

THE ORIENTATION OF UNTRAINED PIGEONS: A DICHOTOMY IN THE HOMING PROCESS

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INTRODUCTION

It had been shown (Matthews, 1951*b*) that reasonably accurate orientation and homing could be obtained with young pigeons after a minimal training up to 25 miles. Recently Kramer & St Paul (1952) and Kramer (1953) have obtained similar results with older pigeons trained up to 10 miles only. Training thus appeared to be rather less essential than had been supposed, and to investigate this further, experiments with completely untrained young pigeons were required.

Table 1. *Results of previous experiments with untrained pigeons*

(Data from Rivière, 1929 (R); Gibault, 1930 (G); Heinroth, 1941 (H); Lockley, 1942 (L); Platt & Dare, 1945 (P)).

Distance (miles)	Released	Returned	Source
34	14	1	H
58	7	7	R
62-93	4	—	H
80	14	—	P
95-102	7	2	R
118	10	5	G
130	4	1	L
136	16	5	G
155	59	1	H
186	10	3	G
215	5	—	L
250-597	7	—	H

Anecdotes of untrained pigeons homing over considerable distances are plentiful, but it is almost impossible to obtain precise details. The very fact that such occurrences are particularly remembered is evidence of their rarity. A number of authors have reported on deliberate releases of untrained pigeons at distances over 25 miles from home, giving the results shown in Table 1. Few birds returned, and those slowly with only four returns on the day of release. Most reports of lost birds came from near the release point (31), but five had gone from 50 to 120 miles, all but one deviating less than 45° from the home line. There is thus a suggestion of navigational ability in these untrained pigeons, but as they stand the results can easily be fitted into a theory of random search for known landmarks such as that discussed by Wilkinson (1952). A considerable variation in the results obtained by different

workers is noticeable. Unfortunately, no details were given of the initial orientation of the birds after release, now recognized to be the keystone of any investigation of their navigational ability, and this could only be obtained by further tests.

MATERIAL AND METHODS

Young pigeons were reared at the Ornithological Field Station, Madingley, Cambridge, from the same breeding stock as those used in the main field experiments (Matthews, 1951*b*, 1953), being the third brood raised in the season. They were kept under normal conditions, and permitted the usual amount of almost daily exercise flights from the loft. The first experimental release (UT 1) showed the birds unwilling to fly far when thrown up for the first time, and so for subsequent tests the birds were previously given several experiences of spending nights in the basket, and of being released singly, all within the home compound, less than 150 yards from the loft.

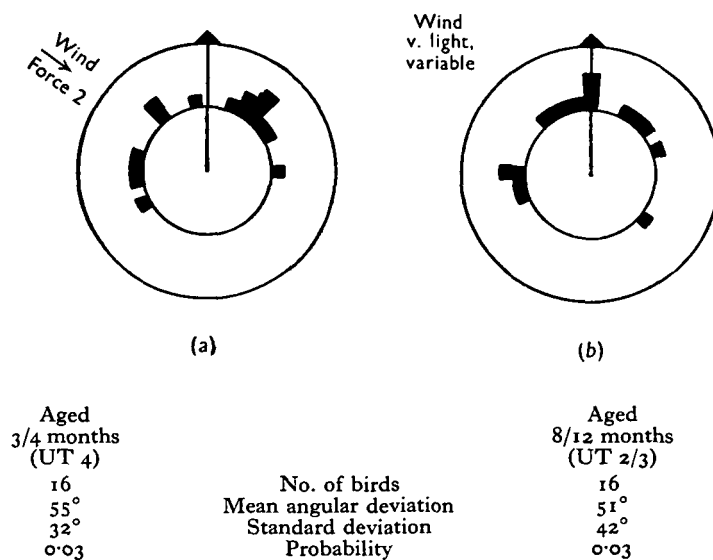


Fig. 1. The initial orientation of untrained pigeons. Explanation: the vanishing points are grouped into 10° sectors; solid arrow, home direction.

