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MAGNETIC FIELDS AND THE ORIENTATION OF HOMING PIGEONS UNDER SUN

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SUMMARY

Applying a magnetic field of 0·1 Gs (1 gauss = 10^{-4}T) to the heads of pigeons homing from unfamiliar release sites significantly increased the scatter of the birds' vanishing bearings. A magnetic field of 0·3 gauss caused no difference between the orientation of birds wearing coils with either their north or south pole up. But a field of 0·6 gauss (equal to that of the Earth) produced a small difference in the vanishing bearings of the two groups. Since an applied magnetic field has an effect on pigeon orientation under sun, it appears that pigeons do not simply switch between a magnetic and a sun compass, but that there is some interaction between the two systems.

INTRODUCTION

The evidence that at least some animals can detect magnetic field is now quite convincing. But the role, if any, that magnetic fields play in the orientation of birds is less clear. Merkel, Wiltschko and their colleagues (Merkel, Fromme & Wiltschko, 1964; Merkel & Wiltschko, 1965, 1966; Merkel & Fromme, 1958; Wiltschko, 1968, 1972; Wiltschko & Wiltschko, 1972; and Emlen *et al.* 1976) have shown that the orientation of caged European Robins can be altered by changing the direction of the applied magnetic field. Southern (1969, 1972) has reported that Ring-billed Gull chicks are disoriented when the earth's magnetic field is disturbed. And Keeton (1971, 1972) has convincingly demonstrated that homing pigeons returning to their lofts under overcast skies are often disoriented when small bar magnets are glued to their backs. Reviews of this work have been published by Emlen (1975) and Keeton (1974*a*).

The magnetic field of a bar magnet is uniform in only a very small area, and to investigate the effect of a well-defined magnetic field on bird orientation it would be highly desirable to surround the bird's head, or wherever the sense organ might be located, with a uniform field that could be accurately controlled in both strength and direction. My colleagues and I have developed a small Helmholtz coil which can be glued to the pigeon's head and produces a relatively uniform field which can be easily controlled by varying the current flowing through the coil.

Experiments using the above uniform-field under total overcast are reported by Walcott & Green (1974). But what would be the effect of uniform magnetic fields if the sun were visible? Lindauer & Martin (1968, 1972) and Lindauer (1973) report that the directional errors in the honey bee's waggle dance are greatly reduced if the strength of the earth's magnetic field is reduced in the hive. This result suggests that the magnetic field might have some effect even on a system that is presumably depending on other environmental cues; in the case of the honey bee, the sun position and gravity. In some early experiments with pigeons, Keeton (1972) reported that magnets frequently disoriented pigeons under sun when the distance was suddenly increased beyond that from which the pigeons are usually released. I have confirmed these results in a small series of releases (Walcott, 1974) and shown in a preliminary trial (Walcott, 1972) that Helmholtz coils with a weak 0·1 gauss field tended to increase the scatter of pigeons' initial orientation. Recently, Keeton (1974*b*) has shown that the vanishing directions that pigeons fly are systematically altered by fluctuations in the earth's natural magnetic field, and that this effect can be abolished by attaching a magnet to the pigeon (Larkin & Keeton, 1976).

This paper will report the results of a series of releases under sun of pigeons equipped with Helmholtz coils inducing a variety of magnetic fields around their heads.

MATERIALS AND METHODS

Pigeons used in this study were bred in the University's lofts in Lincoln, Massachusetts. The original breeding stock was obtained as young birds from successful local pigeon racers. Young birds were trained by successive releases from an automobile at increasing distances along a line to the southeast of the loft. When the flock had been released two or three times at 50 miles from the loft, birds were further trained by being 'single tossed' from the automobile first at 10–20 miles and then at 30–50. Birds returning promptly from these single tosses were released singly 30 miles to the west of the loft for their first off-training line release. Pigeons that returned promptly from this final training release were then used in experiments. In all the experiments reported here pigeons were released from a given release site only once, so there is little chance that they had ever seen it before their experimental release.

The coils used around the birds' heads were wound with #36 enamelled copper magnet wire. One coil, 35 mm in diameter, was placed around the bird's neck; the other, 23 mm in diameter, was glued to the top of the bird's head. Finished coils were wrapped in plastic electrical tape (Scotch #33) for mechanical support. The two coils were connected in series, and to a battery holder, by very flexible wires (phonograph cartridge lead wire, Belden 8430). The mercury battery (Mallory RM-675) could be inserted in the holder with either polarity up. The strength of the field was adjusted by varying the number of turns in the coils and by using a resistor in series with the battery and coils for the very weak fields. The strength of the field between the coils was measured with a Bell Model 620 gauss-meter after attaching the coils to a styrofoam model of the pigeon's head (1 Gs = 10^{-4}T). By orienting the gaussmeter probe so that its direction of maximum sensitivity was at right angles to the normal earth field, the meter read 0 gauss, and the strength of the field due to the coils could be measured even in the presence of the earth's field. Such measurements showed the field to be reasonably uniform: with a 0·6 Gs coil, the field strength with the probe touching either one of the coils was 0·8 Gs. 3 mm away it was 0·6 Gs and remained at this value everywhere between the coils. The field induced by the coils could be either one of two polarities depending on the direction of current flow. The polarity was defined by placing the coils around an ordinary magnetic compass. When the North seeking needle of the compass pointed towards the head coil, that coil was defined as a 'North Up' or NUP for short. The alternative orientation was South Up or SUP.

The coils were attached to the pigeon using F and F Branding Cement (Control Data Corporation, Lincoln, Nebraska) which appeared not to irritate the pigeon's skin and remained sufficiently flexible so that the coils could be removed with minimal disturbance to the pigeon's feathers or skin when the pigeon returned to the loft.

Pigeons were tracked using radio telemetry. Small 148 MHz transmitters (Cochran, 1967) were combined with the battery pack of the coils and the whole assembly glued to the pigeon's back with branding cement. The package weighed about 8 g. The birds were tracked from a portable tracking station which could follow a pigeon for approximately 10 miles from the release site. The tracking distances were measured by following birds from the ground and from an aeroplane (Michener & Walcott, 1967) simultaneously.

Birds were transported to the release site in covered carrying cages in the back of a Volkswagen Squareback. Transmitters and coils were attached to the pigeons immediately before release, and the person who prepared and released the pigeons never informed the person who did the radio tracking what experimental procedure a pigeon had undergone; thus there is no chance that the bearings could have been influenced by a knowledge of a pigeon's experimental treatment.

