Cambridge University Press
978-0-521-09541-9 - Bird Navigation, Second Edition
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CHAPTER I

Field observations of migration

Bird migration has now been studied from so many angles and by so many people that it is doubtful if any one author can still do the whole subject credit, as did Landsborough Thomson (1926). Recent attempts have been made by Schüz (1952), by Dorst (1962) and by Bernis (1966). The present volume concerns itself with only one aspect, the manner in which birds find their way on their journeys, their navigation. However, as this is one of the most fascinating problems in biology, no apology need be made for such specialization.

In the last twenty years in particular there has been a very considerable amount of experimental investigation of bird navigation, and the consideration of this evidence takes up the bulk of the book. But experiments should only be embarked upon against a background of knowledge of what the animal does in its natural state. And so we must first consider the evidence provided by field observation and the collection of specimens.

These together have outlined the remarkable migrations that take place, such as that of the Bristle-thighed Curlew which nests in a coastal strip of Alaska and winters in Pacific Islands 6000 miles away, with minimal sea-crossings of 2000 miles. Although the wintering area covers an arc of 45° from the breeding grounds, the migration must at least have a strongly directional trend. The return journey from the scattered islands to the restricted breeding grounds involves a greater navigational feat, but this pales in comparison with that of the Great Shearwater. These birds range over both Atlantic Oceans up to 60° N. Yet they return in their millions to breed on the Tristan da Cunha islands lying at 40° S, spread over only 30 miles of ocean and 1500 miles from the nearest land mass.

From detailed field observations and examination of plumages we know that in many species the young of the year make their way quite independently of the adult birds. There can then be no question of the latter acting as guides. The cuckoos, of course, provide extreme examples of juvenile independence, and yet the Bronze Cuckoo migrates 2500 miles over the open sea, with minimal sea crossings of 900 miles.

When races can be distinguished in the field or hand, the movements of birds from particular areas can be followed in more detail. Strong tendencies are found for a local breeding population to reassemble in quite localized wintering areas. Thus the six sub-species of the Fox Sparrow, which breed successively down the west coast of North America, are found wintering in the reverse order to the south, the more northerly races having leap-frogged their southern neighbours. Racial discrimination produces many other examples of birds migrating much greater distances than they apparently 'need'. Thus it is the Antarctic race of the Great Skua, not the New Zealand one, which winters off Japan.

But a real upsurge in knowledge came when it was possible to follow the fates of individual birds, by marking them with metal leg bands, bearing an address and a unique number. The method has been widely adopted in the last half-century and its use has reached considerable dimensions. The total number of birds ringed is not known, but it exceeds five million for Great Britain alone. Subsequent reports of birds that have been ringed range from about 20% in species shot for sport or as vermin, to a fraction of 1% in the smaller passerines and in pelagic species. Allowance must be made for some bias in the proportion and location of such recoveries. They will reflect to some extent the distribution of the human population (in particular of that portion of it that is literate), and hunting practices and seasons. Again in most species the bulk of the information will relate to young birds in their first year, which will provide many more recoveries owing to their greater mortality.

On the one hand, some of the most exaggerated migrations have been confirmed, such as that of the Arctic Tern. These birds have been shown to migrate from the Canadian Arctic, where they nest within 10° of the North Pole, to the Antarctic pack-ice via the west coast of Africa. The double journey is equivalent to circling the earth at the equator. On the other hand, it has been established that after long journeys, migrants which return breed year after year in the same nest site. There have been many studies of such *Ortstreue*, diverse examples

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being those on Bank Swallows (Stoner, 1941), various duck (Sowls, 1955), Pied Flycatchers (Haartman, 1960) and Mourning Doves (Tomlinson *et al.* 1960). When allowance is made for natural mortality it is found that practically all surviving adults return to breed in the same area the following year(s). On the other hand young birds returning after their first migration settle and breed over a much wider area. For some species the much more difficult achievement of identifying the same individual repeatedly *wintering* in a small area has been reported (e.g. Tettenborn, 1943). On a more general level the re-forming of localized breeding populations in localized wintering areas has been amply confirmed. Thus Boyd (1964) showed that Barnacle Geese, breeding in Greenland and in Spitsbergen, winter in Scotland only 100 miles apart without intermingling. A third population, breeding in Siberia winters in the north of the Netherlands. Indeed the typical migration has come to have the appearance of a ‘shuttle’ service between two small areas. This would require as a bare minimum of navigational equipment the ability to fly an accurate bearing-and-distance course. In many cases, that of the Great Shearwater for instance, a more precise form of navigation would seem to be needed. But not necessarily so precise as would at first sight be indicated by Richdale’s (1963) finding that Sooty Shearwaters nest, after several migrations of thousands of miles from New Zealand to Japan (Phillips, 1963), an average of 7·7 feet from the point where they were originally marked. A transatlantic airline navigator does not locate his suburban villa by the methods he used to guide his aircraft from New York to London.

