THE BIOLOGY OF THE CLIFF SWALLOW IN CALIFORNIA

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An investigation of the biology of the Cliff Swallow (*Petrochelidon pyrrhonota*) was conducted in California from 1949 through 1956. The most extensive work was done in 1950, 1952, 1953, and 1954. As these birds are present in this area only in the nesting season, the work necessarily has been limited to this period of the life cycle. Circumstances have arisen which necessitate the discontinuance of the investigation along the lines previously used. Therefore, it seems advisable to report the general findings of the study at this time.

ACKNOWLEDGMENTS

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MATERIALS AND METHODS

Trapping and banding.—A large part of the work involved banding as many birds as possible for subsequent recapture. A technique was devised which proved highly successful for capturing large numbers of birds and as many as 1000 were obtained in a single operation. They were caught at night at the nesting sites with the aid of nets and flashlights. Two fish nets of one-half inch mesh, each 30 feet long by 20 feet wide, were used to cover the open ends of the culverts and bridges that are used as nesting sites in central California. With the aid of head flashlights, the birds were flushed from their nests (fig. 1) and captured by hand while they were clinging to the nets that blocked their escape (fig. 2). No young birds were captured unless they were old enough to fly from the nest at night and cling to the nets. The birds were placed in collecting cages as they were caught and they were then banded and immediately released.

The same procedure also was tried in daylight, but trapping efficiency was so low that this was discontinued in favor of night operations. In addition, by trapping at night, it was possible to handle effectively sites that could not be trapped at all in daylight. Figure 3 shows one of the colonies that could be completely sealed off with the nets, permitting almost 100 per cent trapping efficiency at night. Moreover, there were some rather long bridges that could be trapped only at night. The nets were moved from section to section of the long bridges as the birds were removed from the preceding sections. This technique could not be used on moon-lit nights at these large bridges because the birds flushed from their nests readily and could easily find their way past the nets. On dark nights, however, this procedure was quite effective. In spite of the noise produced by our operations, the birds in sections of the bridge not yet trapped would rarely flush until the nets were dropped over their section. They could even then easily

Fig. 1. When nets are dropped into position, birds flush from nests and briefly fly about within the colony. Photograph by Fred Nunn.

evade capture by flying parallel with the long axis of the bridge and escaping around the ends of the nets. Nevertheless, the majority would tend to fly directly at our lights, making capture relatively simple.

Birds were banded in 61 colonies (see fig. 4) in Yolo, Sutter, Placer, Solano, Sacramento, and El Dorado counties in the Sacramento Valley, in three colonies in Stanislaus County in the San Joaquin Valley, and one colony in Riverside County in the San Bernardino Valley. Six colonies in Douglas County, Nevada, also were sampled. The majority of the information to be presented was obtained from the recaptured birds. Table 1 summarizes the capture data, by years, for all the birds that were handled in the course of the investigation.

Sexing adults.—For much of the information that was desired in this study, it was necessary to be able to sex the birds without sacrificing them. However, it appeared to

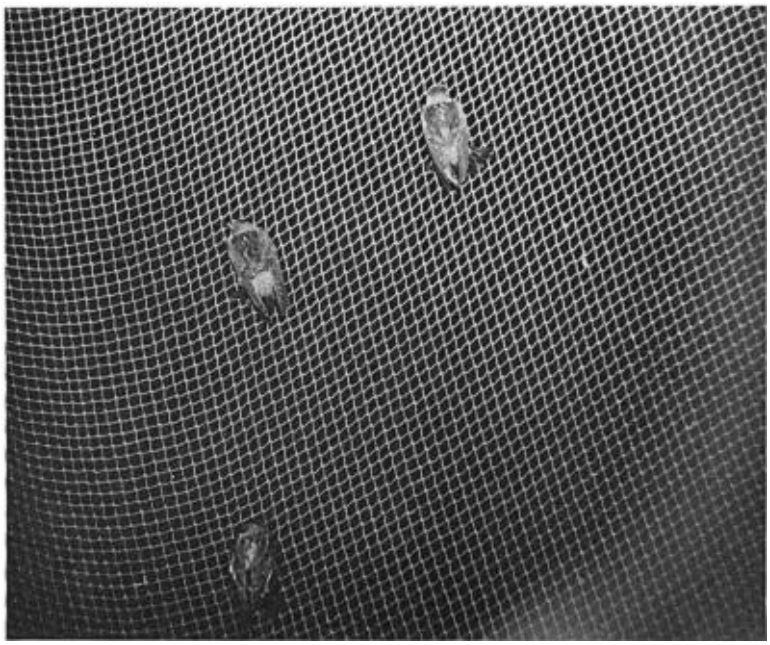

Fig. 2. Birds cling to the nets that block their escape a few moments after they leave nests.

Table 1

Capture Data for All Cliff Swallows Handled

	Year								
	1949	1950	1951	1952	1953	1954	1955	1956	Total
Colonies trapped	5	16	6	43	40*	11	5	3	71*
Adults banded	191	784	236	7249	4476*	1815	607	570	15928*
Young banded	12	230	104	978	442	39	91	180	2076
Total banded	203	1014	340	8227	4918*	1854	698	750	18004*
Repeats[1]	8	173	0	1718	912	343	126	219	3499
Returns[2]	0	49	17	251	2526	1450	658	658	5609
Total recaptured	8	222	17	1969	3438	1793	784	877	9108
Total caught	211	1236	357	10196	8356*	3647	1482	1627	27112*

* Includes 611 birds banded in 6 colonies in Douglas County, Nevada.
[1] A recapture made in the same breeding season.
[2] A recapture made in a later breeding season.

be impossible to determine the sex of the adults on the basis of gross morphological differences. Dr. A. H. Miller (personal communication) said he was unable to detect any measurable characteristic that showed a constant sexual difference. He suggested, on the basis of the work done by Bailey (1952), that perhaps the presence of a brood, or incubation, patch could be used as a means of separating the sexes. Bailey (*op. cit.*:128) had reported the Cliff Swallow as one of the species in which he had found brood patches on females but not on males. Bailey (personal communication) stated that his sample of Cliff Swallows was too small to state positively that only females of this species possess a brood patch, but he felt it was true. Thus, to check further this condition, 60

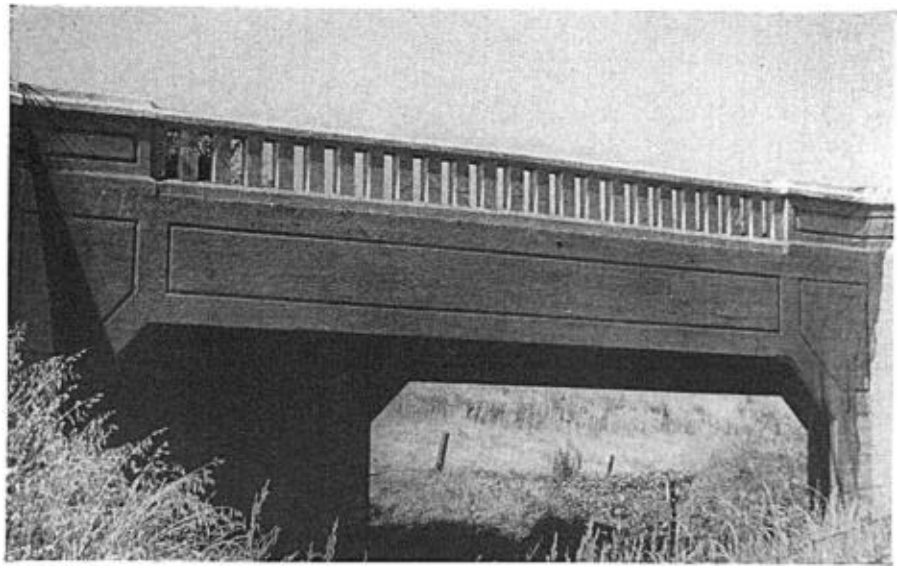

Fig. 3. A colony that can be completely sealed for trapping. Note net hanging in operational position.

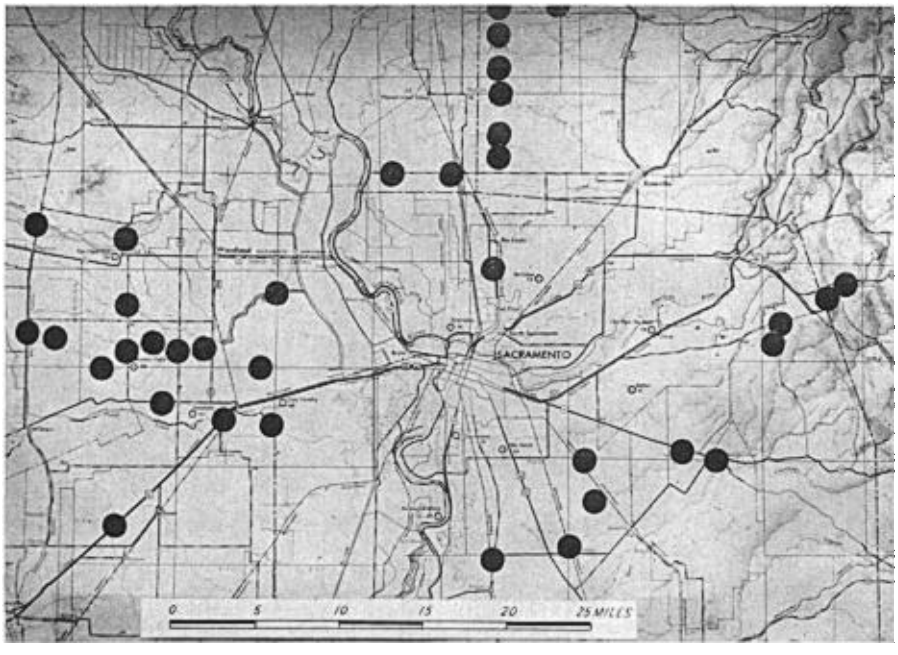

Fig. 4. Black dots represent colonies most intensively trapped in Sacramento Valley study area.

adults (32 males, 28 females) were collected and autopsied in the breeding season (April 4 to June 27). No male collected possessed a brood patch, whereas all but two of the females had a brood patch. Both of these females were collected early in April, and they may not have yet reached breeding condition. Therefore, the presence or absence of a brood patch was used to sex the adults from about the middle of April until the first week of June, since brood patches were most numerous and best developed in this period.

