The Navigation of Homing Pigeons: Do They Use Sun Navigation?

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MANY INVESTIGATORS have followed flocks of homing pigeons as they returned to their home lofts from distant release points (refs. 1 to 6). Yet the track made by a flock of pigeons represents some unknown concensus among the pigeons making up the flock. It could well be that different pigeons use different navigational strategies and that the study of flock behavior would reveal very little about any individual pigeon's technique for finding its loft. For this reason my colleagues and I have spent the past 5 years mapping the tracks of individual homing pigeons as they returned to their lofts. Our hope was that a detailed knowledge of what a pigeon did on its homeward journey might provide some clues to its navigational scheme. In addition we hoped that the effect of our experimental manipulations would be seen more clearly by examining the pigeons' tracks than were revealed in either the initial headings or the overall homing performance.

In this paper I will summarize the results of our analysis of the pigeon's tracks, the effects of short clock shifts, the effects of attempts to disrupt the pigeon's internal clock with heavy water, the transporting of pigeons to the release site under anesthesia, and the effects of placing small magnetic fields around the pigeon's head.

TRACKS

In following individual pigeons returning home from release sites where they had never been released before, their tracks could often be divided into three phases; an initial flight in the compass direction in which the bird had been trained, a segment of track directed toward the loft, and a final turn toward the loft itself. We have called these three phases: compass orientation, true navigation, and landmark orientation. Each will be briefly described below.

Many of the pigeons from the loft at Harvard University in Cambridge, Massachusetts, flew east in their trained compass direction when released from a point off their training line. That this was not simply a tendency to fly in an easterly direction was shown by pigeons that had been trained from other directions—from the north and south; they also would frequently fly for 5 or 10 mi in their trained direction when released at unfamiliar locations. But this compass orientation has become less common in recent years, and the

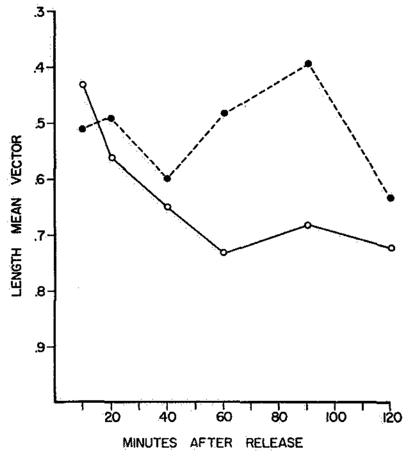

FIGURE 1. Accuracy of homeward orientation of pigeons released off their training line plotted against time after release. Data were derived from tracks of 48 pigeons released at various new release points in different directions from the loft. Bottom solid line represents scatter of homeward bearings measured from release point and graphed as length of mean vector of distribution. Gradual downward slope of the curve simply means that birds flying incorrect courses tend to correct them with time. This distribution also shows a downward trend because as birds fly away from the release point, the angular error to the home loft as measured from the release point tends to decrease. To compensate for this distortion, we have plotted in the upper dashed curve, the mean orientation of 1-mi segments of tract at the specified times. Thus a bird that initially headed away from the release point in the wrong direction would contribute to large scatter in both curves at the outset. As it corrected its course toward the loft, error in its 1-mi track segment might well drop to zero, but its bearing from the release point might still show an error of as much as 180°.

birds in the Lincoln loft rarely show it. One can speculate that this difference may be the result of less extensive training in one direction: the Harvard birds had nearly 30 releases along the training line; the Lincoln birds rarely have more than five or 10 releases in any one direction. Furthermore there is a great variation fom one bird to another in their tendency to fly in the trained compass direction. Some birds often show this behavior often while others almost never do.

