

Overcast tests with clock-shifted pigeons

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Abstract. In order to investigate the pigeon's compass mechanism, a series of overcast tests with clock-shifted birds were run at two familiar release sites. While controls were able to assume a correct homeward direction, the experimental birds' initial orientation cannot be explained either on the basis of a time-compensated sun compass or of a time-independent magnetic compass. Speculative explanations of our paradoxical results are attempted.

Key words. Clock-shift; homing; compass; pigeon.

Having established their geographical position with respect to the goal, homing pigeons are assumed to rely on a time-compensated sun compass to find and maintain a correct homeward route, whereas a time-independent magnetic compass is supposedly used in overcast conditions. Evidence for the existence of a magnetic compass in pigeons is based on a set of empirical data which shows that magnetic disturbance during the homing flight in overcast conditions impairs the birds' orientational ability¹⁻³. In two studies, it was also possible to induce predictably wrong orientation by providing flying pigeons with altered magnetic information^{4,5}. The use of a magnetic compass was also inferred from the results of more complex studies which involved experimental manipulations at the pigeon loft⁶.

It is, however, worth noting that the results of some investigations do not fit with the general picture on which acceptance of the magnetic compass is based^{7,8}, or suggest re-interpretations of previous data^{9,10}. In an attempt to clarify these discrepancies, we ran a series of overcast release tests with clock-shifted pigeons. This experimental design, pioneered by Keeton¹¹, should allow us to verify whether birds actually use a time-independent magnetic compass, or whether they are able to detect the sun's disk through the clouds. In the former case they should assume a correct homeward initial orientation, whereas if clouds are not an impenetrable barrier to sun cues a predictably wrong mean bearing is to be expected.

Materials and methods

The birds used in our experiments, hatched in 1992, were housed in a loft in Arnino (Pisa, Italy). Their pre-test experience mainly consisted of spontaneous

flights and a series (10) of training tosses at two sites 11 and 18 km from home (Livorno and La Costanza, home direction 340° and 190°, respectively). Most of these tosses were carried out in overcast conditions. This procedure was aimed at allowing the birds to develop familiarity with the future test sites and adverse meteorological conditions. Test releases were run in the winter and spring of 1993 and 1994 at the two training sites under overcast skies (the cloud cover was always thick enough to prevent the operators from localising the position of the sun). Two test releases were carried out in sunny conditions, in order to verify the effectiveness of our clock-shifting procedures. In tests, pigeons were randomly allotted to three different groups, which were used in such way that each bird – in each year – was tested not more than once at either familiar site. In each test, there were two groups: controls and 6 h fast clock-shifted experimentals, both kept in artificial light. The birds were released singly, alternating the two treatments, during the morning, shortly before the subjective sunset time of clock-shifted pigeons.

Each set of vanishing bearings (one for controls and one for experimentals in each test) was subjected to vector analysis. Bearing distributions produced in single tests and pooled results were tested for randomness by the Rayleigh test (first order analysis). The Watson U² test was used to test for differences between the bearing distributions of controls and experimentals. The Hotelling test was used for a second order analysis¹². The Mann-Whitney U test was used to test for differences in vanishing time and homing performance¹³.

Results

The results of our tests under overcast conditions are summarised in figure 1 and table 1. They show that clock-shifted experimental birds exhibited worse initial

