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HOMING OF BANK SWALLOWS AND CLIFF SWALLOWS

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INTRODUCTION

The ability of birds to find their way home after being displaced has been known for some species since ancient times, but only recently have the differences in homing ability among species been discovered. At present relatively little is known about the homing abilities of the great majority of passerines (Manwell, 1962).

However, the ability of swallows to home successfully has been recognized for a long time. For example, Pliny wrote (Matthews, 1955) that on occasion a Roman racehorse owner took swallows (species unspecified) with him to the races. These birds, stained with the colors of the winning horses, were released to carry news of the victories back to his friends at home. Fabius Pictor wrote (Lincoln, 1939) that when a certain Roman garrison was besieged by the Ligurians, swallows (species unspecified) were sneaked out of the city and taken to the army advancing to aid the garrison. These birds then were released to return to the surrounded city with knotted strings tied to their feet. The number of knots indicated the number of days before relief could be expected.

Homing experiments have been conducted with several species of swallows in recent years. These include the Barn Swallow, *Hirundo rustica* (Loos, 1907; Ruppell, 1934, 1936, 1937; Wodzicki and Wojtusiak, 1934; Dupond, 1935; Wojtusiak, Wodzicki and Ferens, 1937; Wojtusiak and Ferens 1938, 1947 a, b; Wojtusiak, 1949); Rough-winged Swallow, *Stelgidopteryx ruficollis* (Gillespie, 1934); Purple Martin, *Progne subis* (Southern, 1959); House Martin, *Delichon urbica* (Ruppell, 1934); Bank Swallow, *Riparia riparia* (Loos, 1907; Stoner, 1937; Sargent, 1962); and Cliff Swallow, *Petrochelidon pyrrhonota* (Kirsher, 1955; Mayhew, 1958). Most of the homing data pertaining to the Hirundinidae have been summarized by Griffin (1944), Matthews (1955), Southern (1959) and Sargent (1962).

The object of this paper is to present some additional homing data concerning Bank Swallows and Cliff Swallows.

MATERIALS AND METHODS

Cliff Swallows, nesting in El Dorado, Sacramento and Placer counties, California, were used in homing experiments during 1952 (March and April) and 1953 (March, May, and June). Bank Swallows that nested near the University of Minnesota's Forestry and

Biological Station at Lake Itasca, Clearwater County, Minnesota, were studied during the summer (June and July) of 1957. A total of 13 Bank Swallows and 143 Cliff Swallows (all adults) were released in 7 experiments. These experiments initially were undertaken for somewhat different purposes, so the methods employed were not identical in all cases.

The technique used to capture Cliff Swallows was described previously (Mayhew, 1958). This method could not be applied to the Bank Swallows, however, because they were not nesting beneath bridges and culverts. Instead, the latter birds were nesting in holes in the sheer bank of a gravel pit in a manner similar to that seen in some illustrated Bank Swallow colonies (Stoner, 1936; Peterson, 1955). Consequently, a modified version of Morris' (1942) technique was utilized. Rain damaged the cardboard tubes Morris (*op. cit.*) recommended, so six-fluid-ounce concentrated fruit juice cans were used instead. Both ends of each can were removed and a 3'' x 8'' x 15'' polyethylene bag was attached, by means of a heavy rubber band, over one end. The entrance to each active nest in the Bank Swallow colony was enlarged slightly so that a can would fit snugly into the nest entrance. When the birds attempted to leave the nests, they fell into the bags and remained there until removed.

Many of the birds were reluctant to leave the nest when a can was in place, particularly during the day. Shining a flashlight beam into the nest at night through the plastic bag, however, often produced the desired effect. The light shown on the bird for a minute or two, then was turned off. The birds were captured as they tried to leave the nest after the light was removed.

Both Bank and Cliff Swallows were banded with U. S. Fish and Wildlife Service bands before release. Differently colored model airplane dope was applied to the tips of the outer four primaries of the Bank Swallows to permit identification of each bird in the air. (No color marking was used on Cliff Swallows.) The primaries were spread while the dope dried, so flight would not be impeded by stuck feathers. No difference in flying ability was detected between color-marked and unmarked birds.

