CLOCK-SHIFTING EFFECT ON INITIAL ORIENTATION OF PIGEONS

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IT has long been known that homing pigeons (*Columba livia*) clock-shifted by being held in a light-tight room with artificial lights turned on and off 6 hours out of phase with sun time choose initial bearings roughly 90 degrees different from those chosen by control birds (i.e. ones on normal time) when released at a test site under sunny conditions (Schmidt-Koenig 1958, 1960, 1961; Graue 1963; Keeton 1969). More specifically, a 6 hour slow shift deflects the mean bearing roughly 90° clockwise, and a 6 hour fast shift deflects it roughly 90° counterclockwise.

Because clock-shift experiments of this sort have regularly yielded results consistent with the map-and-compass model of pigeon navigation suggested by Kramer (1953), but not consistent with the sun-arc hypothesis proposed by Matthews (1953), they have been a major factor in the general rejection of the sun-arc hypothesis by present day investigators of pigeon homing. However, Pennycuick (1961) has objected that, during the clock-shifting procedure, the birds are prevented for so long from seeing the sun at home that they might be unable to remember its altitude by the time of the test, and hence be unable to determine their north-south displacement in the manner suggested by the Matthews hypothesis. They might, as a consequence, be forced to resort to sun-compass orientation. If this were so, the results of clock-shift experiments might not be directly relevant as a test of the Matthews hypothesis. Morever, Matthews (1968) has emphasized that a clock-shift might itself be interpreted by a bird as a longitudinal displacement from home.

We have attempted to evaluate these objections by allowing birds undergoing clock-shifting in their home loft to sit in an outdoor aviary during the overlap period between their shifted day and the true day. Thus the birds had a period of unobstructed view of both the sun and the loft's surroundings on each of the 5-7 days of the shifting process. This gave them a daily opportunity to obtain information concerning the sun's arc and its altitude, if such information is important to them, and to see that their incarceration was at home, not at some location 4,000 miles away. The birds were then released for a homing flight to determine whether access to this additional information during the shifting process might result in initial bearings different from those characteristic of ordinary clock-shift tests.

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Methods

For each of the seven tests, control birds and experimentals were drawn at random from a single group of pigeons, and hence had had identical exercise, feeding, and training prior to the test. Clock-shifting was accomplished by putting the birds in a well-ventilated light-tight room in the home loft, where an automatic timer turned the lights on and off 6 hours earlier than sunrise-sunset. During the true morning hours, which was the period of overlap between the shifted day and the sun day, a door leading from the shifting room to a wire aviary was opened and the birds were driven into the aviary; they remained in the aviary 8 hours each day in tests 1–3 and an average of 1.5 hours in tests 4–7. Control birds were in an identical room, but their lights were turned on and off in synchrony with sunrise and sunset.

All test releases were conducted on clear days, when the sun's disk was visible. The birds were carried to the release sites in closed vehicles. They were tossed individually from the hand, the direction of the toss being randomized. Tosses of control and experimental birds were alternated to control for temporally varying conditions. Each bird was watched with 10 × 50 binoculars until it vanished from sight, and a compass bearing was recorded to the nearest 5 degrees. The interval between toss and vanish was timed with a stopwatch. Arrival times were recorded at the home loft so that homing speeds could be calculated.

The mean vector for the vanishing bearings for each treatment in each test was calculated by vector analysis, and this was used in testing for randomness by the V test (Batschelet 1972), with the predicted bearing for the control birds being the home direction and that for the clock-shifted birds being 90° to the left of home.

Differences in vanishing intervals and homing success (based on speeds, with a speed of 0 assigned to lost birds) were evaluated by the matched-pairs signed-ranks test, except in cases where differences in the number of birds homing the day of release made such analysis superfluous.

In Figure 1 each symbol on the periphery of the large circle represents the vanishing bearing of one bird; open symbols designate control birds and solid symbols clock-shifted birds. A small line at the top of the circle locates geographic north, and a dashed line indicates the home direction. The mean vectors are shown as arrows whose length is inversely proportional to the extent of scatter. The mean vectors for control and experimental birds are distinguished by open and solid arrow heads, respectively. The first-given values of N and P (uniform probability under the V test) refer to the bearings of control birds and the second values to those of clock-shifted birds.

Results

Table 1 and Figure 1 show the results of the seven tests performed. In every case the bearings of both treatments were significantly nonrandom, and in every case the mean vector of the clock-shifted birds was to the left of that of the controls, as would be expected in an ordinary 6 hour fast clock shift. Though the magnitude of the angular difference between the two vectors varied from 33° to 137°, such variation is common in ordinary shift tests; the mean of the seven angular differences is 83°, which approximates the predicted 90°.

TABLE 1
RESULTS OF THE SEVEN TEST RELEASES

Test No.[1]	Date	Distance (km)	Home bearing	N[2]	Mean bearing	r	P	Returns same day	Later returns
1 C	24 June 70	33.5	269	10 (9)	263	0.899	<0.001	9	0
E				10 (8)	214	0.700	0.012	1	1
2 C	6 July 70	33.5	269	10	307	0.522	0.034	10	—
E				11 (8)	202	0.737	0.004	6	1
3 C	7 July 70	33.5	269	13 (11)	287	0.720	0.001	13	—
E				11 (9)	199	0.842	<0.001	7	0
4 C	6 July 73	15.4	301	13 (10)	303	0.554	0.012	13	—
E				14 (13)	270	0.775	<0.001	11	2
5 C	10 July 73	73.5	173	9 (7)	206	0.578	0.036	2	5
E				8	90	0.594	0.011	0	4
6 C	18–19 July 73	73.5	173	16 (11)	189	0.821	<0.001	15	1
E				13 (11)	50	0.532	0.018	3	7
7 C	30 July 73	73.5	173	12 (11)	177	0.951	<0.001	6	5
E				12 (7)	129	0.709	0.033	1	11

[1] C designates control birds, E experimentals.
[2] For any release in which bearings were not obtained for all birds, the total number of birds released is given first, followed by the number of bearings (shown in parentheses).

