Topography and Pigeon Orientation*

GERHART WAGNER Swiss National Foundation for Scientific Research

FEW YEARS AGO in Switzerland we started a series of investigations concerning the problem of whether topographical factors influence homing pigeons' orientation. Up to now, the opinions expressed in the literature have been confusing. Some authors (ref. 1) believe that there is no topographical influence at all, whereas others (ref. 2) try to prove that topographical cues alone lead pigeons back to their loft. Kramer (ref. 3) reports a clear influence of the sea coast on the initial orientation behavior of Wilhelmshaven pigeons released from the Danish island of Bornholm. However, it seemed to us that there had not been sufficient experiments conducted specifically to study this question. Most conclusions were drawn from experiments carried out for other purposes.

Switzerland with its high mountain ranges, its valleys and lakes, is a most suitable country for conducting such homing experiments. There is no doubt that the problem is a complex one. It can be divided roughly into two particular problems:

(1) Whether topographical cues influence the initial orientation of the pigeons when released and, if so, how, (2) Whether topographical cues influence the actual and complete homeward flight and, if so, how.

To study the first problem, pigeons can be released in the conventional manner, one by one and in a statistical number, from places of topographical interest. The pigeons then are observed through binoculars as long as possible. The bearings (azimuth) of each pigeon are noted at 20, 40, and 60 sec after release and plotted on concentric circles. Statistical evaluation follows according to the methods of circular distribution: Do the directions chosen by the pigeons show a uniform distribution? If not, is there any evidence of a topographical influence at that particular point of release?

We call the conventional release method the "ground method." Its disadvantage is that one can only follow the pigeons for the first 2 or 3 km of their flight, but one does not know at all what they will do beyond that.

To study the second problem, that is, the actual way home, pigeons have to be followed directly or indirectly in their flight. Such experiments have been performed by different investigators and with different methods. Griffin and others followed displaced seabirds; Matthews followed displaced

259

^{*} The maps in this paper are reproduced by permission of the Swiss National Institute for Topography (Schweizerische Landestopographie).

pigeons on their homeward flight by means of a normal aircraft. However, a normal aircraft cannot fly as slowly as pigeons and, therefore, must fly in curves and circles. Thus, it becomes very difficult for the observer to keep track of the pigeons. Mitchener and Walcott (ref. 4) introduced the "radiotracking" method of following the pigeons. These investigators were able to trace the complete homing flight for a great number of singly released pigeons. The disadvantage of this method, however, is that the pigeons' behavior during the flight, especially their reactions to topographical structures, cannot be observed in detail.

Tracking pigeons by helicopter avoids the disadvantages of both ground and aircraft tracking. By helicopter one can follow the pigeons at their exact speed and even stay very close to them. Their flying behavior can be observed all the time; and, when they are released in a flock, it is possible to study the flock's behavior. We studied the pigeons' actual way home in this manner, and called this method the "helicopter method."

METHODS

Ground Method

To study the influence of topographical cues on initial orientation, we used the conventional releasing method. The topographic structures chosen were water surfaces and mountain ranges. The releasing points in these experiments were normally selected in such a way that, to take the shortest route to their loft, the pigeons had to cross a lake or a mountain range at the beginning of their flight.

The number of pigeons usually released was 20 or more from one loft, sometimes less. The pigeons necessarily originated from different lofts and cannot be considered as homogeneous. This fact, however, did not seem to be a serious disadvantage. On the contrary, it was interesting to study the reactions of different pigeons to the same topographical factors.

Helicopter Method

To study the complete flight of the pigeons from the releasing point to the loft, we used a French Aloutte III helicopter. Since the Swiss army maintains a homing pigeon service and, therefore, was interested in our investigations, we were granted a military helicopter and a pilot for 10 flying hr in 1969 and for 15 hr in 1970.

In our first flights we worked with flocks of 20 to 30 pigeons. It proved to be quite easy to keep them in view, and the birds were not disturbed by the presence of the aircraft even when followed as close as 30 to 50 m. We released flocks of only five to ten pigeons in the 1970 experiments. Sometimes, when the flock divided into smaller flocks, we could follow only one or two individuals.