The birds of both species were sexed by determining the presence or absence of a brood patch. Peterson (1955) indicated only female Bank Swallows possess a brood patch during the breeding season, and Mayhew (1958) showed a similar condition exists in Cliff Swallows. However, some Cliff Swallow releases occurred before the breeding season was well under way, so some birds were unsexed.

In each experiment the birds used were placed together in a screen cage at the time of capture. The cage then was covered with a thick cloth, and the birds were taken by automobile to the release point.

Each Bank Swallow was released individually and its flight was observed with 8X binoculars until it could no longer be distinguished from the other Bank Swallows in the area. The first bird was released facing north. The second was freed as it faced east, the third while it faced south, and the fourth as it faced west. This pattern was followed until all birds were released. An observer was stationed at the nesting colony during my absence in case some of the birds returned before I did.

The Cliff Swallows usually were released in a group. No attempt was made to follow each bird for any extended period of time, although members of the group were watched as long as they could be distinguished from Cliff Swallows living at the release point.

The five per cent probability level has been used in all statistical tests, unless specified otherwise.

All times mentioned are Standard Time for the area concerned.

RESULTS

Bank Swallows

Experiment A. Eleven of the birds used in this homing experiment were captured at night in the manner described above, and held in a screened cage until the following morning. Two other birds were captured the morning of the release (26 June, 1957). No more than one bird was taken from any nest for this experiment, since all occupied nests contained eggs or young. All the Bank Swallows used were females. They were taken 81 kilometers (50 miles) north of the nesting colony and released from the roadside near the western shore of Lower Red Lake, Clearwater County, Minnesota. The area (about 150 meters wide) between the road and the lake was a marsh. The land on the other side of the road contained a willow and aspen thicket, the tallest trees of which were approximately 20 feet high. The first bird was released at 0930, the last bird at 1035. A brisk south-west wind was blowing at the time of release. The sky was completely overcast at first, but occasionally pieces of open sky could be seen for a few moments.

In all cases but one, the birds flew toward the lake shore, no matter which direction they were headed when released. Some birds flew directly to the lake by the shortest route. The rest flew in other directions at first, but they soon circled toward the lake. Other Bank Swallows already were feeding high above the marsh and lake shore when these birds were released. The released birds joined the feeding birds, and usually could not be identified after 2 to 4 minutes. None of the marked birds gave the impression of being in any hurry to leave the area.

No marked birds were observed at the nesting site until 1745 the following day (27 June). Intermittent drizzles had occurred throughout both days (0.26 inches 26 June, 0.33 inches 27 June—weather records of University of Minnesota's Forestry and Biological Station). The sun was visible only approximately 5 minutes (about 1700) 27 June. At 1825 another marked bird was observed entering a nest. The sun was above the horizon for $15\frac{1}{4}$ hours per day during this period (Hansen, 1957), so these birds had taken $23\frac{1}{4}$ and $25\frac{1}{2}$ daylight hours respectively to return 81 km (50 miles) under overcast skies (presumably no flying was done after dark). Thus, they averaged about 3 km (2 miles) per hour. One of these birds had been held overnight before its release, the other was captured the morning of the release.

The sky was clear and no wind was blowing on 28 June. The previously observed marked birds began flying about the nests by 0550, but no other marked birds were visible at that time. Another marked bird (that had been held over-night before release) was seen

at 1215 that day ($35\frac{1}{4}$ daylight hours [$50\frac{1}{4}$ total hours] after the release).

Late that afternoon a gravel dealer began removing gravel from the walls of the pit, thereby destroying or damaging several nests, including those belonging to some of the marked birds. More nests were destroyed the following day, which caused many birds to desert the colony. Possibly other marked birds may have returned to the nesting area, but they escaped detection because their nests were no longer present. Another marked bird was seen 1 July. However, I don't know exactly when it arrived because of the disturbance at the colony. This nesting site was entirely deserted by 16 July. However, on July 10 only young birds that were large enough to fly were present in another colony that had been undisturbed by humans, indicating the homing colony might have been abandoned by 16 July under any circumstances.

