THE EFFECT OF DIRECTIONAL TRAINING ON INITIAL ORIENTATION IN PIGEONS

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SEVERAL investigators (Riviere, 1929; Kramer and St. Paul, 1950; Matthews, 1951; Hitchcock, 1952; Riper and Kalmbach, 1952; Pratt and Thouless, 1955; Michener and Walcott, 1966, 1967) have all reported that when pigeons trained to fly in a single direction were released from points off the training line, the birds continued to fly in the training direction. Wallraff (1959) and Graue (1965) both have reported that even a single flight will influence the vanishing direction of later flights, but Gundlach (1932), Heinroth and Heinroth (1941), Yeagley (1947), and Matthews (1951) present data that do not support such a direction-training effect in pigeons. Matthews (1964) also found no indication of a direction-training effect in Manx Shearwaters.

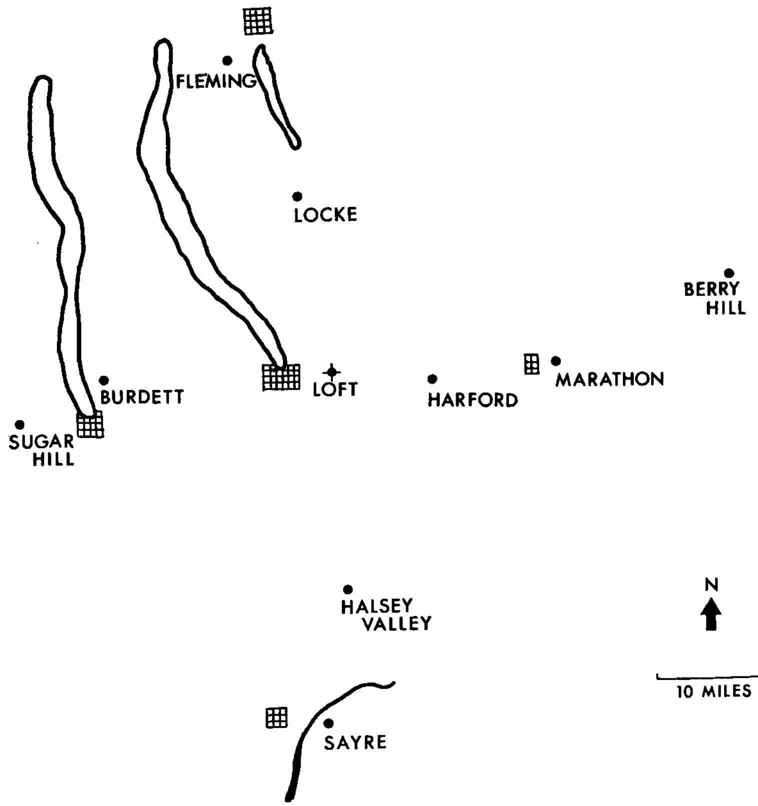
Many of the experiments on this question have been conducted with inadequate controls and with insufficient sample sizes. In several cases data were pooled from many different releases, a procedure that ignores the influence of temporal changes and local variations; when these data are reanalyzed according to releases on the same day from the same site, one often finds statistically random vanishing bearings. Some of the published results that seem to show a direction-training effect are not subject to such criticisms, but they are contradicted by results published by other investigators. Thus, although many workers have investigated the effects of direction training, the question of its effect remains unresolved. After an examination of the literature, we remained unconvinced of the general occurrence of a direction-training effect, and strongly felt that more experiments should be conducted.

GENERAL METHODS

The birds used in these studies were of the Whitney Huyskins-Van Riel, Morris Gordon, and Nemechek Trenton strains; the two groups used in each experiment were of approximately the same strain composition. The birds for any one experiment were kept in the same pen and were handled in the same way, with identical exercise and feeding schedules. In this way it was hoped to minimize any differences in homing performance from differences in physical condition or motivation of the birds.

Birds were placed together in a large carrying basket and transported to the release sites in a closed vehicle. The release sites were all carefully selected to provide a clear, unobstructed view in all directions. Map 1 shows all the test release sites used.

The birds were tossed singly from the hand, randomizing the direction of the toss. Each bird was observed with 10 × 50 binoculars until it disappeared from sight; the vanishing bearing was read to the nearest 5 degrees with a compass. The vanishing interval, i.e. the interval from release of the bird until it was lost from view, was



Map 1. The sites used for test releases are indicated here. The cross-hatched areas indicate the approximate location of cities. The three lakes are, from left to right, Seneca, Cayuga, and Owasco Lakes. The river near Sayre is the Susquehanna.

measured with a stopwatch. Sufficient intervals of time were allowed between releases of successive birds to minimize the possibility that they would join. Each bird was timed upon its return to the loft so that homing speeds could be calculated.

When a test release was being conducted comparing the orientation behavior of two groups of birds, the birds of one group were randomly paired with those of the other group, and then released successively, thus alternating birds from each group (A, B, A, B . . . etc.). This effected a control for any conditions that changed during the period of the release, including wind and weather conditions.

Although some of the training tosses were on cloudy days, all test releases were conducted when the sun was visible. The wind speed ranged from light to moderate (from 0-10 mph) on most releases and had no obvious influence on the orientation of the birds. Details of wind speed and direction for all releases and further details on the training of birds are given in Alexander (1970).