Fig. 5. Artificial Cliff Swallow nest under construction. Note completed nest at right. Photograph by Murray Garrett.

However, this criterion was not relied upon during the remainder of the season. Thus, the sex of birds which were not handled in the period from mid-April to the first week in June is listed as unknown, unless a well-developed brood patch was present.

An attempt was made to use the cloacal protuberance of males, as described by Wolfson (1952:160), to aid in separating the sexes. However, this did not prove to be successful in the present study. Whether it was due to the lack of a well-defined protuberance in this species or to the inability of the investigators to identify such a structure in the beam of a flashlight is not known.

Artificial nests.—In 1955 and 1956, birds in the San Bernardino Valley of southern California (parts of Riverside and San Bernardino counties) have yielded additional observational data. Much of the information obtained in this region was acquired with the aid of artificial nests. A Cliff Swallow nest, which was being used by English Sparrows (*Passer domesticus*), was covered with Blue Diamond casting plaster. After two applications of plaster, the outer surface was covered with varnish. Then the entire nest was removed from the wall of the building, and the mud of the nest washed out of the plaster mold. Additional plaster was added to the inside of the mold to reduce the inside dimensions to those of the normal nest interior.

The plaster mold then was filled with liquid latex, allowed to set for about 10 minutes, and the excess latex was poured out. This left a thin sheet of latex over the entire interior of the mold. When the remaining latex in the plaster mold hardened completely, it was removed. The exterior of the latex mold was an exact duplication of the interior of the plaster mold. The latex mold then was placed upside down on a flat surface and covered with about ¼ inch of wet casting plaster in the manner one would frost a cake (fig. 5). Casting plaster proved to be better than plaster of Paris for nests because it

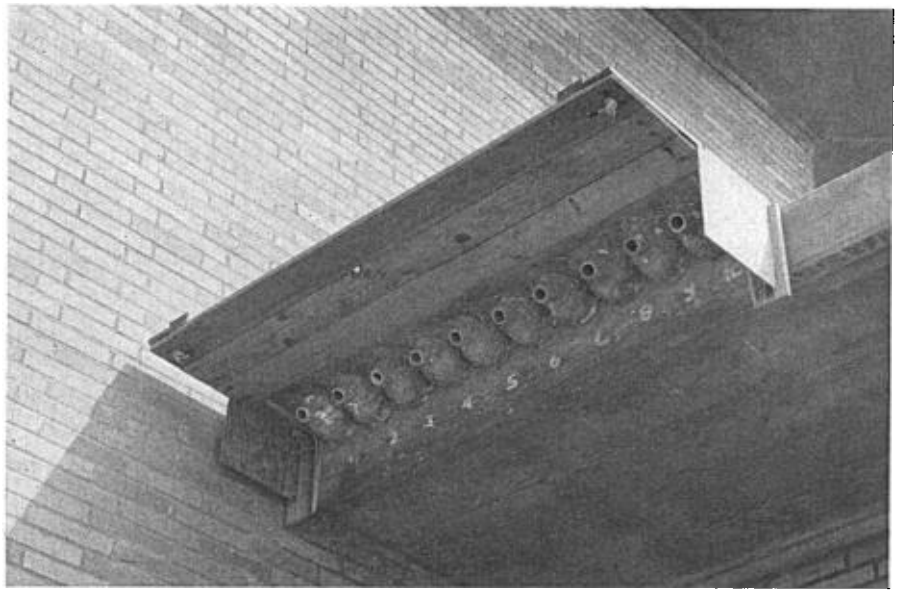

Fig. 6. Experimental colony composed of artificial swallow nests. The interior of each nest is accessible from above (see fig. 7). Photograph by Kenneth Middleham.

did not set as rapidly. A circular piece of cardboard, the diameter of the opening of a natural swallow's nest, was placed at the location of the bird's entrance to the nest. This made certain that this area would remain free of plaster. The cardboard was removed when the nest was almost dry, leaving a smooth, round opening through which the swallows would be able to gain access to the nest. When the plaster had completely hardened (about 15 minutes required), the flexible latex mold was stripped from inside the artificial nest. The exterior of the artificial nest was relatively smooth, rather than roughened like a natural nest. However, the dimensions and shape were identical with those of the original nest.

Ten nests were made on the latex mold, and they were covered inside and out with a coat of mud. These nests then were mounted on a rack made of two 1×12-inch boards 6 feet long which were nailed to each other at right angles along their greatest length. An additional board 18 inches wide was added later as an extension to the roof to give the nests more of an eave (fig. 6). Each nest was mounted to the backboard of the rack by means of a piece of galvanized wire attached to a screw on each side of the nest. A hole 3 inches in diameter was cut in the roof board directly above the cavity of each nest. Each of these holes was filled with the 3-inch plug taken from the hole, to which was nailed a piece of wood 4 inches square (fig. 7). This made a snug-fitting lid for each nest that shut out the light, but it allowed the observer easy access to each nest interior from above. The rack was supported by ropes which held it against the overhang on the second floor of Webber Hall on the Riverside campus of the University of California. The interior of each nest could be examined with ease by an observer standing on the roof of the building and removing the nest doors from above.

HABITAT

Emlen (1954:17) reported that the requirements for a Cliff Swallow colony are: (1) an open area for foraging, (2) a vertical object, preferably with an overhang, for

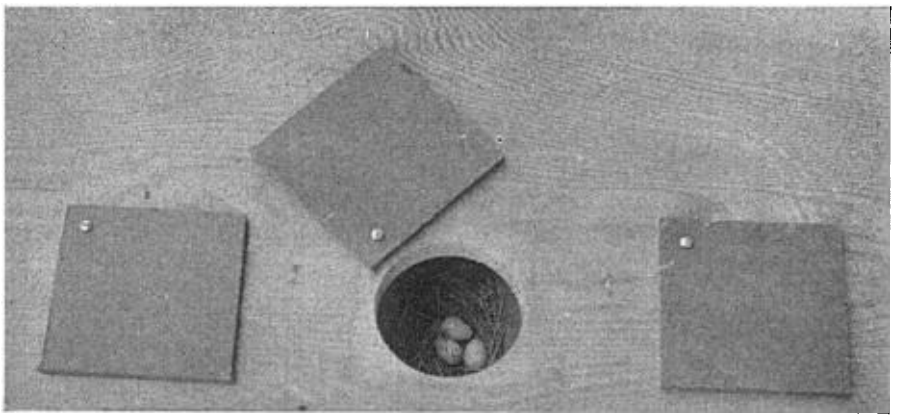

Fig. 7. Observation doors above artificial nests open to permit inspection of nest interiors. Photograph by Murray Garrett.

nest attachment, and (3) a supply of mud of the proper consistency for nest building. In addition to these, Grinnell and Miller (1944:280) list another requisite: some smooth-surfaced fresh water for drinking.

The Sacramento Valley is blessed with an abundance of these necessities. The land is very flat and there are wide expanses of open fields of various types (rice, wheat, barley, and others) that are ideal for foraging. Many bridges and culverts are present that cross gullies and dirt-lined irrigation ditches. These ditches have become quite common in the area in recent years due to the large acreage of rice that is now grown in the region. Almost every colony of swallows that we found in the Sacramento Valley was located beneath a bridge or culvert, although Emlen (1941:248) reported 15 colonies in this area which were on buildings. Spring rainfall, plus irrigation water, in the ditches during the nesting season, provides sufficient mud and drinking water for the birds.

Although superficially the San Joaquin Valley appears to be just as ideal for Cliff Swallows, relatively few colonies were found there. The texture of the soil is much more sandy in the area studied in this valley, which may partly explain the lack of nests, but this is by no means certain.

On the other hand, although these swallows are fairly common in the portion of the San Bernardino Valley investigated, the vast majority of the nests are under the eaves of buildings. Most of the nests are attached to single family homes, but a fairly sizable colony (approximately 200 birds) utilizes buildings on the Riverside campus of the University of California. Bridges and culverts appear to be nearly as common as in the Sacramento Valley, but they are almost completely ignored by Cliff Swallows. Rarely have more than five nests been found under any bridge, no matter how large. The only significant colony located under a bridge was found over a permanent stream. Observations have been made in this area for only two seasons, hence sufficient data are not available as yet to determine the real reason for this, but it appears that the following may be a partial explanation. As this entire region is reclaimed desert or semi-desert, the amount of rainfall is rather small, especially when compared with that of central California, and the rains generally occur before the swallows arrive. Thus, the gullies beneath the bridges and culverts are dry when the birds are looking for mud. However, plenty of mud is available near dwellings where lawns and gardens are watered frequently.

ARRIVAL OF BIRDS

In Cliff Swallows there apparently is considerable diversity in the time of departure from the wintering areas in South America, at least near Buenos Aires, Argentina. Hudson (*in* Sclater and Hudson, 1888:30) stated that "they do not seem to be as regular in their movements as other Swallows here; some years I have observed them passing singly or in small parties during the entire hot season: usually they begin to appear, flying north, in February; but in some years not until after the middle of March. . . . I have known them to continue passing till April, after all the summer migrants had left us . . . ."