But flying in the trained compass direction will not get a bird home if it is released off its training line. And we find that the vast majority of our pigeons do home successfully. In fact our birds are able to orient toward the loft from what is almost surely unfamiliar territory. Several pigeons have shown accurate orientation toward the loft from over the open ocean, well out of sight of land. Furthermore, those birds that don't fly in the trained compass direction orient toward the loft quite rapidly. As figure 1 shows, the tracks show only a gradual decrease in scatter from 10 to 50 min after release. In fact, lumping all off-training line releases from all release points together and plotting the 16-km bearings relative to the homeward direction (fig. 2) reveals that the 16-km bearings are quite tightly grouped with a mean vector differing from the home direction by only a few degrees.

In the last stage of homing when the pigeon arrives in the area near the loft, it appears likely that it uses landmarks to find the loft itself. For birds returning to the loft at Harvard University in Cambridge, it appeared that they made a final course correc-

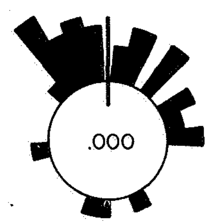

FIGURE 2. 10-mi bearings of 35 birds released from new release points. Bearings are plotted relative to home direction indicated by the line. Number in center is probability that observed distribution is due to chance.

tion when they came within sight of some of the high Harvard buildings—a pigeon flying at tree-top level should have been able to see the buildings when it was about 8 to 16 km (5 to 10 mi) from the loft and indeed most of the pigeons made final course changes within a few km after passing this 8- to 16-km point. (See ref. 7, p. 113 and ref. 8, p. 316 for diagrams.)

It is also possible that landmarks play other roles in the homing process. There is a suggestion from some tracks that landmarks are used as check points by pigeons returning from familiar release points. (See, for example, fig. 4 in ref. 8). But pigeons flying incorrect courses toward the loft do not seem to correct them even when flying through territory that they have flown over many times before (ref. 7, p. 124). It appears then that under sunny conditions, landmarks play only a minor role in homing. But when the Sun was not visible, three pigeons appeared to use landmarks to find the loft. These birds when released along their training line followed a major highway from the release point to the loft. Under sunny conditions their tracks instead of following the highway went straight home.

Pigeons probably use a variety of cues in their homing, and it is a mistake to think that any one single system is totally relied upon. In our years of following individual pigeons, we have been continually impressed with the variation in strategy from one pigeon to another. For example, Blue 77, one of our oldest birds, has been flying for 5 yr. And no matter what experimental regime we subject her to, she always flies straight home, on some occasions with a great deal of sitting. And once when something went wrong with her transmitter harness, she was found slowly walking down a major highway toward the loft.

Another bird, WY, was trained from Orange, Massachusetts, 83 km (52 mi) west of the loft. On the way home all birds from Orange flew past Mt. Wachusett, a conspicuous but not very high mountain, directly on the route home. After training on this line, wherever WY was released the first thing it did was to fly toward the nearest mountain, whether it was Mt. Wachusett, Mt. Monadnock, or Mt. Washington. After circling the mountain, it generally turned and flew directly toward the loft. The final and perhaps the most unusual example was B38 who always navigated very accurately towards the loft. But when it arrived in the region of the loft, it seemed unable to find home. On four of its last five flights, B38 flew past the loft, missing it by only 1 to 2 km and continuing past it for 5 to 16 km (3 to 10 mi). It then landed in the front yard of a house and would allow itself to be captured. The finder then read the label on its transmitter, telephoned the loft, and B38 would arrive home in a taxi. This was a rather unusual strategy but none the less effective.

The moral of these stories is that there is probably a variety of techniques and strategies that pigeons use to find their lofts and that unless the investigator is aware of this diversity, experiments in which pigeons are deprived of one source of information may simply lead the bird to switch to alternate strategies. One of the major advantages of working with individual pigeons is that one can become familiar with the tactics a particular pigeon is most likely to use. Then when one does an experiment, it is easier to assess whether the experimental treatment has had any effect.

