

A STUDY OF HOMING IN THE BANK SWALLOW
(*RIPARIA RIPARIA*)

THEODORE D. SARGENT

A series of field experiments utilizing color-marked Bank Swallows (*Riparia riparia*) was carried out in southern Wisconsin during the summers of 1959, 1960, and 1961. The experiments were designed to test the ability of birds of this species to return to their nesting burrows after geographical displacement. The Bank Swallow was selected as the subject for this study as it is an abundant breeding species in Wisconsin and has the great advantage of being a colonial nester.

Previous studies had indicated that some species of swallows have a well-developed homing ability. Ruppell (1934, 1936, 1937) worked extensively with the Barn Swallow (*Hirundo rustica*) and to a lesser extent with the House Martin (*Delichon urbica*) in Germany. Over several years he released 56 Barn Swallows at distances ranging from 276 to 1,875 km (172 to 1,160 miles) from their nests—of which 21 (40 per cent) returned. The maximum speed of return among these swallows was 412 km (256 miles) per day. The average speed of return was independent of release-point distance, but percentage returns dropped steadily with increasing distance.

Wojtusiak and Ferens (1947a, 1947b) and Wojtusiak (1948) worked further on homing in the Barn Swallow in Poland. They found that swallows released at distances up to 153 km (95 miles) from their nests returned on the day of release, and that homing velocities increased with increasing distance until a maximum of 35 km/hr (22 mph) was reached at distances of 121 to 153 km (75 to 95 miles).

In these studies of the Barn Swallow it was found that adverse weather conditions (rain, strong winds) decisively diminished the mean homing velocity. Likewise, all investigators reported that the swallows headed off in the home direction when released, although they do not mention the possible influence of wind direction or landscape features on these headings.

One record of homing in the Rough-winged Swallow (*Stelgidopteryx ruficollis*) is that of Gillespie (1934), who made two releases of the same male bird at distances of 5.1 and 51 km (3.2 and 32 miles). On both occasions this bird returned to its nest within 12 hours.

Southern (1959) has reported the results of 16 releases of the Purple Martin (*Progne subis*). These birds were transported to distances of 2.8 to 376 km (1.75 to 234 miles) from their home colonies, and all 16 returned. One bird returned 376 km (234 miles) in 8.58 hours (average speed of 43.9 km/hr, or 27.2 mph) under a heavy cloud cover at night.

Very little information on homing in the Bank Swallow is available.

Matthews (1955) has reported the results of 35 releases made during the breeding season in England and Germany. The distances that these birds were transported ranged from 6.4 to 228 km (4 to 142 miles), with the maximum return distance given as 108 km (67 miles). Thirty-seven per cent of the birds released returned to their nests.

In the present study, three indices of homing ability were studied: (1) takeoff directions at release, (2) homing percentages and speeds, and (3) behavior in an orientation cage.

METHODS AND MATERIALS

Eight colonies of Bank Swallows within 16.1 km (10 miles) of Madison, Wisconsin, were utilized. A total of 304 individual releases were made; also 113 individuals were tested in an orientation cage. Forty-eight release points, which ranged from 1.6 to 282 km (1 to 175 miles) from the home colonies, were used.

The birds were trapped at their burrows before dawn. A method of trapping described by Morris (1942) proved the most useful. This involved inserting cardboard tubes with attached plastic bags into each burrow. Mist nets were occasionally used.

When a bird was captured, it was banded with a U.S. Fish and Wildlife band. Each bird was uniquely color-marked by gluing portions of dyed feathers to the upper tail coverts and primary wing coverts.

The swallows were placed in small groups of five to 10 into large cloth bags after capture and banding. They were then transported by automobile to the desired release point. An attempt was made to release all birds at approximately four hours after capture.

