5. Birds of the Refuge and birds observed elsewhere in the Southeastern Coastal Plain of South Carolina and Georgia did not seem to sing with the same zest and abandon as birds of the basswood-maple forests of Minnesota.

6. It is certain that the amount and intensity of song differ in different geographical and ecological communities. Some of the factors discussed that might influence song in different communities were: more non-migratory species; probably less defense of territory; the long nesting season at Savannah spreads the volume of song over a longer period than in the north; temperature influences the amount and volume of song; the difference in bird species composition of areas is important; type of habitat affects song.

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THE BIRD NAVIGATION CONTROVERSY

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SINCE the comprehensive review by Griffin in 1944, new experimental work has brought new interest, new apparent contradictions, and has removed the study of bird navigation from the realm of speculative thought. It is especially stimulating that this progress has been a coöperative endeavor of many of the older disciplines meeting in this field of geophysical ornithology. At this time there is a controversy that may be stated as follows: Is the superior navigation of birds possible because of their possible ability to orient to a Coriolis, magnetic, or other geophysical field of force in addition to keen powers of visual reference? Or do visual reference and sense of direction alone permit these remarkable flights? The evidence prior to 1944 was carfully reviewed by Griffin (1944).

The problem may be divided into two parts: I. Migration from unknown territory to known territory (artificial homing). II. Migration in known territory (the normal condition for the wild bird). "Known territory" implies either learned or inherited knowledge. The present evidence reviewed by Griffin (1944) suggests that the urge for southward flight and the southward flight ability may be inherited, since isolated young birds can make these flights. But the return flight in one species, at least, seems more a function of learning (Valikangas, 1933).

Yeagley, Magnetism, and Coriolis Force

Beginning in 1941, Yeagley (1947) in coöperation with the U. S. Army conducted five sets of experiments with homing pigeons and combined the very old magnetic theory (Viguier, 1882) with his idea of the action of Coriolis force. Thus he postulates that birds can and do orient to a grid formed by lines of equal Coriolis force and lines of equal magnetic dip. He suggests that birds detect the magnetic dip by detection of electromotive force produced within the bird as it flies through the magnetic field of the earth. He postulates that Coriolis force is also detected during flight. His experimental evidence because of its importance is discussed in detail below.

In Yeagley's *first experiment*, eight out of ten trained homing pigeons with an .8 gram copper plate sewed to the metacarpals of each wing returned 65 miles to Paoli, Pennsylvania, on November 7, 1943, within two days after release. Some had lost one or two plates. In comparison, only two out of ten birds with .8 gram magnets returned, and these in four days. He concludes that the magnetic fields of the magnets interfered with normal homing. The statement is made: "Since these birds were well trained and out-standing homing pigeons, Mr. Gable and others expert in the field expected at least two or possibly three of those with two magnets to home, just on the basis of their intelligence and ability to 'hunt' their way home. On the basis of probability and chance a similar prediction would obtain."

These are peculiar statements. The degree to which the birds home by other than visual 'hunting' methods is the thing being tested. How can one know just from experience with pigeons what per cent is due to visual and what per cent is due to sense of direction from the possible magnetic aid that is postulated? And on what basis is such a probability prediction made? As shown below, other workers account for much more rapid returns by random hunting. It seems that this experiment is most important and that it needs to be repeated. It is not impossible that on this one occasion the ratio was accidental or a function of other unknown factors peculiar to the magnets.

The unsubstantiated results so far suggest that a rapidly changing magnetic field interferes with homing. Even if this is true, a change in the electromotive force field of the bird, according to Yeagley's hypothesis, is not necessarily the mechanism of interference. Varian (1948), Slepian (1948), and Davis (1948) independently in letters to the 'Journal of Applied Physics' point out that according to relativity the bird has no way of detecting its own electrostatic field since all of the bird is cutting the magnetic lines and all of the bird has the gradient. As they indicate, even if the bird had the sensory mechanism it must measure the difference between bird and atmosphere. Measuring this gradient of about 10^{-5} volts/cm. by comparison with the atmosphere is not feasible because of the extremely variable atmospheric electrostatic fields of magnitudes up to one volt/cm. or higher in clouds (Gunn, 1948). Thus they reject this mechanism.

