NAVIGATION IN THE MANX SHEARWATER

By G. V. T. MATTHEWS
Department of Zoology, University of Cambridge

(Received 4 February 1953)

INTRODUCTION

Many species of birds have been shown to home from areas of which they could have had no previous experience, but the results were of a nature that did not afford unequivocal evidence of a true navigational faculty. Wilkinson (1952) has demonstrated that the extensive experiments of Ruppell (1935, 1936, 1937) and of Griffin (1940, 1943) produced results that could be explained simply on a basis of random search for known landmarks. Matthews (1951 b) was able to demonstrate true, bico-ordinate navigation in homing pigeons. These fulfilled the two essential criteria by giving initial orientation in the home direction and swift returns. Kramer & St Paul (1952) and Kramer (1953) have substantiated these results. With wild birds the only critical evidence of navigation was that obtained by Matthews (1952a) with Lesser Black Back Gulls, and that only in respect of the initial orientation. Further experiments were therefore needed to settle the question, and to examine the basis of such navigation.

MATERIAL

The Manx Shearwater (Puffinus p. puffinus) breeding on Skokholm Island, Pembrokeshire was the species used. Some account of its breeding biology and migrations has been given by Lockley (1929, 1930, 1942). It has many advantages for this type of work. About 10,000 pairs nest on this small island, in burrows from which they are quite easily extracted. Incubation is shared, each bird taking a spell of several days without feeding, thus allowing transport or experimentation of several days. Being about the size of a pigeon it is easily handled and not fragile. It is very loath to desert, and will continue sitting for many days if the mate is late in homing. The egg is highly resistant to chilling. The incubation period, and hence the time available for homing experiments, is prolonged, about 7 weeks. Although the species is normally diurnal, the birds only come in to their burrows after dark and watch for returns can thus be limited to 2 or 3 hr. a day.

The recoveries of banded birds from Skokholm are discussed in detail in Appendix A. Any release point well inland will be unknown to them, and only the coasts south of Skokholm down West France to North Spain will be well known. There is some evidence that this shearwater, like many of its relatives, migrates into the opposite (southern) hemisphere in winter, and even when breeding the birds may forage up to 300 miles south. Certainly the birds are capable of long, sustained flights, and would be expected to have any possible navigation mechanism developed to a high degree. It flies either in low, careening glides or with beating
Navigation in the Manx Shearwater

wings, but does not normally soar and hence is suitable for orientation observations. Moreover, when released inland it will have no incentive to linger, being such an exclusively pelagic bird.

The main disadvantages lie in the nocturnal return to the burrow. This means that birds will normally only be recovered at the burrow, but frequent checks during the dark period enabled up to 100% recoveries to be made. The birds may well home to the neighbourhood of the Island several hours before they are able to land, and the apparent homing time would be lengthened accordingly. However, allowance can be made for this or the release time adjusted as described later. During the full-moon period the birds show less inclination to come to land if there is little cloud cover, so such periods have to be avoided in planning releases. A further complicating factor is that birds may be at different stages of their 'shift' when taken for homing, and it is not possible to dig sufficient nests and make sufficient inspections to obviate this. But the very fact that large numbers are being used will help to cancel out any effects, and there is no question of the bird's reserves being used up by the end of the usual shift.

The Skokholm shearwaters had been tested in homing experiments previously, by Lack & Lockley (1938) and Lockley (1942). Forty-one birds were released giving seventeen returns at speeds between 8 and 74 miles per day, with the exceptions of one covering 125 miles in 10 hr. and two (released together) 200 miles in 24 hr. As regards initial orientation '...some birds flew off in the direction of Skokholm, others did not, and the former do not appear to form a significant proportion of the whole'. While these results indicated that homing ability existed in this species they did not provide any more conclusive evidence of navigational faculties than other work, despite the much quoted return from Venice (930 miles in 14 days). They did indicate that further critical experiments might be more successful.

METHODS

Only reasonably short burrows, up to about 6 ft., in firm soil and of a simple nature, were used. Plenty of these were to be found within half a mile of the Bird Observatory buildings. The presence of a shearwater is confirmed by the characteristic smell, and the finer points of the burrow's topography determined by a long, flexible probe. An inspection shaft, rarely more than 18 in. deep, is sunk over or slightly to one side of the nesting chamber. The bird is banded and a stone or slate cover, surmounted by the original sod, is placed over the hole to keep it light- and weather-proof yet easily inspected. Secondary shafts are sometimes necessary along the burrow. The nest's position is marked by a white-topped stake and a numbered peg. 441 occupied nests were so prepared in 1951 and 1952, but seventy-seven of these were held by birds that did not lay an egg (or had lost it prior to excavation). These latter were not used for experiments, but only the actively breeding birds. The single egg would appear to be laid during the first 2 weeks of May, laying is certainly virtually complete by the third week. First hatchings occur in the third week of June and are over by the second week in July. A few days after hatching the
parents leave the young and only visit it briefly during the night. It is then much more difficult to check their return. The great majority of homing birds were taken from an egg, all those up to the end of June. Some fifty-two out of eighty-three further releases up to 11 July had perforce to be done with birds taken from young. For transport, fibreboard boxes, 16 x 10 x 10 in. with a diagonal partition, were used, one bird being placed on either side, bedded on dry bracken as in the nest. Ventilation holes, \( \frac{1}{4} \) in. diameter, were punched round the sides near the top. It was generally convenient to collect up twenty birds for a consignment, one per burrow. They were taken by boat 7 miles to Dale Fort, then by van to the railway at Haverfordwest. In most cases it was possible to release the birds within 30 hr. of being placed in the boxes. 338 birds were treated in this way (including sixteen local releases), and the great majority travelled very well and flew strongly on release. Five died in the boxes, but these casualties were sporadic and not proportional to the length of incarceration, one death occurring after only 14 hr.

Release points were chosen in wide open spaces, the birds at Cambridge being released from the University Library tower. The liberators, on whose data the valuable orientation information is based, released the birds one at a time, tossing each one up into the air and following it with binoculars until out of sight before releasing the next in a different direction. The nearest compass point to the bird's position when lost to sight was noted, also the time taken to reach vanishing point. The approximation to compass points (W., W.S.W., S.W., etc.) is considered to be sufficiently accurate and, moreover, was made necessary by the unreliability of compasses on top of a steel frame building. All releases except that at Llandovery (p. 382) were in full daylight, between 07.00 and 19.00 hr. (all times B.S.T.). The positions of the release points, and the numbers of birds released there, are shown in Fig. 1. They are all in areas that can be considered to be unknown to the birds from Skokholm. Inland releases in England, with two long north/south coast lines, form especially stringent tests of navigation in a normally pelagic bird. If only random wandering was the basis of homing the chances of reaching the wrong coast and then searching along it are equal at Haydon and weighted against the birds at Cambridge. The latter is clearly one of the best possible release points, quite apart from convenience of laboratory accommodation, etc. The other points were necessary to check that orientations were not due to some local peculiarity of topography, or, say, a simple tendency to fly west when released inland. Also when it was possible to use the same birds a second time another release point in a different direction was needed. That planned in Eire could not be brought into operation because of foot-and-mouth restrictions. The release in the open Atlantic was from the Ocean Weather Ship, *Weather Recorder*.

Burrows at which homers were due were visited and inspected several times in rotation from midnight until 2 or 3 o'clock in the morning, while there was yet any traffic among the shearwaters. Homers were marked with a spot of light paint on top of the head, making it easy to distinguish them from their mates, though band numbers were of course checked as well. These regular checks were maintained up to the tenth night from release, or longer if the mate was still sitting. Stragglers
coming in after this period have little interest in a study of navigation, but irregular checks were maintained for as long as possible. The number of nests to be visited per night had to be limited in this way to about forty, otherwise the necessary frequent visits could not be made.