Each bird was released singly, and its flight was followed with 7×50 binoculars. Disappearance time and compass direction were obtained for each bird. Extensive weather observations were made at each release point. Particular attention was paid to the wind direction (given in degrees from true north) and velocity (given in terms of the Beaufort Wind Scale) and to details of the cloud cover.

After the releases on a given day, observations were carried out at the home colony for the remainder of that day and for portions of two succeeding days. If it seemed probable that some birds might arrive at home before I did, an assistant was stationed at the home colony from the time of capture until I returned.

Generally the burrows were deserted if the captured member of a pair did not return within 24 hours. Thus, this observational method of accounting for returning birds certainly resulted in minimal figures, as many birds returning after 24 hours had elapsed were seen for only a few minutes.

TABLE 1
PERCENTAGE RETURNS OF THE BANK SWALLOWS FROM VARIOUS DISTANCES
(The numbers in parentheses refer to the total number of swallows released
in each case.)

<i>Categories of releases and percentage returns</i>	<i>Distance (miles) of releases from home colony</i>			
	<i>1-25</i>	<i>25-50</i>	<i>50-100</i>	<i>175</i>
A. Adults in incubating stage of breeding cycle released first time	80% (30)	87% (15)	39% (136)	33% (9)
B. Adults in incubating stage of breeding cycle released second time	100% (2)	86% (7)	50% (12)	
C. Adults in incubating stage of breeding cycle released third time		100% (1)	100% (4)	
D. Adults in preincubating stages of breeding cycle			14% (22)	
E. Adults in parental stages of breeding cycle	80% (5)		36% (11)	
F. Adults (incubating stage) released at night, returning same night	0% (2)		0% (4)	
G. Juveniles			0% (16)	

The orientation cage, in which the directional tendencies of 113 swallows were tested, was 92 cm (three feet) in diameter, 30 cm (one foot) high, and constructed of quarter-inch-mesh hardware cloth. The bottom was a piece of Plexiglas and was marked off into 12 numbered 30° sectors. The cage had a small circular wire perch in the center, and a larger one (79 cm in diameter) running around the periphery. The entire cage rested on a card table, the top of which had been removed, and which was draped with heavy, black cloth extending to the ground. Observations were always made from beneath the cage, where the relative darkness prevented the birds from perceiving the observer. A siding of uniform, heavy paper could be attached around the cage, shutting off the bird's view of the surroundings and leaving only a view of the sky.

Each bird was placed into the cage through a door in the top, and the sector of the cage in which the bird was located was recorded at five-second intervals. It was soon discovered that the birds remained active in the cage for only about 10 minutes. Therefore, data were taken for each bird for 10 minutes, with the siding either up or down.

RESULTS

Percentage Returns

Table 1 presents the percentage returns of the swallows released in this study. The total number of birds is divided into several categories, and