Varian and Davis instead suggest that there might be some direct magnetic mechanism. Such a mechanism presumably would not depend on motion of the bird. Attempts to train three homing pigeons to respond to a magnetic field were negative (Griffin, 1944) whereas success was obtained with light responses or air current stimuli. As yet, apparently, there are no instances known among animals where even large magnetic fields have been detected.

Henderson (1948) opposes the magnetic theory. During the war he served on a Canadian mine sweeper. He describes the reactions of wild birds to intense magnetic fields used in mine detection. "Birds appeared to be supremely indifferent to magnetic fields even at the sudden beginning of magnetic pulsing." On the other hand there are some observations that claim interference by radio stations with homing (Aymar, 1936). These are mostly fragmentary.

In addition to direct magnetic detection and detection of the electrostatic field created by flight through the magnetic field of the earth, there is the third possibility that the rapidly moving magnets on the wings might be felt by the bird whereas constant magnetic and electrostatic fields might not be felt. Varian and Davis independently make the excellent suggestion that the homing experiments be repeated with magnets attached to the body.

Dr. J. T. Zimmer (personal communication) has pointed out that the pigeon wing beat (about 8 per second) is far less than the 180 beats per second that Yeagley used in figuring .12 microvolts/cm. as the magnitude which alternates from positive through zero to negative for each beat. Thus, if the bird can detect this oscillation it is even more sensitive than Yeagley postulates in his paper.

Apparently satisfied with magnetism of the earth playing some role, Yeagley next experimented to see if the pigeons would home to a point in Nebraska which had approximately the same magnetic and Coriolis force field (although reversed in east to west direction) as the place in Pennsylvania where the pigeons were trained. Since the magnetic poles do not correspond to the regular poles, the circles of equal vertical component of magnetic force intersect the Coriolis force lines (which coincide with the latitude lines) in two places.

In this *second experiment* 43 birds were reported by telegraph out of 98 Pennsylvania-trained birds, which were released at eight points on eight days, 25–100 miles in all directions from Kearney, Nebraska. Six of eight of the vector sums of each day's returns converge on the Coriolis-magnetic conjugate point corresponding to the Pennsylvania training. Only one bird actually found a loft. Certainly visual orientation as stated by Yeagley is indicated in these experiments as the mechanism within ten miles, since the loft was rarely found. Apparently, the lofts with birds that were moved to Nebraska were kept near Kearney and thus near the conjugate point prior to their release. It would have been better if the loft had been kept elsewhere so as to eliminate the possible use of sense of direction of some sort. Twelve additional birds liberated 100 miles east of the conjugate point, apparently without ever having been near the conjugate, gave a good vector for six reported birds. The winds for the 14th to the 17th of May, 1944, were SE, SSE, and SW, roughly giving a resultant to the north. Here the birds were evidently unaffected by the wind. Twelve untrained birds that had spent a year caged in Pennsylvania gave a random pattern in Nebraska. This was interpreted as showing that the magnetic orientation in homing pigeons had to be trained.

G. E. Hutchinson (1948) pointed out that the returns from the west were not as satisfactory as the others. At the time of the main experiment the weather map shows winds: NE, E, SE, S, NE, E, SE, E, S, respectively, from June 29 to July 7. The total vector of winds is very roughly to the WNW. In the first two days the wind was ENE. In this case, at least, the winds might be considered as contributing to the vector sums from the east. Finally twelve young birds trained in Nebraska were liberated 100 miles south of the Pennsylvania conjugate; the vector sum of reported birds was northward toward the conjugate. The weather map shows SE flow on these days. This might have had an effect.

Considering all the releases of this experiment, there apparently is confirmation for the latitude-magnetic grid orientation theory. But these results are possibly subject to the criticisms above and those to follow. Unfortunately three out of ten old birds from Nebraska with long flight experience, when released in Pennsylvania homed to Nebraska, and three more went part way in this direction.