The pairing of the two groups of birds on test releases permitted the use of the Wilcoxon matched-pairs signed-ranks test (Siegel, 1956) to compare the vanishing intervals and homing speeds. Vector analysis was used to calculate the mean vanishing bearing for each release. The Rayleigh test, as prepared by Greenwood and Durand (1955), was used to test the bearings for randomness. In all but the releases of Series I, the Wheeler and Watson (1964) distribution-free two-sample test on a circle was used to determine whether the bearings of the two groups were significantly different; because of the large number of tie values, the bearings of the two groups in Series I were compared using the modified F test proposed by Watson and Williams (1956) and summarized by Batschelet (1965).

SERIES I RELEASES

Preliminary studies were begun in the fall of 1967, in an attempt to confirm the reported "training effect." Two groups of experienced birds were used, with one receiving six successive training releases from the east (Marathon, 20.8 miles), the other from the west (Burdett, 21.1 miles). Figures 1A and 1B show the well oriented vanishing bearings of the birds on their last training tosses. Then both groups were taken 16.6 miles north (Locke) and released alternately in single tosses. The direction of their vanishing bearings (Figure 1C) showed a significant difference ($P < 0.05$); the birds trained from the west had a mean bearing to the east of the true home bearing, while those trained from the east had a mean bearing to the west of the true home bearing, as would be predicted by the training-effect hypothesis (Table 1).

The training of the birds was then reversed in an attempt to reverse the bias shown on the first test release. Thus after the birds that had been previously trained from the east had been retrained from the west (Figure 1D), and those from the west had been retrained from the east (Figure 1E), both groups were again taken north for a test release (begun 7 November and completed 10 November). If indeed a training effect exists, one might expect that now the birds would orient in the opposite way from that displayed on their first release from the north. There was no significant difference in their mean bearings on either day, or when the data for the two days were combined. Furthermore the small difference between the mean bearings for the pooled data was in the same direction as before (Figure 1F); no reversal had occurred.

Thus the first test release seemed to indicate that the initial orientation of the pigeons was influenced by their previous training flights, but the second test release failed to confirm this.

SERIES II RELEASES

As the preliminary experiments were inconclusive, we began another series of more carefully designed experiments. We thought that perhaps any possible bias in Series I might be difficult to detect because the training flights were superimposed on top of the birds' extensive previous experience. Therefore, we decided to try young birds with no previous homing experience.

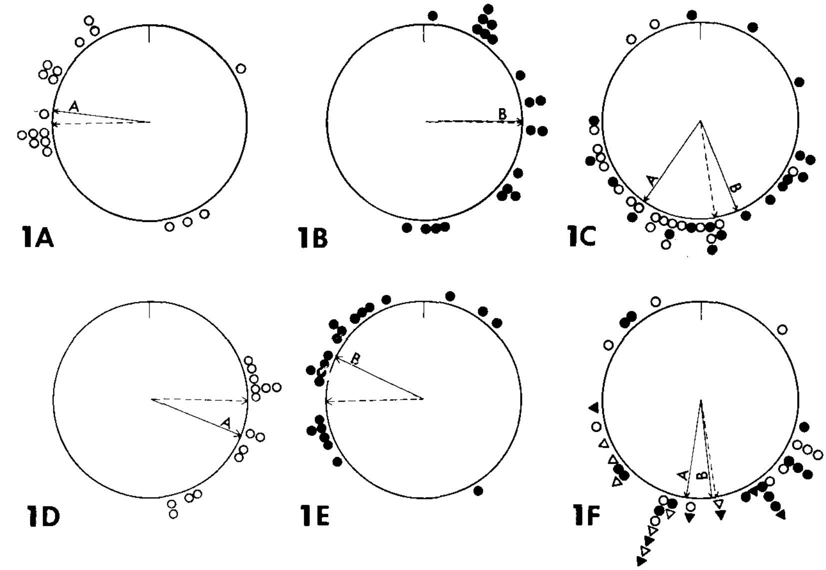


Figure 1. Series I. A, training release, Marathon, New York, 10 October 1967, 20.8 miles, home direction 269°; mean bearing 277° (oriented, $P = 0.002$). B, training release, Burdett, New York, 10 October 1967, 21.1 miles, home direction 91°; mean bearing 90° (oriented, $P < 0.001$). C, test release, Locke, New York, 17 October 1967, 16.6 miles, home direction 171°; mean bearing of Group A 215° (oriented, $P < 0.001$), mean bearing of Group B 158° (oriented, $P = 0.010$). D, training release, Burdett, New York, 31 October 1967, 21.1 miles, home direction 91°; mean bearing 112° (oriented, $P < 0.001$). E, training release, Marathon, New York, 26 October 1967, 20.8 miles, home direction 269°; mean bearing 296° (oriented, $P < 0.001$). F, test release, Locke, New York, 7 November (circles) and 10 November 1967 (triangles), 16.6 miles, home direction 171°; 7 November: Group A not homeward oriented ($P = 0.234$), mean bearing of Group B 163° (oriented, $P = 0.016$); 10 November: mean bearing of Group A 210° (oriented, $P < 0.001$), mean bearing of Group B 185° (oriented, $P = 0.006$); composite of both days: mean bearing of Group A 188° (oriented, $P = 0.008$), mean bearing of Group B 173° (oriented, $P < 0.001$). [In these and all later figures true north is indicated by a line at the top of the circle, the home direction by an unlabelled dashed arrow, and the mean bearings by solid arrows labelled A (Group A) or B (Group B). Each open symbol on the periphery of the large circle indicates the vanishing bearing of one bird of Group A, and each solid symbol the bearing of one bird of Group B.]

