HOMING OF SINGLE PIGEONS—ANALYSIS OF TRACKS

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INTRODUCTION

The way in which homing pigeons find their home lofts is still obscure despite a long history of investigation. Since the work of Kramer & St Paul (1950a, 1952) and of Matthews (1951, 1953), it has been widely believed that some homing pigeons possess the ability to navigate. This belief is now based on the results obtained by many workers (see Schmidt-Koenig, 1965, for a critical review), which indicated that some pigeons arrived home from unfamiliar territory too quickly to be explained by their simply having searched for familiar landmarks. Other investigators found that pigeons released from unfamiliar locations showed an initial orientation toward the home loft. But there has always been a wide variation of the pigeons' homing times and a large scatter of the initial departure directions in such studies. This scatter has limited the usefulness of these data in deciding exactly what environmental cues were important for the pigeons' homing.

In the belief that a knowledge of the pigeons' flight-path from release point to home might reduce this scatter and thus yield more information about the method the pigeons use to orient, Griffin (1952a) and Hitchcock (1952, 1955) used aeroplanes to follow visually the homeward flights of the pigeons. In their separate studies of small flocks of pigeons, both investigators reported that the pigeons were generally well oriented to the loft even in unknown territory. But the behaviour of a flock is always some unknowable consensus of the reactions of the individual birds and is thus difficult to analyse. Hitchcock (1955) reported following single pigeons visually by aeroplane but found that they frequently flew very erratically and often landed in trees. Because of the difficulty of keeping single pigeons in sight, the study did not provide conclusive information about the tracks taken by individual birds.

Clearly, any real understanding of pigeon navigation must be based on what individual pigeons do on their flights home. Fortunately, the use of radio telemetry has enabled us to overcome many of the problems of following single pigeons. In this paper, we will report the results of tracking sixteen birds on 136 trips to their home loft, and we will discuss what these tracks imply about the pigeons' homing.

MATERIALS AND METHODS

Birds

The study was begun in the spring of 1964 with a pre-established loft at Cambridge, Massachusetts. All the pigeons we have used come from native racing stocks which are

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considered by local racers to be above average in homing performance. The twenty pigeons used during the 1964 season were 2- and 3-year-old adults whose previous detailed experience is unknown. The previous owner of the loft had released these pigeons from places on a line W.N.W. of the loft at distances up to 100 miles (160 km.). The birds had never been taken to any place off this training line but may well have flown over almost any part of southern and eastern New England on their homing flights. During the year between the spring of 1963 and the beginning of the study in 1964 the pigeons were totally confined to the loft. Other pigeons used during the 1965 and 1966 seasons were either obtained as fledgling young from local racers during the springs of 1964 and 1965 or were bred from our stock birds.

Lofts

One of the two lofts used in this study was located in the Harvard Biological Laboratories on the top (fifth) floor, 50 ft. (15·2 m.) above the street level in the city of Cambridge. The room was 10 ft. by 9 ft. (3·0 × 2·7 m.), with a large window in the southern wall containing the landing shelf with a one-way gate. A wire cage, 7 ft. by 3 ft. (2·1 × 0·9 m.), was suspended over the landing shelf and communicated with the loft by one open window, allowing the pigeons to sit outside the loft at any time. This cage provided the birds with a 180° view of the buildings and the sky south of the loft.

The other loft was a small building approximately 8 ft. by 20 ft. (2·4 × 6·1 m.) located in the country in Lincoln, Mass., about 10 miles (16 km.) west of Cambridge. The arrangement of the loft was similar to that at Harvard except that the large viewing cage was located on top of the loft rather than on its side and was only accessible to the pigeons on days when they were not free to fly outside the loft. Water and grit were provided in excess in the lofts at all times, and food was administered once daily. The pigeons were allowed to fly outside the loft almost every day, usually just before being fed.

Pigeon transmitters

Each pigeon to be tracked is equipped with a small radio transmitter similar to those described by Lord, Bellrose & Cochran (1962). The whole transmitting package weighs 25–30 g., including harness, batteries, oscillator, and antenna. The components and the batteries are enclosed in waterproof capsules and wrapped in plastic tape to hold them to the harness. The oscillator is a single transistor, crystal-controlled unit, which delivers the 52 mHz signal to a 15 in. (38 cm.) whip-antenna through a small loading coil. The antenna projects backward over the pigeon's tail and is made of 0·023 in. (0·6 mm.) diameter copper-plated music wire, which is stiff enough so that the birds do not hook it around objects during their normal activities (Fig. 1).

The transmitter is mounted on a wire platform and is attached to the pigeon by a harness made of five rubber bands. We found that placing the transmitter over the pigeon's centre of gravity greatly interfered with the pigeon's wing movements during flight, so it was moved back over the bird's rump.

The harness alone, although weighing only 1½ g., caused many pigeons to show agitation and 'discomfort' when it was first put on them. Frequently, when a harness alone was first installed, the bird would run backwards, somersault, and apparently attempt to get rid of the device. This behaviour never lasted longer than 15 min. after the harness was put on, and by training the birds with dummy transmitters this

reaction was almost totally eliminated. Most pigeons wearing a new transmitter would preen and quickly settle down to normal life again. Males were frequently seen to court females without seeming to be aware of the device. This same pattern of behaviour was observed whether the harness alone was put on the pigeon or whether the harness had an antenna and transmitter attached to it.

No differences could be seen, even by experienced pigeon racers, in the flight of a bird with or without harness and transmitter. Even when pigeons were not given a chance to preen, but were tossed upward immediately after harnessing, we frequently saw them circle, climb, glide, and land without unusual effort.
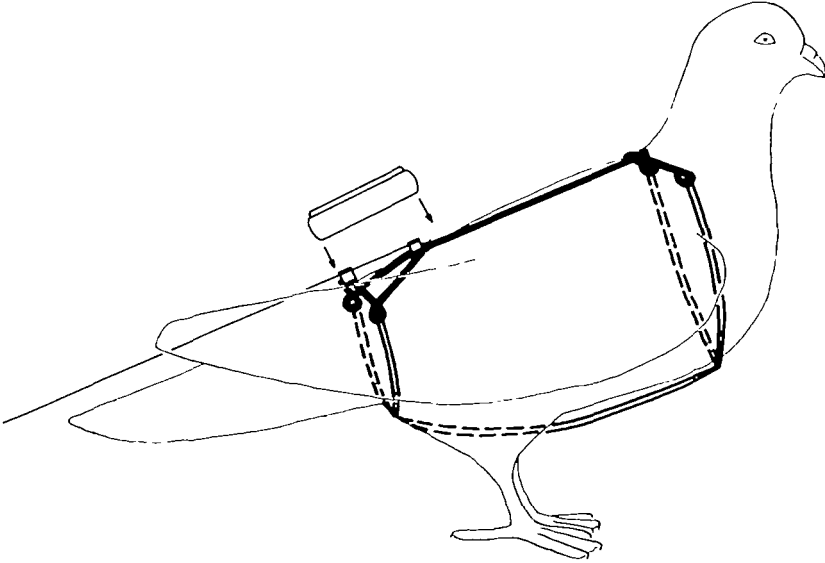

Fig. 1. Diagram of pigeon with harness and antenna. The heavy wire on the back is held by two rubber bands around the neck and two rubber bands around the tail, joined underneath by a fifth rubber band (shown looser than normally). The antenna is fastened to two insulators above the rump. The transmitter and batteries are then taped to the wire platform on the rump.

Another piece of incidental evidence suggests that at least some of the pigeons could adapt to the transmitter quite well. One bird was lost on a routine training flight while wearing an operating transmitter. It returned after an absence of 1 month still wearing the unit, in good health, and with no signs of abrasion from the harness. When the batteries were replaced, the transmitter worked immediately. One can assume that this bird did not enter another loft, because the owner would probably have removed the device to examine it, and would than have opened the plastic tape to look inside, whereas the tape was intact as originally placed. Yet the bird was not excessively thin, so it must have lived off the land during the month it was away.

Comparative releases of the birds with and without transmitters showed no marked differences in the birds' best homing speeds (Michener & Walcott, 1966). Therefore, no further effort was made to reduce the weight of the transmitting package.

Training

We trained our pigeons by releasing them in flocks at increasing distances along a line to the W.N.W. of home. This training-line procedure was chosen in order to

develop each pigeon's ability to fly and to bring it into good physical condition, while still keeping the area of countryside it might see to a minimum. This procedure also gave each pigeon an opportunity to learn a small area of landmarks very well, and enabled us to compare the bird's orientation in such presumably familiar regions with that in less familiar places. It also provided the pigeons with a well-defined training direction, which simplified the later analysis of their tracks from new release points.

After being trained in a flock from points up to 40 miles (65 km.) away, the birds were individually released along the same training line at increasing distances from the loft. Pigeons that were selected for tracking were always released singly, because it was desirable to develop whatever abilities each possessed to orient individually without its being able to rely on other members of the flock to find the loft. It was therefore frustrating to observe that single pigeons often waited after being released until another bird was set free, and then flew home directly in the company of the other bird. Even when birds were released from a moving automobile ¾ mile (1 km.) apart, they developed good skill at finding each other and flying home in pairs, as shown by observations at the loft of arriving groups. This agrees with the findings of many pigeon racers and of Kramer & St Paul (1950a). This behaviour made intensive training of more than a few birds from a single release point impossible, because each had to be released only after it was certain that the preceding bird had left the area.

It is important to remember that all the birds we have tracked were trained in this way. This means that we cannot rigorously exclude the possibility that an individual bird was familiar with a wide range of landmarks and with places well off the training line. However, the behaviour shown in their tracks (as will be discussed) seems to imply that such previous familiarity with landmarks is not very important.

Tracking

The pigeons were tracked with a National HRO 500 radio receiver and a Techcraft converter in a Cessna 180 single-engine aeroplane. The receiving antennas were a pair of dipoles stretched from each wing strut back to the side of the fuselage just in front of the tail. In this way, the fuselage acts as a shield between the two antennas; the antenna on the right mainly picks up signals on the right. By switching between the two antennas as the plane turns, it is possible to determine the pigeon's direction from the plane within a few degrees. The strength of the signal is a measure of how far away the pigeon is from the aeroplane. Using this system, we have been able to hear a pigeon from as far away as 20 miles (32 km.). This range has enabled us to leave pigeons when they stop flying at night, and then to find them in the same location before sunrise the next morning. In addition, we could leave a flying pigeon to refuel the airplane, and then find it once again even though it had flown several miles. Thus, during the 3-day life of the transmitter batteries, we could almost always find the pigeon again after leaving it for any length of time.

At first we tracked by continuously circling the pigeon with the aeroplane. This procedure proved disturbing to the pigeon (Michener & Walcott, 1966), and it was discarded in favour of our remaining as far away from the bird as possible while still being able to obtain an accurate set of fixes. The new pattern that was developed in mid-summer 1964, prior to most of the tracks off the training line, is as follows. After releasing the pigeon from the ground at the airport we waited until it had flown

far enough for the signal to fade noticeably ($\frac{1}{2}$–3 miles). We then took off and by the time we had caught up with the pigeon it had already gone about 5 miles (8 km.). This allowed the bird to begin its course without reference to the operations of the aeroplane. The plane was then flown so as to keep it over the territory from which the pigeon had just come. This allowed the pigeon to choose almost any course, except straight backward, without encountering the aeroplane. In order to obtain the radio fixes on the bird, we would then fly toward the bird until we were about $\frac{3}{4}$ mile from it, then make a 180° turn and fly away again, back toward the area we had just covered. When we were 5–10 miles behind the pigeon we turned again toward the signal source. This tracking pattern was not oriented in any way to the loft or the release point, *per se*, but only to the path which the bird had chosen most recently.

The data were collected as the aeroplane made the turn nearest the homing pigeon and were recorded as dots on aeronautical maps of the terrain. The time of each fix was also recorded to the nearest minute. Since we could use the radio tracking system to locate light-coloured pigeons visually whenever we tried, these fixes probably represent the pigeons' actual positions to an accuracy of less than $\frac{1}{4}$ mile (350 m.). The fixes were then connected by a line to indicate roughly the course taken by the pigeon. Lapses in tracking are indicated on the maps by a series of widely spaced dashes which are arbitrarily drawn straight from the point where the bird was lost to the point where it was found again. Places where the pigeons perched for any length of time are indicated by crosses on the maps.

<div align="center">RESULTS</div>

The pigeons were tracked repeatedly from their training points in order to explore the daily variations in their homing behaviour. The resulting variations in straightness were tested to find if they were correlated with any feature of the weather, the particular release point, or any other variable.