In Yeagley's *third experiment* he tested to see if there was a tendency for the birds to retrace the path along which they were transported. Fifty-four were reported out of 250 pigeons released in Nebraska on one day. Most were untrained and the flight vectors were short. Of the few trained birds, six made flights toward original homes in the southeastern U. S. even though they had come to Nebraska via New Jersey. However, a look at the weather maps for the 30th of September and 1st of October, 1944, shows that a cold front passed on the 30th of September with the usual accompanying strong NW winds at all levels. It is not apparent why the untrained birds were used since it is already accepted that homing ability in pigeons must be brought out by training, although the capacity is inheritable. Thus the data of six birds is not convincing. It seems too bad that in other experiments the loft was carried first to the conjugate point prior to birds being released near by.

In the *fourth experiment,* 44 birds trained in Pennsylvania were released in a band between Pennsylvania and Nebraska. The latitude lines and magnetic lines become parallel in a region half way between so that it was expected that birds in this region would go either east or west. The resulting vectors of birds reported confirmed expectations, with birds east of the parallel region going east, those west going west, and those within 100 miles of the parallel region going both ways. There were flight components in direction of conjugates of about 2300 miles compared to perpendicular coördinate components of about 500 miles. The eastern-released birds went east and the western-released birds went west for 1950 miles compared to 76 miles in the unexpected direction. The behavior of the western group seems to be Yeagley's best evidence for the theory, especially since the birds had never been west before. It should be noted that the birds were carried in an east–west direction prior to their release. The point of lowest elevation is half way between the conjugate points. The weather maps show a stationary front oriented from NE to SW half way along the route so that there was a tendency for NE winds in the west and SW winds in the east. Thus Yeagley's evidence is here subject to three additional interpretations.

In Yeagley's *fifth experiment,* 200 birds were trained to return to the Pennsylvania station always from release points to the northwest.

These same birds were released to the northeast of the Nebraska conjugate point. The 32% recovery had vectors with components of 2621 miles toward the point compared to 43 miles away from the point. The winds on the weather map were NW for three days, becoming S and E. So in this case the winds support the experiment. This confirms earlier experiments indicating that Pennsylvania birds tend, when released east and northeast of the Nebraska point, to go toward the conjugate. The components perpendicular to the release-conjugate line were about equal on either side, although Yeagley minimized this by adding them algebraically. Although a portion of his data does not apply, there is definitely an apparent confirmation at least of there being a latitude-longitude grid of some detectable quantity which reversed direction half way between Pennsylvania and Nebraska. But more controls are needed with releases other than in the east–west band and in other pairs of conjugate points. Experiments are needed to rule out winds and other effects such as elevation that are inherent in the geographical situation. A very important fact not pointed out is that the Platte River runs from a point NE of the conjugate at Kearney toward the town and then NW. A bird flying up river or toward the river would have a component toward Kearney. As previously stated the western results were not good.

It is unfortunate, from the nature of the bird recoveries, that the speed of their movements is not known. If the birds were to scatter in a random manner, the center of distribution would shift in the direction of the net wind vector during the two to six days in which most of the recoveries of Yeagley's experiments were made. Or if the birds maintained a constant latitude, the longitudinal center of distribution would shift in the direction of the net east–west wind component. In Yeagley's experiments the birds might have flown toward the conjugate in two hours and then spent the rest of the time wandering in the vicinity of the conjugate. If, on the other hand, the flight of these birds was evenly distributed over the several days before telegraphed reports came in, then their speed is extremely low. For example, in Yeagley's first Nebraska experiment, the vectors amount to only 6 to 18 miles per day whereas such a movement could be made in less than an hour, or the wind could have blown the birds that far in less than an hour. It is thus highly desirable that such experiments be closely tabulated with wind vectors. In any case, if this magnetic effect is a valid one it is not possible to tell from these experiments whether there is any real aid to the bird. As Griffin has shown, a wandering search by the birds could get them home quicker than the time of this experiment. Yeagley's experiments don't tell us which is the case.

These pigeon experiments differ in one major way from remarkable homing in wild species such as the homing of Noddy Terns from Texas to Tortugas. Pigeons have to be trained, which apparently allows them to learn part of a region among other things. Wild birds already know a region and may inherit some responses. This might be the only difference. There is no reason why the urge to migrate and the path taken are different from other inherited behavior patterns with visual releasers.

