

BIRD NAVIGATION

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Abstract: The paper reviews the methods by which birds orientate themselves and navigate to a desired destination. Homing is classified; theories are presented; experimental proofs and negations observed are reviewed. Methods of studying bird flight are described. A series of experiments on short-range navigation by pigeons conducted by the author are described and results interpreted.

INTRODUCTION

This report presents some of the more prevalent theories and ideas concerning bird navigation. The few theories that have withstood experimental scrutiny may answer the still-unsolved problem of how birds navigate, orientate, and home.

In this paper orientation, navigation and homing are defined as follows:

Orientation is the ability of a bird to know its geographic position at all times with reference to some cue.

Navigation is the ability of a bird to take off in a certain direction and keep its course during flight. The bird recognizes its goal when it arrives.

Homing is the ability of some birds to find their way back to their loft (or home) when released in unfamiliar territory. This means they can judge their home direction.

CLASSIFICATION OF HOMING

There are three ways birds navigate on homing flights (Griffin 1952):

Type I: "Contact Flying". Reliance on visual landmarks in known territory and undirected wandering in unfamiliar territory.

Type II: The ability to fly in a certain direction, even in an unfamiliar area, not necessarily the active homeward direction.

Type III: The ability to home even when released in unfamiliar territory and when the correct direction of the homing flight has no relation to directions that have been flown in training flights.

Contact flying does not seem to be hard for humans to comprehend. It is the long flight over unfamiliar territory that seems to puzzle us.

Watson and Lashley (1915) suggested that we must distinguish between types of homing (cited in Hochbaum 1955, and Griffin 1952). Hochbaum (1955) suggested we should not make this distinction since Type I is a part of Types II and III.

Kramer (1952) has carried out extensive experiments over a number of years to show that, in Type II navigation, the sun serves as a guide to compass direction for birds. When birds are flying inland in unfamiliar territory when the sun is not visible, there is confusion and random scatter in their flight paths. In the absence of the sun, or in journeys over the ocean, the orientation of waves may be a possible cue to direction (Hochbaum 1955; Griffin 1952). Clouds may also be a cue in the absence of the sun, either by their texture overhead or on the horizon (Hochbaum 1955).

Type III homing navigation has been observed in common terns (Sterna hirunda) (Griffin and Goldsmith 1955); swallows (Hirundinidae spp.) (Wojtusiak, R. J. 1949); and homing pigeons (Columbidae spp.) (Matthews 1953) within two miles after being released. Matthews (1953) found that his homing pigeons orientated quickly only when the sun was plainly visible. Birds with good homeward orientation in sunny weather scattered at random with overcast skies.

Homing experiments show that some birds released in unfamiliar territory orientate homeward quicker than those set free at a closer distance (Matthews 1953). Failure of birds to return home from strange but nearby places is due to the inability of birds to detect changes in the arc angle of the sun close to home according to Matthews. Based on his experiments, Matthews (1951) concluded that perhaps 50 miles is the critical point for pigeons between nearby and long-distance homing.

Possibly the critical point varies between species, but it appears to lie roughly between 50 and 100 miles. However, it is also probable that some of the data scatter and uncertainty are due to the different native ability and motivation of the birds used in the experiments.

Since man has depended heavily on the magnetic compass for navigation, some students have attempted to attribute a biological awareness of the magnetic pole to birds (Hochbaum 1955; Allen 1948; Yeagley 1947, 1951). However, Gordon (1948) showed that birds have no structure that could possibly react to the magnetic field. Forces are produced by putting non-magnetic materials in a magnetic field, but they are far too small to give any serious consideration. Griffin and Hock (1948), Henderson (1948), Van Riper and Kalmbach (1952), and Wilkinson (1949) failed to find any sensitivity to magnetic fields in birds. Pigeons orientating their flight in the training direction have been undisturbed by powerful magnets swinging below the head or attached to the wings (Matthews 1951).

Ising (1946) suggested that the navigation of birds is based upon perception of mechanical forces related to the rotation of the earth. Ising discusses the physical forces upon which sensitivity might be based (cited by Griffin 1952). Thorpe and Wilkinson (1946) and de Vries (1948) have adversely criticized this theory (cited by Griffin 1952). Griffin (1952) concludes that "Ising's theory that bird navigation is based upon perception of mechanical forces stemming from the earth's rotation has the great advantage of postulating a type of mechanical sensitivity that is qualitatively present in virtually all animals. But the quantitative requirements of differential sensitivity exceed by roughly two-hundredfold the capabilities of any known mechanical receptors."

Winds may play a role in bird navigation, orientation, and homing (Landsberg 1948); (Suffern 1949; Odum 1948; Lowery 1951; as cited by Griffin 1952), but there is little evidence that it is a major factor in orientation (Hochbaum 1955; Griffin 1952).