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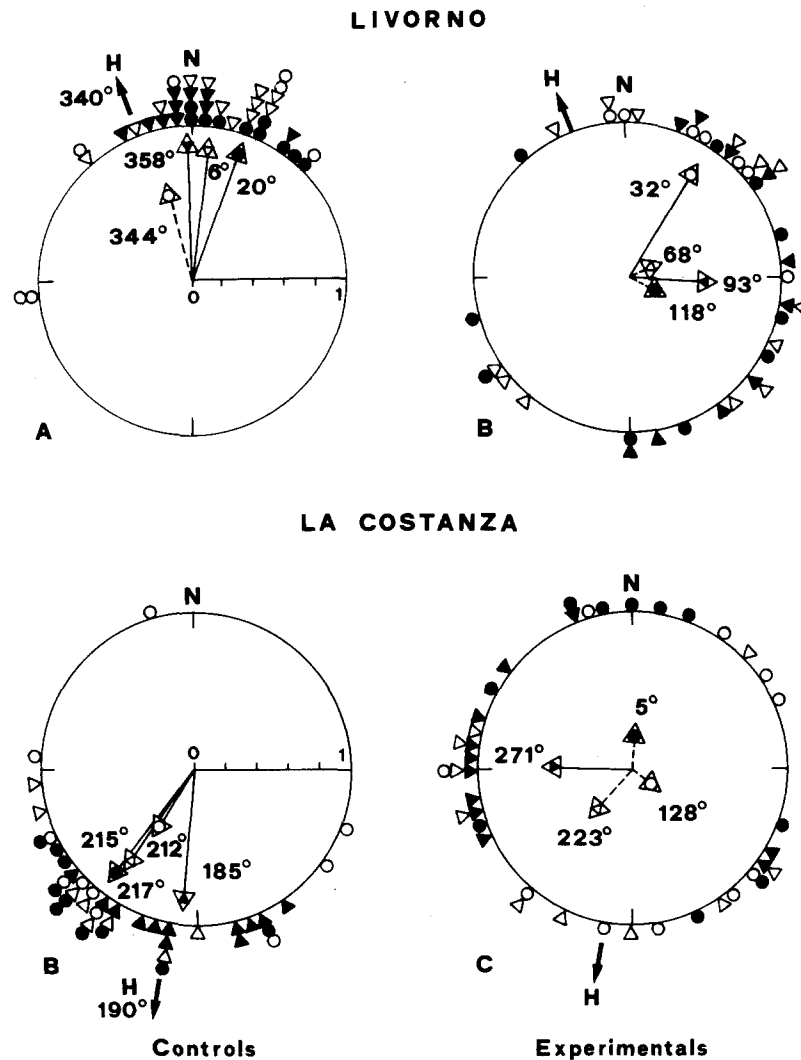


Figure 1. Orientation performance in overcast tests at the two familiar release sites (Livorno and La Costanza). Each symbol on the periphery of the circles represents the vanishing bearing of a single bird. Four different symbols refer to four different tests. Each inner arrow represents the mean vector of a bearing distribution recorded in a single test (symbols within arrowheads agree with those used for the related bearing distributions). The lengths of the vectors can be read on the scale in the left-hand diagrams (dashed arrows indicate that the related bearing distribution is not different from random according to the Rayleigh test). External arrows indicate the home direction (H). Diagrams A and C refer to control birds, B and D to 6 h clock-shifted pigeons. Other explanations in text.

orientation, with respect to homeward oriented controls, in all but one of the eight experiments (this result is different from random: binomial test, $p < 0.035$), as indicated by shorter length of their mean vectors and smaller values of homeward component. This difference between controls and clock-shifted experimentals is significant, according to the U^2 test, in 4 out of 8 cases. The difference between treatments, however, is not in agreement with what was expected as a result of the clock-shift treatment which the experimentals had been subjected to. In overcast tests, experimental birds did not in fact exhibit the expected counterclockwise deviation of their initial bearings. Deviations of mean bearings with respect to controls were actually clockwise in 6 out of 8 cases (table 1). Experimental birds showed a large scatter of their

vanishing bearings, which were not different from random in 5 out of 8 tests. The second order statistics show quite a clear picture: while controls turn out to be globally oriented, the experimentals' mean vector distribution does not significantly differ from random (Hotelling test: $p < 0.001$ and $p > 0.1$, respectively). Conversely, quite a different picture emerges from the two tests run in sunny conditions (fig. 2). In one of these two tests the deviation of the experimental birds' initial bearing was much larger than expected (fig. 2B). This was probably due to the fact that the birds released at the eastern periphery of Livorno tended to fly around the city. The expected westward direction would in fact have led them across the city, an environment that our birds – housed in the open countryside – tend to avoid (our unpublished data).

Table 1. Results of clock-shift experiments.

Home dir.	Home dist. Km	Date	Treat.	n (N)	r	α	Δh	Δc	hc	U ²	Homing success
340° Livorno	10.6	6.4.93	Co	10 (11)	0.96***	020°	+40°		0.83	**	10-1-0
			So	10 (10)	0.24	118°	+138°	+98°	-0.15		8-2-0
		27.2.94	Co	7 (9)	0.62	344°	+4°		0.61	-	8-1-0
			So	7 (14)	0.86**	032°	+52°	-48°	0.64		13-1-0
		1.4.94	Co	10 (10)	0.96***	358°	+18°		0.96	***	10-0-0
			So	10 (10)	0.56*	093°	+113°	+95°	-0.13		9-0-1
		19.4.94	Co	12 (13)	0.94***	006°	+26°		0.85	**	not rec.
			So	12 (12)	0.33	068°	+88°	+62°	0.01		not rec.
		12.4.95	Cs	12 (12)	0.96***	345°	+5°		0.96	***	11-1-0
			Ss	12 (12)	0.90***	173°	-167°	-172°	-0.87		10-2-0
190° La Costanza	18.0	18.3.93	Co	10 (12)	0.91***	217°	+27°		0.80	***	11-0-1
			So	10 (11)	0.30	005°	+175°	+148°	-0.30		11-0-0
		10.4.93	Co	10 (12)	0.49*	212°	+22°		0.45	-	10-0-2
			So	10 (10)	0.23	128°	-62°	-84°	0.11		7-1-2
		25.1.94	Co	12 (13)	0.90***	185°	-5°		0.89	***	12-1-0
			So	12 (13)	0.59*	271°	+81°	+86°	0.09		11-2-0
		24.2.94	Co	9 (11)	0.87**	214°	+24°		0.79	-	9-2-0
			So	10 (11)	0.43	223°	+33°	+9°	0.36		10-1-0
		15.3.93	Cs	10 (10)	0.98***	205°	+15°		0.95	***	10-0-0
			Ss	11 (11)	0.77**	112°	-78°	-93°	0.16		11-0-0