**EVIDENCE OF TRUE, BICO-ORDINATE NAVIGATION**

From the data provided by the liberators, radial histograms can be constructed as in Figs. 2 and 3, the length and breadth of the various rays being proportional to the number of birds lost from sight in those directions. In Fig. 2 are collected the releases made under cloudless skies. It will be seen that there is a marked home-ward tendency which becomes very striking when the results are summed in the central figure. The chances of such an orientated distribution being derived from
a chance scatter are quite negligible \((P<0.001, \text{ as determined by a } t\text{ test regardless of sign, the method described in Matthews, 1953a})\). Fig. 3 shows the orientations obtained from releases under variable, high thin cloud, with the sun visible throughout. The homeward orientation is only slightly (not significantly) less marked than in Fig. 2, and again cannot be attributed to chance \((P=0.002)\). The time for which the birds were in sight, averaging 3.0 and 3.1 min. respectively, also showed no difference between the two categories.

We have here, then, extremely strong, concrete evidence that the shearwaters were at least roughly orientated towards home within about 3 min. of release, arguing that they must possess some form of navigational mechanism. It is particularly important to note that the results are repeatable and are not dependent on any one observer, release point, home direction or wind direction and the orientation is shown both on land and at sea. The results are all the more remarkable when it is remembered that the whole experience of transport and release is
novel and presumably somewhat disturbing to the birds, particularly those finding themselves for the first time out of sight of the sea.

(a) Haydon A
25. v. 52, W. J.

(b) Haydon B
22. vi. 52, W. J.

(e) All releases

(c) Birmingham A
11. vi. 51, C. A. N.

(d) 'Weather Recorder'
20. vi. 52, A. W. F.

Fig. 3. Initial orientations under lightly clouded skies, sun visible throughout.

The returns achieved from releases under cloudless or lightly clouded skies (including those for which sufficient orientation data are not available, such as birds flying very low and lost in less than a minute behind trees, etc.) are listed in Table 1.

Table 1. Returns from releases under cloudless or lightly clouded skies

<table>
<thead>
<tr>
<th>Released</th>
<th>Date</th>
<th>No.</th>
<th>Returned on nights</th>
<th>Returned later</th>
<th>Missing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cambridge D</td>
<td>22. v. 52</td>
<td>20</td>
<td>2 7 1 . . . 1 . 2</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>Hayward A</td>
<td>25. v. 52</td>
<td>20</td>
<td>6 2 2 2 2 . 1 1 1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Slimbridge</td>
<td>2. vi. 51</td>
<td>2</td>
<td>. . . . . . . . .</td>
<td></td>
<td></td>
</tr>
<tr>
<td>London A</td>
<td>3. vi. 51</td>
<td>10</td>
<td>2 1 1 1 1 . 1 .</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Cambridge A</td>
<td>7. vi. 51</td>
<td>15</td>
<td>4 5 2 2 2 . . . .</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Birmingham A</td>
<td>11. vi. 51</td>
<td>20</td>
<td>2 6 4 1 . x x x x</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>W. Recorder</td>
<td>20. vi. 52</td>
<td>20</td>
<td>1 5 2 1 2 4 1 . 1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Haydon B</td>
<td>22. vi. 52</td>
<td>20</td>
<td>1 3 1 1 1 . 3 1 . 1</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>Cambridge G</td>
<td>26. vi. 52</td>
<td>19</td>
<td>3 . . 1 1 2 1 x x</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td>146</td>
<td>16 27 19 10 3 8 6 9 2 2</td>
<td>9</td>
<td>35</td>
</tr>
</tbody>
</table>

Note. No watch kept for returns from Cambridge H, or on nights marked x.
Attention may first be called to the fact that sixteen of these birds released in unknown areas were back in their burrows on Skokholm the same night. Dividing the straight-line distance by the time between release and recapture gives them minimal homing speeds:

<table>
<thead>
<tr>
<th>Released between</th>
<th>At</th>
<th>Miles per hour</th>
</tr>
</thead>
<tbody>
<tr>
<td>07.05 and 07.30 hr.</td>
<td>London A</td>
<td>12.2, 12.2</td>
</tr>
<tr>
<td>07.31 and 08.33 hr.</td>
<td>Birmingham A</td>
<td>8.7, 8.8</td>
</tr>
<tr>
<td>10.30 and 12.14 hr.</td>
<td>Haydon A</td>
<td>17.4, 17.9, 18.2, 18.5, 19.3, 20.0</td>
</tr>
<tr>
<td>15.16 and 15.34 hr.</td>
<td>Cambridge D</td>
<td>21.5, 22.0</td>
</tr>
<tr>
<td>18.21 and 18.42 hr.</td>
<td>Cambridge A</td>
<td>28.0, 29.4, 29.4, 35.2</td>
</tr>
</tbody>
</table>

Thus the releases earlier in the day gave lower minimal speeds, from which we may infer that such birds had completed their journey back to Skokholm in daylight and had to wait some hours before they came in to land. Since the flight speed of the shearwater can be taken as around 30 m.p.h. (Lockley, 1942) we have evidence, incontrovertible in some cases and strongly inferential in others, that these birds flew almost directly back to Skokholm. Since they formed a substantial proportion (18%) of their releases, we are clearly not dealing with purely chance happenings. The importance of this evidence, in conjunction with the orientation behaviour, will be clear. For the first time, it has been demonstrated that a species of wild bird can, given the correct conditions, fly straight home across a wide stretch of unknown country. Still considering these five releases it will be seen that the proportion of first and second night returns are interrelated, 6 and 2 for Haydon A but 2 and 7 for Cambridge D and so on. By reason of the late starts from Cambridge, instead of the birds having to wait about before landing, only the faster returns will be able to reach Skokholm in time to land, say by 02.30 the next morning. In fact, it seems that only those which reach a well-known strip of coast by dusk would be able to pilot their way through the darkness (p. 382). It seems very probable, therefore, that returns on the second night had homed very much faster than the extra 24 hr. elapsed would suggest. The distribution of returns shown in Fig. 4, with 53% back by the second night and 75% by the fourth is clearly very different from that which would be expected on the basis of random search.

The remaining three releases in Table 1 gave poorer returns, despite the fact that the birds were well orientated on release. That from the Weather Recorder may be considered separately since the distance was nearly twice as great, the birds had had 4 nights in the boxes instead of one, and being at sea there would both be less compulsion to keep flying and more temptation to rest and feed. The releases at
Navigation in the Manx Shearwater

Haydon and Cambridge are, however, directly comparable to the earlier ones as in Table 2. The significant differences lie in swift returns and in the missing birds.

Table 2. Returns from sunny releases at 155-265 miles

<table>
<thead>
<tr>
<th>Dates of releases</th>
<th>No.</th>
<th>% returning on nights</th>
<th>% returning later</th>
<th>% missing</th>
</tr>
</thead>
<tbody>
<tr>
<td>22. vi.-11. vi.</td>
<td>85</td>
<td>44 19 21</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>22. vi.-26. vi.</td>
<td>39</td>
<td>10 13 28</td>
<td>49</td>
<td></td>
</tr>
</tbody>
</table>

(Returns from sunny releases at 155-265 miles)

(P < 0.001 in both cases), and some seasonal factor must be concerned. All these birds were taken from eggs so there would be no less likelihood of their being checked at the burrow. The embryo is perhaps less resistant to chilling at this late stage, but many of the missing birds’ eggs were being covered by the mate, and the fact that an egg is dead or addled does not seem to prevent the birds brooding for at least the normal spell. It would seem unlikely that the birds would desert more readily late in incubation or lose the urge to home. Of nineteen birds released 65 miles away in special circumstances (see p. 382) on 28 June 1952, eleven were back by the second night. Again, six local releases on Skokholm 9 July 1951 in the late afternoon (having been held for 39 hr. in boxes) gave five returns that night, with the last in on the second night. The urge to home would thus appear to be present at this late stage, and the most plausible explanation of the falling off in returns would attribute it to a decline in general stamina.

