

ORIENTATION AND HOMING ABILITY OF THE BARN SWALLOW

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Many studies have monitored the homing ability of various animals, particularly birds. The mechanisms employed in navigation to a specific site or home area are not well understood; in fact, much work remains to be done in clarifying which species exhibit homing behavior. Also, few studies have examined the differential homing ability of males vs females during egg-laying and incubation. One might inherently expect females to exhibit a stronger homing tendency during this period, regardless of the distance or direction of the displacement from the home colony.

This study was designed to quantify and statistically determine if Barn Swallows (*Hirundo rustica*) home during nesting and, if so, how effectively. Barn Swallows were chosen as research animals because they may be found nesting colonially with colonies ranging from several to approximately 50 nests per site (Snapp 1976). This allowed efficient capture and recapture. I measured: (1) the ability to home from varied distances and compass directions, (2) the ability to orient toward home from release sites of different distances and directions from nest sites, and (3) the homing and orientation abilities of males and females.

STUDY AREA AND METHODS

The study was done at the University of Pittsburgh Laboratory of Ecology on the Pymatuning Reservoir in Crawford Co., northwestern Pennsylvania. Six colonies of nesting Barn Swallows were located within a 10 km radius of the Field Station. Three of the colonies were under bridges: Colony A—10 active nests, B—12 active nests, and C—4 active nests. The remaining three colonies were in barns or abandoned buildings: Colony D—12 active nests, E—6 active nests, and F—4 active nests. Most data were collected during May through July of 1976, with some investigations in 1975 and 1977. During the pilot study in 1975, Barn Swallows homed to the nest site with great proficiency. A return rate of 89% was recorded for 137 displacements made at distances ranging from 0.8 to 16 km from the home colony. I decided to extend distances for the 1976 experiment.

Swallows were caught with mist nets draped over the sides of bridges or erected in building openings. Swallows became net-shy and many were picked off the nest or roost before dawn. All captures were made during egg-laying or incubation stage. Only breeding birds were used as test animals (presence of cloacal protuberance or incubation patch) in order to avoid the possibility of displacing non-breeding birds or transients.

Each bird was banded with a U.S. Fish and Wildlife Service band, and

sexed using methods described by Samuel (1971a,b), which were slightly modified to include characteristics of the outer rectrices, incubation patch, and the intensity of the orange on the upper breast and forehead (U.S. Fish and Wildlife Service and Canadian Wildlife Service 1977). The swallows were placed in holding boxes covered with dark cloth and transported to release sites between dawn and 10:00. The 32 release sites were located north, south, east, and west, at points 16.6, 25, 33.3, 41.6, 50, 66.6, 83.3, and 100 km from the colonies. Three birds were released at each site. Birds were released one at a time; the second and third birds were released only after the preceding bird had disappeared from sight. Upon release, each swallow was observed with binoculars until it assumed a final heading which was recorded. Weather conditions were noted during each release. Birds were not released if high winds or heavy rains persisted.

Effort was made to recapture the swallows at the home colonies. Netting and night captures continued daily throughout the breeding season (through July) to insure that if a transported bird returned to its home colony it was recorded. However, if homing occurred, the swallows usually returned within 2 days. Many returned the evening of the day of release.

Homing and orientation abilities were tested using confidence limits for percentages and the G-statistic (Sokal and Rohlf 1969).

RESULTS

Confidence limits for percentages of swallows which homed successfully were calculated for both distance and direction of displacement (Mainland et al. 1956). At the 95% confidence level all of the confidence limits overlap (Table 1). Therefore, in order to verify this independence

TABLE 1. Barn Swallow returns to the colony for each distance-direction release point. Three birds were released at each point. n/T is the number (n) of birds returning of the total number (T) of birds released for that row or column. The percent of the returnees (and 95% confidence intervals) are also shown.