Therefore, it is not surprising that the date of the first spring arrival of these birds in California has been variously reported by different authors. For example, Willett (1933:114) told of seeing birds in Los Angeles on February 15, while Gross (*in* Bent, 1942:483) stated that the earliest arrival in California was February 26 at Los Angeles. Grinnell and Wythe (1927:127) indicated that these birds generally arrived in the San Jose area about the first week in March, whereas Grinnell and Linsdale (1936:87) told of seeing them in the Point Lobos region for the first time on March 28. On the other hand, Grinnell and Miller (1944:278) reported that the dates of arrival and departure are greatly variable with year and locality, but in general these birds arrive in California in mid-March.

Some variations in the time of arrival of other species of North American hirundines have been reported, as by Allen and Nice (1952:608 ff) in Purple Martins (*Progne subis*) and by Peterson (1955:238 ff) in Bank Swallows (*Riparia riparia*). Edson (1942:5; 1943:396) has shown that there is a great deal of variation in arrival dates of Violet-green Swallows (*Tachycineta thalassina*). In the course of this investigation considerable variation has been found in the time of arrival of birds from one year to the next at a given colony. Figure 8 shows examples of the variation in the time of arrival that occurred at some of the colonies. Unfortunately, a close check on the time of arrival at all colonies each year was impossible.

A possible explanation for variation in arrival time is readily apparent. These birds feed almost exclusively on flying insects, and they are not able to survive in a region when it is so cold that no flying insects are available. Therefore, temperature would seem to play an important role in governing the time of arrival at the colony sites. No insect counts correlated with temperature were obtained in the course of this study to

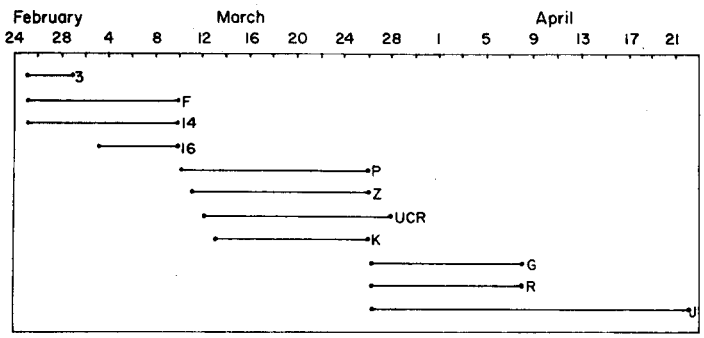

Fig. 8. Extreme dates for first arrival of Cliff Swallows at some representative colonies. Legend: 3 = 5 mi. E Folsom, Sacramento County; F = 7 mi. S Sacramento, Sacramento County; 14 = 4.5 mi. SE Florin, Sacramento County; 16 = 1 mi. N Elk Grove, Sacramento County; P = 4 mi. W Davis, Yolo County; Z = 2 mi. NE Davis, Yolo County; UCR = University of California campus, Riverside, Riverside County; K = 7 mi. W Davis, Yolo County; G = 6 mi. NW Davis, Yolo County; R = 5 mi. NW Davis, Yolo County; J = 7 mi. W Davis, Yolo County.

support this statement. However, Glick (1939:94), working in the southern United States, found the number of insects in the air during the day increased sharply when the air temperature rose above 55°F. Freeman (1945:144), from his work in England, likewise showed that the density of the population and the total number of species of insects increased with rise in temperature over a range from 43° to 83°F. For example, all species of some groups of insects were taken only when the temperature was above 61°F. Both of these investigators stated that temperature is considered one of the most important meteorological factors controlling flight of insects.

The four most abundant orders of insects collected during the day below 1000 feet by Glick (*op. cit.*) were Diptera, Coleoptera, Hymenoptera, and Hemiptera (Homoptera), in that order. He found that Hemiptera were most numerous when the temperature of the air ranged from 70° to 79°F., Coleoptera and Diptera from 75° to 79°F., and Hymenoptera from 85° to 89°F.; thus fairly high temperatures are necessary before any of these groups becomes very abundant. Beal (1918:7 ff) reported that the most numerous food items found in the stomachs of 375 Cliff Swallows, collected from March to September, belonged to the insect orders Hymenoptera, Coleoptera, Hemiptera, and Diptera, in that order; these are the same major groups reported by Glick (*op. cit.*). This would indicate that temperature indeed would play an important role in determining the presence or absence of food for Cliff Swallows.

Allen and Nice (*op. cit.*), in their investigation of Purple Martins, and Peterson (*op. cit.*), in his study of Bank Swallows, showed a correlation of time of arrival of the birds with mean temperatures. However, it is believed that mean temperatures have little value, since this is not the condition experiencd by the birds. Rather, it is felt that the extremes of temperature to which the birds and their food supply are actually exposed should be the ones under consideration. Therefore, in the present study, daily maximum temperatures are used.

Figure 9 shows the maximum daily temperatures for early spring recorded at the Sacramento office of the United States Weather Bureau and the time of arrival of the first birds on the major study area in 1952, 1953, and 1954. Admittedly, temperatures taken at the weather station will not be exactly the same as those at the individual colonies, but they will be of the same order of magnitude. Also, the temperature is measured a number of feet above the ground, which is where the birds feed, and where Glick (*op. cit.*) and Freeman (*op. cit.*) made their observations. In addition, the city of Sacramento is centrally located in relation to most of the colonies studied in the Sacramento Valley.

In each case, the birds arrived during, or just after, a few days of relatively warm weather (above 60°F.). As shown in figure 9 there were two definite times of arrival in 1952. The first arrival was noted at only two colonies in El Dorado County. This date was followed by an extensive period of relatively cool weather. The majority of the colonies observed that year did not have any birds until the second date indicated in figure 9, at which time nearly every colony under observation was occupied. It would be interesting to know whether the few birds that had reached the two colonies on the earlier date remained at those colonies during the colder weather or whether they moved to some other area. Based on observations made in southern California, it is felt that they probably moved out during this period, since this has been found to occur in periods of inclement weather before the nests are completed. However, Kimball (1889:338), in his work in Illinois, reported dead Cliff Swallows in nearly every nest during a spring when a prolonged cold period occurred after the birds arrived. At any rate, instead of having a slow but steady influx of birds at the colonies, as usually occurred at the beginning of the season, there were large numbers of birds at each of the colonies within

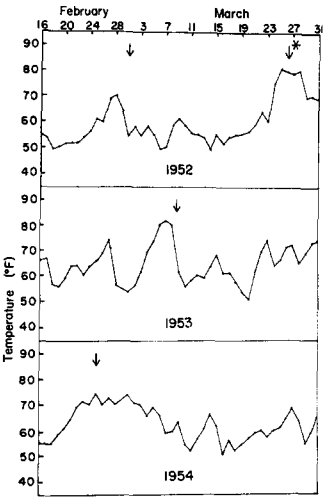

Fig. 9

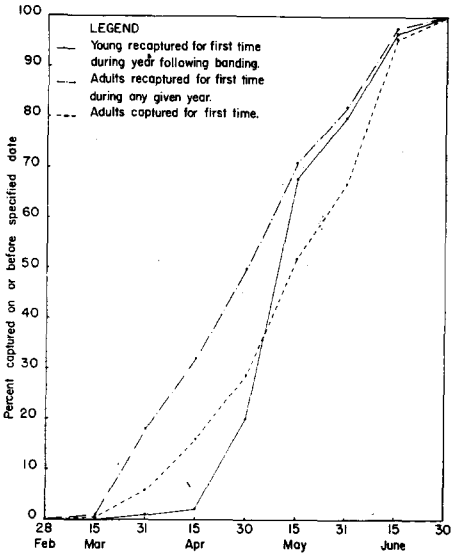

Fig. 10

Fig. 9. Maximum daily temperatures recorded by Sacramento office of United States Weather Bureau. Arrows indicate dates first Cliff Swallows were seen on study area.

Fig. 10. Rate at which banded birds (both yearlings and returnees) are recaptured for the first time in subsequent breeding seasons compared with newcomers. Results are based on 181 yearlings, 3489 returnees, and 4376 newcomers caught at the same colonies involved in table 4.

24 hours of the first arrivals. Therefore, although this scant bit of evidence is far from conclusive, it tends to indicate that the birds generally arrive after food becomes available.

It is more difficult to attempt to explain the variation in time of arrival at different colonies in the same year. The dates of first arrivals at different colonies in the Sacramento Valley range, for example, from March 1 to April 22 in 1952. This year showed the greatest variability, but the same phenomenon was exhibited in the other years to a lesser degree. In one case, the first birds arrived at a culvert on March 26, but none occupied a culvert 200 yards away until April 22, at which time there were only six birds present. More amazing, the second culvert appeared to human eyes to be much superior for Cliff Swallow nesting. There was no apparent decrease in the nesting population in the first culvert, so it was not merely a shift in the local population. Each of these culverts eventually contained approximately 200 nesting birds that year. At present no information is available to explain this great diversity in arrival time at different colonies.

PAIR FORMATION

The data available at present essentially agree with those of Emlen (1954:25) in regard to pair formation. It appears that some of the birds are paired either before they arrive at the nesting colony or they become paired immediately upon arrival. On the day of arrival, many of the old nests are occupied and actively defended by two birds. The urge to defend the nests is strong in these birds in the morning, but it decreases perceptibly in the afternoon. So far it has not been possible to tell what percentage of the population of a colony is paired at this time. However, it is felt that most birds are

paired very shortly after arriving in this region. By using new techniques that are being developed in conjunction with artificial nests, it is expected that more information on this point will be forthcoming.

Present evidence indicates that new pairs are formed each year. A series of nests was numbered so that individual birds could be identified with a given nest. On 25 occasions both members of a pair have been captured and banded at a numbered nest. In none of the five instances where these birds have been caught subsequently in succeeding years have both members of the pair been taken together. Unfortunately, this sample is quite small, due to the difficulty of accurately identifying two birds with a particular nest at the time of capture. Nevertheless, even this small sample indicates that the birds probably do not form the same pairs in succeeding years except by chance.

