarkably strong homeward tendency (e.g., ±0, three; ±1, six; ±2, two; –3, one; –7, one; in all 92 per cent within ±3). This might suggest that experience was beginning to tell, but 11 (85 per cent) of these birds on their previous sunny release had been within ±3 compass points of home. It might be that they were a superior set of navigators or that they learned to ignore disturbance more readily. A much bigger sample of repeat releases in good weather is needed, it being particularly unfortunate that the summer in which most third and fourth sorties were made was a bad one, even by British standards. However, with 37 third or fourth sorties in cloudy conditions it is possible to state that experience does *not* lead to orientation in the absence of the sun—the scatter still being essentially random (49 per cent within ±3 points).

Homing performance.—In contrast to the initial direction tendencies, the homing performance clearly improves as a result of test experience. In Table 4 the homing times of birds which returned on both first and second or second and third sorties are compared. Losses on the second (or third) sorties cannot be considered at this point since losses on the first (or second) sortie will automatically have been excluded from the comparison. The improvements shown in homing on the second and third release are therefore *not* due to the elimination of inferior birds.

Slower returns could be expected when the shearwaters were released in overcast conditions and/or late in the breeding season, i.e., after mid-June (Matthews, 1953b). The comparisons in Table 4 must therefore be examined further lest the improvement was wholly due to a change in release

TABLE 5

PERCENTAGE DISTRIBUTION OF HOMING TIMES OF INDIVIDUAL SHEARWATERS, UNDER DIFFERENT SETS OF RELEASE CONDITIONS

Night of return	*Conditions on second release**					
	Worse		*Similar*		*Better*	
	A	*B*	*A*	*B*	*A*	*B*
1st–2nd	29	44	28	51	15	50
3rd–4th	27	29	26	30	16	27
5th–10th	17	17	19	8	40	15
11th–20th	17	7	12	7	6	2
Later	10	3	15	4	23	6
Number of sorties	41		53		48	

* The conditions on the second sortie (B) are compared with those on the first (A). See text for definitions of "better" and "worse."

conditions. In Table 5 the pairs of sorties have been regrouped. In the first pair of columns one or both (5 cases) of these factors at the second release (B) were worse, i.e., sun in A, cloud in B and/or early season in A, late in B. In the second pair of columns conditions were basically the same or a change for the worse in one factor was matched by a change for the better in the other (19 cases), e.g., sun/late matched with cloud/early. In the third pair of columns one or both (14 cases) of the factors were better on the subsequent occasion.

It may be concluded that improvement on a subsequent release occurs regardless of conditions pertaining, but that the *degree* of improvement does depend on the conditions at the first sortie, i.e., there is more improvement when there is more room for it. The indications are that as birds gain in experience the conditions at release will have less relevance to homing performance. This is brought out by further regrouping of the data, in Tables 6 and 7. As shown in Table 6 there is a strong contrast between first sorties in sunny and in cloudy conditions, particularly in regard to the swiftest returns. On the second and third sorties the difference is much less, and birds released in cloudy conditions on their second sortie give a better performance than birds released in sunny conditions on their first sortie. Similarly (Table 7), a marked difference between early season and late season releases on the first sortie is much reduced by the second and possibly eliminated by the third (though the number of late sorties is then too small for a real comparison). Birds making late second sorties returned rather better than those on early first sorties.