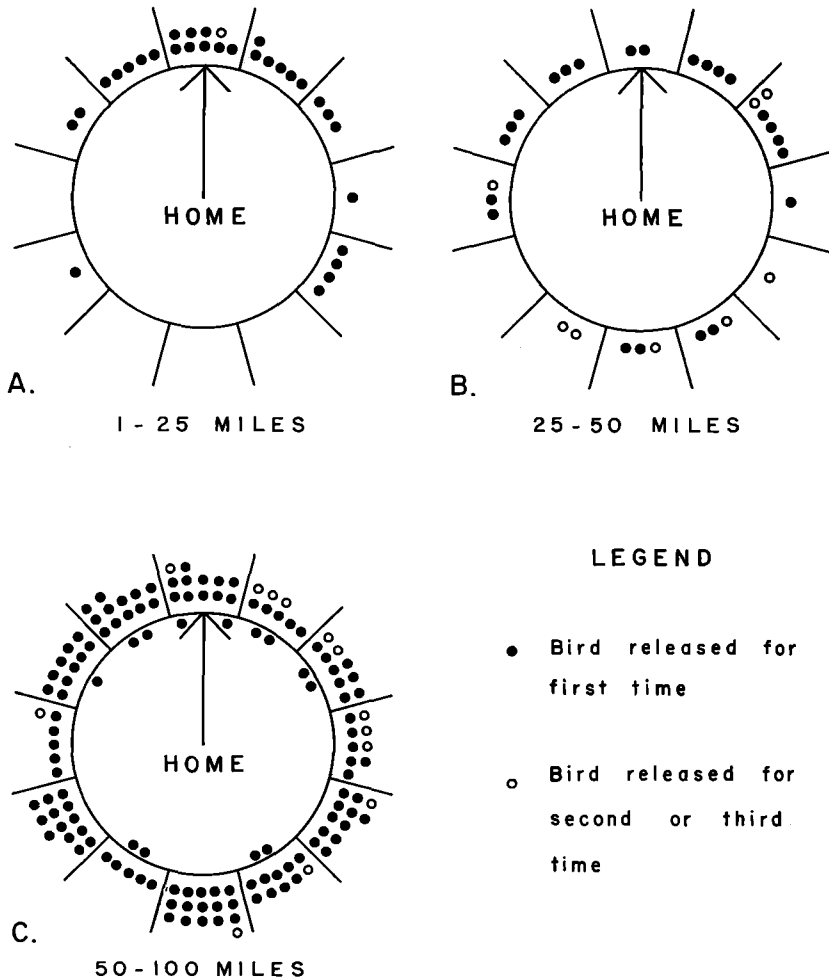


Figure 1. The disappearance points of the swallows from all release points with relation to the home direction for each of three distance groups.

percentage returns are given as a function of four distance units. Five results should be noted:

1. Percentage returns were much smaller for distances beyond 80 km (50 miles) than for those under 80 km (Table 1, category A).
2. Swallows released on more than one occasion generally showed better homing success than those released for the first time (Table 1, categories B and C). All of the swallows that were released more than once were released at different points, at least 90° apart, on each occasion.
3. Percentage returns were approximately equal for birds in incubating