Distance (km)	Compass direction				n/T	% (C.I.)
	North	South	East	West		
16	1	2	2	3	8/12	66.7 (34.8-90.1)
24	3	2	1	2	8/12	66.7 (34.8-90.1)
32	3	1	2	2	8/12	66.7 (34.8-90.1)
40	1	1	1	1	4/12	33.3 (9.9-65.1)
48	2	2	0	2	6/12	50.0 (21.0-78.9)
64	2	1	3	1	7/12	58.3 (27.7-84.8)
80	1	2	3	1	7/12	58.3 (27.7-84.8)
96	2	1	1	1	5/12	41.7 (15.1-72.3)
n/T	15/24	12/24	13/24	13/24	53/96	55.2 (44.5-65.1)
% (C.I.)	62.5 (40.6-81.2)	50.0 (29.1-70.9)	54.2 (32.8-74.4)	54.2 (32.8-74.4)		

TABLE 2. Comparison of the number of Barn Swallows homing successfully by distance, direction, and sex. Data are presented in the format (number of birds returning/number of birds released). There were no significant differences in homing ability by direction, distance, or sex (see text).

Distance (km)	Direction				Sex		Total
	North	South	East	West	Males	Females	
16-40	8/12	6/12	6/12	8/12	8/15	20/33	28/48
48-96	7/12	6/12	7/12	5/12	10/23	15/25	25/48
Total	15/24	12/24	13/24	13/24	18/38	35/58	53/96

of either distance or directional effects, the data were pooled 2 ways. First, the distances 16-40 km and 48-96 km and the 4 cardinal directions (N, S, E, W) were compared to homing ($G = .672$, $df = 3$, $.5 < P < .9$, Table 2). Thus, the frequency of Barn Swallow homing is independent of the direction and distance of release. Second, in order to determine if there was some relationship between sex, the distance of release, and ability to home, these data were pooled by distance classes and sexes compared ($G \text{ adj} = .616$, $df = 1$, $.1 < P < .5$, Table 2). Barn Swallows home equally well regardless of their sex and the two distance classes of displacement.

Upon release, Barn Swallows circled and finally flew off in a particular direction. Home direction was determined by position on a topographic map and the use of a compass. If the swallows flew off within the quadrant of the home bearing, they were considered to positively orient themselves. Most birds oriented homeward (Fig. 1). Confidence limits for percentages were determined and, at the 95% level of significance, the overlap implies the tested distances do not have a significant effect on orientation (Mainland et al. 1956). To verify this, these data were pooled. Pooled distances (16-40 km and 48-96 km) were compared to the cardinal directions ($G = 1.622$, $df = 3$, $.5 < P < .9$, Table 4). Frequency of Barn Swallows which oriented correctly towards home is independent of distance and direction of release. I also determined whether sexes show a differential tendency to correctly orient themselves in the home direction. I examined their ability at two different distance classes ($G \text{ adj} = .424$, $df = 1$, $.5 < P < .9$, Table 4). There was no association between sexes and distance classes in the ability to orient in the direction of the home colony. Males oriented equally as well as females.

DISCUSSION

Although a number of authors have examined homing behavior in swallows, none have examined differences in homing ability as related to distance, direction, and sex in a quantitative manner.

Southern (1959) displaced 16 Purple Martins (*Progne subis*) at distances of 2.8 to 376 km with a 100% return rate. Sargent (1962) studied