The pairing bond may not be as strong in Cliff Swallows as it is in some other species of birds. For example, Forbush (1929:147) reported that E. O. Grant saw three Cliff Swallows build a nest together, and all took turns incubating the eggs (he thought they were two males and one female). Brewster (1906:301) occasionally found three birds in nests he examined, and he stated that he believed there is good reason to suspect these birds sometimes practice polygamy or polyandry.

Some evidence was obtained in this investigation to indicate that all pairs may not remain together for an entire nesting season. From the numbered nests, it was found that the majority of pairs recaptured remained together throughout the breeding season. However, there were some cases where three birds were captured from a nest in a single season, but never more than two birds were captured at a time. Originally it was thought that one member of the pair had died and been replaced. This may have been true in these instances, but judging from more recent information, this is not necessarily true. A more detailed discussion of this follows.

VAGRANCY AND HOMING

As Farner (1945:84) stated, a great deal of data has been accumulated relating to the return of swallows to their birthplaces, and several references have been found that deal with movements of these birds between breeding colonies (Uchida, 1932; Stoner, 1941; Bergstrom, 1951; Allen and Nice, 1952; Chapman, 1955; Kirsher, 1957). However, there seems to be relatively little information on the movements of swallows between colonies in a single breeding season. For example, Robertson (1926:244) reported two nestling Cliff Swallows captured five days following banding about ½ mile from the original site. Wharton (1952:30) told of two adult female Tree Swallows (*Iridoprocne bicolor*) being recaptured at locations about 20 miles from the banding sites. In the case of one of these birds, both of the captures were made in the same breeding season. Bergstrom (1951:60) enumerated three instances where adult Bank Swallows were recaptured three miles from the banding site in the same year they were banded.

The data obtained in the present study indicate that membership in a breeding colony of Cliff Swallows may not be as stable as previously assumed. Although most recaptured adults were caught at the original banding sites, many birds were found to change colonies in a single breeding season. A recapture that is made in the same breeding season is called a repeat. Table 2 shows that a small percentage of these repeats have been taken at locations other than the previous trapping sites. The term vagrancy is being used to describe this situation. The proportion of vagrants each year was approximately the same. The greater number of female vagrants is highly significant statistically.

As the birds are captured at night, it is assumed that the banding site is the summer home of the individuals captured. Most vagrant birds joined colonies that were from

one to five miles from the original nesting sites. The longest movement noted to date has been approximately 25 airline miles. The most notably vagrant birds found thus far have been two females that were captured three times in one season, each time at a different site.

Table 2

Vagrants Compared with All Repeats

	Males	Females	Sex unknown	Total	Per cent of vagrants
Repeats	1493	1629	377	3499	
Vagrants	111	175	18	304	9

Microscopic examination of the testes of two vagrant males collected revealed all stages in the formation of gametes from spermatogonia to mature spermatozoa, corresponding to stage 7 of Blanchard (1941:55). Thus, they appeared to be potentially breeding birds. Likewise, the well-developed incubation patches on the female vagrants examined indicated that they were potential breeders as well.

At first, when an effort was made to try to interpret these results, it was felt that the night banding operations might have caused birds to change colonies. This possibility still cannot be ruled out completely. However, more recent work tends to discredit this explanation. For example, some birds have been captured as many as ten times over a five-year period without causing them to desert the original colony. Also, several homing experiments have shown that many of the transplanted birds have a strong attachment to a particular nesting site. These particular homing experiments were planned to determine whether the birds could find their way back to their nests the morning after their release at the trapping site. They were not designed to study the phenomenon of homing *per se*. It was felt that perhaps, since the birds were in the dark several hours after their release, they might be unable to find their way back to the nest site if they happened to have wandered into unknown territory.

Homing experiments.—Only two previous homing experiments with North American swallows have been noted in the literature. Gillespie (1934:44) released the same adult male Rough-winged Swallow (*Stelgidopteryx ruficollis*) on successive occasions at 4 miles, 7 miles, and 32.8 miles from the nest site. Each time the bird returned to its nest within a matter of a few hours. Stoner (1937:18–19) released an adult Bank Swallow three miles from its nest in a light rain, and it was found in the same nest the following day.

For most of the present experiments, birds were captured at night and carried in covered collecting cages to the release point. Most birds were held in these cages until the following morning, but some that were released near Davis, Yolo County, California, were freed the same night they were captured. Birds taken to Minden, Douglas County, Nevada, were caught in daylight and released the same day they were captured. All birds in each experiment were released in a group.

A relatively small number of birds was involved in each of the releases shown in table 3. In the three Davis releases, the percentage that returned was approximately the same whether the birds were released in daylight or in the dark. The greatest differences recorded here, namely 39 per cent and 57 per cent, are not statistically significant at the 5 per cent level. (The 5 per cent level of significance has been used in all statistical calculations.)

Even greater obstacles did not prevent some birds from returning to their nesting sites. For instance, birds were taken from the Sacramento Valley over the crest of the Sierra Nevada to Minden, Nevada, and released. The lowest pass through the mountains

Table 3

Results of Homing Experiments

Site of capture	Folsom, Sacramento Co., Calif.	Clarksville, El Dorado Co., Calif.	Clarksville, El Dorado Co., Calif.	Clarksville, El Dorado Co., Calif.	Riego, Placer Co., Calif.	Riego, Placer Co., Calif.
Site of release	Davis, Yolo Co., Calif.	Davis, Yolo Co., Calif.	Davis, Yolo Co., Calif.	Minden, Douglas Co., Nev.	Berkeley, Alameda Co., Calif.	Farallon Islands
Distance (miles)	40	45	45	70	85	115
Date and time of release	Apr. 5 Day	Mar. 31 Day	Mar. 26 Night	June 2 Day	May 24 Day	May 24 Day
Number birds released	18	49	28	10	19	19
Number returned same year	7	25	16	3	7	3
Per cent returned same year	39	51	57	30	37	16
Additional birds recaptured in other years	3	7	3	....	5	4
Total number returned	10	32	19	3	12	7
Total per cent returned	56	65	68	30	63	37
Number homing birds returned after experiments for:						
1 year	6	15	6	....	6	3
2 years	1	5	....	....	....	2
3 years	....	1	4	1	....	....
4 years	....	1	....	....	....	....

available to them was 7382 feet above sea level. However, three of these birds were back at the banding sites four days later. They probably arrived sooner, but we were unable to return to the colony earlier. None of the other birds taken on this trip has been recaptured.

A number of birds was caught at one colony in the Sacramento Valley, divided into two equal groups, and released the following morning. One group was released in Berkeley, Alameda County, California; the other group was released on the Farallon Islands, about 25 miles off the coast of California near San Francisco. Although a greater percentage returned from Berkeley than from the Farallon Islands, the difference is not statistically significant. Two of the birds released in Berkeley were recaptured at their nests within 17 hours of their release. They probably arrived earlier than this, but it was impractical to trap them earlier.

None of the transplanted birds in any experiment has been recaptured at the point of release, even though some of the birds were released at frequently trapped colonies.

Thus, although it is possible that a bird may wander about for the remainder of the night after its release at a banding site, it is capable of finding its way back to its nest when daylight returns.

Discussion.—Rarely are more than 50 per cent of the birds recaptured on subsequent trips to a colony in the same breeding season. At first glance, this might be considered sufficient reason to view the trapping methods as the causative factor of this phenomenon. However, there appears to be an influx of unbanded adults into colonies that have been trapped several times in the same breeding season, which could not be

Table 4

Comparison of Number of Recaptured to Newly Captured Adults in Successive Trapping Attempts

	Trapping	Date	Number recaptured	Number newly captured
1952				
1 mi. W Clarksville, El Dorado Co.	1st	Mar. 30	.....	344
	2nd	May 23	164	347
	3rd	June 14	225	54
5 mi. E Folsom, Sacramento Co.	1st	Apr. 4	.....	112
	2nd	May 24	54	67
3 mi. SE Folsom, Sacramento Co.	1st	Apr. 4	.....	145
	2nd	June 8	69	182
3 mi. NE Riego, Placer Co.	1st	May 8	.....	638
	2nd	June 6	143	112
7 mi. W Davis, Yolo Co.	1st	Mar. 29	.....	81
	2nd	Apr. 22	56	117
1953				
1 mi. W Clarksville, El Dorado Co.	1st	Mar. 26	.....	182
	2nd	Apr. 17	88	324
	3rd	June 6	362	236
5 mi. E Folsom, Sacramento Co.	1st	Mar. 22	.....	121
	2nd	May 22	90	148
	3rd	July 3	100	8
3 mi. SE Folsom, Sacramento Co.	1st	Mar. 22	.....	94
	2nd	May 22	56	185
3 mi. NE Riego, Placer Co.	1st	Apr. 24	.....	654
	2nd	June 16	192	26

the fault of the capturing technique. Table 4 shows examples of this over a two-year period at five optimum colonies. These colonies are so situated that the number of birds escaping is virtually nil. Therefore, these additional birds must have joined the colonies between trapping attempts. The evidence from other colonies is not as good, because many of the sites cannot be completely sealed. Nevertheless, the indications are that this influx of birds occurs at all the sites. It may be argued that these additional birds came from a non-breeding reservoir and that they moved into the colony because of available space created by the removal or voluntary departure of earlier birds. For example, Emlen (1952:195; 1954:26) stated that he believed many of the Cliff Swallows that he called raiders may be non-nesting birds. Nero (1956:140), speaking of Red-winged Blackbirds (*Agelaius phoeniceus*) in Wisconsin, said that "territory-seeking males appear commonly on the breeding area throughout the season." The presence of a non-breeding reservoir (especially males) has been reported for many species of breeding birds in a Maine spruce-fir forest by Stewart and Aldrich (1951), and by Hensley

and Cope (1951). Nevertheless, several species studied in the Maine forest showed little or no increase in number of birds on the study area in the course of the investigations. If it is argued that the trapping operations in this investigation created available territory for the late arrivals by causing earlier birds to depart, what created this available territory for the banded vagrants that moved to previously untrapped colonies? In 10 colonies that never had been trapped before, a total of 197 previously banded birds were recaptured. Although some of these birds were recaptured for the first time that season, many were repeats of birds trapped earlier in the same season at other colonies.