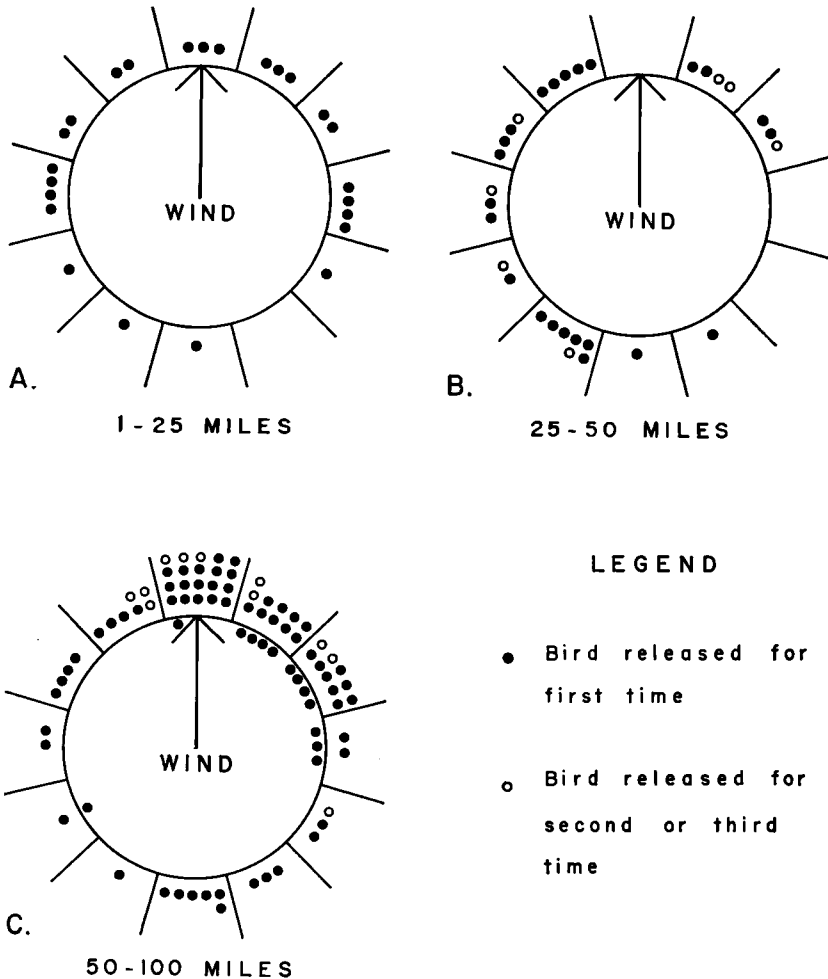


Figure 2. The disappearance points of the swallows from all release points grouped around the common wind direction (where wind velocities exceeded 8 km/hr or 5 mph) for each of three distance groups.

and parental stages of the breeding cycle (Table 1, categories A and E), but the returning percentage of preincubating birds was small (Table 1, category D). Data obtained from the preincubating birds are not included in other tables and figures as they are probably not comparable with those from incubating and parental birds. The actual dates of the releases seemed relatively unimportant in affecting percentage returns. Breeding cycle stages were not closely related to dates, as birds released as early as 23 May and as late as 10 July were known to be incubating.

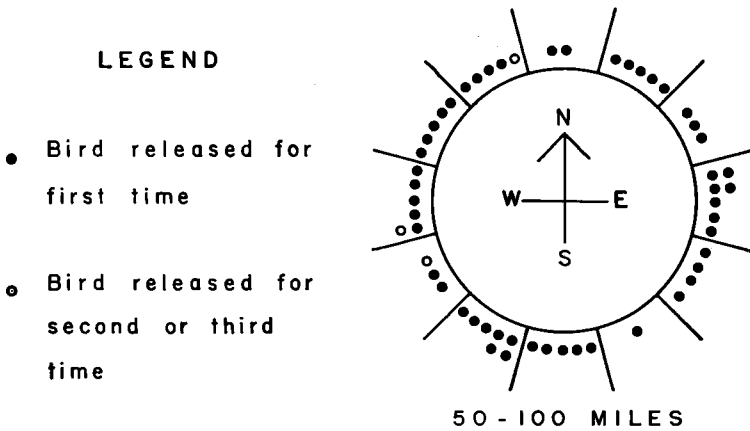


Figure 3. The disappearance points of 53 swallows released at distances of from 80 to 160 km (50 to 100 miles) when wind velocities were less than 8 km/hr (5 mph), plotted around common compass directions.

4. None of the swallows released at night (Table 1, category F) were known to return during the night of the release.

5. No juveniles were known to home at all (Table 1, category G).

The extent of cloud cover had no discernible effect on percentage returns from any distance, but no birds were released on days when the cloud cover was sufficiently heavy to obscure completely the sun's position.

Initial Directions at Release

Figures 1, 2, and 3 show the initial directions taken by the Bank Swallows at all release points. The only birds whose disappearance points are not included in these figures are those few that landed immediately after release or that were lost in less than one minute against vegetation (usually while feeding). Typically the swallows would initially gain altitude by spiraling irregularly upward for several seconds and then take off in a reasonably constant compass direction. Most birds were lost against the sky after two to five minutes. The swallows flew at altitudes of from about 30 to 150 meters (100 to 500 feet) above the ground.

Figure 1 shows the disappearance points of the swallows grouped around the home direction for each of three distance groups. At the 1- to 40-km (1- to 25-mile) distance, a highly significant number of birds disappeared from sight within the home quarter of the compass (chi-square = 24; $p < 0.01$). At the 40- to 80-km (25- to 50-mile) distances, twice as many birds disappeared in the home half of the compass as in the half away from home. This orientation is not statistically significant (chi-square = 5.4; $p < 0.20$). Beyond the 80-km (50-mile) distance, the distribution

of disappearance points with respect to the home direction is completely random (chi-square = 0.19; $p > 0.95$).