It is clear, then, that different factors are concerned with orientation and with the return home in shearwaters, much as they are in pigeons (Matthews, 1953 b). Nevertheless, there is a general association between a good start and a swift return. Birds starting within two points of the home direction gave 33 % (of 72) returns on the first and second nights as against 16 % (of 49) of those making starts wider of the mark (P = 0.04). This suggests that the initial direction of flight is maintained for some time at least, as also do the few recoveries of birds that met with accidents after release. These were found as shown in Table 3. These recoveries are indicated on Fig. 1. Not only is there a strong association between the initial and final bearing, but these recoveries support the evidence that the birds are seeking home directly and not making for the nearest coast. Bird (a) is particularly eloquent in
this respect, and with (b) and (d) recalls the recoveries of three starlings not far from
the direct line home by Ruppell (1937). These five birds, with another that came to
grief soon after release, are included in the 'missing' totals since there is no evidence
to show whether others that were missing had not met a similar fate. A considerable
proportion do survive, for 27% of those thirty-three 'missing' from 1951 were
found in burrows on Skokholm in 1952, as compared with 52% of the fifty-six
known to return in 1951 ($P = 0.03$).

In pigeons it has been possible to demonstrate wide variation in orientation and
homing ability (Matthews, 1951*, 1952**, 1953*), the birds giving consistently good
(or bad) performances for a number of releases from different points. This is in
itself confirmation of the existence of a true navigational ability. The shearwater
offers unusual opportunities for similar individual testing since it has a strong
tendency to return to the same burrow year after year. It was not considered
feasible to use the same bird twice in the same season because of the increased risk
of desertion. Of eighty-nine used on homing tests in 1951 thirty-eight were
recovered on Skokholm in 1952, but only twenty-four were in the right breeding
state and available when required for testing by release at a second point in a different
direction. Because of variations in release conditions, etc., this is not considered
a sufficient sample for detailed analysis. This should be possible after the 1953
season when it is hoped to obtain some sixty additional records. Mention may be
made, however, of one bird that returned from Cambridge on the first night in
1951 and from Haydon on the first night in 1952 (8:0 and 14:6 hr.).

The array of evidence from initial orientation and swift returns is far more
convincing evidence of navigational ability than any isolated homing feat, however
remarkable. Against this background one such case can now be presented and
properly appreciated. In 1952 two shearwaters were sent by air to Boston, U.S.A.
Although the journey only involved 3 nights in the box one died en route, the other
was released in good condition in bright sunshine at 13.15 B.S.T. on 3 June. It flew
east (seawards). Watch was commenced at the two burrows on 12 June, and on
16 June at 01.30 AX 6587 was back, replacing the mate that had been there an hour
earlier. It is interesting to note that confirmation that this bird alone had been
released arrived by boat some 10 hr. later! The shortest distance (great circle)
between Boston and Skokholm is 3050 miles. This had been covered in 124 days,
a minimal daily average of 244 miles—the equivalent of a Cambridge-Skokholm
flight every day. It is by far and away the longest successful homing flight obtained
with any species of bird, previous long distance flights being:

<table>
<thead>
<tr>
<th>Species</th>
<th>Distance (miles)</th>
<th>Miles per day</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>White Stork</td>
<td>1400</td>
<td>117</td>
<td>Wodzicki et al., 1938</td>
</tr>
<tr>
<td>Swallow</td>
<td>1150</td>
<td>164</td>
<td>Ruppell, 1937</td>
</tr>
<tr>
<td>Alpine Swift</td>
<td>1000</td>
<td>333</td>
<td>Schifferli, 1943</td>
</tr>
<tr>
<td>Manx Shearwater</td>
<td>930</td>
<td>66</td>
<td>Lack &amp; Lockley, 1938</td>
</tr>
</tbody>
</table>
Even so only the last was definitely well outside country it might have known on migration. Homing pigeons have returned over 1000 miles, but only after considerable training over part of the course. The minimal speed of AX 6587 was also in excess of most previous flights, even those over much shorter distances. While there is no direct evidence that the bird maintained an undeviating line for home little room is left for diversions and none for random search.

![Clouds and orientations](image)

(a) Cambridge C 8.vii.51, W.H.T.  
(b) Cambridge B 5.vii.51, W.H.T.  
(c) Cambridge E 29.v.52, R.A.H.  
(d) Birmingham B 1.vi.52, C.A.N.

Fig. 5. Initial orientations under heavily clouded skies.

*Note. Amounts of cloud are roughly average for period of releases.*

**THE PHYSICAL BASIS OF THE NAVIGATION**

We have seen that shearwaters released in sunny conditions have given very clear evidence of the existence of a navigational ability. Those released under conditions of heavy cloud present a very different picture. Their initial scatters are shown in Fig. 5. Homeward orientation has completely broken down, in fact there is a distinct \( P=0.006 \) tendency for the birds to leave in the opposite direction. Examination of the individual release diagrams shows that the wind direction will account for this tendency, i.e. under these conditions the birds are not orientated
and tend to drift down wind. Further evidence of disorientation with heavy cloud is given by the results of an experimental release, Cambridge F (p. 385, Fig. 6). The time the birds were in sight was longer than in the case of sunny releases, the average 4.2 min. being markedly higher ($P < 0.001$) than 3.0 and 3.1 min. for the latter. This can be taken as reflecting a general state of disorientation with the birds hesitating and circling near the release point.

The returns obtained from releases made in cloudy conditions are set out in Table 4. They are seen to be very much poorer than those for sunny conditions (Table 1), but the difference may be exaggerated since clouded releases also show a fall in homing success with the advancing season (Table 5). As with sunny

Table 4. *Returns from releases under heavily clouded skies*

<table>
<thead>
<tr>
<th>Released</th>
<th>Date</th>
<th>No.</th>
<th>Returned on nights</th>
<th>Returned later</th>
<th>Missing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cambridge E</td>
<td>29. v. 52</td>
<td>20</td>
<td>3 2 3 1 2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Birmingham B</td>
<td>1. vi. 52</td>
<td>20</td>
<td>6 2 2 2 2 2 6 6</td>
<td></td>
<td>6</td>
</tr>
<tr>
<td>Manchester</td>
<td>2. vi. 52</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Newcastle</td>
<td>4. vi. 52</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>London B</td>
<td>18. vi. 52</td>
<td>6</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Cambridge B</td>
<td>5. vii. 51</td>
<td>20</td>
<td>2</td>
<td>2 6</td>
<td>16</td>
</tr>
<tr>
<td>Cambridge C</td>
<td>8. vii. 51</td>
<td>20</td>
<td>3 1 1 3 3 3 3 1 3</td>
<td>1 5 6 6 6</td>
<td>40</td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td>90</td>
<td>9 6 6 3 5 3 2 1 3 6</td>
<td>15 40 26</td>
<td>26</td>
</tr>
</tbody>
</table>

*Note. No watch kept for returns on nights marked ×.*

Table 5. *Returns from clouded releases at 155–265 miles*

<table>
<thead>
<tr>
<th>Dates of releases</th>
<th>No.</th>
<th>% returning on nights</th>
<th>% returning later</th>
<th>% missing</th>
</tr>
</thead>
<tbody>
<tr>
<td>29. v.–18. vi.</td>
<td>50</td>
<td>18 16 40 26</td>
<td>26</td>
<td>26</td>
</tr>
<tr>
<td>5. vii.–8. vii.</td>
<td>40</td>
<td>18 16 40 26</td>
<td>26</td>
<td>26</td>
</tr>
</tbody>
</table>

releases, the later tests gave fewer fast returns and more were missing ($P < 0.001$ in both cases). As the late clouded releases were well after the late sunny ones, and twenty-two of the birds of the former were taken from chicks, with less chance of being checked on return, it is probably best to compare the effect of release conditions only among the earlier ones. Comparing these in Tables 2 and 5 it will be seen that sunny releases gave a higher proportion of quick returns than the clouded releases, the latter showing a higher proportion of late returns (44% vs. 18%, 21% vs. 40%, $P = 0.02$ in both cases). The bad starts in clouded conditions had the effect of slowing up returns without significantly lowering the proportion finally reaching home. The effects of a bad start are carried over into homing success despite the possibility of subsequent orientation as and when cloud cover was reduced.