The species of birds studied in Wisconsin (Nero, *op. cit.*) and in Maine (Stewart and Aldrich, *op. cit.*; Hensley and Cope, *op. cit.*) required relatively large territories for nesting, whereas Cliff Swallow territories consist of only the nest site. There was quite a bit of variation in the number of nests in a colony from year to year, but there was still space for nests, even at the end of the breeding season, in the great majority of colonies every year. This means that these additional birds did not have to wait for the removal or departure of earlier arrivals before being able to nest themselves. It was found that these new adults usually were approximately evenly divided as to males and females. Thus, these birds apparently did not have to wait until earlier pairs were broken by death, or other means, before being able to acquire a mate. Therefore, it is felt that these birds either are late arrivals from the wintering area (see Sclater and Hudson, 1888:30), or that they are vagrants of the type described previously.

NEST CONSTRUCTION

Nest construction has been described extensively by Emlen (1954:17 ff), so it will not be discussed at length here. In addition it has been found, from numbered nests and marked birds, that Cliff Swallows normally do not return to the same nest each year. So far, only one bird has been taken from the same nest in two successive years. In some colonies in which there are several sections to the bridge, the great majority of birds have been observed to nest in one or two sections one year and in other sections the following year. This often occurs even though many old nests are still available. Apparently when a bird uses the same nest again, it is purely on the basis of chance and is not done intentionally. This does not mean, however, that old nests normally are not used, because actually this practice is very common.

It also has been determined that the birds do not spend the night at the nesting colony until the nests are almost completed. This is not particularly noticeable in colonies where many old nests of previous years are still present, because the majority of these nests usually will be occupied almost as soon as the birds arrive. It is very evident, however, in colonies that have lost all the old nests in the course of the winter. Such a colony may be bustling with nest-building activity during the day, but birds will not be found there at night until their nests are nearly ready for eggs.

There are several cases on record of Cliff Swallows converting the nests of other birds for their own use. For instance, Carpenter (1918:90) described these birds using Bank Swallow nests, Whittle (1922:214) observed them using Robin (*Turdus migratorius*) nests, and Reed (1927:110) saw them convert a Phoebe (*Sayornis phoebe*) nest. Goodsell (1919:175) reported Cliff and Barn swallows (*Hirundo rustica*) using the old foundations of one another's nests. The author has seen a pair of Cliff Swallows occupy an old Barn Swallow nest and change it into a typical Cliff Swallow nest.

On the other hand, there are many instances of other species using Cliff Swallow nests. For example, numerous authors, among them Brewster (1906:300), Forbush (1929:145), Burleigh (1930:48), Herman (1935:137), Grinnell (1937:207), and Sooter, Bennington, and Daniels (1954:309), have reported English Sparrows occupy-

ing Cliff Swallow nests, in so doing often driving out the rightful owners. Sibley and Hemphill (1940:224) saw a Plain Titmouse (*Parus inornatus*) use a Cliff Swallow nest. A. H. Miller reports a similar instance involving the Chestnut-backed Chickadee (*Parus rufescens*). Sooter, Bennington, and Daniels (*op. cit.*) listed the Say Phoebe (*Sayornis saya*) as a species seen using a nest of the Cliff Swallow. Shepardson (1915:101) described House Finches (*Carpodacus mexicanus*) using nests of this species, as well as apparently parasitizing a nest containing Cliff Swallow eggs. Friedmann (1929:234; 1931:63) told of Cowbirds (*Molothrus ater*) parasitizing this species, and Stoner (1939: 221) reported one instance in which a pair of Cliff Swallows was parasitized by English Sparrows. In addition, the present author has observed English Sparrows, House Finches, and Bewick Wrens (*Thryomanes bewicki*) successfully reproducing in artificial Cliff Swallow nests described earlier.

Nests of Cliff Swallows are used by some species during the winter, according to Sooter, Bennington, and Daniels (*op. cit.*). They have noted Rosy Finches (*Leucosticte tephrocotis*), Black Rosy Finches (*Leucosticte atrata*), and Canyon Wrens (*Catherpes mexicanus*) using Cliff Swallow nests in Colorado. Recently, Kirsher (1957:3–4) has reported finding several Say Phoebes and one Sparrow Hawk (*Falco sparverius*) using Cliff Swallow nests in winter and a Screech Owl (*Otus asio*) sitting (in the day time) in a partly completed Cliff Swallow nest in the breeding season.

Also, several species have been seen nesting in close proximity to Cliff Swallows, even though neither was using the nests of the other. For instance, Coues (1878:434–435) saw Cliff Swallows building nests among the outer sticks of a Great Blue Heron (*Ardea herodias*) nest, and others constructed nests near that of a Prairie Falcon (*Falco mexicanus*). Herman (*op. cit.*) has found Eastern Bluebirds (*Sialia sialis*) nesting in a Cliff Swallow colony. McCanne (1936:84) and Goodsell (*op. cit.*) both reported Barn and Cliff swallows nesting at the same site. Bailey (1907:169), Skinner (1933:241), and Pitelka (1944:34) have all seen White-throated Swifts (*Aëronautes saxatalis*) nesting with colonies of Cliff Swallows. In the course of the present investigation, Black Phoebes (*Sayornis nigricans*), English Sparrows, and Barn Swallows have been found nesting with colonies of Cliff Swallows, and several Red-shafted Flickers (*Colaptes cafer*) have been found roosting at night under the bridges and culverts used by Cliff Swallows for nesting (see Kirsher, *op. cit.*).

Grinnell, Dixon, and Linsdale (1930:292) indicated that the Cliff Swallows sometimes use nesting sites alternately. A few examples of this were observed in the course of the present investigation. In one instance, a colony had birds in 1950, but none was found there at any time after that date. However, no check was made on this colony after 1954. In another instance, birds were captured in a colony in 1949 and 1950. In the breeding seasons of 1951 and 1952 the site was unused, but birds were captured again at this colony in 1953. Although every bird in this rather small colony was captured at the time, no banded birds were in the group. In still another case, a colony that was known to have contained no birds, at least since 1948, was occupied in 1953.

Grinnell, Dixon, and Linsdale (*op. cit.*:293) thought it possible that this alternate use of nesting sites is due to an over-abundance of ectoparasites in the nest. However, it is rather hard to attribute alternation to that cause in the present case, since all the old nests were destroyed by winter rains in the two cases where the colonies were not used in subsequent years.

EGG-LAYING, INCUBATION, AND BROODING

Apparently there is a good deal of variation in the time eggs are laid in central California, both within a colony and between colonies. On several occasions, eggs under-

going incubation were found in colonies that also possessed flying young. Likewise, some colonies had large numbers of young in the air while the majority of nests in other colonies in the study area had newly completed clutches of eggs. Gross (*in* Bent, 1942:484) lists 109 egg records from California, ranging from April 27 to July 5. In the present study, eggs have been found in nests from April 5 to July 3, with the majority being found from about April 20 to the end of May.

On the other hand, Myres (1957:314) has reported that the Cliff Swallows he studied in British Columbia laid their eggs in any one colony in a very short period of time. However, the largest colony he investigated contained only 54 nests, which would be a rather small colony in the study area currently under discussion. Therefore, it appears likely that each of his colonies was occupied by a single wave of migrants, which would be expected to nest at about the same time. In the larger colonies studied in central California the nesting sites are occupied in successive waves; birds arrive at these colonies over an extended period of time. These differences may be due not only to the size of colonies studied but also to the fact that fewer waves of migrants may reach the more northerly areas. This could explain the differences in the results obtained.

Grinnell, Dixon, and Linsdale (1930:292) reported that Cliff Swallows in the eastern Great Basin portion of northern California nest nearly one month later than those that live in the northern Sacramento Valley of this state. My investigations show that the same general difference prevails between the southern Sacramento Valley and the Great Basin area near Minden, Douglas County, Nevada. On June 2, 1953, the majority of nests in that area of Nevada contained incomplete clutches, and no young were found in any nest. On this same day, however, in the Sacramento Valley, several young birds were captured that were already flying, and a large number of flying young was banded in the Sacramento Valley four nights later. Grinnell, Dixon, and Linsdale (*op. cit.*) believed it probable that this was due to a greater amount of food for the young becoming available earlier in the western region. This explanation seems reasonable when one considers the difference in temperature between these regions at that time of year.

Gross (*in* Bent, *op. cit.*:474) stated that the number of eggs in a clutch varies from 3 to 6, with 4 or 5 being the usual number. Storer (1927:106), reporting on observations made in central California, found 5 young and 1 egg in one nest, and 3 young and 2 eggs in another nest. However, most of the nests he investigated possessed from 2 to 4 eggs each. Rarely were more than 4 eggs found in any nest in the course of the present investigation, and often only 3 were found. It is felt that 3 to 4 eggs per clutch is the normal condition in this area. Recently Myres (*op. cit.*:313 ff) has shown that early clutches contain the larger number of eggs (4 or 5), whereas later clutches usually contain only 3 eggs. He found the average clutch size ranged from 3.6 to 3.9 eggs. From observations made in artificial nests, it was found that the eggs are laid on consecutive days until the clutch is completed. This has been confirmed by Myres (*op. cit.*:313), and other investigators have found that the same situation exists in other species of hirundines.

Brood patches were seen on females from April 3 to July 3, but as stated earlier, they were most numerous and best developed from about the middle of April until the first week in June. It was not determined whether males assisted with incubation. However, both members of a pair were almost always found in the nest at night.

