AN ANALYSIS OF CLOCK-SHIFT EXPERIMENTS: IS SCATTER INCREASED AND DEFLECTION REDUCED IN CLOCK-SHIFTED HOMING PIGEONS?

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Summary

Clock-shifting (altering the phase of the internal clock) in homing pigeons leads to a deflection in the vanishing bearing of the clock-shifted group relative to controls. However, two unexplained phenomena are common in clock-shift experiments: the vanishing bearings of the clock-shifted group are often more scattered (with a shorter vector length) than those of the control group, and the deflection of the mean bearing of the clock-shifted group from that of the controls is often smaller than expected theoretically. Here, an analysis of 55 clock-shift experiments performed in four countries over 21 years is reported. The bearings of the clock-shifted groups were significantly more scattered than those of controls and less deflected than expected, but these effects were not significantly different at familiar and unfamiliar sites. The possible causes of the effects are discussed and evaluated with reference to this analysis and other experiments. The most likely causes appear to be conflict between the directions indicated by the sun compass and either unshifted familiar visual landmarks (at familiar sites only) or the unshifted magnetic compass (possible at both familiar and unfamiliar sites).

Key words: pigeons, *Columba livia*, clock-shifting, navigation, scatter, deflection, homing.

Introduction

The process of clock-shifting (altering the phase of a bird's internal clock) has been a vital tool in investigating the mechanisms involved in pigeon navigation. At a release site, clock-shifted pigeons (*Columba livia* L.) use their internal clock to compensate for the sun's movement and to take up a bearing appropriate to their subjective time of day. Since their internal clock is shifted, they 'mis-read' the azimuth of the sun, and their mean vanishing bearing from a site is deflected from that of controls by approximately 15° for each hour that their clocks are shifted (Schmidt-Koenig *et al.* 1991). The existence of this deflection allows the experimenter to conclude that the pigeons must have been using their sun compass to determine the home direction. Despite their long use, clock-shift experiments have two common and largely unexplained effects: the clock-shifted group usually shows greater scatter (a shorter vector length) than the control group and a smaller deflection than would be expected theoretically (for discussion, see Neuss and Wallraff, 1988; Wiltschko *et al.* 1994). These effects occur both during release experiments (Schmidt-Koenig, 1979; Schmidt-Koenig *et al.* 1991) and in some experiments directionally testing pigeons in outdoor open-field arenas (Chappell and Guilford, 1995; Gagliardo *et al.* 1996; Hagmann *et al.* 1994). These two clock-shift phenomena will be collectively referred to as 'clock-shift effects'.

There have been few attempts to determine whether these effects are widespread and, if so, to determine their cause. Indeed, the only experiment specifically designed to examine these clock-shift effects found no evidence of them, even though they are common in the literature (Neuss and Wallraff, 1988). The only other systematic examination of these effects was by Wiltschko *et al.* (1994), in an analysis of 103 releases performed over 17 years. However, since all the releases used pigeons bred at the Frankfurt loft at release sites around Frankfurt, the analysis may suffer from the problem of pseudo-replication: it only showed that the effects were significant for Frankfurt-bred pigeons released around Frankfurt, and not that they were general effects of clock-shifting.

The present study reports an analysis of the results of a number of experiments involving 6 h clock-shifts, performed in a number of different countries, that were available from the literature. Ideally, one release from each loft would have been used as a data point, but this would have resulted in an insufficient sample size. Nevertheless, the data represent releases from a wide range of geographical areas, diverse experimental techniques and training regimes, and by a number of different authors.

My aims were as follows: (1) to establish whether there is a significant decrease in vector length relative to controls, and a deflection significantly smaller than theoretically expected in clock-shifted pigeons, (2) to determine whether releases at

familiar and unfamiliar sites differ in these effects, and (3) to use the results of the analysis together with the results of other experiments to try to determine a possible cause (or causes) of the effects.

Materials and methods
Data set

The data were collected from the literature by a computerized on-line search of published papers using appropriate key words and from unpublished experiments performed by researchers in Oxford University. In order to be considered, each study needed to include certain specific information, such as the mean bearing and vector length of the clock-shifted and control groups, the place and approximate date of release and whether the pigeons had been released from the site previously. After rejecting studies which did not provide this information, 60 releases involving a 6 h clock-shift (22 from familiar sites, 38 from unfamiliar sites) from 13 experiments remained. These releases are therefore not an exhaustive sample of all clock-shift experiments ever performed, but they do represent all the experiments that I could find that included the necessary information and which did not involve other sensory manipulations (e.g. anosmia or deprivation of vision). They cover releases in four countries (USA, Germany, Italy, UK) and were performed over 21 years. Thus, it can be reasonably assumed that any statistical effect is a general and widespread effect of clock-shifting, independent of other extraneous factors.

