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THE ORIENTATION OF PIGEONS AT GRAVITY ANOMALIES

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The means by which homing pigeons determine the direction to their home loft when released in unfamiliar territory remains a mystery. Hypotheses involving the sun (Matthews, 1953, 1955), Coriolis force and the earth's magnetic field (Yeagley, 1947, 1951), inertial cues (Barlow, 1964, 1966), infrasound (Kreithen & Quine, 1979), have been advanced but currently there is no strong empirical support for any of these hypotheses. Recently Papi (see Papi, 1976; Papi *et al.* 1980 for reviews) and Wallraff (1980) have proposed that olfactory cues are the basis of the pigeons' position-finding ability but not all investigators are convinced by the evidence (see e.g. Able, 1980; Keeton, 1980; Schmidt-Koenig, 1979; Walcott & Lednor, 1983).

One cue from which pigeons could, in principle, derive position-finding information is gravity. Due to the spheroidal shape of the earth and the centrifugal forces associated with its rotation there exists a regular gradient (of 0·73 mgal km^{-1} at 32 °N) in the force of gravity between the geographic equator and the poles (Dobrin, 1976). If birds were sensitive to such minute changes in gravity, and were able to compensate for the variation in gravity with altitude, they could determine their latitude. Alternatively, as suggested by Keeton (1980), birds might use the direction of the gradient of gravity as a true north-south reference which would enable them to measure magnetic declination.

To test the possible role of gravity in pigeon navigation Larkin & Keeton (1978) repeatedly released the same group of birds at a particular release site. They found a correlation between the birds' mean vanishing bearings and the day of the lunar synodic month, that is, the birds' bearings were deflected as a function of the lunar cycle. Although the authors could not directly show that tidal variations in gravity (at peak approx. 0·3 mgal) were responsible, the results suggest this possibility.

A second hint that gravity might be involved comes from studies of the effect of magnetic anomalies on pigeon orientation. Following up reports by Graue (1965), Talkington (1967) and Wagner (1976), Walcott (1978) and Kiepenheuer (1982) have shown that experienced pigeons released under sunny conditions are disoriented when released at localized magnetic anomalies, locations where the earth's magnetic field is distorted by underground deposits of a magnetic mineral. By releasing birds at a series of different magnetic anomalies, Walcott (1978, 1980) showed that the degree of scatter of the pigeons' bearings correlated well with an index of the magnetic

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irregularity at each anomaly. This result suggests that the disturbance of magnetic cues is the cause of the birds' disorientation, but another possibility exists. The magnetic anomalies studied by Walcott are produced, at least in the cases for which we have accurate geological data, by large subsurface bodies of magnetite. This ore, besides being magnetic, is also more dense ($5{\cdot}2\,g\,cm^{-3}$) than average crustal rock ($2{\cdot}7\,g\,cm^{-3}$) (Parasnis, 1973). Due to this density contrast, positive gravity anomalies are normally associated with deposits of magnetite. It might be that the disturbed gravity field plays a role in disorienting pigeons at these anomalies.

To clarify this problem and to test further the possible role of gravity cues in pigeon orientation, we released pigeons at gravity anomalies occurring over salt domes in Texas, U.S.A. Since salt is normally less dense than the surrounding rock it gives rise to a negative gravity anomaly or gravity minimum (Dobrin, 1976) but, as it is not magnetic, no magnetic anomaly is produced. Experiments were conducted at six salt domes in east Texas. The amplitudes of the anomalies ranged from −2 to −10 mgal and their approximate diameters from 7·9 to 12·2 km. Aeromagnetic maps (flown at about 120 m above mean terrain) showed no magnetic disturbance over the salt domes and this was confirmed by ground level surveys. Using a proton precession magnetometer (Geometrics model G-816) the total intensity of the earth's field was measured at about ten stations in and around each anomaly. While measurements at a number of locations within the magnetic anomalies studied by Walcott (1978) often yielded differences of over 1000 nT, the magnetic variability found at the salt domes was much smaller, of the order of 40 nT.

The pigeons used in these tests were all young birds raised and trained by local pigeon flyers. All birds had been trained along a line and some, in addition, had been given off-line training flights. Tests were conducted by synchronously releasing pigeons at a site near the centre of each anomaly and at a site just outside the anomaly. Each bird was fitted with a small radio transmitter (Cochran, 1967), released singly,

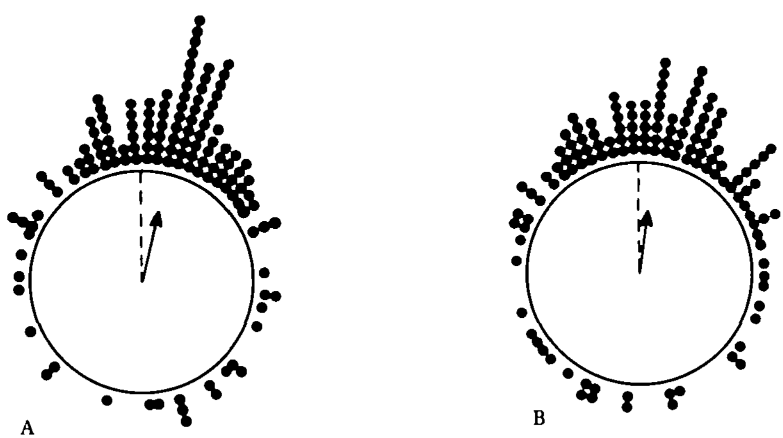

Fig. 1. Pooled results of all releases outside the gravity anomalies (A), and inside (B). Each point plotted on the circle represents the bearing of a single pigeon. All bearings have been referenced to home direction as 360°. The arrow at the centre of the circle represents the mean vector. Each distribution of bearings is non-random under the Rayleigh test: A; $N = 132$, $r = 0{\cdot}657$, $a = 13{\cdot}4°$, $P < 0{\cdot}0001$. B; $N = 127$, vector length (r) = $0{\cdot}566$, mean angle (a) = $8{\cdot}4°$, $P < 0{\cdot}0001$.