No experimental work was done to test the Coriolis force theory. The only evidence at this stage for Coriolis force orientation is that birds seem to orient to latitude, and Coriolis force lines parallel latitude lines. Coriolis force is discussed below in connection with Ising's theory. Yeagley, like most other students of migration, applied his theories to both homing from unknown regions and movements in known regions.

Ising and Coriolis Force

Independently at the same time, the Swedish physicist, Ising (1946), postulated the theory that birds (or other animals) might orient themselves by detecting the Coriolis force in the semicircular canals or other organs whenever the organ was subjected to velocity relative to the earth. He visualized birds turning their heads so that the rotation of the earth's horizon plane including them might be felt as an extremely small force on some sensory hairs or other sensory mechanism. This is somewhat different from Yeagley's idea of the Coriolis force acting because of the flight velocity of the whole bird. (*Coriolis force is the force exerted by the rotating earth upon any object which has velocity relative to the earth. A train traveling across the earth has a velocity relative to space. The earth in rotation is rotating the horizon plane (and thus the rails) to the left (in the Northern Hemisphere or right in the Southern Hemisphere). The moving train thus experiences a force from the right rail. This changes the direction of motion with respect to space. Similarly there are vertical components of Coriolis force. The horizontal component is zero at the equator since the plane of the horizon is not rotating. That is, two objects do not turn laterally about each other with respect to space. The horizontal components of Coriolis force are maximum at the poles where the horizon plane rotates at the same rate as the earth or once a day. The force is proportional to the velocity of the object relative to the earth. Thus the acceleration works out to be*

$$A = 2\omega V \sin \theta.$$

where ω is the angular velocity of the earth, V the velocity of the object relative to the earth and θ the latitude measured in degrees.)

Ising constructed a rotating device and actually measured the calculated force in good agreement.

Thorpe and Wilkinson (1946) discussed Ising's work. They pointed out that the magnitude of the Coriolis force in small birds would be of the same order of magnitude as forces resulting from Brownian movement and thus not to be considered as detectable without further heretofore unknown mechanisms. The forces acting on the whole bird in flight, as suggested by Yeagley, would be larger but would still be very small and, as pointed out by Hutchinson (1948), difficult to prove physiologically. Davis (1948) suggests the possibility of detection of Coriolis force on moving blood streams. However, Varian (1948) suggests that a supersensitive new organ other than one already in use for other sensory detection is less likely to evolve without natural selection, and natural selection could not act until the organ became supersensitive. This would be true if more than one or two mutations were involved.

As pointed out independently by Hutchinson (1948) and Davis (1948), the bird, in order to evaluate the Coriolis force, must know the velocity of his head in the case of the Ising idea or his ground speed in the case of the Yeagley proposition. It was already noted that the electromotive force interpretation of magnetic orientation required a ground speed determination also. The idea was brought out by Yeagley that in haze and fog birds get lost and homing pigeons can't home. Of course, if visual orientation is the only navigation method, then it, too, would be thus interrupted. As seen below, some homing is independent of visual references. Bender (1948), in his review of Yeagley, pointed out that over water ground speed could not be obtained. However it should be pointed out that this is not a valid objection. Almost never is the sea smooth. Ripples, swells, and whitecaps, although in motion themselves, serve as enough reference up to 4000 feet for detecting ground speed. That this is true is known from the standard procedure of aviation over the ocean whereby the wing velocity of the air mass in which the plane is embedded is told from 'double drift' measurements in reference to the sea surface. The surface wind, when over 10 knots as it usually is, may be told easily by the direction of streak of the whitecaps. Of course there would be much greater error due to movement of water patterns in the case of birds than with airplanes because of the smaller air speeds of birds. Incidentally, pigeons as well as other birds home successfully from miles at sea.

But there seems to the reviewer that there is a more fundamental objection to the Coriolis force determination by a bird in flight.