During the flight we could not only trace the exact homing route on the map, but also measure the altitude over ground as well as the horizontal and vertical speed.

GROUND-METHOD RELEASES UNDER ALPINE CONDITIONS

When released under alpine conditions, the diagrams of the bearings soon after release show clearly a topographical influence. This influence is demonstrated in the following three examples.

Release Nr. 14/68 1

This release in the Toggenburg valley re-

260

¹ From Wattwie (600 m alt) to Wetzikon: 22 km at 270° az; Sept. 30, 1968; 1126-1530 hr.

sulted in a clear bimodal distribution as shown in figure 1. The bottom of the valley, 600 m above sea level, is about 1 km wide, and the mountain ranges on both sides rise up 1000 to 1300 m within a distance of 2 to 3 km. The home direction includes an angle of 70° with the downward direction of the valley. On both sides, villages of about 5000 inhabitants were visible in the valley axis and at a distance of about 2 km. The sky was completely covered that day by very low clouds with a moderate wind blowing from the southwest.

The pigeons, taken from a loft at Wetzikon, were trained from different directions. They clearly preferred the axis of the valley in both directions. Although the number of pigeons is only 13, the distribution of the vanishing points is obviously not uniform. All the 13 vanishing points are located within the two 90° sectors covering the upward and the downward direction of the valley. Statistical evaluation using the Roa test, (ref. 5) shows that the hypothesis of a uniform distribution can be rejected with an error probability of about 7 percent. Table 1 shows the preference for the two sectors covering the valley's axis immediately after release.

In this case, however, it is possible or even likely that the strong bimodal distribution is due to the location of the two villages in the axis of the valley and not so much to the two mountain ranges. The pigeons' loft was located in a village of similar size. This conjecture is supported by the fact that during the first minute after release, most of the pigeons flew in the direction of the nearest village. At the vanishing point, however, most of them had chosen the opposite sector which was in better agreement with the home direction. We made the same observation in many other releases; i.e., pigeons living in a village are often attracted by the view of other villages.

- FIGURE 1. Release no. 14/69 in the Toggenburg Valley. Vanishing diagram (● ●) shows a clear bimodal distribution with modes in directions of the valley's axis. The 20-sec diagram (black spots) already reveals a preference for the valley. Home bearing is indicated by arrow.

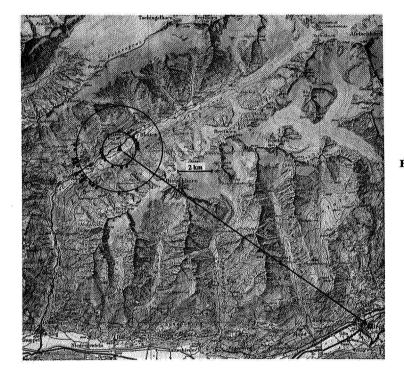


FIGURE 2. Release no. 8/ 68 in the Loetschental. Bimodal distribution after 20 sec but unimodal "downward" distribution of vanishing points. Home bearing (arrow) hits the Bietschhorn massif (3934 m).

Release Nr. 8/68²

This release (fig. 2) shows a strongly unimodal vanishing distribution. We obtained it in the Loetschental, an alpine valley below the timber line. The releasing point was located at the bottom of the valley, 1450 m above sea level. The valley's bottom was only 500 m wide, and the slopes of both sides ascended up to 3200 m and more within a horizontal distance of only 3 km.

The valley floor had a moderate descent of 5 percent from NE to SW coming down in a straight line from a large glacier. Downward, the valley turned to the left at a distance of 4 km from the releasing point into a very steep and deep gorge, leading out to the main valley of the upper Rhone. The loft was located at Brig in the Rhone valley at a distance of 18 km. The straight line home hit the Bietschhorn, the highest point of the region—nearly 4000 m above sea level. The sky was cloudless that day; all the mountains around were clearly visible. The temperature at the releasing point was 17°C and a moderate wind of 1.5 m per second blew from the southwest.