For many years there was great controversy as to the method of migration. There were those, following Middendorf (1855), who believed that migration took place in one general direction, on a broad front. Opposing them were the followers of Palmen (1876) who insisted that the migrants passed along certain restricted routes, on a narrow front. As is so often the case in biological controversy the correct answer is a compromise. Geyr von Schweppenburg (e.g. 1922, 1963) formulated such a theory. He suggested that there was indeed a directional trend to migration, the birds flying in a ‘standard direction’, typical of their particular population, while over uniform terrain or the sea. But in addition there were ‘leading-lines’ formed by the boundaries between favourable and unfavourable terrain,

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between land and sea, hill and plain, forest and savannah, desert and fruitful land. When the birds encounter such a leading-line they tend to fly along it, forming a narrow and concentrated stream just as if they were passing along one of Palmen's 'routes'. But when the obstacle is passed, or the urge to fly in the standard direction becomes paramount, the stream widens out into the broad front again.

As long as field observations were confined to counting and identifying birds that had landed or were passing within the range of unaided vision, little progress could be made in the study of the way in which migration proceeded and of the factors influencing it. We now know that such observations represent but a small and variable proportion of migratory streams. Thus, when they encounter head winds birds fly lower and are so more easily seen. Again, migrants may only appear on the ground when they have been drifted there by unusual winds and/or 'precipitated' by encountering fog or heavy cloud and rain.

The initiative for a more comprehensive study of migration was provided by Kramer (1931), who observed that birds migrating overhead by day could be detected with binoculars at considerable heights. It has since been determined that the bulk of migration occurs within a mile of the surface and is therefore accessible to this technique. The new method was seized upon with enthusiasm, and gazing through upturned glasses became widespread in North-west Europe, see, for example, Svärdson (1953) and more recently in North America (Newman & Lowery, 1962). Tinbergen (1956) and Gruys-Casimir (1965) provided a summary of daylight observations in the Netherlands, especially in so far as they illuminate the problems of bird navigation, and Perdeck (1961, 1962) has made detailed studies on Chaffinch migration.

Some evidence on the numbers and species of birds passing by night has been provided by 'kills' at lighthouses and more recently airport 'ceilometers' (Howell *et al.* 1954) and television masts (Cochran & Graber, 1958). Spectacular slaughter has been recorded, such as 50,000 birds of fifty-three species in one night (Johnston & Haines, 1957) but these happenings are abnormal both as regards the birds' behaviour and the weather conditions implicated. Attempts to probe the normal course of nocturnal migration started when Scott (1881) conceived the idea of using a telescope to count birds passing across the moon's disc. Lowery (1951) took up this method and organised a network of observers in Northern America, and eventually (Lowery & Newman, 1966) published results for four nights. Strömberg (1961) used the technique in Sweden. Since the apparatus is simple and portable it is useful for small expeditions working away from base facilities, such as in Greece (Bateson & Nisbet, 1961) and Spain (Walraff & Kiepenheur, 1962). Elaborate calculations are needed to ascertain the effective size of the cone of observation which is swept across the sky, but these can be reduced to tabular form (Nisbet, 1959). A more basic limitation is that observations are confined to one-third of each month, centred on the full-moon period.

Both moon-watching by night and sky-watching by day are frustrated by cloudy weather. In places like Britain this greatly reduces their utility. Mention may be made of the technique, started by Libby (1899), of counting flight calls of migrants invisible on moonless nights or above low cloud. The unaided human ear (e.g. Ball, 1952) cannot pick up normal flight calls above 1500 feet and can give but little indication of direction. Graber & Cochran (1959, 1960) have overcome these difficulties by using a parabolic reflector and an amplifier, extending the range to 10,000 feet or more. There remains the difficulty of relating the number of calls heard to the number of birds passing, for the rate of calling undoubtedly varies between species and according to weather and time of night. However the opportunity it affords for identifying species makes it a useful accessory to other methods.

Radar has undoubtedly revolutionized the field study of bird migration and made observations almost independent of weather and fully comparable by day and by night. There was a gap between the first statement of radar's potentialities for the study of bird migration (Lack & Varley, 1945) and its actual use. Suitable microwave equipment had to be developed and research workers had to be insinuated as tolerated parasites on equipment serving airports or military requirements. The snags of the radar tool are its expense and the skilled maintenance required. Moreover, its primary users have no reverence for the 'angels' that clutter up their display screens, and strive towards technical improvements that will eliminate them. Opportunities to use such equipment may thus be passing ones, but ornithologists have seized theirs in Switzerland (Sutter, 1957; Gehring, 1963), England (Harper, 1958; Tedd & Lack, 1958; Eastwood *et al.* 1960), Sweden (Mascher *et al.* 1962), Cyprus (Adams, 1962), New England (Drury & Keith, 1962), Illinois (Graber & Hassler, 1962), Finland (Bergman & Donner, 1964) and the Mediterranean (Casement, 1966).