Each pigeon was then tracked from points from which it had never been released before. These new release points lay off the training line, in order to enable us to distinguish between the birds' use of landmarks, fixed-direction orientation and true orientation to the loft by other means. The results of each of these procedures will be discussed in sequence.

<div align="center">*Training releases and tracks*</div>

Sixteen pigeons were trained by successive releases and then tracked to the loft more than four times from the training point. During 1964, Fitchburg Airport at North Leominster, Mass., was used exclusively as the training point; in 1965 and 1966, Worcester Airport, at Worcester, Mass., Orange Airport at Orange, Mass., and Manchester Airport at Manchester, New Hampshire, were also used.

Fig. 2 shows all the training tracks of Blue Y AL from Worcester, Blue W AL* from Manchester, and Blue R-19 from Orange. The training tracks of four other birds are included in Figs. 3–6. The 33 tracks of these 7 birds are typical of the 78 training tracks we observed.

It is clear that no two tracks of any bird coincided for appreciable segments, even

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* The names of the pigeons are based on their plumage and bands. This pigeon had 'Blue' plumage, a White band on its left leg, and an ALumininum band on its right leg. Those pigeons with only one band are referred to by the colour and number of this band, as in Blue Red-19. The colours are W = white, R = red, Y = yellow, B = blue, X = no band.

though no bird flew more than 10 miles (16 km.) from a straight line. In order to assess the straightness of these tracks, two measures have been found helpful. One will be called *deviation*, and expresses the average extent to which the track differs from a perfectly straight line between release point and loft. It is calculated by sampling the distance between the track and the straight line at ten or more points, regularly spaced along the track. The absolute values of these samples are then summed and divided by the number of samples (averaged). The result is the average number of miles that the pigeon was off course along the length of the track. For a given angular inaccuracy,
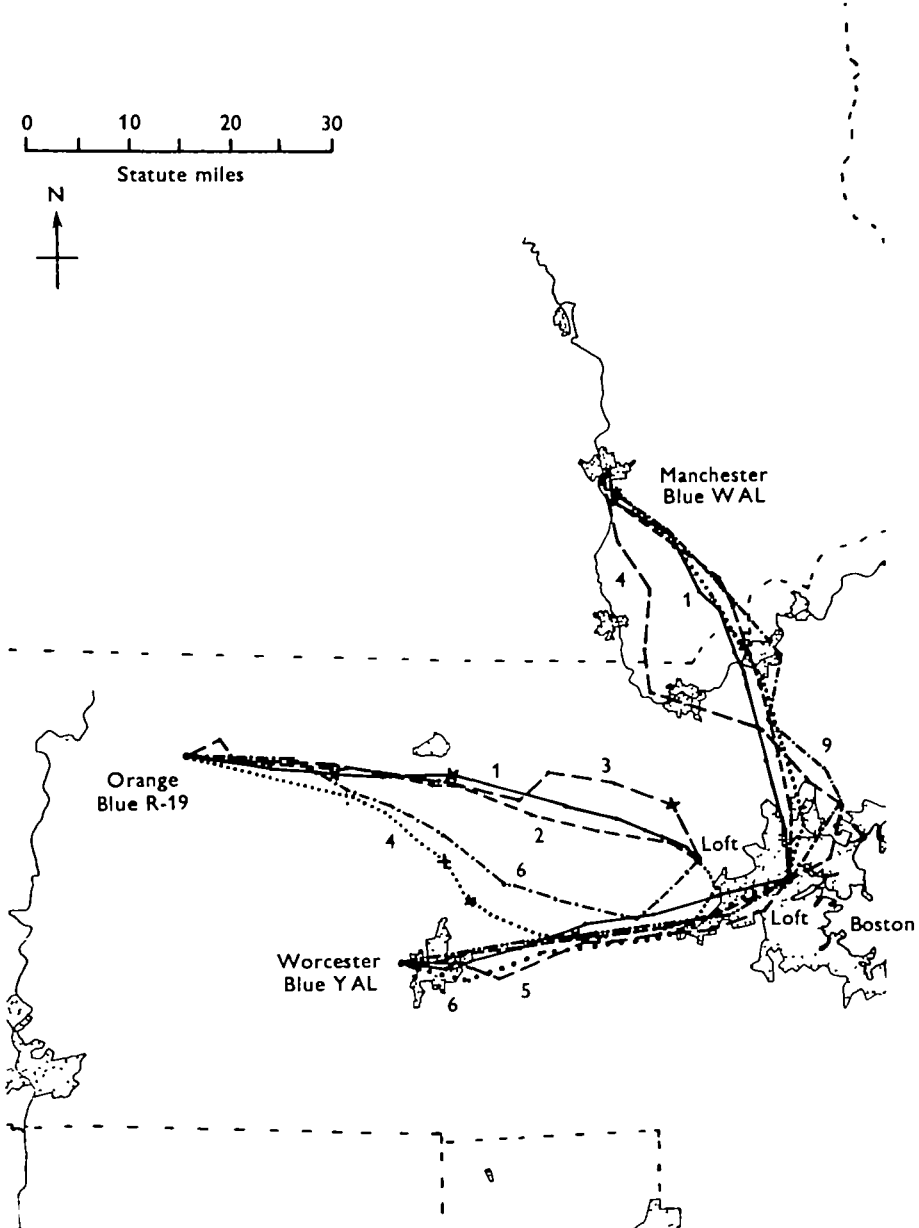
Fig. 2. For legend see facing page

however, this linear distance should be larger as the release distance increases. There-fore, the average deviation of each track is divided by the straight-line distance from release to loft (release distance), and the result is expressed as a percentage deviation.

The other measure is more useful on tracks where a bird changes course frequently but does not fly very far away from the straight line. It will be called the 'length ratio', and is simply the total distance the bird flies divided by the release distance. This measure shows how much farther a pigeon flew than the straight line distance to the loft, and is expressed as a decimal ratio. A ratio of 1·000 is an ideal flight, and would, of course, have a deviation of 0·0 %.

Table 1 gives the deviations and length ratios of all the tracks of the sixteen birds studied to date (exclusive of those given in the legends of Figs. 2–6 and 8). For most of the training tracks the deviations lay between 1 % and 10 %, and the length ratios between 1·02 and 1·20. This means that for a typical release distance of 40 miles (65 km.) the birds' tracks were, on the average, 0·4–4 miles (0·6–6 km.) from a straight line, and the birds flew 0·8–8 miles (1·3–13 km.) farther than they would have had to if they had gone directly home.

In order to see if there were consistent differences in the straightness of different birds' tracks from the same release point, we compared the deviations and length ratios. Taking all the birds from the same release point, two at a time, a *t* test was employed to find out if their tracks were significantly different. Among the five birds tracked from Fitchburg only one of the ten possible tests showed significant differences in the tracks' deviations ($P < 0.05$), whereas three tests showed significant differences

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Legend to fig. 2

Fig. 2. Tracks from the training points of Blue W AL, Manchester, N. H.; Blue Y AL, Worcester, Mass.; Blue R-19, Orange, Mass. Stippled regions show major cities, thin lines are rivers. For explanation of weather symbols, see Table 1. Track 7 not shown.

	Track no.	Release point	Date	Release time (E.S.T.)	Sky	Visi-bility (miles)	Wind Direc-tion	Wind Speed (m.p.h.)	Devia-tion (%)	Length ratio
			Blue W AL							
———	1	Manch.	31. iii. 65	09.40	O	40	330°	18	8·8	1·060
– – – –	3	Manch.	12. v. 65	07.20	O	40	320°	8	10·5	1·079
— —	4	Manch.	21. v. 65	09.48	O	40	170°	6	6·4	1·503
. . . . .	5	Manch.	26. v. 65	08.53	◑	10	340°	12	10·5	1·053
	7	Manch.	16. vi. 65	11.23	◑	15	090°	5	11·3	1·113
·—·—·	9	Manch.	27. vi. 65	11.17	◑	15	270°	12	13·1	1·180
			Blue Y AL							
———	2	Worc.	1. vi. 65	09.52	◑	40	290°	10	1·9	1·008
– – – –	3	Worc.	11. vi. 65	10.35	◑	—	320°	14	3·5	1·024
— —	5	Worc.	27. vi. 65	08.48	◑	15	270°	12	6·8	1·087
. .	6	Worc.	2. vii. 65	08.28	O	40	230°	8	5·4	1·024
·—·—·	8	Worc.	15. vii. 65	13.27	◑	20	320°	14	3·4	1·024
			Blue R-19							
———	1	Orange	12. vi. 66	09.34	O	40	150°	10	4·2	1·030
– – – –	2	Orange	19. vi. 66	09.45	◑	—	Light		3·2	1·020
— —	3	Orange	21. vi. 66	10.15	◑	15	320°	8	Incomplete	
. . . . . .	4	Orange	3. vii. 66	10.45	◑	12	300°	10	10·5	1·240
·—·—·	6	Orange	16. vii. 66	14.15	◑	—	270°	15	6·3	1·100

Table 1. *Data for all the tracks from the training points, excluding those given in the figure legends in this report*

Track no.	Release point	Date	Release time (E.S.T.)	Sky*	Visi- bility (miles)	Wind† Direc- tion	Wind† Speed (m.p.h.)	Devia- tion (%)‡	Length ratio‡
				Silver AL Y (referred to as 'Silver' in previous papers)					
1	Fitchburg	18. iv. 64	07.00	○	—	290°	10	4·9	1·04
2	Fitchburg	19. iv. 64	12.03	○	—	050°	15	5·7	1·065
3	Fitchburg	21. iv. 64	14.48	◐	10	120°	10	7·7	1·095
4	Fitchburg	25. iv. 64	09.20	◐	12	Calm		6·1	1·035
5	Fitchburg	26. iv. 64	06.41	◐	10	250°	5	8·7	1·085
6	Fitchburg	2. v. 64	16.49	○	30	100°	5	3·2	1·06
7	Fitchburg	3. v. 64	13.11	◐	12	120°	8	2·5	1·08
8	Fitchburg	6. v. 64	10.20	○	6	120°	5	1 8	1·055
9	Fitchburg	30. v. 64	16 02	◐	15	140°	10	4·3	1 095
10	Fitchburg	31. v. 64	12.39	○	—	120°	15	10·2	1 21
		Blue B AL Fitchburg, see Fig. 6 (referred to as 'Blue' in previous papers)							
				Red W Y					
1	Fitchburg	7. v. 64	11.49	◐	8	240°	8	4·6	1·325
2	Fitchburg	29. v. 64	13.45	◐	20	340°	10	14·2	1·155
3	Fitchburg	30. v. 64	08 05	◐	15	Light		11·2	1·085
4	Fitchburg	31. v. 64	08.53	◐	15	Light		4·3	1·11
				Blue X W					
1	Fitchburg	6. iv. 64	11.43	◐	10	230°	17	7·8	1·91
2	Fitchburg	11. iv. 64	10.23	○	—	Light		Incomplete	
3	Fitchburg	21. iv. 64	17.03	◐	10	120°	10	16 9	1·635
4	Fitchburg	26. iv. 64	13.38	◐	10	250°	5	14·2	1·54
5	Fitchburg	27. iv. 64	16.32	◐	—	270°	10	2 2	1·225
6	Fitchburg	30. iv. 64	13.43	○	30	120°	10	Incomplete	
7	Fitchburg	1. v. 64	09 15	○	—	090°	10	2 6	1·195
8	Fitchburg	2. v. 64	08.21	○	30	120°	10	4·6	1·19
9	Fitchburg	31. v. 64	08.53	○	—	Light		6·0	1·30
				Silver W R					
1	Fitchburg	12. v. 64	15.50	◐	8	130°	14	2·0	1 080
2	Fitchburg	29. v. 64	06.39	◐	15	300°	10	0·5	1·020
3	Fitchburg	11. vi. 64	09.18	○	40	320°	15	1 1	1·015
4	Fitchburg	15. vi. 64	11.19	◐	—	Light		5·0	1·110
5	Fitchburg	18. vi. 64	09.18	○	40	Light		0·7	1·015
6	Fitchburg	5. vii. 64	16.12	◐	8	Calm		10·1	1·225
7	Fitchburg	14. viii. 64	12.48	◐	30	290°	12	2·1	1·030
				Grizzle 431					
1	Manchester	17. iii. 65	12.56	○	40	330°	10	2·5	1·21
2	Manchester	31. iii. 65	11.57	○	40	330°	17	6 0	1·038
3	Raymond	1. iv. 65	11.06	○	40	310°	12	5·6	1·203
4	Manchester	5. iv. 65	16.23	○	40	360°	7	3 0	1·026
5	New place								
6	New place								
7	Manchester	12. v. 65	09.06	○	40	320°	8	10·5	1·060
8	Manchester	1. vi. 65	12.18	◐	40	290°	10	10 7	1·097
				Silver 442					
1	Worcester	21. vii. 65	13.00	◐	40	280°	8	2·9	1·055
2	Worcester	29. vii. 65	10.50	◐	40	290°	12	2 3	1·007
3	Worcester	30. vii. 65	13.48	◐	40	260°	7	2·4	1·007
4	New place								
5	Worcester	24. viii. 65	11.48	◐	15	290°	12	3·7	1·027