After further investigation, four unfamiliar-site releases and one familiar-site release from this data set of 60 releases were omitted from the analysis: these were from Neuss and Wallraff (1988), Schmidt-Koenig et al. (1991), Wallraff et al. (1994) and Wiltschko and Wiltschko (1980). This was because the results they reported were for several releases pooled from different sites. Pooled data might obscure differences between the control and clock-shifted groups that were specific to a particular release site. Since orientation behaviour varies greatly according to the release site (Wiltschko et al. 1994), the present analysis was designed to compare the behaviour of control and clock-shifted pigeons at each particular release site. It was also difficult to determine an accurate estimate for the expected deflection for pooled releases performed over a period of time. However, data from these five studies are given in Tables 1 and 2 for comparison, and it can be seen that they follow the general trend of the data set. The studies included in the analysis were: Alexander and Keeton (1974), Edrich and Keeton (1978), Foà and Albonetti (1980), Füller et al. (1983), Wiltschko et al. (1976), Wiltschko and Wiltschko (1981), A. Ferry (unpublished data) and R. Holland, F. Bonnadonna, S. Benvenuti, L. Dall'Antonia and T. Guilford (unpublished data).

Release-site classification

The releases were categorized into those from familiar and unfamiliar sites. A familiar site was defined as one at which

the pigeons had been released previously at least once, and an unfamiliar site as one at which a pigeon had never been released previously. Clearly, some pigeons may also have been familiar with the general area of the release site from previous flights. However, since it is almost impossible to quantify the size and extent of familiarity with this area, I used the more stringent criterion stated above to classify the releases. In eight releases (marked with an asterisk in Tables 1 and 2), three different clock-shift groups were released with one control group. Since these groups were all released on the same day, and there was no a priori reason to suppose that the bearings of the clock-shifted groups should differ substantially from those of the controls (the groups were merely housed in different conditions), a second-order mean (Batschelet, 1981) was used to calculate a mean vector for all the clock-shifted groups. The number of vanishing bearings per group for each release ranged from five to 23. Normal quartile plots of a selection of the data established that the vector lengths were normally distributed, but the prediction differences (see section below on deflection) were not. Thus, parametric tests were performed on the vector-length data and non-parametric tests on the prediction-difference data.

Data analysis and statistics
Vector lengths

Since the vector lengths of the control and clock-shifted groups were not strictly independent, the difference in vector length between the two groups was calculated for each release, and a one-sample t-test was performed on these differences for familiar and unfamiliar sites separately. The vector length of the clock-shifted group was subtracted from that of the control group, so that a positive difference would indicate that the clock-shifted group was more scattered than the control group. The vector-length differences for familiar and unfamiliar sites were then compared using a two-sample t-test.

Deflection

The mean deflection for each release was determined by the angular difference between the mean bearings of the control and clock-shifted groups. The sign of the deflection indicates whether the clock-shifted group was counter-clockwise (a fast shift) or clockwise (a slow shift) relative to the control group. However, the sign was ignored in the analysis as fast and slow shifts do not appear to result in systematically different degrees of deflection (Wiltschko et al. 1994). The angular difference between the control and clock-shifted groups (and not between the home direction and the clock-shifted group) is the correct method of determining deflection, as at many sites release site biases or preferred compass directions result in control pigeons being oriented in a direction other than that of home (Wiltschko et al. 1994).

In some cases, the expected deflection was given in the same paper (see Tables 1, 2), but for the majority, the expected deflection had to be calculated. To accomplish this, a set of equations that define the sun's position (Linacre, 1992) was

incorporated into a Pascal computer program which calculated the sun's altitude and azimuth at any time and site on Earth, once the sun's declination (d) in degrees and the equation of time (E) in minutes were known (see Fig. 5.1 in Linacre, 1992).

The equations were as follows:

$$Tt = Tu - \frac{L}{15} + \frac{E}{60} \ , \qquad (1)$$

where Tt is true solar time in hours (time on a sundial set to true solar noon), Tu is universal time or Greenwich Mean Time in hours, L is the longitude of the site in degrees and E is the equation of time in minutes.

$$H = 15(Tt - 12), \qquad (2)$$

where H is the hour angle (the difference of time from solar noon, expressed as $15\,^{\circ}\mathrm{h}^{-1}$ of difference).

$$\sin sa = (\sin d \times \sin A) + [(\cos d \times \cos A)\cos H] \ , \qquad (3)$$

where sa is the sun's altitude in degrees above the southern horizon, d is the sun's declination and A is the latitude of the site in degrees.

$$\sin az = -\cos d \times \frac{\sin H}{\cos sa} \qquad (4a)$$

or

$$180\,^{\circ} - az = -\cos d \times \frac{\sin H}{\cos sa} \ . \qquad (4b)$$

$$\cos az = \frac{\sin d - (\sin A \times \sin sa)}{\cos A \times \cos sa} \qquad (5a)$$

or

$$360\,^{\circ} - az = \frac{\sin d - (\sin A \times \sin sa)}{\cos A \times \cos sa} \ . \qquad (5b)$$

where az is the sun's azimuth in degrees (clockwise from north). Since the azimuth angle satisfies equations 4 and 5, and both equations have two solutions (a and b), the angle common to equations 4 and 5 is the true azimuth angle.

