

PIGEONS AT MAGNETIC ANOMALIES: THE EFFECTS OF LOFT LOCATION

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Summary

Homing pigeons from our old lofts at Fox Ridge Farm in Lincoln, MA, were disoriented when released at places where the earth's magnetic field was irregular – so-called 'magnetic anomalies'. The orientation of pigeons raised in our lofts at Cornell in Ithaca, NY, was unaffected by anomalies. Further experiments in Lincoln showed that sibling pigeons raised and trained to lofts only 2.5 km apart behaved differently when released at a strong magnetic anomaly. Pigeons from the loft situated in a magnetic gradient of 450 nT km^{-1} were disoriented at anomalies, whereas birds raised in a loft in a magnetic gradient of 88 nT km^{-1} were well oriented. This suggests that the location of the home loft may play an important role in determining which cues pigeons use for their navigation, and that these cues are learned sometime after weaning from their parents at 4–6 weeks after hatching.

Introduction

There is a continued debate about whether homing pigeons use magnetic cues as part of their 'map' or position-finding system (Wallraff, 1983; Walcott, 1991; Gould, 1985; Presti, 1985). As Skiles (1985) and Wiltschko and Wiltschko (1988) have pointed out, the earth's magnetic field varies in both strength and direction over its surface. If pigeons could measure these tiny changes (of the order of 7 nT km^{-1}), they would, in theory, have a way of locating their position. By comparing differences in the field between the release point and the home loft they might be able to determine their position relative to home. If pigeons were using such a scheme, then any small artificial change in the magnetic field might be expected to alter their orientation. The evidence that pigeons might use magnetic map cues is largely based on this kind of indirect evidence.

Disturbances in the earth's magnetic field are of two kinds: variations of the field over time, due to diurnal fluctuations in the field or to magnetic storms, and irregularities of the field in space. Pigeons' vanishing bearings are known to be altered by changes in both of these factors, although small magnetic fields applied

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to the pigeons head seem to have very little effect under sunny conditions (Walcott, 1977; Lednor and Walcott, 1983; Visalberghi and Alleva, 1979). Yet the orientation of pigeons' vanishing bearings is frequently altered by changes in the earth's magnetic field some hours before the pigeons are released (Keeton *et al.* 1974; Wiltschko *et al.* 1986; Kowalski *et al.* 1988). In terms of geographical disturbances, large-scale maps of the earth's magnetic field make it appear that the field is uniform and varies in a predictable fashion, yet detailed measurements of the local field show considerable irregularity (Skiles, 1985; Lednor, 1982; Walcott, 1991). Some of this irregularity is due to changes in the magnetic permeability of the underlying bed rock. Large deposits of iron-containing rock, like magnetite, distort the earth's magnetic field. This distortion results in locally anomalous areas called 'magnetic anomalies'. The orientation of homing pigeons released at such places tends to be more scattered than when they are released at magnetically uniform locations (Graue, 1965; Talkington, 1967; Walcott, 1978, 1986; Kiepenheuer, 1982, 1986).

In Switzerland, where the anomalies are relatively weak (80–100 nT with a gradient of only 10–12 nT km⁻¹) and the field at the anomalies is fairly regular, pigeons tend to fly down the magnetic gradient (Frei and Wagner, 1976; Wagner, 1983; Frei, 1982). In both the United States and Germany there are much stronger and more irregular anomalies with changes of intensity of several thousand nanotesla and gradients as strong as 8000 nT km⁻¹. Pigeons released at these places are disoriented. Since in both the United States and Germany the scatter of the pigeons' vanishing bearings is correlated with the magnetic variability at the release site and since the disorientation occurs under sunny conditions when, as Kiepenheuer (1982, 1986) has shown, the vanishing bearings of pigeons can be altered in the predicted direction by clock shifting, these results further suggest that the variable magnetic field was having its effect on the pigeon's 'map' rather than its compass. The implication is that pigeons might be using some feature of the earth's magnetic field as part of their position-finding system or 'map' (Walcott, 1982; Kiepenheuer, 1982). Furthermore, pigeons seem to be disoriented at anomalies only on their first release there (Kiepenheuer, 1986), although extensive training at a series of anomalies does not improve their orientation at a test anomaly (Lednor and Walcott, 1988). All in all, the pigeons behavior at magnetic anomalies is the strongest evidence we have that pigeons use some aspect of the earth's magnetic field as part of their map.

A continuation of these experiments with pigeons bred or housed in our lofts at Cornell in Ithaca, NY, as well as other lofts near Boston, MA, has revealed that how pigeons behave at anomalies may depend on the location of the loft where they were raised. Furthermore, changes in pigeon behavior when they are released at the same anomaly over a period of years have suggested that other features at the anomaly besides magnetic ones may also be important. All these findings show that how pigeons orient at magnetic anomalies is more complicated than we had originally expected. This paper describes the experiments that led to this conclusion.

Materials and methods

Homing pigeons were bred from the stock of birds maintained as breeders in our lofts in Ithaca, NY. For stocking the lofts in Lincoln, MA, these birds were supplemented by young birds contributed by Boston, MA, pigeon fliers. Young birds were raised in the Ithaca lofts and, when they were newly weaned from their parents at about 4–6 weeks of age, they were settled in Lincoln. When they reached approximately 8 weeks of age, they were trained first by being allowed free flights around the loft and then by being released along a line to the SSE of the loft at gradually increasing distances up to 50 miles (80 km). Initially the birds were released as a group but these ‘flock tosses’ were supplemented by a few releases where each pigeon was released individually. A final flock release at 25 miles (40 km) north of the loft completed the training. None of the birds released at a test site had ever been there before. This procedure is similar to that used by Walcott (1978).

Since none of the magnetic anomalies was located in areas that permitted visual tracking each pigeon was fitted with a small radio transmitter. The signal from this beacon was followed by a directional antenna and the bearing at which the radio signal disappeared was recorded as the radio vanishing bearing. For each pigeon we recorded the vanishing direction, the time to vanish and, for some birds, the time they returned to the home loft.