Cliff Swallows

Experiment B. Birds (18) were captured at night (5 April 1952) 1 mile east of Folsom, Sacramento County, California, and transported 58 km (36 miles) west to Davis, Yolo County, California. This was the first capture for all these birds. The following morning they were taken to an active Cliff Swallow colony (a bridge) 6.5 km (4 miles) west of town and released at about 0900 under a cloudless sky. The released birds joined the local Cliff Swallows feeding above the surrounding wheat fields, and soon were indistinguishable from the resident population. The colony at the release site was trapped that night to see if any of the released birds had remained at that location. Although every bird under the bridge that night was captured, none of the released birds were found. Seven of these birds (2 males, 5 females) were recaptured at the original site on 8 June, which was the first time we returned to that colony after the release.

Experiment C. The 49 birds used in this experiment were trapped the night of 31 March 1952 near Clarksville, El Dorado County, California. Four birds were returns from the previous year, the remainder were captured for the first time that night. The birds had arrived at this colony only 7 days earlier. The captives were transported 66 km (41 miles) west to Davis that night, then released at 0900 the following morning at the same colony used in Experiment B. The weather was clear and calm. This time all the released birds flew west, rising to a great height very quickly. They were soon lost to view, still climbing and flying west. Twenty of these birds (5 males, 12 females, 3 sex unknown) were recaptured at the original colony the first time we trapped there after the release (23 May). Five additional birds (3 males, 2 females) were recaptured at the same site during the remainder of the 1952 breeding season. One other bird (male) was recaptured at a colony 0.8 km (0.5) mile east of the original colony during the same year. None of these birds ever were captured at the release colony.

Experiment D. Two weeks after the spring arrival of Cliff Swallows, 28 birds were caught and released at the same colonies used in Experiment C. This was the first capture for all the birds involved.

They were released at 0130 the same night they were captured (26 March 1953). This was 4 nights before the full moon, so there was bright moonlight at the time of release. All the birds immediately flew to a considerable altitude. They were seen for only a few seconds after their release, but they could be heard calling for quite a distance. As with the previous experiments, none of these birds were ever recaptured at the release point. However, 10 of them (5 males, 3 females, 2 sex unknown) were recaptured at the original site the first time we trapped that colony (17 April) following their release. Six additional birds (5 males, 1 female) used in this experiment were recaptured during the same breeding season.

Experiment E. Ten birds were captured in early afternoon (2 June 1953) at the colony trapped for Experiments C and D. Two of the birds (both females) were returns from the previous year, and another (female) had been captured once earlier in 1953. They were taken 112 km (70 miles) east over the crest of the Sierra Nevadas and released the same afternoon (1730) near Minden, Douglas County, Nevada. The release occurred at an active Cliff Swallow colony in open country that was used for grazing cattle. The weather was clear and calm. The released birds flew above the residents that were feeding over a small body of water nearby, and soon were lost to sight. None of these birds were captured at the release colony that night. It rained at the original colony for the next three days, so we were unable to trap until the fourth night. However, we recaptured three released birds (all females) that night. All of them had been captured for the first time in 1953. None of the others were ever seen again.

Experiment F. A colony near Riego, Placer County, California was trapped the night of 23 May 1953. One-half the captured birds were retained for this experiment, and one-half were kept for Experiment G. Nine of the birds used in this experiment were returns from the previous year, and six of these had been recaptured once previously in 1953. They were transported that night 136 km (85 miles) west to Berkeley, Alameda County, California and released at 0530 the following morning. They were freed at a yacht harbor that did not contain a Cliff Swallow colony. There were no clouds or wind. All the birds started to fly south from the release point. Shortly they turned east and continued to climb to a considerable height. Two of these birds (both females) had returned to the original colony by sundown that evening (1930), 14 hours after their release. Thus, a minimum speed of 10 km (6 miles) per hour was required of these birds in order for them to home during this time interval. However, both birds may have arrived long before sundown. One had been captured in 1952, the other was caught for the first time the night before the release. William Kirsher recaptured 4 additional birds (3 males, 1 female) the following night at the trapping site (these birds, previously unreported, account for the difference in returns in Table 3 [Mayhew, 1958: 19] and Figure 1 [this paper] for this experiment). Two had been captured in 1952, the other two were caught for the first time the night before the re-

lease. A total of 11 birds (4 males, 7 females) returned to the nesting colony during the 1953 breeding season.