Table 1 (*cont.*)

Track no.	Release point	Date	Release time (E.S.T.)	Sky*	Visibility (miles)	Wind† Direction	Speed (m p.h.)	Deviation (%)‡	Length ratio‡
			Blue Y AL, Worcester (see Fig. 2)						
			Blue W AL, Manchester (see Fig. 2)						
			Blue R-9						
1	Manchester	14. viii. 66	09.48	O	40	Calm		7 4	1·189
2	Manchester	25. viii. 66	10.13	◑	30	330°	7	2·4	1·055
3	Manchester	27. viii. 66	11.40	O	40	280°	10	5·4	1·189
4	Manchester	29. viii. 66	13.18	O	40	Calm		Incomplete	
5	Manchester	1. ix. 66	12.50	◑	10	Light		6·6	1·055
6	Manchester	6. ix. 66	13.21	◑	40	250°	13	0·3	1·00
			Grizzle R-10, Orange (see Fig. 4)						
			Blue R-19, Orange (see Fig. 2)						
			Blue R-22						
1	Orange	1. viii. 66	10.36	O	30	Light		3·1	1·175
2	Orange	7. viii. 66	12.00	O	6	180°	12	Incomplete	
3	Orange	12. viii. 66	14.12	◑	10	270°	17	3·3	1·065
4	Orange	14. viii. 66	13.52	◑	40	230°	10	1·8	1 008
			Blue W W						
1	Orange	8. vii. 66	10.04	◑	20	270°	7	1·5	1·014
2	Orange	23. vii. 66	13.34	◑	7	180°	10	2·8	1·025
3	Orange	25. vii. 66	10.30	O	10	Light		4·3	1·042
			Blue W Y, Orange (see Fig. 5)						
			Blue B-77, Orange (see Fig. 3)						

* The standard meteorological symbols mean: O, clear; ◑, scattered clouds; ◑, broken clouds; ⊕, overcast clouds.
† Number of degrees clockwise from true north from which the wind blows. Speed is in m.p.h.
‡ Discussed in text.

between the length ratios. With the three birds trained from Manchester one of the three pairings showed significant differences in the deviations, but none of the comparisons of the length ratios was significantly different. The tracks of the two birds trained from Worcester were not significantly different in either measure of straightness, nor were any of the tests between the six birds trained from Orange significantly different in either respect.

It is interesting that, when all the tracks from each release point were grouped and compared with those from other release points, more rather than fewer significant differences were found. Among the deviations, there were three of the six pairs of comparisons where $P < 0.05$, and three of the six tests of the length ratios were also significantly different. Considering the track deviations alone Manchester tracks differed significantly from both Worcester and Orange tracks but not from Fitchburg tracks (which, in turn, differed significantly only from Orange tracks). This pattern was only partly reflected in the length ratios: Fitchburg differed from Orange as before, but it also differed from Worcester. Manchester only differed significantly from Worcester, but not from Orange.

It is difficult to evaluate these analyses. They seem to indicate, first, that there are significant differences between straightnesses of the tracks of some individual birds, and second, that there are significant differences in straightness of all the tracks from some different release points. As yet there is insufficient data to determine whether these results are caused by differences between individual birds or are characteristic
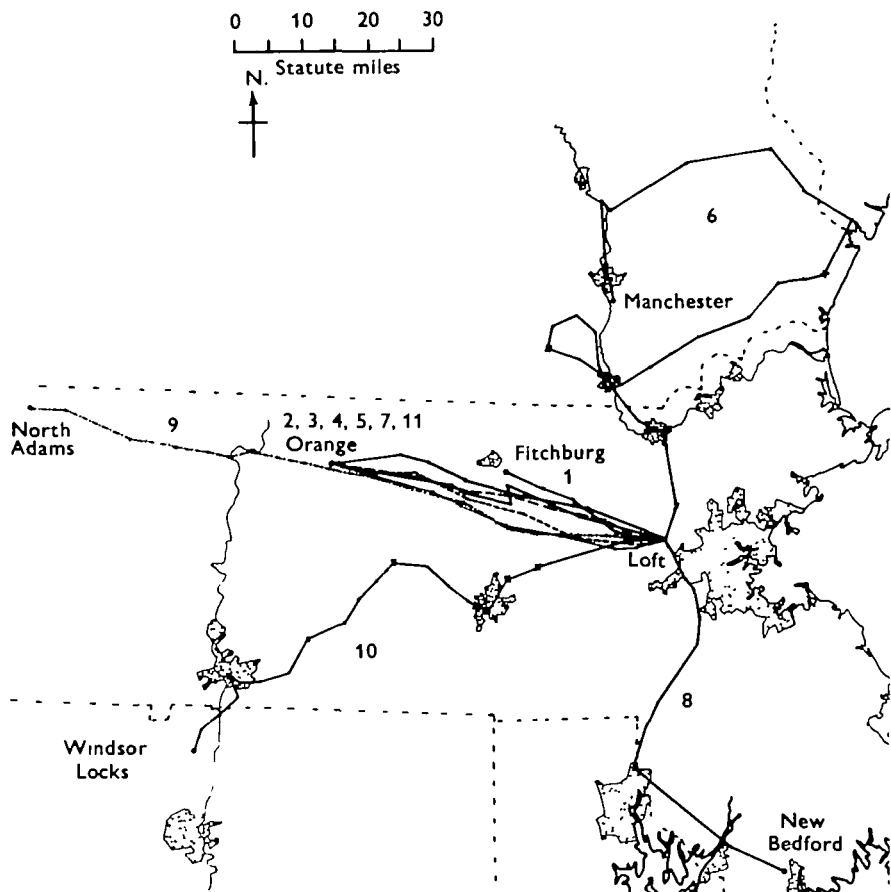

Fig. 3. All the tracks of Blue B-77. For several days prior to track 10 the bird was kept under an artificial light/dark regime. Track 4 not shown. For explanation of weather symbols, see Table 1.

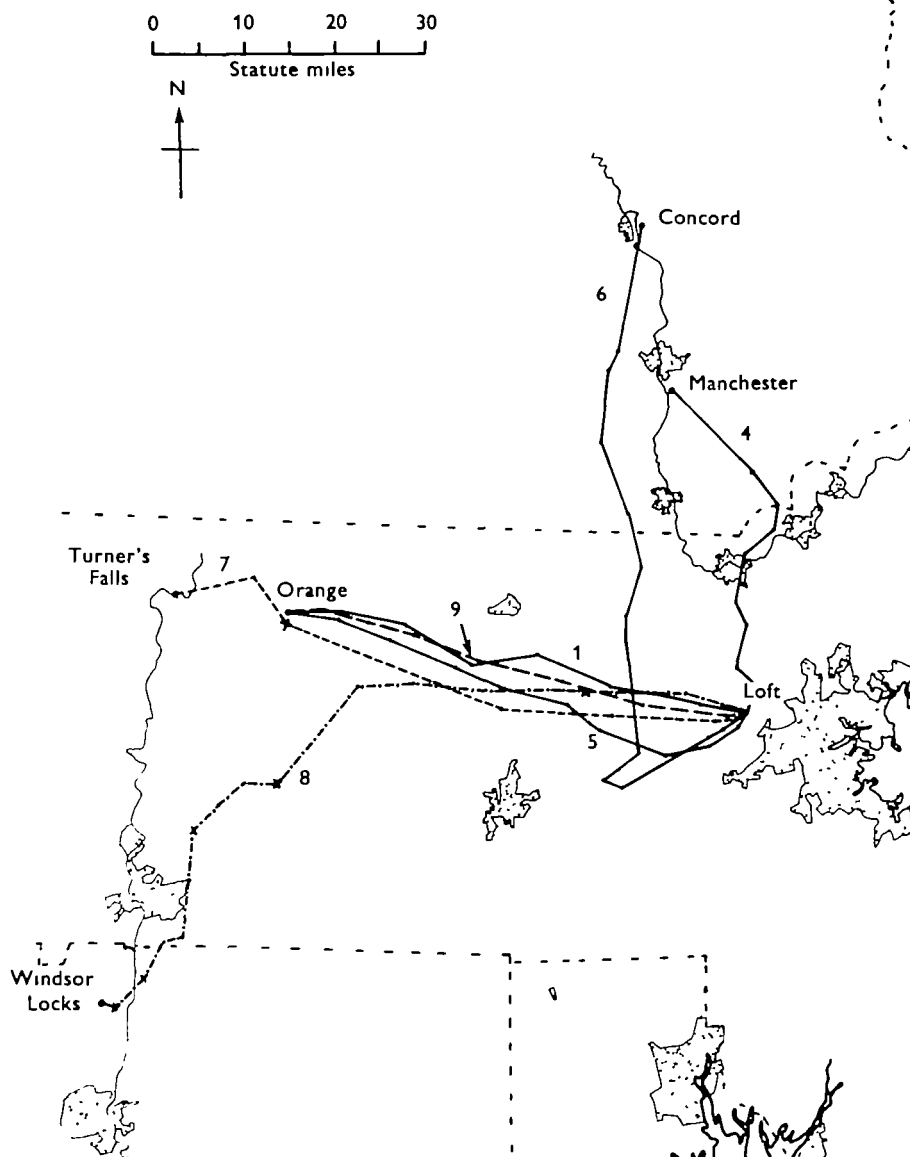|	Track no.	Release point	Date	Release time (E.S.T.)	Sky	Visi-bility (miles)	Wind Direc-tion	Wind Speed (m.p.h.)	Devia-tion (%)	Length ratio
———	1	Fitchburg	15. v. 66	14.35	O	20	140°	10	2·2	1·000
———	2	Orange	18. vi. 66	09.34	O	40	330°	10	1·0	1·075
———	3	Orange	22. vi. 66	12.33	O	40	080°	5	4·8	1·015
	4	Orange	29. vi. 66	10 53	O	40	180°	8	Incomplete	
- - - -	5	Orange	1. vii. 66	11.15	O	40	330°	15	1·8	1·010
———	6	Manch	9. vii. 66	09.54	O	40	350°	6	43·0	4·52
.. ...	7	Orange	16. vii. 66	09.57	①	—	315°	15	4·3	1·010
———	8	N. Bedford	18. vii. 66	11.24	O	10	230°	15	12·0	1·197
·—·—·	9	N. Adams	22. vii. 66	10.47	①	20	320°	5	1·2	1 005
———	10	Windsor L.	4. viii. 66	10.28	O	30	Light		7·2	1·190
— —	11	Orange	12. viii. 66	11.41	①	10	270°	17	1·3	1·020

Fig. 4. All the tracks of Grizzle R-10. For several days prior to track 6 the bird was kept under an artificial light/dark regime. Tracks 2 and 3 not shown. For explanation of weather symbols, see Table 1.