Gross (*in* Bent, *op. cit.*:474) stated that the incubation period for Cliff Swallows is from 12 to 14 days in length, which is the same as that reported by Burns (1915:286). Myres (*op. cit.*:311) gave 14 days as the incubation period but stated that 13 days may be more accurate. Gross (*in* Bent, *op. cit.*) observed one nest in which the time from the laying of the last egg to the hatching of the first young was 13 days. However, the meas-

urement of incubation time used in this study is that recommended by Nice (1953:81) and others, namely "counting the time from the laying of the last egg to the hatching of the last egg, when all eggs hatch." No complete records of incubation time were made in the Sacramento Valley. However, with the aid of artificial nests, it was found that 16 days elapsed between the time the last egg was laid and the last egg hatched. This was true for both clutches that were watched for the entire incubation period. As the time from the laying of the last egg to the hatching of the first egg was 15 days in both nests, it appears that incubation may normally begin one day before completion of the clutch. At least, some development in earlier eggs must occur before the last egg is laid to produce such a result. The number of clutches watched so far is very small and may not be typical of the species in general. Also, as stated earlier, these nests were built of casting plaster with a mud lining. It is conceivable that this nest material may prolong incubation slightly by allowing uncovered eggs to cool more rapidly than similar eggs in mud nests. Nevertheless, it is felt that 16 days is probably close to the normal incubation period for this species.

Kendeigh (1952:240 ff) did not mention the Cliff Swallow in his review of the literature concerning incubation time in the Hirundinidae. Nevertheless, it can be seen from his report that the incubation time for all North American hirundines included in his survey (4 species) ranges from 14 to 16 days. Allen and Nice (1952:630) included an additional North American species of hirundine (not the Cliff Swallow) in their summary of length of incubation in swallows, and its incubation time also agreed with the data considered by Kendeigh (*op. cit.*). It seems unlikely that Cliff Swallows should vary to any extent from this time interval.

Unusual nesting behavior.—Cliff Swallows nesting, or continuing to nest, under peculiar circumstances have been reported in the literature on several occasions. For example, there have been instances reported in which the adults accepted the young in a substitute nest after an accident had befallen the original nest. Wright (1924:153) gave an account of adults accepting an old tomato can as a nest after it had been nailed in the location of the natural nest and the nestlings placed in it. The adults began to build a mud neck over the open end of the can within a few hours after it was placed in position. Reed (*op. cit.*) told of an old strawberry box being utilized in the same manner.

On the morning of June 8, 1955, a nest containing three half-grown young birds fell from its attachment above a loading dock at the Physical Sciences building on the Riverside campus of the University of California. Some students brought the fledglings to the Life Sciences Division, and Dr. Irwin M. Newell placed them in a shoe box and kept them overnight. He fed them a thin gruel at frequent intervals with an eye-dropper. On the afternoon of the accident, he propped one of the artificial nests, described earlier, into the position of the old nest by means of a long stick. Late the following morning, upon the author's return from a trip, the young birds were placed in this new nest. Although the parents had not seen the young birds for more than 24 hours, by early afternoon they were carrying food to the young and adding mud to the artificial nest. The young birds successfully reached flying age, and they abandoned the nest 10 days later. At that time it was found that the adults had placed mud, about ¼ inch thick, around the entire inner surface where the nest touched the building. There was sufficient mud to support the nest, since, when the stick was removed, the nest remained in position. The parents' acceptance of an artificial nest that closely resembled one of their own is not very surprising. However, the length of time that elapsed between the loss of the original nest and the return of the young in a new nest is felt to be unusual.

Apparently young Cliff Swallows can survive relatively long periods without food, if they remain inactive. This was demonstrated when one young bird, which was old

enough to fly from the nest at night, inadvertently was detained. The bird was captured on the night of May 25 during routine trapping operations. While the writer was storing banding cages late in the afternoon of May 27, the bird was discovered in the corner of one cage. It could not have eaten for at least 46 hours, but upon its release at a colony, it flew off with no apparent difficulty. It immediately joined the flock that was feeding above the bridge and was soon lost in the crowd.

Mortality of eggs and young.—During the incubation and early brooding periods, it was rather difficult to make many of the adults flush from the nests at night. This was rather disturbing, because the nesting birds were needed for study, but it was felt that perhaps our activities in these periods might cause a higher than normal mortality among the eggs and young. Since it had been learned early in the investigation that none of the adults returned to the nests on the night of their release, it was feared the eggs or recently hatched young might suffer from the lower temperature caused by the absence of the adults. Therefore, both air and nest temperatures were recorded at one colony that contained a large number of eggs, and a series of nests was marked for continued investigation. Both air and nest temperatures were 23°C. at the time the first measurement was made at 9:30 p.m. When the second record was taken 3½ hours later, the air temperature had dropped to 18.5°C., whereas the nest temperature remained at 23°C.

The maintenance of a rather constant temperature in the nest interior is not altogether surprising when one considers the construction and the location of these nests. The mud used in nest building is a rather poor heat conductor. Also, there is a single opening into the nest, about two inches in diameter, which prevents drafts of air passing through the nest. In addition, most of the nests in the primary study area are attached beneath cement bridges and culverts, which tend to retain heat long after the sun has gone down.

Of the 24 marked nests containing full clutches, 20 successfully produced broods. This would indicate that no appreciable harm was done to the eggs by the overnight absence of the adults.

Later a colony was visited in which the majority of the nests contained newly hatched young. No thermometer was available to measure the temperature on this occasion, but the weather was so cool that the investigators were uncomfortable, even though working physically. It was felt that if any additional mortality were to occur among nestlings, due to our activities, this set of circumstances would be responsible. A sample of 23 of these nests with young was marked, and the future progress of each nest was noted. It was found that 21 of the 23 marked nests showed no mortality of young up to the time the birds left the nest. Therefore, it was felt that the trapping operations at night produced little, if any, deleterious effect upon the Cliff Swallow populations on the study areas.

Fledging.—Young birds from clutches hatched in the artificial nests were first seen flying 23 days after hatching. They returned to the nest for another two to three days before deserting it permanently. This generally agrees with the summary by Burns (1921:179), in which he listed published reports that recorded the length of nestling life in Cliff Swallows as varying from 16 to 24 days. Similar results have been reported for several other species of North American swallows. For example, Kendeigh (1952:286) summarized observations on several species of the Hirundinidae, and he stated that the period in the nest ranged from 18 to 28 days. Allen and Nice (1952:633) recorded that the length of time in the nest for the Purple Martin varies from 27 to 35 days, but usually it is about 28 days. However, this is the largest swallow in North America, so the slight extension of the nestling period in this species is readily understandable.

Allowing 3 to 6 days for egg-laying, 16 days for incubation, 23 days for reaching

flying age, and 2 to 3 days for leaving the nest, 42 to 45 days would be required from the laying of the first egg to flying young, or 44 to 48 days would be required until the young would leave the nest permanently. This roughly corresponds to the findings of Grinnell (1937:207), who observed a minimum interval of 48 days from the date of first arrival of adults until there were flying young. The minimum interval recorded by Grinnell was probably obtained from birds that utilized old nests, since these birds would possibly be able to complete nesting first.

The earliest flying young were found about the middle of May, and there were large numbers of young in the air by the first of June. By the end of June, almost all birds, both young and adults, had deserted the nesting sites. In only three years of the eight-year investigation period were birds found at any colony after July 1, and these birds were relatively few in number. Birds were never found in any nesting colony after the middle of July.

On most occasions, the adults had deserted the nesting site at night by the time the young could fly well. Many colonies were trapped in late June when only young birds, or at most a few adults mixed with large numbers of young, would be captured. It appeared that there was insufficient room in the nest for two parents and three or four young birds that were nearly as large as the adults by the time they could fly. Apparently, therefore, the adults left the nest entirely to the young for a few days before the nestlings also deserted the nest site. The exact length of time the young are brooded was not determined. Beyer (1938:134) and Peterson (1955:256) both have reported a similar situation in the Bank Swallow in which Peterson (*op. cit.*) found that "the parents rarely spent the night in the nest after the young were 12 days old." Allen and Nice (*op. cit.*:634) stated that brooding by adult Purple Martins stops altogether by the ninth or tenth day. Austin and Low (1932:43) found that neither adult spends the night in the nest after young Tree Swallows are one-half grown. Combellack (1954:441) observed that young Violet-green Swallows are brooded by an adult for only 10 nights.

Number of broods.—J. G. Cooper (*in* Sharp and Wyatt, 1885–1894:544) was quoted as saying that Cliff Swallows raise two broods in most of California. Willett (1933:114) stated that at least two broods a season are produced by this species, and Gross (*in* Bent, 1942:474) reported that "most all observers agree that cliff swallows in general raise two broods of young during any one breeding season. Hatch states that even three broods are sometimes reared, but I am inclined to believe that is very exceptional."

On the other hand, E. Coues (*in* Sharp and Wyatt, *op. cit.*:540) stated that probably only one brood is reared each season. Buss (1942:158) believed it likely that only a single brood a year is produced by these birds, since he wrote "it seems more likely that these incubating birds are not raising a second brood but are re-nesting birds whose first nests fell from the barn."

The production of two broods may be possible in some parts of the United States, but it does not appear to be true in the areas of California under investigation. Since, as was previously mentioned, most of the birds in the region under discussion lay their eggs after April 20, and the majority of adults leave the nesting colonies by June 30, this allows approximately 70 days to complete two broods. Again, this agrees roughly with the observations of Grinnell (1937), who reported that these birds usually were at the Life Sciences Building on the Berkeley campus of the University of California from about May 1 to July 10, a period of 71 days. If it requires from 42 to 48 days to produce and raise a single brood in California, not counting the time necessary to build a nest, there is not time for a second brood to be successfully raised in most cases. Usually there are a few birds that lay before April 20, and there are occasional instances of birds nesting beyond the end of June, but these are exceptions. It is possible that these late nesters

are actually raising a second brood, but it is more likely that they are re-nesting because of destruction of a previous nest or brood. If these birds are raising a second brood, they certainly are in the minority.