The vanishing bearings have been treated with the conventional statistical methods; distributions were compared with the Watson U^2 -test (Batschelet, 1981). Except for Carthage, the magnetic anomalies we used are shown on a map in Walcott (1978) and were located from aeromagnetic maps published by the U.S. Geological Survey. The Carthage anomaly is strong, with a magnetic variability of 3000 nT over 1 km in the homeward direction. It is located in the town of Carthage, NY, at 44°N, 75.5°W, approximately 185 km at 22° from our loft in Ithaca, NY. For most anomalies the magnetic variability was confirmed by ground surveys using a proton precession magnetometer or a Develco portable, three-axis, flux-gate magnetometer.

Results

Cornell loft pigeons at the Carthage anomaly

Old, experienced pigeons raised in the lofts at Cornell were taken to a large magnetic anomaly in Carthage, NY. The position of the anomaly was determined from magnetic maps and confirmed by an extensive ground survey of total magnetic intensity. Two groups of birds were released simultaneously; one at the peak of magnetic intensity inside the anomalous region and another group at a magnetically normal release site a few miles away. Two releases were conducted in 1983; as the Watson U^2 -test revealed no significant difference in the vanishing bearings between the two releases, the bearings at each site were pooled (open circles in Fig. 1A,B). Clearly, the birds released at the center of the anomaly were better oriented towards home than the birds released from the control site. The

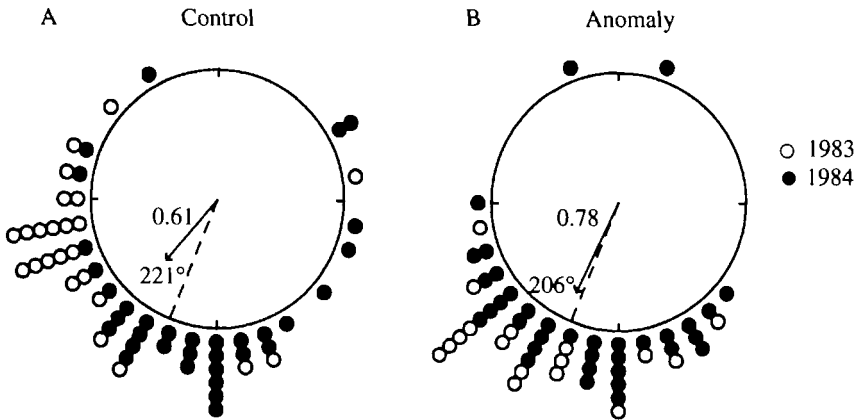


Fig. 1. Vanishing bearings of pigeons from the Cornell loft in Ithaca, NY, released at the magnetic anomaly in Carthage, NY. Each pigeon was new to the site and each vanishing bearing is indicated by an open circle (for 1983) or a solid circle (for 1984) on the periphery of the circle. The dashed line indicates the direction to home, the solid arrow is the mean vector. The length of the vector indicates the degree of clumping of the vanishing bearings; 1.0 indicates that every pigeon vanished in the same direction, a vector length of 0 indicates a random distribution. The angle of the vector is indicated near its tip. (A) Pigeons released at a control site. (B) Pigeons released at the peak of the magnetic anomaly. Although there is a statistically significant difference (Watson U^2 , $0.05 > P > 0.01$) between the two pools, birds released at the anomaly are clearly well oriented towards home.

Watson U^2 -test shows that the two distributions are significantly different ($P = < 0.005$), but it is the controls that are less well oriented towards home that accounts for this difference.

In 1984, we repeated this experiment with young pigeons that had received training from several directions within 15 miles (24 km) of the loft as well as with experienced older birds. The results were essentially identical to those of the year before; the young birds showed a somewhat greater scatter in their vanishing bearings than the older birds, but none of the groups showed any significant difference in orientation between the anomaly and the control site (filled circles, Fig. 1A,B). Although overall there is a significant difference between the vanishing bearings of birds released at the anomaly and those of the birds released outside it (Watson U^2 , $0.05 > P > 0.01$), it is clear that the pigeons released at the Carthage anomaly are well oriented towards the loft. Why there should have been a difference in the orientation of birds at the control sites between the two years is unknown.

This result is in such contrast to what we experienced with our Lincoln, MA, pigeons that we wondered why there was a difference. Three alternatives seemed possible. (1) The magnetic anomaly at Carthage was somehow different from the ones near Boston, MA, that we had been using. (2) The Cornell birds were somehow different in their genetic stock, making them unresponsive to magnetic

anomalies. (3) Growing up in Ithaca, NY, as opposed to Lincoln, MA, might make the difference.

Cornell pigeons at Massachusetts anomalies

To test the possibility that the magnetic anomaly at Carthage was somehow different from the ones we had previously used in Massachusetts, we began by releasing Cornell pigeons at the magnetic anomaly near Worcester, Rt 20, MA. This is a large magnetic anomaly at which we have released over 80 Fox Ridge Farm, Lincoln, MA, pigeons over a 5 year period (see Fig. 2B). We have an even larger pool of data for Lincoln pigeons released at Worcester airport, a magnetically normal site (Fig. 2A). Experienced Cornell pigeons trained along a line to 162 km east of Ithaca with flock releases in other directions were released at the Worcester, Rt 20, anomaly and at the magnetically normal site at Worcester airport. In the initial releases, Cornell birds were as well or better oriented at the anomaly than they were at the control site. We followed up this finding for a total of seven releases over a 2 year period; the combined pool is shown in Fig. 2C,D. Although both groups of vanishing bearings are well oriented, the birds at the anomaly show better orientation towards home! The same was true of Cornell birds released at the strong magnetic anomaly at Iron Mine Hill in Woonsocket, RI (Fig. 2E). Cornell birds released at the relatively weak magnetic anomaly at Lynnfield, MA, were also well oriented (Fig. 2F). Taken together, these results clearly demonstrate that Cornell pigeons are well oriented at Massachusetts anomalies, places where birds from our old lofts at Fox Ridge Farm were consistently disoriented. This result rules out the possibility that the orientation of Cornell birds at the Carthage anomaly was due to some kind of difference between the magnetic anomaly there and the ones around Boston.