This disorientating effect of heavy cloud is precisely the same as in the case of homing pigeons (Matthews, 1953a) and Lesser Black Back Gulls (Matthews,
Now that parallel evidence of this nature has been obtained for three species of very different habits, the suggestion that a form of sun navigation (Matthews, 1951a, b) is concerned would seem to be very plausible. The most likely form that such navigation would take has been discussed in detail by Matthews (1953a), to which reference should be made. Stated very briefly, the bird is required to estimate the sun’s arc by observation of its movement over a small part of that arc. Measurement of the highest point gives local altitude and noon. Comparison with home altitude and noon gives the difference in latitude and longitude and hence the direction of home. The experimental investigation of this hypothesis has proceeded fruitfully with pigeons, and parallel attempts with shearwaters will be described. It may be noted that complete overcast is apparently not essential for disorientation. This can be incorporated in the hypothesis since very brief glimpses of the sun would not permit the appreciation of its movement. Even with more prolonged appearances, detection of its true movement might be confused by massive clouds moving in close proximity.

EFFECT OF THE INCUBATION CYCLE ON HOMING

Before passing to the experimental investigation of the sun navigation hypothesis, a further factor which can affect homing may be considered. As explained earlier, it was not possible, in view of the large numbers of birds being used, to dig a large surplus of burrows and check each daily to ensure that all birds were sent off when they had had the same amount of time on the egg. This would in any case run counter to the policy of disturbing the birds as little as possible before and after the homing test, and would increase the risk of desertion before the birds could be used. In any case, any differences in performance resulting from difference in incubation cycles should cancel out if large numbers are used. A check of this assumption can be made from the data collected when inspecting the nests for returning homers.

There do not appear to be any marked fluctuations in the nocturnal visitations for the island as a whole (except in connexion with the full-moon period), and we can assume that change-over of the individual pairs is independent of those of their neighbours. On any one night the proportion of change-overs should be constant and depend on the average length of the incubation shift. The arrival of the relieving bird is a good indication of the end of the sitting bird’s shift, though individuals may be overkeen to brood and arrive early, and others may arrive late. The burrows are inspected on the first night after release; for those listed in Tables 1 and 4 this is the second night after the removal of the homer, except for the Weather Recorder release. In 40% of cases the mate was found to have arrived, corresponding to a 5-night incubation shift. As some mates may have returned on the night following removal of the homer, and not remained in the burrow, the actual change-over proportion may well be rather higher, say 50%, for the 2 nights, corresponding to a 4-night shift. In these cases the homer was probably on its last, or penultimate, day of its shift when removed. Table 6 demonstrates that the proportion of such birds was practically the same in the various conditions of release that have been discussed earlier, i.e. any effects were distributed equally
throughout and would not affect the conclusions reached. The table also shows that
those birds which were probably at an early stage of their shift gave more swift
returns than those due for relief. The difference is only of significance in the case of
the early releases in sunny conditions ($P = 0.01$) and this indicates that the effect is
a subsidiary one which only becomes important when the conditions and period of
release already give good returns. As further indication of this, the effect is then
seen mainly in the returns on the first 2 nights from release, 56% of those early and
27% of those late in their shifts ($P = 0.01$). Birds that are due for relief are thus less
likely to hurry back than those in which the urge to incubate is still strong.

Table 6. Effect of incubation cycle on swiftness of return

<table>
<thead>
<tr>
<th>Conditions and period</th>
<th>Total</th>
<th>% reliefs</th>
<th>% returned on nights 1-4</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Early in shift</td>
<td>Late in shift</td>
</tr>
<tr>
<td>Sunny, early</td>
<td>85</td>
<td>39</td>
<td>73 45</td>
</tr>
<tr>
<td>Sunny, late</td>
<td>39</td>
<td>44</td>
<td>27 24</td>
</tr>
<tr>
<td>Clouded, early</td>
<td>50</td>
<td>44</td>
<td>83 43</td>
</tr>
<tr>
<td>Clouded, late</td>
<td>40</td>
<td>35</td>
<td>8 14</td>
</tr>
<tr>
<td>All</td>
<td>214</td>
<td>40</td>
<td>45 30</td>
</tr>
</tbody>
</table>

INVESTIGATION OF THE SUN-NAVIGATION HYPOTHESIS

The well-known fact that pigeons will not fly through the night, and very rarely
after sunset (Matthews, 1953 a), cannot be cited as strong evidence for sun naviga-
tion since the pigeon is so strictly diurnal. The undoubted existence of nocturnal
pilotage in shearwaters opens a way to test further the hypothesis that their naviga-
tion is dependent on the sun. Their night vision may not be very good, they tend to
blunder into novel obstacles such as the human observer. But they are able to fly
direct to the immediate neighbourhood of their burrow and select the right one
from scores of others even if the mate is not present to assist such pin-pointing by
calling. Indeed, despite the recognizable individuality of the flight calls, the re-
sultant cacophony may be akin to that produced by traffic in eastern cities, expres-
sive of a desire to avoid collision, of nervous tension and general excitement. The
first night returns from Cambridge A (p. 376) must have completed their journey
in darkness, but they had of course been orientated during daylight.

As will be seen from Appendix A, an inland release point, even at no great
distance, will be unknown to the birds. If released there after dark they should only
be able to reach home the same night if they had some navigation device not
dependent on the sun. The local release described on p. 377 showed that no difficulty
would result from an unusually close association of the disturbance of capture and
boxing with the release point. The test release was made with nineteen birds from
a point in the hills near Llandovery (Fig. 1). To establish the existence of non-sun
navigation, nine of these would have to be back the first night, for one or two might
be expected to arrive if the birds scattered at random and flew steadily in the initial
directions. The birds were released in quick succession from 23.30 on 28 June 1952,
and thus had 3 hr. to cover the 65 miles direct to Skokholm. The sun had set some 2 hr. before, the sky was locally overcast, but quite clear at Skokholm. It was not possible to follow the birds for more than a few seconds in this light. Watch for returns was prolonged till dawn, and a confirmatory check made during the day. Not one of the birds returned on the first night. The following night the unusually high total of eleven returns was found at the first check. Thus the birds had survived the night release and maintained the urge to home, but had been unable to complete the short journey in the hours of darkness and to arrive before it was too light for them to land on Skokholm. Two more returns came in up to the sixth night when watch had to be stopped. This experiment has shown that shearwaters are not possessed of any mysterious agency that enables them to navigate in the dark, and forms a useful piece of negative evidence for a form of sun-navigation.