Experiment G. The remainder of the birds captured near Riego 23 May were also transported to Berkeley that night, then taken by boat the next morning to the Farallon Islands. These islands lie off the California coast approximately 40 km (25 miles) west of San Francisco, and 184 km (115 miles) west of the capture site. The birds were released at 1030 on shore, under favorable weather conditions. They all started south, but soon turned east toward the California coast. They continued to climb until they were out of sight. Only 3 of these birds (1 male, 2 females) returned during 1953 (2 caught 1 June, 1 caught 9 June).

Homing success

Fig. 1 compares the homing success of Bank and Cliff Swallows during the year released. The gravel removal at the Bank Swallow colony during Experiment A makes it rather difficult to evaluate Bank Swallow homing ability, as far as percentage of returns is concerned. However, in spite of this disturbance, the proportion of Bank Swallows that were observed to return to the colony was not significantly less than for Cliff Swallows returning from a comparable distance (Experiments B, C, D). In addition, overcast skies and rainy weather prevailed during the Bank Swallow experiment, whereas no cloud cover interfered with the aforementioned Cliff Swallow experiments. Thus, it seems reasonable to assume that Bank Swallows and Cliff Swallows are able to home equally well.

Although there was considerable variation in the percentage of

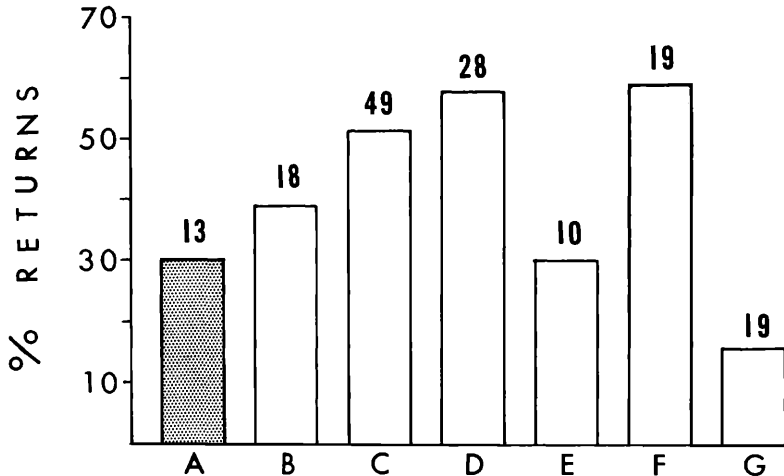


Figure 1. Percent of birds successfully homing during the year released. Bank Swallows are represented by shaded rectangle, Cliff Swallows by unshaded rectangles. Numbers above rectangles indicate sample sizes. Letters beneath rectangles designate different homing experiments (see text for details).

birds that returned, the differences in most cases were not statistically significant. An exception occurred between the birds released at Berkeley (Experiment F) and at the Farallon Islands (Experiment G). The difference in homing success in these two experiments was significant at the five percent level, but not at the one percent level. Apparently the 40 km (25 miles) of ocean was a navigational hurdle too difficult for most of these birds to overcome.

Night-released Cliff Swallows returned successfully in greater proportion than birds released at the same site in daylight (Experiments C and D, Fig. 1). However, the difference was not statistically significant.

Although slight differences were found in the number of homing male and female Cliff Swallows (Table 1), these differences were not statistically significant. It should be noted, however, that females usually were the first to return from the longer trips, and only females returned in one experiment (Experiment E).

The stage in the breeding cycle seemed to make little difference in Cliff Swallow homing success. Experiments C and D were conducted before nesting had started. Experiment B was undertaken on the earliest date that eggs had been found in nests (Mayhew, 1958). Experiments E, F and G were carried out while eggs or young were in the nest. Nevertheless, as large a percentage returned from the experiments conducted before eggs were laid as home in the middle of the breeding season (Fig. 1). This contrasts with Sargent's (1962) observations on Bank Swallows.

