

Bird Navigation

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1 Aims of the series of lectures

This is the first of two lectures I give in the course. The first is on Bird Navigation and the second is on modelling behaviour. There is a common theme: how do we design experiments that tell us what is going on inside the animal. Sometimes the theme is illustrated by successes, where something was learned about the inner workings. At least as often, the theme is illustrated by failure and the question becomes: how can we learn from mistakes? To achieve this aim the lectures trace an episode in the history of each subject.

This lecture and the notes should give a fairly full account of historical developments in the study of bird navigation; modern studies are cited but not described and students are encouraged to read the modern citations themselves.

2 Aims of this lecture

There has been intense research on bird navigation and, even 30 years ago, [Matthews \(1968\)](#) cited over 700 references going back well over 100 years. The aims of the lecture are to:

1. Show what birds achieve
2. Discuss current views of how they do it
3. Illustrate the way various systems may interact, and how birds calibrate one system from another.

4. Review the way research has progressed and to learn from the mistakes that have been made.

3 Types of navigation

3.1 Piloting (the use of landmarks)

How do birds navigate? The simplest hypothesis was that they rely exclusively on landmarks they have already learned. Thus when released in unfamiliar territory they search randomly until they come across a known landmark. It is often difficult, even in homing experiments over long distances, to exclude the use of landmarks ([Matthews, 1970](#)) especially because of the height birds may fly. However, in many species the young migrate through unfamiliar territory without accompanying adults. Young bronze cuckoos, for example, leave New Zealand some time after the adults and cross 2,500 miles of ocean to winter in the Solomon Islands. This involves non-stop flights of at least 900 miles where compass errors of a few degrees must be fatal. Thus, while known landmarks may be important, it is clear that many species use a *compass sense* and often with startling accuracy.

3.2 Compass orientation

In principle, migrants could alternate between summer and winter quarters by setting out in an appropriate direction in autumn and reversing it in spring. This would require no more than a compass sense and

genetic coding of the appropriate direction. In practice, young birds of several species seem to show exactly this on their autumn migration. When trapped and artificially displaced, young starlings continued to head in the same direction instead of correcting for the displacement and so ending up in the appropriate winter quarters (Fig. 1) (Perdeck (1958) reviewed by Matthews (1968); Schmidt-Koenig (1965)).

More recently, Helbig (1996) studied the genetic basis of inherited migratory directions while Thorup et al. (2000) and Mouritsen (2000) have debated the evidence from models used to simulate the geographic distribution of ringing recoveries in young pied flycatchers (*Ficedula hypoleuca*). It appeared that the ringing recoveries were more narrowly distributed than would be predicted by a model with compass direction alone, leading to the claim that young birds were compensating for the previous night's wind drift. The study is interesting but difficult to interpret.

3.3 True navigation

In Perdeck's experiments, displaced adults compensated for the error and most recoveries occurred in the normal winter quarters or on the way to it. Thus the adult birds were able to determine which compass direction would lead them to their goal. This additional ability is usually referred to as *true navigation*.

Landmarks, compass orientation, and true navigation are of course used together by many species. The best studied example is the homing pigeon and Michener and Walcott (1967) have tracked individual pigeons homing from unfamiliar territory (Fig. 2). Flights often showed three phases:

1. Flight in a 'preferred direction', for five miles or more, not usually towards home. A compass sense is all that is needed to explain this phase.
2. Flight heading towards home for many miles with errors often less than two degrees. This illustrates both the ability to maintain a compass bearing and the accuracy of their estimate of the home direction.