To calculate a mean expected deflection for each release, the sun's azimuth was calculated for two pairs of times, each representing a 6 h interval that gave approximately the minimum and maximum angular differences in azimuth (09:00–15:00 h and 12:00–18:00 h). The angular difference was calculated for each pair, then the mean of both pairs was calculated to give the mean expected deflection (range 80–150 °). The date of the release (used to calculate d and E), and the longitude and latitude of the release site were needed for these calculations. Where only the month of release was given, I calculated d and E for the middle of that month.

The observed mean deflection (the angular difference between the control and clock-shifted group) was subtracted from the expected deflection for the release to give the prediction difference (p). Positive values of p indicate that the observed deflection was smaller than expected, and negative values that it was greater than expected. A one-sample Wilcoxon signed-ranks test was performed on p for familiar- and unfamiliar-site releases separately to determine whether the median was significantly different from zero (that is, whether pigeons show a significantly different deflection from that expected). I also used a Mann–Whitney U-test to compare p in familiar- and unfamiliar-site releases to determine whether the deficit was different at the two site types. Finally, I suspected that the familiar-site releases might be somewhat heterogeneous: pigeons in releases close to home ($\leqslant 10\,\mathrm{km}$) might be very familiar with the area as well as the release site, while those released at a greater distance might only be familiar with the release site itself. Therefore, the familiar releases were divided into short- ($\leqslant 10\,\mathrm{km}$) and long-distance ($>10\,\mathrm{km}$) releases, and a Mann–Whitney U-test was used to compare p in the short and long releases. Since one observation from a pigeon carrying a route recorder has suggested that pigeons may spontaneously range up to 30 km from the loft (R. Holland, F. Bonnadonna, S. Benvenuti, L. Dall'Antonia and T. Guilford, unpublished data), it seems reasonable to assume that pigeons may be very familiar with the area within a radius of 10 km from the loft. A regression of p on the distance of the release site (for familiar sites) was also performed to determine whether the variance of p could be explained by the distance of the site.

Other analyses

The percentage of the expected shift that was observed was calculated [(observed shift/expected shift) $\times$ 100 %], and this was compared with the absolute value of the expected shift using a Spearman rank correlation to determine whether the percentage of the expected shift that was observed was proportional to the expected shift.

Since scatter and deflection can vary independently, a Spearman rank correlation was used to determine whether the vector length of the clock-shifted group was correlated with p for both the site types separately. A χ^2-test was used to determine whether the pattern of reduced deflection and/or increased scatter was significantly different from that expected at each site type. Each release was categorised according to whether there was an increase in scatter only, a decrease in deflection only or both. An increase in scatter was classified as a 10 % or greater difference between the control and clock-shifted vector length, and a decrease in deflection was classified as a 10 % or greater difference between observed and expected deflection.

Results

All the analyses reported below were performed on the subset of data suitable for the analysis (releases 1–21 at familiar sites and releases 1–34 at unfamiliar sites, see Tables 1, 2).

Table 1. *Summary of the data from familiar site releases*

No.	Clock-shift r	Clock-shift n	Control r	Control n	ϕ_{diff} (degrees)	ϕ_s (degrees)	Reference	Comments
1	0.95	11	0.95	11	−28	81	Foà and Albonetti (1980)	
2	0.89	11	0.90	10	−31	81	Foà and Albonetti (1980)	Some CS allowed flight during shift
3	0.90	11	0.90	10	−66	81	Foà and Albonetti (1980)	
4	0.89	12	0.98	11	−34	81	Foà and Albonetti (1980)	2–4 years old
5	0.71	11	0.96	8	−73	81	Foà and Albonetti (1980)	6 h fast
6	0.94	20	0.98	19	+18	80	Foà and Albonetti (1980)	6 h slow
7	0.99	19	0.99	16	+16	80	Foà and Albonetti (1980)	6 h slow
8*	0.36	9.3	0.92	12	−74.6	119	Edrich and Keeton (1978)	Young birds
9*	0.47	12.3	0.88	13	−121.8	119	Edrich and Keeton (1978)	6 h fast
10*	0.48	14	0.76	13	−59	119	Edrich and Keeton (1978)	6 h fast
11*	0.75	10.3	0.92	10	−93	119	Edrich and Keeton (1978)	6 h fast
12	0.60	12	0.96	12	+91	92	Füller *et al.* (1983)	Very experienced birds
13	0.91	11	0.96	16	+93	87	Füller *et al.* (1983)	6 h slow
14	0.74	8	0.52	10	−105	132	Alexander and Keeton (1974)	6 h fast
15	0.84	9	0.72	11	−88	132	Alexander and Keeton (1974)	6 h fast
16	0.53	11	0.82	11	−139	129	Alexander and Keeton (1974)	6 h fast
17	0.71	7	0.95	11	−48	129	Alexander and Keeton (1974)	6 h fast
18	0.76	13	0.98	13	+38.3	121	A. Ferry (unpublished data)	Very close to home
19	0.75	13	0.81	10	−94	120	R. Holland, F. Bonnadonna, S. Benvenuti, L. Dall'Antonia and T. Guilford (unpublished data)	Approximately 10 km from home
20	0.77	9	0.94	11	−35.82	94		
21	0.82	7	0.65	7	−64.36	99		
22	*0.52*	*65*	*0.76*	*60*	*−99*	*125†*	*Wallraff* et al. *(1994)*	*Experienced birds 1–2 years old*
Mean	0.75		0.88		67.19°	103.6°		
N	21		21		21	21		
S.D.	±0.17		±0.12		±34.61°	±20.75°		

The vector length (**r**) and number of vanishing bearings (*n*) are shown for the clock-shifted (CS) and control (C) groups.