Two groups of pigeons were used in the summer of 1968, each group composed of 25 birds about 2 months old that had never been taken away from the loft. Group A was trained only from the east and Group B only from the west. The initial training release for each group was from a point ½ mile from the loft; then 1-, 2-, 3-, 4-, 8-, 10-, and 20-mile releases were made. These flock releases were followed by three single

TABLE 1
DATA FROM TEST RELEASES

Release	Number of birds[1]	Mean bearing (degrees)[2]	Deviation from home (degrees)	Length of mean vector	P Rayleigh test	Number of day birds	Mean speed of day birds (miles/hour)	Mean vanishing interval (minutes)
Series I, test 1								
Group A	22 (19)	215*	44.4	0.70	<0.001	22	23.0	5.5
Group B	23 (19)	158*	–12.5	0.48	0.010	21	17.7	7.4
Series I, test 2								
Group A	24 (19)	188	17.4	0.49	0.008	23	26.7	6.6
Group B	23 (21)	173	2.0	0.61	<0.001	22	25.2	6.8
Series II, north test								
Group A	25	151	–12.8	0.74	<0.001	21	24.7	2.8
Group B	25	150	–13.9	0.84	<0.001	22	26.3	2.7
Series II, south test								
Group A	25	344*	–19.2	0.81	<0.001	23	26.5	2.2
Group B	25	307*	–56.0	0.81	<0.001	24	23.5	2.2
Series III, east test								
Group A	21	316*	57.3	0.89	<0.001	5	19.0	2.9
Group B	21	287*	28.8	0.80	<0.001	15	19.8	1.8
Series III, west test								
Group A	9	343	–100.4	0.64	0.020	7	12.1	2.7
Group B	13	307	–135.8	0.91	<0.001	11	14.9	2.0
Series IV, test 1								
Group A	8	250	–18.7	0.41	0.276	4	19.4	3.1
Group B	10 (9)	267	– 2.2	0.95	<0.001	10	18.4	3.3

Release	Number of birds[1]	Mean bearing (degrees)[2]	Deviation from home (degrees)	Length of mean vector	P Rayleigh test	Number of day birds	Mean speed of day birds (miles/hour)	Mean vanishing interval (minutes)
Series IV, test 2								
Group A	12	245	−23.5	0.79	<0.001	4	20.1	2.7
Group B	9	268	− 0.5	0.81	0.001	5	17.5	2.3
Series V, east (1)								
Group A	16 (14)	242	−26.5	0.79	<0.001	16	19.0	3.4
Group B	17 (14)	276	6.9	0.81	<0.001	17	24.9	2.1
Series V, south								
Group A	16	314	−44.1	0.88	<0.001	14	20.9	3.1
Group B	16 (15)	297	−61.4	0.95	<0.001	16	27.5	3.3
Series V, west								
Group A	15	36	−55.3	0.38	0.115	13	16.8	4.3
Group B	16	344	−107.4	0.27	0.311	15	19.1	3.5
Series V, north								
Group A	15	222	51.8	0.45	0.047	15	18.7	4.0
Group B	16	242	71.6	0.63	0.001	15	27.1	5.2
Series V, east (2)								
Group A	15	281	12.1	0.90	<0.001	14	23.2	3.3
Group B	16 (15)	283	14.5	0.90	<0.001	16	23.9	2.1

[1] For any release in which bearings were not obtained for all birds (because the bird landed, or was lost before the binoculars could be focused on it, and so forth), the number of birds for which bearings were obtained is shown in parentheses.
[2] An asterisk follows the mean bearings for those tests in which the vanishing bearings of the two groups were significantly different.