Further analysis must of necessity involve the birds being kept away from the sun for a number of days, and the advisability of such incarceration must be considered. The shearwater is one of the few wild birds that could be used because of its habit of spending several days at a time down its dark burrow. The incubation shift varies in length, Lockley (1942) gives 3–5 days as normal extending to 10 days over moonlit periods. During this period the sitting bird does not feed, but subsists on reserves, losing weight in the process. It is improbable that it drinks either, and in view of its pelagic habits it is quite possible that shearwaters, like seals (Irving, Fisher & McIntosh, 1935) obtain all their water requirements from their food. This would be an interesting physiological problem in its own right, as is that of their prolonged fasting. It might be conjectured that a bird taking over incubation just before the full moon period might have laid on extra reserves of fat, but the shift can also be extended without ‘warning’ during the moonless periods. Thus if we consider those cases in which a homing bird had not returned by the fourth night, and omitting those in which the mate only appeared once or not at all, we find mates sitting continuously for the following number of nights:

<table>
<thead>
<tr>
<th>Season</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
<th>15</th>
<th>16</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mid-June</td>
<td>5</td>
<td>8</td>
<td>12</td>
<td>6</td>
<td>8</td>
<td>6</td>
<td>4</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>.</td>
<td>.</td>
<td>.</td>
<td>1</td>
</tr>
<tr>
<td>Mid-July</td>
<td>9</td>
<td>9</td>
<td>12</td>
<td>7</td>
<td>3</td>
<td>4</td>
<td>4</td>
<td>7</td>
<td>2</td>
<td>2</td>
<td>.</td>
<td>.</td>
<td>.</td>
<td>.</td>
<td>.</td>
<td>1</td>
</tr>
</tbody>
</table>

i.e. about half the birds would remain sitting voluntarily for more than 5 nights in the absence of their mates, and their tenacity did not alter with the advancing season. These figures are in many cases minimal since they probably included an extra night before the homer was released, when the nest was not inspected, and in a number of cases were terminated by the arrival of the homer or the end of watching. The bird which was still sitting on the sixteenth night was still present on the twenty-second and twenty-third nights, after which it deserted. In view of the above evidence, it would seem reasonable to carry out experiments which involved delaying release until after 4 nights from capture. Two birds were kept in boxes for this period and inspected at intervals. They remained quiescent during the day, at night there would be some scuffling and calling. On release (5 June 1952) they were
still lively and flew well. Further confirmation is afforded by the returns obtained from the Weather Recorder (Table 1) after the birds had been confined for the same period. In the experiments described below the birds were taken just before the full-moon period, when they might be expected to be in the best condition. They were sprinkled with water each day and kept in cool, well-ventilated rooms.

It has been demonstrated that pigeons are using the sun's altitude to estimate their north/south displacement (Matthews, 1953a). The birds were kept out of sight of sun and sky for 6-9 days in mid-September when the sun's altitude was decreasing rapidly (being near the equinox), and fell in those intervals 2° 19' and 3° 28'. The pigeons were then released 1° south of the loft and, with few exceptions, were apparently unable to allow for the unobserved decrease in altitude and flew southwards. Control birds, allowed full view of the sun during incarceration, orientated correctly northwards. This method is not easily applicable to shearwaters. First, there is the theoretical objection that, unlike pigeons, periods when they do not see the sun for several days are of frequent occurrence in their lives, and there is much more likelihood of a corrective factor being selected into their navigational mechanism. Secondly, there is the practical difficulty that the period when the birds are available and in good condition for homing work, mid-May to mid-July, is close to the solstice when the daily changes in altitude are minimal. For example, from 2. vii to 6. vii the fall is only 20', or the equivalent of 23 miles in latitude. For birds released at Cambridge it would have the effect of depressing the homeward line by less than a third of a compass point, which certainly could not be detected by the present rather crude observational method. Releases to the south would show no effect, and there would be the additional complication that the known area for shearwaters from Skokholm lies in that direction. Use of the birds later in the season would run the risk that a continuation of the decline in stamina would make them much less resistant to prolonged incarceration—they do not remain in the burrow over the day at all and so probably do not lay up food reserves when visiting the chick. Even in mid-August when desertion of the young has begun and ties with the colony loosened, the fall in altitude over 4 days is still only 1° 16', and any effect would remain very difficult to detect. It seems that with shearwaters this aspect of their navigation can only be investigated by trans-equatorial experiments.

Prolonged incarceration in the homing season will not then produce any observable systematic errors of orientation in latitude. Determination of longitude must essentially be bound up with the estimation of time by some internal physiological 'chronometer'. It was possible that the disturbance of prolonged captivity might upset such a mechanism. Eight birds were therefore kept boxed for 4 days at Cambridge, in a room which the sun did not penetrate directly, with the normal light/dark alternation of day and night. Their orientation on release (Cambridge H, 6 July 1952) was compared with that of ten other birds brought direct from Skokholm and spending only the one night in the boxes. In this and the subsequent experiments the birds were as usual released singly, two controls following two experimentals. The results are shown in Fig. 2 (d), the long-duration birds being
shown in black, the short-duration in white. The sky was quite clear at release and an excellent homeward orientation was obtained for both groups with no discernible differences between them. We can therefore conclude that these experimental conditions will have no effect on orientation, either directly by upsetting the navigational mechanism or indirectly by psychological disturbance breaking the urge to home.

The good orientation obtained from the Weather Recorder is additional evidence for this conclusion (Fig. 3 (d)), the birds there having been in the boxes over 4 nights, though here, of course, there were no controls.

Although a 'chronometer' would presumably have a basis of internal rhythms, it is probable that external 'pace-makers' would play a part in maintaining its synchronization. The experimental alteration of potential 'pace-makers' is therefore a method of attack which can be employed if longitude determination, according to the present hypothesis, is to be disturbed. The most obvious candidate for selection is the daily alternation of light and dark. A 6-day treatment of irregular light/dark periods, accompanied by irregular feeding, produced a random scatter in pigeons as against orientation by controls (Matthews, 1953a). In shearwaters feeding is often very irregular and is unlikely to be a factor in time-keeping, and could not be altered experimentally in any case. The coming of day and of night, however, have a peculiar importance in their lives at the breeding season which should add to their importance as 'pace-makers'.

A first experiment, aimed at producing as little general psychological disturbance as possible, was made by keeping twelve shearwaters boxed for 4 days and nights in a lightproof room which was kept strongly lit continuously throughout the period. For the same time twelve other birds were kept in a separate wing of the laboratory at Cambridge and subject to the normal light/dark alternation, i.e. in the same conditions as the experimental birds in Cambridge H. Unfortunately, weather conditions were not satisfactory for the release on 11 June 1952. The forecast held no promise of improvement, and delay for a further day or two would run the risk of weakening the birds. Accordingly, they had to be released under a heavy cloud cover, 5/10ths increasing rapidly to 9/10ths, as and when the sun appeared in gaps. The results shown in Fig. 6 are quite inconclusive from the present point of view,
although they confirm the disorientating effect of heavy cloud cover even with the sun visible at intervals (p. 381). As we should now expect from a clouded release, returns were slow, by the sixth night only five were back (four were controls). Eventually eight returned from each group (67%). This proportion accords well with that (65%) returning from an earlier clouded release at Cambridge (E. 29 May 1952), and absolves their incarceration from any prolonged ill-effects.

This experiment was a passive attempt to desynchronize the 'chronometers' by the absence of a dark period. The next experiment attempted actively to produce a systematic error by altering the time at which the dark period occurred. While in their burrows, only a dim light will filter to the shearwaters, and the oncoming of night may become apparent less by the change of illumination as by the arrival of the shearwaters from the sea, heralded by their wild clamour. To take this factor into account and complete the illusion that they were still on Skokholm, nine shearwaters were subjected to the following routine during the 4 days and nights that they were in the laboratory at Cambridge. From 20:30 the lights were cut down in the lightproof room until complete darkness was achieved at 21:00.

<table>
<thead>
<tr>
<th>Control</th>
<th>Experimental</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cambridge I</td>
<td></td>
</tr>
<tr>
<td>9.VN.52, G.V.T.M.</td>
<td></td>
</tr>
</tbody>
</table>

Fig. 7. Initial orientations after active desynchronization treatment. See text.

A record of the nocturnal flight uproar (recorded by Dr Ludwig Koch) was then played until 23:00 when the lights were increased again to full illumination at 23:30. The lights were kept on continuously until 20:30 the next day. 'Night' for these birds thus fell some 3 hr. early, and it was hoped that their 'chronometers' would be similarly put forward. Then on release they would find the sun time well behind their 'chronometer' time, interpret this as being due to displacement westwards from Skokholm, and react by orientating to the east. Ten control birds kept for the same period in the separate wing of the laboratory with the normal light/dark sequence should orientate correctly homewards, to the west.