Codman Farm pigeons at anomalies

The next two possibilities were that either the genetic strain of the birds or the location in which they were reared was important. To test this idea we re-established a loft of pigeons in Lincoln, MA. Unfortunately, our old site at Fox Ridge Farm was not available but we were able to put a small portable loft at Codman Farm only 2.5 km WNW of our old location. This loft was stocked with young birds from our lofts at Cornell as well as with young birds obtained from local Boston pigeon racers. These birds were trained in the same way that all our previous Lincoln birds had been and were then released and tracked from several different magnetic anomalies as well as from control sites.

The first question was whether there was any difference between birds from Ithaca stock hatched in our lofts at Cornell and birds raised from Boston stock. Fig. 3 shows the results of a small release of these two groups of birds at the strong magnetic anomaly at Iron Mine Hill, near Woonsocket, RI. Although the sample is small, both groups of birds were well oriented towards home and there was no difference in their vanishing bearings. Whether the pigeons came from Ithaca or Boston stock made little obvious difference to their orientation.

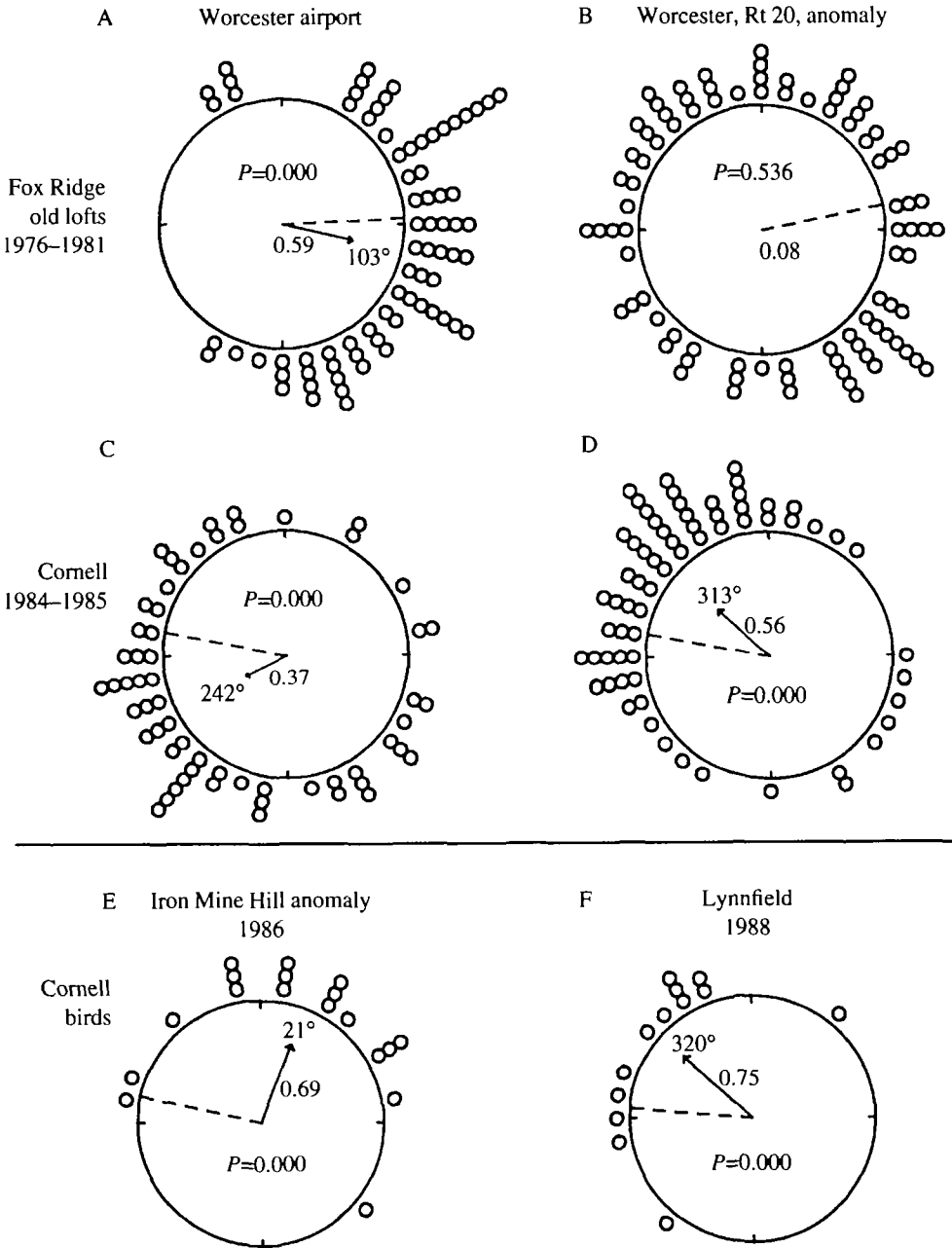


Fig. 2. Pigeons from our old lofts at Fox Ridge Farm released (A) at Worcester airport, a magnetically normal site and (B) at Worcester, Rt 20, a strong magnetic anomaly. This is a pool of data from releases in 1976–1981. Experienced, old Cornell pigeons raised and housed in lofts in Ithaca, NY, released (C) at Worcester airport, (D) at Worcester, Rt 20, (E) at Iron Mine Hill, a strong anomaly, and (F) at Lynnfield, a weak anomaly. Conventions as in Fig. 1.