Each line of data represents one release, except those marked by an asterisk: in these, more than one CS group was released for each C group, so a second-order mean was calculated for the CS group (Batschelet, 1981).

$\phi_{diff} = \phi_{CS} - \phi_C$, where ϕ is the mean bearing of the group and ϕ_{diff} is the mean deflection for each release.

ϕ_s, expected theoretical deflection; *N*, number of releases.

†Expected shift given in the source paper (see text).

Release 22 (in italics) was excluded from the analysis because the data were pooled from several releases.

Experimental birds were shifted either counter-clockwise (fast) or clockwise (slow) relative to the control group.

Vector lengths

Tables 1 and 2 show the vector lengths (**r**) for clock-shifted and control groups at both familiar and unfamiliar sites. Vector lengths varied greatly (range 0.36–0.99), but in most cases the vector length was shorter for the clock-shift group than the corresponding control group, indicating greater scatter in the former (24 out of 34 releases at unfamiliar sites, 18 out of 21 at familiar sites). The mean difference (±S.E.M.) in vector length between clock-shifted and control groups was 0.13±0.04 at familiar sites and 0.11±0.03 at unfamiliar sites. A one-sample *t*-test revealed that the mean was significantly different from zero at both familiar-site releases (*t*=3.01, *N*=21, *P*=0.007) and unfamiliar-site releases (*t*=3.55, *N*=34, *P*=0.0012). However, a two-sample *t*-test comparing the vector length differences between familiar and unfamiliar sites revealed no significant difference (*t*=0.26, *N*=55, d.f.=53, *P*=0.79).

Deflection

Fig. 1 shows the prediction difference (*p*) for each release at familiar and unfamiliar sites. In most of the releases, *p* was positive, indicating that the observed deflection was smaller than expected (18 out of 21 for familiar sites, 27 out of 34 for unfamiliar sites).

Interestingly, the releases where the pattern of deflection went against the trend did not correspond to the releases where the pattern of vector lengths went against the trend. The mean value of *p* (±S.E.M.) was 36.43±6.09 for familiar sites and 38.24±7.95 for unfamiliar sites. A one-sample Wilcoxon signed-ranks test on the values of *p* obtained for each site type revealed that the median was significantly different from zero in both familiar-site releases (Wilcoxon statistic 221.0, *N*=21, *P*<0.0001) and unfamiliar-site releases (Wilcoxon statistic 527.5, *N*=34, *P*<0.0001). Thus, the observed deflections were significantly different from the expected deflections.