The theory that birds have a built-in recording sense to remember an outward route taken when being transported has also been disproven by researchers. Matthews (1953), in his experiments, transported his birds in a covered van. Thus, a recording sense would have to function while the birds were sleeping, and this is highly improbable.

Undoubtedly some birds do use visual contacts with remembered landmarks to return home. As one example, Matthews (1952), in experiments with lesser black-backed gulls (Larus fuscus graellsii) and herring gulls (Larus argentatus argentatus) concluded: "A large proportion of the gulls were undoubtedly homing by the relatively inefficient method of random

exploration for visual landmarks. A minority, however, were apparently using a method that was not dependent on the distance or familiarity of the area in which they were released." It seems reasonable to assume that while sight navigation may be used on short flights, it is unlikely that birds on longer flights rely solely on sight. As a general rule birds fly low, but, even if they flew high in the sky, there is a definite limit of vision imposed by the curvature of the earth (horizon).

Experiments by Griffin and Goldsmith (1955) and Matthews (1951) show that pigeons and gulls, released at 10 to 25 miles from home (within sight of home) homed well by seeing familiar landmarks. Between 30 to 50 miles, the birds homed poorly. Beyond 50 miles, orientation was good again. The results of these experiments seem to bring together sensory perception with the sun-arc hypothesis.

Kramer (1952) proved conclusively that birds use the sun as a navigational cue or reference. Kramer conducted two experiments in proving this thesis. The first was based on the fact that birds tend to flutter in a preferred direction during migration. Starlings (*Sturnus vulgaris*) were placed in a circular cage which could be rotated and from which only the sky was visible. The directional movements of the birds could be estimated by an observer lying under the cage looking up through the glass bottom. When the sky was overcast there was no directional orientation whatsoever, but when the sun was out the birds became strongly orientated. If mirrors were used to alter the apparent position of the sun, the birds' directional tendencies were appropriately changed. In the second experiment, starlings were trained to one particular compass direction. Then 12 food containers were placed in a half circle. The birds went only to the food container that was in the training direction. To make sure it was not just the particular food container, the containers were rotated. When the sky was cloudy, the birds chose the containers at random. If mirrors were used to deflect the sun, the birds were fooled and the choice of container was changed accordingly. Even an artificial sun, a 250-watt light bulb, changed the birds' orientation.

Neither Matthews (1953) nor Kramer (1952) claim the sun to be the sole factor in directional orientation, but it seems to be the primary factor. Wallraff (1966, 1967) and Walcott and Michener (1967) provide evidence to show birds use sun, experience, and area familiarity and that all these play a part in pigeon homing ability.

While sun-orientation as a navigation aid has been found to possess all the properties needed to explain day-time migrations, it is not satisfactory to assume that for night migrants sun-orientation supplies the starting direction, and that this is maintained throughout the night by flying straight ahead. Strong night migrations proceed with or without a moon--so moon-orientation isn't the answer (Kramer 1952). Star orientation

may be a possibility. But certainly, further study of, and search for, other orientation methods--based upon stimuli available throughout the night--is needed.

Sun-Arc Hypothesis (grid derived from the sun's coordinates).

Matthews (1951) proposed a hypothesis for complete sun navigation, deriving both latitude and longitude from the sun's position. The suggestions of the hypothesis are:

1. By observation of the sun's movement over a small part of its arc, and by extrapolation, the highest point is determined and this gives geographical south and local noon (assumes the bird is in the Northern Hemisphere when it refers to geographical/south).
2. Comparison of the remembered noon altitude at home with the observed or extrapolated noon altitude gives the differences in latitude.
3. Comparison with home position in azimuth at local noon gives the difference in longitude.
4. All measurements and comparisons are automatic.

Good orientation in birds has been obtained when the horizon was not clear because of haze. It seems safe to conclude that birds have the equivalent of bubble sextants or artificial horizons.

The sun's arc rises and falls across the sky changing with the seasons, reaching maximum altitude on June 22, and minimum on December 22 (two solstices). At these dates, the daily rate of change in altitude is very small, about 10" of arc. It increases to maximum of about 1400" of arc at the two equinoxes, March 21 and September 23. Even if the maximum rate of change (27 miles of latitude) was not allowed for by the bird, no great error would result according to previous experiments.

Existence of some form of accurate time mechanism is an essential part of the sun-arc hypothesis, although, in theory, latitude could be figured without a chronometer from the altitude of the highest point of the sun's arc (Matthews 1953).