Unfortunately, cloud conditions on the release day, 9 July 1952, were again not satisfactory. At the start there was less than 1/10th cloud and during the following hour nine birds were released. Cloud had increased to 5/10ths by then and was soon about 8/10ths. It showed no signs of clearing so seven birds were released in these conditions when the sun appeared in gaps. The sky then became completely overcast until 3 hr. later when it cleared temporarily to 4/10ths and the last three birds
were released. The results are shown in Fig. 7, the birds released in sunny conditions being shown in black, the others in white. Only the former can give any evidence of the effect of the experimental procedure, and they do show a difference in orientation, in the sense predicted by the hypothesis. But with the small numbers available the difference is not sufficient to be considered significant ($P = 0.07$). The experimental birds also took longer to get away, in sunny conditions, than the controls averaging 4.6 min. $v.$ 3.4, again this is not significant. Thanks to the vagaries of the English weather this result is inconclusive like the last. But it is certainly more suggestive, and more tests of this nature are required and are planned for the coming season—under blue skies it is hoped.

**DISCUSSION OF PREVIOUS WORK**

The existence of a true navigational capacity has been demonstrated beyond doubt in the homing pigeon, in the Manx Shearwater and (less certainly) in the Lesser Black Back Gull. How far does the evidence obtained with these three diverse species imply that other birds with homing capacities are likewise equipped? In other words, how far has the lack of any unequivocal evidence of navigational ability been due to inadequate experimentation or the use of incorrect techniques or unsuitable material?

Until recently, far too little attention was paid to the orientation behaviour of homing birds on release. In any case the small numbers used by most workers would preclude any definite decision. In many cases the birds used were unsuitable for such observations, being birds which progress largely by soaring, e.g. Gannets, or small passerines which are likely to perch after release and in any case would be difficult to follow far. Griffin (1943) did analyse the headings of twenty-five Herring Gulls and found no tendency to start in the home direction, but the birds were released in cloudy conditions, and moreover are prone to soar.

The lack of any previous demonstration of straight line homing by a wild bird requires more explanation. The results obtained with the Lesser Black Back Gulls serve as a pointer. It was possible to demonstrate initial orientation, but the return was generally so slow that the second criterion of navigation was not fulfilled. It was suggested that this might be due to the birds adopting their normal, leisurely pace of travel, a conclusion now strengthened by the demonstration that different factors govern orientation and the actual return, in both pigeons and shearwaters. It can therefore be argued that swift returns over considerable distances should only be expected if the species used is one that normally travels fast and far. But only with exactly the right conditions can even the right sort of species be expected to put up the outstanding performance needed. We have seen that with the Manx Shearwater a high proportion of first and second night returns can only be expected when the birds are released: (1) in sunny conditions, (2) relatively early in incubation (before mid-June), (3) near the beginning of an individual incubation shift. The factors are listed in descending order of importance. To them we may add the probable existence of individual variations in orientation and homing powers. Further, the release must not be too distant or too late in the day for the birds to return by the
end of darkness. There are indications that about 300 miles, representing 10 hr. flying, is about the limit for 1 day’s flight for shearwaters.

On grounds such as these can we find the explanation for the inability of Lack & Lockley (1938) to demonstrate straight-line homing from unknown country, although using the same species. Of forty-one birds used, nine were taken from empty burrows or simply picked off the ground, and might well have been non-breeders. Then half the experiments were carried out after the third week in June when homing performance would be poorer. Lastly, continued nightly watch at the burrow was not practical for an active farmer. Orientation evidence was lacking because of small numbers and many of the releases took place on the coast whose topography would, at least temporarily, be an over-riding factor. Griffin (1940) failed to obtain evidence of navigation in an allied species, Leach’s Petrel. This much smaller petrel, about a tenth the weight of the Manx Shearwater, is much more delicate and easily weakened by transport. Thus after ‘nearly 3 days’ 50% were in poor condition. Secondly checks for returns were not possible in several cases until the fourth night after liberation, and only late in the season was the procedure of ‘inspecting the burrows at regular intervals throughout the nights’ adopted. Most of the releases were at sea where it would be difficult to follow so small a bird for long and there were no inland releases.

Previous failures to demonstrate navigation ability in the many species shown to be capable of homing cannot therefore be taken to mean that such ability is lacking. Indeed it would be safer to assume its presence until it is definitely shown to be absent. And since three such very dissimilar birds, pigeon, shearwater and gull, are apparently using the same type of navigation, it is presumably of wide-spread occurrence in birds.

APPENDIX A

The range of shearwaters from Skokholm

Thanks to the pioneer work of R. M. Lockley, and years of steady banding by the Skokholm Bird Observatory, some forty thousand of the numbered leg bands issued under the auspices of the British Trust for Ornithology have been put on Skokholm shearwaters. Even so, as would be expected in a bird of pelagic habits, the number of recoveries away from the breeding colony have been relatively few, 202 up to June 1952. The great majority of the birds are banded as adults picked up off the ground at night. Large numbers are obtained in this way but the method gives no information as to the individual’s age or breeding status. Comparatively small numbers of fledged young are banded, and hence recoveries are mainly of adults, in strong contradistinction to most other species, e.g. gulls (Matthews, 1952a).

The locations of recoveries are indicated in Fig. 8. They emphasize the pelagic nature of the species, there being only nine recoveries inland, of which four are of immature birds. All occurred in September and can be attributed to the birds being blown inland by autumnal gales, as can the inland occurrences of Manx
Shearwaters in general (Kenrick in Lack & Lockley, 1938). It is therefore safe to assume that shearwaters released any distance inland will be in an area unknown to them, and one which they will leave as quickly as possible.

The coastal recoveries are concentrated to the south of Skokholm, south Wales, Devon and Cornwall, west France and north Spain—there being only four isolated recoveries to the north of Skokholm. Only three recoveries came from the English Channel, again immatures in September and probably gale-blown. The east coasts of Britain can thus be classed as unknown to Skokholm shearwaters, and most of the west coasts as probably unknown.

Fig. 8. Distribution of recoveries of banded birds from Skokholm. Note. Majority of recoveries along shaded coasts, totals in distance brackets shown in circles. Isolated recoveries shown as dots.

For many years the southwards recoveries terminated abruptly at north Spain, and it seemed that the Manx Shearwater, unlike many of its relatives, had a fairly circumscribed annual range. But there was a complete dearth of recoveries from the beginning of November until February, which suggested that the birds wintered at least well out to sea. Manx Shearwaters had been known to occur regularly off Brazil and Argentina (Murphy, 1936), but as there had been reports of this species breeding in the Bermudas (Reid, 1884; Nichols & Mowbray, 1916; Dwight, 1927) it seemed likely that birds from there or from other undiscovered colonies in, say, the West Indies, would provide the migrants in South American waters. On the eastern side of the Atlantic the species breeds as far south as Maderia and, possibly, the Canaries (Bannerman, 1914), very much closer to South America than is Skokholm. However, in 1951 an immature bird ringed on Skokholm was
recovered only 6 weeks later in October off Rio de Janeiro (Brazil), and since this
analysis was made a further report has arrived of an adult ringed in 1947 and
recovered 200 miles south of Buenos Aires (Argentina) in October 1952. While
further recoveries of this nature must be awaited before we draw definite conclu-
sions it seems probable that the Skokholm population moves much farther south
than had previously been suspected. This conclusion is important for the present
work in that it places the Manx Shearwater among those trans-oceanic wanderers
in which any navigational faculties should be especially highly developed. Occur-
rences in North America are extremely rare and appear to be only accidental
(Dwight, 1923).