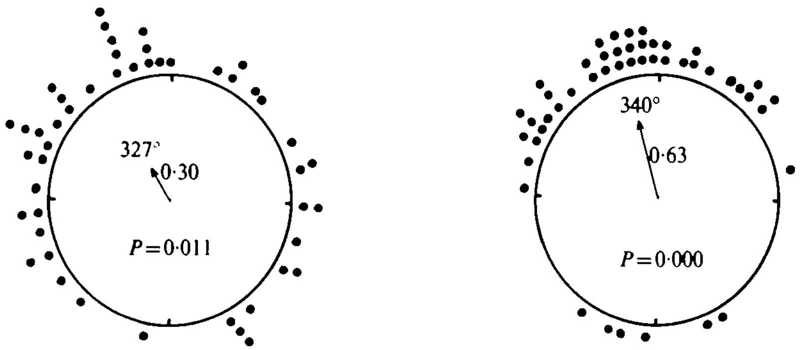
Weather data were always collected at the release site. The sun was said to be visible if its disc could be seen.

After release, the bearing to the pigeon was recorded every min. The 'vanishing bearing' is the direction in which the signal was last heard, and a pigeon was said to have vanished if no signal was heard for 3 consecutive min. The time of the pigeon's arrival at the home loft and the condition of its coils and batteries was also recorded. Since each pigeon required from 10 to 90 min to disappear from radio range, the number of birds released each day was limited. Thus each experiment required several releases, often from different release points. Data from several release points have been combined in the vanishing diagrams which follow, by plotting the vanishing bearings of the pigeons relative to home. The significance of the mean vector of the resulting distribution was determined with a Raleigh test (Batschelet, 1965), the probability of homeward orientation with the V test, and confidence intervals of the direction and length of the mean vector as described by Batschelet (1965, 1972). The Watson U^2 test (Watson, 1961, 1962; Batschelet, 1972) was used to assess differences between the distribution of vanishing directions.

RESULTS

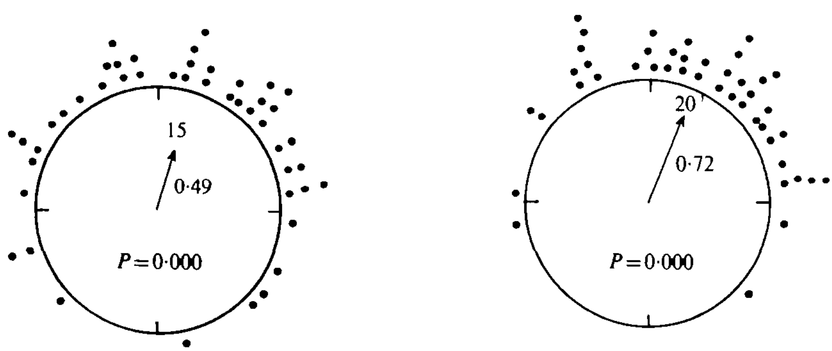
0·1 *gauss coils*

In 1970 a series of experiments was begun to see whether a very weak magnetic field would alter the initial orientation of homing pigeons. A total of 9 releases from



0·1 gauss No Current

Fig. 1. Diagram showing direction in which the radio signal was last heard from each pigeon at a distance of about 10 miles (16 km) from the release point. Each dot represents the vanishing bearing of one bird, the home direction is at the top of the diagram (360°). The arrow in the centre is the mean vector of the distribution; its length is indicated by the decimal number, and its direction in degrees is shown at the tip. *P* is the probability that the observed bearings were drawn from a random sample. These releases were carried out in 1970. The length of the mean vectors of the two distributions is significantly different ($P = 0·05$ or less).



0·1 gauss No Current

Fig. 2. A series of releases similar to that shown in Fig. 1, but made with a different group of pigeons released at different sites than in 1970. This series was done in 1971. The vector lengths are significantly different ($P = 0·02$).

locations 30 to 50 miles North and South of the loft were made. Experimental pigeons carried coils which induced a field of 0·1 Gs around the pigeon's head. No attention was paid to the direction of the field. Control birds carried identical coils and batteries but the wire was not electrically attached to the battery so no current passed through the coils.

The 10-mile vanishing bearings for all nine releases are summarized in Fig. 1. Both experimentals and controls show significant homeward orientation (V test, Expt. $P = 0·007$, Cont. $P = 0·000$) and neither the time to vanish from radio contact nor the speed of homing to the loft was significantly different for the two groups. However, the birds with current in their coils had a greater scatter in their vanishing directions than did the controls. The length of the mean vector of the distribution is a convenient measure of this scatter; the vector length for the experimentals was

Table. 1. *Orientation of birds with 0·1 Gs coils released North and South of the loft*

	Number of birds	Length unit vector	Mean vector direction (home, 360°)
	1970		
North			
With magnetic field	25	0·44	318°
No magnetic field	25	0·61	316°
Difference		0·17	2°
South			
With magnetic field	23	0·18	250°
No magnetic field	23	0·75	260°
Difference		0·57	10°
	1971		
North			
With magnetic field	26	0·57	14°
No magnetic field	27	0·76	15°
Difference		0·19	10°
South			
With magnetic field	20	0·38	19°
No magnetic field	17	0·69	28°
Difference		0·31	9°

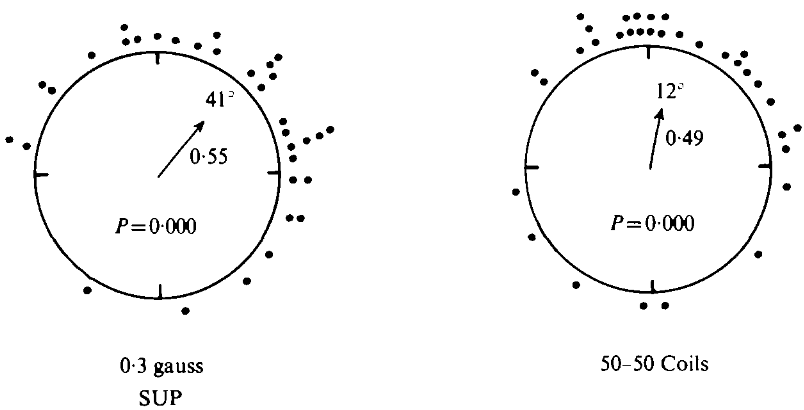


Fig. 3. Vanishing bearings of birds with 0·3 Gs SUP (South pole up) coils compared with birds carrying coils with half the turns in each coil reversed. Such 50–50 coils have no net magnetic field in the region between the two coils, but there is an irregular field near each of the individual coils due to non-uniform placement of the wires.

less than half the length of the controls, a difference significant at $P = 0{\cdot}05$ or less. Furthermore, in eight of the nine individual releases the controls showed less scatter than the experimentals. This experiment was repeated the following year, with a new group of pigeons from different locations, using the same treatments. Once again the same pattern is evident; both groups were significantly oriented towards home (V test, Expt. $P = 0{\cdot}000$, Cont. $P = 0{\cdot}000$) (Fig. 2). Vanishing times and homing performance were identical, but the experimentals' vanishing bearings were significantly more scattered than those of the controls. Of the nine individual releases (combined in Fig. 2) the controls were better orientated in six. The pooled results [of] these 2 years (a total of 18 releases of 185 birds) showed that in 14 of the 18