There was no significant difference in *p* between familiar

Table 2. *Summary of data from unfamiliar site releases*

No.	Clock-shift r	Clock-shift n	Control r	Control n	ϕ_{diff} (degrees)	ϕ_s (degrees)	Reference	Comments
1	0.86	10	0.86	10	−88	81	Foà and Albonetti (1980)	See Table 1
2	0.69	10	0.74	6	−187	81	Foà and Albonetti (1980)	6h fast
3	0.94	23	0.99	23	+49	80	Foà and Albonetti (1980)	6h slow
4	0.69	15	0.94	16	+83	80	Foà and Albonetti (1980)	6h slow
5	0.83	10	0.66	11	+49	119	Edrich and Keeton (1978)	See Table 1
6	0.58	9	0.83	9	+36	119	Edrich and Keeton (1978)	6h slow
7*	0.57	13.3	0.96	9	−73.8	95	Edrich and Keeton (1978)	6h fast
8*	0.54	11.3	0.99	11	−48.4	95	Edrich and Keeton (1978)	6h fast
9*	0.68	8.3	0.58	16	−42	84	Edrich and Keeton (1978)	6h fast
10*	0.50	20.3	0.83	19	−69.7	129	Edrich and Keeton (1978)	6h fast
11	0.81	8	0.91	9	+116	119	Wiltschko *et al.* (1976)	6h fast
12	0.77	6	0.62	7	+36	119	Wiltschko *et al.* (1976)	6h slow
13	0.72	10	0.85	10	−108	122	Wiltschko and Wiltschko (1981)	Young birds
14	0.51	10	0.55	10	−45	122	Wiltschko and Wiltschko (1981)	6h fast
15	0.86	10	0.85	8	−109	125	Wiltschko and Wiltschko (1981)	6h fast
16	0.69	10	0.86	10	−28	125	Wiltschko and Wiltschko (1981)	6h fast
17	0.54	11	0.75	9	−132	125	Wiltschko and Wiltschko (1981)	6h fast
18	0.75	11	0.74	10	+11	125	Wiltschko and Wiltschko (1981)	6h fast
19	0.90	11	0.90	10	−133	125	Wiltschko and Wiltschko (1981)	6h fast
20	0.50	11	0.90	10	−16	125	Wiltschko and Wiltschko (1981)	6h fast
21	0.68	11	0.68	14	−110	125	Wiltschko and Wiltschko (1981)	6h fast
22	0.61	11	0.65	11	−58	125	Wiltschko and Wiltschko (1981)	6h fast
23	0.44	13	0.98	10	−62	125	Wiltschko and Wiltschko (1981)	6h fast
24	0.52	5	0.86	9	−60	125	Wiltschko and Wiltschko (1981)	6h fast
25	0.58	11	0.88	10	−151	118	Wiltschko and Wiltschko (1981)	6h fast
26	0.80	10	0.76	8	−64	118	Wiltschko and Wiltschko (1981)	6h fast
27	0.82	10	0.85	10	−100	118	Wiltschko and Wiltschko (1981)	6h fast
28	0.82	10	0.80	11	−40	118	Wiltschko and Wiltschko (1981)	6h fast
29	0.63	12	0.81	10	−124	118	Wiltschko and Wiltschko (1981)	6h fast
30	0.57	11	0.51	10	−83	110	Wiltschko and Wiltschko (1981)	6h fast
31	0.70	11	0.93	10	−85	110	Wiltschko and Wiltschko (1981)	6h fast
32	0.70	8	0.90	9	−49	132	Alexander and Keeton (1974)	See Table 1
33	0.78	13	0.55	10	−33	129	Alexander and Keeton (1974)	6h fast
34	0.59	8	0.58	7	−116	129	Alexander and Keeton (1974)	6h fast
35	*0.60*	*24*	*0.60*	*24*	*−119*	*119†*	*Neuss and Wallraff (1988)*	*6h fast*
36	*0.47*	*383*	*0.71*	*344*	*−71°*	*NA*	*Schmidt-Koenig* et al. *(1991)*	*6h fast*
37	*0.35*	*334*	*0.68*	*348*	*+83°*	*NA*	*Schmidt-Koenig* et al. *(1991)*	*6h slow*
38	*0.71*	*56*	*0.66*	*67*	*+108°*	*126°*	*Wiltschko and Wiltschko (1980)*	*6h slow*
Mean	0.68		0.80		76.3°	114.6°		
N	34		34		34	34		
S.D.	±0.13		±0.14		±41.38°	±16.19°		

The vector length (**r**) and number of vanishing bearings (*n*) are shown for the clock-shifted (CS) and control (C) groups.

Each line of data represents one release, except those marked by an asterisk: in these, more than one CS group was released for each C group, so a second-order mean was calculated for the CS group (Batschelet, 1981).

$\phi_{diff} = \phi_{CS} - \phi_C$, where ϕ is the mean bearing of the group and ϕ_{diff} is the mean deflection for each release.

ϕ_s, expected theoretical deflection; *N*, number of releases.

†Expected shift given in the source paper (see text).

NA, the expected shift could not be calculated because the time/place of the release was not available.

Releases 35–38 (in italics) were excluded from the analysis because the data were pooled from several releases.

Experimental birds were shifted either counter-clockwise (fast) or clockwise (slow) relative to the control group.

and unfamiliar sites (Mann–Whitney *U*-test, W=564.5, N=55, P=0.69). W is the test statistic (sum of the ranks of the first sample), sometimes called U_s. There was also no significant difference in p between short- ($\leqslant$10 km) and long-distance (>10 km) familiar-site releases (W=144.5, N=21, P=0.105) using a Mann–Whitney *U*-test. Furthermore, a regression of p
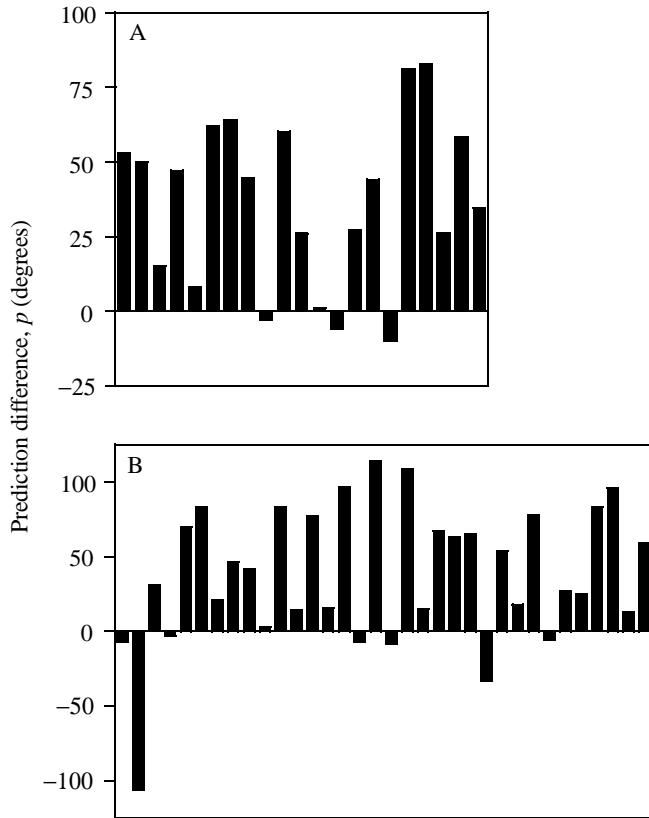
Fig. 1. Prediction difference (p) (the difference between the expected and the observed shift, in degrees) for each release from a familiar site (A) and an unfamiliar site (B). Positive values indicate that the observed shift was smaller than expected, negative values indicate that the observed shift was greater than expected.