During our early tracking, we were impressed with how reluctant our pigeons were to fly if the Sun was not visible. Pigeons flying courses toward the loft would frequently stop and sit when the Sun became obscured; still other pigeons would refuse to fly at all if the Sun were not visible. Only after extensive training under overcast could we presuade our pigeons to home successfully without the Sun. These observations led us to wonder if perhaps the pigeons were not only using the Sun as a compass, but also as the basis of their navigation, as Matthews (ref. 9) suggested. But the evidence for Matthews' theory and for Pennycuicks' (ref. 10) modification of it rests on two sorts of experiments: clock shifts on the one hand and the confinement of birds during the autumnal equinox on the other. A repetition of the crucial experiments by other investigators has yielded different results (refs. 11 to 16). It could be argued that pigeons using Sun navigation exposed to 3- or 6-hr clock shift would simply not "believe" the amount of displacement that such a shift would indicate (ref. 17). For example, a 3-hr shift is equivalent to moving several thousand km on the surface of the Earth, and for pigeons trained to fly only a few hundred km, such a shift might conceivably be ignored.

What we sought to do was to expose pigeons to very small clock shifts of only a few minutes, small enough to lead to only a trivial error in their Sun compass but to a relatively-easy-to-assay error in their navigation. For example, a 5- or 10-min clock shift would generally lead to only a 2° to 3° error in a Sun compass but in terms of Sun navigation would be equivalent to a displacement of 80 to 160 km (50 to 100 mi). These experiments were performed by confining pigeons, whose normal homing performance was known, to clock shift boxes. These boxes were equpped with artificial lights and timers arranged to turn the lights on and off the appropriate number of minutes either before or after local sunrise or sunset. Details of the procedure and results are given in reference 8.[1] Pigeons were exposed to "0" shifts (lights on at local sunrise and off at local sunset) and to shifts of 5, 10, 15 to 20, and 120 min. The birds were then equipped with radio beacons and taken in covered containers to release points where they had never been before and released. They were tracked by airplane and by ground tracking stations. Figure 3 shows the bearings of each bird relative to the home loft when it was 16 km (10 mi) from the release point, as well as its bearing plotted relative to the "false home," i.e., that location where the local time agrees with the shifted time imposed on the pigeons.

It is obvious from the figure that there is no consistent orientation toward the false home nor is there any significant difference in the accuracy of the homeward orientation of the different shifts. There is, however, an interesting change in the mean vector of the birds given various shifts; the mean vector moves from left to right as one looks at controls, 0 shift, 5-min, 10-min, 15- to 20-min, and 120-min shifts.

An examination of the longer shifts, namely 120 min and 6 hours, shows that the 120-min birds are deviating to the right of the homeward direction. Applying a correction for the Sun-azimuth change involved in the 2-hr shift gives a distribution (fig. 4) that is much closer to the true homeward direction. The 6-hr shifts are really too scattered to analyze and the fact that we lost three of the five birds made us reluctant to increase the sample.

The results suggest that small clock shifts have little effect upon the initial orientation of the pigeons. A detailed analysis of the track of each bird shows no consistent differences between birds given a clock shift and birds taken directly from the loft (table 1). In no case did any bird ever fly to its false

[1] Also, WALCOTT, C.; AND MICHENER, M. C.: Sun Navigation in Homing Pigeons—Attempts to Shift Sun Coordinates. J. Exp. Biol., vol. 54, 1971, pp. 291–316.