	Track no.	Release point	Date	Release time (E.S.T.)	Sky	Visibility (miles)	Wind Direction	Wind Speed (m.p.h.)	Deviation (%)	Length ratio
———	1	Orange	23. vi. 66	09.48	①	—	130°	5	2·0	1·015
	2	Orange	27. vi. 66	12.26	①	7	270°	12	Incomplete	
	3	Orange	1. vii. 66	14.26	○	—	300°	15	Incomplete	
———	4	Manch.	11. vii. 66	13.32	◐	—	360°	12	7·6	1·215
———	5	Orange	17. vii. 66	14.15	①	—	225°	15	5·5	1·032
———	6	Concord	27. vii. 66	10.38	○	40	330°	10	9·9	1·465
– – – –	7	Turner's F.	3. viii. 66	10.25	①	40	320°	18	4·3	1·030
·—·—·	8	Windsor L.	6. viii. 66	11.28	○	15	050°	6	14·2	1·130
– – –	9	Orange	13. viii. 66	13.10	①	—	270°	12	1·7	1·000
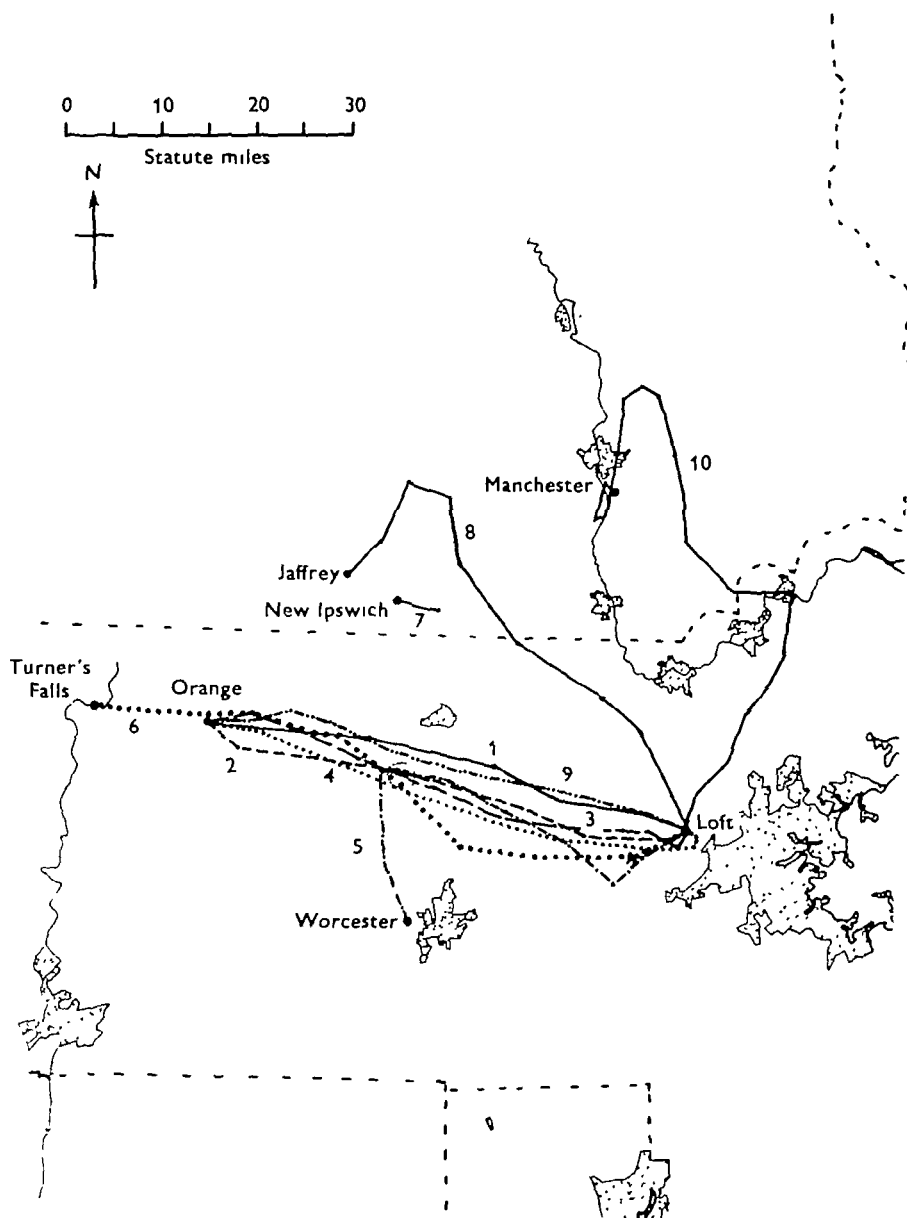
Fig. 5. All the tracks of Blue W Y. Some of the highest mountains are shown on this figure as rings of dots. For several days prior to track 5 the bird was kept under an artificial light/dark regime. For explanation of weather symbols, see Table 1.

	Track no.	Release point	Date	Release time (E.S.T.)	Sky	Visibility (miles)	Wind Direction	Wind Speed (m.p.h.)	Deviation (%)	Length ratio
———	1	Orange	23. vi. 66	12.14	①	10	270°	10	3·1	1·020
– – – –	2	Orange	30. vi. 66	11.34	①	15	360°	12	2·3	1·024
— —	3	Orange	2. vii. 66	13.43	①	—	310°	8	3·1	1·039
. . . . .	4	Orange	4. vii. 66	10.53	①	30	350°	10	4·2	1·077
·—·—	5	Worcester	17. vii. 66	09.44	①	15	260°	14	23·7	1 735
. . . . . .	6	Turner's F.	21. vii. 66	10.31	①	40	340°	5	5·4	1·075
———	7	N. Ipswich	29. vii. 66	12.26	①	15	315°	10	Incomplete	
———	8	Jaffrey	3. viii. 66	14.15	①	—	340°	12	15·0	1·38
·—··—··	9	Orange	7. viii. 66	08.00	①	5	Light		2·9	1·017
———	10	Manch.	25 viii. 66	14.13	①	20	Light		18·3	1·93

of the different release points. Because there are no obvious differences in the birds' headings from any of these points, more data are needed to understand the meaning of these statistical differences.

The general variability of the tracks suggests that the pigeons were not following a fixed sequence of landmarks, but without our knowing how high they flew on each occasion it is impossible to judge which landmarks may have been visible to them. Hitchcock (1952) and Griffin (1952 a) reported that their pigeons flew nearly at tree-top level. We did not usually observe our birds directly but have, on twenty occasions, seen the pigeons we were tracking flying within 100 ft. (30 m.) of tree-top level. On a few occasions we observed them flying much higher—even as high as 2000 ft. (600 m.) above the ground. It is therefore difficult to assess the significance of the differences between daily tracks *per se*.

A careful examination of the training tracks showed, however, that the birds made no major turns at obvious landmarks. The pigeons, in fact, flew unaltered courses over conspicuous rivers, roads, fields, woods, hills, valleys, lakes, towns, railroads and airports. The question of interest becomes: how close to a major highway or other such landmark must a pigeon fly in order to keep it in sight? Suppose the highway makes a gap about 150 feet (46 m.) wide through an otherwise hilly, forested region (such as several of the major highways do in much of the region the pigeons crossed). If the trees are about 50 ft. (15 m.) tall, a pigeon flying even as high as 250 ft. (76 m.) above the ground could only see the roadway when less than 750 ft. (230 m.) from it. These simple calculations were confirmed by direct observations from aircraft 1000 ft. (300 m.) above the ground; it was nearly impossible to locate the largest roads in rural Massachusetts when only ¾ mile (1200 m.) from them, even when we knew exactly where to look. Most of the pigeons' tracks did not follow any features within a distance of ½ mile (0·8 km.), so that, in general, inspection of the tracks from the training points suggests that the birds ignored roads and other landmarks of this sort on their homeward flights.

Since each pigeon's tracks were somewhat different from one day to another, we looked for correlations between these daily variations and various aspects of the weather.

Visibility

If the pigeons were relying on distant landmarks in order to find their loft they should show a poorer orientation to it on days when the visibility was poor. We therefore compared the average deviations, the length ratios, and the initial orientation of the birds on days with greater or lesser visibility. The average deviations of 61 tracks from training points on days with greater than 15 miles (24 km.) visibility was 5·38 %; that for 17 other tracks of these same birds from the same training points with less than 15 miles visibility was 4·59 %. The length ratios show a similar lack of correlation with visibility. But the possibility still remains that poor visibility might affect the birds' initial orientation at the release point. To examine this, the initial track error was considered in relation to visibility.

We will define the 'initial track error' as the angle between the home direction and the pigeon's position as it crosses a circle 10 miles in radius from the release point. On 17 days with less than 15 miles visibility the mean initial track error was 9·4°,

whereas when the pigeons could see more than 15 miles, on 66 other days, the mean error was 11·1°. From these results, it seems unlikely that the pigeons were relying on landmarks more than 15 miles distant, such as tall buildings or radio towers, to find their loft from the training points.
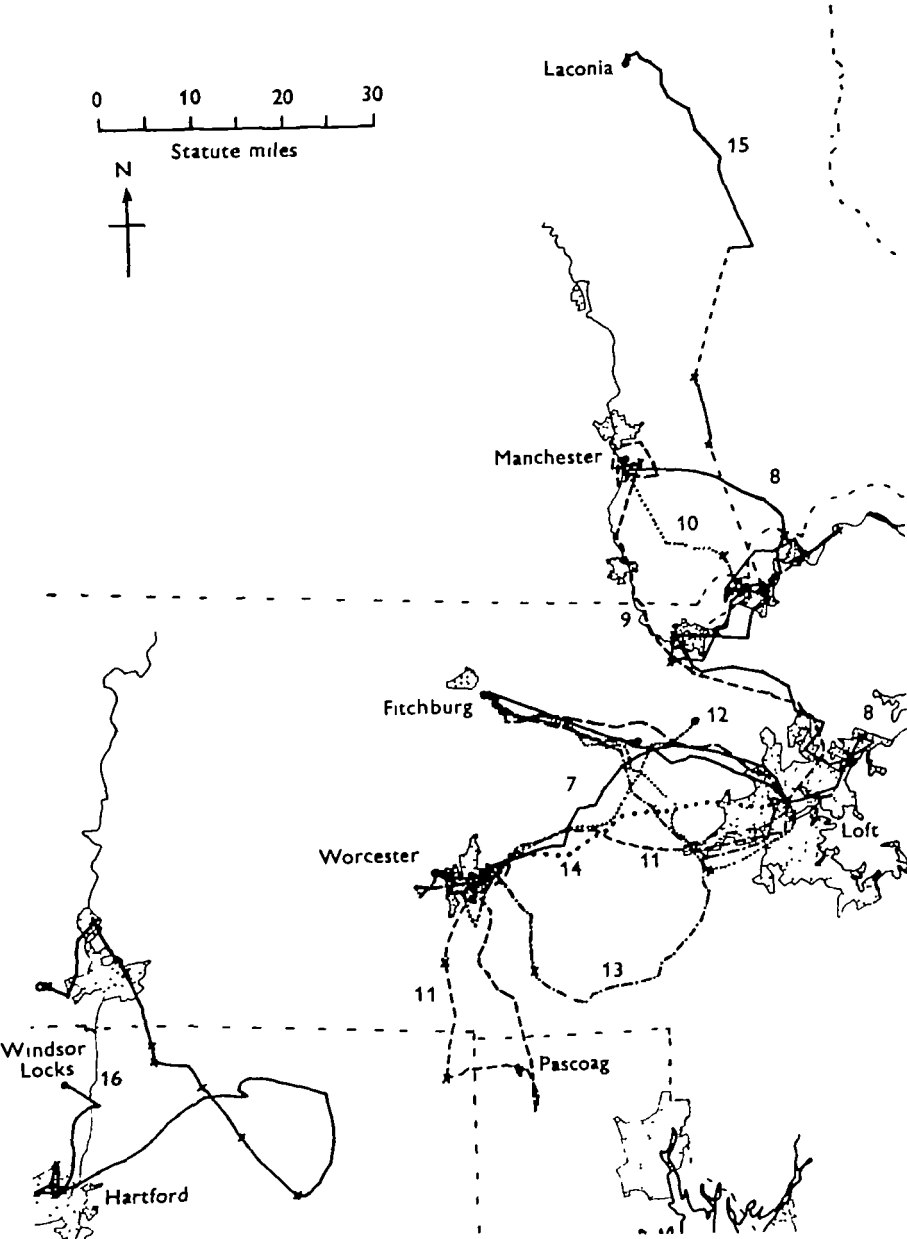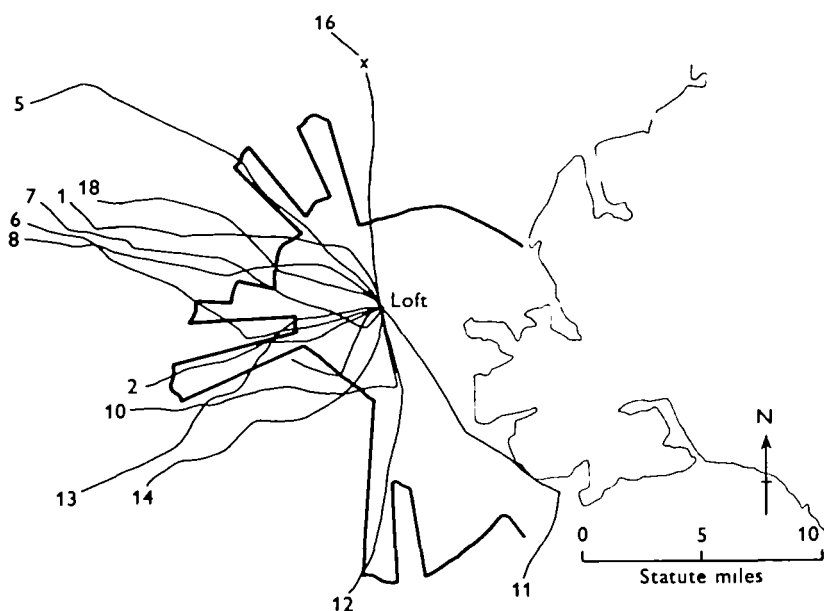

Fig. 6. For legend see facing page.