Another problem that has a strong bearing on the navigational and flying
capacities of the Manx Shearwater is that of its feeding range while incubating. As
will be seen from Table 7, there have been a number of recoveries 500-600 miles
south of Skokholm during the months May/July when there are eggs or young on
the Island. Lockley (1935) reasonably concluded that such recoveries were of late
breeders or non-breeders, in view of the indiscriminate banding technique. Later

Table 7. Distribution of coastal recoveries south of Skokholm

<table>
<thead>
<tr>
<th>Distance (miles)</th>
<th>May/July (%)</th>
<th>Aug./Oct. (%)</th>
<th>Nov./Jan. (%)</th>
<th>Feb./Apr. (%)</th>
<th>Total no.</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-100</td>
<td>23</td>
<td>28</td>
<td>.</td>
<td>1</td>
<td>30 + 1*</td>
</tr>
<tr>
<td>100-200</td>
<td>48</td>
<td>33</td>
<td>.</td>
<td>18</td>
<td>58</td>
</tr>
<tr>
<td>200-300</td>
<td>4</td>
<td>24</td>
<td>.</td>
<td>10</td>
<td>24</td>
</tr>
<tr>
<td>300-400</td>
<td>23</td>
<td>13</td>
<td>.(100)</td>
<td>70</td>
<td>71 + 1*</td>
</tr>
<tr>
<td>400-500</td>
<td>61</td>
<td>1</td>
<td>72</td>
<td>188</td>
<td></td>
</tr>
<tr>
<td>500-600</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total no.</td>
<td>52</td>
<td>61</td>
<td>1</td>
<td>72</td>
<td></td>
</tr>
</tbody>
</table>

Plus 1, Brazil, 1, Argentina, October. * No date.

(1942) he abandoned this cautious attitude following the recovery of two birds in
this group that had been ringed the same spring in Skokholm. These recoveries,
with the others ringed in previous years, were then considered to have 'settled once
and for all the truth that our shearwaters are feeding in the farthest corners of the
Bay of Biscay at the same time as they have nests and eggs at Skokholm—that they
are, in short, flying distances of 600 miles to feed!' But not one of these birds had
been banded on a nest with egg or young in that season, or, for that matter, in any
other season. A sixth of the occupied burrows prepared for the present study
contained birds that visited them irregularly but produced no egg (or had lost it
before excavation). An unknown and probably greater number of non-breeders
would be unable to obtain a burrow of their own. Lockley himself estimated that
40% of those which produced eggs were unsuccessful in rearing young. The chances
of a non-breeding bird being banded by the pick-up technique are thus substantial,
and certainly the mere presence of a bird at the colony during the breeding season is
no evidence that it is itself actively breeding.

In the course of the present work 724 birds were banded on egg or chick. One
was recovered away from Skokholm in May/July. This bird was the mate of a
Navigation in the Manx Shearwater

homer that had failed to return 10 days after release. Desertion of the burrow and chick might well be expected, but cannot be affirmed. Five days after last being checked at the burrow this bird (AX 3263) was recovered at Concarneau, Finistère, on 19 July 1951, 280 miles south. While there is serious doubt as to whether this bird was still persisting in breeding, its recovery is one of a substantial number off Finistère in May/July (Table 7). Again none of the others was definitely breeding, and only two had been ringed the same spring. But it cannot be denied that there is a possibility that active breeders range south across the mouth of the Channel (where we can expect no records) up to 300 miles from home. Again, the comparative importance of recoveries off Finistère may be exaggerated by the shooting by local fishermen, a factor absent in British coastal waters. Table 7 shows a marked hiatus in the May/July recoveries between 300 and 500-600 miles, the group Lockley was primarily concerned to allot to active breeders. Such a distribution suggests that we may be dealing with two classes of birds, e.g. breeders and non-breeders and not with the general spread from the breeding centre.

There have been reports of many thousand Manx Shearwaters passing by day southwards off Cornwall (Wallis, 1924; Thorpe, 1935; Hartley, 1935) and northwards off Ushant, Finistère (Meinertzhagen, 1948) which may be such feeding movements in progress. So far the most spectacular movements have been observed in April, before egg laying has begun and when potential breeders might be ranging farther afield than when actually incubating.

As most birds have been banded and recovered as adults little can be said about the age composition of the population, the age at which the birds first breed and other interesting points. It is hoped that data on adult mortality rates will be extracted from the mass of recoveries that have been made on Skokholm, where in the main colony about 40% of the birds picked up in a night have been banded previously. Some birds used in the homing tests had been banded up to 5 years previously as adults, but the bands generally wear through in this time and banding had come to a stop during the war, so this is by no means the upper age limit.

APPENDIX B

Use of flight-duration recorders

We have seen that well-orientated shearwaters returning on the first or second night will have flown in a more or less direct line from their inland release points to the neighbourhood of Skokholm. We must investigate the performance of such birds as these, and not that of stragglers, if the basis of bird navigation is to be found. It follows that the exact homeward track is now of only minor interest. Wilkinson (1950) had designed a radio-active flight-duration recorder to determine the approximate length of the homeward track, before concrete evidence of true navigation had been obtained. Recorders of this type have been tested extensively on pigeons (Matthews, unpublished) and over a hundred were used on shearwaters in 1951. There was little difficulty in recovering the recorders from returned birds
such as had been met in Lesser Black Back Gulls (Matthews, 1952a) and sixty-three recorders were recovered after flights.

Great difficulty was experienced in the matter of waterproofing the recorder, the interior of which must be kept completely dry to prevent the ball-bearing shutter from sticking, or the film emulsion from being damaged. Various waxed and rubberized wrappings were tried out, but only by embedding the recorder wholly in wax within a further capped dural container, liberally sealed with Bostik, could the penetration of water be avoided. This increased the bulk and weight (c. 1 g.) of the

Table 8. 'Flight' duration records obtained with Manx Shearwaters

<table>
<thead>
<tr>
<th>Release point</th>
<th>Time from release to recapture (hr.)</th>
<th>'Flight' time (hr.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cambridge</td>
<td>6:7</td>
<td>7:2</td>
</tr>
<tr>
<td>Local</td>
<td>7:7</td>
<td>3:5</td>
</tr>
<tr>
<td>Local</td>
<td>7:9</td>
<td>4:5</td>
</tr>
<tr>
<td>Cambridge</td>
<td>8:9</td>
<td>9:5</td>
</tr>
<tr>
<td>Cambridge</td>
<td>8:0</td>
<td>12:0</td>
</tr>
<tr>
<td>Cambridge</td>
<td>8:4</td>
<td>11:7</td>
</tr>
<tr>
<td>London</td>
<td>17:7</td>
<td>14:8</td>
</tr>
<tr>
<td>Birmingham</td>
<td>17:7</td>
<td>22:1</td>
</tr>
<tr>
<td>Birmingham</td>
<td>17:8</td>
<td>21:8</td>
</tr>
<tr>
<td>Slimbridge</td>
<td>28:5</td>
<td>11:0</td>
</tr>
<tr>
<td>Birmingham</td>
<td>30:2</td>
<td>20:4</td>
</tr>
<tr>
<td>Cambridge</td>
<td>30:3</td>
<td>15:2</td>
</tr>
<tr>
<td>Cambridge</td>
<td>30:3</td>
<td>21:1</td>
</tr>
<tr>
<td>Birmingham</td>
<td>30:4</td>
<td>28:6</td>
</tr>
<tr>
<td>Cambridge</td>
<td>31:2</td>
<td>25:2</td>
</tr>
<tr>
<td>Birmingham</td>
<td>42:3</td>
<td>84:1</td>
</tr>
<tr>
<td>Birmingham</td>
<td>42:3</td>
<td>24:5</td>
</tr>
<tr>
<td>Slimbridge</td>
<td>52:3</td>
<td>36:1</td>
</tr>
<tr>
<td>Cambridge</td>
<td>56:9</td>
<td>36:7</td>
</tr>
<tr>
<td>Birmingham</td>
<td>64:6</td>
<td>43:9</td>
</tr>
<tr>
<td>Cambridge</td>
<td>78:1</td>
<td>37:4</td>
</tr>
<tr>
<td>Cambridge</td>
<td>129:0</td>
<td>166:3</td>
</tr>
</tbody>
</table>

attachment to a point where it could begin to be an encumbrance to a bird of the present size.