In this case, the flight directions after 20 sec yielded a clear bimodal distribution with modes in the axis of the valley. However, flight directions into the upward sector (with a view toward the glacier) decreased during the following minute. The vanishing diagram showed a typically unimodal distribution with the mode in the downward direction of the valley.

The bimodal distribution at the beginning as well as the unimodal distribution in the

² From Loetschental (1450 m alt) to Brig: 18 km at 125° az; Sept. 24, 1968; 1038-1233 hr.

TABLE	11	Distribu	ution	of	Fligh	t D	irections	
on	the	Four	90°	Se	ctors	in	Release	
Nr	. 14/0	68						

Time from release to bearing check (sec)	N	E	S	w	Total	¢(Roa test)
20	4	1	5	1	11	>0.05
40	3	1	6	2	12	>0.05
60	3	1	6	1	11	>0.05
120	1	0	7	0	8	<0.01
V	8	0	5	0	13	>0.05
All values	19	3	29	4	55	<0.01

TABLE 2.—Distribution of Flight Directions in Release Nr. 8/68

Time from release to bearing check (sec)	1ª	2 ^ь	3°	4 ^b	Total	¢(Roa test)
20	6	2	6	1	15	>0.05
40	5	5	9	2	21	>0.05
60	4	4	8	0	16	>0.05
120	2	2	13	1	18	<0.01
v	0	2	17	1	20	<0.01

^a 90° sector in the upward valley direction

^b Sectors rectangular to the valley

° 90° sector in the downward valley direction

vanishing points can easily be explained by the topographical situation. The homeward direction does not seem to play an important role in the initial orientation under these conditions. Table 2 shows the distribution on the four sectors and their significance levels after the Roa test.

Release Nr. 9/68 3

This release (fig. 3) was performed under high alpine conditions above the snow line. The releasing point was the top of the Langfluh near Saas Fee in the Wallis canton. The Langfluh is a long shaped rock ascending 2500 to 2900 m above sea level. In all directions, except a narrow northeast sector where the tourist center of Saas Fee was visible, there was nothing but snow and ice. The home direction almost coincided with the direction to Saas Fee. The weather during this release was excellent; the temperature was 12°C with a moderate wind blowing from the mountain side (SW). The pigeons used in this experiment had been trained

³ From Langfluh (2885 m alt) to Brig; 27 km at 17° az; Aug. 25, 1968; 1000-1133 hr.

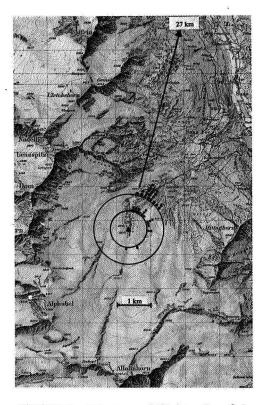


FIGURE 3. Release no. 9/68 from Langfluh (2885 m). Strong unimodal distribution of the 20-sec and the vanishing diagram. Home bearing is indicated by arrow.

within the valleys of the region but not in the high mountains. They were released in 20 groups of two individuals.

The cumulative influence of topography and home direction in this case resulted in a unimodal distribution that was narrower than any we had ever observed before. Forty seconds after release, no pigeon was observed out of a sector of 60°. The 20-sec distribution is also strongly unimodal and far from uniform, although four groups of pigeons had not yet chosen the final direction. The level of significance is already less than 0.01 for the 20-sec distribution. As figure 3 shows, the pigeons left the icy region as soon as possible.

GROUND-METHOD RELEASES FROM LAKES

Water surfaces of relatively small size proved to be as efficient as mountain ranges or snow surfaces in determining the initial bearings.

Release Nr. 1/65 4

This experiment was carried out with a small number of homing pigeons from the Swiss Pigeon Service during a military course in 1965 under good weather conditions. It was the first experiment that revealed an evident influence of a lake surface on the direction chosen by the pigeons at the releasing point. The 17 pigeons had been taken from four different lofts, all situated beyond the lake of Neuchatel at a distance of 15 to 25 km. They had a small amount of training that spring but not from this particular direction. Lake Neuchatel has a width of 6 km. We released the birds in groups of two and only measured the vanishing directions.