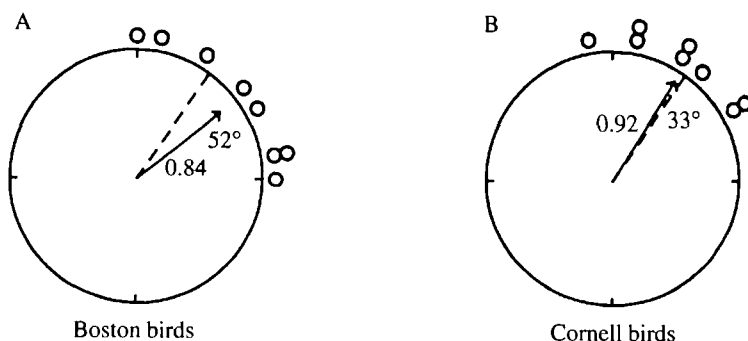


Fig. 3. The vanishing bearings of pigeons of (A) Boston stock, hatched in Boston lofts but settled and trained at Codman Farm in Lincoln, MA, and (B) pigeons of Ithaca stock hatched at Cornell but settled at Codman Farm. Both groups of birds were released simultaneously at the Iron Mine Hill magnetic anomaly. Conventions as in Fig. 1.

We pooled the vanishing bearings of birds from the two stocks, and the left-hand column of Fig. 4 shows the bearings of Codman Farm birds at both anomalous and control release sites. In every case the pigeons were well oriented towards home and there was no difference in their orientation at magnetic anomalies or at magnetically normal sites. Furthermore, pigeons raised in the Codman Farm loft from the egg were as well oriented at anomalies as young birds raised in Ithaca and moved to Codman farm soon after they had been weaned from their parents.

Fox Ridge Farm and Codman Farm compared

These results seemed to leave us at a dead end unless there was some difference between the behavior of birds raised at sites only 2.5 km apart. To test this unlikely possibility, we re-established a loft about 400 m SE of our original lofts at Fox Ridge Farm. This loft and the identical one at Codman Farm were stocked with young pigeons just weaned from their parents in our loft in Ithaca, NY. Of the two young from each nest, one was put into each loft. In this way we tried to make the genetic stock of pigeons in each loft as similar as possible. The birds from both lofts were then trained together and finally were visually tracked from a normal release site and then radio-tracked from several magnetic anomalies. The right-hand column of Fig. 4 presents the pooled vanishing bearings from these releases.

Although the vanishing bearings of both groups of pigeons were similar at the normal control site at Regis College, as well as at two of the three magnetic anomalies, at Iron Mine Hill they were dramatically different (Watson U^2 , $0.01 > P > 0.005$). At Iron Mine Hill, Codman Farm birds were well oriented towards home whereas the vanishing bearings of the Fox Ridge Farm pigeons were not significantly different from a random distribution.

Worcester, Rt 20, anomaly

One mysterious result of these experiments was that pigeons raised at both Fox

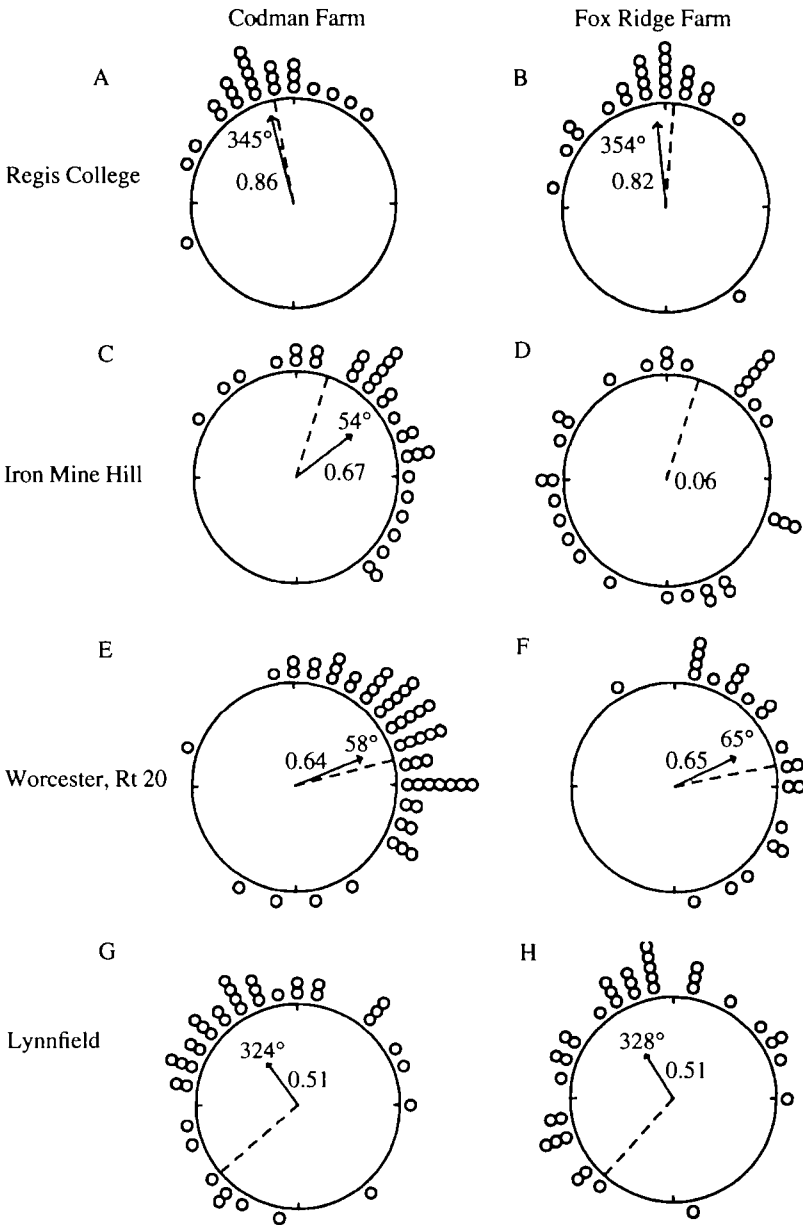


Fig. 4. The vanishing bearings of young pigeons raised in identical lofts at Codman Farm and Fox Ridge Farm both in Lincoln, MA. (A,B) Visual vanishing bearings at Regis College, a magnetically normal site. There is no significant difference between the two distributions. (C,D) Vanishing bearings at the strong magnetic anomaly at Iron Mine Hill. Watson U^2 -test shows the two distributions are different ($0.01 > P > 0.005$). (E,F) Releases at the strong anomaly at Worcester, Rt 20. There is no difference between the two distributions. (G,H) Vanishing bearings at the weak anomaly at Lynnfield; there is no difference between the two distributions. Conventions as in Fig. 1.