A bird experiencing adverse (cloudy) conditions at a period (late season) when its homing urge may have diminished or its general physical condition may be poorest, might well be easily discouraged when subjected,

TABLE 6

DECREASING EFFECT, WITH INCREASED EXPERIENCE, OF POOR RELEASE CONDITIONS ON HOMING TIMES OF SHEARWATERS*

Night of return	*First sorties*		*Second sorties*		*Third sorties*	
	Sun	*Cloud*	*Sun*	*Cloud*	*Sun*	*Cloud*
1st–2nd	26	13	47	38	72	54
3rd–4th	24	11	29	34	21	28
5th–10th	24	33	16	7	7	18
11th–20th	7	15	3	14	–	–
Later	19	28	5	7	–	–
Number of sorties	54	46	58	42	14	28

* Expressed as percentages of the sorties under each set of conditions.

in addition, to the novel trauma of an experimental displacement. On subsequent occasions alarm and general disturbance should be less, and so the bird might press on with more determination and not be unduly disturbed if unable to determine its home bearing at release. Overcast conditions are unlikely to continue for a long period or over a wide area. The suggestion is, then, that improvement in the homing performance is largely a matter of habituation to the disturbance imposed by the experimenter. It may also be that an age factor is involved, older birds perhaps having a stronger impulse to return and/or being less easily deflected. The original age of the individual adults used was not known but they would certainly be a year older on each subsequent sortie.

Positive learning must also be considered. This is unlikely to concern the navigational process whereby the bird determines its position relative to home. All the birds used were adults with considerable migratory experience and we have seen that initial homeward tendency did not improve with experience when sorties were made from different release points. Sorties were, deliberately, only arranged from the *same* release point when

TABLE 7

DECREASING EFFECT, WITH INCREASED EXPERIENCE, OF RELEASE LATE IN BREEDING SEASON ON HOMING TIMES OF SHEARWATERS*

Night of return	*First sorties*		*Second sorties*		*Third sorties*	
	Early	*Late*	*Early*	*Late*	*Early*	*Late*
1st–2nd	32	8	45	35	57	(72)
3rd–4th	22	14	30	35	29	(14)
5th–10th	10	46	12	13	14	(14)
11th–20th	18	6	9	4	–	–
Later	18	26	4	13	–	–
Number of sorties	50	50	77	23	35	7

* Expressed as percentages of sorties under each set of conditions.

TABLE 8

HOMING TIMES OF SHEARWATERS WITH REFERENCE TO THE BEARINGS OF THEIR EARLIER RELEASE POINT OR POINTS*

Previous flight direction(s)	*Night of return*					*Number of sorties*
	1st–2nd	*3rd–4th*	*5th–10th*	*11th–20th*	*Later*	
			Second Sorties			
Same	42	34	8	8	8	12
Similar	32	34	13	15	6	67
Different	59	31	7	–	3	29
			Third sorties			
One the same	53	29	18	–	–	17
Neither the same	60	28	12	–	–	25

* Expressed in percentages of sorties under each set of conditions.

nothing better could be done with the birds. In three cases (of six) the second sortie was in cloudy conditions and the deviations from home were +1, +2, and –4 compass points, no more than a suggestion that memory of landmarks might make the birds independent of sun navigation. It has been found, incidentally, that homing pigeons are slow to learn landmarks at the release point (Matthews, 1963). The homing performances on these repeat sorties improved in four cases, but one bird was lost, making the results inconclusive. For the majority of sorties made from a different point on the subsequent release, learning of landmarks on the return journey should be more likely when the homing directions approximated one another. Using the groupings as for Figure 2, second sorties can be related to the first according to whether they were in (1) the *same* direction, (2) *similar* directions, i.e., NE : NW or E : NE and vice versa, (3) *different* directions, i.e., E : NW or NW : E.

Since we are not making comparison with the homing performance on the first sortie we may now include a further ten birds for which that information was lacking. There were 16 second sorties in the first category, 79 in the second, and 29 in the third. The failures to home were respectively 4 (25 per cent), 12 (15 per cent), and 9 (24 per cent). So a previous flight in the same direction did not reduce the likelihood of losses, which may be largely accidental anyway. The performance of these birds which did return was also unrelated to the likelihood of their having previous experience of the terrain (see Table 8). In the case of birds making a third sortie, their experience may be divided according to whether one of the previous sorties had been in the same direction (18 cases) or whether both had been in different directions (26 cases). In each category one bird was lost, and there was no real difference between the performances of successful homers. We can therefore conclude that landmark learning