The diagram shown in figure 4 suggests a *From L'Abbaye to four lofts beyond the Lake

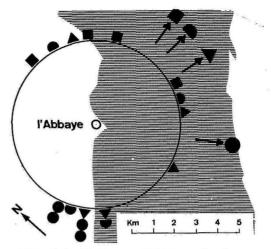


FIGURE 4. Release no. 1/65 from the shore of the Lake of Neuchâtel. Four arrows show (with different symbols) directions of four lofts from which pigeons were taken. Vanishing diagram (circle) is trimodal with two modes in the shore directions and one across the lake.

preference for the two shore directions (eight and five pigeons, respectively); However, four pigeons disappeared directly across the lake. No pigeon vanished in the opposite direction. Consequently the resulting diagram is trimodal, but statistical evaluation shows that this distribution can be considered as uniform.

Release Nr. 21A and 21B/67⁵

The 22 pigeons used for this experiment (fig. 5) were taken from a loft in Bettwiesen, a small country village 38 to 40 km from the two releasing points. Although they were well selected racing pigeons, they were trained only from the opposite direction.

The release Nr.21A was carried out from Erlenbach, a village located at the right shore

of Neuchatel: 15-25 km; May 7, 1965.

⁵ (A) From Erlenbach to Bettwiesen: 38 km; and (B) from Horgen to Bettwiesen: 40 km; May 17, 1967.

of Lake Zurich. The experiment was arranged in such a way that, in their home direction, the pigeons had to fly straight away from the Lake.

The vanishing diagram shown in figure 5 reveals that the directions chosen by the pigeons were in good agreement with the home direction within the first 20 sec after release. The length of the mean vector which deviated from the home direction by only 4° was 0.88 (p<0.01, Rayleigh Test). Immediately after releasing 16 pigeons from Erlenbach, we crossed the lake by boat with the remaining 12 birds from the same loft, releasing them from Horgen on the opposite side of the lake. Now the directions chosen resulted in quite a different diagram. Soon after release, most of the pigeons chose a direction parallel to the eastern shoreline of the lake. In this case also, the distribution of the vanishing directions is not uniform. The length of the mean vector is 0.64 (0.01 , but its deviation from the home direction is 79°. The average homing time was distinctly longer than in the Erlenbach experiment. It is possible that most of the pigeons were able to fly around the lake in the time observed for homing.

Release Nr. 3/67 6

This release was made from a motor boat in the middle of Lake Konstanz, one of the largest water surfaces in central Europe. The distance from the releasing point to each shore was at least 5 km. The 34 pigeons used were taken from the loft in Bettwiesen. They had limited experience that spring. The weather was hazy, but both shores were clearly visible, the northern shore having better sunlight than the southern; the wind was

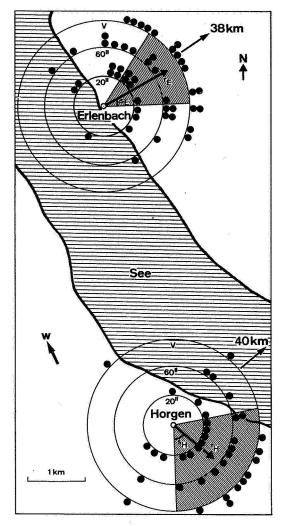


FIGURE 5. Release no. 21A and 21B/67 from the shore of the Lake of Zurich. (A) Release from Erlenbach (E) with home bearing away from the lake. (B) Release from Horgen (H) with home bearing across the lake. Both diagrams are unimodal (20 sec, 60 sec and (V) as well); but in case B the mean vector's (r_{II}) deviation from the home direction is 79°, and in case A (r_E) it is only 4°. The hatched area shows the sector within the mean angular deviation $(s_E = \pm 28^\circ, s_H = \pm 49^\circ)$. W is wind direction.

^e From middle of Lake Konstanz to Bettwiesen: 33 km at 247° az; Apr. 3, 1967; 1330–1530 hr.