Fig. 7. The final turns of Silver AL Y near the Cambridge loft. The track numbers correspond to those used in earlier results. The heavy line divides the area around the loft into two parts: inside the line an observer at treetop can see the top of the tallest building in Cambridge; outside the line the hills around the city obscure this building. The thin line represents the shoreline around Boston. Many of the tracks make the final turn directly toward the loft within 2 miles after crossing the heavy line.

Legend to fig. 6

Fig. 6. All the tracks of Blue B AL. Track 6 not shown.
For explanation of weather symbols, see Table 1.

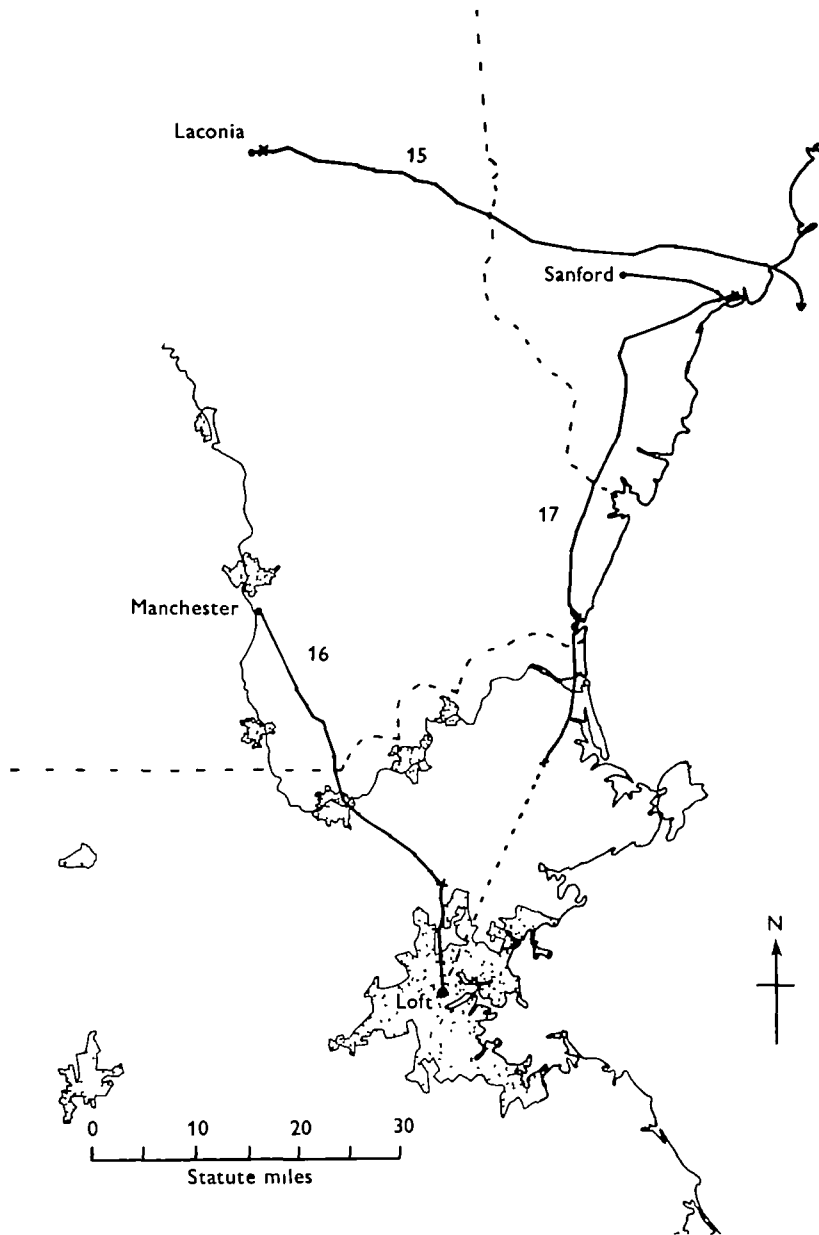|	Track no.	Release point	Date	Release time (E.S.T.)	Sky	Visi- bility (miles)	Wind Direc- tion	Wind Speed (m.p.h.)	Devia- tion (%)	Length ratio
————	1	Fitchburg	14. vi. 64	09.48	◐	15	300°	18	1·0	1·015
– – – –	2	Fitchburg	18. vi. 64	08.45	◐	40	310°	15	1·4	1·020
— ·—	3	Fitchburg	19. vi. 64	08.36	○	5	210°	12	4·4	1·083
· · · · · ·	4	Fitchburg	23. vi. 64	09.50	○	17	170°	12	10·4	1·415
· —· —· —	5	Fitchburg	25. vi. 66	09.01	◐	15	325°	15	10·0	1·220
	6	Fitchburg	5. vii. 64	10.12	◉	15	090°	16	Not tracked	
————	7	Worcester	16. vii. 64	13.24	◐	15	315°	8	8·9	1·23
————	8	Manch.	17. vii. 64	12.57	◐	7	250°	10	15·5	3·14
– – – –	9	Manch.	20 vii. 64	11.10	◉	25	180°	10	9·0	1·50
· · · · ·	10	Manch.	27. vii. 64	13.57	◐	15	Light		Incomplete	
– – – –	11	Worcester	30. vii. 64	09.52	◐	30	315°	12	21·3	2·75
· · · · ·	12	Worcester	4. viii. 64	10.03	◐	30	050°	12	Incomplete	
· —· —· —	13	Worcester	6. viii. 64	10.32	◐	40	315°	15	20·5	2·03
· · · · · ·	14	Worcester	9. viii. 64	13.57	◐	40	315°	15	2·3	1·045
————	15	Laconia	16. viii. 64	11.30	◐–⊕	10	Light		Incomplete	
————	16	Windsor L.	20. viii. 64	11.27	◐–⊕	20	Light		Incomplete, lost!	

Fig. 8. Three releases from new places of Silver AL Y. For all other tracks of this bird, see Walcott & Michener (1967). For explanation of weather symbols, see Table 1.

						Wind			
Track no.	Release point	Date	Release time (E.S.T.)	Sky	Visi- bility (miles)	Direc- tion	Speed (m.p.h.)	Devia- tion (%)	Length ratio
15	Laconia	13. viii. 64	12.11	◑-◑	40	Light		Incomplete	
16	Manch.	18. viii. 64	12.23	⊕-○	25	Calm		3·0	1·09
17	Sanford	25. ix. 64	13.39	⊕-◑	8	315°	10	Incomplete	

Winds

In order to calculate how fast the pigeons flew through the air (airspeed), we have vectorally subtracted the wind velocity from the bird's ground velocity. This calculation can be used as a good approximation of airspeed over any straight segment of track. When this was done the results showed that each pigeon flew a nearly constant airspeed along the entire length of its track, and was quite consistent from day to day. For instance, the airspeeds of Blue B AL along its five tracks from Fitchburg (Fig. 6) were 33, 29, 31, 31 and 29 m.p.h. (standard deviation 1·7 m.p.h.) respectively, whereas the ground speeds on these trips were 53, 40, 30, 28, and 40 m.p.h. (standard deviation 10·0 m.p.h.). The variations in the calculated airspeeds are within the accuracy with which the wind velocity is known. The airspeeds of the different pigeons studied were found to be constant from day to day and lay between 28 m.p.h. and 40 m.p.h., which agree with previously published estimates (Kramer & Seilkopf, 1950).

Since the pigeon's ground speeds vary with the wind, it is interesting to investigate whether their tracks are blown to the left or right by crosswinds. We will follow the same conventions as used by Drury & Nisbet (1964) to discuss the birds' flight directions: 'track' or 'path' will refer to a pigeon's flight relative to the ground, whereas a bird's 'heading' is its direction relative to the air, i.e. the direction in which it is pointing.

The captions of Figs. 2–6 give the wind velocity during the flights of these 7 pigeons from their training points. Of 55 tracks from training points for 9 pigeons, 15 had crosswinds of greater than 10 m.p.h. Of these 15, 7 tracks deviated primarily to the side which would be expected if the birds were being blown off course, four tracks deviated mostly opposite to the wind, and four tracks deviated equally right and left of a straight line. Thus on about half the tracks the pigeons compensated fully or more than necessary for wind drift. Therefore, the pigeons must head at some angle to the home direction to achieve this compensation for the wind drift. This is more than a trivial correction. For instance, with a 10 m.p.h. crosswind (at right angles to the track), a flight of 40 miles (65 km.) would miss the home loft by about 13 miles (21 km.), instead of approaching it within a typical error of less than 2 miles (3·6 km.), as we observed.

The notion of compensation for wind drift raises the question of whether the pigeons' tracks deviated, in general, more on days with strong crosswinds than on calm days. On the fifteen tracks with more than 10 m.p.h. crosswind component the average path deviation was 6·2 % (length ratio average 1·17), whereas the same nine pigeons on forty other tracks with less than 10 m.p.h. crosswind component showed an average deviation of 5·7 % (length ratio average 1·11, neither significantly different, $P > 0.05$). The pigeons therefore seem to be able to compensate rather precisely for crosswind error, but they maintain a preferred flying airspeed and do not speed up or slow down to adjust their ground speeds.

Various other factors

Several other factors differing between daily training releases were analysed to see if they had any effect on either measure of path accuracy. As already mentioned elsewhere (Michener & Walcott, 1966), there was no noticeable change in track direction

or track deviation with time of day of release, even though birds were released from 07.00 through 16.00 E.S.T. The mean release time for one bird, for example, on six tracks with greater than 10° initial track error was 10.54 E.S.T., whereas for four other tracks with less than 10% initial track error the mean time was 11.16 E.S.T.

Daily temperature variations seemed to have no effect on individual tracks, but, when taken all together, tracks flown at higher temperature had significantly lower deviations than those flown at lower temperatures. Temperatures were recorded on fifty-two training tracks of sixteen pigeons, The median temperature was 75° F. (24° C.), with a range from 12° F. ($-11°$ C.) to 95° F. (35° C.). There was a significant negative correlation between the track deviations and the temperature ($r = 2.88$, $P = 0.04$) but not between the length ratios and temperature ($P > 0.40$).

At first glance, these results might be taken to agree with those reported by Kramer (1954) and by Wallraff (1960), but all fifty-two of these flights were made during the 6 months of celestial summer (March 20 through September 23) and Wallraff's 'temperature effect' was only found during the celestial winter. We believe that this correlation we have observed in our tracks may be fortuitous—at least it is hard to see how this effect could be related in any causal way to our pigeons' repeated homing from the same training points, and why the length ratios should not also reflect this effect if it were of biological importance. This temperature effect may simply be a reflexion of our more intensive experiments, and therefore of the pigeons' better training, during the warmer summer months.

We have tracked pigeons to two lofts and have compared the flights to each. The fifty training tracks to Cambridge had an average deviation of 5.95% (length ratio of 1.132) while the twenty-eight to Lincoln had an average deviation of 3.88% ($P = 0.02$) and an average length ratio of 1.062 ($P = 0.05$). Thus, both measures of track straightness show significantly straighter tracks to the Lincoln loft. The reason for this difference is unknown.

Sun visibility

As we have discussed previously for the 1964 results (Michener & Walcott, 1966), the pigeons we have studied generally refused to fly unless the sun was visible to them when they were more than 10 miles from the loft. This was not a correlation with with cloud cover (*per se*) or precipitation, but was related directed to the sun's visibility.

In all 3 years, on 177 tracks, 23 were flown under cirrus cloud overcast through which the sun was clearly visible, and the pigeons homed directly; on 35 tracks the sun was not visible during more than 15 min. of the time that the pigeons were under observation. Of these 35 tracks, 18 were from places within 10 miles of the loft and the pigeons homed quickly, 17 were from longer release distances and the pigeons perched in each case whenever the sun was not visible. On only one track, Silver AL Y flew more than 5 miles (from Sanford) without the sun, and this will be discussed later.

In an effort to study this problem more fully three adult pigeons which had been trained to fly from Orange to the Lincoln loft were retrained only on overcast days. These three homed at normal speed when released from 2 miles, but when first released singly from 30 miles (48 km.) west of the loft none returned on the first day under overcast. All three homed on the next day, however, which was sunny. Two of these birds (Blue R-2 and Blue R-28) were next released 13 miles (21 km.) west of the loft

when thesun was not visible. They both homed together in 90 min. without the sun. These two were then released from 30 miles. On the day of release the sun was intermittently visible and they took 3 hr. to return. On the next release from the same place the sun was also intermittently visible and the two birds homed in $2\frac{1}{2}$ hr. The birds were then released from Orange (their previous training point, 52 miles, 84 km., west) under overcast conditions. One bird came home in the continued fog and overcast the next day in 31 hr., and the other homed in 50 hr. During this period of heavy overcast the sun was never visible to a human observer at the loft. It is therefore unlikely that the birds saw any celestial features during this 2-day period. At no time during these tests did any of these birds wear transmitters or harnesses, nor were they tracked. The results show that our pigeons performed very poorly when they were unable to see the sun, even when there was no possible influence from our tracking procedures. We are now making arrangements to track them under overcast conditions to investigate this effect more fully.