Ridge Farm and Codman Farm were well oriented at the magnetic anomaly at Worcester, Rt 20. This is a dramatic contrast to the behavior of our old birds from Fox Ridge Farm at that same site (Fig. 2B). There would seem to be two alternative explanations: either (1) the anomaly itself had changed in some way, or (2) pigeons raised in a loft 400 m away from the old loft location at Fox Ridge Farm were, in some way, different from birds raised in the old lofts.

Neither of these explanations seems very probable; magnetic anomalies are the result of distortion of the earth's magnetic field by subsurface minerals. It is hard to see how this could change over the years. Second, a difference in loft location of 400 m, a very much shorter distance than the pigeons range over on their practice flights, would seem highly unlikely to make a difference. Yet I would have said the same thing about the 2.5 km separation of the Codman Farm and the Fox Ridge Farm lofts; indeed, even at that distance there were a few pigeons that commuted between the two lofts!

To resolve this issue we moved the loft from Codman Farm back to the location of the old lofts at Fox Ridge Farm. In this way we had two identical lofts at Fox Ridge Farm; one on the site of the old, original lofts, one 400 m away near the road. Both lofts were stocked with breeding birds from Ithaca. One egg from each clutch of two was exchanged between the two lofts, ensuring as much genetic similarity as possible. In addition, a few young birds from both Ithaca and Boston stocks were added to both lofts to make up for early losses. As a result, the genetic stock in the two lofts was not as similar as we would have liked. As the birds grew up birds from both lofts were trained together as previously described.

Pigeons from the two lofts were then taken to Worcester, Rt 20, and radio tracked. Fig. 5 shows the result; both groups of birds were clearly and unambiguously oriented towards home. The Watson U^2 -test showed no significant difference between the two distributions. This implies that the difference we see at Worcester, Rt 20, is not the result of the loft location. Compare the pool of these results to the pool of all the previous Fox Ridge Farm, old-loft birds released at the same site (Fig. 4C,D). The Watson U^2 -test shows that these two distributions are significantly different ($P < 0.001$). The only reasonable conclusion seems to be that something about the anomaly has changed over time.

Discussion

The importance of a pigeon's behavior at magnetic anomalies is in what it tells us about the pigeon's use of the earth's magnetic field for position finding. If pigeons are able to use some aspect of the regular, geographic change in the earth's magnetic field to determine the direction to home, it follows that they might be disoriented when released at places where the field is locally distorted, at magnetic anomalies. And the finding that pigeons released at anomalies both in New England and in Germany were disoriented even under sunny skies was certainly consistent with this idea (Kiepenheuer, 1982, 1986; Walcott, 1978). It was also a consistent and repeatable effect; our experiments in Lincoln, MA, extended

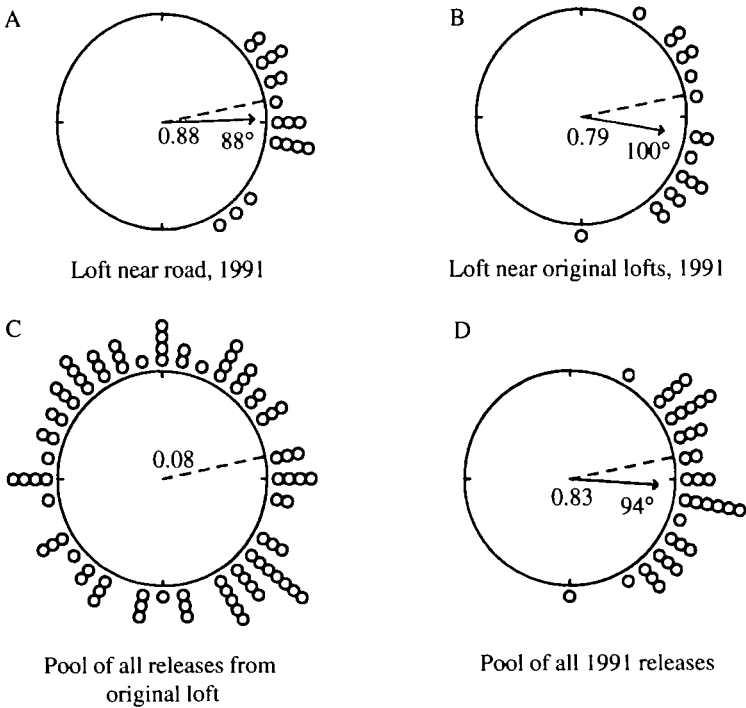


Fig. 5. (A,B) Vanishing bearings of sibling pigeons from identical lofts at Fox Ridge Farm released at the strong magnetic anomaly at Worcester, Rt 20. There is no significant difference between the two distributions. (C) A pool of 78 previous releases of Fox Ridge Farm birds in 1976–1981 at Worcester, Rt 20. Compare this pool of old data to the pool of 1991 releases (D). The difference is highly significant (Watson U^2 , $P < 0.001$). Conventions as in Fig. 1.

from 1976 to 1983 and involved hundreds of pigeon releases at six anomalous sites. The scatter of the pigeon's vanishing bearings was proportional to the degree of magnetic variability in the homeward direction (Walcott, 1980).

It was, therefore, a totally unexpected finding that pigeons raised at Cornell were well oriented at the large magnetic anomaly in Carthage, NY. Pigeons raised at Cornell were released at the same Massachusetts anomalies we had used before; they were all well oriented. This clearly demonstrates that it was not a difference in the anomaly; it must have been either the stock of the pigeons or the location of the loft.