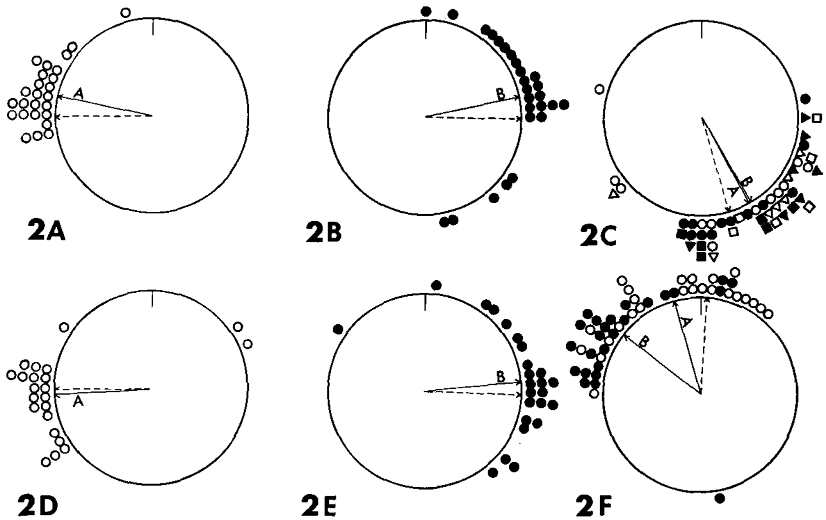


Figure 2. Series II. A, training release, Marathon, New York, 16 July 1968, 20.8 miles, home direction 269°; mean bearing 281° (oriented, $P < 0.001$). B, training release, Burdett, New York, 17 July 1968, 21.1 miles, home direction 91°; mean bearing 78° (oriented, $P < 0.001$). C, test release, Fleming, New York, 18 July (circles), 19 July (triangles), and 20 July 1968 (squares), 30.4 miles, home direction 164°; 18 July: mean bearing of Group A 165° (oriented, $P = 0.003$), mean bearing of Group B 158° (oriented, $P < 0.001$); 19 July: mean bearing of Group A 148° (oriented, $P = 0.005$), mean bearing of Group B 125° (oriented, $P = 0.001$); 20 July: mean bearing of Group A 134° (oriented, $P = 0.003$), mean bearing of Group B 164° (oriented, $P = 0.001$); composite of all three days: mean bearing of Group A 151° (oriented, $P < 0.001$); mean bearing of Group B 150° (oriented, $P < 0.001$). D, training release, Marathon, New York, 25 July 1968, 20.8 miles, home direction 269°; mean bearing 266° (oriented, $P < 0.001$). E, training release, Burdett, New York, 25 July 1968, 21.1 miles, home direction 91°; mean bearing 83° (oriented, $P < 0.001$). F, test release, Sayre, Pennsylvania, 26 July 1968, 32.5 miles, home direction 3°; mean bearing of Group A 344° (oriented, $P < 0.001$), mean bearing of Group B 307° (oriented, $P < 0.001$).

tosses at approximately 20 miles. The vanishing bearings for the single tosses of each group (Figures 2A and 2B) were well-oriented in the homeward direction, with little scatter.

After this extensive training from the single direction, the first half of the test release was conducted on 18 July; half of the birds from each group, selected randomly, were released from a point 30.4 miles north, at Fleming, New York. The release of the second half of the birds was begun the next day, but was discontinued because the sky became overcast. The release was completed the following day. At this north point the vanishing bearings for the two groups showed no significant difference on any of the 3 days (P = 0.491, 0.396, 0.716, respectively) or when the data for the 3 days were combined (P = 0.397) (Figure 2C); both the groups were well oriented homeward on all 3 days. The mean vanishing intervals and the mean homing speeds for the two treatments were not significantly different. Nor was there any difference in homing success; almost all the birds returned home in good time on the day of the release, with only five Group A birds and three Group B birds taking longer than 1 day.

The birds were next given two flock tosses followed by a single toss from the 20-mile release points in the original training directions, Group A from the east and Group B from the west. After this reinforcing of the original directional training (Figures 2D and 2E show that the birds were well-oriented), the birds were given a second critical test release from a point 32.5 miles south, near Sayre, Pennsylvania. This time there was a significant difference between the vanishing bearings (P = 0.020), but the difference was opposite to that predicted on the basis of previous training (Figure 2F). Again the two groups showed very little difference in homing performance, with both having similar vanishing intervals and homing speeds. The homing success was also similar, with only two Group A and one Group B birds not returning in good time on the day of release.

Thus, in this second series of experiments, extensive training from a single direction had no detectable effect on the vanishing bearings of later flights.

Series III Releases

The same procedure used in Series II was followed in this third series to see if the results would be the same when the tests were done from different directions. Two groups were sett up, each of 25 young inexperienced birds; Group A was trained only from the south and Group B only from the north. The training was carried out in the same manner as in the previous series, with the initial flock release from ½ mile, and succeeding ones from 1, 1½, 2, 3, 4, 5, 7, 10, 15, and 20 miles. After two single tosses at approximately 20 miles, the birds were well-oriented in the homeward direction (Figures 3A and 3B).

The first test release was conducted at Berry Hill Firetower, 37.9 miles east of the loft. Although the mean vanishing bearings of both groups were north of the true homeward direction, the difference between the bearings of the two groups was significant (P = 0.007) and in the direction predicted on the basis of previous training (Figure 3C). The two groups also showed a difference in homing success. Only 5 of the 21 Group A birds returned the day of release, and 4 more returned in the next few days; of the 21 Group B birds, 15 returned the day of release and 4 more returned later.