Summary of training tracks

Most of the factors studied had little or no consistent effect on the pigeons' orientation, except that the sun's disk apparently had to be visible for the birds to show good homing performance from distances of greater than 13 miles (21 km.). This finding strongly suggests that the pigeons do not use familiar landmarks alone to fly to the loft, but is not entirely conclusive. It is still possible that the pigeons piloted some of their courses to the loft by a detailed knowledge of some landmarks. The fact that poor visibility had no effect on the straightness of the tracks would require that the pigeons at least know enough landmarks to remain oriented by them on days when they could see no more than 5 miles. The effect of the sun suggests that the pigeons were returning by some orientation other than piloting: either by establishing a learned fixed compass direction to fly, or by navigating by some co-ordinate system to the loft. In order to investigate this observed orientation we next released the pigeons from unfamiliar places off the training line.

Releases off the training line

A bird released off the training line at a place where it has never been before would seem to have three alternatives: (1) it could search until it found familiar landmarks; (2) if it were using a sun-based compass it could fly in the training compass direction; (3) if it were able to navigate, it could fly directly towards the home loft. Such off-training-line releases provide a way of discriminating between these three techniques.

This experiment has been tried with eight different pigeons for a total of twenty tracks. Figs. 3–6 give all the tracks of Blue B-77, Grizzle R-10, Blue WY, and Blue B AL respectively. Others are shown in Michener & Walcott (1966) and Walcott & Michener (1967). Table 2 contains an analysis of all twenty tracks.

A cursory examination of the tracks from these new points shows that the birds' behaviour was complex. Close examinations of Fig. 6 reveals, however, an important point: Blue B AL was flying a course on track no. 12 which was not directed to the loft, but which crossed many previous tracks. At these crossings the bird did not alter its *incorrect* course in any way. This lack of response to what one might expect was familiar territory has been observed 69 times. It will be discussed more fully below.

Table 2. *The twenty tracks from new places off the training line*

(Those releases which were conducted with birds kept on artificial light/dark cycles, as well as those from new places on the training line are omitted. For explanation of symbols, see Table 1.)

Track no.	Release point	Date	Release time (E.S.T.)	Sky	Visibility (miles)	Wind Direction	Wind Speed (m.p.h.)	Deviation (%)	Length ratio
	Silver AL Y, trained from Fitchburg to Cambridge: tracks 15–17 in Fig. 8								
11	Worcester	12. vi. 64	09.32	O	30	315°	8	26·5	2·57
13	Windsor Locks	7. viii. 64	11.51	◐	10	200°	10	2·0	1·105
15	Laconia	13. viii. 64	12.11	◑	40	Light		Incomplete	
16	Manchester	18. viii. 64	12.23	⊕-O	25	Calm		3·0	1·090
17	Sanford	25. ix. 64	13.39	◐-⊕	7	315°	10	Incomplete	
	Blue B AL, trained from Fitchburg to Cambridge: see Fig. 6.								
7	Worcester	16. vii. 64	13.24	◐	15	315°	8	8·9	1·23
8	Manchester	17. vii. 64	12.57	◐	7	250°	12	15·5	3·14
15	Laconia	16. viii. 64	11.30	◐-⊕	10	Light		Incomplete	
16	Windsor Locks	20. viii. 64	11 27	◐-⊕	20	Light		Bird never homed	
	Blue W AL, trained from Manchester to Cambridge								
6	Fitchburg	12. vi. 65	10.27	O-⊕	15	Light		Incomplete	
10	Gardner	8. vii. 65	12.24	◑	—	Light		Incomplete	
	Blue R-9, trained from Manchester to Lincoln								
7	Worcester	8. viii. 66	10.38	◐	15	Light		62·0	4·35
	Grizzle R-10, trained from Orange to Lincoln: see fig. 4								
4	Manchester	11. vii. 66	13.32	◑	—	360°	12	7·6	1 215
8	Windsor Locks	6. viii. 66	11.28	O	15	Light		14·2	1·130
	Blue R-19, trained from Orange to Lincoln								
7	Laconia	21. vii. 66	14.18	◐	40	Light		Incomplete	
	Blue W Y, trained from Orange to Lincoln: see Fig. 5								
7	New Ipswich	29. vii. 66	12.26	◐	15	315°	10	Incomplete	
8	Jaffrey	3. viii. 66	14.15	◐	—	340°	12	15·0	1·380
10	Manchester	25. viii. 66	14.13	◐	20	Light		18·3	1·93
	Blue B-77, trained from Orange to Lincoln: see Fig. 3								
6	Manchester	9. vii. 66	09.54	O	40	Light		43·0	4·52
8	New Bedford	18. vii. 66	11.24	O	10	230°	15	12 0	1·197

It implies that pigeons did not rely on fixed sequences of landmarks to find the loft, and leads us to believe that they did not make much use of landmarks at all, even in the region between the training point and the loft.

There remains the question of what strategy the birds did use when released from unfamiliar places. As we have reported elsewhere, many pigeons seemed to fly first in the compass direction that they had repeatedly taken from their training point. To gather statistical data on this point for all eight pigeons, we have defined, for each track, an 'initial compass error', which is the angular difference between the position of the track 10 miles from the release point and the pigeon's previous training direction.

For the eight birds on their first releases off the training lines the median initial compass error was 8°, and 50 % of the values lay between 7 and 17°. This is noticeably smaller than the angular difference between the track 10 miles from the release point and the true direction to home (the initial course error), which had a median of 49°

with a scatter of 50 % of the values between 40° and 64°. Thus the tracks were much more nearly oriented to the previous training direction than they were to the proper homeward direction.

On subsequent releases off the training line pigeons showed a slight decrease in their tendency to orient to the previous compass direction, so that the overall results for all the tracks from off-training-line releases show a greater compass error than the first releases alone. The median initial compass error for all twenty tracks was 15° with a 50 % range of values between 5° and 36°, while the median initial course error was 45°, range of 29–62°. This tendency to fly in the trained direction, then, seems to decrease slightly with subsequent releases from new directions.

As far as we can tell from our data the release point has little influence on this initial orientation. It appears that for most flights the direction taken for the first 10 miles depends solely on the previous training direction of flight. This is an additional argument against the birds' using landmarks at the release point to determine the direction in which to fly.

In one case (Michener & Walcott, 1966) a pigeon learned to fly in a new compass direction after three successive releases from a new release point. Although this experiment has not been repeated with other birds, we have noticed a difference in individual pigeons' tendencies to fly in the single training direction. Blue B-77 on one of its releases (Fig. 3, track 6), initially flew in a direction that was inexplicably different from either the correct homeward direction or the trained compass direction. This bird was exceptional, however, and the other seven birds studied frequently showed a clear initial orientation in the previous training direction.

Orientation to the loft from unknown territory

A bird which flies only in a trained compass direction will not get home from a release point off the training line. Yet in all but one of the twenty first releases from new places the birds did get home. An inspection of these tracks (especially Figs. 6 and 8) and of those in our previous papers shows that the birds, after flying in the trained compass direction, begin to correct their course and eventually arrive at the home loft. But much of the flight path of the pigeons cannot simply be separated into either 'homeward-directed' or 'training-directed' segments.

In order to simplify our discussion of the tracks we have tried to develop objective criteria for the accuracy of the birds' orientation. To reduce the possibility of the pigeons' using landmarks for orientation we will examine only those portions of the tracks which lie more than 10 miles away from all previous tracks. We will refer to this region as 'unknown territory', even though there is a remote chance that the pigeons might have seen this area on some previous, untracked release.

When pigeons were observed in such presumably unfamiliar territory they frequently seemed to fly a very straight course, accurately directed either in the previous training direction or toward home. As an analytical criterion for such apparent straightness we have chosen the following: the section of track in question must fit within a rectangle only 2 miles (3·2 km.) wide and 20 miles (32 km.) or more long. We have examined all of eight birds' tracks for segments which fit these criteria. For each straight track segment we recorded both the total length of the portion fitting inside a 2-mile-wide slit, and the compass direction of its long axis. Track segments were

chosen so that each straight segment did not overlap any other straight segment, thereby making them all mutually independent. Table 3 lists all the straight track segments found in the twenty-four tracks in 'unknown territory'. It also includes the bearing of previous training direction and the bearing toward the loft at the beginning of each straight-track segment. The 'compass error' is the angle between the straight segment and the previous training direction (direction of home from training point). The 'home error' is the angle between the straight segment and the direction in which home lay when the straight segment began.

Table 3. *Straight track segments more than 20 miles long in tracks through unknown territory*

All bearings and errors in degrees, length of segments in miles.

Bird	Track no.	Straight segment Bearing	Length	Home Bearing	Error	Compass Bearing	Error	Lesser error*	
Silver AL Y	11	112	24	073	+39	109	+3	Comp.	3
	13	048	20	065	−17	109	−61	Home	17
	13	072	27	070	+2	109	−37	Home	2
	15	108	26	170	−62	109	−1	Comp.	1
	15	099	28	187	−88	109	−10	Comp.	10
	16	156	25	157	−1	109	+47	Home	1
	17	198	29	199	−1	109	+89	Home	1
Blue B AL	15	152	24	171	−19	080	+72	Home	19
	16	060	21	063	−3	?	?	Home?	3
	16	313	23	053	−100	?	?	?	
Blue W AL	6	165	25	105	+60	157	+8	Comp.	8
	6	166	38	055	+111	157	+9	Comp.	9
	6	011	26	016	−5	157	−146	Home	5
	10	155	29	105	+50	157	−2	Comp.	2
Blue R-9	7	058	26	088	−30	170	−112	Home	30
Grizzle R-10	4	140	21	165	−25	105	+35	Home	25
Blue R-19	7	121	36	184	−63	105	+16	Comp.	16
	7	231	31	209	+22	105	+126	Home	22
Blue W Y	8	132	29	139	−7	105	+27	Home	7
	10	163	22	173	−10	105	+58	Home	10
	10	204	28	203	+1	105	+99	Home	1
Blue B-77	6	068	23	171	−103	105	−37	Comp.	37
	6	242	37	211	+31	105	+137	Home	31
	6	129	22	149	−20	105	+24	Home	20
	8	309	30	341	−32	105	−156	Home	32
	8	022	28	007	+15	105	−83	Home	15

* Comp. = compass.

Our tracking experience suggested that straight track segments either have small compass errors or small home errors. The data in Table 3 support this impression overwhelmingly for three of the eight birds. In all the tracks of Silver AL Y, Blue W AL, and Blue W Y, thirteen of the fourteen straight segments lay within 10° of either the training direction or of home. The exception was Silver AL Y's track from Windsor Locks, Conn., where the straight segment was 17° from the home direction. But it is clear, once again, that pigeons show considerable individual differences. What little data we have for Blue R-9, Grizzle R-10 and Blue R-19 shows that they seem to have

been less accurate than the aforementioned three, yet fairly well directed toward one of the two choices of directions. Blue B-77 was consistently inaccurate; its straight-track segments lay between 20° and 40° of either training or home directions. Yet in spite of these relatively large errors this bird's overall performance was good (see Fig. 3). Blue B AL's first two straight-track segments were nearly homeward directed (19° and 30°), but the last segment (shown in Fig. 6, track 16) stands in contrast to all other such straight segments observed: the direction was more than 90° from both home and any reasonable estimate of a training direction. This was the wrong direction to fly by any standard, because the pigeon never returned to the loft after this track, whereas all the other tracks containing these straight segments ended successfully.

The switch to loft orientation

It appears that most of our pigeons flew first in a trained compass direction and then switched to a system of loft orientation. What factors lead them to change from one to the other? In the case of Blue B AL (described in Michener & Walcott, 1966) it appeared that this switch was due to the absence of landmarks that were familiar from the training releases. Such an argument could apply to Silver AL Y's track from Windsor Locks (shown in Michener & Walcott, 1966) and to Blue B AL from Laconia, N.H. (Fig. 6). But this does not apply to all tracks. Blue B AL from Windsor Locks (Fig. 6) and Blue W Y from Jaffrey (Fig. 5) show a transition from compass to home-ward flight that is hard to relate to local landmarks. Perhaps the answer is that time is required for the pigeon to make use of its system of home orientation. If it cannot navigate immediately on release it may either perch at the release point, as did Silver AL Y at Manchester (Fig. 8) and Grizzle R-10 at Manchester (Fig. 4), or it may fly off in some direction.