Although the birds almost completely abandoned the nesting colonies in the Sacramento Valley by July 1, Cliff Swallows were seen there for several weeks. The latest date birds were seen in any of the study areas in the course of this investigation was August 18. However, Grinnell and Miller (1944:278) state that these swallows remain in California until September, and sometimes they are found in October in the southern part of the state. Willett (1933:114), for example, stated that J. G. Cooper saw this species at San Diego, San Diego County, on October 5, 1862, and Gross (*in* Bent, *op. cit.*:483) told of some of these birds being seen at Kernville, Kern County, on October 28. Van Rossem (1911:133) found some of them apparently wintering in the Salton Sea area of Imperial County, since he collected specimens there on December 18, 1910.

RETURN OF BANDED BIRDS

To simplify discussion, the following terms will be used in this paper hereafter: recaptured birds that were banded as adults, or birds banded as young but recaptured more than one year following banding, will be called *returnees*; recaptured birds that were banded as young the preceding year will be called *yearlings*; adult birds that were captured for the first time will be called *newcomers*.

In this section the following points will be established:

1. When Cliff Swallows arrive in spring, returnees that have nests in a given colony arrive first; these are followed by newcomers and yearlings.
2. Many more adult returnees than yearlings return to the original colony the year following banding.
3. After yearlings nest once, they tend to return to the same nesting site, which may or may not be the hatching site.
4. More females, banded as adults, return in succeeding years than do males, but this does not seem to be true for yearlings.
5. Among adults that return, there is a higher percentage of females that go to other nesting sites in the area. This sexual difference is not so pronounced in yearlings.
6. The annual mortality among adults appears to be about 50 per cent, with few birds living more than 4 or 5 years.
7. Certain types of injuries apparently do not result in death of the injured birds.

Arrival of returnees, newcomers, and yearlings.—Table 5 was compiled from data collected at five colonies which could be completely sealed for trapping purposes. As trapping efficiency was much greater in such colonies, it is believed one is more justified in basing assumptions on this sample than on data from many colonies which could be only partly sealed. The columns of table 5 labelled "seasonal catch to indicated dates" contain the total number of birds captured for the first time by the specified date over a period of several years. This does not mean the first time these birds were ever captured, but the first time they were caught seasonally.

Evidence from these colonies indicates that when Cliff Swallows return to the nesting sites the following spring, returnees that have nested previously in a particular region tend to be the first to arrive in that area. Newcomers, which never have been trapped hitherto and are assumed never to have been in the area before, arrive in larger and larger numbers as the breeding season progresses. Shortly after the middle of May, the colonies contain about equal numbers of returnees and newcomers. A small percentage of the banded birds that return are yearlings, but the relative number is so small that it is ignored in table 5.

Table 5

Changes in Proportion of Newcomers to Returnees, According to Time of Arrival, in Five Optimum Colonies[1]

Date	Seasonal catch to indicated dates Total number[3]	Newcomers[2] Number[3]	Per cent	Returnees[2] Number[3]	Per cent
Feb. 28	6	2	33	4	67
March 15	52	10	19	42	81
March 31	871	244	28	627	72
April 15	1820	695	38	1125	62
April 30	3038	1262	42	1776	58
May 15	4923	2298	47	2625	53
May 31	5964	2946	49	3018	51
June 15	7807	4207	54	3600	46
June 30	8046	4376	54	3670	46

[1] Same colonies involved in table 4.
[2] See text for definition of terms.
[3] The numbers in these columns are cumulative.

Figure 10, however, shows that many of the returnees return earlier in the season than do yearlings. This indicates that since the adults have made the return trip from the wintering area at least once before, many of them tend to return to the breeding area more rapidly than those birds that have not made the trip previously. When yearlings return to nest in subsequent years, however, they return earlier in the season, as do other returnees. This pattern could be produced by: (a) young birds traveling together over unfamiliar migratory routes without adults to guide them, (b) differences in response to stimuli that cause migration, due to age, or (c) a combination of these two. Sufficient data are lacking at present to state which, if any, of these explanations is correct.

The curve for newcomers in figure 10 shows a condition intermediate to the other two curves early in the season. This is to be expected, since the group consists of adults that have nested in other colonies previously and young birds. Presumably many of these young birds have hatched in other sites the preceding year, although it is quite likely that some of the young birds had hatched at the same colony but escaped banding because of their age at the times the colony was trapped that year.

By the middle of May, the curve for newcomers falls below that of both yearlings and returnees. This could be explained by the probability that the majority of adults have arrived in the area by this time and the remainder of the birds consist primarily of young of the preceding year. Therefore, the curve for these birds should approximate that of the yearlings, although possibly it would be somewhat lower, because many of these birds might not be familiar with the area. However, added to this would be the number of vagrants that change colonies in the course of a season, as described earlier (see table 2). The majority of vagrants are detected in the middle and late stages of the breeding season, at a time when most birds have arrived at a nesting site. These birds, therefore, tend to obscure the actual situation concerning the original time of arrival of birds in the nesting area. Vagrants moving out of a colony would be undetected, whereas the addition of unbanded vagrants to a colony would increase the total number of birds considered as newcomers.

To use a hypothetical example, assume that 1000 newcomers arrive in a colony in a given nesting season and 100 of these birds are captured before April 15. This would mean that 10 per cent of the new birds had arrived by that particular date. If, to this number, are added 200 unbanded vagrants that move into the colony later in the season

from other colonies, the total number of unbanded birds captured at the colony is 1200. Therefore, the 100 birds that are captured before April 15 appear to show that only 8 per cent of the new population has arrived by that particular date. It appears, therefore, that a combination of the late arrival of birds that probably hatched in other colonies the preceding year and the arrival of vagrants could produce the type of curve shown.

Number of returnees versus yearlings.—Table 6, using data from the same five colonies, shows that a much larger number of returnees than yearlings return to the original colony the year following banding. A similar situation has been shown to exist in other species of swallows (table 7). Although there is some changing of colonies in both age groups of Cliff Swallows, it appears that birds which once have nested at a particular

Table 6

Comparison of Returns of Young and Adults Captured at Five Colonies[1]

	Young		Adult	
	Number	Per cent	Number	Per cent
Total banded	1098	100	4376	100
Recaptured year following banding	181	16	2036	47
Recaptured year following banding at same sites	104	57	1668	82
Recaptured year following banding at other sites	77	43	368	18
Ever recaptured	212	19	2093	48

[1] Same colonies involved in table 4.

Table 7

Comparison of Total Reported Returns for Several Species of Swallows According to Age at Banding

Species	Age	Per cent returned	Author
Cliff Swallow (*Petrochelidon pyrrhonota*)	Young	19	Mayhew (this study)
	Adult	48	
Barn Swallow (*Hirundo rustica*)	Young	0.2	Uchida, 1932
	Adult	46	
Purple Martin (*Progne subis*)	Young	1	Allen and Nice, 1952
	Adult	....	
Tree Swallow (*Iridoprocne bicolor*)	Young	11	Low, 1933
	Adult	31	
	Young	4	Chapman, 1955
	Adult	38	
Bank Swallow (*Riparia riparia*)	Young	1	Stoner, 1941
	Adult	4	
	Young	5	Bergstrom, 1951
	Adult	12	

colony have a stronger desire to return to that colony than young birds which were hatched there. This difference is highly significant statistically.

The percentage of returned Cliff Swallows recaptured in both age groups, however, is higher than that reported for any other species of swallow that occurs in North America (table 7). (The investigation of Uchida (1932) included in table 7 was not carried out in North America but was conducted on a species that occurs here.) It is not known whether this is an actual difference between species, or whether it is due to the various capturing techniques used by different investigators.

Nesting of yearlings.—Table 8 indicates that birds that are in the year after they are yearlings tend to return to the previous nesting site. In a slight majority of cases, this is also the hatching site for these birds. This partly agrees with the statement of Lincoln (1934:151) that "attachment to the breeding . . . [site] involves only adult birds." He felt that, generally speaking, the homing instinct is not strong until after a bird has nested, and that the first nest location is primarily a matter of chance.

Table 8

Yearlings Which Were Recaptured the First Two Years Following Banding

	Number	Per cent
Total recaptured	54	100
Returned to banding colony each time	32	59
Returned to previous nesting colony, if other than banding colony	11	20
Total nested at same colony each time	43	79
Nested in banding colony, then another colony	2	4
Nested in another colony, then banding colony	6	11
Captured in different colony each year	3	6

Thomas (1934:124), basing an opinion on his data from Starlings (*Sturnus vulgarus*), Stoner (1936:228; 1937:14; 1941:108), on the strength of his studies of Bank Swallows, and Chapman (1955:55), from his work on Tree Swallows, expressed essentially similar views. However, other investigators, such as Allen and Nice (1952:655) and Farner (1945:81 ff), do not feel that random dispersal of the young is necessarily true. They apparently felt that the small number of young that return to the hatching area is due primarily to the difference in mortality between young and adults. Farner (*op. cit.*) has presented a rather complete review of the controversy up to the date of his publication.

It is the opinion of the author that Lincoln and his supporters are probably most nearly correct in their evaluation of the situation, at least as far as Cliff Swallows are concerned. The young birds reported in the present investigation were banded only after they were old enough to fly from the nest after dark. Therefore, most of the relatively high mortality that usually occurs among nestlings of many altricial species already had occurred by the time these birds were banded. Admittedly, it is possible that among the young and adults released at night, there was greater mortality among the young. However, judging from the very small number of dead birds found around any of the colonies, it is believed that there was no appreciable difference in mortality due to this circumstance. Also, it is quite probable that more young birds than adults are lost on the migratory flights to and from the wintering area. Nevertheless, it is felt that the difference in percentage of returns of the two age classes presented in this study was due primarily to an actual difference in development of a homing instinct for a particular area and secondarily to a difference in mortality after the birds deserted the breeding sites.

