TO FIND A WAY HOME

by Philip Martin, Seattle, Washington

Each year, from around the end of May until the beginning of November, Greater Shearwaters cruise off the New England coast and throughout the North Atlantic. The entire estimated world population of five million birds, however, nests on three small islands in the South Atlantic, two million pairs alone on Nightingale Island, a speck of land no more than one square mile in extent, about half-way between Buenos Aires, Argentina, and Cape Town, South Africa. How do the shearwaters find their way over the boundless seas to their ancestral "needle-in-a-haystack" colony?

This is a dramatic, but by no means unique, illustration of the remarkable homing and navigational abilities of birds. The problem of how birds orient themselves and find their way from place to place has puzzled animal behaviorists for years. We are still a long way from truly understanding the phenomenon, but there have been intriguing advances in the field over the past twenty years.

Perhaps the problems of a navigating bird can be made more tangible if we compare them to the problems faced by a lost person. In order to find one's way in the trackless wilderness, one needs to know direction; in other words, a compass is necessary. However, we are not out of the woods yet; it does a lost person little good to have a compass if he does not know which direction to take. A map, too, is essential. In the figurative sense, birds too must have a map and compass.

What cues might birds use for navigation? Man has long used celestial information, the position of the sun and the stars, but until recently there was very little evidence to support the notion that birds also used a "sun-compass" or a "star-compass." Now it is virtually certain that some birds, at least, have this ability. Much of the experimentation that has been done has used our familiar friend the pigeon (albeit especially talented individuals bred for their homing ability) and Keeton (1974) has presented an excellent summary of the most important discoveries made in pigeon homing experiments.

Some of the first advances in the study of the sun-compass were made by Gustav Kramer in the early 1950's, using starlings as subjects. Kramer kept his birds in circular cages with several food cups located around the edge. He found that it was quite easy to train starlings to seek food at a cup located in a particular compass direction, regardless of whether the cage was rotated or moved to a different location. On sunny days the birds were able to locate a specific cup consistently; however, on overcast days the starlings' cup choice became random, and when the sun's apparent position was altered with mirrors, the starlings' cup choice was altered to match! This experimental evidence certainly indicated that starlings were able to use the sun as a compass, but there is a further complication. The sun is not a stationary light source; its position in the sky shifts approximately 15 degrees per hour (360 degrees of the circle divided by 24 hours in the day). If the birds were using the sun as a compass they must be able to correct for this apparent motion of the sun. Sure enough, when placed under an artificial light source which acted as a stationary "sun," the starlings shifted their cup choice approximately 15 degrees per hour to compensate for the movement their internal clock told them must have occurred! (Griffin, 1964; Keeton, 1974).

This result indicates an accurate internal time sense must be operating in the birds, although we really don't know how accurate or very much about what keeps the clock ticking. The concept of an internal clock should be very familiar to anyone who has experienced "jet lag" after a transatlantic flight, or anyone who usually wakes up 10 minutes before the alarm clock is set to go off. We know that internal clocks and calendars function in many areas of animal behavior, bird migration and navigation among them. We shall return to this subject in discussing experiments which use manipulation of the birds' time sense to test certain theories.

The experiments of Kramer and others showed that birds could make use of the sun as a compass, but the "map" element of a navigation system was still unknown. In 1953, another of the pioneers in this field, G. V. T. Matthews, proposed what is known as the sun-arc hypothesis of bird navigation, which elegantly describes how a bird could get all of the information needed for navigation from solar cues (see Figure 1). There has been much argument about whether birds actually have the sensory capability to analyze solar movement with the accuracy demanded for this system. Most experimental evidence indicates that birds do not use this system, and one experiment described by Keeton is worth recounting here. In this test, the internal clocks of homing pigeons were disrupted. They were "time-shifted" six hours behind real time; this was done by keeping them in an enclosed room where the lights were turned on and off six hours after sunrise and sunset, respectively. (Day length and light/dark cycles are intimately associated with the maintenance of internal clocks and calendars in many animals and plants too.) These time-shifted birds were then released 100 miles south of home at noon, which was 6:00 a.m. to our time-shifted subjects. If a bird were using the sun-arc system it would "think" something like this, "It is 6:00 a.m. at home, but here the sun is in the noon position, therefore I must be horribly far east of home, and I must fly west." In actuality, the pigeons in this experiment headed in the opposite direction, to the east!