If one considers the length of time a bird takes between release and when it shows a loft-directed straight segment, we find a median figure of 121 min. with the values lying between 6 and 1140 min. The most rapid orientation toward the loft was per-formed by Blue B-77 on its release from New Bedford, Mass. (Fig. 3, track 8). On this occasion it oriented to within 32° of the correct homeward direction 6 min. after release.

The other possibility is that some sort of physical displacement might be necessary for the pigeons to employ their homeward orientation. Such a possibility is ruled out, however, by the flights of Silver AL Y from Manchester (Fig. 8), Blue B AL from Laconia (Fig. 6) and Grizzle R-10 from Manchester (Fig. 4). On these tracks the pigeons perched at the airports for some time and then oriented accurately toward the loft when they first took off.

From these results it appears that different pigeons may use different factors to trigger the onset of their homeward orientation. Probably the two most important are the passage of time after release and the use of landmarks as checkpoints to terminate incorrect flights.

Landmarks near the loft

As we have discussed previously (Walcott & Michener, 1967), when our pigeons approached the region around the Cambridge loft they frequently made abrupt turns exactly towards it. These sudden, final course corrections suggested that the pigeons switched, at this time, to orienting to the loft by familiar landmarks.

Fig. 7 shows a map of the loft area with a heavy line drawn on it, inside of which an observer at tree-top level could just see the tallest building in Cambridge, which stands within 100 m. of the loft entrance. This map was prepared by observing the limit of the visual horizon from the top of this building. A homing pigeon flying at tree-top level would be expected to first see this building and reorient its flight directly toward the loft just after crossing this line. Silver AL Y was tracked all the way to the loft 14 times; 10 tracks turned toward the loft within 2 miles after crossing this line, 1 turned 4 miles after crossing the line, 1 was already going straight toward the loft, 1 curved toward the loft after crossing the line and the remaining one turned toward the loft 6½ miles before crossing the line. In this last case the pigeon had perched for 22 min. on a water-tower in Reading, Mass., north of the loft, and may have been able to see enough of the city to judge its course to the loft correctly without having seen the building in question. Thus 10 of the 14 tracks show the behaviour expected of pigeons using this building to pilot to the loft.

As discussed previously (Walcott & Michener, 1967) the tracks of Blue B AL are in similar agreement, eight of the ten tracks turned toward the loft within 2 miles after crossing this dividing line. For these two pigeons (the only two tracked repeatedly near the loft in sufficient detail to draw any conclusions) eighteen out of the twenty-four tracks (75 %) change course in agreement with the supposition that they were using the top of the tallest building near the loft as a guidepost.

The Lincoln loft has no obvious landmarks associated with it, and so no similar analysis is possible. But there is no reason to suppose that the birds behaved any differently in the region near the loft, because the tracks also show sharp turns during the last 5-10 miles of flight.

To summarize our results, it appears most likely that our pigeons use a variety of methods of orientation on their homeward flights. They often flew in a trained compass direction from 0 to 70 miles (113 km.), then they switched to some fairly accurate orientation to the loft and finally used landmarks within the last few miles to locate the loft itself.

<div align="center">DISCUSSION</div>

The sequence of methods of orientation we have observed in this study is very much like that suggested by Griffin (1952 a, b) for his homing flocks of pigeons. Schmidt-Koenig (1965) has sub-divided Griffin's basic three methods of homing. We will review this more complete classification here:

(1) *Piloting* (Griffin's type I). The use of familiar landmarks to find a goal. If a bird is released in unfamiliar territory, it may use a random or an organized search process to locate familiar objects.

(2) *Directional orientation* (Griffin's type II). The process of flying on a fixed compass bearing without reference to goals or landmarks. This may be further subdivided into methods which are compensated for wind-error and those which are not, learned or innate, eventually used or not used to find a goal, steered by inertial, geodesic, or celestial features.

(3) *Navigation*. The process of flying with reference to a goal without landmarks. This may be by:

(a) *Reversed displacement navigation*: to reach a goal by using the actual or summed

information gathered during the displacement process. This may be divided into that which works during self-displacement and that which can work if the animal is artificially displaced. The information might be gathered inertially or by a combination of a compass and a distance sense.

(b) *Bi-coordinate navigation* (Griffin's type III). The use of co-ordinates other than landmarks to establish reference to the goal without information being gathered during displacement. This will be referred to as 'true navigation'.

We will discuss each one of these possible methods of orientation in sequence, and the relationship which our results have to each.

The use of landmarks for piloting

The tracks from the training points were examined to discover which, if any, landmarks were correlated with turns in the pigeon's tracks, and which might serve as orientational references. They will be treated in three categories: (a) landmarks at the release points, (b) those along the main paths, (c) those around the home loft.

(a) Landmarks at the release points

The pigeons released repeatedly at Fitchburg Airport appeared to know the area there, since some individuals often chose to perch on the same trees and power-line poles on many different days. This seemed also true to a lesser extent with pigeons trained from the other release points. When these pigeons were released from new release points, however, they flew off in the same compass direction, as a rule, as they had from the training points. They seem therefore to have behaved as though they did not 'recognize' that they were at a different release point. It seems unlikely, at first glance, that the pigeons would fail to react to the rather different surroundings at the different release points, but there are several other interpretations of these results. The pigeons may have reacted as though they had been released farther out along the training line, i.e. our training procedure may have conditioned them not to attend to landmarks at each release point. It also may be possible that most airports look the same to pigeons.

A more specific comparison is possible in only one other case. Blue B AL was released once from Worcester after its training from Fitchburg, then three times from Manchester, then from Worcester again (Fig. 6). On this last trip the bird flew south, as though released from Manchester for a fourth time. Since the bird had been released from Worcester 2 weeks previously, its incorrect choice of a southerly course seems to mean that it failed to recognize the Worcester airport and city, in spite of the 15 min. it spent circling over the city at the start of this track. In contrast to the Worcester release there is no city placed east of and near to the Manchester airport, so the pigeon seems to have ignored Worcester in order to choose its southerly course. These findings agree, as far as they go, with Matthews (1963), who reported having to release pigeons five times from a release point before they showed evidence of recognizing it in test releases.

(b) Landmarks along the main path

We found no evidence to indicate that our pigeons piloted their courses by familiar landmarks even when flying home from the training points. It may be worth while to examine in detail the different possible ways in which a pigeon could use landmarks to

find its loft. Probably the simplest method would be for it to learn some tall landmark near the loft (such as a radio tower near Boston) and use this as a guide. This method would break down on days with bad visibility. Our pigeon's tracks, however, were no more inaccurate on such days than normally, which indicates that the birds were not relying on this system. A more complex method might be for each pigeon to learn a single sequence of closely spaced landmarks, leading from the training point to the loft, so that on days with less than 4 miles visibility it could still fly from object to object. These landmarks would obviously have to be closer than 4 miles to one another. Such a scheme should lead to a much closer coincidence between each bird's tracks from one day to the next than were observed, especially since the birds could probably not see very far while flying within 100 ft. of the trees through this hilly country. Thus the extent of the daily track variations of each bird's route suggests that none of them followed such simple sequences of landmarks.

Table 4

	No. of crossings
Course already within 10° of home	
Course changed	4
Course continued	22
Course incorrect	
Changed toward home	14
Changed toward previous path	3
Changed away from both	18
Course continued	69

The only remaining method of piloting that appears left for our pigeons to have used is for them to have known the area between their training points and the loft so well that they could have chosen almost any path without losing sight of a familiar landmark. This would require such a high degree of familiarity with this region that one would expect the pigeons to be able to orient quickly toward the loft from almost anywhere within this area. One of the few ways to investigate this prediction is to see what a pigeon does when it flies through such a region. If it has been flying on an incorrect course and encounters a path it has recently flown, it should either turn toward home or turn and follow its previous path. In such an analysis, it is hard to tell whether the pigeon turned at that place by coincidence or whether it reacted to the previously encountered landmarks. Obviously, if pigeons flying incorrect tracks consistently corrected their orientation toward the loft on encountering their previous paths, the evidence for their piloting by landmarks would be greatly strengthened. Table 4 summarizes the results of the eight pigeons' thirty-nine tracks from non-training points. There were 130 cases where a bird's track crossed its previous path. A bird was judged to be on a correct course if its track was already within 10° of the home direction. A course was said to have changed if a bird turned more than 10° within 1 mile of crossing a previous track. Each change fell into one of three categories: either it turned toward home, toward the previous path, or toward neither.

It is interesting that the percentage of correct tracks which were changed within 1 mile of a crossing (15·4%) is not significantly different ($P = 0·15$) from the percentage of incorrect tracks changed (33·6%) at crossings. This suggests that the changes in path direction are not causally related to whether a pigeon is on a homeward course

or not. Furthermore, those pigeons on incorrect paths which did change course chose worse bearings more often than they chose improved bearings. Of the 14 improved courses, 8 later became worse in their home error, 5 were very slight improvements in the homewardness of the course, and only 1 resulted in a course that was within 10° of the loft.

The three tracks that turned to follow the previous tracks do not look very convincing either; they all diverged from the previous course after less than 6 miles, and the birds did not then home directly, but showed several apparently random turns later in the track. This is about the same distribution of errors as one might expect if the pigeons' course changes were entirely random. There is certainly no evidence that flying through 'familiar regions' of the sort described here improved the pigeon's orientation toward the loft.

Evidence that the pigeons could not pilot their way to the loft is impossible to obtain, but this is certainly strongly suggested by the correlation between sun visibility and homing at distances of more than 10 miles from the loft. Even the birds especially trained on overcast days took from 3 to 30 times longer than usual to home when the sun was not visible. It is conceivable that these pigeons used a search process to find the familiar territory near the loft; further releases are under way to clarify this point. The existence of a familiar area near the loft is indicated by the distance-dependence of the sun's effect: the birds would home directly from 10 miles or less either with or without the sun. At greater distances, however, the dependence of homing on the sun supports the conclusions from the analysis of track crossings.

(c) Landmarks near the loft

The analysis of the turns in the tracks near the Cambridge loft suggests that the tallest building in Cambridge served two pigeons as a guide to the loft once they were inside the rim of hills surrounding Greater Boston. There are, however, no objects near the Lincoln loft with which such a comparison could be made. Nevertheless, the tracks to the Lincoln loft show frequent turns and near-misses, which suggest that some similar recognition of landmarks also occurs in this region as it did at the Cambridge loft.

Other reactions to landmarks

In several tracks from releases off the training-line other abrupt changes in course direction have occurred. Many of these turns occur near obvious landmarks—not necessarily landmarks that the birds had actually seen before. These reactions can be divided into two categories: (1) those in which a pigeon reacted as though it had arrived in the home area, and (2) those in which the pigeon apparently either saw a landmark which was inappropriate to its present course, or it failed to see, at the proper distance, an appropriate landmark signalling its arrival in the home area.

All the clear-cut examples of the first kind of reaction come from one pigeon: Blue B AL. Its reactions were mainly to cities, and it is interesting to note that the pigeon had been trained over an entirely rural course, which ended at its loft in the densely populated city of Cambridge. The bird's tracks are all shown in Fig. 6. As previously described (Michener and Walcott, 1966), this bird flew around the cities along the Merrimack River on its first release (track 8) from Manchester, N.H.; it spent some considerable time in the city of Worcester, Mass. on its third release

(track 12) from the Worcester Airport; it spent almost an entire day flying and perching in Hartford, Conn., on its first (and last) release from Windsor Locks, Conn. (track 16). It is tempting to infer from this behaviour that the pigeon mistook these cities for the region around its loft, in which case its ability to remember specific visual objects must have been rather poorer than a human's.

The use of landmarks as checkpoints is documented for only a few of our pigeons. The best example of this reaction has been discussed briefly (Michener & Walcott, 1966). Blue B AL had been released once from Worcester, then three times from Manchester. On its second Worcester release (Fig. 6, track 11) it flew southward, in a direction more appropriate to its last three Manchester releases. The pigeon reversed course abruptly over a wooded, rural section of countryside, flew north again, then landed at Pascoag, R.I. On its flights from Manchester this bird had always crossed a string of industrial cities after flying south about 20 miles (32 km.), and its point of reversal on the second Worcester flight was just 25 miles (40 km.) from the release point. The supposition that the bird was reacting to a *lack* of cities is further supported by its behaviour at Pascoag; it landed on the only factory in sight. It seems possible that the lack of cities south of Worcester was the first clue that the pigeon had that it had been flying on an inappropriate course for 25 miles.