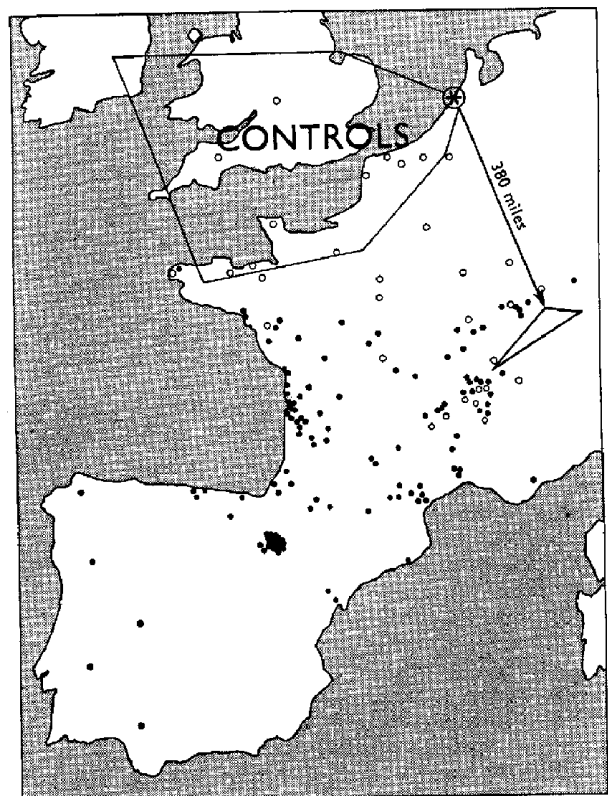


Figure 1: Recoveries of starlings displaced from Holland to Switzerland while on autumn migration. Open circles: adults; filled circles: juveniles (From Matthews, 1968, p. 14, after Perdeck, 1958). Note that the young birds continued to migrate in the direction needed to reach the usual wintering area (controls) from Holland, but this was now inappropriate. The adults mostly changed direction back towards the usual wintering area.

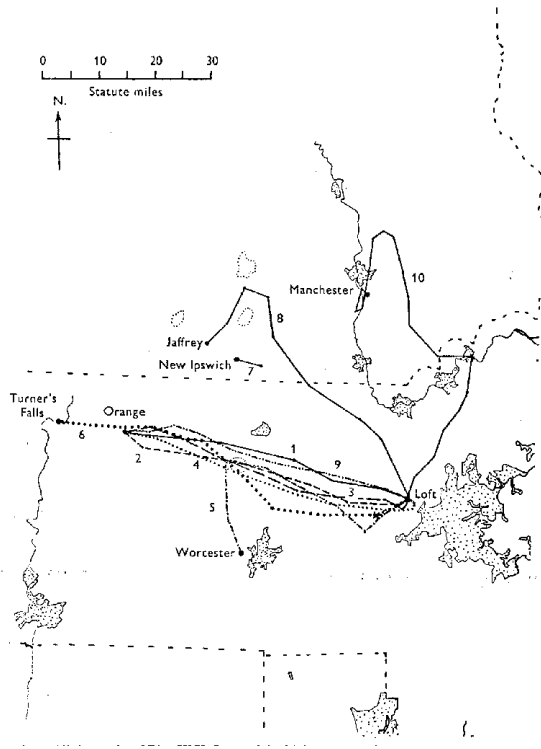


Figure 2: All the tracks of Blue W Y. Some of the highest mountains are shown in this figure as rings of dots. For several days prior to track 5 the bird was kept under an artificial light/dark regime. (From Michener and Walcott (1967)).

3. Within ten miles of the loft pigeons appeared to respond to landmarks.

4 Sensory cues

The sensory cues underlying these three types of orientation have been studied intensively. Unfortunately much of the work before 1965 was unreliable because the problems of circular statistics were not well understood. Another early misunderstanding arose because authors assumed that birds could use only one set of cues. The fallacy can be illustrated by imagining a man heading north with a compass.

Take the compass away and he manages by the stars, does this prove he was not using the compass. It seems very obvious, but Pennycuik set out the requirements for any successful navigation hypothesis and his first requirement was that the proposed cues must be available under all conditions in which birds are known to navigate. He was not alone in making this error. Thus [Matthews \(1951\)](#) concluded that magnetism had no role in bird navigation after showing that pigeons homed successfully with bar magnets attached. Later, [Keeton \(1971\)](#) found evidence that, under overcast skies, an attached magnet caused disorientation while a brass bar did not. Both groups could navigate while the sun was visible. You should be sceptical, therefore, of experiments which seem to rule out a cue because the bird does not use it. It may be that other cues were available.

A third problem is that many authors studied the vanishing directions of birds at the release site. As [Michener and Walcott \(1967\)](#) showed, the first phase of flight is often in some preferred direction, unrelated to the home direction. This phase can extend for ten miles: well beyond the point of vanishing. Care is needed in interpreting vanishing directions and their response to various treatments, although this was not understood in the early studies.

The cues on which piloting is based are presumably visual, and depend on what landmarks the bird has learned. Pigeons fitted with frosted-glass contact-lenses return to within a few hundred metres of the loft, but fail to reach it, so visual landmarks seem to be essential for the final approach. Piloting cues are much more boring than those which underly compass orientation or true navigation. It is best to consider these latter types of orientation separately.