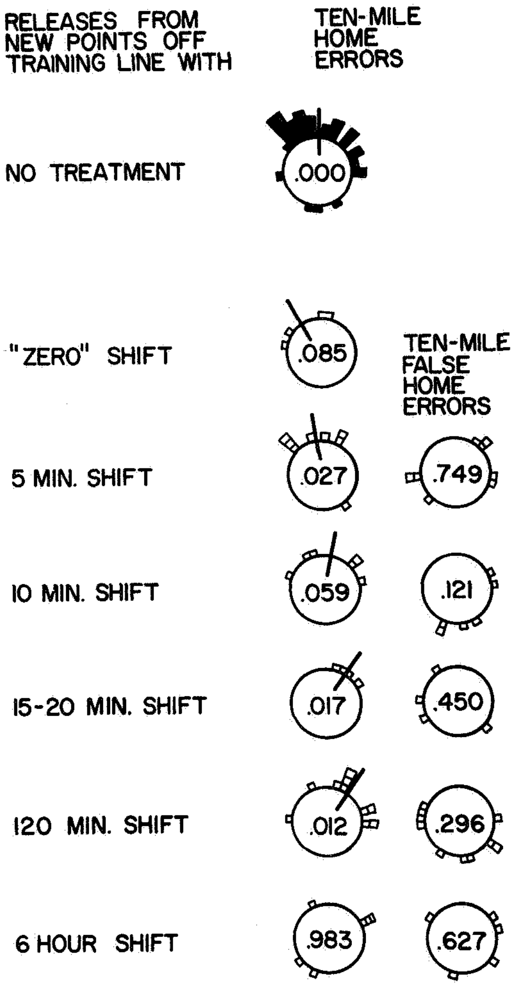

FIGURE 3. Orientation of pigeons at 10 mi from the release point after being subjected to various artificial light regimes. Left column shows bearing of each bird plotted relative to true direction to the loft; home is at the top of circle. Number in the center is probability that distribution is random: the line indicates mean bearing of distribution, given only if probability of randomness was less than 0.1. In the right-hand column, the same bearings are replotted in relation to the "false home." If birds were flying to this false home, their bearings should be tightly grouped around the top of the circle. All except the 6-hr shifted birds show better orientation to home loft than to false home.

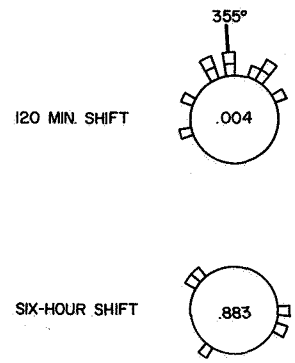

FIGURE 4. Bearings, relative to home, of birds given 2- and 6-hr shifts corrected for change in Sun azimuth caused by the shift. This procedure corrects for error the shift would have caused in a Sun compass. In the case of birds given a 120-min shift, this correction has resulted in a tighter grouping of 10-mi bearings (p is 0.004 compared with 0.012 before the correction) and a smaller difference between mean vector of distribution and the home direction (5° instead of 37°). Distribution of 6-hr shift bearings is unchanged.

home. The only consistent effect resulted from the 6-hr shifts; only two of the five birds ever homed after this treatment, and the other two homed significantly more slowly than normal. These results are in contrast with those we reported earlier (ref. 8). Apparently the small sample we reported on at that time was not typical of what we have now found. Short clock shifts had little or no effect on the birds' navigation, but larger shifts did affect the Sun compass. But Hoffmann (ref. 18) has suggested that the pigeon might use a two-clock system—one clock rigidly fixed to loft time and highly resistant to shifting which would be used for navigation, and another clock that was easily reset to local time at the release point which was to be used for a Sun-compass clock. As Snyder (ref. 19) has pointed out, it is very hard to imagine how a bird could have a clock that would be able to compensate for the constantly changing solar

TABLE 1.—*Some Aspects of the Tracks and the Homing Performance of Pigeons Subjected to Various Experimental Regimes*[a]

Treatment	Number of tracks	Homing speed	Length ratio	Tract deviation	Home/ compass ratio
No treatment	35	12.6± 9.5	1.785±1.14	21.0±18.8	23:9
Cloth box	7	11.5±10.5	1.809±1.13	15.7± 6.0	5:2
0 shift	5	6.0± 6.9	1.420±0.237	19.8± 9.9	3:1 1?
5-min shift	8	10.3±10.6	1.860±0.638	21.6±11.6	7:1
10-min shift	6	15.8±11.3	1.790±0.933	21.9±14.4	2:4
15 to 20-min shift	4	16.1± 8.8	1.756±0.577	7.0± 1.8	3:0 1?
120-min shift	10	12.3± 6.3	1.506±0.550	11.4± 9.8	7:2 1?
6-hr shift [b]	5				
Mirror box	10	5.5± 6.6	1.454±0.280	11.9± 3.5	8:2