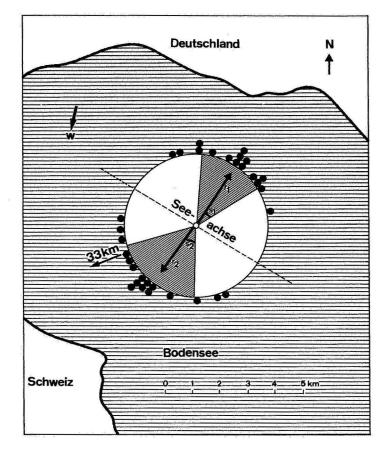


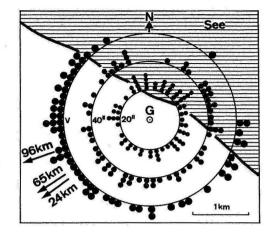
FIGURE 6. Release no. 3/67from the middle of the Lake of Konstanz. Vanishing diagram is clearly bimodal with modes in the two shore directions. r_1 and r_2 indicate mean vectors of the two groups taken independently; s_1 and s_2 , the mean angular deviations ($\pm 26^\circ$ and $\pm 35^\circ$, respectively).

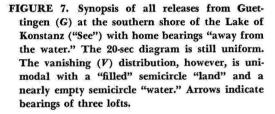
moderate from the north. Immediately after release, the pigeons chose one of the two shore directions. In the first 20 sec, the wrong northern shore was clearly preferred. The vanishing diagram, however, shows a symmetrical bimodal distribution.

Let us consider the northern and the southern groups separately (fig. 6). For each we calculated the mean vector and the mean angular deviation. The length of the mean vectors then are 0.81 and 0.89, respectively. The directions of the two vectors are clearly oriented to the nearest points of the northern and southern lakeshore and seem to be quite independent of the home direction. Both groups show symmetry with respect to their mean vector. The distribution is not uniform with a significance level of p < 0.01.

The northern group clearly needed more time for homing than the southern one; i.e., 122 min instead of 80 min. Nevertheless, it is likely that some pigeons of the northern group turned to the southern side after having vanished from our binoculars but before reaching the northern shore.

The conclusion of this experiment, as well as of the two experiments related before, is that during the initial orientation (i.e., during the first minutes after release) water surfaces can influence the flight directions to a large extent and eliminate, more or less, the long distance orientation.





Figures 7 and 8 show the influence of the lake surface on a larger statistical basis for the case of shore releases. Figure 7 resumes the bearings of three releases from one point (Guettingen) located at the southern side of Lake Konstanz. Overall, the lofts were situated in about the same direction from the lake but at different distances. The great majority of the vanishing points is situated within the correct semicircle.

Figure 9, on the other hand, summarizes the vanishing bearings of three releases from one point (Langenargen) located on the northern side of Lake Konstanz. The 55 singly released pigeons were taken from the same three lofts as in the three releases from the south side (fig. 7), but this time the home bearings were directed across the lake. The great majority of the vanishing directions is again clearly oriented to the land side, but this is the incorrect semicircle. The two shore

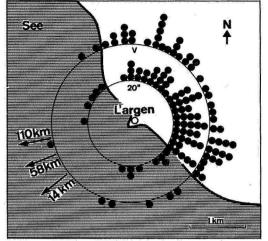


FIGURE 8. Synopsis of all releases from Langenargen (L) at the northern shore of the Lake of Konstanz ("See") with home bearings "across the water." Unimodal distribution of the 20-sec and the vanishing diagram (V). The "correct" semicircle "water" is empty, and the "wrong" semicircle "land" is filled. The same three lofts (directions indicated by arrows) were used as in the case of figure 7.

directions, however, show clear modes within the semicircular distribution.

HELICOPTER-METHOD RELEASES

What is the pigeon's flight path after vanishing from the view of the ground-observer's binoculars? Do they fly around a large lake? In the mountains, do they follow the valleys and passes to overcome the mountains—or, do our observations, using the ground method, give a wrong impression? To answer this question, we used the helicopter method for extended observations.