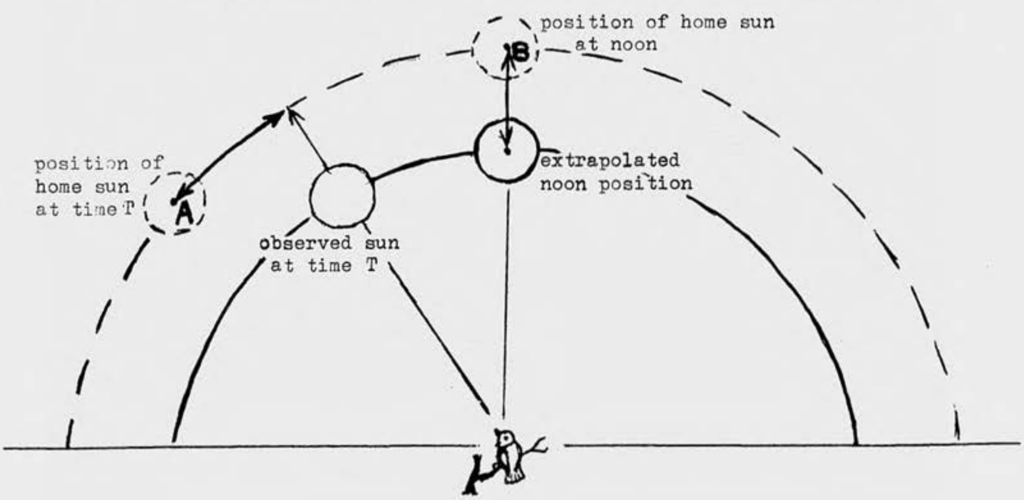


Figure 1. THE SUN-ARC HYPOTHESIS works like this: the bird who is displaced looks at the sun at time T and notes its position. By watching the sun's movement the bird extrapolates where the sun will be at its highest point--the noon position. The bird compares this noon position with the noon position of the sun at home by memory. In this case, the noon position at home is point B and since the noon position at the bird's present location is lower, it knows that it is north of home. The east/west displacement can be determined by comparing the observed position of the sun at time T with the bird's memory of how far along its arc the sun would be at time T at home. In this case, at home the sun would be at point A, not so far along its arc, so the bird knows it is east of home. To get back, it must fly in a southwesterly direction.

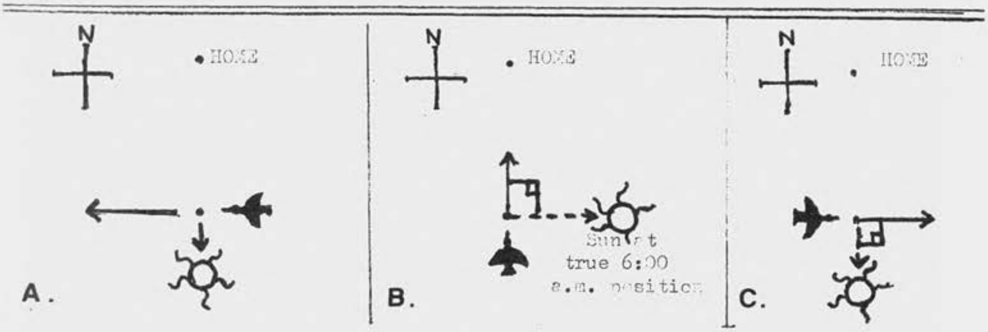
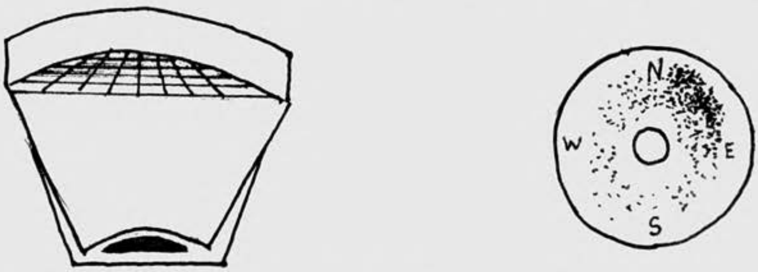


Figure 2. Figure 2A shows the predicted flight line of the time-shifted bird if it is using the sun-arc method. It sees the sun in the noon position (to the south) and since it thinks it is only 6:00 a.m., figures that it is drastically far east. It then flies off to the west. The experimental birds did not do this, they flew off to the east. If we take it for granted that the "map" tells the bird that it has to fly north, then thinking that the sun is at the normal 6:00 a.m. position in the east the bird would fly 90 degrees counter-clockwise from the sun as in Fig. 2B. However, since the bird is time-shifted six hours behind, and the sun is in the noon position, the same line of reasoning leads the bird to fly due east, as in Fig. 2C.