Table 2. *Comparison of birds released with 0·3 gauss coils and birds with 0·3 gauss coils with half the turns in one direction, half in the other*

	Number of Birds	Length unit vector	Mean vector direction (home 360°)	*P*	Time to vanish (min)	Homing speed (mile/h)
8 July 1971 Providence, R.I.						
0·3 Gs	7	0·889	78°	0·002	22·6	18·0
50–50	6	0·454	53°	0·290	17·4	3·4
10 July 1971 Monson, Mass.						
0·3 Gs	7	0·105	335°	0·925	13·5	5·5
50–50	5	0·019	222°	0·998	13·5	5·7
11 July 1971 Monson, Mass.						
0·3 Gs	3	0·270	94°	0·804	17·5	2·6
50–50	3	0·898	15°	0·079	10·6	15·7
12 July 1971 Portsmouth, N.H.						
0·3 Gs	4	0·952	20°	0·018	42·0	14·5
50–50	6	0·655	348°	0·071	29·3	5·2
13 July 1971 Hancock, N.H.						
0·3 Gs	6	0·579	329°	0·130	14·5	12·6
50–50	6	0·631	340°	0·086	24·6	9·6
15 July 1971 Hancock, N.H.						
0·3 Gs	6	0·675	30°	0·059	33·8	14·1
50–50	6	0·829	24°	0·010	18·2	15·3
North						
0·3 gauss SUPs	16	0·580	12°	0·003	18·0	10·1
50–50 Coil	18	0·588	360°	0·001	14·6	6·9
Difference		0·008	12°			
South						
0·3 gauss SUPs	16	0·614	68°	0·001	28·6	13·6
50–50 Coil	15	0·389	36°	0·1	24·0	10·0
Difference		0·225	32°			

releases the vanishing bearings of the controls were less scattered than those of the experimentals. Furthermore, dividing the results into two groups (those from release points North and South of the loft) shows that there was a greater scatter from release points South of the loft (Table 1). It is possible that this north–south difference might be related to the birds' southeasterly training direction, but if this were the case, the birds should be better oriented when released from the South, in their training direction, than when released from the North. In fact, the coils had their greatest effect in releases from the South.

The pigeons' initial orientation is thus disturbed by the experimental procedure even under sunny conditions. But whether this effect is due to the magnetic field generated by the coil or to some extraneous side effect of the current is not clear. One could imagine, for example, that it was the heating effect of the current through the coil rather than the magnetic field that caused the increase in scatter. To test this idea, three sorts of controls were used.

0·3 *gauss vs. scrambled coils*

The effect of 0·3 Gs SUP coils was compared to that of two types of 'scrambled coils', i.e. coils with little or no magnetic field. The first of these types had the sa

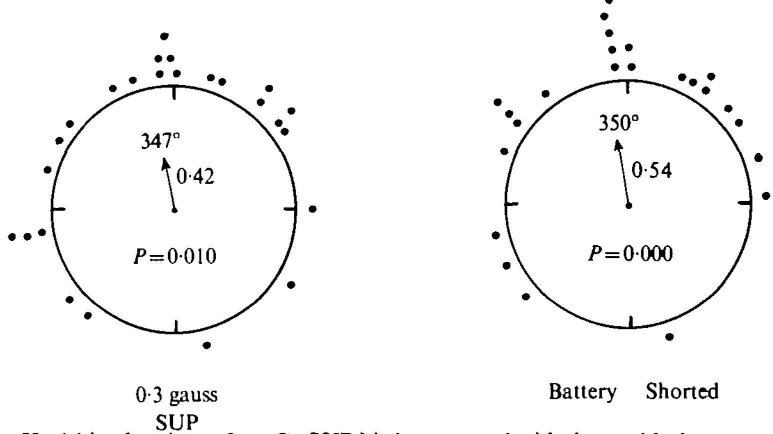


Fig. 4. Vanishing bearings of 0·3 Gs SUP birds compared with those with the same coils as in Fig. 3 but with no current flowing through the coil and a resistor across the battery. Since this resistor was located in the neck coil, the same current flowed from the battery and through the connecting wires to the coil but no current flowed through the coils themselves. The vanish directions of the 0·3 Gs SUPs are more scattered than that of the controls.

Table 3. *Orientation of birds with 0·3 gauss coils compared to that of pigeons with a resistor substituted for the coils*

	Number of birds	Length unit vector	Mean vector direction (home 360°)	P	Time to vanish (min)	Homing speed mile/h
18 July 1971 Slocum, Mass.						
0·3 Gs	6	0·835	27°	0·010	15·8	19·6
50–50 shorted	6	0·875	42°	0·006	10·8	12·2
20 July 1971 Providence, R.I.						
0·3 Gs	6	0·506	284°	0·213	37·5	7·2
50–50 shorted	6	0·800	313°	0·015	27·2	4·4
21 July 1971 Providence, R.I.	6	0·654	356°	0·071	88·2	10·8
0·3 Gs	6	0·654	356°	0·071	88·2	10·8
50–50 shorted	6	0·359	326°	0·462	19·0	9·6
22 July 1971 Providence, R. I.						
0·3 Gs	7	0·261	306°	0·620	40·3	7·5
50–50 shorted	6	0·698	351°	0·047	19·3	13·4
Summary						
0·3 Gs	25	0·420	347°	0·006	45	11
50–50 shorted	24	0·547	350°	0·000	19	13

number of turns and the same amount of current as the SUP coils but had half the turns of wire made in one direction and half made in the other. Such coils, '50–50 coils,' have no detectable magnetic field in the region between the two coils although there is a small and variable field near each of the two individual coils. This residual field is due to the opposing fields of each coil not balancing one another perfectly.