Figure 2 shows the disappearance points of the swallows with relation to the wind direction (where wind velocities exceeded 8 km/hr (5 mph)), again for three distance groups. From 1 to 40 km (1 to 25 miles) and from 40 to 80 km (25 to 50 miles) from home, the disappearance points are randomly distributed with respect to the wind direction (chi-square values of 3.3 and 3.6 with $p > 0.30$ for the two distance categories). For birds released at distances of 80 to 160 km (50 to 100 miles) from home, a highly significant downwind effect on initial headings is indicated (chi-square = 34; $p < 0.01$). Wind, therefore, affected the takeoff direction only in birds released at distances where homeward orientation was lacking (Figure 1C).

Figure 3 presents an analysis designed to determine whether the swallows had any tendency to choose one constant compass direction when released. Only those 53 birds that were released at distances beyond 80 km (50 miles) when wind velocities were less than 8 km/hr (5 mph) are considered. A completely random distribution of disappearance points is seen (chi-square = 0.2; $p > 0.95$).

Speed of Homing

None of the swallows released in this study achieved homing speeds approaching the maximum flight speed of 52 km/hr (31 mph) recorded for this species by Harrison (1931).

The maximum speed achieved by a homing bird was 22 km/hr (13.7 mph) (from an 18-km (11-mile) distance). Of the 45 birds that returned from distances under 80 km (50 miles) from home, 36 per cent exceeded 8 km/hr (5 mph) homing speeds; whereas of the 136 birds that homed from distances over 80 km (50 miles) from home, only 15 per cent exceeded 8 km/hr (5 mph). (Two of these latter birds arrived at home on the day following their release. Their speeds were calculated by subtracting eight hours from the total elapsed time to allow for the hours of darkness.) Thus, contrasting with the data on Barn Swallows (Wojtusiak, *op. cit.*), homing speeds did not increase with distance. However, the homing speeds of the Bank Swallows from all distances are so slow that speed is not considered to be a sensitive indicator of homing ability in this species.

Wind direction and velocity had no effect on the homing speeds achieved. Some of the fastest homing flights from distances of less than 80 km (50 miles) were made against head winds, under overcast skies, in haze, and through general shower activity. However, all 18 birds returning on the

TABLE 2
TOTAL PER CENT OF BIRDS HOMING, AND PER CENT OF BIRDS HOMING WITHIN 24 HOURS, FROM THE FOUR COMPASS DIRECTIONS, AT
VARIOUS DISTANCES

Distance of releases from home	Compass direction of releases from home colony											
	North			East			South			West		
	Total birds released	% homing	% homing within 24 hours	Total birds released	% homing	% homing within 24 hours	Total birds released	% homing	% homing within 24 hours	Total birds released	% homing	% homing within 24 hours
1-25 miles	7	71	71	9	78	56	11	73	55	17	88	71
25-50 miles	22	32	5	20	30	25	34	24	9	6	100	100
50-75 miles	25	40	16	7	43	0				27	59	7
75-100 miles										12	42	0

day of release from distances of greater than 80 km (50 miles) did so under clear skies.

Homing Success from the Four Compass Directions

Table 2 shows the percentages of swallows returning from each of the four compass directions for several distances. The homing percentages are calculated for all birds returning in less than 84 hours and birds returning within 24 hours. The number of birds released from each compass direction in each of the distance zones is too small to permit a statistical evaluation of the data, but it appears that no direction produced markedly superior performance, either in percentage returns or in speed of homing.

Performance in the Orientation Cage

Figure 4 shows graphically the performances of the swallows tested in the orientation cage. Each graph is considered below:

A. The four birds tested within sight of their home burrows demonstrate that this method of testing for a directional preference is valid. The small peak to the right of the home peak indicates that some individuals might perform erratically in trying to escape, necessitating samples of several individuals at each test site.