Two main types of radar have been employed (usually operating on 10 or 23 cm bands), the ones used at airports which give coverage within a radius of 10 miles, and the high power early warning sets which sweep a vast area, detecting small birds out to 80 miles or more. The former is the tactical instrument and offers the opportunity to investigate the nature of the echoes by visual and auditory checks. One of the main limitations of radar at present is the difficulty of identifying echoes beyond the broad categories of passerines, waders or wildfowl. Much experimental investigation of 'echo' characteristics such as that of Edwards & Houghton (1959), Gehring (1967*b*) and Schaefer (1968) is needed. The bigger set can paint in majestically a complete migratory movement, enabling a strategic appreciation of the situation as a whole. Permanent photographic records can be made of the display screens at short intervals or projected as a cine-film so that the movements of the individual echoes are readily apparent. Dyer (1967) has developed a photoelectric cell technique for analysing film of radar scans. A *caveat* must be entered concerning the quantitative analysis of radar traces. So many factors, beside the actual density of the birds, are concerned in producing the density of 'angels' observed, that only very broad categories of enumeration would seem to be justified (Nisbet, 1963*b*). Nevertheless the use of radar has built up a formidable number of data on the phenology of bird migrations (Lack, 1959/63; Lack & Eastwood, 1962; Lack & Parslow, 1962; Parslow, 1962), on the heights at which they occur (Lack, 1960*a*; Nisbet, 1963*a*; Eastwood & Rider, 1965; Gehring, 1967*a*), on their manner of flight (Eastwood & Rider, 1966), on the influence of weather (Lack, 1960*d*; Hassler *et al.* 1963) and especially on the effects of wind on migrants moving over the open sea (Lack, 1958, 1959, 1960*a*, *b*, *c*; Drury & Nisbet, 1964; Nisbet & Drury, 1967; Bergman & Donner, 1964), or overland (Bellrose & Graber, 1963; Evans, 1966*a*; Bellrose, 1967*a*). Lack (1962) condensed the light that radar threw on the problems of bird orientation and Evans (1966*b*) has essayed a comparison between the results obtained by visual and by radar observations, while Eastwood (1967) has gathered into book form much of the published data.

We may now attempt to summarize the information garnered by the various methods of field observations, giving preference to radar evidence when there is a conflict. The close linkage between the main migratory movements and the breeding seasons has been fully confirmed. We are not here concerned with the factors governing the latter, summaries having been published by Marshall (1961), Wolfson (1966) and Farner (1967). On the other hand, radar has revealed quite substantial movements throughout the year and the formerly sharp distinctions between the normal (spring and autumn) migrations, 'reversed' migrations and hard-weather movements can no longer be maintained. There follows the implication that navigational faculties cannot be rigidly seasonal.

Even in the normal migratory periods, movements are not spread evenly and the bulk of the migration tends to be concentrated in short periods of a few days. These movements are usually initiated during periods of undisturbed weather with clear skies and light winds. Moderate or strong winds are avoided unless they are favourable. There is no question of the birds simply flying downwind with any wind; they appear to wait for one blowing in the general direction in which they should migrate. There is some evidence of still finer adjustment of headings at the start of the flight, so that the resultant track is in the proper direction.

Once started, a migratory movement may well encounter cloud and unfavourable winds. It may be 'precipitated' over land when it meets the turbulent conditions of a cold front. Over the sea migrants which enter cloud or mist banks become disorientated, milling in all directions and inevitably drifting down wind. There is little direct evidence to support Williamson's (1955) suggestion that in such conditions they descend near the sea, determine the wind direction with reference to the wave patterns and actively fly downwind. Such visual observations as have been made of lowflying birds in mist, rarely migrants (King, 1959), more often foraging seabirds (e.g. Drury, 1959), suggest that they can maintain a heading, probably with reference to the wave pattern, but are completely

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disorientated when fog closes right down. Well-directed movements continue above fog or low cloud, when ground and sea features are obscured but not astronomical clues. On the other hand there are numerous instances of migration continuing in the normal direction under layer cloud heavy enough to eliminate directional clues afforded by the sun, stars or moon. These instances were over land or at no great distance from the coast; sufficient topographical features would then be available for a point-to-point maintenance of *direction*. Bergman (1964) has shown this to be so in practice. Even at night the ground is sprinkled with a galaxy of lights in densely inhabited areas which would be visible far out to sea from the coasts of (for example) New England. If migration continues for several days in heavily clouded conditions it becomes noticeably less well orientated. Bellrose (1967*a*) produces rather convincing evidence that airborne birds may be able to determine the wind direction and strength directly, provided that the airflow is turbulent. Vleugel in many papers (e.g. 1959, 1962) has stressed the possibility of wind direction acting as a secondary orientation clue, by day and night.