Release points were in open country with good all-round views. The birds were taken there in covered baskets and kept covered until release. In all cases this was in bright sunshine, with cloud 4/10th or less, the birds thrown up singly and followed with 16 × 40 binoculars until out of sight. The bearing of the vanishing point (Initial Orientation) and the time between release and vanishing (Orientation Time) were noted. The scatter diagrams (Fig. 1) obtained by plotting the vanishing points relative to the home direction were tested for statistical significance by comparing the mean angular deviation (regardless of sign) with that of a random distribution by means of a *t* test, as described in Matthews (1953).

RESULTS

Five pigeons, aged 13/14 weeks, were released singly at a point 78 miles distant, home bearing 345° , on 20 September 1951. This site had been used in a number of previous experiments, and scatter diagrams for these—T 9, 21, 28, 36—are available for comparison in Matthews (1953). In this first release (UT 1) no evidence on orientation was obtained. Four birds came down in distant trees. Another release was made at this point on 20 September 1952 (UT 4), using sixteen pigeons aged 13/16 weeks, which had had the basket training described earlier. These flew well and produced the initial scatter diagram shown in Fig. 1(a). This shows a definite homeward orientation, the t test giving $P=0.03$.

Not one of the twenty-one birds from these two releases returned home. The only one reported elsewhere had flown to a point 67 miles away only 22° off the home line, its error in latitude being only 7 miles. Too much emphasis cannot be laid on this, as the bird was not secured until 6 months after the release, although there is some evidence that it might have been present for a long time. Allowed to breed at Madingley it was released without further training on 16 September 1952, 65 miles WSW. Nothing further has been heard of it, and one cannot assume that it was a particularly gifted bird.

As it was possible that the distance was too great for the young, untrained birds, other tests were made with older birds, also untrained, at a shorter distance. Six cocks aged 31/33 weeks, which had been prevented from mating, were released at 50 miles, home bearing 022° , on 13 April 1952 (UT 2). An excellent orientation resulted, but again there were no returns. Birds with an even greater incentive to get home were therefore used in the next test (UT 3), eight cocks and four hens which had reared two broods of young and were starting a third, aged 39/52 weeks. To avoid any topographical bias, they were released at a similar distance to the NNW. instead of to the SSW., distance 53 miles, home bearing 158° . Two were 'treed' but the others gave an orientation similar to that in UT 2, and can be considered together with that in Fig. 1(b). The homeward trend is again statistically significant, $P=0.03$. Indeed the two distributions (a) and (b) are so similar that the chances of their being drawn from the same population are $P=0.8$, i.e. they can be considered together. The chances of such an overall orientation being produced by non-orientated birds are correspondingly lower, $P<0.001$. We can therefore have no hesitation in asserting that untrained pigeons show a homeward orientation when released in unknown country.

Even with the strong motivation presumed in UT 3 only one of the twelve birds returned home, being back early next morning. This cock was subsequently trained in the normal way and proved to be above the average in performance.

The results obtained with these untrained birds can be compared with those of birds which had had various amounts of training, as in Table 2. Scatter diagrams for the trained birds are figured in Matthews (1953). Training was by increasing steps in one direction to the distance shown, the birds then being released roughly at right angles to this training line. Those in T 9 were released in the opposite direction,

but at right angles to the previous critical test, T 8. Kramer's (1953) training was in all directions, so that the area flown over by his birds was 20 miles wide. His birds were released in small groups (all the others being singles) and include only those released after a short exposure to the sky, i.e. in comparable circumstances to the other tests. He gives no details of orientation times, and the proportion homing cannot be taken into account since it would be misleading. The releases of the untrained birds in his case were closely interspersed with those of birds that had already flown from the same point, and there is a strong possibility of the untrained birds joining with these potential guides out of sight of the release point.