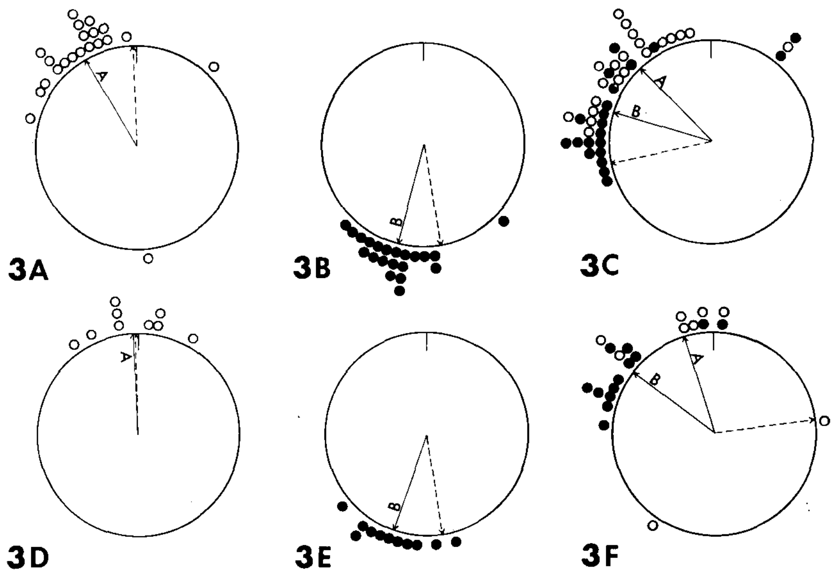


Figure 3. Series III. A, training release, Halsey Valley, New York, 12 October 1968, 20.3 miles, home direction 358°; mean bearing 330° (oriented, $P < 0.001$). B, training release, Locke, New York, 16 October 1968, 16.6 miles, home direction 171°; mean bearing 195° (oriented, $P < 0.001$). C, test release, Berry Hill, New York, 18 October 1968, 37.9 miles, home direction 258°; mean bearing of Group A 316° (oriented, $P < 0.001$), mean bearing of Group B 287° (oriented, $P < 0.001$). D, training release, Halsey Valley, New York, 30 October 1968, 20.3 miles, home direction 358°; mean bearing 357° (oriented, $P < 0.001$). E, training release, Locke, New York, 30 October 1968, 16.6 miles, home direction 171°; mean bearing 199° (oriented, $P < 0.001$). F, test release, Sugar Hill, 1 November 1968, 29.3 miles, home direction 83°; mean bearing of Group A 343° (oriented, $P = 0.020$), mean bearing of Group B 307° (oriented, $P < 0.001$).

The birds were next given two flock tosses and one single toss from the 20-mile release points in the original training directions, Group A from the south and Group B from the north. Both were well-oriented homeward (Figures 3D and 3E). Then the birds were released singly for the second test release from Sugar Hill Firetower, 29.3 miles west. The number of birds released was only 22 because of the poor returns, especially in Group A, from the east test release. The homeward orientation of all the birds was very poor, being considerably north of the true home direction (Figure 3F). Although the mean bearings of the two groups differed by 36 degrees, this difference was not significant ($P = 0.244$). Homing success was comparable in the two groups, with two birds out of each group not returning on the day of release. The homing speeds were somewhat slower than on the previous releases, perhaps correlated with the large deviations from the true homeward direction.

The results of this third series are not so clearcut as in the second series. On the first test release, each group did seem to have a bias in the appropriate direction, corresponding to the homeward direction of the training flights. It is difficult to interpret the results of the second test release in this series as both groups showed large deviations from the homeward direction, but we do not consider that it provides convincing evidence of a training bias.

In summary, although the first test release in this third series yielded results consistent with training bias, neither this series as a whole nor the second and third series combined provided convincing evidence for the existence of an influence of training flights on the initial orientation of later flights.

Series IV Releases

The most dramatic published results of the effect of direction training are those Wallraff (1967) presents, based on tests with birds with no previous experience. It seemed possible that our pigeons had been given so many training flights that they became better at the homing process, so that the effect of any possible bias was not observable. Therefore an additional series of releases was set up to test the possibility that the first release might have a more noticeable biasing effect on untrained birds than later releases have on experienced homing pigeons.

Naive birds, that is, birds that had been permitted exercise flights at the loft but had never before been transported away from the loft, were divided into two groups, A and B, of 10 birds each. A single training release was given to both groups: Group A was released in single tosses from 16.6 miles north (Locke), while Group B was released in single tosses from 9.4 miles east (Harford) on the same day. Both groups showed good initial orientation in the homeward direction (Figures 4A and 4B), and returns were very good, with 8 out of 10 returning from the north and 10 out of 10 from the east. Several days later both groups were released alternately in single tosses from 20.8 miles east (Marathon). If the direction of the first release influences the initial orientation of later releases, it would be expected that Group A, whose first release was from the north, might show a bias toward the south of the true home bearing on this second release, while Group B, whose first release was from the same direction as the second, might continue to show clear homeward orientation toward the west. The vanishing bearings obtained on this test release indicated a difference in the orientation behavior of