[a] The homing speed is given in statute miles per hour followed by the standard deviation of the mean. The length ratio is the actual length of the track divided by the straight line distance from release to home. The track deviation is determined by measuring the deviation of the track from a straight line at 10 points, averaging these measurements and expressing this average as a percentage of the straight line distance from release to loft. The home/compass ratio is the number of birds whose 16-km (10-mi) bearings are closer to the home direction or closer to the trained compass direction. The three cases where these two errors are equal are indicated by ?.

[b] Only two of five birds returned.

day and still be rigidly fixed to solar time at the home loft. Indeed there is really no direct evidence to suggest that such a clock exists. But postulating the existence of such a clock, it becomes interesting to think about ways of upsetting it.

It has been shown that heavy water (D_2O) slows down the expression of the clock in a variety of organisms (refs. 20 and 21). Snyder (ref. 19) has shown that 30 percent D_2O in drinking water slows down the circadian activity rhythms of pigeons by about 4 to 6 percent. This finding led us to perform a "disruption" experiment. Pigeons were confined to a shift box with a random light schedule of the same kind used by Matthews (ref. 22). In addition, for their 10 days to 2 weeks of confinement, they were given 30 percent D_2O in their drinking water. Such birds, we reasoned, should have little recollection of time at the home loft; and not only would their clocks be running slow, but the random lights should have upset their circadian rhythms. But clearly the compass clock would also be upset by this procedure; and looking at the pigeons homing performance, it would be hard to distinguish any effect on navigation from the errors in the compass. To resolve this ambiguity, we took the pigeons from their shifting container and transported them in closed containers 400 km (250 mi) to the west where they were held for us in open cages by William Keeton at Cornell University in Ithaca, N. Y. In the week to 10 days they were held with a view of the Sun, the birds had an ample opportunity to reset their compass clocks to local Ithaca time. If their navigation clocks were also reset, they would have to be set to Ithaca time as well. At the end of 10 days the birds were equipped with transmitters and tracked from the ground and by airplane from Orange, Massachusetts, (about 88 km west of the loft and exactly on the same line as the loft) and Ithaca. Figure 5 shows the results of this release; both the experimental birds and the controls were well oriented toward the home loft. This result suggests that nei-

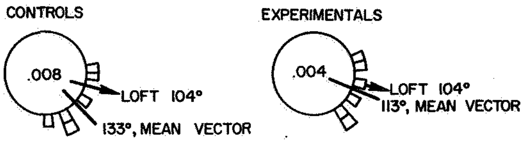

FIGURE 5. Comparison of orientation of pigeons that had been given heavy water, random light schedules, exposure to the Sun 250 miles west of the loft, and then released with pigeons taken directly from the loft. In each case the loft was at a bearing of 104° from the release site. The probability that the observed distribution arose by chance is indicated in the center of each circle: bar indicates mean vector of the pigeon's bearing at 10 mi from release. Experimental birds are as well or better oriented to the loft than the controls.

ther the D_2O, the random light schedule, nor the holding at Ithaca had any major effect on the pigeons' ability to fly home.