Table 2. *Performances of untrained and trained young pigeons*

Test	Distance (miles)	Age (months)	Training (miles)	No.	Orientation (°)		Orientation time		Returns (%)
					Mean	s.d.	Mean	s.d.	
UT 1/4	78	3/4	Nil	21	55	32	5.6	2.4	Nil
UT 2/3	53	8/12	Nil	18	51	42	5.7	2.6	6
Kramer	200	13/19	10	10	46	24	N/A	N/A	N/A
T 12	49	4/5	25	10	47	31	5.8	4.2	70
T 15	62	4/5	50	10	67	51	4.1	2.5	80
T 36 C	78	4/6	80	13	45	22	3.8	2.3	76
T 8	79	5/6	130	47	45	30	3.3	1.1	87
T 9	69	5/6	130 + T 8	33	45	33	4.4	2.3	94
T 35 C	80	6	200	13	54	44	3.2	1.1	77

From Table 2 we can conclude that:

(1) The accuracy of orientation shows no significant improvement with training, the difference between the worst untrained and the best trained having $P=0.3$. This is not to be confused with the undoubted improvement that does occur *on* the training line due to a blunting of true navigational ability by constant release at one time and in one direction. Overtraining in this way may lower the accuracy of orientation off the training line as, respectively, in T 15 and T 35, as discussed in Matthews (1953).

(2) The orientation time becomes reduced with training, the fall being sharpest after the 25-mile stage, and the extreme values differing significantly.

(3) The proportion of returns mounts very rapidly with a small amount of training. Thereafter there may be some further improvement, but this is not consistent.

These conclusions suggest that there is an essential dichotomy in the homing process, namely between the factors governing initial orientation, which are completely innate, and those governing the actual return, which are largely dependent on individual experience. Orientation time falls in the latter group, and it is probable that in the good conditions of these tests it bears little relation to the orientation process, although when the latter is disturbed (Matthews, 1953) there is a corresponding rise in the orientation time. A less definite term, such as 'Time in sight' would probably express this measure of performance better.

The nature and basis of the process producing initial orientation has been examined in another paper (Matthews, 1953), in which the conclusion was reached that a form of sun navigation, as proposed earlier (Matthews, 1951*a, b*), is probably concerned. This would be a highly complicated process which certainly could not be learnt by an individual, and so is in accord with the demonstrated innate nature of the orientation process. The young birds of course had no opportunity to 'practice' such a mechanism in their restricted exercise flights from the loft. The slight improvement in orientation with experience is probably due to a weeding out of imperfectly equipped birds, and to less loitering near the release point which means less chance of a bird being lost on evolutions not connected with orientation.

The factors which are concerned with the actual successful return, and which are developed by individual experience can probably be placed in three groups:

(*a*) *Psychological*. Training gives a bird the experience of flying considerable distances back to the loft, implanting the information that flying long enough in the direction indicated by the orientation mechanism will produce the desired result. The 'confidence' thus imparted also increases the willingness to start out alone (witness the decrease in 'orientation' time) and makes the bird less likely to be diverted from its course by joining strange flocks of pigeons. The awareness that food will be waiting at the end of the journey will also prevent foraging and possibly fatal delay.

(*b*) *Topographical*. Young untrained pigeons do not go far from the loft on exercise flights; repeated observation makes it doubtful if they explore more than a mile radius. Certainly it is possible to lose them at short distances on the initial training steps— $\frac{1}{2}$, 1, 2, 4, 6 miles—eighteen young birds disappeared from these releases in 1951 and 1952, 13% of the total. With such a small 'target' the chances of even a well-orientated and 'confident' bird reaching home from 50 or 80 miles would be understandably slight. Training that increases the 'target' width to 20–30 miles brings it within the limits of accuracy that could be postulated for sun-navigation.

(*c*) *Physical*. The development of strong muscles and stamina would be hastened by training, but this is less likely to be critical. The untrained birds at 12 months were certainly stronger than the trained youngsters a third the age.