How to explain this result? If we assume that some unknown "map" tells our pigeon that it is south of home, then it would "think," "My clock tells me it is 6:00 a.m. and the sun is therefore in the east. I want to fly north which should then be 90 degrees counter-clockwise from the sun's direction." (Hang in there, Figure 2 should help you wade through all of this.) Since it is really noon, and therefore the sun is to the south, this 90 degree swing points the pigeon east. The catch in this explanation is that nobody has been able to identify the "map," so we are at something of an impasse, except that we are pretty sure that the pigeons are not using the sun-arc system.

There are large groups of migrants which are surely not using solar cues much for navigation--most passerines, some shorebirds, and sometimes loons, ducks, geese and alcids are nocturnal migrants. The orientation system of one nocturnal migrant in particular, the Indigo Bunting, has been the subject of intensive examination by Stephen T. Emlen of Cornell University. His experiments are worth looking at not only for what they tell us about buntings, but also as a study in creative ornithology. The following account has been gleaned from several of his articles (Emlen, 1967a, 1967b, 1969, 1975).

Emlen's first experiments were designed to test the buntings' ability to use stars as an aid to navigation. A total of 33 buntings were captured during the spring seasons of 1964 and 1965, and kept in aviaries in, or near, Ann Arbor, Michigan. Experiments were conducted in spring and fall, when the birds showed readiness for migration, which can be determined in several ways. Prior to migration many migrants deposit large amounts of body fat as fuel for the journey (often 30% to 40% of the body weight). More important for these experiments is the phenomenon known as "Zugunruhe," a German term generally translated as "migratory restlessness." It has long been known that diurnal birds, which are usually quiescent during the nighttime, may shift their behavior dramatically during migration periods. They become very active from evening through most of the night; if they are in captivity the birds flutter against the cage repeatedly. It was also noticed that often these flutterings were oriented in the appropriate direction for migration (i.e., north in spring, south in fall), and this has become a valuable tool for experimentation.



Figures 3. At left is the Emlen bunting cage in cross-section. The floor is an ink pad; the sloping sides are covered with blotting paper, and a screened top permits a view of the sky. When the bunting undergoing migratory restlessness flutters up along the sides, its inky feet make marks on the blotting paper. At the right is a representation of a blotting paper record of a typical spring bird. As one would expect, the marks are heavily concentrated to the northeast.

When Emlen's buntings showed signs of migratory restlessness they were placed in specially designed cages (see Figure 3) with sloping sides covered with blotting paper and an ink pad for a floor. Thus, when a bird hopped up from the floor and fluttered against the side of the cage, its footprints were recorded on the blotting paper and later these marks could be analyzed to determine whether the bunting had a tendency to flutter in any particular direction. Some of the buntings were tested outdoors under natural sky conditions, and some were tested in a planetarium where the skies were subject to the whims of the experimenter. The birds tested outdoors over the two-year period generally showed the expected orientations--south in fall, and northeast in spring.

Tests in the planetarium yielded similar results, but there were some added twists. When south-orienting birds in fall were exposed to a reversed sky pattern, in which the north star was actually projected on the south side of the planetarium, the birds reversed their orientation to correspond to the star pattern. During the spring, birds normally orienting northeast would head towards the southerly sector of their cages when faced with a reversed star pattern. Birds tested in the planetarium became less active and their orientation deteriorated markedly when the stars were turned off and diffuse "moonlight" introduced.

Having established that buntings did indeed orient by the stars, Emlen then set out to discover how they were doing it. He came up with two alternative possibilities.

1. They were locating a particular star or group of stars and then flying at a certain angle with respect to that star. Just as Kramer's starlings did with the sun, the buntings would have to compensate for the apparent movement of the stars across the sky, again dependent on an accurate internal clock. Only in this case the birds would have to deal with a vast number of stars, as opposed to only one sun. Furthermore, facing the north in the northern hemisphere the stars rise on the right and set to the left; in the southern half of the sky the stars rise on the east and set to the right. A bird would have to know what stars it was looking at in order to make the proper correction for their change in position.

2. The second possibility is that buntings were using fixed star patterns to point the way. We do this when we locate the north star, Polaris, by following an imaginary line passing through the "pointer stars" in the Big Dipper. The advantage of this system is that an internal time sense is unnecessary; the Big Dipper rotates around Polaris, but the pointers always point to Polaris, which is always in the north.