Co and So = controls and 6 h clock-shifted experimentals released in overcast conditions; Cs and Ss = controls and 6 h clock-shifted experimentals released in sunny conditions.

n (N) indicate the number of bearings recorded in a single test, and that of birds actually released.

r and α = mean vector length and direction, respectively.

Δh and Δc = deviation of the mean vector from the home direction, and deviation between controls' and experimentals' mean vectors, respectively.

hc = homeward component.

Levels of statistical significance of the Rayleigh test (r column) and Watson U² test (U² column) are given as asterisks: *p < 0.05, **p < 0.01, ***p < 0.001. As regards the homing success, the three figures refer to the number of birds that homed the same day as release, of birds that homed later and of birds lost, respectively.

While the experimental treatment clearly affected the birds' initial orientation, it had no consistent effect on vanishing times and homing performance (table 1). As regards the vanishing times, controls were significantly faster than experimentals only in one out of 8 overcast releases (La Costanza, 18.3.93: Mann-Whitney U test, $p < 0.025$). A significant difference between treatments in homing performance was recorded only in one case (Livorno, 1.4.94; $p < 0.05$) in which controls homed faster than experimentals.

Discussion

On the basis of Kramer's classical map and compass concept, the navigational performance of birds can be impaired by altering either the map or the compass system. From a long series of experiments, run mainly in Italy and Germany, it turns out that the pigeon's map of unfamiliar areas is based on olfactory cues^{14,15}. In familiar areas, olfactory cues appear to be unimportant¹⁶, whilst visual landmarks are involved¹⁷. In the release tests reported here, which were carried out from

familiar sites, we made no manipulations of either olfactory cues or visual landmark information, so it is unlikely that the map component was altered. The aim of our experiments was to alter only the compass component of navigation.

As regards the compass system of pigeons, the proposed existence of a magnetic compass is based on the fact that the birds are actually able to orient homeward under overcast skies, whereas they lose this ability if they are exposed to magnetic disturbance during the homing flight^{1,2,4,5}, or are subjected to appropriate experimental treatment at the loft⁶.

However, this convincing picture is dimmed by the following facts: 1) homing performances of magnet-carrying pigeons are globally not significantly different from those of brass-equipped controls, leading to the conclusions that magnets exert a transitory effect, and that the observed impairment is easily overcome soon after vanishing^{2,8}; 2) an analysis of the late Keeton's data carried out by Moore⁸, and unpublished data reported in the same paper, revealed that the expected effect of magnetic disturbance failed to manifest itself in