on the distance of the release site revealed that the variance in p between releases could not be explained by distance of the site ($F_{1,19}$=1.98, P=0.176). Fig. 2 shows the value of p plotted against the distance of the release site.

It could be argued that it is incorrect to analyse p separately without taking the vector length of the sample into account. A very scattered sample might generate confidence intervals which include the predicted deflection, even if the mean deflection of the sample appears to be very different from the predicted deflection. The 95 % confidence intervals were therefore calculated for each release, using the vector length and size of the sample (Batschelet, 1981), and then it was determined whether the predicted deflection was included in the confidence interval. Releases where the predicted deflection did not fall within the confidence interval (those where the observed deflection was significantly different from the expected deflection) were classified as having an observed deflection either larger or smaller than predicted. Using a χ^2-test, I found that the frequency of deflection type was significantly different from that expected for both familiar and unfamiliar sites (familiar, χ^2=12.0, d.f.=1, P<0.001; unfamiliar, χ^2=14.22, d.f.=1, P<0.0005): smaller-than-predicted deflections were more frequent than expected. Thus,
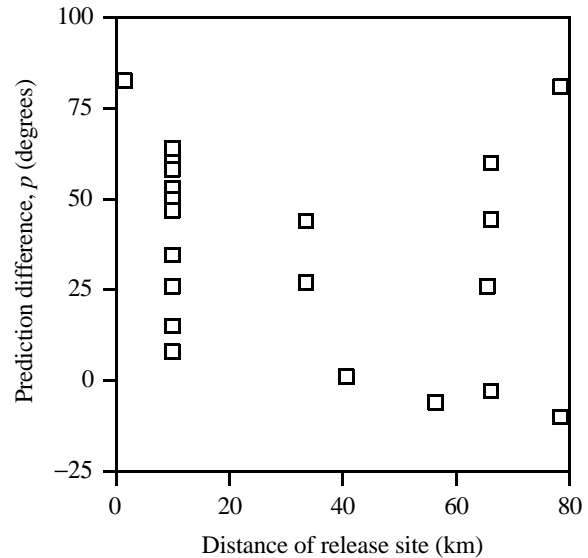

Fig. 2. Prediction difference, p (expected shift minus observed shift) *versus* the distance of the release site for familiar-site releases. There was no significant relationship between p and release-site distance.

it does not appear that using this method alters the general conclusions of this study. Furthermore, since **r** and the mean bearing (ϕ) can vary independently, and since there is no significant correlation between **r** and p (see below), it would seem permissible (even desirable) to analyse **r** and ϕ or p separately.

Other analyses

A Spearman rank correlation showed that there was no significant correlation between the percentage of the expected shift observed and the absolute value of the expected shift for familiar sites (r=0.295, N=21, P>0.05), but that there was a significant negative correlation for unfamiliar sites (r=−0.355, N=34, P<0.05). There was also no significant correlation between the vector length of the clock-shifted group and p for either site type (familiar sites, r=0.304, N=21, P>0.05; unfamiliar sites, r=−0.132, N=34, P>0.05) using a Spearman rank correlation. There was no significant difference between the observed pattern of reduced deflection and/or increased scatter and the pattern expected by chance at either site type using a χ^2-test (familiar sites, χ^2=3.707, d.f.=2, P>0.05; unfamiliar sites, χ^2=4.903, d.f.=2, P>0.05).

Discussion

These results show that clock-shifting pigeons does result in significantly increased scatter in vanishing bearing relative to controls and a significantly smaller deflection than expected, confirming the general findings of Wiltschko *et al.* (1994). However, the magnitude of the prediction difference p is not significantly different between familiar and unfamiliar sites. Furthermore, the two-sample t-test showed that the differences between the vector lengths of clock-shifted and control groups

between familiar and unfamiliar sites were not significant. These results have important implications. It is commonly assumed that it is viewing familiar landmarks in conflict with the shifted sun compass that leads to clock-shift effects (see Foà and Albonetti, 1980), but the similarity of the effects at both site types argues against this assumption (if the cause is common to both site types). If the causes differ at familiar and unfamiliar sites, conflict with familiar landmarks may occur at familiar sites, but another process must be invoked to explain the effects at unfamiliar sites. Furthermore, the causes must be sufficiently similar that they result in statistically indistinguishable effects. Possible causes of the effects will be discussed later, but first it must be considered whether the effects are linked.