These experiments—the clock shifts, the disruption, and several others reported [2] (ref. 19)—suggest that the pigeons are probably not using the Sun as a navigational reference although they do seem to use it as a compass. Matthew's crucial experiments have not been successfully repeated, and indeed Keeton's (ref. 23) demonstration that shifted birds homed under total overcast strongly supports the idea that the Sun is not essential for homing. In short, considering the evidence that is currently available, it is hard to accept the view that pigeons use the Sun for navigation. This conclusion raises real questions about what the pigeons do use and where and when they obtain the information that leads them home. It might be that they are gathering information on the journey out to the release site. This seems unlikely to us because pigeons that have been carried in the back of the airplane all day while following birds released earlier homed as well as control pigeons. To examine the question further, we have transported pigeons to the release point while:

(1) Unable to see the outside
(2) Jiggled in the back of a car
(3) In varying magnetic fields
(4) While anesthetized

Such pigeons showed as accurate a homeward orientation at 8 to 16 km (5 to 10 mi) from the release site as did control pigeons taken directly from the loft. While it is obviously hard to argue that the pigeons could not have gathered any information while being transported to the release site in this way, the treatment certainly makes it less probable.

Most recently we have begun a series of experiments based on Keeton's findings (reported elsewhere in this volume) that small magnets attached to a pigeon's back sometimes cause both poor initial orientation to the loft and slower homing speeds. But the use of magnets in this way results in a rather non-uniform magnetic field around the pigeon's head. It seemed possible that a uniform field around the head might give clearer results. To produce such a uniform field, a small pair of Helmoltz coils were arranged around the pigeon's head and neck (see fig. 6), and an additional battery was added to the transmitter pack glued on the pigeon's back. A current of between 10 and 15 mA through the coils gave a field of 0.8 to 1.2 G in the region between the coils. The uniformity and magnitude of the field was measured with the small probe of a Bell gausmeter. Control birds carried coils, batteries, and connecting wires, but no current was passed through the coils. Thus the only difference between the experimentals and the controls was the presence or absence of current through the coils.

In performing the eight releases we have made to date, pigeons were taken from the

[2] WALCOTT, C.; AND MICHENER, M. C.: Sun Navigation in Homing Pigeons—Attempts to Shift Sun Coordinates. J. Exp. Biol., *ibid.*

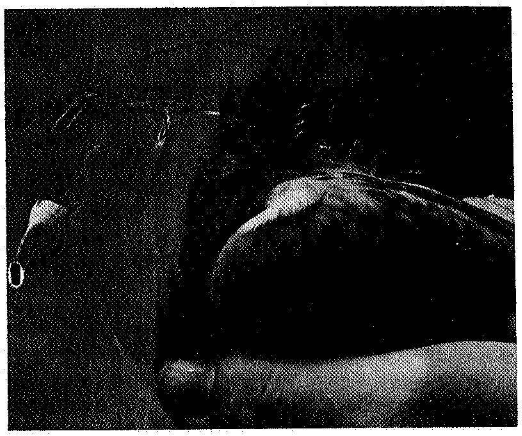

FIGURE 6. Pigeon equipped with pair of Helmholtz coils and small radio beacon for tracking.

loft and transported to a new release site. Before each bird was released, it was equipped with coils, battery, and transmitter and then released and tracked from the ground. Experimentals and controls were released alternately, and as far as possible a bird that served as an experimental one day was used as a control the next and vice versa. This procedure enabled us to compare the performance of the same birds under both experimental and control conditions but from different release sites. The results of these preliminary experiments are shown in figures 7 and 8. An examination of the degree to which each distribution of 16-km (10-mi) vanishing points might be due to chance shows that, in seven out of the eight releases, the control birds were more closely grouped than the experimentals. Combining the results of all eight experiments in a single distrubution makes the difference in the homeward orientation of controls and experimentals clearer. In fact comparing the home errors (i.e., the number of degrees each bird's track deviates from the homeward direction) of both groups using the Mann-Whitney U test, corrected for ties, shows that the controls