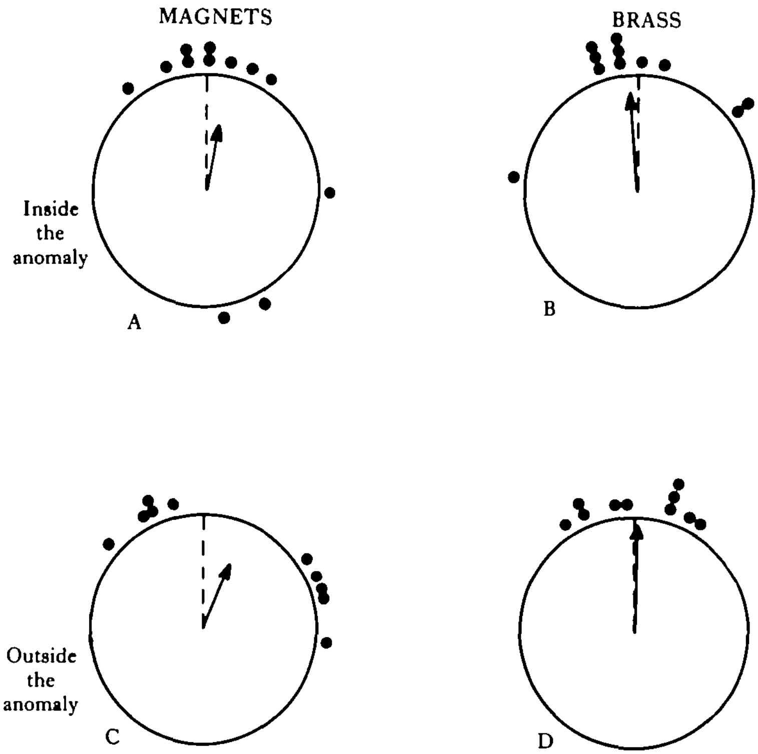

Fig. 2. Bearings of birds released inside the gravity anomaly wearing magnets (A) or brasses (B), or outside the anomaly with magnets (C) or brasses (D). Symbols and conventions as in Fig. 1. All distributions are different from random under the Rayleigh test. A; $N = 12$, $r = 0{\cdot}563$, $a = 12{\cdot}6°$, $P = 0{\cdot}019$. B; $N = 11$, $r = 0{\cdot}834$, $a = 355{\cdot}8°$, $P < 0{\cdot}0001$. C; $N = 10$, $r = 0{\cdot}622$, $a = 22{\cdot}3°$, $P = 0{\cdot}017$. D; $N = 10$, $r = 0{\cdot}928$, $a = 1{\cdot}1°$, $P < 0{\cdot}0001$.

and tracked with a directional antenna for 30 min, or until it vanished. All releases were conducted under sunny skies at test sites unfamiliar to the birds.

The pooled results of these tests are shown in Fig. 1A,B. There is no difference in the distribution of bearings of birds released inside and outside the anomalies ($P > 0{\cdot}1$ Watson U^2 test). The mean vanishing interval of birds leaving in less than 30 min is slightly longer (15·5 min, $N = 104$) for birds released inside the anomalies than those released outside (13·0 min, $N = 107$) ($P < 0{\cdot}005$, Mann-Whitney U test). Twenty-three birds were still in radio range at 30 min inside the anomalies compared to 25 birds released outside. Two additional tests were conducted with birds carrying either small cylindrical magnets (0·64 cm×0·25 cm in cobalt-samarium, pole strength 0·75 T) or brass pieces of equal weight and similar size. The magnets or brasses were mounted at the base of the pigeons' necks immediately prior to release. No difference was found in the distribution of bearings of the birds wearing magnets or brass pieces and released inside the anomaly (Fig. 2A,B). At the control site outside the anomaly, birds carrying magnets were significantly more scattered ($P < 0{\cdot}05$ Watson U^2 test) than those carrying brasses, a result that contrasts with the slight effects of applied magnetic fields under sunny skies reported by Keeton (1971) and Walcott (1977).

There was no difference in the vanishing intervals of the two treatments either ins[illegible] or outside the anomaly.

The results presented in Fig. 1 show clearly that the initial orientation of young but experienced pigeons was not affected by the gravity anomalies. It appears, then, that gravity cues do not form an essential part of the pigeon's position-finding system. Had the birds been using gravity cues to determine their latitude, or as a directional reference, an effect on the scatter or mean direction of their bearings would have been expected. A second conclusion relates to the effects of magnetic anomalies. The results presented in Fig. 1 suggest that disturbance of the gravity field probably does not account for the disorientation observed at magnetic anomalies. Further, since birds wearing magnets were as well oriented as controls when released inside the gravity anomaly, it seems to rule out the idea that the combination of disturbed magnetic and gravity fields are responsible for the scattered orientation of the birds tested by Walcott (1978) and Kiepenheuer (1982).

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