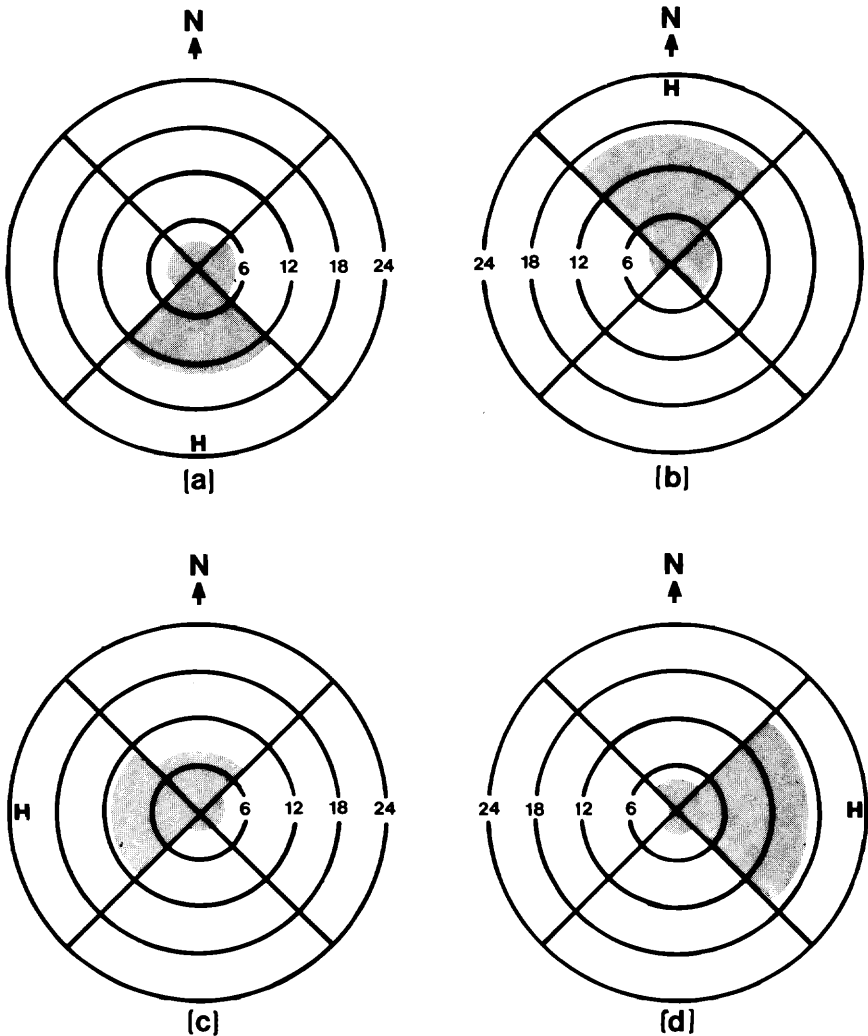


FIGURE 1. Comparison of release directions (a, b, c, d) in relation to home colony and the direction of Barn Swallows' initial orientation. The shaded area represents the number of birds out of a possible total of 24 which demonstrated a post-release orientation in a given 90° quadrat (a = released north of colony, b = released south of colony, c = released east of colony, and d = released west of colony; N = north, H = home colony direction).

Bank Swallows (*Riparia riparia*) in Wisconsin and found strong homeward orientation at release points 1.6 to 40 km from the colony. He observed no significant orientation from over 40 km away and, at 80 to 160 km, orientation was totally random, but with a strong tendency to go downwind.

TABLE 3. Number of Barn Swallows correctly orienting in direction of colony for each distance-direction release point. Three birds were released at each point. The heading, n/T, indicates the number of birds orienting in the correct direction over the total number of birds released for that row or column. Birds were given two minutes to orient themselves. The percent of released birds demonstrating a correct post-release orientation (and 95% confidence intervals) are also shown. (See Table 1.)