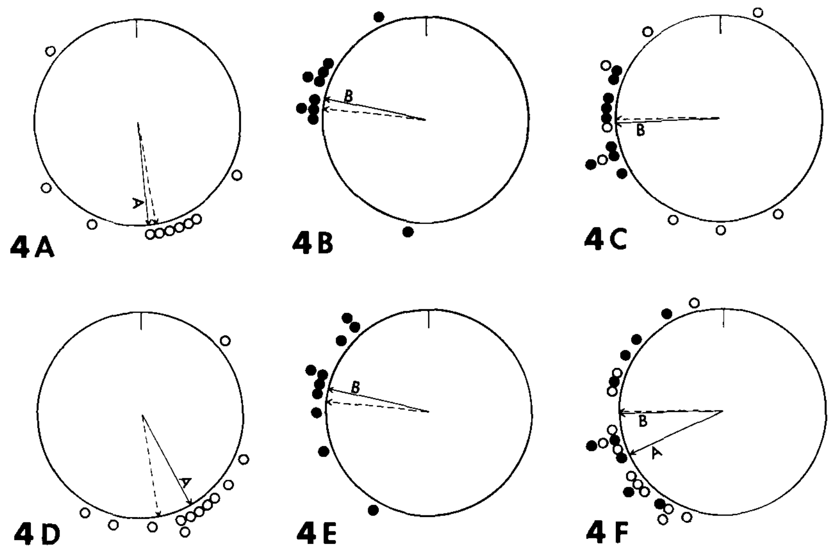


Figure 4. Series IV. A, first release of inexperienced birds, Group A, Locke, New York, 25 April 1969, 16.6 miles, home direction 171°; mean bearing 175° (oriented, $P = 0.004$). B, first release of inexperienced birds, Group B, Harford, New York, 25 April 1969, 9.4 miles, home direction 276°; mean bearing 282° (oriented, $P < 0.001$). C, test release, Marathon, New York, 30 April 1969, 20.8 miles, home direction 269°; Group A birds not homeward oriented ($P = 0.276$), mean bearing of Group B 267° (oriented, $P < 0.001$). D, first release of inexperienced birds, Group A, Locke, New York, 2 May 1969, 16.6 miles, home direction 171°; mean bearing 152° (oriented, $P < 0.001$). E, first release of inexperienced birds, Group B, Harford, New York, 2 May 1969, 9.4 miles, home direction 276°; mean bearing 283° (oriented, $P < 0.001$). F, test release, Marathon, New York, 5 May 1969, 20.8 miles, home direction 269°; mean bearing of Group A 245° (oriented, $P < 0.001$), mean bearing of Group B 268° (oriented, $P = 0.001$).

the two groups, not in the expected deviation in mean vanishing bearings, but in the fact that the birds whose first flight had been from the east were well-oriented toward home ($P < 0.001$), whereas the birds whose first flight had been from the north now vanished randomly ($P = 0.276$) (Figure 4C). The two groups exhibited no significant differences in vanishing intervals or homing success.

A replicate of this experiment using additional untrained birds was performed. On the training flights both groups were well-oriented in the homeward direction (Figures 4D and 4E). But the results of the test release differed from those of the first test; this time both groups were well-oriented homeward (Figure 4F) and there was no significant difference in their mean vanishing bearings ($P = 0.754$).

Series V Releases

Thus far we had failed to demonstrate that the direction of previous flights had any significant effect on the initial orientation of later flights. Next we tried still another method, an approach similar to that of Graue (1965), using experienced birds.

Two groups, A and B, were set up, with 15 very experienced birds in each. Both groups were given a preparatory release at the 20-mile east point, and then Group A was released on 4 successive days from the 20-mile (approximately) release points at 90° intervals clockwise, and Group B counterclockwise. That is, on the 2nd day Group A was released from the south, Group B from the north; on the 3rd day both groups from the west; on the 4th day Group A from the north, Group B from the south; and on the 5th day both groups from the east.

This experimental design allows a comparison to be made at each release point of the initial orientation behavior of two groups of birds whose previous flights were from opposite directions. For example, at the west point the previous release of Group A was from the south, while that of Group B was from the north. At two of the four release points (west and east) the birds from each group were released alternately on the same day under the same environmental conditions.

On the preparatory release from the east (Marathon), both groups were moderately well-oriented in the homeward direction and there was no significant difference between them ($P = 0.103$) (Figure 5A).

At the south point (Halsey Valley), the mean vanishing bearings of both groups were to the west of the true homeward direction (Figure 5B), as is normal for birds from our loft at this point. The difference between the bearings of the two groups, which was the reverse of what would have been expected if there were a bias from the previous release, was not significant ($P = 0.759$).

On the third release, when both groups were released from the west (Burdett), both groups gave random bearings (or perhaps bimodal) for some unknown reason and there was no significant difference between them ($P = 0.391$) (Figure 5C).

At the north point (Locke), both groups gave mean vanishing bearings to the west of the true homeward direction (Figure 5D). The mean bearing of Group B, whose previous release was from the east, was indeed to the west of the mean bearing for Group A, whose previous flight was from the west, but, the difference in the bearings was not significant ($P = 0.271$).

On the final release, from the east (Marathon), both groups were very well-oriented in the homeward direction with little scatter, and the difference in their bearings was not significant ($P = 0.889$), the two