It seems possible that other birds also used landmarks as checkpoints to tell if their courses were correct. Silver AL Y, on its first release from Windsor Locks, Conn. (Walcott & Michener, 1967, Fig. 5), stopped flying its incorrect course just after crossing the Connecticut River. This is probably the only large river that this bird had seen that summer. The pigeon perched for nearly an hour, then took off and headed very nearly exactly toward home. Furthermore, on its first release from Sanford, Maine (Fig. 8), this bird stopped flying upon reaching the seashore, a landmark clearly inappropriate for finding the Cambridge loft. It later oriented toward the loft successfully.

Other than these reactions there were only a few occasions where pigeons seemed to be piloting by landmarks for portions of their flights outside the immediate area around the loft. In two cases the pigeons seem to have chosen the flight direction before encountering the landmark in question. Blue B AL, on its second flight from Manchester (Fig. 6), flew directly south from the release point toward home, then encountered and followed the Merrimack River for 11 miles (18 km.). As the river curved eastward, however, the bird crossed it and continued southward away from the river toward the loft. In another case Silver AL Y flew east from Sanford, Maine (Fig. 8), perched, then flew west, and finally turned south. The southerly course was directed toward the loft, but when the sun was obscured by a cloudbank in the west, the bird's track curved eastward, encountered the seacoast, and it perched again. It took off and flew along the coast, without the sun's disk being visible, for another 14 miles (23 km.). This is the only instance where a pigeon more than 10 miles from the loft flew for more than a few miles when the sun's disk was not visible, and in this case the bird seems to have continued on a previously chosen course by simply following along the seacoast.

One pigeon apparently reacted to a single landmark 30 miles (48 km.) from the Lincoln loft: Wachusett Mountain, 2006 ft. (611 m.) above sea level. This is the tallest hill in eastern Massachusetts, and can be seen from 100 ft. above tree-top level for

more than 30 miles in most directions. Blue W Y was trained from Orange, Mass., and thus it had to pass by Mt Wachusett on each of its training flights. On Blue W Y's first release from Worcester (Fig. 5), which was complicated by our having kept the bird on an artificial light/dark cycle for 9 days, it flew directly north and passed 2 miles west of the summit of Mt Wachusett (shown as an ovoid dotted line). The bird then turned eastward and flew more or less directly towards the loft. On a subsequent release from Jaffrey, N.H. (Fig. 5), the bird seems to have oriented also to Mt Monadnock (also shown as a ring of dots) before turning and flying to the loft. It is, in many respects, surprising that more of the pigeons did not show orientation to this kind of landmark, but, to date, only this one bird out of the sixteen studied has shown such a reaction.

To summarize, there is no evidence that most of our pigeons used piloting as a major method of orientation more than 10 miles from their lofts. This conclusion agrees with those of Matthews (1955), Kramer & St Paul (1952) and others (see Schmidt-Koenig's review, 1965). The area round the loft within which pigeons apparently do use landmarks has been repeatedly discussed by many authors (Schmidt-Koenig, 1965) and seems from our results to be determined by the kinds of landmarks around the loft. For the pigeons homing to the Cambridge loft familiar territory seemed to extend W.N.W. to Bedford Airport, but was otherwise confined to areas from which the tallest buildings in Cambridge could be seen.

Directional orientation

Most of our pigeons released at new places for the first time started off in the compass direction that they had previously flown from the training point to the home loft.

In 11 out of 20 such releases off the training line the birds flew for 5 miles or more in a direction within 10° of their previous training. The analysis of the straight-track segments also show this accuracy clearly (Table 3). This compass orientation may continue for a variable distance before the pigeon corrects its course toward home, and while some tracks began with no flight in this direction at all others continued in the training direction well beyond the distance at which the birds were accustomed to finding home. As shown in Fig. 8, Silver AL Y flew 51 miles (82 km.) on such a course from Laconia, even though the training distance had been 35 miles (57 km.). Similarly, Blue W AL followed a southerly training-direction course from Fitchburg (not shown) for 72 miles (116 km.), whereas it had been trained from 40 miles (65 km.). These flights suggest that the birds reacted as though they had been released further out along the training line. It should be stressed, however, that such long flights in the training direction were rare, since the pigeons mostly reoriented to their lofts directly before flying this far.

This orientation in the trained direction has been shown by many studies in which the birds were released along a line in a fixed compass direction. Matthews (1951), Kramer & St. Paul (1950a), Hitchcock (1952) and Griffin (1952a) reported such instances of training-direction flights. This directional orientation seems to be completely learned from the birds' past experience. We only tried to retrain one pigeon from a new place, and, as discussed elsewhere (Michener & Walcott, 1966), the bird showed the new orientation (Fig. 6, track 11) after only three consecutive releases (tracks 8–10). We have found no evidence in our results for the existence of any inherited tendency to fly in a specific direction. One bird trained from Manchester

(see Fig. 2, Blue W AL) showed a slight tendency to fly eastward, but otherwise the directional orientation was always parallel to the training line.

The fact that our pigeons flew only when they were either in familiar territory or could see the sun suggests that they were using the sun as a directional reference. It has long been widely accepted that many different animals use the sun's azimuth as a compass reference. Kramer & St Paul (1950b) and Kramer & Reise (1952) showed that birds could compensate for the sun's apparent motion and orient to a fixed direction at any time of day. It is, however, a much more difficult process to orient by the sun and still to compensate for crosswinds. This requires that the pigeons be able to project their courses in some way along the terrain in front of them and to maintain a heading different from their chosen direction of flight in order to produce a corrected course across the land. In order to fly a course with an accuracy of less than 10°, compensations on the order of 20° in heading must be made for even moderate crosswinds. Drury & Nisbet (1964) reported a similar correction at night in migrating songbirds, which also must be intrinsically more difficult over ocean than over land.

Preliminary investigations of the effect of exposing pigeons to artificial light/dark schedules (Walcott & Michener, 1967) has raised some doubt as to whether the pigeons really do use a simple sun-azimuth compass of the sort described by Kramer & Reise (1952). Further experiments are presently under way to investigate this point more fully.

Reverse-displacement navigation

On several tracks, after ceasing to fly in their trained compass directions, birds flew back almost to the release point before turning toward the loft. Silver AL Y, on its track from Sanford (Fig. 8), and Blue B AL, on its second trip from Worcester (Fig. 6, track 11), showed this tendency most clearly. This may be taken as a kind of voluntary reverse-displacement navigation. It was observed on only three occasions, however, and therefore does not seem to be an essential part of the pigeons' orientational processes. The performance in these examples requires, it should be noted, no particular inertial sense, and might well have been accomplished by the pigeons' having integrated the distance and direction they had flown, using a time sense and a compass reference, such as the sun.

In our experience no pigeon ever returned to the loft along the same path by which it had been taken to the release point, so there is no suggestion that they find their lofts by reproducing the turns and accelerations experienced during their displacement. These negative data agree with many other reported findings (see Schmidt-Koenig, 1965).

Orientation to the loft

Inspection of the tracks of pigeons released from new places (Figs. 3–6, 8) leaves little doubt that the pigeons were oriented to the loft better than at random. Nearly all the tracks lie completely within ±30° of the home direction (as viewed from the release point), even though the bearing of the release points from home varied from 165° to 015°, a span of 210°.

The results of the analysis of straight-track segments showed that at least three pigeons could consistently choose straight courses (over presumably unknown territory) that were oriented to within 10° of the loft. The average accuracies of these birds' homeward-directed straight segments were: Silver AL Y 5·4°, Blue W AL 5·0°, and

Blue W Y 6·0°. The only other birds for which we have sufficient data to analyse meaningfully were Blue B AL (11·5°) and Blue B-77 (24·5°). It is clear that the probability of these birds having chosen such accurate courses at random, while not actually computable, is very small. Even the least accurate of these five pigeons, Blue B-77, oriented a great deal better than at random.

When considered all together, the dependence of this orientation upon the sun, the remoteness of the chance that these pigeons had seen the areas in question even once before, and all the evidence *against* the pigeons' using landmarks extensively strongly suggests that this orientation to the loft represents some form of true navigation.

Griffin (1952*a*) and Hitchcock (1952) reported that their flocks were generally well oriented to the loft even when in unfamiliar territory, but that these flocks often turned on to incorrect headings and, generally, did not fly toward the loft in the same direct manner as the single birds we have observed. For these reasons, they did not conclude that their flocks had definitely demonstrated true navigation. Hitchcock (1955) found direction-orientation with his single birds, but, again, presented no conclusive evidence for true navigation. The homing times and initial orientations of pigeons reported by Matthews (1951) and Kramer (1953) strongly suggested that the birds could orient to the loft from unknown territory. The sensory basis of this orientation was the subject of considerable discussion, and Kramer and Matthews have repeatedly suggested that it depends, in part, upon the sun.

The simplest form of one-coordinate sun navigation was proposed by Tunmore (1960). It depended only on the instantaneous measurement of the sun's altitude (angle between the sun and the ideal level horizon). If the sun appeared at release higher than the bird remembered it would be at that time at the loft, the bird would, as a first approximation, be able to orient in a general direction of the loft if it simply flew away from the sun. If the sun appeared too low, the bird should fly toward it. This hypothesis predicts therefore that the birds' flight will be directed toward or away from the sun. The tracks of our pigeons show that this hypothesis is inadequate to explain the accuracy of the observed navigation. The birds showed no simple tendency to fly along a compass direction related directly to the azimuth of the sun.

Matthews (1953) suggested that pigeons might make use of a two-coordinate sun navigation. This idea was developed more explicitly by Pennycuick (1960). This 'sun-arc' navigation, in its most general form, relies on the sun's altitude and its change of position to provide a pigeon with information about the direction of the home loft. Kramer (1953) claimed that his pigeons showed truly navigated flight directions within 1 min. after their release, and that this did not allow the birds to see enough of the sun's movement to obtain sufficiently accurate information from it to navigate by the proposed sun-arc method. In contrast, our results from pigeons trained along a compass line indicated that the initial orientation depended only on the birds' previous experience, and did not show any such accurate navigation. In fact, with our pigeons, much more time was apparently necessary for navigation to be manifest. The average time between the moment when our pigeons could first see the sun and the moment when they displayed accurate loft-orientation in unfamiliar territory was 176 min., with the values ranging between 6 min. and about 19 hr. The most rapid examples of loft-orientation from new release points were not the most

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accurate: Blue B-77, released from New Bedford (Fig. 3, track 8), oriented to within 32° of the loft direction in about 6 min., and Blue B AL, on its first release from Worcester (Fig. 6, track 7), oriented to within 25° of home in 24 min. All other loft-directed straight-track segments were only manifest more than 50 min. after release. During 50 min., furthermore, the sun moves through a great circle arc of $11\frac{1}{2}$–$12\frac{1}{2}°$ (depending on the time of year), or about 23–25 of its diameters. This amount of arc would be sufficient for quite accurate information to be obtained by such methods of sun navigation as proposed by Matthews or Pennycuick.

Thus our data generally support the notion of bi-coordinate sun navigation as proposed by Matthews and Pennycuick. If their hypotheses are correct then it should be possible to manipulate a bird's navigation by very small shifts in its (presumed) internal clock. A few preliminary trials (Walcott & Michener, 1967) have shown promising results; further experiments are under way.

Our pigeons, then, seem to have used three basically different methods of orientation during many of their flights. They started out orienting in their previous training direction. Since this directional orientation depended on the visibility of the sun, yet occurred quickly after release, it was probably based on the sun's position and a time-dependent angular compensation process. When the pigeons had flown until they could employ their navigation system, they reoriented toward the loft. This process probably also involved some aspect of the sun's position, and allowed them to navigate to within 5 or 10 miles of the loft. Within this region they seemed to abruptly reorient their flights directly to the loft by using some familiar landmark(s).

SUMMARY

1. Pigeons trained by releases along a constant compass line were repeatedly tracked to their lofts from the same training points 30–50 miles away. Their tracks differed from day to day by several miles, and the birds usually did not follow any obvious landmarks.

2. The pigeons were released from new release points and on many of the tracks followed a definite sequence of orientation methods: the birds began flying in the same compass direction that had got them home from the training point, then they apparently switched to a rather accurate navigation method which got them to within 10 miles of the loft, where they seemed to pilot by a few familiar landmarks to the loft entrance.

3. There is no evidence that most of the pigeons learned or could use landmarks extensively more than 10 miles from the loft, even over area which they crossed more than twenty times.

4. The flight of pigeons from the training points and new release points at distances of 13 miles or more depended strictly on the visibility of the sun.

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