Establishing a loft of pigeons at Codman Farm in Lincoln, MA, 2.5 km NNW of our original loft site, gave us the opportunity to distinguish between these two possibilities. Since pigeons settled in the Codman Farm loft, whatever their origin, proved to be as well oriented at magnetic anomalies as they were at normal release sites, the genetic stock of the birds was clearly not the crucial factor. This suggested that it was the location of the loft that was important. To test this idea, a new loft was placed at Fox Ridge Farm, about 400 m east of our old lofts. Sibling

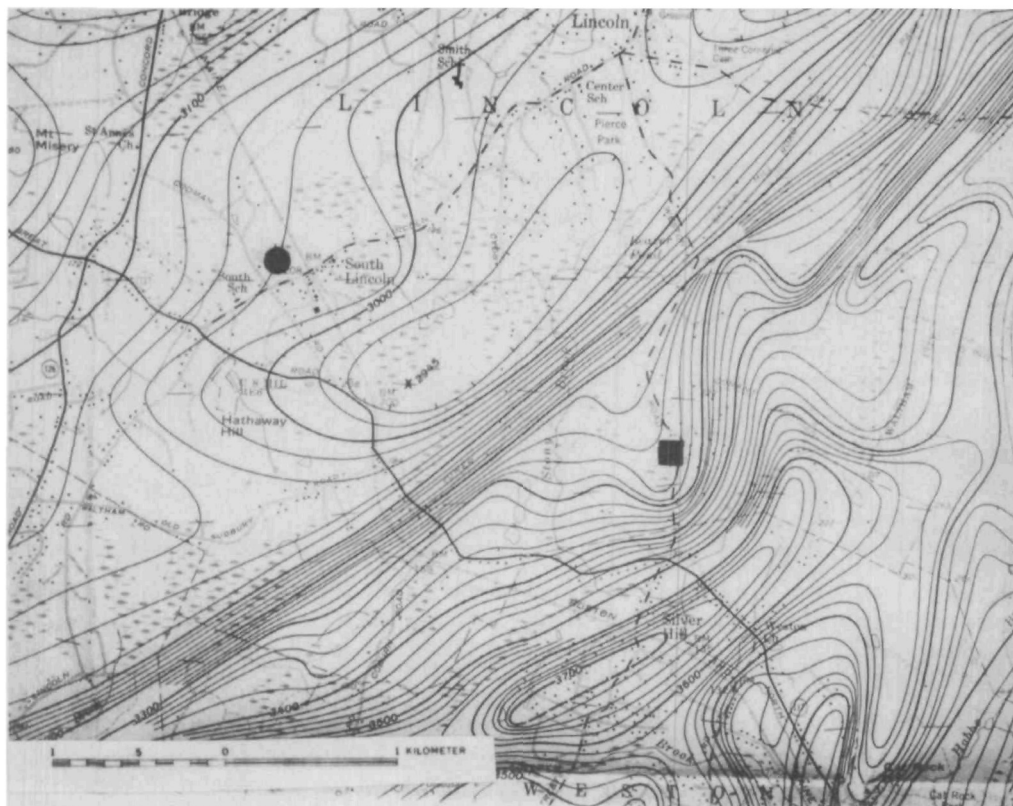


Fig. 6. A portion of the aeromagnetic map showing the location of the two lofts in Lincoln, MA, and the magnetic topography. The filled square indicates the location of Fox Ridge Farm; the filled circle, Codman Farm. The two sites are separated by 2.5 km. The lines of equal magnetic intensity show that there is a steep magnetic gradient on both sides of the Fox Ridge Farm loft, but a much weaker gradient at Codman Farm.

pigeons raised at Fox Ridge Farm and Codman Farm lofts were equally well oriented at Regis College, a magnetically normal site, but Fox Ridge Farm birds were disoriented at the magnetic anomaly at Iron Mine Hill whereas Codman Farm birds oriented towards home. Clearly, the pigeons' behavior at magnetic anomalies was a function of loft location rather than of their genetic stock.

What differs between the two lofts that could possibly account for the difference in the pigeon's behavior? The lofts themselves were identical, as was the training of the birds. Even the environment around the loft was generally similar. Yet, an examination of the magnetic map of the Lincoln area (Fig. 6) shows an intriguing difference: Codman Farm, where the birds are well oriented at anomalies, is located in a region of relative magnetic calm; the total magnetic variability as measured from the aeromagnetic map within 1 km of the loft is only 88 nT. At Fox Ridge Farm, in contrast, there is a very steep magnetic gradient; close to

450 nT km⁻¹. Magnetic measurements made at ground level reveal even greater differences. One might speculate that young birds learning to fly around the Fox Ridge Farm loft learn that the magnetic field provides useful information whereas birds growing up in the magnetic calm of Codman Farm ignore the earth's magnetic field in favor of some other orientation cue.

It is interesting that the difference in orientation at the Iron Mine Hill anomaly was not due to where the pigeons had been hatched; young birds raised in Ithaca and settled in the experimental lofts behaved no differently from birds that had been raised there from eggs. Something happened in the weeks after weaning from their parents at 4–6 weeks of age, being settled in the new loft, and their test at the magnetic anomaly. It is during this time that the young birds learn to fly and are trained to return to the loft. Presumably this is the time that the birds become familiar with their local environment. But why should there be any difference in the behavior of birds from lofts located only 2.5 km apart? After all, young birds on their ranging flights might well be expected to fly over the other loft.

It is well established that pigeon orientation depends upon some characteristic of the loft in which the birds are kept. For example, Schmidt-Koenig's cross-loft experiment (Schmidt-Koenig, 1963) clearly showed differences in the orientation of pigeons at the same site that must have been due to home loft location. The Wiltschkos found that pigeons raised on the roof of the Zoological Institute responded to being made anosmic by disorientation. Their siblings from a loft in the garden were unaffected (Wiltschko and Wiltschko, 1989). Pigeons from our loft at Cornell were disoriented when released at Jersey Hill Fire Tower, but birds from other lofts, even young birds from the Cornell loft raised in New Jersey, were well oriented at Jersey Hill (Walcott and Brown, 1989). All of these results support the notion that how pigeons orient may be altered by changes in their home loft environment.

But why might that be? One obvious suggestion is that pigeons use multiple cues and that pigeons growing up in different environments learn which cues are useful in that environment. This process may well take place during practice flights around the loft or on their first return from an artificial displacement sometime around the third month of their life as Wiltschko (1991) suggests.