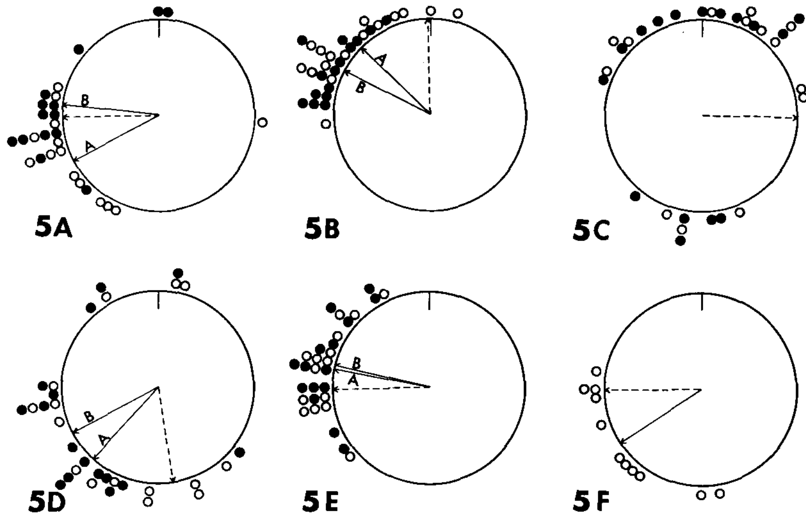


Figure 5. Series V. A, Marathon, New York, 9 June 1969, 20.8 miles, home direction 269°; mean bearing of Group A 242° (oriented, $P < 0.001$), mean bearing of Group B 276° (oriented, $P < 0.001$). B, Halsey Valley, New York, 20.3 miles, home direction 358°; mean bearing of Group A, on 10 June 1969, with previous release from east, 314° (oriented, $P < 0.001$), mean bearing of Group B, on 12 June 1969, with previous release from west, 297° (oriented, $P < 0.001$). C, Burdett, New York, 11 June 1969, 21.1 miles, home direction 91°; Group A, with previous release from south, not homeward oriented ($P = 0.115$), Group B, with previous release from north, not homeward oriented ($P = 0.311$). D, Locke, New York, 16.6 miles, home direction 171°; mean bearing of Group A, on 12 June 1969, with previous release from west, 222° (oriented, $P = 0.047$), mean bearing of Group B, on 10 June 1969, with previous release from east, 242° (oriented, $P = 0.001$). E, Marathon, New York, 13 June 1969, 20.8 miles, home direction 269°; mean bearing of Group A, with previous release from north, 281° (oriented, $P < 0.001$), mean bearing of Group B, with previous release from south, 283° (oriented, $P < 0.001$). F, Campbell, New York, 9 June 1969, 545 miles east of Palos Park, Illinois, home direction 269°; mean bearing 236° (oriented, $P < 0.001$).

means differing by only two degrees (Figure 5E). Note that this was less difference than in the release of Figure 5A, when the previous experience of the two groups was identical.

Thus this series of experiments presented no evidence that the initial orientation of the pigeons was influenced by the direction of the preceding flight.

Release of Illinois Birds

In a last attempt to demonstrate a direction-training effect, we performed a release using 12 birds borrowed from a pigeon racing fancier in Palos Park, Illinois. The birds had been trained and raced up to 300 miles from the west, but had never been released from east of Palos Park (Gobert, 1970). We single-tossed these birds on 9 June 1969, at Campbell, New York, 545 miles east of Palos Park. The birds departed well-oriented in the homeward direction (Figure 5F), and had unusually short vanishing intervals (mean, 2.7 minutes). Obviously then, these Illinois pigeons showed no observable directional bias, exhibiting no hesitation in choosing a direction opposite to the one they had had to take on all their previous flights. In numerous releases at this site, Cornell birds have never vanished in the direction the Illinois birds chose, which indicates that the pigeons were not simply flying in a direction dictated by local topography.

Our results in this test agree with those reported by Goswick (1970). This fancier raced his pigeons up to 300 miles as young birds and to 700 miles as old birds, along a course southwest of his loft in Tulsa, Oklahoma. When the racing season was over, he released 14 of these birds at a site 600 miles northeast of the loft. Only one of the birds was lost, and the homing speed of the others was "equal to their speed on the regular race course." Though Goswick did not report vanishing bearings, it seems clear that these birds, which had never flown from any direction but southwest, had no difficulty homing rapidly over a very long distance from the opposite direction.

Discussion

Only three of our tests gave significant differences in vanishing bearings between the two experimental groups; in two cases the difference was in the direction expected if the previous training exerts a bias, and in the other it was in the direction opposite to that predicted. If we examine all the tests without regard for whether the difference between treatments was significant, but omitting the two tests (IV-1, V-W) where the birds of one or both treatments vanished randomly and also the one test (III-2) where the data cannot easily be interpreted with reference to the predictions, we see six tests in which the differences are in the direction predicted if previous training influences later flights, and three tests in which the differences are opposite to the prediction; the binomial probability (one-tailed) that such a result would be obtained by chance is 0.254. It should be noted that this 6:3 split includes two releases (II-1, V-E) in which the difference between the means of the treatments is two degrees or less; differences this small are essentially meaningless because they are well below the grouping unit of five degrees used in recording field data. If these two releases are omitted from the analysis, we obtain a split of 4:3, for which the chance probability is 0.500. We conclude that training biases either do not occur in our birds or are of negligible importance.

Most of the release points used in our experiments have been used many times previously, and we were familiar with the usual orientation of our birds at these points. Reasonable sample sizes were used to permit valid statistical analysis. All experiments except the ones in the last series were conducted so that on test releases two groups of birds of different experience were compared on the same day from the same release site. Pigeons from one group were released alternately with pigeons from the other group; this controlled for factors that may have changed during the course of the release. In these ways, we hoped to provide adequate controls for our experiments.

One might ask why different researchers have obtained conflicting results. A detailed and critical review of the literature on this subject is given in Alexander (1970); we shall include only a brief treatment here.