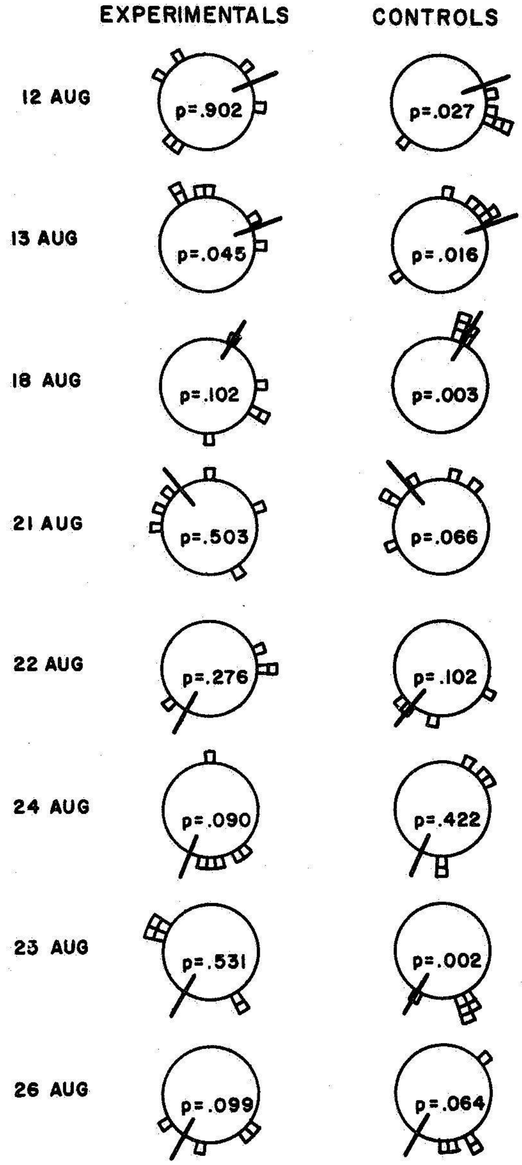

FIGURE 7. Departure bearings measured 10-mi from release points for pigeons equipped with Helmholtz coils. Both experimental and control birds were equipped with identical apparatus, but only the experimental birds had coils that were connected to batteries and were therefore carrying current. Figure in the center of each distribution is probability that observed distribution is due to chance; line indicates direction to loft.

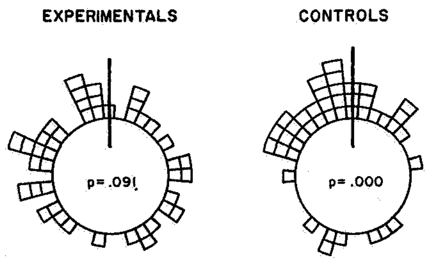

FIGURE 8. Bearings of pigeons shown in figure 7 replotted with home direction at top of diagram.

had significantly smaller home errors than the experimentals.

In addition to this difference, a number of the pigeons perched in trees when they were released. Of the 43 control birds, two sat, whereas of the 43 experimentals, 14 sat, a difference that is highly significant. The homing performance of the two groups was not significantly different. Although there is not accurate quantitative data available, it appears that all except one of the experimental birds returned with either broken coils or dead batteries whereas the majority of the control birds returned with their coils intact. These results, although based on a small number of releases, do offer the hint that magnetic fields may have some effect upon the pigeon's orientation.

To summarize our experiments to date, it seems increasingly likely that pigeons do not use the Sun as a basis of their navigation although they can make use of the Sun as a compass. Furthermore, whatever the basis of their navigation may be, information gained on the trip to the release point seems to be of less importance than cues gained at the release point itself. What the nature of these cues may be is completely unclear.

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DISCUSSION

GWINNER: Do you measure any circadian function to ascertain whether the pigeons' circadian rhythm(s) had in fact been shifted?

WALCOTT: Yes, we have activity rhythms which show that at least the activity rhythms were shifted about; but whether this means that the clocks were shifted or not, I don't know.

ENRIGHT: In your clock shift experiments, how long did you expose the animals to the new light cycle?

WALCOTT: About 10 days. Snyder has exposed them for a month and a half and got exactly the same shift and effects as when they were exposed for 5 days.

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