The results of six releases with these coils is shown in Fig. 3. Here the scatter of the two groups is about the same (0·55 vs. 0·49). But in five of the six releases (Table 2) the birds with 0·3 Gs SUP coils vanished on a bearing which was to the right of the birds with 50–50 coils; the sixth release was random. This difference in vanishing bearings is reflected in the 29° difference between the two mean vectors in Fig. 3. Furthermore, although neither the direction nor length of the two vectors in Fig. 3

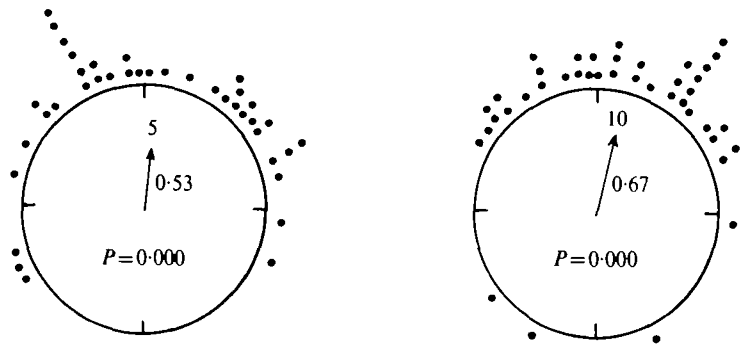


Fig. 5. A summary of vanishing directions of all the paired NUP–SUP releases with 0·3 Gs coils. The two distributions are not significantly different.

are significantly different, the birds with the 0·3 Gs coils headed in a direction which differs from home at the 98% confidence level. Finally, at release sites North of the loft, the length of the mean vector is the same for both groups (0·58 for the 0·3 Gs birds, 0·59 for the 50–50), but from the South there was a greater difference (the 0·3 Gs birds had a vector length of 0·60 whereas the 50–50's were 0·39). The angular difference was also greater in the South than in the North (32° vs. 12°). There were no significant differences in time to vanish or in homing speeds for the two groups.

Although the behaviour of the two groups of birds appears substantially similar (Fig. 3) there are differences in the results from North and South release points. Surprisingly, these differences coincide with those found for birds exposed to the 0·1 Gs field. But the vanishing bearings of the birds with 50–50 coils seem more scattered than those of birds with no current (the controls in Figs. 1 and 2). This was probably due to the small, residual field near each of the two coils.

It seemed possible that the current flowing from the battery through the wires attached to the coils might have caused the above effect rather than the field of the coils themselves. To test this possibility we made a series of four releases in which the control birds carried coils and batteries but the current flowed through a resistor and not through the coils, i.e. there was a field generated by the battery and the wires but there would be no field from the coils. The results of these releases (Fig. 4) show that the SUPs were slightly more scattered in their initial orientation. Table 3 summarizes the results of the four releases shown in Fig. 4. The SUPs did take significantly longer to vanish than the birds with no current in their coils (Mann–Whitney U test, $P = 0{\cdot}005$), but the homing speeds were not significantly different. The above results suggest that there could be an effect due to the field of the coils, but it would be hard to detect among the usual scatter of pigeon vanishing bearings. The effect becomes clearer with individual release data rather than the pooled summaries. For example, 5 of the 6 SUPs went right of the 50–50 coil birds and 3 of the 4 SUPs were to the left of the birds with shorted coils. But the effect is quite small.

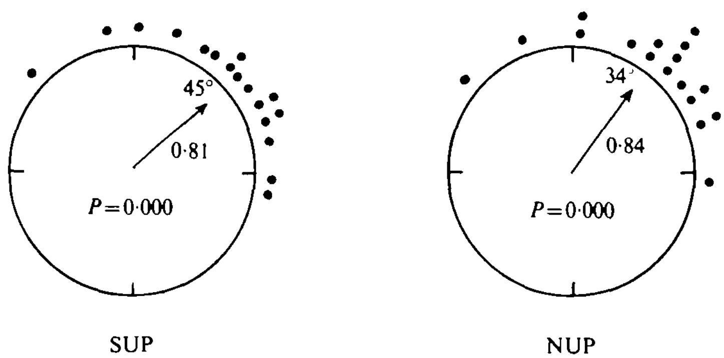


Fig. 6. The vanishing directions of the three releases of pigeons wearing 0·3 NUP and SUP coils from Carver, Massachusetts, 43 miles south of the loft. The vanishing bearings of both NUP and SUP birds are deflected to the right (east) of the home direction. But as Fig. 9 shows, birds with no coils normally vanish 40° to the right of home from Carver, so this easterly deflexion simply represents the normal release bias at Carver. The 10° difference between NUPs and SUPs not significant.

NUPs vs. SUPs

A total of 8 releases of birds with 0·3 gauss coils were made under sunny conditions. The 80 vanishing bearings are shown in Fig. 5. The vanishing directions of birds with SUP and NUP coils were similar with no significant difference in either the direction or length of the mean vectors, nor was there any difference in homing. Yet Table 4 shows that of the 8 groups of SUPs and the 8 groups of NUPs released, 14 of the 16 deviated to the East of the correct home direction. There was a diversion to the left for birds released from the North and to the right from the South (Fig. 6). The vanishing directions of birds with no coils released from Carver (Fig. 9) are almost identical. It seems likely that the eastward deviation of the initial headings is not a consequence of the applied magnetic field, but is the result of release point bias. To test whether increasing the magnetic field strength of the coils might increase the effect, a series of coils producing 0·6 Gs, a strength equal to the Earth's field, was prepared.

0·6 *Gs coils*

The overall results of releases with coils of 0·6 Gs under sunny conditions is shown in Fig. 7. Although the Watson U^2 test shows no significant differences ($P = 0{\cdot}1$) between these two distributions of vanishing directions, a χ^2 test (Batschelet, 1965) shows them to be different at the $P = 0{\cdot}01$ level. The SUPs oriented on the average to the right of the NUPs and the NUPs are a little more scattered than the SUPs. Both groups were more scattered than birds with no coils at all.

In releases from both North and South of the loft, the SUPs vanished to the right of the NUPs although in neither case is the angular difference statistically significant (Figs. 8–10). The results of the 20 individual releases with 0·6 Gs coils failed to reveal any clear pattern (Table 5). For example, in releases from the North the NUPs are slightly more scattered than the SUPs or the birds carrying coils with no current. Yet out of 9 individual releases from the North the NUPs were more scattered on occasions. Of the 5 releases from the south, the NUPs were more scattered on 2. But from the West it was 3 out of 3. Nor were the angular deviations in any way

Table 4. *A comparison of the orientation of birds carrying* 0·3 *Gs NUP and SUP coils*

	Number of birds	Length unit vector	Mean Vector direction (home 360°)	*P*	Time to vanish (min)	Homing speed (mile/h)
North						
9 Aug. 1971, Swanzee, N.H.						
NUP	5	0·261	34°	0·711	30·4	11·2
SUP	5	0·521	339°	0·255	20·2	15·2
12 Aug. 1971, Swanzee, N.H.						
NUP	6	0·878	334°	0·005	14·6	11·3
SUP	5	0·654	311°	0·112	12·8	24·7
13 Aug. 1971, Swanzee, N.H.						
NUP	5	0·589	332°	0·173	28·4	6·7
SUP	3	0·804	292°	0·137	17·0	14·6
24 Aug. 1971, Pittsfield, N.H.						
NUP	5	0·805	338°	0·001	25·8	3·2
SUP	6	0·982	6°	0·031	35·6	6·0
29 Aug. 1971, Pittsfield, N.H.						
NUP	3	0·952	331°	0·050	14·0	3·1
SUP	3	0·960	341°	0·050	21·3	7·5
North Summary						
NUP	24	0·656	348°	0·000	23·0	6·8
SUP	22	0·628	323°	0·000	22·4	14·4
South						
14 Aug. 1971, Carver, Mass.						
NUP	5	0·956	64°	0·005	21·0	19·4
SUP	5	0·851	40°	0·019	14·0	20·7
16 Aug. 1971, Carver, Mass.						
NUP	6	0·806	18°	0·014	42·3	11·8
SUP	6	0·643	31°	0·078	13·5	16·5
17 Aug. 1971, Carver, Mass.						
NUP	6	0·765	46°	0·004	30·6	13·9
SUP	6	0·904	42°	0·023	22·6	9·9
South summary						
NUP	17	0·810	34°	0·000	31·9	15·1
SUP	17	0·839	46°	0·000	16·9	15·7

consistent in the individual releases. In short, considering only the vanishing directions there was no substantial difference between the two groups.