B. A homeward preference is clearly marked in the birds tested at 1- to 8-km (1- to 5-mile) distances. The three hilltops used as test sites for these birds allowed views of from 5 to 8 km (3 to 5 miles) through at least 225° of the compass.

C. The birds tested at 8- to 24-km (5- to 15-mile) distances again show a homeward tendency. The four test points included the roof of a building (allowing a view of approximately 8 km (5 miles) in almost every direction), and three hilltops that allowed views of from 5 to 8 km (3 to 5 miles) through at least 200° of the compass.

D. A homeward preference is apparently shown again in the birds tested at 24- to 40-km (15- to 25-mile) distances (three home colonies were involved). The hilltop used allowed a view of about 24 km (15 miles) through 300° of the compass. The state capitol building in Madison (27 km, or 17 miles away) was visible from this point.

E and F. At distances greater than 56 km (35 miles) from home, when the birds were allowed a view of their surroundings, no homeward tendency is noted. The four test points were hilltops that enabled the birds to see from 5 to 16 km (3 to 10 miles) through at least 200° of the compass.

G, H, and I. No homeward preference is shown by birds tested in the cage when landmarks were screened from view by an opaque siding. In all of these instances the cage was set up in an open area, where only the sky and sun were visible to the birds.

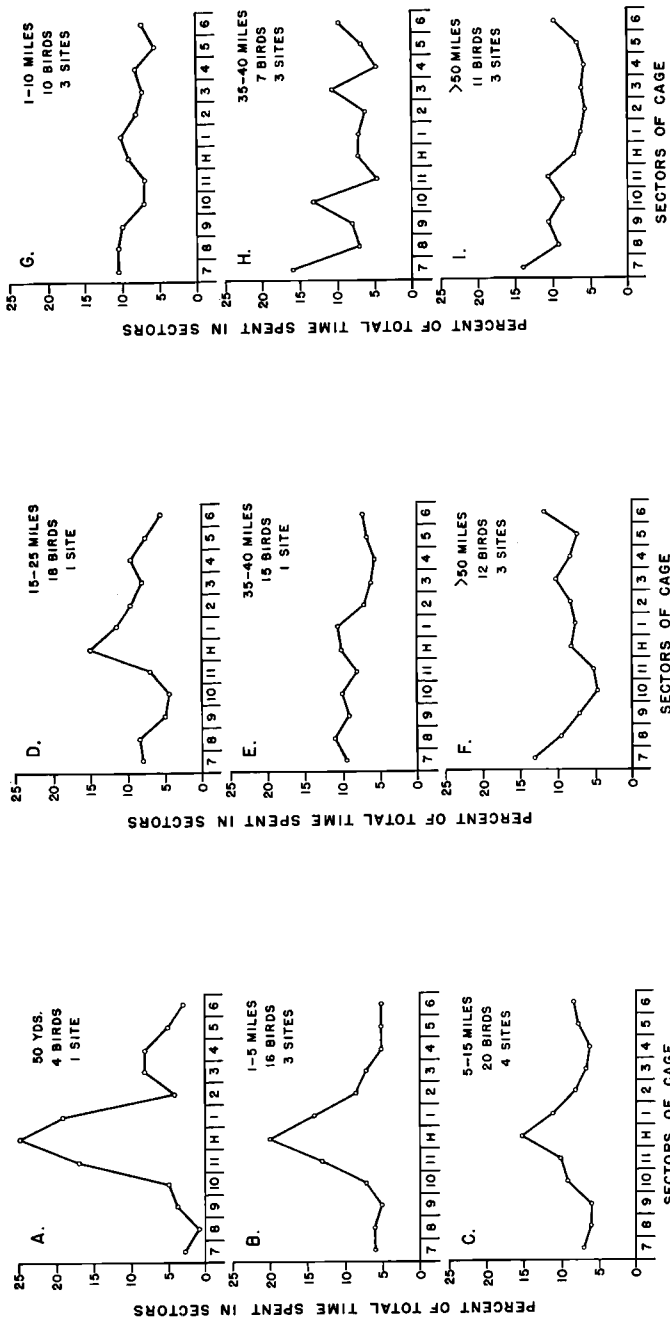


Figure 4. The performance of Bank Swallows in an orientation cage at several distances from home. Each graph shows the average per cent of total time spent by several test birds in each of 12 sectors of the circular cage during a 10-minute test period. The home sector is at the center of each abscissa. A through F represent performances when the birds had a complete view of the surroundings; G through I represent performances when the birds could see only the sky overhead.

DISCUSSION

Griffin (1955) recognizes three types of orientation in birds:

Type I. The use of random search patterns and familiar landmarks.

Type II. The ability to choose a constant compass direction.

Type III. True navigation: the ability to recognize displacement in any direction with respect to a particular geographical point.

There is no evidence in the present study for Type II orientation being used by displaced Bank Swallows. No initial preference of the birds for a particular compass direction could be detected, and no compass direction produced markedly superior homing percentages or speeds. The experimental findings have to be explained on the basis of Type I or Type III orientation.

Evidence that Type I orientation was utilized is provided by the fact that several measures revealed better performance at shorter distances. Such improvement at shorter distances is expected when a Type I mechanism is involved, but is not seen (and may even be reversed) when a Type III mechanism is used (Matthews, 1955).