In 1969 and 1970 we performed 12 helicopter experiments. In three cases only we could follow the pigeons on their complete flight from the releasing point to the loft. In five cases the pigeons landed before reaching

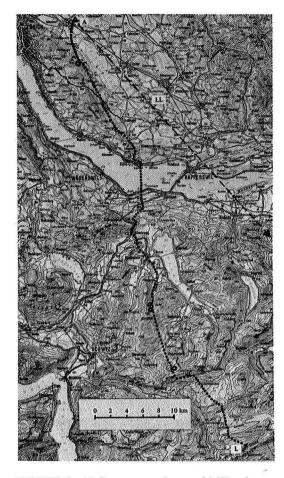


FIGURE 9. Helicopter track no. 3A/69. A, releasing point; LL, leading line to the loft (110 km); L, landing point after an effective track of 70 km within 60 min.

the loft. In two cases we lost them from view under difficult terrain and weather circumstances (rocks, rainfall). In two other cases we had to quit tracking because of lack of fuel. Nevertheless, the experiments yielded many interesting observations concerning the main question of whether topography does influence the pigeons' orientation behavior. In the following paragraphs we describe two cases of alpine flights.

Helicopter Flight Nr. 3A/69⁷

This experiment (fig. 9) was performed under good weather conditions with a flock of 27 pigeons trained to home from north. At two critical points the flock divided into smaller flocks. The flock that we followed consisted of 13 pigeons at the end of the flight.

The first 20-km leg of this flight was within the Swiss middleland, a landscape comprised of hills rising not over 1000 m above sea level and valleys lying at 400 to 500 m above sea level. After crossing Lake Zurich, the subalpine level was reached, becoming rougher and rougher with tops over 2000 m. The loft was located within the typically alpine canton of Graubuenden which is in a deep valley. Therefore, the direct homing line crossed many mountain ranges and valleys.

Soon after release, the pigeons chose a direction with a deviation of about 20° to the right of the home direction. This deviation can probably be ascribed to the influence of the training direction. As we had observed in previous experiments, the pigeons generally flew very low over the ground (often within 10 m or less), especially when the ground was ascending. They flew directly toward topographical obstacles such as hills and rocks, turning only at the very last moment and then flying around and not over it. Arriving after 40 km flight in the alpine region, this pattern of behavior implied that the pigeons often followed high vertical rocky walls at a distance of only a few meters. Topographical lines were never followed unless they had the same orientation as the pigeons' actual flight.

Lake Zurich, which had seriously influenced the pigeons' initial orientation in

⁷ From Duebendorf to Tiefencastel: 110 km at 138° az; Jul. 17, 1969.

ground-method experiments, was crossed after 20 km of flight. A slight deviation from the course was observed, however, in the sense that the birds chose the shortest way over the water using a small peninsula as a rudimentary "landbridge."

During the first 60 min the pigeons had flown an effective distance of about 70 km. Then they approached a very high rocky mountain range presenting a nearly vertical wall of 700 m height rectangular to the flight direction. In this situation, the pigeons landed near a small mountain lake 1800 m above sea level; i.e., above the timber line in the alpine rubble. We also landed with the helicopter at a distance of about 100 m from the pigeons. They began to preen, then fed between the rocks and probably drank water from a tiny rill.

After 45 min the pigeons did not manifest any intention to continue their flight. We then started our engine and tried to chase them up by approaching the birds very closely with the helicopter, but the downward wind produced by the rotor pressed them to the Earth. We broke off the experiment and flew over to the Engadine valley to start another homing experiment with more pigeons we had on board.

Helicopter Flight Nr. 3B/69⁸

In this experiment (figs. 10 to 12), the arrangement was opposite that of flight Nr. 3A: The pigeons had to start in the middle of the alps, in the Engadine valley. The straight line to the loft crossed the high alpine massif of Piz Kesch (3421 m). The releasing point was situated at 1700 m above sea level in the bottom of the valley. The 20 birds were taken from the Bettwiesen loft,

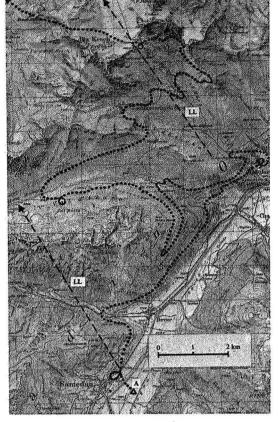


FIGURE 10. Helicopter track no. 3B/69. Track of the first 35 min after release crossing the massif of Piz Kesch (3417.7 m). *A*, releasing point; *LL*, home direction (leading line).

had good homing experience from different directions, but had never been released from Graubuenden.