The evidence for some form of general time-keeping mechanism is quite widespread in animals (Matthews 1953). A more particular time sense has been found in insects (Belings 1935) and in passerine birds (Stein 1951), in which the animals could be trained to come for food at a certain hour of the day (cited in Matthews 1953). Stein claimed that for passerine bird this time was not disturbed by the animal being kept in constant light, by varying the length of fasting before feeding, or by injection of metabolic

The present hypothesis is different from other "super" sensitivity theories in two important ways. If the distance from home is great (500 miles or more) and is traveled rapidly and at a high altitude, a human could find a rough position without instruments easily, especially in latitude (Hochbaum 1955). If this is easy for a human, it is simple for birds. Secondly, in 50 to 130 miles of displacement from home, the differences in sun angle to be measured lie within the estimated powers of the avian (bird) eye. Pumphrey (1948) estimated, on the basis of the retinal structure of the bird, that the limit of distinction between two objects at a distance away from them is about 10" of arc (cited in Matthews 1953). This is about three times better than the human eye. Even with indirect methods of experiments, Grundlach (1933) found pigeons were making distinction down to 23" of arc (cited in Matthews 1953). This distinction limit also compared with the required solar angular resolution at distances of 50 miles from home. Displacement of 50 miles in latitude results in a change in the sun's angle of altitude 260 times the bird's power of resolution. A displacement of 50 miles in longitude (at 52°N) results in a change of azimuth 420 times that power. It seems quite possible that the bird's eye could detect the smallest angular changes required of it. Displacement of 50 miles in longitude (at 52°N) represents a time change of under five minutes, which indicates the limits of accuracy required in the bird's chronometer.

Though the angular and time differences needed to distinguish between two suns would seem to lie inside the limits of the bird's sensory equipment, an objection is that the bird does not have the chance to compare the positions of two observed suns. It compares the positions of the observed sun with that of the visualized sun. Pigeons have excellent memories for landmarks once they are learned, but the recognition of one skyline from another depends on a comparison of all the small angular differences that make them different. Perhaps it is only unfamiliarity of the idea that makes it hard to credit the memory and visualization of the sun arc at home. Furthermore, increased experience does not bring improvement in orientation, but only in speed and success of actual homing (Matthews 1951).

Experiments by Matthews (1953) with 230 birds released north to south, and 76 released westerly relative to the home point appeared to verify the sun-arc hypothesis. They also confirmed the increased accuracy of orientation around noontime. Experiments run in two different years, 1951 and 1952, showed that birds became disorientated when they were not able to take into account seasonal changes in the sun's altitude. The size of the experiment and variation of homing ability do not conclusively prove anything either way. Limited experiments on the chronometer during the same years with up to 20 birds supported the theory that longitude determination is based on a time reference.

Taking all the facts about the sun-arc hypothesis into consideration, it seems very likely that birds use a "grid" derived from the sun's coordinates in navigation.

Experiments in Short-Range Bird Navigation

The author conducted some brief experiments designed to establish more precisely the type of homing near their loft.

The experiments were carried out with four mature male homing pigeons. Three of the four were mated, and two had squabs in the loft. All four had been in the same loft for the previous three years so they were quite familiar with the immediate area around the loft, but they had not been taken away and released before.

The birds will be identified in the report as follows: No. 1 - mated, no squabs, five years old; No. 2 - unmated, four years old; No. 3 - mated, squabs in loft, five years old; No. 4 - mated, squabs in loft, three-four years old.

The four birds were divided into two groups termed White and Grey. There were two different release points, one four miles to the west, and one four miles to the north of the loft. Seven flights were made from the western point and five from the northern point. The White group contained birds No. 1 and No. 2, and the Grey group contained birds No. 3 and No. 4 when they were released to the west. When they were released to the north, the groups were changed so that the White group contained birds 2 and 4. This was done to see if teaming of birds' talents affected their homing ability.

Watches for timing release and return were coordinated before each flight. The birds were taken to the release point in black-out conditions and released two to five minutes apart. The release times and the times the birds landed at the loft were noted together with weather conditions, etc. The experiments included three variables:

1. Direction (west and north),
2. Time of day (Morning, noon or early afternoon, and late afternoon or evening),
3. Weather condition (sunny and cloudy).

The data from the flights in this experimental program support the idea that use of sun position, force grids, etc., is not employed by pigeons to home at distances of four miles from the loft. This conclusion results from the fact that generally the same results were obtained on all flights even though conditions such as weather, time of day, and

directions were varied. Natural flight ability, flight experience, and training all appear to have the greatest influence on the navigational ability of birds near the loft. The limited data obtained with the unmated bird tend to show that the drive to return to a mate in homing pigeons is not the predominant factor in the ability of pigeons to home at short distances from the loft.

Conclusions

Man has wondered for hundreds of years how birds are able to navigate, and much research and experimentation has been done on this subject to try to answer this question. There have been, it seems, innumerable hypotheses proposed to provide this answer. Many of these hypotheses have become theories, but then, when researched more carefully, they are found to be impossible or improbable explanations of the problem.

In all of the many theories and/or hypotheses reviewed, it appears that only one, the sun-arc hypothesis, is very substantial for long-range navigation, and even this may be disproven or shown to be only a partial answer. This problem is still unsolved.

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