Further indications of the nature of the orientation are suggested by the orientation cage experiments. A homeward tendency was shown when the birds were within 40 km (25 miles) of home and had long observation distances, including prominent buildings and other topographic features. The homeward tendency disappeared when this view was screened off, and when the tests were carried out beyond 40 km (25 miles) from home. The good homing performance displayed by released birds to distances of 80 km (50 miles) would seem to reflect the advantage of their elevated viewing position relative to the ground-level cage birds.

The relatively poor performance of swallows from distances beyond 80 km (50 miles) suggests that more random search for familiar landmarks was necessary at these longer distances. No data were obtained that would necessitate invoking a Type III mechanism to explain Bank Swallow homing.

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SUMMARY

Homing experiments utilizing color-marked Bank Swallows were carried out in the southern half of Wisconsin during the summers of 1959, 1960, and 1961. The swallows were captured at their burrows before daybreak, transported by car, and released individually at distances of from 1 to 280 km (1 to 175 miles). A total of 304 releases were made. Homing records were obtained by watching for returning individuals at the home colony. In addition, 113 swallows were tested for directional preferences in a portable orientation cage.

The major results may be summarized as follows:

1. Percentage returns decreased with increasing distances. Over 80 per cent of the birds released at distances of 1-40 and 40-80 km (1-25 and 25-50 miles) from home returned, while less than 40 per cent of the birds released at 80-160 km (50-100 miles) returned.

2. Swallows released at distances under 80 km (50 miles) from home showed initial homeward takeoff headings. Swallows released at distances beyond 80 km (50 miles) from home showed a random scatter of initial takeoff headings with respect to home.

3. Wind direction exerted no effect on the initial headings of the birds released under 80 km (50 miles) from home, but exerted a strong downwind effect on the initial headings of birds released at distances over 80 km (50 miles) from home.

4. Birds upon release showed no tendency to fly in any one compass direction.

5. Homing speeds were somewhat greater at shorter distances.

6. Birds tested in a portable orientation cage showed preferences for the home direction at distances of less than 40 km (25 miles) from home, provided a view of surroundings was available to them, but showed no such tendency at greater distances.

It is concluded that random search patterns and landmark recognition were used by displaced Bank Swallows in homing. No evidence for the use of true navigation was found in these experiments.

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Department of Zoology, University of Wisconsin, Madison 6, Wisconsin.