The ground experiments previously described suggested that the pigeons would follow the valley's axis in one direction or the other. An Earth observer indeed would have reached the same conclusion in this case. The helicopter method, however, revealed that the pigeons followed the axis of the valley for 8 km only, then turned around and followed the valley's slope in the opposite direction,

^e From Samaden to Bettwiesen: 125 km at 330^e az; Jul. 17, 1969; 1427-1600 hr.

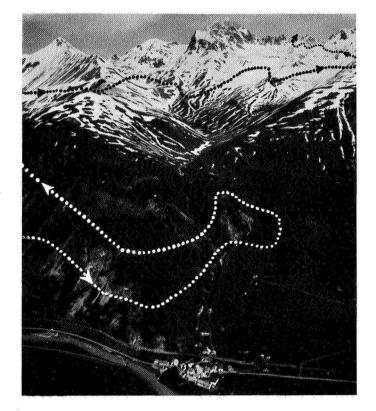


FIGURE 11. Helicopter track no. 3B/69. General view of the Piz Kesch massif from southeast with the pigeons' track.

flying very close to the ground but continually ascending. In this way they reached the Albulapass after having flown different curves and circles. The Albulapass is an important communication line to the Engadine with an alpine road. Having reached the highest point of that pass, the pigeons turned again and approached the massif of Piz Kesch. Following the wild and steep slopes of that massif in constant ascent, they reached a high alpine passage, the Porta d'Escha, 3008 m above sea level and crossed it in good home direction.

After this immense obstacle the rest of the way home presented no problems. Some smaller massifs were crossed in an analogous manner. Several valleys were crossed at 800 to 1000 m above ground. Even the large valley of the Rhine, although leading in approximate home direction, was crossed in direct flight toward the next massif, that of the Calanda (2808 m). This massif, too, was crossed in the typical way.

Unfortunately 20 km later, before the last high rocky barrier on their way home, the pigeons landed at 2000 m in almost vertical rocks near a water rill. It was quite impossible for the helicopter to go down at that point, and we had to terminate the experiment.

In a nonstop flight, the pigeons had covered a distance of 125 km in 93 min, which means their mean speed was 80 km per hour. They had never been more than 7 km away from the shortest line to the loft. Most of them arrived in the loft the same evening.



FIGURE 12. Helicopter track no. 3B/69. *A*, releasing point; *LL*, leading line to the loft (125 km); *L*, landing point of the pigeons after an effective track of 125 km within 93 min.

SUMMARY AND CONCLUSIONS

Two types of homing experiments have been performed with pigeons to study the question of topographical influences on the birds' orientation behavior:

(1) Ground experiments by releasing the pigeons one by one in the conventional manner at points of topographical interest.

(2) Helicopter experiments by following small flocks of pigeons on their homing flight.

The ground experiments clearly revealed a strong influence of topographical factors on the initial orientation; i.e., during the first minutes of flight:

(1) When released at lake shores with home direction across the lake, pigeons generally avoided the water surface.

(2) When released in valleys between mountain ranges, the pigeons preferred the valley axis.

(3) When released in the neighborhood of alpine snow and ice, pigeons avoided flying over the snow.

(4) When released in the neighborhood of a village, the village often attracted pigeons originating from another village.

The helicopter experiments, however, proved that the observations from the ground experiments do not allow conclusions concerning the actual homing way of the pigeons:

(1) Lakes as well as mountain ranges did not affect the general flight direction once the pigeons had recognized the approximate home bearing; both were crossed, if necessary, directly. Never did the pigeons follow a topographic leading line for a long time.

(2) A local influence of topographical factors could sometimes be observed during the homing flight. Mountain massifs can oblige the pigeons to fly many curves and circles to get over the obstacles. Topographic structures that are familiar to the pigeons

from home range, e.g., villages or woody hills, can attract the pigeons temporarily and sometimes in a persistent manner. Water surfaces of 2 to 3 km width were of small influence once the pigeons were flying in the proper direction.