The Cliff Swallow colonies used as trapping sites were ones that could be completely sealed at night. This insured that nearly all birds in the colony could be captured each time. Therefore, it was assumed that birds captured for the first time were ones that had occupied the colony for a relatively short time compared to either repeats or returns (see Table 1, footnote, for definitions). Repeats, on the other hand, were felt to have been residents for a shorter time than returns. Table 1 compares Cliff Swallow homing success the year of release, according to the relative lengths of time the birds resided at a colony before the homing experiments. It appears that newly captured birds were more successful in returning home than either repeats or returns. However, the differences are not statistically significant.

In all, 85 (59 percent) of the experimental Cliff Swallows were recaptured at least once after being released, and 65 (45 percent) of these were recaptured during the year of release. Twenty-nine of the latter group also were recaptured the following year. In addition, 17 birds were recaptured only in the year following release. Also, 2 were recaptured for the first time two years after the release, and another three years later (released 26 March, 1953 - recaptured 27 March, 1956).

DISCUSSION

Both Cliff and Bank Swallows are trans-equatorial migrants—Cliff Swallows have been reported in Argentina (Selater and Hudson, 1888), Bank Swallows in Argentina (Dabbene, 1926) and Peru

TABLE 1. COMPARISON OF HOMING SUCCESS IN CLIFF SWALLOWS, BY SEX AND LENGTH
OF RESIDENCE AT NESTING COLONY

Experiment	No. Released	Newly Captured		% Returned	No. Released	Returns ¹		% Returned	No. Released	Repeats ²		% Returned
		Returned	No. Returned			No. Returned	No. Returned			No. Returned	No. Returned	
<i>B</i>												
Males	3	2		67								
Females	6	5		83								
Sex Unknown	9	0		0								
<i>C</i>												
Males	9	8		90	1	1	100					
Females	15	14		93	2	0	0					
Sex unknown	22	2		10								
<i>D</i>												
Males	11	10		91								
Females	5	4		80								
Sex unknown	12	2		17								
<i>E</i>												
Males	5	0		0								
Females	2	2		100	2	0	0	0	1	1	100	
<i>F</i>												
Males	3	3		100	4	2	50					
Females	6	3		50	5	3	60		1	0	0	
<i>G</i>												
Males	4	0		0	4	1	25		2	0	0	
Females	3	0		0	5	2	40		1	0	0	
<i>TOTALS</i>												
Males	35	23		66	9	4	44		2	0	0	
Females	37	28		76	14	5	36		3	1	33	
Sex Unknown	43	4		9								

¹A recapture made in a later breeding season²A recapture made in the same breeding season

(Bergstrom, 1951). Consequently, one would expect such long-distance migrants to be capable of homing from considerable distances. However, most birds of both species performed relatively poorly when required to home from fairly distant release points.

The direction of flight taken by these birds when freed indicated they did not know the direction of the home colony at the time of release. All the Bank Swallows and some of the Cliff Swallows circled above the release point for some time. Many of the Cliff Swallows left the release point in the opposite direction from home (Experiment C), but the majority of these birds still were able to find the original colony again (Fig. 1).

The speed of homing, in those experiments where this could be measured reasonably well, indicated that most Bank and Cliff Swallows return home at a leisurely pace, at least from the distances used in these experiments. A few birds returned fairly rapidly (i.e. two birds in experiment F), but most of them did not.

The present Bank Swallow experiment was conducted under rather adverse circumstances. However, the number of Bank Swallows that returned in experiment A approximated the proportion of incubating birds that returned (released for the first time) from a similar distance in other Bank Swallow experiments (Sargent, 1962). Therefore I feel the results were fairly typical for this species.

Thorpe (1949: 89) pointed out most homing experiments have been conducted where the birds might have had considerable previous knowledge of the country. Thus, if a bird has not been taken out of familiar territory, it can return by following known landmarks.

Cliff Swallows are strong fliers that are capable of covering many miles in a day. Thus, it is conceivable release sites 64-72 km (40-45 miles) west of the nest colonies were within familiar territory for the birds. This might explain the high percentage of returns before nesting began in earnest, as well as the relatively equal returns from day and night releases at the same colony. Velocities were not checked on any experiments from these distances, so return speeds are unknown.