It was demonstrated earlier (Matthews, 1951*b*) that there were wide individual variations in homing ability. This, of course, only confirmed the opinions of practical fanciers who treat their champion racers as individuals—making allowance for one always flying itself to exhaustion, another always taking its time, for one homing faster to eggs, another to young, and so on. Indeed the multiplicity of their schemes for success reflects the highly complicated nature of the problem. Statistical confirmation of this point, and of the contrast with the relatively unitary nature of the orientation process, can be obtained from a consideration of the individual case histories of the birds used in previous tests. Details of initial orientation, time in sight and homing success are recorded for each sortie flown. The individual performance over the season can be reduced to numerical indices

by awarding arbitrary points according to the method described by Matthews (1952*b*). The justification for the values allotted and other features of the scheme is given therein; here the basic details are set out baldly in Table 3. Limiting consideration to those birds which made at least two individual sorties from 50 miles or more in sunny conditions, but otherwise taking all available data, we have indices for 104 birds, covering 482 sorties.

Table 3. *Arbitrary system of points awarded for performances*

Initial orientation				
Deviation from home ...	0-30°	-45°	-60°	-90°
On training line	20	15	5	2
Off training line	40	30	10	4

Returns					
Back on ...	1st day, speed above average	1st day, speed below average	2nd day	3rd day	Later
On training line					
50 miles	20	10	5	2	1
80 miles	40	20	8	3	2
Off training line					
50 miles	40	20	15	6	3
80 miles	80	60	10	10	5

Notes. (1) repeat performances rated at half the values shown; (2) allowance for tests missed by bird's own shortcomings made by adding percentage of possible points to total gained; (3) resultant totals scaled down so that best performance in each section rates 100.

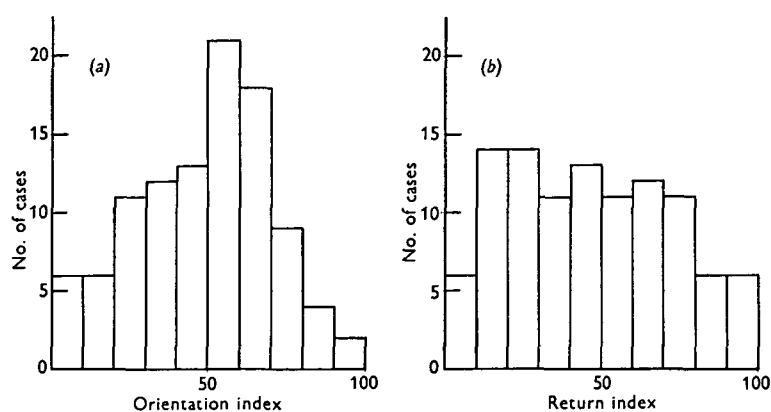


Fig. 2. Frequency distribution of indices of orientation and return.

The frequency histograms for the resultant indices of orientation and return are shown in Fig. 2(a), (b). They have mean values close to the median value, 47 in each case, indicating an adequate sample. But the distributions are very dissimilar ($P=0.01$). That of the orientation index approaches the form of a normal curve which would result if we were dealing with a single quality (or group of interdependent qualities) varying about its mean. On the other hand, that of the return

index departs strongly from normal and is of the form that would be expected if we were measuring the effects of a large number of independent factors.

The relation between the two indices is shown by the contingency table (Table 4). There is a general overall association between them ($P=0.01$) as would be expected with qualities which both contribute to homing success and thus likely to be selected out together to some extent. At the same time, since such a large number of factors is concerned, the chances of their being equally developed in one bird are small, and the correlation is by no means strict. It is strongest in the case of birds showing poor orientation ability, such birds generally producing poor returns. With good or moderate orientation ability the factors governing the return assume the greater importance. We have a further indication here that the orientation mechanism need not be of phenomenal accuracy, its main function being to impart a homeward trend to the flight from unknown country, home being pin-pointed by pilotage rather than navigation.