TABLE 9

HOMING TIMES OF INEXPERIENCED AND EXPERIENCED SHEARWATERS RELEASED ON THE SAME DAY*

Class	*Night of return*					*Number of sorties*
	1st–2nd	*3rd–4th*	*5th–10th*	*11th–20th*	*Later*	
Inexperienced	40	18	16	17	9	57
Experienced**	49 (24)	18 (19)	17 (24)	13 (14)	3 (19)	75

* Expressed in percentages of the total sorties for each class.

** Experienced birds' previous sorties resulted in the figures in parentheses.

over a wide area played little part in the improvement of homing by these shearwaters.

It would be expected that where experienced and inexperienced birds were released on the same day at the same place the former would give better returns. There were eight experiments in which very similar numbers of both experienced and inexperienced birds were involved (Haydon, 25-V-52, 22-VI-52, 20-V-53, 30-V-54; Manchester, 2-VI-52; Reading, 12-VI-54; Kildare, 24-VI-54). These gave 83 birds with a previous known homing time and 71 birds hitherto unused. Of the experienced birds 10 per cent were lost and of the inexperienced 20 per cent, a significant and expected difference. But the inexperienced birds that did return put up a good performance compared with that of the experienced birds (Table 9). This suggests that as individuals these inexperienced birds were the rather better homers. This is borne out by the poorer *previous* performances of the experienced birds set out in the last line of Table 9, though these are not directly comparable since the release conditions would have been different.

Adequately to test individual differences in homing performance would require a series of releases for each individual in approximately the same (preferably good) conditions. Only seven birds had three releases in sunny weather. Such consistency of performances as is shown is therefore of most value in underlining the reality of some form of navigational ability, in contrast to homing by random wandering. The latter process would not have allowed 40 per cent of the 40 birds with a sequence of three checked homings to return each time by the fourth night. Even more striking are individual performances such as that of bird No. 1, which in four successive seasons was shipped away to Cambridge, Haydon, Kildare, and Dunmanway and returned on the first, first, second, and second nights, respectively. For the first three releases sunny conditions prevailed and the bird was lost to sight respectively to the west (±0), south-south-east (–2), and east-northeast (–3).

CONCLUSIONS

It would seem that, as with pigeons (Matthews, 1952b, 1953a, 1963), the homing process in Manx Shearwaters is dichotomous. First there is the homeward orientation, probably achieved by a form of sun navigation, innate and but little influenced by experience (though the home coordinates must presumably be learned by each individual). Secondly there is the completion of the homeward journey which depends on a number of factors varying with the individual and its experience. Pigeons for instance must, in the course of their "training," be given knowledge of a sufficient area around their home to form a reasonable target—there being good evidence that the navigational process, as opposed to the following of recognized landmarks, breaks down when distances much less than 50 miles are concerned. In the case of adult shearwaters such information would have been imparted in the course of feeding and migratory flights.

Then again pigeon training is much concerned with getting the birds used to handling and to traveling in containers, as well as imparting "confidence" to fly alone over strange country. It has been suggested above that the overcoming of the disturbance factors may play an important part in improving the homing performance of Manx Shearwaters. It is not unlikely that experience would also give the birds confidence to continue flying straight over land instead of being diverted by rivers, lakes, and coast lines. Lastly, considerable individual differences in homing ability have been found with pigeons and there is now suggestive evidence that such differences exist in Manx Shearwaters.

These considerations have a practical bearing on future work with Manx Shearwaters or related species. It should be possible to build up a stock of experienced homers by releasing them twice at, say, 150 miles in two different directions. These birds could then be used with confidence for really long-distance experiments such as that made with the Skokholm bird released in Boston, Massachusetts, more than 3,000 miles away. It is probable that by a lucky chance a good homer was selected, which returned in 12½ days (Mazzeo, 1953); but, regrettably, it did not reappear in subsequent seasons to have its ability checked. It is also possible that after repeated sorties the initial homeward tendency might be sharpened by the elimination of irrelevant meandering. Experimental changes in the orientation, for instance by the manipulation of the birds' time-keeping mechanism, would then have a greater chance of being successfully demonstrated.