Yeagley's mechanism of detection of Coriolis force involves the bird feeling the deviation of his flight path produced by the earth rotating him. This action by the earth presumably acts through the medium of the atmosphere. However, the air is not rigidly attached to the earth. Movements of the atmosphere are most often initiated by differences in the pressure gradient and thus determined by the positions of highs and lows, etc. The air begins to move across the pressure gradient but the horizon plane of the earth is rotating beneath it and, so to speak, out from under the air flow. To the observer on the ground the air flow is being forced to the right whereas in relation to space it is the observer whose line of vision is being rotated to the left (Northern Hemisphere). Eventually the air flow obtains an equilibrium, with the apparent Coriolis force balancing the pressure gradient force and the air flowing parallel to the lines of equal pressure. The main point is that the positions of these high and low pressure areas are subject to many other meteorological factors and their own cycles so that they change in position and intensity with time, place and altitude even in the regions of the earth where the pressure systems are fairly constant. Furthermore, a bird flying across the earth's surface is crossing from one pressure pattern to another. Thus the air velocities and accelerations in horizontal and vertical are a function of changing patterns as well as the continual rotation of the horizon plane. A bird thus flying in the air must be able to distinguish which of the forces that it feels is due to wind systems and which is due to Coriolis acceleration. This seems impossible. And it must make these very small measurements and correlate with a very accurate determination of ground speed. For these reasons detection of Coriolis force is considered skeptically at this time. Once again these discussions apply both to homing from unknown regions and migration over known regions.

GRIFFIN: VISUAL RECOGNITION AND WANDERING

The theory of visual orientation really has two parts.

A. First, a bird in unknown territory wanders perhaps with a sense of returning to an altitude, to a given sun orientation, to a given vegetation appearance, or to some other visual gradient until it finds a recognizable landmark.

B. Secondly, a bird in known territory may seek other territory by following recognizable geographical patterns and by flying directed headings between recognizable landmarks. This latter ability is apparently a function of:

(1) learned behavior and

(2) inherited responses coupled with

(3) an ability to maintain constant flight direction.

This ability to fly straight may be a function of:

(a) the ability to remember direction changes just as a person in a train knows when it is turning; and

(b) the ability to maintain a constant angle with respect to heavenly bodies or some terrestrial objects.

It is generally accepted that some of bird navigation especially over short distances is accomplished by this visual recognition theory. The question is how much? Griffin (1944, 1948) is one of the main modern proponents of this theory which he clearly formulated although slightly differently from the expression above. He suggests that this method of orientation is adequate to account for all but a few unsubstantiated cases.

Griffin and Hock (1948), with an airplane, followed 9 out of 16 Gannets from a release point 100 miles inland from their nests. The paths as far as they were followed were looped, twisted, and of the wandering type. These authors ruled out the airplane as having affected the flight path because the birds followed for one to nine hours arrived back at the nest at the same rate as the other birds. The average speed of return of 99 miles per day compared well with speeds of homing of six other wild species of 38–141 miles per day. Pigeons over previously flown routes have covered 500 to 1000 miles in a day. This speed discrepancy suggests a difference between wandering from unknown territory and movements in known territory. But Yeagley's pigeons had net vectors that were only a fifth of that of the wild birds in apparently unknown territory. As mentioned above there is no way to tell if this is an artifact of the experiments or not. As Griffin pointed out (1944), if a bird flew outward in an Archimedes or other more random spiral it would be flying rapidly enough to account for almost all homing records. The Gannet results seem to confirm this idea and suggest that magnetic detection in pigeons is grossly ineffective or not present at all. Of course there is the possibility that the birds followed by airplane made up for lost time later, and if otherwise undisturbed would have flown direct courses. More birds should be followed. A very short wave PPI radar scope would be ideal for this job. Perhaps the coöperation of aviation may be secured for this purpose. Saville (1948) draws a distinction between migration and homing on the basis of the much greater speeds with migration under certain conditions and because migration seems more inherited than homing. However from the point of view of navigation ability, once the bird has the mental behavior patterns established, either by inheritance or by learning, the problem is the same. The difference between migration and artificial homing can be considered as being the difference between movement in known and unknown territory.