To test these hypotheses Emlen placed buntings under planetarium skies which were shifted out of phase with the birds' internal clock. If the buntings were using system #1 this would produce a situation where the birds' internal clock would lead them to make improper compensation.

As a hypothetical example, let us say the skies are shifted four hours ahead, then a bird's "reasoning" would run something like this, "My clock tells me that it is 10:00 p.m. and I should therefore fly 20 degrees to the right of star X in order to go north." But since the skies have been shifted, star X is really in the 2:00 a.m. position and is rotated 60 degrees counter-clockwise from where the bird thinks it is. That 20 degree compensation then is inappropriate and sends the bird off in the wrong direction.

On the other hand, if the bird was using system #2, then time-shifting would have no effect. In fact, when the experiment was conducted, with skies three, six, and twelve hours ahead of and behind real time, the bird was still able to orient correctly. This indicates that it was using star patterns, a system independent of time sense.

What star patterns were the buntings using, then? Emlen was able to play with nature on a grandiose scale in the planetarium, removing and replacing sections of the sky, individual stars, or constellations. He found that the buntings rely on the stars that lie within 35 degrees of

Polaris (including the constellations Cassiopeia, Cepheus, Draco, and Ursa Major, the Big Dipper). However, there was considerable variation among his test subjects regarding which stars were essential for navigation, and there seemed to be considerable redundancy in their guidance systems; that is, if one group of stars were blocked out, another group would suffice. Considering the situation on a partly overcast night, this would be a useful ability.

Later experiments showed that it is the rotational axis of the night sky (with stars rotating around Polaris) that serves as a reference system for buntings in learning to navigate. To investigate the development of navigational ability, it was necessary to raise young buntings from 4-10 days old (no mean feat in itself). The young birds were divided into three groups, raised under varying conditions.

Group I was raised in a diffusely lit room, without ever being exposed to a point source of light. During their first fall they were tested in the planetarium under simulated normal autumn skies. Their orientation was random.

Group II was raised without a glimpse of the sun, but they were allowed to view a simulated night sky in the planetarium every other night during August and September. The night sky was rotated in a normal fashion to duplicate natural conditions. Unlike the first group, these birds were able to orient south consistently.

Group III was also allowed to view the planetarium sky. However, instead of rotating around Polaris, the sky was made to rotate around Betelgeuse, a very bright star in the constellation Orion. When nocturnal restlessness began, these birds oriented 180 degrees away from Betelgeuse, responding as if it were the north star!

Apparently, young buntings learn how to navigate by observing the arcs of the stars' paths, thus locating the axis of rotation. Since older birds can orient under a fixed star pattern in a planetarium, the relationship of the stars is apparently learned and subsequently the buntings can navigate without actually observing any actual motion. Emlen suggests a fascinating hypothesis on the value of having young birds learn the axis of rotation, rather than having a fixed hereditary instruction which says something like, "Thou shalt follow the North Star in spring." He notes that there is a wobble in the direction to which the earth's axis of rotation points (like that seen in a spinning top) which causes the position of the pole in the sky to swing around in a circle 47 degrees in diameter every 26,000 years. Though the rate of this change may seem very gradual to us, it seems impossible that a genetically coded set of instructions could keep pace. By having each generation learn anew where the polar axis is located the problem of obsolete instructions is avoided.

Once the bird has learned how to locate the north/south axis, what tells it to fly one way along the axis in spring, and the opposite way in fall? Emlen sought to answer this question with an experiment involving "photoperiodism," the effect of day length on the physiological state. Photoperiod effects have been known for centuries--the ancient Japanese art of Yogai consisted of artificially lengthening the day lengths for cage birds by candle-light in order to induce mid-winter song (Welty, 1975).

Photoperiod has profound effects on the levels of production of many hormones, and these in turn have complex and interrelated effects on basic body functions and behavior, including the breeding cycle. Even a cursory look at this subject is beyond the scope of this article, but the reader should be aware of the basis for Emlen's tinkering in the experiment described below.

A group of male buntings were captured and kept in captivity over the winter. One group (the control) was exposed to day-lengths similar to what they would experience on their wintering grounds, as simulated by the lights in their flight room. These birds molted from winter brown to spring blue in February and April and began to show migratory restlessness in May. The second group was subjected to manipulations of the day-length as follows: in early fall the lights in their flight room were kept on for longer periods of time, simulating spring day-lengths of 15 hours. This caused the buntings to molt into spring plumage in January. Beginning in March, the day-lengths were shortened, so that by May they molted back to basic brown, and they too showed migratory restlessness.