Over the sea well away from coasts the birds fly on a straight course by day and by night and do not appear to compensate for the effect of changes in wind direction. They may thus drift off their intended track and make landfall far from that indicated by their heading at departure. Thus many of the arrivals of continental birds on the east coasts of Britain can be related to easterly winds acting on a south or SSW movement out of Scandinavia. Occasional observations have been made of wind-drifted night migrants abruptly changing their direction at dawn to a course that offset the drift (Lee, 1963; Myres, 1964). It is not clear yet whether this indicates the operation of a superior navigation by day or a rather stereotyped directional response to finding themselves still over the sea. If migrants coming in off the sea show any reaction to the coast (and they generally proceed straight on) they turn and fly along it in the upwind direction. Radar observations have yet to give unequivocal examples of movements of wind-drifted migrants which have subsequently re-determined the position of their goal. Ringing recoveries certainly indicate that this does occur and there is a little evidence that even juvenile birds on their first migration are so gifted (Evans, 1968).

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Although the concept of 'standard directions' governing the migratory flights of species, or even local populations, has been fully justified, it is clear that in many cases a single compass course will not take the birds to their winter quarters. Thus warblers and flycatchers travelling SSW to SW across western Europe must at some time swing to east of south to reach their wintering grounds in tropical Africa, while other species which leave to the SE must turn in a clockwise sense (Moreau, 1961). Chaffinches from Norway have been shown to fly a whole series of courses, starting SE, changing at intervals right round to NW. This has the effect to bring them to Britain without crossing the main North Sea (Perdeck, 1962). Such changes of course are not necessarily associated with topographical features (Mook *et al.* 1957), but the possible influence of experienced birds cannot be ignored. Vleugel (1953) suggested that the increasingly westward trend in autumn could be due to failure to allow for the changing position of sunrise.

To sum up then—if we were restricted to the evidence of field observations, we could certainly conclude that migrant birds, even inexperienced juveniles, at least have the ability to fly on straight compass courses and know which direction is appropriate to the season and the stage of migration. There is evidence that adults have a firm knowledge of the position of the breeding site and probably of the winter quarters and can return to them if displaced by their own efforts or by the wind. Topographical features may temporarily deflect the more low-flying migrants or concentrate them into apparent 'streams'. Landmarks may also serve as reference points for the correction of wind drift or the maintenance of a predetermined direction. Corrections may also derive from an intimate appreciation and assessment of air flow structure. The basic navigational information, however, is most likely derived from astronomical clues. The field evidence thus is that birds are guided almost exclusively by visual stimuli. With this background we may now consider the experimental evidence.

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CHAPTER 2

Experimental evidence for bearing-and-distance navigation

In those species where the young migrate independently of the old we have a natural experiment showing that any tendency to fly in one direction must be part of the bird's innate behaviour; the young Cuckoo provides an extreme example. Where young and old migrate together the former could possibly *learn* the migration direction as well as the final location of the wintering area. This can be tested by holding young birds in the area of their breeding until all others of their species have departed. Rowan (1946) reported briefly that fifty-four Prairie Crows gave 'some 60 %' recoveries of which 'not a single bird had deviated significantly from the standard fall direction'. Schüz (1949) obtained sixteen reports from 247 delayed White Storks, all in the normal migration direction but rather more scattered than usual.

To eliminate the possibility that the unlearned direction was imposed by geographical or meteorological features, Schüz took 144 White Storks from nests in the Baltic region and reared them in West Germany. Released after all local migrants had passed, the tracks followed by the birds (which had colour marks on their plumage as well as leg rings) could be mapped (fig. 1). They show a strong tendency to lead SSE, the appropriate direction for the population from which they were drawn, but quite distinct from that (SW) for the species in the release area.

A more stringent test is to rear and release young birds in areas where the species does not breed. Schüz (1938*b*) reared 21 White Storks from the Baltic in England; Drost (1955, 1958) 953 Herring Gulls from the Freisian Islands inland in Germany; Bloesch (1956, 1960) 192 White Storks from Algeria in Switzerland; Vaught (1964) 377 Blue-winged Teal ducklings from Minnesota in Missouri. The recoveries indicated migration in the direction normal for the population from which the birds