There was a difference in the time required to vanish from radio range; birds with NUP coils were significantly slower to vanish than birds with no current in their coils or no coils at all (Mann–Whitney U test, $P = 0{\cdot}005$). The difference in vanishing times between NUPs and SUPs was not significant ($P = 0{\cdot}1$), and there was no significant difference in homing speed.

If the coils and magnetic fields had affected orientation, differences between the various groups might be clearer immediately after release than when the birds actually disappeared from radio contact at the release point. Perhaps the coils exerted an immediate disorienting effect but the birds were able to correct for it in the 10–25 min period before they vanished. To test this idea, the length of the mean vector of the distribution of bearings was plotted for each min for each of the three treatments. In

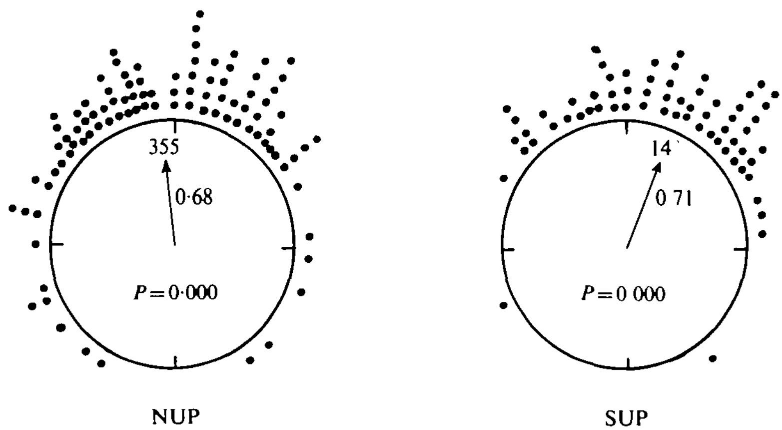


Fig. 7. The results of all the releases with 0·6 Gs coils under sun. The Watson test shows that there is no significant difference between the two distributions (P = 0·1) but a χ^2 test (Batschelet, 1965) shows that they are different at P = 0·01 – 0·02. Notice that the SUPs are 19° to the right of the NUPs.

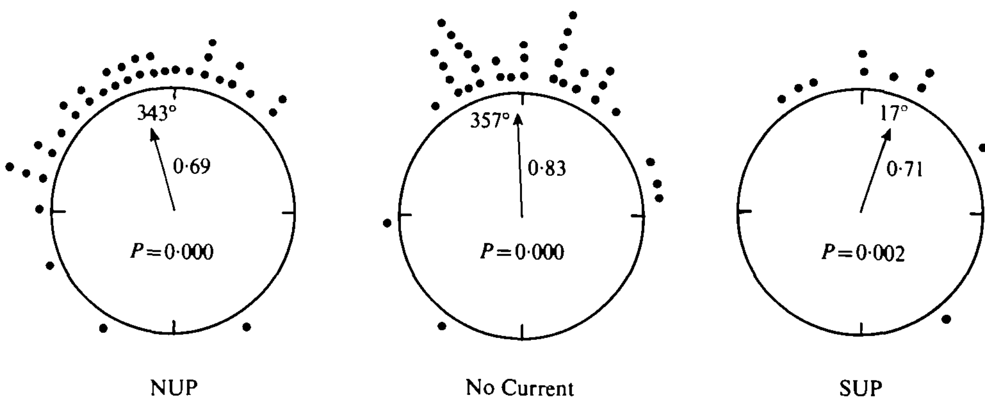


Fig. 8. A composite of all the releases from Concord, New Hampshire, 90 miles north of the loft. The vanishing bearings of birds with 0·6 Gs NUP and SUP coils is compared to that of birds with coils but no current flowing through them. Notice that the mean vector of SUPs is deflected to the right of that of the other two groups.

the birds were to leave the release point in a variety of directions (i.e. were to be very scattered at the outset), then the length of the mean vector would be very short. Yet if, with time, the orientation of the birds were to improve and more of them head in the same direction (whether or not this direction was related to the homeward direction) the length of the mean vector should increase. However, this is not the case (Fig. 11), for the length of the mean vector is not greatly different from the 1st to the 15th min. However, it is interesting that at each min the NUPs are consistently less uniform in their direction of flight than either the SUPs or the birds with no coils. The graph shows a change about 9 min after release (Fig. 11) After that point birds with no coils or no current appear to become less well oriented and the SUPs appear to improve. These changes are a consequence of the way in which the curve was measured. Each point on the graph was derived from the bearings of all the birds that were in radio contact at that time. The dip in the curve for no-current birds

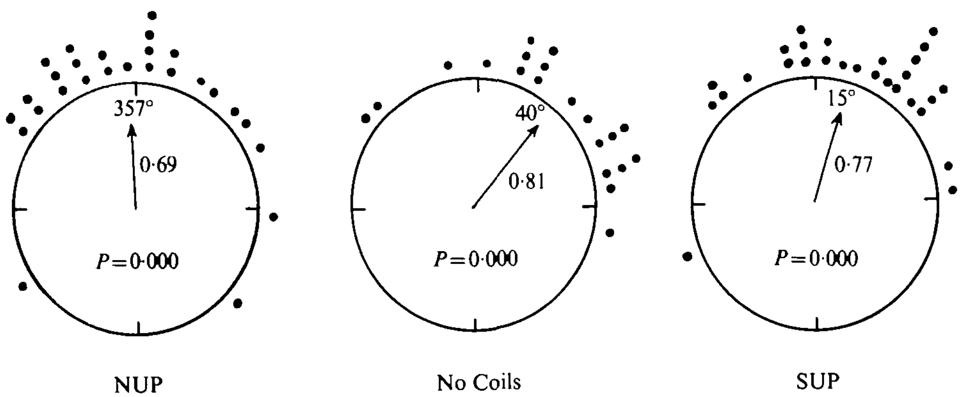


Fig. 9. A composite of all the releases from Carver, Massachusetts, 43 miles south of the loft. Notice that SUPs are less scattered than NUPs and their mean vector is right of the NUPs, but that both NUPs and SUPs are to the left of birds with no coils.