Essentially then, Emlen had produced two groups of birds--one group physiologically ready for spring, the other for autumn. When tested under identical spring night skies in the planetarium, the "spring" birds headed north, while the "autumn" birds headed south, demonstrating that the directional choice was under physiological control. A similar result has been achieved with White-throated Sparrows, by administering directly doses of two hormones, prolactin and corticosterone.

These experiments have given us a better understanding of the migratory behavior of buntings than perhaps any other species, but there are still many gaps to be filled. The fact that the bunting navigation system seems to function independently of any internal time sense rules out the possibility that some nocturnal equivalent of the sun-arc system could be utilised to determine latitude, or tell a bird which way to go if it is forced off course. In other words, as with the pigeons' sun-compass, we have discovered the "compass" but the "map" element of the system remains unknown.

In contrast, early experiments by Sauer indicated that European warblers <u>were</u> capable of true bi-coordinate navigation by the stars. This points up one of the major difficulties in the field: there is no reason to expect all birds to navigate in the same manner. Rather, it is <u>probable</u> that different species use different systems, and perhaps the individual bird has a number of systems at its disposal.

This last possibility was strongly suggested to William Keeton when he noticed that some of his homing pigeons made it home on overcast days, hence without benefit of the sun-compass. Clock-shifted pigeons, while disoriented on sunny days, performed as well as normal birds under overcast skies. These results suggested an alternate system, independent of sun <u>or</u> internal clock that could be called upon when needed. What could this be? Obviously, homing pigeons can use simple visual cues when covering familiar ground, but they also home from unfamiliar locations <u>and</u> some pigeons can home while blind-folded.

One suggestion has been some kind of inertial guidance system, similar to that used in modern rocketry. For instance, a homing pigeons being carried away from the home loft would sense the direction and magnitude of each acceleration over the entire journey, derive the vector sun and come up with a resulting distance and direction of displacement. Stranger things have happened but the theory has met with a good deal of skepticism.

However, another theory long held in disrepute has gained more acceptance in recent years. Researchers are coming up with more and more evidence to support the idea that birds may be able to detect magnetic fields, specifically the general dipole field of the earth and use this information for navigation purposes.

In the 1960's experimentation primarily by German scientists using the European Robin proved that directional choices could be influenced by subjecting the birds to an artificially produced magnetic field of similar intensity to the earth's at temperate latitudes. Later studies showed, surprisingly, that the horizontal component of the magnetic field (represented by the direction of a compass needle) did not influence orientation, while the vertical component (represented by the "dip" of a compass needle) did. The robins were apparently responding to the angle between the vertical component of the field and the pull of gravity (Wiltschko and Wiltschko, 1972).

Homing pigeons have also been found to be sensitive to magnetic fields. Magnets placed on the pigeons' heads did not interfere with their orientation on sunny days, but on cloudy days their orientation was reduced to random. In another experiment, devices known as Helmholtz coils were attached to pigeons' heads, powered by batteries strapped to their backs. The Helmholtz coil produces an electromagnetic field that can be reversed in direction. Again, no effect was produced on sunny days, but on cloudy days an amazing result occurred--when the electromagnetic field was oriented in one direction, the birds flew homeward, but when the field was reversed they tended to fly directly away from home!

A recent study used radar tracking of migrating birds passing over the antennas of the Navy's Project Seafarer site in Wisconsin. There are two antennas there which generate an ac current; at a distance of 100 to 900 meters, the strength of the magnetic field was calculated to be less than one percent of the earth's. The tracks of the migrants, as they flew over the antennas, were classified as "linear" if they proceeded in a straight line without deviation, or "non-linear" if they seemed to swerve over the antennas. The results were correlated with the condition of the antennas: whether they were off, whether either or both were on, or "changing" the current from 0-75 amps or 75-0 amps. Here are the results:

antennas condition	# linear	# non-linear
off	157	6 (4%)
on	204	28 (12%)
changing	53	21 (28%)

The significantly higher percentages on non-linear tracks in the second two categories indicates that migrants may be sensitive enough to shifts in magnetic field to react within minutes (Larkin and Sutherland, 1977).