Ganzhorn (1990) has shown by a multivariate analysis technique that pigeon orientation and the cues that they are using may well vary from release site to release site. He finds that at some clusters of sites the disturbance of olfactory cues seems to disturb orientation while at other clusters magnetic cues may be important. This raises the disturbing notion that not only might which sensory cues a pigeon uses be a function of the environment at the loft but of that at the release site as well!

It is also clear that the pigeon's behavior at a release site can change. In years past, Worcester, Rt 20, was a classic anomalous site causing our old Fox Ridge Farm birds to vanish in such a scattered fashion that the average vector length for the 87 pigeons we released there was only 0.08. Now, not only are Cornell loft pigeons and Codman Farm birds well oriented there but so are birds from both

lofts at Fox Ridge Farm. Something has obviously changed and one real possibility is the release site itself. When we first used Worcester, Rt 20, the site was a turnout in the road, surrounded by trees, fields and a few small buildings. Now, most of the trees are gone and the area is fast becoming an industrial park, with the field across the road replaced by a giant municipal incinerator. There has been a great change in the appearance of the site; the huge incinerator building with its high smoke stacks is certainly a striking landmark, visible for miles! It is possible that the presence of the incinerator has altered other cues as well; maybe there are changes in the available odors, maybe the huge smokestacks generate low-frequency sounds; the list of potential changes is almost endless. Still, none of these activities should have profoundly altered the anomalous magnetic field in the area. Yet the behavior of the pigeons released there is now clearly different.

Such changes are known in other areas. At Castor Hill the pronounced release site bias (Keeton, 1973) vanished for several years but now is back (I. Brown and C. Walcott, unpublished data). There are other release sites where pigeons used to show excellent homeward orientation where now, for no apparent reason, pigeons vanish in very scattered directions. Wallraff (1959, 1986) reports the same kind of temporal variability in Germany.

The important point from all of this is that the pigeon's orientation at a release site is some complex function of both the loft environment in which it was raised and some characteristic of the release site itself. At Jersey Hill, Cornell birds show no agreement on the home direction and vanish at random. Presumably they cannot interpret the map cues. At Castor Hill, birds agree on a biased home direction. At Iron Mine Hill, Fox Ridge Farm birds are lost until they get outside the anomalous area, then they orient towards and return home. The obvious interpretation of these results is that pigeons are comparing some factor remembered from the home loft with its value at the release point. In some way this comparison yields the direction towards home.

What do these results tell us about the possibility of a magnetic map? Our earlier findings that pigeons were reliably disoriented at magnetic anomalies under sunny skies and that, further, the degree of disorientation was correlated with the magnetic variability at the anomaly all hinted that these birds were using some kind of magnetic map information. Furthermore, the extensive experiments of Lednor and Walcott (1988), in which pigeons were trained at a wide variety of anomalies and then tested at another anomaly, showed that the trained pigeons fared no better at the test anomaly than did naive pigeons straight from the loft. This experiment suggested that the map was not redundant and that, in some way, magnetic cues were essential.

The current results certainly make one wonder about the generality of this conclusion. Magnetic anomalies have no effect on pigeons from either the Cornell lofts or from the Codman Farm loft. Furthermore, the effect of Worcester, Rt 20, one of the stronger anomalies in our study, has changed over the years. Finally, we should remember Lednor's (1982) caution that the magnetic field is so locally irregular that it is hard to see how it could be used as a map reference except on the

very broadest scale. This conclusion is supported by careful ground-based measurements of the field reported in Walcott (1991).

All in all, the pigeon's response to magnetic cues is both puzzling and variable. Given the behavior of birds from both Cornell and the Codman Farm lofts it is hard to believe that magnetic cues play any essential role in the pigeon's map. Yet the continued disorientation of Fox Ridge Farm pigeons at the anomaly at Iron Mine Hill shows that the basic phenomenon still exists: that is, some pigeons are still disoriented under sunny skies when released in the distorted magnetic field of a magnetic anomaly.

I thank the many people who helped with the experiments reported here. Irene Brown supervised many of them and greatly assisted with the writing of this paper. Stanley Chick trained the Fox Ridge Farm pigeons and helped with the test releases at Worcester, Rt 20, in 1991. The trustees and manager at Codman Farm kindly allowed us to set up a loft. Mr and Mrs Jerome Hunsacker graciously welcomed us back to Fox Ridge Farm. Financial support came from a National Science Foundation Grant no. BNS-85-13839, The Whitehall Foundation, The American Racing Pigeon Union and from individual pigeon fliers.

References

- BATSCHULET, E. (1981). *Circular Statistics in Biology*. New York: Academic Press.
- FREI, U. (1982). Homing pigeons' behaviour in the irregular magnetic field of western Switzerland. In *Avian Navigation* (ed. F. Papi and H. G. Wallraff), pp. 129–139. Berlin, Heidelberg, New York: Springer-Verlag.
- FREI, U. AND WAGNER, G. (1976). Die Anfangsorientierung von Brieftauben im erdmagnetisch gestorten Gebiet des Mont Jorat. *Rev. suisse. Zool.* **83**, 891–897.
- GANZHORN, J. U. (1990). Towards the map of the homing pigeon? *Anim. Behav.* **40**, 65–78.
- GOULD, J. L. (1985). Are animal maps magnetic? In *Magnetite Biomineralization and Magnetoreception in Organisms* (ed. J. L. Kirschvink, D. S. Jones and B. J. MacFadden), pp. 257–268. New York, London: Plenum Press.
- GRAUE, L. C. (1965). Initial orientation in pigeon homing related to magnetic contours. *Am. Zool.* **5**, 704.
- KEETON, W. T. (1973). Release-site bias as a possible guide to the 'map' component in pigeon homing. *J. comp. Physiol.* **86**, 1–16.
- KEETON, W. T., LARKIN, T. S. AND WINDSOR, D. M. (1974). Normal fluctuations in the earth's magnetic field influence pigeon orientation. *J. comp. Physiol.* **95**, 95–103.
- KIEPENHEUER, J. (1982). The effect of magnetic anomalies on the homing behavior of pigeons: An attempt to analyze the possible factors involved. In *Avian Navigation* (ed. F. Papi and H. G. Wallraff), pp. 120–128. Berlin, Heidelberg, New York: Springer-Verlag.
- KIEPENHEUER, J. (1986). A further analysis of the orientation behavior of homing pigeons released within a magnetic anomaly. In *Biophysical Effects of Steady Magnetic Fields* (ed. G. Maret, N. Boccaro and J. Kiepenheuer), pp. 148–153. Berlin, Heidelberg, New York, London, Paris, Tokyo: Springer-Verlag.
- KOWALSKI, U., WILTSCHKO, R. AND FULLER, E. (1988). Normal fluctuations of the geomagnetic field may affect initial orientation in pigeons. *J. comp. Physiol.* **163**, 593–600.
- LEDNOR, A. J. (1982). Magnetic navigation in pigeons: Possibilities and problems. In *Avian Navigation* (ed. F. Papi and H. G. Wallraff), pp. 109–119. Berlin, Heidelberg, New York: Springer-Verlag.
- LEDNOR, A. J. AND WALCOTT, C. (1983). Homing pigeon navigation: The effects of in-flight exposure to a varying magnetic field. *Comp. Biochem. Physiol.* **76A**, 665–671.