In summation, our experiments under Swiss conditions yielded the following results. It is true that topographical factors may influence pigeons' homing behavior in many ways. However, such factors always make homing more difficult and not easier. There are no topographical structures or lines that lead pigeons home. Their long distance orientation system is not affected by topography.

DISCUSSION

QUESTION: Did all of the birds return home?

WAGNER: In the described experiments we used a total of 182 pigeons; 162 of them (90 percent) returned the day of release, 16 the following day. Only three were lost, two in the release Nr. 3A/69and one in the release Nr. 3/67.

GRIFFIN: Would you give us some information concerning cases when pigeons flew through cumulus clouds?

WAGNER: We performed one experiment in the Alps on a very cloudy day when a thunderstorm was starting. The pigeons had very bad orientation that day. They did fly into a large cumulus cloud once but only for a short time.

WILLIAMS: Did you have any chance to observe pigeons when the sky was totally overcast and the Sun was hidden from view?

WAGNER: Not with the helicopter method, but with the ground method. We obtained well-oriented vanishing diagrams even under complete overcast.

QUESTION: Do two pigeons released at the same time vanish in the same direction?

WAGNER: Generally they fly together and as a consequence vanish together. When released in a flock, the flock will also stay together.

WALCOTT: Did you see any effect of the helicopter on the behavior of the pigeons? Was the homing time of the pigeons who were followed roughly comparable with the pigeons who were not followed? WAGNER: The homing time in the helicopter experiments was quite normal. We could see a disturbing influence of the helicopter only when we came within 10 to 15 m of the pigeons.

GAUTHREAUX: Did you ever think that you had a steering effect when you were following the pigeons with the helicopter?

WAGNER: No. I think this possibility can be excluded.

GAUTHREAUX: Did the helicopter take off simultaneously with the pigeons as they were re-leased?

WAGNER: The helicopter is waiting in the air when the pigeons are released. After their normal initial circles, we follow them. For technical reasons it is not possible to start with the helicopter after the pigeons have been released.

GRIFFIN: In what position was the helicopter flown relative to the pigeons—behind them or above them?

WAGNER: Behind them; sometimes above, sometimes beneath. It was best to fly slightly beneath them.

REFERENCES

- MATTHEWS, G. V. T.: The Experimental Investigation of Navigation in Homing Pigeons. J. Exp. Biol., vol. 28, 1951, pp. 508-536.
- 2. ARNOULD-TAYLOR, W. E.; AND MALEWSK, A. N.: The Factor of Topography in Bird Hom-

ing Experiments. Ecology, vol. 36, 1955, pp. 641-646.

- 3. KRAMER, G.: Ueber Flüge von Brieftauben über See. In: Steiniger, Natur und Jagd in Niedersachsen, Hannover, 1956.
- MITCHENER, M. C.; AND WALCOTT, C.: Homing of Single Pigeons—an Analysis of Tracks. J. Exp. Biol., vol. 47, 1967, pp. 99–133.
- ROA, J. S.: 1969. Some Contributions to the Analysis of Circular Data. Ph.D. Thesis, Calcutta.
- WAGNER, G.: Verfolgung von Brieftauben im Helikopter. Rev. Suisse Zool., vol. 77, 1970, pp. 39–60.

BIBLIOGRAPHY

- BATSCHELET, E.: Statistical Methods for the Analysis of Problems in Animal Orientation and Certain Biological Rhythms. Washington, D.C.: Am. Inst. Biol. Sci., 1965.
- GRIFFIN, D. R.: Airplane Observations of Homing Pigeons. Bull. Mus. Comp. Anat., vol. 107, 1952, pp. 411–440.
- GRIFFIN, D. R.: Bird Migration. Doubleday and Co., 1964.
- HITCHCOCK, H. B.: Airplane Observations of Homing Pigeons. Proc. Am. Phil. Soc., vol. 96, 1952, pp. 270–289.
- HITCHCOCK, H. B.: Homing Flights and Orientation in Pigeons. Auk, vol. 72, 1955, pp. 355-373.