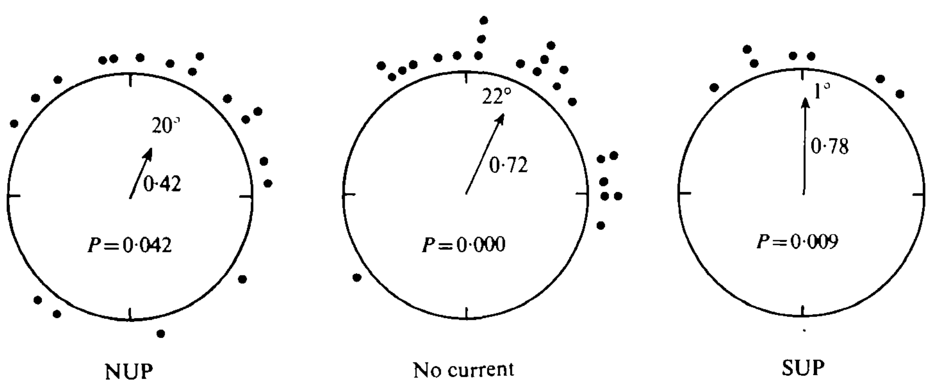


Fig. 10. All the vanishing bearings from Orange, Massachusetts, 50 miles west of the loft. The vanishing bearings of the NUPs are more scattered than those of either the SUPs or of birds with no current in their coils.

reflects the rapid departure of well oriented birds. For example: at 9 min, 20% of the birds with no field had already vanished; at 10 min, 31%; and at 13 min, 53% had disappeared. The data for all three treatments are given in Table 6. The NUPs and SUPs appear to be leaving at about comparable rates, whereas the birds without any magnetic field leave faster. Thus the drop in the length of the mean vector for these birds is a consequence of the best oriented among them leaving the release point more rapidly than either the SUPs or NUPs. The mean time to vanish averages 12 min longer for the NUPs than for either the SUPs or birds with no coils. Furthermore, the homing speed of the birds with no field is greater than either the SUPs or NUPs.

Using this same procedure we can plot the bearing of the mean vector for each group of birds as a function of the time after release. Figs. 12 and 13 show the results for a release point North and South of the loft. There is no dramatic change in bearing from min 1 to min 15 after release. But in both cases the curve for the NUP birds is separated from the SUPs and the SUPs are to the right of the NUPs. This further strengthens the information, given in the vanishing diagram, by showing that the

Table 5. *The orientation of birds carrying 0·6 Gs NUP and SUP coils*

	Number of birds	Length unit vector	Mean vector direction (home 360°)	*P*	Time to vanish (min)	Homing speed (mile/h)
North						
18 June 1972, Concord, N.H.						
NUP	4	0·600	27°	0·236	40·8	8·7
SUP	4	0·790	14°	0·073	19·5	2·3
28 June 1972, Concord, N.H.						
NUP	3	0·313	20°	0·745	52·5	2·8
SUP	3	0·930	30°	0·064	19·0	10·6
2 July 1972, Concord, N.H.						
NUP	4	0·669	328°	0·162	46·8	2·0
SUP	4	0·512	355°	0·349	22·5	2·2
4 July 1972, Concord, N.H.						
NUP	7	0·743	327°	0·016	18·9	10·4
UNC	8	0·785	335°	0·004	13·1	12·0
7 July 1972, Concord, N.H.						
NUP	5	0·934	300°	0·007	37·2	9·1
UNC	6	0·698	331°	0·047	20·4	12·7
22 July 1972, Concord, N.H.						
NUP	6	0·957	324°	0·000	34·2	12·6
UNC	5	0·973	355°	0·004	11·6	23·7
26 July 1972, Concord, N.H.						
NUP	6	0·909	360°	0·003	20·7	26·5
UNC	6	0·958	357°	0·002	24·2	21·8
27 July 1972, Hancock, N.H.						
NUP	7	0·859	19°	0·003	21·4	18·2
SUP	7	0·961	15°	0·000	34·1	26·3
28 July 1972, Hancock, N.H.						
NUP	6	0·974	16°	0·001	30·3	11·3
SUP	6	0·786	354°	0·018	27·7	15·2
North Summary						
NUP	48	0·709	348°	0·004	32·1	12·7
SUP	24	0·792	10°	0·000	26·3	13·6
UNC	25	0·830	357°	0·000	17·3	17·5
South						
5 July 1972 Carver, Mass.						
NUP	6	0·799	314°	0·016	22·3	13·1
SUP	6	0·731	8°	0·034	20·3	11·9
8 July 1972 Carver, Mass.						
NUP	7	0·629	5°	0·070	22·2	14·2
SUP	7	0·365	17°	0·003	14·4	15·0
9 July 1972 Carver Mass.						
NUP	7	0·265	22°	0·030	23·1	16·9
SUP	7	0·366	17°	0·011	18·9	11·8
10 July 1972 Carver, Mass.						
NUP	7	0·905	358°	0·001	13·4	28·0
SUP	8	0·749	358°	0·007	15·3	25·2
1 Aug. 1972 Willimantic, Ct.						
NUP	6	0·769	28°	0·022	15·3	22·3
SUP	6	0·839	30°	0·009	9·3	27·0
22 June 1973 Carver, Mass., No coils	8	0·847	39°	0·001	16·0	32·5
25 June 1973 Carver, Mass., No coils	3	0·864	332°	0·097	11·0	21·7

Table 5 (*cont.*)

	Number of birds	Length unit vector	Mean vector direction (hm 640°)	*P*	Time to vanish (min)	Homing speed (mile/h)
29 June 1973 Carver, Mass.,						
No coils	9	0·902	59°	0·000	13·3	20·7
South Summary						
NUP	33	0·687	3°	0·000	19·2	19·1
SUP	34	0·781	18°	0·000	17·1	17·2
No coils	20	0·810	40°	0·000	14·1	24·9
West						
24 July 1972 Orange, Mass.						
NUP	7	0·549	346°	0·117	18·4	17·6
SUP	7	0·780	1°	0·009	18·4	20·7
26 July 1972 Orange, Mass.,						
UNC	4	0·939	33°	0·022	15·0	14·7
29 July 1972 Orange, Mass.,						
UNC	5	0·938	4°	0·005	15·8	21·4
30 July 1972 Orange, Mass.,						
UNC	4	0·861	12°	0·042	14·0	18·0
11 Aug. 1972 Orange, Mass.						
NUP	5	0·438	85°	0·382	22·8	17·8
UNC	4	0·547	341°	0·301	9·1	18·3
16 Aug. 1972 Orange, Mass.						
NUP	6	0·560	23°	0·148	36·8	11·5
UNC	6	0·730	62°	0·035	16·3	18·8
West summary						
NUP	18	0·416	20°	0·041	25·8	15·6
SUP	7	0·780	1°	0·009	18·4	20·7
UNC	23	0·719	22°	0·000	14·3	18·4

directional choices of the two groups of birds are consistent and stable over at least the first 15 min after release.