- LEDNOR, A. J. AND WALCOTT, C. (1988). Orientation of homing pigeons at magnetic anomalies: The effects of experience. *Behav. Ecol. Sociobiol.* **22**, 3–8.
- PRESTI, D. E. (1985). Avian navigation, geomagnetic field sensitivity and biogenic magnetite. In *Magnetite Biomineralization and Magnetoreception in Organisms* (ed. J. L. Kirschvink, D. S. Jones and B. J. MacFadden), pp. 455–482. London, New York: Plenum Press.
- SCHMIDT-KOENIG, K. (1963). On the role of the loft, the distance and site of release in pigeon homing (The 'Cross-Loft Experiment'). *Biol. Bull. mar. biol. Lab., Woods Hole* **125**, 154–164.
- SKILES, D. D. (1985). The geomagnetic field: Its nature, history and biological relevance. In *Magnetite Biomineralization and Magnetoreception in Organisms* (ed. J. L. Kirschvink, D. S. Jones and B. J. MacFadden), pp. 43–102. London, New York: Plenum Press.
- TALKINGTON, L. (1967). Bird navigation and geomagnetism. *Am. Zool.* **7**, 199.
- VISALBERGHI, E. AND ALLEVA, E. (1979). Magnetic influences on pigeon homing. *Biol. Bull. mar. biol. Lab., Woods Hole* **156**, 246–256.
- WAGNER, G. (1983). Natural geomagnetic anomalies and homing in pigeons. *Comp. Biochem. Physiol.* **76A**, 691–700.
- WALCOTT, C. (1977). Magnetic fields and the orientation of homing pigeons under sun. *J. exp. Biol.* **70**, 105–123.
- WALCOTT, C. (1978). Anomalies in the earth's magnetic field increase the scatter of pigeon's vanishing bearings. In *Animal Migration, Navigation, and Homing* (ed. K. Schmidt-Koenig and W. T. Keeton), pp. 143–151. Berlin, Heidelberg, New York: Springer-Verlag.
- WALCOTT, C. (1980). Effects of magnetic fields on pigeon orientation. In *Actis XVII Congressus Internationalis Ornithologici* (ed. R. Nohring), pp. 588–592. Berlin: Deutsche Ornithologen-Gesellschaft.
- WALCOTT, C. (1982). Is there evidence for a magnetic map in homing pigeons. In *Avian Navigation* (ed. F. Papi and H. G. Wallraff), pp. 99–108. Berlin, Heidelberg, New York: Springer-Verlag.
- WALCOTT, C. (1986). A review of magnetic effects on homing pigeon orientation. In *Biophysical Effects of Steady Magnetic Fields* (ed. G. Maret, N. Boccara and J. Kiepenheuer), pp. 146–147. Berlin, Heidelberg, New York, London, Paris, Tokyo: Springer-Verlag.
- WALCOTT, C. (1991). Magnetic maps in pigeons. In *Orientation in Birds* (ed. P. Berthold), pp. 38–51. Basel, Boston, Berlin: Birkhauser.
- WALCOTT, C. AND BROWN, A. I. (1989). The disorientation of pigeons at Jersey Hill. In *Orientation and Navigation: Birds, Humans and Other Animals*. Cardiff, England: Royal Institute of Navigation.
- WALLRAFF, H. G. (1959). Ortlich und zeitlich bedingte Variabilität des Heimkehrverhaltens von Brieftauben. *Z. Tierpsychol.* **16**, 513–544.
- WALLRAFF, H. G. (1983). Relevance of atmospheric odors and geomagnetic field to pigeon navigation: What is the 'map' basis? *Comp. Biochem. Physiol.* **76**, 643–663.
- WALLRAFF, H. G. (1986). Directional components derived from initial-orientation data of inexperienced homing pigeons. *J. comp. Physiol. A* **159**, 143–159.
- WILTSCHKO, R. (1991). The role of experience in avian navigation and homing. In *Orientation in Birds* (ed. P. Berthold), pp. 250–269. Basel, Boston, Berlin: Birkhauser.
- WILTSCHKO, R. AND WILTSCHKO, W. (1989). Pigeon homing: Olfactory orientation – a paradox. *Behav. Ecol. Sociobiol.* **24**, 163–173.
- WILTSCHKO, W., NOHR, D., FULLER, E. AND WILTSCHKO, R. (1986). Pigeon homing: The use of magnetic information in position finding. In *Biophysical Effects of Steady Magnetic Fields* (ed. N. Boccara, G. Maret and J. Kiepenheuer), pp. 154–162. Berlin, Heidelberg, New York, London, Paris, Tokyo: Springer-Verlag.
- WILTSCHKO, W. AND WILTSCHKO, R. (1988). Magnetic orientation in birds. In *Current Ornithology*, vol. 5 (ed. R. F. Johnston), pp. 67–121. New York, London: Plenum Press.