One of the mechanisms of orientation of some insects involves a combination of landmark recognition, following olfactory trails, and orientation to a constant angle with the sun by means of two rigid compound eyes. This latter is the light compass reaction known to exist in ants. Insect orientation is summarized by Wigglesworth (1947). That birds may maintain constant angles of visual reference is not unreasonable especially since there is an eye on each side of the body axis in birds and since there is little eyeball movement. It should be mentioned that the pecten projecting into the eyeball might possibly have some effect here. Crozier and Wolf (1943) postulate that the pecten increases contrast. The pecten theories were discussed recently by Pumphrey (1948). If a bird were maintaining an orientation to a heavenly body on the horizon, with the rise of this object above the horizon the bird might, in the course of time, shift its orientation to the next appearing heavenly body. Or at least it might gradually shift its orientation. For north–south flight the rotation of the earth changes the elevation of heavenly bodies mostly at right angles to the flight path in comparison with a change of flight direction which would change the azimuth. It is an interesting possibility that an illuminated terrestrial object at night might serve as an orientation reference. A bird under these conditions might converge in a logarithmic spiral as suggested for insects because of its flying at a constant angle (Buddenbrock 1917). Sometimes lighthouses get large concentrations of birds which strike or fly around, confused. Constant flight direction over the sea may be accomplished by visual reference to the ocean swell patterns that are almost always present.

Sense of direction without visual reference is a different thing. Brewster has cited homing of auklets and murres to Alaskan rookeries through fog. It is likely that birds are very sensitive to any accelerations produced by change of flight direction just as a person on a train senses a turn. There may be some gyroscopic stabilization by the wing beat. But this sense is apparently not the orientation method for artificial homing experiments where the bird is initially lost. Exner obtained usual homing by birds anesthetized, rotated, and electrically shocked during transport. However, these experiments have been criticized by Griffin (1944).

Infra-red light has been suggested as an aid through clouds, at night, and around the curvature of the earth. However, as yet all experiments on birds show negative sensitivity (Hecht and Pirenne, 1940; Matthews and Matthews, 1939).

In oceanic regions, especially in the trades, the typical air mass is modified somewhat in passing across islands so that the lee flow has different cloud appearances. This might enable birds to locate these islands visually.

CONCLUSION

1. The extreme smallness of the Coriolis force of the order of magnitude of Brownian movement forces, the absence of experimental or direct theoretical support, and in the case of the flying bird the impossibility of separating the Coriolis acceleration from atmospheric accelerations and the difficulty of making the necessary correlations with ground speed seem to rule out the Coriolis force as a factor in bird navigation.

2. Experiments testing the direct action of magnetism on homing pigeons, although positive, seem unsatisfactory and need to be repeated and enlarged.

3. It is unlikely that magnetism can be detected by a bird through the mechanism of the electrostatic field induced within the bird as it flies through the earth's magnetic field. This is because there is no way to measure the force, since the variations in the atmospheric fields are of large magnitude.

4. There is either positive experimental evidence that the earth's magnetic field in some completely unknown way affects the homing of pigeons which are in unknown regions or alternately this same evidence indicates that in the Nebraska to Pennsylvania region there is some effect coincidental with the magnetic hypothesis in ultimate effect that causes the peculiar homing of the pigeons in two opposite directions.

5. The homing of birds from territory new to them is of a speed and nature that supports the hypothesis of the birds wandering until known visual references are located.

6. The navigation of birds over territory previously visited or territory which visually releases inherited behavior patterns seems to be adequately accounted for by apparently acute ability to choose the correct flight direction and procedure from memory or inheritance after visual landmark recognition so as to fly from landmark to landmark and to follow geographical lines such as coast lines and rivers. Two effects permit them to maintain flight direction between landmarks: (a) Birds may maintain their sense of direction apparently just from memory of movements as in fog for short distances at least,

although fog prevents navigation if the bird is initially lost; (b) It is possible that birds can maintain their sense of direction by light compass orientation and by maintaining a constant flight angle with some visual references such as ocean swells.

7. The wandering and visual orientation theory is certainly part of the correct explanation. The magnetic theory is lacking in theory and upheld by experiments which for various detailed reasons need to be repeated. Even if valid magnetic effects exist, that they are anything but grossly inefficient has yet to be shown. The burden of proof still seems to lie with the proponents of the magnetic theory.

ACKNOWLEDGMENTS

This review was made at the suggestion of the editor. The author wishes to express his sincerest appreciation to Dr. G. E. Hutchinson for comments and stimulating suggestion and to Dr. S. C. Ball for aid with the literature.

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