SUMMARY

1. In all, 144 individual Manx Shearwaters were released two, three, or four times from distances between 65 and 415 miles.

2. The same birds gave a crude initial homeward tendency in sunny conditions and scattered at random when released under heavy cloud. The orientation of the individuals shifted according to the direction of home. There was no indication of a "nonsense" orientation in a fixed compass direction.

3. Experience of homing had little effect on orientation, but led to marked improvement in the swiftness of return. This occurs regardless of release conditions, which become less and less important on each release.

4. Improvement in homing performance is not so much brought about by the learning of landmarks as by an habituation to the experimental disturbance.

5. There are indications of individual variations in homing ability.

6. The similarity of the results to those obtained with pigeons is discussed, and future experimental procedure is suggested.

ACKNOWLEDGMENTS

Many of the birds were released, and their initial behavior recorded, by A. W. Ford, M. Hewitt, R. A. Hinde, W. Johnson, R. E. Jones, G. T. Mack, A. G. Mason, J. F. Monk, C. A. Norris, J. E. O'Donovan, W. G. Reade, G. Tharp, W. H. Thorpe, H. R. H. Vaughan, and D. H. Wilkinson. The Wardens of Skokholm Bird Observatory, P. J. Conder and P. E. Davies, and of Dale Fort Field Centre, J. H. Barrett, provided invaluable assistance and transport. The Royal Society gave a grant to cover expenses, the work was done while in receipt of a grant from the Department of Scientific and Industrial Research, and this analysis was made while I was holding a post at the Wildfowl Trust financed by the Nature Conservancy. To all these persons and bodies I would like to express my sincere thanks.

LITERATURE CITED

BELLROSE, F. C. 1958. Celestial orientation by wild Mallards. Bird-Banding, **29:** 75–90.

GRIFFIN, D. R. 1943. Homing experiments with Herring Gulls and Common Terns. Bird-Banding, **14:** 7–33.

GRIFFIN, D. R., AND T. H. GOLDSMITH. 1955. Initial flight directions of homing birds. Biol. Bull., **108:** 264–276.

GRIFFIN, D. R., AND T. H. GOLDSMITH. 1956. Further observations of homing terns. Biol. Bull., **111:** 235–239.

LACK, D., AND R. M. LOCKLEY. 1938. Skokholm Bird Observatory homing experiments. I. 1936–37. Puffins, Storm Petrels and Manx Shearwaters. Brit. Birds, **31:** 242–248.

MATTHEWS, G. V. T. 1952a. An investigation of homing ability in two species of gulls. Ibis, **94:** 243–264.

MATTHEWS, G. V. T. 1952b. The relation of learning and memory to the orientation and homing of pigeons. Behaviour, **4:** 202–221.

MATTHEWS, G. V. T. 1953a. The orientation of untrained pigeons: a dichotomy in the homing process. J. Exp. Biol., **30:** 268–276.

MATTHEWS, G. V. T. 1953b. Navigation in the Manx Shearwater. J. Exp. Biol., **30:** 370–396.

MATTHEWS, G. V. T. 1954. Some aspects of incubation in the Manx Shearwater *Procellaria puffinus*, with particular reference to chilling resistance in the embryo. Ibis, **96:** 432–440.

MATTHEWS, G. V. T. 1955a. An investigation of the 'chronometer' factor in bird navigation. J. Exp. Biol., **32:** 39–58.

MATTHEWS, G. V. T. 1955b. Bird navigation. Cambridge, Cambridge Univ. Press.