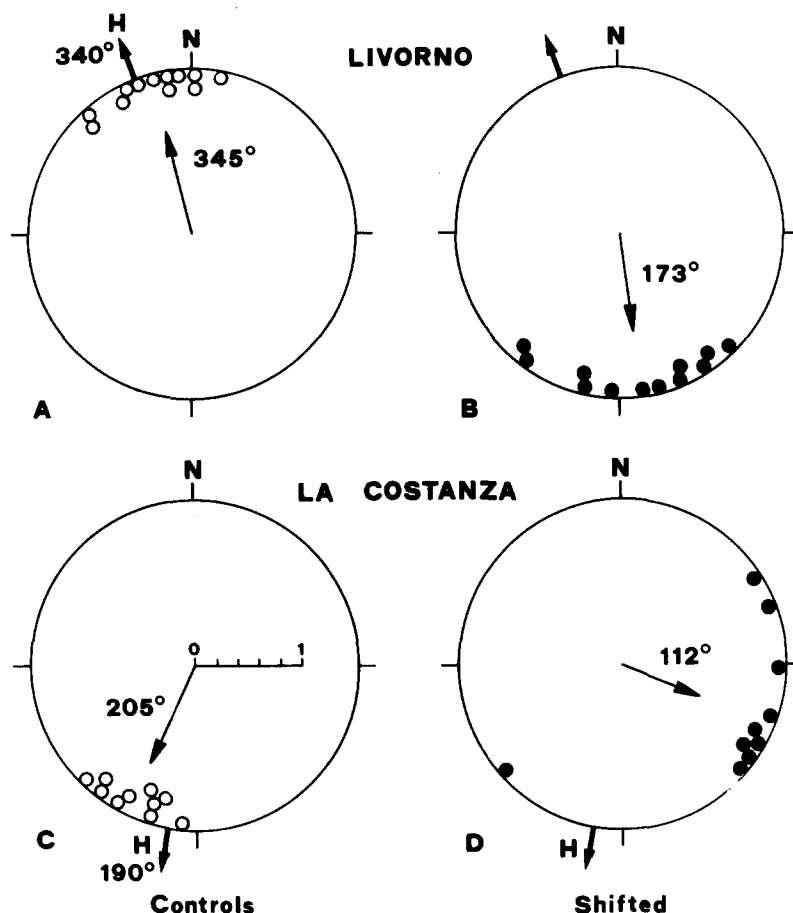


Figure 2. Orientation performance in sunny conditions at the two familiar sites. In each couple of diagrams (A-B and C-D) the result of a single test is reported. Other explanations in figure 1 and in text.

many tests and in pooled data; 3) bar magnets produced disorientation in some overcast tests^{1,2} and reversed azimuth in other tests³; 4) recent studies on possible non-specific effects of magnetic treatments – related to an influence on the opioid system^{9,10} – cast a new light on the interpretation of previous results on this topic. Our experimental design, similar to that reported by Keeton¹¹, was planned with the view that clock-shifted experimentals, tested under overcast skies, would have allowed us to verify whether pigeons actually use a magnetic compass or whether they, unlike humans, are able to detect the sun through a thick cloud cover. This idea has not so far been supported by any experimental data on birds. In our expectation, this ability would have been revealed by a counterclockwise deviation of the experimental birds' initial bearings – with respect to the controls' bearings – in agreement with the clock-shift treatment. In fact we found no such effect. Neither can the lack of any consistent deviation of experimental birds in our tests be regarded as being in agreement with the idea that our birds were using a magnetic compass. This view is in fact contradicted by the impaired orientational ability of the experimental group. If

the orientation of the controls was based on a magnetic compass, we see no plausible reason why experimentals were not capable of the same performance, given that – as far as we know – the physiological processes which the magnetic compass is based on are not ruled by an internal clock. The idea which emerges from our results is that clock-shifted birds, in contrast to controls, are not able to use any kind of compass when confronted with overcast conditions. Homing performances, however, were globally not influenced by the experimental treatment, which leads us to conclude that the disturbance of the initial orientation was soon overcome after vanishing. So far, we have no data to establish whether the recovery from the initial impairment is related to the familiarity with the release area. Although it is possible, it seems unlikely that experimental birds' impaired orientation was due to a non-specific influence of the clock-shift treatment on homing motivation, related to the fact that they were released close to their subjective sunset. In fact, such an effect has never been recorded in tests run in sunny conditions.

Our results seem to disagree with those reported by Keeton¹¹; in three overcast tests run by the American

author no significant difference between controls and clock-shifted birds was reported. The number of field tests, however, is too small to allow a qualified discussion of the discrepancy between Keeton's and our results (but see Moore⁸).

So far we have no firm explanation for our results, which may have been caused by yet unknown factors interacting with the pigeon's compass system; among various possible hypotheses, we might suggest that pigeons' sensitivity to magnetic cues, or the ability to use them, varies with subjective sunset time (the condition of clock-shifted birds at the time when tests were run). It can also be supposed that controls had a better opportunity – relative to clock-shifted birds – to localise weak sun cues, given that at familiar release sites they know where the sun should be at the time indicated by their internal clock. This possibility could be tested by running tests at unfamiliar sites, where neither group (controls and clock-shifted experimentals) would have an opportunity to figure out the position of the sun's disk with respect to visual landmarks. We are aware that this view implies that pigeons may not be able to use a magnetic compass, an idea that clashes with a classical concept concerning the pigeon's orientational system. The paradoxical aspects which emerge from our results certainly deserve further investigation, since they have important impli-

cations for the actual role of the magnetic compass in the pigeon's navigation system.

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