The conclusions reached by Riviere (1929), Hitchcock (1952), Riper and Kalmbach (1952), Pratt and Thouless (1955), and Michener and Walcott (1966) are open to question, as they all made observations on very small samples, and, in most cases, without adequate controls. Several workers have used large enough samples for statistical analysis. Kramer and St. Paul (1950) performed two series of releases that consisted of training birds from one direction and then releasing them from a crosswise direction. In the first series the birds were trained from the south, in the second from the southeast. Some of the birds used in the second test release had already participated in the first test; these experienced birds gave random bearings on the second test. As they had had so much training from one direction, the south, if there indeed is a "training effect," one might expect these birds to exhibit a strong northerly tendency, which, in fact, they did not. These results do not seem conclusive, but as the vanishing points for the whole group were mostly in the training direction on the cross release, Kramer and St. Paul concluded that birds do indeed tend to fly in the training direction when released from points off the training line. At certain release sites pigeons are known to orient consistently in one direction, and not necessarily in the homeward direction; this "place-specific" bias must be considered when interpreting the results of orientation studies. Kramer and St. Paul present no evidence of how pigeons normally orient from the sites used in their critical tests, and they used no controls in their one-sample releases from the south and southeast.

Matthews (1951) investigated this problem, and in preliminary experiments found that the birds showed a strong tendency to vanish in the training direction, but in later experiments he found that the birds were able to orient successfully toward home when released in unknown areas. Matthews (1968) later acknowledged that other workers have found that pigeons fly in the training direction when released off the training line, and he appears to have accepted the general validity of the training-bias concept.

Wallraff (1959) reported on 3 years of experiments to investigate the problem of directional training. The difference between the means of the vanishing bearings of the two groups in his 1956 release was not significant. In his 1957 test release one group gave random vanishing bearings, which makes comparing the two groups difficult. His 1958 series of experiments consisted of releasing different groups of naive birds from the four compass directions and then giving them a release from a crosswise direction. In analyzing these experiments, Wallraff combined data from releases from three different years and from many different release points. As Schmidt-Koenig (1965) has pointed out, this procedure fails to consider variations caused by temporally changing parameters and local deviations. When Wallraff's data from releases of birds on the same day from the same release point are examined as Schmidt-Koenig (1965) did, one finds that several of the groups are too small to be submitted validly to statistical procedures, and for several other groups the small sample size gives statistical randomness. Thus overall, Wallraff's (1959) results are inconclusive.

In a later paper Wallraff (1967) reported the results of a release of birds with only one previous flight, that vanished in the direction corresponding to the home direction of their first release. Taken alone the result of this test is impressive, but Wallraff states that "this result is a rather extreme one; in most cases the effect is smaller." As the number of these other cases is not mentioned, it is difficult to evaluate the importance of the selected test.

Graue (1965) set up a complex series of experiments to test whether the initial orientation of pigeons was influenced by the home direction of the preceding flight. He concluded that a single release can influence the initial orientation on the succeeding release and that the effects of several releases are averaged to influence the orientation on later flights. Comparisons between groups of birds with different experience were made at each of 12 release points, and, in fact, the predicted deviations were observed in all cases. In analyzing these experiments it must be kept in mind that they included many variables for which there were no adequate controls. The releases that he compares were made on different days and even different years, under different environmental conditions. The birds were in different physiological condition over the weeks and years of the experiment. The release points were only 10 miles away from the home loft, and it seems likely that the birds, while circling after release, could see the nearby release points. Certainly after 6 weeks of daily release from the same points it seems that the birds would be very familiar with the territory. The fact remains that in every one of the numerous comparisons set up by Graue's design, the means differ (though usually not statistically) in the direction predicted by training bias. The criticisms we have enumerated here do not therefore negate the fact that Graue's results remain the strongest evidence to date that training biases may occur in some pigeons.

A possible explanation for different results being obtained might be that different strains of homing pigeons differ in their response to direction training, but we used birds of three different strains in our experiments and found no obvious differences. More important might be the differences in handling the birds. It is well-known among pigeon fanciers that time of feeding, quantity and quality of grain fed, amount of exercise, breeding condition, and other factors play an extremely important role in homing performance. Perhaps if the birds are not maintained in peak condition, they are less able to orient successfully in the homeward direction (Gobert, 1969). It is interesting that Walcott and Michener (1967) and Michener and Walcott (1966, 1967) report finding evidence of a directional effect from their loft at Cambridge, Massachusetts, but that Walcott (pers. comm.) has found no evidence of such an effect from his new loft at Lincoln, Massachusetts. The birds at this new loft are of the same stock as the ones at the Cambridge loft and apparently have been handled and trained similarly.

Another possible cause for different results might be that certain conditions exist under which birds are more readily influenced by previous training. For example, a directional bias might be more pronounced after extensive training from a single direction, or naive birds might be more easily influenced by directional training. For this reason we performed six different series of experiments approaching the problem in a variety of different ways. In none of these did we find significant evidence of such a directional effect. We conclude, then, that it is not a general phenomenon.

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Summary

Six series of experiments were conducted using several different approaches to the problem of directional training. These included

extensive training in a single direction for pigeons with previous homing experience (Series I) and for pigeons with no previous experience (Series II and III); using naive birds to determine the effect of a single flight (Series IV); using an approach similar to that of Graue (1965) to determine the effect of the preceding flights on experienced birds (Series V); and testing at very long distances pigeons with much long-distance racing experience from the opposite direction. In these exhaustive experiments we found no conclusive evidence of any direction-training effect. We conclude, therefore, that if such an effect exists, it is of minor importance in the orientation of pigeons.

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