DISCUSSION

It is difficult to evaluate the results presented here because whatever effect a weak magnetic field may have upon the pigeon's orientation under sunny conditions, the effect is quite small and tends to get lost in the natural unpredictability of the pigeons' normal homing performance. Table 7 summarizes the results of the various experiments. The weakest field used, 0·1 Gs, caused an increase in the dispersion of 10-mile vanishing bearings. It also seemed to cause the experimental birds to deviate somewhat to the left of controls. The comparison between 0·3 Gs SUP coils and the 50–50 coils is hard to interpret because of the variable, local fields produced by the unevenness of winding of the 50–50's. The 0·3 Gs SUPs and the controls with no current in their coils but normal battery current show a small difference – the 0·3 Gs birds are more scattered in their vanishing bearings and the mean vector falls to the right of the controls. In addition the SUPs took significantly longer to vanish. Comparing birds with 0·3 Gs fields which differed only in the polarity of the field, there is no difference between the two groups. The only noteworthy feature is that almost all the vanishing bearings are deflected to the east of the correct homeward bearing.

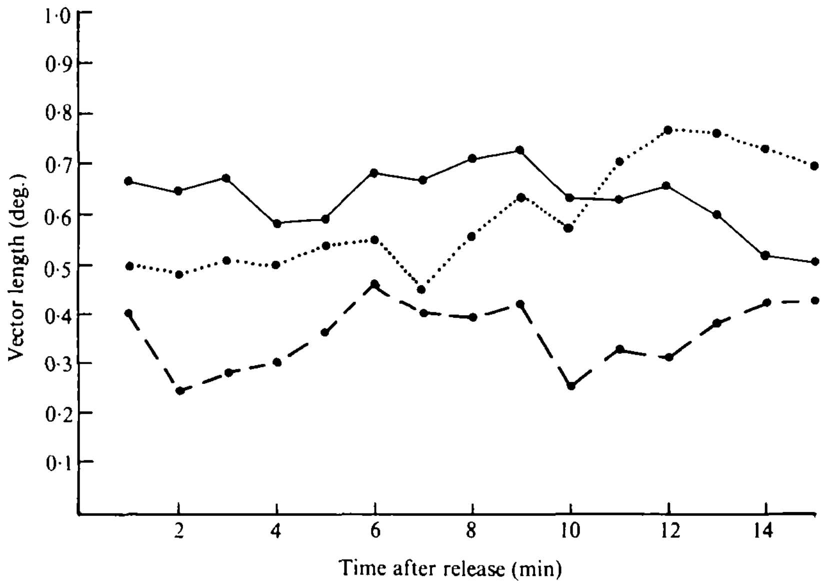


Fig. 11. The degree of scatter of each of the three groups of birds as a function of time after release. Birds with coils but no current are shown by the solid line. Birds with 0·6 Gs NUP coils are indicated by the lower dashed line and the 0·6 Gs SUPs are indicated by dots. The drop in the curve for birds with no current 10 min after release is due to the rapid departure of well-orientated birds (see Table 6).

Table 6. *The percentage of birds in radio contact as a function of time after release*

Time after release	Birds in radio range % 0·6 Gs NUPS	0·6 Gs SUPS	No coils or coils but no current
1	100	100	100
2	100	100	100
3	100	100	100
4	100	100	98
5	98	94	98
6	98	89	93
7	96	89	91
8	89	89	87
9	83	86	80
10	78	81	69
11	78	75	67
12	70	72	62
13	65	61	47
14	60	61	42
15	60	56	42
Mean time to vanish (mins)	28·4	17·9	15·8
Homing speed (mile/h)	14·8	12·9	20·9

The birds with 0·6 Gs coils showed a difference between the two groups in their vanishing bearings, with the SUP birds vanishing to the right of the NUPs. Furthermore, the NUP birds take significantly longer to vanish than birds with no magnetic field and their poorer orientation to home (indicated by greater scatter in their bearings) is consistent from the first to the 15th min after release. Similarly the mean

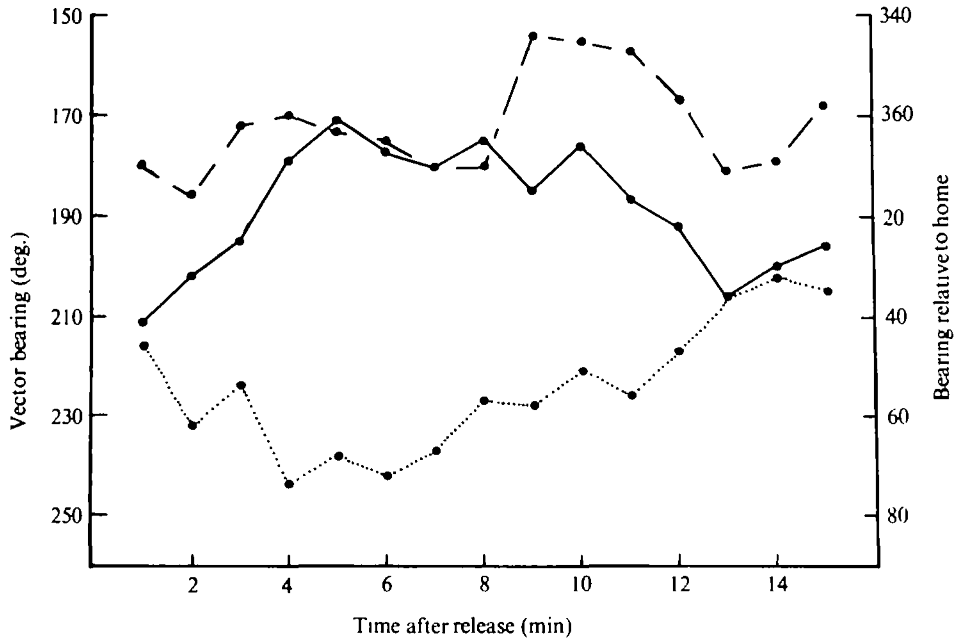


Fig. 12. The direction of the mean vector of the distribution of vanishing diagrams plotted as a function of time after release. These birds were released from Carver, Massachusetts, south of the loft. Labels are the same as in Fig. 11.