5 Sensory cues underlying compass orientation

5.1 Sun

[Kramer \(1951\)](#) suggested that the sun was used as a compass, being south at noon and moving approximately 15° per hour. This was based on experiments in which starlings were placed in circular cages with

perches around the walls. Kramer recorded the number of times each perch was used and the birds preferred those in the direction they would have taken on migration. They became completely disoriented under overcast but, in later studies, took up appropriate orientation when the sun was ‘moved’ by reflection.

To use the sun as a compass, a bird must allow for its movement through the sky (about 90° every six hours). Numerous experiments (eg. by Kramer, 1952) have demonstrated this ability in caged starlings (Fig. 3). He also shifted their internal clocks by six hours and demonstrated errors of about 90° . Finally, he arranged a ‘stationary’ sun and showed that the birds’ preferences moved around the cage in the predicted way. Numerous experiments (reviewed by Matthews, 1968, Ch. 3), and since, have confirmed the view that the sun is used as a compass.

5.2 Stars

The majority of migrants fly at night. The evidence for compass orientation by the stars is good (Matthews, 1968, Ch. 4).

The first experiments were by Sauer and Sauer (1955); Sauer (1957) who showed that hand-reared blackcaps and garden warblers took up their appropriate autumn migration directions in Kramer cages under a planetarium sky, even though they had never seen a natural sky. The birds reversed their migratory direction when tested in spring.

Emlen (1972) gave an example of planetarium experiments and tackled the problem of how birds learn to use the stars. He showed that indigo buntings learned where north is from the rotation of the stars. The north star is the one that moves least. Emlen used a planetarium to rotate the stars with other constellations as the centre of rotation and the birds adopted these constellations as ‘north’. These results have been confirmed innumerable times and a particularly good study is by Mouritsen and Larsen (2001) who compare five hypotheses in a single experiment.

Radar studies (e.g. Bellrose, 1967; Griffin, 1973) indicate that night migrants are not disoriented under overcast, so they appear to be able to maintain a course without seeing the stars. However, occasional glimpses of the stars may be enough to set the direc-

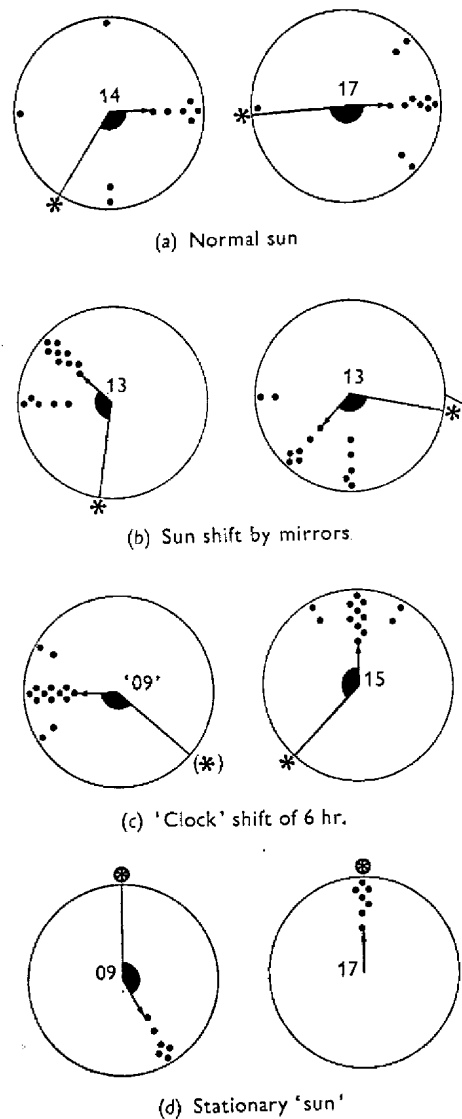


Figure 3: Analysis of sun-compass orientation in caged starlings. (a) The birds select the same direction at different times of day. (b) The orientation is changed by displacing the sun’s apparent position by mirrors. (c) The orientation can equally be changed by shifting the bird’s internal ‘clock’. (d) The angle taken up with reference to a stationary ‘sun’ changes through the day. Time is shown in hours in the centres. Dots represent activity periods (a,b) or food choices (c,d). (From Matthews (1968)).

tion and the set direction could then be maintained using other cues such as wind.