In only two of the present experiments was it reasonably certain the birds were taken outside familiar country. As Cliff Swallows have not been found on the Farallon Islands (Grinnell and Miller, 1944: 278), the birds used in Experiment G probably were outside the normal range of the species.

Experiment E birds also probably were released in unfamiliar territory, but this is more difficult to establish with certainty. Miller (1957) showed that migrant birds in California tend to use passes through mountain ranges, and tend to follow paths of least resistance. It seems reasonable to suppose that Cliff Swallows, nesting on each side of the Sierra Nevadas, would have reached their nesting grounds by migrating parallel to the Sierras rather than crossing this mountain mass. This supposition is supported by some circumstantial evidence. A total of 9,784 young and adult Cliff Swallows were banded at 65 colonies during the four years preceding Experiment E. These colonies were scattered across the entire

width of the Sacramento Valley of California at the latitude of the Nevada release point. Not one of these birds was recaptured at any of the six sites trapped in Nevada. In addition, none of the 611 birds banded near Minden, Nevada on the release date (Experiment E) were recaptured in the Sacramento Valley during the three years following the experimental release, even though 6,756 Cliff Swallows were captured in central California during this period. It was shown previously (Mayhew, 1958: 18) that about 9 percent of Cliff Swallows in California change colonies during a single breeding season (vagrants). Also, 43 percent of young birds and 18 percent of adult swallows were recaptured the year following banding at other sites (Mayhew, 1958: 29). Thus, it is evident these birds move about rather extensively. Consequently, if Cliff Swallows normally flew through the only readily accessible pass (Echo Summit—7382 feet elevation) that has been shown to be used by some species in that portion of the Sierras (Miller, 1957: 165), one would expect to find a few birds that were banded on one side of the Sierras recaptured on the other side. Admittedly, the sample sizes are not particularly large, considering the size of the territory involved. Nevertheless, the colonies utilized in these experiments were among the closest to the pass in question, so they should have been most likely to show this movement, if any occurred.

The proportion of returns from each of the two experiments mentioned above was approximately that postulated by Thorpe (1949: 89) which could be expected to return from unknown territory by random radial search or spiral exploration (see Griffin [1944: 18] for description). Although each of the birds in Experiment G was last seen flying toward the California coast, there was no assurance all of them continued in that direction until, or after, they reached the mainland. Consequently, random scatter or spiral exploration could have occurred beyond the observer's range of vision. At least 48 hours transpired before any of the Farallon Island birds returned to the nesting colony, indicating a very slow return velocity.

The evidence from the experiments reported herein suggest that Bank and Cliff Swallows utilize Type I (Griffin, 1955) orientation in homing from unknown territory. This type of orientation has been proposed for Bank Swallows previously (Sargent, 1962).

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SUMMARY

Thirteen Bank Swallows (*Riparia riparia*) were used in one experiment in Minnesota, and 143 Cliff Swallows (*Petrochelidon pyrrhonota*) were utilized in 6 experiments in California.

Bank Swallows were taken 81 kilometers (50 miles) from the nesting colony. Cliff Swallows were transported from 64 km (40 miles) to 184 km (115 miles) and released. The only statistically

significant difference in the proportion of Cliff Swallow returns occurred between birds taken to Berkeley, California (136 km) and those transported to the Farallon Islands, 40 km off the California coast (184 km from the nest site). Apparently the 40 km of ocean was a navigational hurdle too difficult for most of the birds to overcome.

The direction of flight taken when released indicated the swallows did not know the direction of the home colony at the time of release.

The Bank and Cliff Swallows whose homing speed was measured reasonably accurately indicated most of them home at a leisurely pace, at least from the distances used in these experiments.

Cliff Swallows that had been released at night homed as well as those released at the same site in daylight.

There was no significant difference between male and female Cliff Swallows in their ability to home. The stage in the breeding cycle also seemed to make little difference in Cliff Swallow homing success.

There was no significant difference in the proportion of returns of Cliff Swallows that were new arrivals and birds than had lived at the colony in preceding years.

It was suggested that both Bank and Cliff Swallows use random radial search or spiral exploration to find home when they are released outside familiar territory.

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