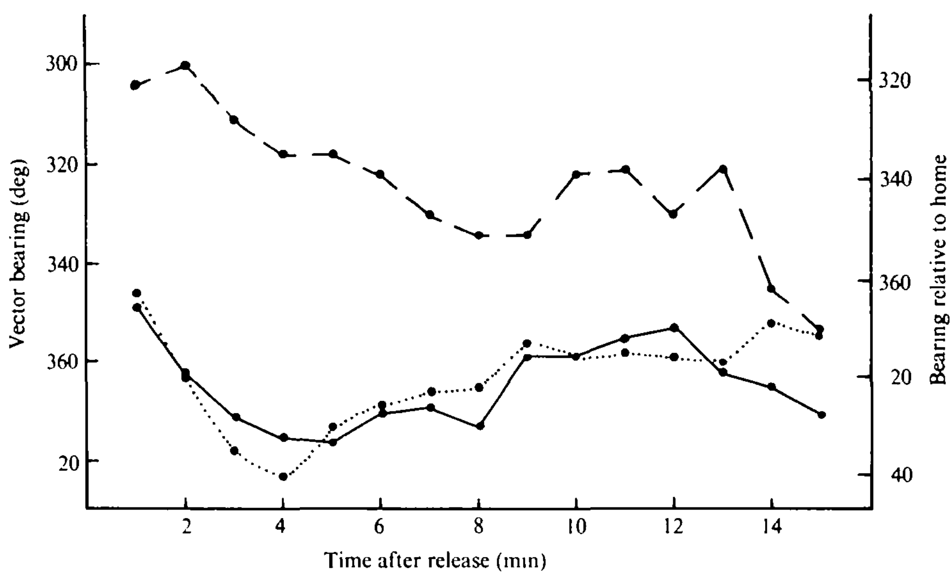


Fig. 13. The same diagram as Fig. 12 but plotted for birds released in Concord, New Hampshire, to North of the loft. From both Carver and Concord it appears that the NUPs and SUPs are clearly separated at all times after release. There is a trend, however, for the differences in bearings to decrease with time, so that at vanishing the direction of the two groups is quite similar. Notice also that in releases from the South, the curve for birds with no current through their coils is quite similar to the SUPs, whereas from the North, the no-current birds are closer to the NUPs.

Table 7. *A summary of the various results*

	Length of mean vector	Bearing of mean vector relative to home	Time to vanish	Homing speed
0·1 Gs 1970	0·1 < C*	0·1 Gs 13° left C	Same	Same
0·1 Gs 1971	0·1 < C*	0·1 Gs 5° left C	Same	Same
0·3 Gs vs. 50–50	0·3 > 50–50	0·3 Gs 29° R 50–50	Same	Same
0·3 Gs vs. battery shorted	0·3 < BS	0·3 Gs. 4° left BS	0·3 Gs longer*	Same
0·3 NUP vs. SUP	N > S	NUP 5° R SUP	Same	Same
0·6 G NUP vs. SUP	S > N	SUP 19° R NUP	No field < NUP*	Same

* Significant, P is 0·05 or less.

vector of the SUPs is consistently to the right of the NUPs over this same time period. Both SUPs and NUPs homed more slowly than birds with no coils.

To summarize these results, I believe that these relatively weak magnetic fields affect the initial orientation of pigeons even when the sun is visible. However, the effect is very small: a general increase in the scatter of 10-mile vanishing bearings and, with a field strength of 0·6 Gs, a spread of about 20° in the bearing of the mean vectors of the two groups. These results contrast with the situation when the sun is obscured. Walcott & Green (1974) observed a difference in the behaviour of the 0·6 Gs SUPs and NUPs under overcast conditions. The SUPs appeared to be well oriented to the home loft but the NUPs were divided; some went towards home but a substantial fraction flew in the opposite direction. When the sun was visible, pigeons with 0·6 Gs coils responded as they did in the releases reported here. These results agree in a general way with those of Keeton (1971). He found that bar magnets led to disorientation when the sun was not visible, but had much less effect under sunny conditions. Unfortunately, he did not record the polarity of the magnetic field induced by his magnets so a direct comparison with the coils is impossible.

Recently Keeton (1974*b*) has reported that the orientation of pigeons changes with variations in the Earth's magnetic field. He finds that with increasing 'K' values, the birds' vanishing bearings are deflected to the left. In addition, Larkin & Keeton (1976) report that bar magnets also deflect vanishing bearings in the same direction. The results of the releases of birds equipped with 0·1 gauss coils show that the birds with the added field from the coil vanished to the left of the controls. Both SUP and NUP birds (released at Carver with 0·6 Gs coils) vanished to the left of birds with no coils at all. The other releases are not as clear.

That an applied magnetic field can increase the scatter of vanishing directions but not slow down homing may seem surprising. Homing speed is extremely variable even among birds given no experimental treatment; this variability obscures differences between experimental and control groups. For example, even though birds with no coils vanished significantly faster than the 0·6 Gs SUPs or NUPs, and the homing speed was 6 mile/h faster, the difference was not significant.

It is difficult to draw definite conclusions from these experiments. An obvious possibility is that pigeons might have a dual compass system: one based on a time-compensated sun compass and the other, perhaps, on the earth's magnetic field. When the sun is visible, the sun compass is used; under thick overcast they might use the earth's magnetic field. The possibility that migratory birds use the Earth's magnetic field has been suggested by the work of Wiltschko, Emlen and their colleagues (Merkel & Wiltschko, 1965, 1966; Wiltschko, 1968, 1972; Emlen *et al.* 1976). They have demonstrated that the European Robin and the Indigo Bunting show biologically appropriate orientation in an artificial magnetic field, at least in an orientation cage. Wiltschko (1972) also found that the intensity of the magnetic field was critically important; orientation only occurred when the field strength was between 0·34 to 0·68 Gs. Furthermore, Robins were responding to the angle between the earth's magnetic field vector and the gravity vector rather than to the horizontal projection of the earth's magnetic field as a compass does. For pigeons carrying coils, the total magnetic intensity is a function of both the earth's field and that of the coils. When the pigeon is flying in one direction, these fields add; in the other they subtract. Similarly the angle of the total magnetic field vector sensed by the pigeon also varies with its direction of flight. Because of the complexity of these interactions perhaps we should not be surprised that the pigeon's behaviour is hard to predict.

The finding that applied magnetic fields have any effect under sunny conditions raises doubts about the idea that pigeons simply switch from one compass system to the other depending on sun visibility. Rather it argues that there may be some sort of interaction between the two systems, although under sunny conditions birds rely less on the magnetic than on the sun compass. The effect we see is reminiscent of that reported by Lindauer & Martin (1968) in which the 'Missweisung' of the honey bee waggle dance is greatly reduced by lowering the strength of the earth's magnetic field in the hive. The parallel is interesting because we know that the honey bee waggle-dance involves a sun compass and the translation of the food-sun angle into a food-gravity angle within the hive. Thus at least some of the same components (i.e., sun and gravity) are present in the bees' world as they are in the pigeons'. Only further experimentation on the effect of magnetic fields on the orientation of pigeons will show whether such a comparison is valid.

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