5.3 Wind

Nisbet (1955) and Bellrose (1967) discuss the possibility of birds using wind direction as a cue, the latter providing some evidence. A flying bird may sense wind direction by the shape of the gusts. These begin suddenly and die away gradually so the highest accelerations are felt in the direction of the wind. This information may be enough to allow a bird to maintain a course after it is set by other cues.

5.4 Magnetism

In the 1960s, magnetism was thrown out as a cue for bird orientation in no uncertain terms; it is now well demonstrated that birds use magnetism as a compass. The attitudes and misunderstandings do little credit to the scientific community. One of our Ph.D. students found evidence of magnetic orientation in nematodes in the late 1960s but was told by his supervisor that he would fail his Ph.D. if he included it in the thesis.

The first convincing evidence came from insect behaviour (Lindauer and Martin, 1972).

At about the same time, Keeton (1971) showed that magnets could confuse pigeons forced to home under overcast. At Cornell University, where Keeton worked, it is cloudy almost all the time so pigeons get lots of practice under overcast. Keeton's results showed:

Cloud cover:	Clear	Overcast
With magnets	oriented	disoriented
With brass bars	oriented	oriented

It was not clear whether the magnets interfered with compass orientation or with true navigation, under overcast. However, Wiltschko and Wiltschko (1972) showed that robins have a *compass* response to magnetic fields of the *same intensity as the earth's*. They failed to respond to much stronger or weaker fields.

It came as a complete surprise that the robins did not follow the north or south pole of the field, but

followed the angle of dip. Walcott and Green (1974) then showed that pigeons were disoriented by an electrically induced magnetic field. They had fitted coils round the heads of their pigeons and the direction of current determined the magnetic field. When the field was North up (NUP) the pigeons headed in the opposite direction (until the batteries ran out). With SUP the orientation was normal. Hence, their results fitted well with Wiltschko and Wiltschko (1972).

Modern studies have confirmed responses to the angle of dip in many species (eg. Able and Able, 1996) and increased the range of species known to use magnetic cues (eg. Gudmundsson and Sandberg, 2000).

5.5 Polarised light

Brines (1980); Phillips and Waldvogel (1982, 1988) showed that birds responded to the way patterns of polarised light rotated during the day. More recent studies have shown that it is the rotation of polarised light rather than the sun itself which is used for fine tuning the magnetic compass (Able and Able, 1993). This is especially interesting in the light of Mouritsen and Larsen (2001).

6 Cues underlying true navigation

If, in a particular example, we can rule out the use of landmarks, then a homing bird must be using true navigation, ie. it must determine its present position in relation to home or goal. The adult starlings displaced by Perdeck (1958) corrected for the displacement and flew to their normal winter quarters. And the tracks of homing pigeons, recorded by Michener and Walcott (1967) leave no doubt about the accuracy with which pigeons can determine their home direction from many miles away. However, the first phase of a homing flight is often in the wrong direction and these 'vanishing directions' have been used in experiments. When the vanishing direction is disturbed by a treatment it could be that the bird has the wrong idea about the home direction, or it

could be that the compass it is using has been disturbed. These complications make it even more difficult to identify the navigation cues than it has been to identify the compass cues.

To date, there have been four serious hypotheses explaining true navigation:

1. That the bird computes every twist and turn of the outward journey and so, by a highly sophisticated sense of direction, keeps in mind the home direction. Birds have been transported in rotating drums, while anaesthetised, in varying magnetic fields and unable to see the outside. In all cases homing was unimpaired but recent studies have revived the debate (Wallraff, 2000; Wiltschko and Wiltschko, 2000).
2. That birds find their position by celestial cues. Because the earth rotates, this requires that the birds have an internal clock. A bird displaced to the east, for example, would find the sun at a given height earlier than at home. One displaced to the south would find the sun higher, at a given time of day, than it should expect at home at the same time of day.
3. That the birds use magnetic variations across the earth's surface.
4. That birds learn to associate a particular odour with a particular direction of the wind at their home site. Then they fly in the opposite direction when they detect the odour at the release site.

6.1 Celestial navigation

The details of the various celestial navigation hypotheses are set out in Matthews (1968). All such hypotheses require that a bird can detect the sun's position accurately. However, pigeons have been known to home while wearing frosted glass contact lenses which excluded any precise judgement of the sun's position. So if they do use the sun normally, they must be using some other navigation system when wearing frosted glass contact lenses.