The returns are not all in by any means. For instance, Emlen (1970) reported no apparent use of geomagnetic cues in Indigo Bunting orientation and found no evidence that they could detect magnetic fields. We have no idea what sense organs birds might use to detect magnetic fields, and very little idea of how they would actually translate this information to navigational instructions. Incidentally, it has been suggested that since anomalies in the earth's magnetic field often correspond to the position of mid-oceanic islands, sea birds such as the Greater Shearwaters mentioned at the beginning of this article might use this to locate their breeding colonies (Freedman, 1973).

It is difficult for us to deal with magnetic field detection because it is a sensory capability which we, ourselves, do not possess. Perhaps birds are capable of gathering other sensory input which we cannot detect. A recent study on homing pigeons incidates that they are capable of detecting very low frequency sound in the vicinity of 10 Hertz (Hz),* referred to as infrasonic radiation. Two shock electrodes and two ECG electrodes to monitor heart rate were placed in the pigeons. Infrasonic stimulus was given for ten seconds, followed by an electric shock, which resulted in acceleration of heart rate. After a few trials, a conditioned response occurred so that the heart rate increased when the birds were exposed to the sound stimulus even in the absence of the shock. Later experiments involving surgery proved that the receptors for infrasonics are located in the inner ear (Yadlowski, Kreithern, and Keeton, 1977).

There are many sources of infrasonic radiation: wind, thunderstorms, weather fronts, auroras, ocean waves, earthquakes, and many man-made devices. It would seem beneficial for birds to be able to detect many of these things, but it is not at all clear how they would use this information for navigation. (If birds do use infrasonic cues, one can idly speculate whether the ever-increasing presence of man-made devices producing low-frequency sound results in an adjunct occurrence of stray birds whose navigational systems have been "jammed".)

Beyond this, our theories get more and more speculative. When it is all said and done, we really have many more questions than answers about the riddle of bird migration. Recently, on a foggy morning at sea about 40 miles east of Cape Cod, I saw scores of warblers flying low over the water in all directions. It was a startling reminder of the fact that millions of avian deaths must result each season as migrants are lost at sea. However, the truly astonishing fact is that so many make it--hundreds and thousands of miles there and back again (Williams, et. al., 1977). Meanwhile, I think it is rather exciting that there is still such a basic unsolved mystery in ornithology. For the present, in the field of bird orientation and migration, we are almost as much in the fog as those warblers.

* To give some idea of what this means, the note middle C has a pitch of 256 Hz (often referred to as "cycles per second"). The note C an octave above middle C has a value of 512 Hz, double that of middle C. An octave below middle C has a pitch of 128 Hz, half the frequency of middle C, and so on. Our range of hearing is about 20 Hz to 20,000 Hz (about 10 octaves, if you work it out) although the lower end of this range is "heard" as vibration, and lower pitched sounds produced at sufficient volume are felt as pain, not sound. Ten Hz, therefore, is about an octave below the threshhold of human hearing.

REFERENCES

Emlen, S. T. 1967a. Migratory Orientation in the Indigo Bunting, Passerina cyanea. Part I. Evidence for Use of Celestial Cues. Auk, 84: 309-342.

__________ 1967b. Migratory Orientation in the Indigo Bunting, Passerina cyanea. Part II. Mechanism of Celestial Orientation. Auk, 84: 463-489.

__________ 1969. Development of Migratory Orientation in Young Indigo Buntings. The Living Bird, Vol. 8, 118-126, Cornell University.

__________ 1970. The Influence of Magnetis Information on the Orientation of the Indigo Bunting, Passerina cyanea. Animal Behavior, 18: 215-224.

__________ 1975. The Stellar Orientation System of a Migratory Bird. Scientific American, 233: 102-111.

Freedman, S. J. 1973. Orientation of Birds by Geomagnetic Field. In Bateson and Klepfer (ed.). Perspectives in Ethology. Plenum Press, New York.

Griffin, D. R. 1964. Bird Migration. Natural History Press, Garden City, New York.

Keeton, W. T. 1974. The Mystery of Pigeon Homing. Scientific American, 231: 96-107.

Larkin, R. P. and P. J. Sutherland. 1977. Migratory Birds Respond to Project Seafarer's Electromagnetic Field. Science, 195: 777-779.

Williams, Timothy C., et al. American Birds, 31: 251-267.

Welty, J. C. 1975. The Life of Birds, 2nd ed. W. B. Saunders Company, Philadelphia.

Wiltschko, W., and R. Wiltschko. 1972. Magnetic Compass Orientation of European Robin. Science, 176: 62-64.

Yodolowski, M. L., M. L. Kreithen, and W. T. Keeton. Detection of Atmospheric Infra-sound by Homing Pigeons. Nature, 265: 725.