The mean bearing and vector length of a group of pigeons are both components of the mean vector, but they can vary independently. For example, if clock-shifted pigeons became confused and therefore selected the home bearing less accurately than controls, the vector length of the group would decrease, but the mean bearing would remain centred on the expected direction. This implies that the confusing factor is non-specific: it increases the variance in vanishing bearings without skewing the distribution in any one direction. Alternatively, clock-shifted pigeons might select a bearing other than the expected direction. If all the pigeons chose a similar bearing, the mean bearing would shift but the vector length would stay the same. However, if pigeons compromise between two alternative directions, either by individuals choosing an intermediate direction or by individuals unambiguously choosing one or other of the alternatives, the vector length and the mean bearing would change simultaneously. The results of the χ^2-tests showed that the distribution of these three types of effect was not significantly different from that expected by chance within each site type, nor was there a significant correlation between the vector length of the clock-shifted group and the prediction difference. This raises two possibilities. First, the clock-shift effects may result from a number of different processes causing a combination of confusion, change of strategy and compromise between strategies. These processes must influence the outcome of releases with approximately equal probability, because the distribution of these effects was not significantly different from that expected. Alternatively, there may be only one cause of the effects, equally likely to result in confusion, change of strategy or compromise. From the results of the present analysis it is impossible to distinguish between these possibilities.

Causes of the clock-shift effects
Product of shifting the internal clock

It is possible that the process of shifting the bird's internal clock might, in itself, have physiological or motivational consequences. Thus, pigeons that have their internal clocks shifted might show an increase in scatter because of disturbance unconnected to their navigational systems. Other experimental treatments such as an altered magnetic field

(Papi and Luschi, 1990), transport in the dark and immobilisation (Del Seppia *et al.* 1996) appear to increase scatter by increasing stress in the pigeons. This hypothesis could be tested by clock-shifting and directionally testing pigeons indoors where the sun compass is unavailable. If the increase in scatter is due to the process of shifting the internal clock itself, the clock-shifted pigeons should show a similar increase in scatter relative to controls to those tested outdoors. One such experiment (Chappell and Guilford, 1997) does not support this hypothesis: the bearings of the clock-shifted group were less scattered than those of the control group.

Incomplete compensation for the sun's movement

In order to use the sun compass, pigeons must compensate for the rate of change of the sun's azimuth over time, which varies with time of day, time of year and latitude. It is not known exactly how this is achieved (see Ranvaud *et al.* 1991 for discussion; Schmidt-Koenig *et al.* 1991), but it is possible that the decreased deflection observed at both sites is due to incomplete compensation for the sun's actual rate of azimuth change. This raises questions concerning our assumptions about the pigeons' method of calibration of the sun compass. The expected clock-shift deflection in this and most other experiments (see Wiltschko *et al.* 1994) was calculated using the actual angular displacement of the sun over 6 h, which assumes that the pigeon has perfect knowledge regarding the sun's movement (a perfect 'ephemeris function'). One of the alternatives is that pigeons always use a constant rate (the mean daily rate of azimuth change), which is $15\,°\,h^{-1}$ (Neuss and Wallraff, 1988). Clock-shift deflection reflects (amongst other things) the angle through which the pigeon estimates the sun to have moved in 6 h, so pigeons using this constant rate of compensation would always expect the sun to have moved $90\,°$ in 6 h. This would result in an increasing discrepancy between the observed and expected deflection as the absolute size of the actual expected deflection increased. There was indeed a significant negative correlation between the percentage of the expected deflection that was observed and the value of the expected deflection for the unfamiliar-site releases, but no significant correlation for the familiar-site releases. Wiltschko *et al.* (1994) performed a similar calculation on their data and found no significant correlation. This could account for the reduction in deflection observed at unfamiliar sites. However, at both site types, pigeons generally reduced their deflection more than would be predicted by the incomplete-compensation hypothesis alone: the mean predicted difference (familiar $36.4\,°$; unfamiliar $37.2\,°$) was greater than the difference between the mean expected deflection and $90\,°$ (familiar $13.6\,°$; unfamiliar $24.7\,°$). Furthermore, a similar negative correlation between the percentage of the expected deflection that was observed and the value of the expected deflection might be predicted if pigeons experiencing a very large conflict between the sun compass and other cues (see discussion below) were to switch to an alternative strategy, thus showing a reduced or absent deflection.