The results obtained from the films in successfully waterproofed recorders are shown in Table 8. These are corrected for the theoretical decay of the source strength between the date of flight and that of subsequent calibration for a known time. It will be at once apparent that in a number of cases the ‘flight time’ exceeded the maximum possible. This was, at least in part, due to false ‘flight’ recording while the bird was still in the box. This is shown by the readings of recorders removed after the bird had spent a period in the box, before release:

<table>
<thead>
<tr>
<th>Hours in box</th>
<th>Recorded as ‘flight’ (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>32</td>
<td>2</td>
</tr>
<tr>
<td>30</td>
<td>4</td>
</tr>
<tr>
<td>32</td>
<td>5</td>
</tr>
<tr>
<td>30</td>
<td>8</td>
</tr>
<tr>
<td>32</td>
<td>8</td>
</tr>
<tr>
<td>30</td>
<td>8</td>
</tr>
<tr>
<td>32</td>
<td>12</td>
</tr>
<tr>
<td>32</td>
<td>14</td>
</tr>
<tr>
<td>32</td>
<td>21</td>
</tr>
<tr>
<td>32</td>
<td>73</td>
</tr>
<tr>
<td>32</td>
<td>83</td>
</tr>
</tbody>
</table>

The proportion of box time recorded as ‘flight’ is both substantial and variable, not entirely related to the period of imprisonment, i.e. 1 or 2 nights. It is therefore impossible to apply a standard correction. The position of the recorder, stuck with Bostik over the manus on the inside of the wing, cannot be improved upon to give
wider differences in attitude between flight and rest. The 1 mm. steel ball shutter of the original design had already been replaced by a 1.8 mm. lead ball as the heavier shutter had reduced similar false recordings by pigeons in baskets, to some extent. A denser ball might help even more but the diameter cannot be increased further without scaling up the instrument as a whole. In pigeons the problem was avoided by hardening on the wing a permanent bucket into which the recorder could be slipped just before release. But with shearwaters the elaborate waterproofing required that the complete assembly be hardened into place as a unit, and this can only be done when the bird is confined in the box. The only solution would be to attach a second recorder as close as possible to the first for removal before release. This would double the already considerable amount of work involved—the few results given here resulted from the individual counting of 186,000 alpha particle tracks under the microscope.

The false 'flight' record is presumably built up by the birds scuffling about in the box, or resting with one wing up against the side. It is not wholly due to the unnatural circumstances, since birds remaining in the nest also produce 'flight' records:

<table>
<thead>
<tr>
<th>Hours in burrow Recorded as 'flight' (%)</th>
<th>34</th>
<th>53</th>
<th>34</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>5</td>
<td>12</td>
</tr>
</tbody>
</table>

This would also have to be allowed for if there was any delay in recapturing the bird on its return. And if so much 'flight' is recorded while the bird sits quietly in its burrow, how much more will be recorded when resting, preening or feeding on the water? Further, the shearwaters that assemble on the sea off Skokholm from 19.00 onwards do not sit quietly and wait for night to fall. They frequently take off and fly for several minutes at a time. The total amount of flying done in this way is very variable, but is estimated to be between 1 and 2 hr.

Lastly, it has now been found that the apparent reduction in source strength is variable and in most cases faster than would be predicted theoretically, i.e. the 'flight' times in Table 8 would be too high in any case. This discrepancy is not due to flight conditions alone as it occurs when the recorders are standing in the laboratory. This is a problem in radio-chemistry, which might be solved by using a source other than polonium and/or improving the present method of electrolytic deposition on silver foil from dilute nitric acid solution.

**SUMMARY**

1. Homing experiments were carried out with 338 Manx Shearwaters from Skokholm Bird Observatory, Pembrokeshire. The especial advantages of this species for such work are described.

2. With sunny conditions, strong homeward orientation was shown by birds released at points unknown to them. Early in the season these releases gave very fast, complete returns, more than half back on the first 2 nights. Those on the first night were unequivocal evidence of long, direct flights over unknown country.

3. One shearwater homed at least 3050 miles across the Atlantic in 12.5 days.
4. There was a decline in the proportion of returns later in the season, probably due to a loss of stamina.
5. With conditions of heavy cloud the homeward orientation broke down and returns were poorer.
6. The stage of the individual incubation shift has some effect on the homing performance.
7. For the first time we have a demonstration of complete evidence for navigational ability in a wild bird. The suggestion of a form of sun navigation is in line with evidence obtained with pigeons and gulls. The failure of workers with other species to produce such evidence is not considered to weigh against the possibility of navigational ability of this kind in all proven homers.
8. The sun-navigation hypothesis is investigated. Although shearwaters fly to the burrows after dark they are unable to navigate after sundown. Determination of the latitude from the sun's altitude can only be tested in this species by trans-equatorial experiments.
9. Determination of longitude by time differences was tested by attempting to desynchronize the necessary internal 'chronometers'. The first attempt was inconclusive owing to cloudy conditions at release. A second attempt was also partially thwarted by the weather, but gave suggestive results favouring the hypothesis. More experiments of this nature are required.
10. An analysis of the range of shearwaters from the colony, based on banding results, is given.
11. The Wilkinson flight-duration recorder was used on this species, but did not give satisfactory results.

My thanks are due to Prof. J. Gray for his interest in and facilitation of this work. Dr W. H. Thorpe has been a constant source of encouragement, and in addition undertook the liberation of many birds. The Council for the Promotion for Field Studies permitted the use of their Centre, Skokholm Bird Observatory, whose Warden, P. J. Conder, and his wife, have been extremely helpful. The Warden of the Dale Fort Centre, J. H. Barrett, and his staff, undertook the arduous task of ferrying the birds by boat and van to the railway. Many visitors to Skokholm helped with digging, box making and other tasks, and their help is in no way forgotten if special mention is made of M. Hewitt, R. Orpin and M. W. Reade who gave practically full-time assistance during their stay.

The main liberations (Figs. 2, 3 and 5) were carried out by Captain A. W. Ford, Dr R. A. Hinde, Wm. Johnson, C. A. Norris, Dr W. H. Thorpe and Dr D. H. Wilkinson—who also gave much help with his flight-duration recorders, whose source material was prepared by Dr A. G. Maddock. Smaller numbers of birds were released by M. Hewitt (London A), E. Godfrey (Newcastle), R. E. Jones (London A), G. T. Mack (Manchester), R. Mazzeo (Boston), G. Tharp (London B), M. R. Williams (Slimbridge), and Captain H. R. H. Vaughan (Llandovery). Permission from the Air Ministry for the release from O.W.S. Weather Recorder was obtained through the good offices of the Marine Superintendent, Cmdr. C
Navigation in the Manx Shearwater

Frankcom. Weather information and forecasts were obtained from the Air Ministry, Harrow and Mildenhall. R. M. Lockley gave advice and was instrumental in enabling the transatlantic flight to take place. Miss E. P. Leach was of great help in the matter of recoveries, and the organization of the British Trust for Ornithology is of course responsible for the data on Skokholm to which I had access by the courtesy of the Warden. Dr Ludwig Koch’s recording of the Manx Shearwater was loaned by the British Broadcasting Company, through the good offices of E. Simms. The University Librarian kindly permitted the use of the Tower.

The Royal Society provided a grant to cover the experimental expenses, and the work was done while I was in receipt of a research grant from the Department of Scientific and Industrial Research.

For all this assistance, personal and financial, all too briefly summarized, I am most profoundly grateful.

REFERENCES