Table 4. *Relation of indices of orientation and return*

		Orientation		
Index		0-33	-67	-100
Return	0-33	18	17	5
	-67	5	23	11
	-100	5	14	6

It would clearly be desirable to follow up these individual variations in ability on a genetical basis, but this would be extremely difficult, if not impossible, with such a relatively slow breeding animal, quite apart from difficulties of measuring the factors under consideration. There is no doubt that the selection imposed by racing the birds, and by 'intuitive' cross-breeding, can improve their homing qualities. The differences between performances of birds given the same training and tests, but coming from separate stocks was demonstrated earlier (Matthews, 1951 *b*), and that conclusion is confirmed by the more refined method of assessment used in the present paper. Thus the birds used in 1949 from Duxford (27) and from Sawston (25) which had sufficiently complete case-histories gave distributions of indices as follows:

	Orientation		Returns	
	Duxford	Sawston	Duxford	Sawston
Mean	49	67	52	67
S.D.	25	21	28	20

The Sawston stock gave a higher mean value and less variation in both cases, particularly in the (innate) orientation process, the differences being significant with $P=0.009$ and 0.04 respectively.

DISCUSSION

Now that the very different natures of the orientation and homing processes, and their hereditary basis, have been demonstrated, the reasons for conflicting results obtained with pigeons by various authors will be clear. Many doubtless worked with birds of inferior stock, often just to test some private theory, and without taking the necessary step of getting to know one's experimental animal. Also attention was concentrated on the returns rather than on the initial orientation. The basis of the navigational process is the problem of the greatest theoretical interest (although it may yet have practical implications), and it is now clear that it will be solved by investigation of the orientation behaviour. It is even doubtful if observation of the homeward track by aircraft or more subtle devices will be as useful. The amount of training given to pigeons before an experimental release can be much reduced, *provided* the birds are derived from a stock with homing qualities highly developed. This will reduce the amount of work for a given result, and also reduce the number of birds lost on routine training, and thus 'wasted'.

It is at least probable that a similar dichotomy in the homing process will be present in wild birds, the 'training' being provided by migration experience. The only comparable experiment to those described for pigeons was that by Ruppell & Schein (1941) with young starlings. These were prevented from migrating and kept over winter in an aviary until they began breeding. Taken to a point 71 miles away they all failed to home, although starlings similarly treated after several return migrations homed well. The vital orientation data are lacking however, as the birds simply flew into trees on release. It must be emphasized that for parallel studies on navigation in wild birds, a species that has suitable release behaviour must be used. Ideally this is a bird that is unwilling to settle (i.e. released over unfavourable terrain) and which depends on flapping flight in these circumstances (i.e. not soaring birds).

Such studies as have been made with non-migratory birds (e.g. Creutz, 1949) have indicated a very restricted homing ability, but again adequate orientation data are lacking. Matthews (1952*a*) showed that the Herring Gull, a restricted nomad, was a much poorer homer than the migratory Lesser Black Back Gull, but that (statistically insufficient) traces of homeward orientation could be found in the former. This raises the speculative point of whether an orientation mechanism could remain in a population not making active use of it. It must be remembered that migration is a somewhat flexible habit. Lack (1943) showed that birds of a single species in one area varied in their migratory habits, and differences in this respect between local groups of a species are well known, e.g. Herring Gulls in Britain and on the Continent. Moreover, the Lesser Black Back Gull in Britain has in the last 100 years (say in some twenty generations) changed from being mainly resident throughout the year to a total migrant, and is now showing signs of reverting to its former status. Even with such flexibility a navigation mechanism that had no other function might well be eliminated in a sedentary population. But if the mechanism was based on an organ, such as the eye, and on physical data, such

as the sun's co-ordinates, which both play other vital roles in the animal's life, then it might well continue, dormant, ready to become effective if circumstances suddenly demanded it.

SUMMARY

1. It is demonstrated that young pigeons without any previous training show a definite homeward orientation at a distance, yet home very badly.
2. The results are compared with those of birds with varying amounts of training. An essential dichotomy in the homing process is revealed, between the orientation process which is innate and the process of return which is governed by factors developed by individual experience.
3. The further contrast between the unitary nature of the orientation process and the multiplicity of factors concerned in the return is supported by statistical consideration of the individual variation in ability.
4. The practical and theoretical implications of these conclusions are considered.

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