In releases 1, 6, and 7, simple inspection of the number of birds that got home the day of release (Table 1) indicates that the control birds had greater homing success than the clock-shifted birds. In the other four cases, statistical analysis shows significantly better performance by control birds in releases 2, 3, and 5 ($P = 0.005$, 0.013, 0.046, respectively); only in release 4 was the difference insignificant ($P = 0.11$).

In none of the seven tests were the vanishing intervals of the controls and experimentals significantly different.

DISCUSSION

If homing pigeons were truly responsive to the sun's movement in arc or to the sun's altitude, one might expect that the daily opportunity to observe these during the shifting process might influence the effect of the clock-shifting treatment on initial orientation. For example, if the birds could determine local sun time by observation, then the daily opportunity to do so might act as a *Zeitgeber*, thereby preventing the shifted L:D cycle from entraining the birds' circadian clocks; the result, in a test release, would be vanishing bearings not significantly different from those of the controls. Or perhaps the daily conflict between home time as determined by observation of the sun at the home loft and "home" time as indicated by the bird's shifted internal clock (which would indicate a different value each day during the shifting process) would result in confusion, leading to random vanishing bearings in the test release.

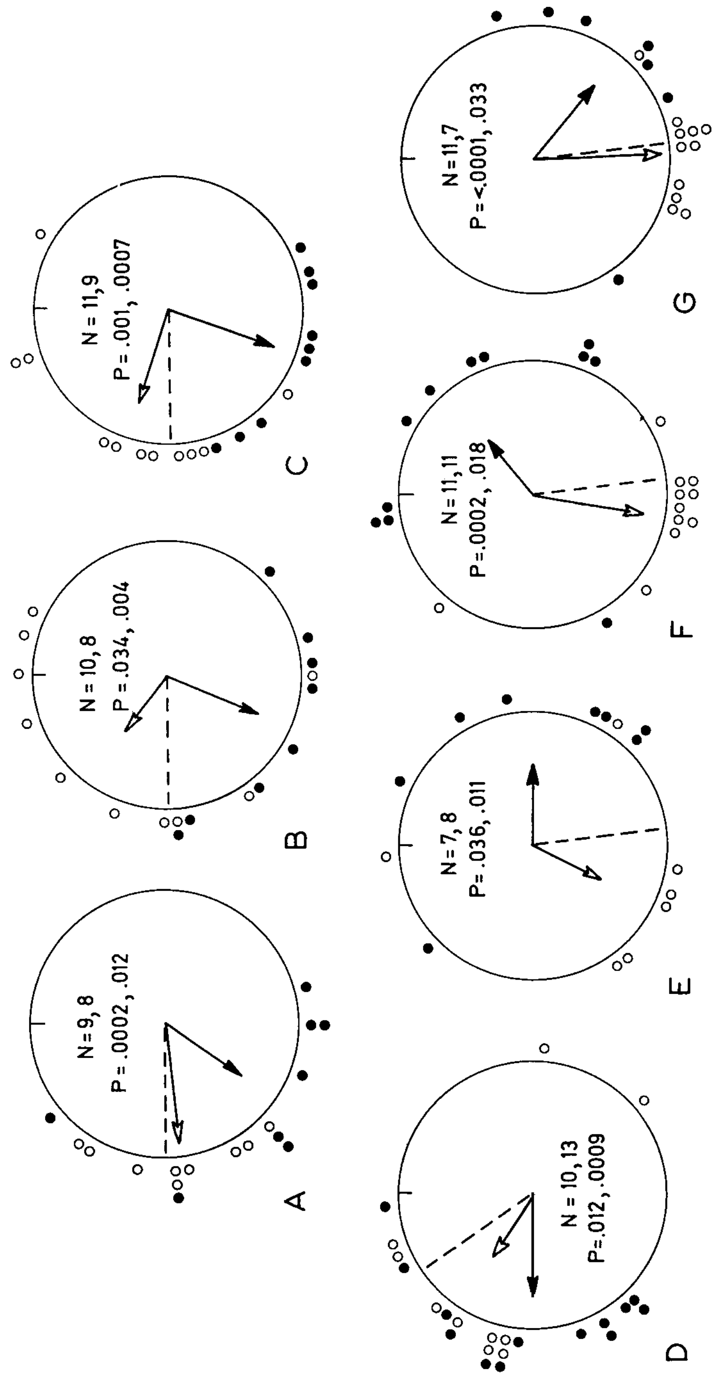

Figure 1. Vanishing bearings from the seven test releases. A–C, tests 1–3, from Marathon, New York. D, test 4, from Padlock Fire Tower, New York. E–G, tests 5–7, from a drumlin N of Weedsport, New York.

The clock-shifted birds showed no such aberrant behavior. They indicated, both by deflected vanishing bearings and by poorer homing success than the controls, that they were behaviorally the same as birds given no opportunity to observe the sun during the shifting process. We conclude, therefore, that the only orientationally relevant information the birds in the aviary derived from their observation of the sun was that the light was on. There is no evidence whatever that the sun's altitude, rate of change of altitude, or position in arc was biologically meaningful to the pigeons.

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