MATTHEWS, G. V. T. 1961. "Nonsense" orientation in Mallard *Anas platyrhynchos* and its relation to experiments on bird navigation. Ibis, **103a:** 211–230.

MATTHEWS, G. V. T. 1963. The orientation of pigeons as affected by the learning of landmarks and by the distance of displacement. Animal Behaviour, **11:** 310–317.

MAZZEO, R. 1953. Homing of the Manx Shearwater. Auk, **70:** 200–201.

RÜPPELL, W. 1935. Heimfindeversuche mit Staren 1934. J. f. Orn., **83:** 462–524.

SARGENT, T. D. 1962. A study of homing in the Bank Swallow (*Riparia riparia*). Auk, **79:** 234–246.

SPAEPEN, J., AND P. DACHY. 1953. Het oriëntatieprobleem bij de Trekvogels. III. Verdere homing proeven met Gierzwaluwen (*Apus apus* L.). Gerfaut, **43:** 327–332.

WATSON, J. B., AND K. S. LASHLEY. 1915. An historical and experimental study of homing in birds. Publ. Carneg. Inst. Wash., **7:** 7–60.

WOJTUSIAK, R. J., AND B. FERENS. 1938. Untersuchungen über die Orientation und Geschwindigkeit des Fluges bei Vogeln. IV. Heimkehrgeschwindigkeit und Orientierungart bei den Rauchschwalben (*H. rustica* L.). Bull. Acad. Pol. Sci., **2:** 173–201.

The Wildfowl Trust, Slimbridge, Gloucestershire, England.

APPENDIX

RELEASE POINTS, DATES, AND WEATHER FOR RELEASES

Release point	*Date*	*Number released*	*Medium and/or low cloud (eighths)*	*Wind direction/force*
		1951		
London	3 June	4	0	Nil
Cambridge	7 June	6	0	N. 2
Birmingham	11 June	6	0	SE. 2
Cambridge	5 July	10	7–8	W. 3
Cambridge	8 July	11	8	SW. 3
		1952		
Cambridge	22 May	10	0	N. 1
Haydon	25 May	14	0	W. 2
Cambridge	29 May	7	6–7	NW. 5
Birmingham	1 June	7	3–6	SW. 3
Manchester	2 June	1	4	NW. 3
Cambridge	11 June	9	2–4	NW. 2
London	18 June	1	5	W. 4
Weather ship	20 June	11	0	WNW. 4
Haydon	22 June	12	0	W. 2
Cambridge	26 June	4	0	E. 3
Llandovery	28 June	8	8	Nil
Cambridge	6 July	1	0	E. 2
Cambridge	9 July	7	1–7	W. 1
		1953		
Haydon	20 May	17	4–8	W. 2
Cambridge	28 May	6	3	N. 3
Haydon	7 June	15	3	E. 2
Kildare	11 June	26	1–7	NW. 1
Manchester	14 June	14	4–8	SSE. 2
Cambridge	24 June	14	8	N. 3
Kildare	30 June	14	1	N. 3
Cambridge	8 July	4	0	WNW. 5
		1954		
Dunmanway	30 May	17	7–8	ESE. 3
Haydon	30 May	12	0	NE. 1
Kildare	3 June	20	8	SE. 3
Haydon	6 June	20	8	ENE. 3
Tenbury	6 June	2	8	E. 3
Reading	12 June	16	8	ESE. 4
Cambridge	16 June	1	3–7	SW. 3
Kildare	24 June	8	8	SW. 5
Manchester	27 June	3	4–7	SE. 3
Reading	29 June	5	0	NE. 1

A total of 343 sorties was thus made by the 144 birds with two or more sorties to their credit. Satisfactory data on their homing performances were obtained for 334 sorties and on their orientation behavior for 304 sorties. Consignments were usually made up to about 20 birds and in this way 341 further birds were released once only, bringing the grand total for the whole series to 684 sorties.