Conflict with other elements of the navigational system

Conflict within the sun compass. It is generally accepted that birds, along with most other animals that use a time-compensated sun compass, only use the azimuth component of the sun's arc and not its altitude above the horizon (see Papi, 1992). Thus, the usual explanation for their behaviour under clock-shift is that they maintain a bearing to the sun appropriate to their subjective time, even though the altitude of the sun might be totally inappropriate for this subjective time. While pigeons certainly do not appear to use the altitude of the sun in their compass, it is still possible that they notice the discrepancy and, consequently, become confused. In addition, there are numerous other celestial cues that might allow a pigeon to detect an error in the sun compass, such as the apparent size and colour of the sun's disc or the colour temperature of the ambient light. Also, ultraviolet receptors in the pigeon's retina may allow it to perceive that the hue of a cloudless sky changes throughout the day (Coemans and Vos, 1992). The perception of an error in the sun compass might result in confusion and an increase in scatter, or the pigeon might switch to another navigational system, resulting in decreased deflection. Bingman and Jones (1994) trained pigeons directionally in an outdoor open-field arena (without providing directional visual cues within the arena) and found that the clock-shifted pigeons showed approximately the expected deflection (94°) with very little scatter (clock-shift, **r**=0.94; control, **r**=0.98). This suggests that the conflict between the sun compass and the other celestial cues does not completely account for the clock-shift effects.

Conflict between the sun compass and visual landmarks. At familiar sites, visual landmarks provide a potential source of conflict with the sun compass. Pigeons' response to this conflict depends upon how they are using the visual landmarks. If visual landmarks are used directly to locate the home direction (Griffin, 1955), a system called pilotage by several authors (e.g. Papi, 1992), there will be a conflict between the directions indicated by the sun compass and the visual cues, and pigeons might attempt to compromise between the two directions (Wallraff, 1991). If they include the sun as a mobile element in the landmark array (Bingman and Ioalè, 1989), they might also attempt to compromise between the shifted position of the sun and the rest of the landmark array. However, if they use landmarks merely to identify a site to which a sun compass bearing is attached, there may not be a conflict, and pigeons may take up the shifted sun-compass bearing (Chappell and Guilford, 1995). Evidence of both strategies has been found at familiar sites (Bingman and Ioalè, 1989; Luschi and Dall'Antonia, 1993; Wallraff *et al.* 1994) and sometimes within one release (R. Holland, F. Bonnadonna, S. Benvenuti, L. Dall'Antonia and T. Guilford, unpublished data). Their strategy might depend on previous experience at that site, general homing experience in the area, the age of the bird or the type of landmarks at a site (see Chappell and Guilford, 1997). Most of these factors could not be investigated in the present analysis, either because the information was unavailable or because pigeons of mixed age and experience were released together. The only factor that was investigated was distance of the release site, which might influence the pigeons' familiarity with the release area. However, there was no linear relationship between *p* and the distance of the release site, and the variation in *p* at any one site distance (e.g. 10 km in Fig. 2) suggested that the other factors listed above probably influenced deflection much more than did distance of the release site. Wiltschko *et al.* (1994) did find that age and experience affected deflection: the bearings of older pigeons shifted progressively less than expected. However, as these results were pooled from familiar and unfamiliar sites, this relationship cannot be completely explained by older pigeons compromising more between the directions indicated by the sun compass and the visual landmarks.

Conflict between the sun compass and the magnetic compass. The other main source of conflict is between the sun compass and another, unshifted, compass. The only other diurnal, non-time-compensated compass which has been investigated in pigeons is the magnetic compass. A clock-shifted pigeon might detect a conflict between the directions indicated by the sun compass and the magnetic compass. Again, the pigeon might choose either of the directions or a compromise bearing. Since the magnetic compass is available at both familiar and unfamiliar sites, this conflict might be the cause of the effects at both site types. However, pigeons tested directionally in an outdoor arena with no internal directional visual cues added did not appear to show either of the usual clock-shift effects, even though these pigeons presumably had a conflict between their sun compass and magnetic compass (Bingman and Jones, 1994). Furthermore, in a similar open-field arena experiment indoors, where pigeons were provided with directional visual cues which were shifted 90° before testing, the pigeons shifted their bearings appropriately (Chappell and Guilford, 1997). Even though these pigeons were not clock-shifted, the shifted visual cues were still presumably in conflict with the magnetic compass. Finally, the magnetic compass appears to be important to young pigeons, but then seems to decline in importance once the sun compass has developed (Wiltschko and Wiltschko, 1988). In the analysis of Wiltschko *et al.* (1994), it was the youngest birds that showed the greatest degree of deflection which, as they pointed out, seems rather counterintuitive.

In conclusion, the clock-shifting process itself, incomplete compensation for the sun's movement and conflict within the sun compass all seem unlikely to contribute greatly to the observed clock-shift effects. It seems more likely that conflict with familiar visual landmarks causes the effect at familiar sites. It is possible that a similar conflict with the magnetic compass could cause the effect at both site types, although this is not supported by some of the experimental evidence available. Both types of conflict result in a similar degree of discrepancy between cues, which might result in similar effects at both familiar and unfamiliar sites.

Since it appears that clock-shift effects are a general and widespread effect of clock-shifting pigeons, more research is

needed to clarify the causes of these effects. Such research could shed valuable light on the mechanisms that underlie pigeons' navigational systems at both familiar and unfamiliar sites.

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