Dis- tance (km)	Compass direction				n/T	% (C.I.)
	North	South	East	West		
16	2	2	1	2	7/12	58.3 (27.7-84.8)
24	1	2	3	1	7/12	58.3 (27.7-84.8)
32	2	1	2	2	7/12	58.3 (27.7-84.8)
40	1	2	1	2	6/12	50.0 (21.0-78.9)
48	2	1	2	1	6/12	50.0 (21.0-78.9)
64	1	3	2	3	9/12	75.0 (42.7-94.5)
80	2	3	0	3	8/12	66.7 (34.8-90.1)
96	3	2	0	3	8/12	66.7 (34.8-90.1)
n/T	14/24	16/24	11/24	17/24	58/96	60.4 (49.5-69.8)
% (C.I.)	58.3 (36.7-77.9)	66.7 (44.7-85.3)	45.8 (26.6-67.2)	70.8 (48.9-87.4)		

Ruppell (1934, 1936, 1937) studied the Barn Swallow in Germany. He displaced 56 Barn Swallows 276 to 1875 km from their nests—twenty-one (40%) returned. The maximum speed of return among these swallows was 412 km per day. Average speed of return was independent of release point distance, but percent returns dropped steadily with increasing distance.

Wojtusiak and Ferens (1947) and Wojtusiak (1948) studied homing of Barn Swallows in Poland. Swallows released up to 153 km from their nests returned on the same day, and homing speed increased with increasing distance until a maximum of 35 km/h was reached at distances of 121 to 153 km. These studies showed that adverse weather conditions (rain, strong winds) drastically diminished the mean homing velocity. The investigators also reported that the swallows oriented in the home direction when released.

TABLE 4. Comparison of the number of Barn Swallows which correctly oriented in the direction of the home colony after release. Data are presented as in Table 2. There were no differences in orienting ability in any of the comparisons.

Distance (km)	Direction				Sex		
	North	South	East	West	Males	Females	Total
16-40	6/12	7/12	7/12	7/12	9/15	18/33	27/48
48-96	7/12	9/12	4/12	10/12	14/23	16/25	30/48
Total	13/24	16/24	11/24	17/24	23/38	34/58	57/96

Matthews (1963) suggested for certain species of birds a "hiatus" or confusion area at approximately 40 km from home site where displaced birds home poorly. He attributed this to the possible switching of their homing mechanisms from familiar landmarks to some other means of successful navigation. Poorer homing ability at 40 km is not suggested by my data.

This study supports recent literature with regard to the Barn Swallow's ability to home to its nest when displaced varied distances. Additionally, I present data that illustrate that both male and female Barn Swallows home and orient equally well from distances up to 96 km in directions N, S, E, and W from the home colony. These data pose some interesting questions. For example, why do males home and orient as well as females? The implication is that male parental investment is greater than once believed. The post-copulatory role played by the male (nest building, incubation, feeding of the nestlings, and nest defense) is likely significant enough to mandate his presence throughout nesting to insure reproductive success. What mechanisms of navigation are being employed by swallows? Sargent (1962) suggested a random search pattern which uses familiar landmarks. This however, fails to explain the orienting ability of swallows documented in this and other papers. Swallows were released from directions and distances (e.g., 96 km N) which should have presented landmarks unfamiliar to the orienting animal. Further research is necessary to elucidate the navigation mechanisms which are used in short- to mid-distance homing.

SUMMARY

Homing and orienting experiments were carried out on marked Barn Swallows in northwestern Pennsylvania during the summers of 1975, 1976, and 1977. The swallows were captured using mist nets and pre-dawn "picking off" the nests and nearby roosts. The birds were transported by auto to release sites 16 to 96 km in the 4 cardinal directions from the home colony. Upon release the birds were observed until they flew off in a specific direction, which was recorded. Concerted recapture efforts were made throughout the breeding season to determine if displaced birds returned. Confidence limits for percentages and the G-statistic were used to test for homing and orienting abilities.

The major results are summarized as follows: (1) the frequency of Barn Swallow homing is independent of the direction and distance of release; (2) Barn Swallows home equally well regardless of sex and distance of displacement; (3) the frequency of Barn Swallows orienting toward their home colony is independent of the distance and the direction of release; and (4) no differences between males and females and the ability to orient homeward were found for the distance classes examined.

It may be concluded that Barn Swallows home and orient equally well from the tested distances and directions and that they home and orient equally well regardless of their sex.

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