Keeton (1969) not only demonstrated that pigeons can home adequately under overcast, but that the errors that time-shifted birds made when the sun was visible were the errors that would be predicted if the bird were using the sun as a compass. The errors were not those predicted on any hypothesis which involved a sun-based true navigation. Keeton's results are summarised below.

Cloud cover:	clear	overcast
Time-shifted pigeons	sun compass errors	no errors
Control pigeons	no errors	no errors

Michener and Walcott (1967) originally thought that they had evidence for the sort of errors predicted on a sun-based navigation hypothesis, but Walcott (1972) became convinced that the sun was used as a compass and no more. This shift of opinion was based on a long series of experiments. Schmidt-Koenig (1972) also comes down firmly on the side of the sun compass and no more. Numerous more recent studies confirm this view.

6.2 Is there a magnetic map?

In principle, magnetic variations across the earth's surface could provide a magnetic map. The evidence is discussed by Wiltschko and Wiltschko (1996) who point out: that birds would have to detect minute differences in the magnetic field (of the order of 0.03%); that the map would be irregular and show great local variations and that daily fluctuations would complicate the pigeons's task.

At present it is not clear how a magnetic map would work, but we should not discount a possibility because we do not understand it yet.

The previous sentence remains true in the light of a very recent study on spiny lobsters (*Panulirus argus*) by Boles and Lohmann (2003). They showed that lobsters displaced up to 18 km walked in the direction of home and that the walking direction could be altered by simulating the magnetic field of an alternative site up to 400 km away. The walking direction in simulated magnetic fields suggested that the lobsters were using angle of dip as part of their 'map' in a case of true navigation.

6.3 Are odours important in determining the home direction?

Wallraf (1967) mystified his audience at the International Ornithological Congress in Oxford when he described experiments in which pigeons were kept in lofts where they could not see the sun. But they found home when released.

Another group were kept in a loft where they could see the sun all the time but were screened from the wind by glass screens. These birds could not find home when released.

One possibility was that pigeons learned to associate particular smells with the wind direction experienced when they occur: they smell sea smells when the wind comes from the west, say. Then, when released to the west of their loft, the sea smells are stronger and the birds head east.

In 1972 Papi and his colleagues started a series of experiments which showed disorientation of anosmic pigeons (no sense of smell). There is now a great deal more evidence but some bitterness on both sides of the debate. Three papers in the special navigation issue review the evidence: (Wallraf, 1996; Wiltschko, 1996; Able, 1996). And the most recent paper is by Odetti et al. (2003)

7 Calibrating the systems

Birds are not born with a star map and, as they migrate, the pattern of stars changes. Similarly, the magnetic compass is based on the angle of dip which becomes zero and then reverses for those migrants which cross the equator. How do they learn the appropriate direction?

Able and Able (1996) give an excellent account of the development of abilities. Hand reared savannah sparrows which have never seen the sky show a preference for the southwest in autumn when placed in a magnetic field. In other words, the response to the magnetic compass is genetically programmed. Helbig (1996) has studied the genetic control of migratory direction and found that hand-reared blackcaps exhibited preferred directions which were population-specific and were heritable. It appears that only a

few major genes control the preferred direction.

Migratory song birds also have a genetically controlled response to the axis of celestial rotation (Able and Able, 1996) but they also adjust the magnetic compass if it conflicts with celestial cues (Bingman, 1983). This is important for migrants because the preferred direction may change during different legs of the the flight. It is especially important for birds that cross the equator because the angle of dip reverses and the magnetic compass must be adjusted if it is to go on working. In a more recent study, Sandberg et al. (2000) found birds of four species were able to calibrate their star maps using magnetic information.

8 Redundancy and the balance between systems

When the sky is overcast, Keeton's pigeons use their magnetic compass. On a sunny day they cannot be disoriented by bar magnets. We now know there are multiple systems but we do not know how much attention birds give to each system. Studies in learning show that learning two cues at once tends to reduce learning of either and it seems very likely that individuals differ considerably in the weight they give to the different systems. That would explain why some pigeons are disoriented at particular release sites while others are not. Again some are disoriented by particular treatments, others are not.

It may explain such differences, but it also makes it very difficult indeed to design conclusive experiments.

9 Recent papers

A number of recent papers are of interest: Mouritsen and Mouritsen (2000); Baeckman and Alerstam (2003); Nehmzow and Wiltschko (2000) Wehner (2001); Wiltschko and Wiltschko (2003) Bonadona et al. (2000) Mouritsen et al. (2003).

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