The number of breeding birds present in the colonies under consideration did not change appreciably in the course of this investigation. Since approximately one-half of the adults fail to return, most of the remainder of the birds in a colony must consist of those hatched the previous year. It can be seen in table 6 that approximately 18 per cent of the adults go to other colonies the next year, but this is believed to be balanced by birds from other colonies moving into the one under consideration. Therefore, some of the newcomers captured could have been adults the year before and were moving from colonies that had not been trapped the previous year. Nevertheless, this still leaves approximately one-half of the colony to be composed of young birds. As it has been shown (table 6) that only 16 per cent of the young birds produced at a particular colony return to that colony the following year to nest, it requires the addition of a fairly large number of young produced in other colonies to bring the number of breeding birds back to the level of the previous year. This means, therefore, that a number of young birds must nest in colonies other than the one in which they hatched. Table 6 shows that approximately 43 per cent of the returning yearlings produced in one colony go to other colonies to nest.

It is felt that the dispersal of young is not necessarily random throughout the entire range of the species, but that it is random in the general area of the hatching site. As was stated earlier, nesting space is not at a premium in most of the colonies studied, so it seems unlikely that competition for space with older birds plays an important part in causing the young of this species to nest elsewhere.

Farner (1945:95) stated that "it seems possible in Robins that the tendency among adults is to return to the immediate locality of the previous breeding season whereas among first-year birds the tendency is one to return to the general vicinity of the birthplace." Probably a similar situation exists in Cliff Swallows.

Return of males versus females.—There is a statistically significant difference in the returns of males and females (table 9). More females than males are recaptured in succeeding years. This is not true for young birds returning to nest for the first time, however. It indicates the possibility of a different death rate in the sexes, similar to that found in other organisms, including man.

Table 9

Number of Years Birds Recaptured, Arranged by Age and Sex

	Number of years					
	1	2	3	4	5	Total number returns
Adults (number)						
Males	1184	309	59	26	2	2093
Females	1447	433	82	14	2	2625
Sex unknown	428	49	2	0	1	537
Total adults	3059	791	143	40	5	5255
Young (number)						
Males	80	27	7	2	0	163
Females	66	15	10	1	0	130
Sex unknown	52	3	1	0	0	61
Total young	198	45	18	3	0	354
All birds (number)						
Males	1264	336	66	28	2	2256
Females	1513	448	92	15	2	2755
Sex unknown	480	52	3	0	1	598
Total birds	3257	836	161	43	5	5609

Based on a sample of more than 4700 recaptures, it was found that female returnees are more apt to go to a different nesting colony the following year than are male returnees (table 10). The difference is statistically significant. However, this difference is not so pronounced in birds nesting for the first time. Although a much larger percentage of the younger age group go to a different colony, the difference between the sexes is not statistically significant. No reason can be given at this time to explain the sexual difference in returnees.

Table 10

Number of Birds Recaptured at a Different Site the Following Year, According to Age and Sex

	Number	Per cent that changed sites[1]
Adult		
Males	347	16
Females	542	21
Sex unknown	96	18
Total adults	985	19
Young		
Males	60	37
Females	55	42
Sex unknown	32	52
Total young	147	42
All birds		
Males	407	18
Females	597	22
Sex unknown	128	21
Total birds	1132	20

[1] See table 9 for total number of returns.

The greatest distance traveled between colonies in successive years by any returnee was about 40 airline miles. The greatest distance between hatching site and nesting colony for any yearling was approximately 48 airline miles.

Longevity and mortality.—Birds banded as adults were recaptured as long as five years after banding (tables 9, 11), but these were few in number. These birds would have a minimum age of 6 years at the time they were last captured. (This year four birds have been recaptured that are known to be at least 7 years old.) It appears, however, that a relatively small number of birds live more than 4 or 5 years. It is believed that no birds banded as young were recaptured this many years because relatively few young were marked in the early years of the study, and a rather small number of these marked birds returned (table 11).

It is possible that birds of both age groups, banded in 1949 and 1950, returned after the date shown in table 11. Unfortunately, relatively few colonies were trapped in those years, and it was impractical to return to these particular sites after 1953. Therefore, table 11 is somewhat misleading in this regard. However, the number of these individuals captured in 1953 indicates that very few, if any, would have been recaptured in 1954. Therefore, it is felt that the earlier statement concerning longevity is valid.

The data obtained from adult birds banded in 1951 (table 11) are probably most nearly accurate in determining the proportion of birds returning year after year, since these colonies have been trapped every year since that time. One can see that, of those

Table 11

Yearly Distribution of Returns Recaptured According to Age at Banding

Year banded	Number banded[1]	Year recaptured						
		1950	1951	1952	1953	1954	1955	1956
1949								
Adults	182	47	3	21	6			
Young	12	2	1	1	0			
1950								
Adults	316		10	107	28			
Young	134		3	7	5			
1951								
Adults	238			111	67	31	10	5
Young	102			4	3	0	0	0
1952								
Adults	6145				2339	702	125	64
Young	912				78	65	16	11
1953								
Adults	1476					561	135	72
Young	384					91	20	12
1954								
Adults	1201						351	194
Young	0						0	0
1955								
Adults	554							286
Young	86							18

[1] Number banded at colonies that were retrapped the following year (see table 1 for total number banded each year).

present one year, approximately one-half return the following year. It appears, therefore, that a rather high mortality occurs among adults as well as young.

Injured birds.—A number of previously injured birds have been found in the course of this study, but in most cases their activities did not seem to be unduly impaired by their physical disabilities. For example, birds were captured that were missing toes and even, in some cases, a leg. Nevertheless, judging from the healed condition of the wounds, these birds had been competing successfully with other members of the species for some time. Several were recaptured in subsequent years. As these birds spend little time on the ground, the loss of toes or a leg would not seem to be as serious in this species as in birds that depended upon their legs for digging, walking, and capturing prey.

One female was banded that had the outer layer of bone missing over most of the cranium. The damage apparently had happened much earlier because there was old scar tissue around the entire edge of the opening. The injury evidently caused the bird little trouble, however, since it was recaptured the following year.

SUMMARY

Over an eight-year period, 18,004 Cliff Swallows were banded, and 9108 recaptures were made in 71 colonies. The majority of these birds were caught in three areas of California, but one area in Nevada was sampled. A technique was developed, using artificial nests, to gain additional observational information. Incubation patches were found useful in determining the sex of live adults during a portion of the breeding cycle.

In the interior valleys of northern and central California, most of the birds nest

under culverts and bridges. However, buildings are used primarily for nesting sites in southern California.

The time of spring arrival varies greatly from year to year at a given colony. In general, the birds usually arrive between late February and the end of March. An attempt has been made in this paper to show that the time of arrival probably is correlated with temperature and the dietary habits of the birds. There is also variation in time of arrival between colonies in the same year, for which no explanation is available at this time.

Some birds appear to be paired upon arrival at the nesting sites; others become paired almost immediately. New pairs apparently are formed each year.

The pairing bond may not be as strong in Cliff Swallows as in some other species. A condition called vagrancy is described, in which potential breeders have been found to change colonies in the middle of the breeding season. A greater number of females have been recaptured as vagrants, and this result is statistically significant. It is possible that some of the movement between colonies may be due to the disturbance caused by night banding operations. However, it is felt that this plays a relatively minor part, since some birds have been caught as many as 10 times over a five-year period without causing them to desert the original colony. In addition, several homing experiments have shown that many of the transplanted birds have a strong attachment to a particular nesting site. Also, previously uncaptured adults are caught each time a colony is trapped in the course of a season, indicating probable movement from untrapped colonies.

Although nests built in previous years are often repaired and used, individuals do not tend to use the same nests each year. It has been found that the birds do not spend the night in the nesting colonies until nests are almost complete. The intermittent use of nesting sites has been noted.

A review of species reported to use Cliff Swallow nests, Cliff Swallows found using the nests of other species, and species seen nesting with Cliff Swallows is included with additional data obtained in the present investigation.

There is considerable variation in the time eggs are laid, both within a colony, and between colonies. Three to four eggs seems to be the normal clutch in this area; the eggs are laid on consecutive days until the clutch is completed. The observed incubation period, from the laying of the last egg to the hatching of the last egg, is 16 days. Nest temperatures at night remain rather constant, even without adults being present in the nest. Night trapping operations did not seem to produce any additional mortality in eggs or in very young nestlings. The young birds are brooded at night in the early stages of nestling life, but they are left to themselves at night near the end of this period. Young birds usually fly about 23 days after hatching.

Based on the length of time required to raise one brood, and the length of time adults remain in the nesting colonies, it is thought that only one brood is produced each year by the great majority of birds in this region. Most nesting colonies are empty by July 1, and all birds are gone from these sites by July 15. However, nearly all the birds remain in the general area for some time after they have deserted the nesting sites.

When birds return the following spring, evidence indicates that adults which have nested in a given colony arrive first. They are followed by previously uncaptured adults and young produced the preceding year. A much larger number of "returnees" than "yearlings" return to the original colony the year following banding. Although there is some shifting between colonies in both age groups, birds that once have nested at a particular colony appear to have a stronger desire to return to that colony than do young birds that were hatched there. When birds return to nest the second year after hatching, they tend to return to the previous nesting site.

More females banded as adults return in succeeding years than males. This does not

appear to be true for young birds returning to nest for the first time. Among adults that return, there is a significantly higher percentage of females that go to other nesting sites in the area. This sexual difference is not so pronounced in birds hatched the preceding year.

Some birds are known to have lived for at least 7 years, but few are believed to live more than 4 or 5 years. The annual mortality among adults seems to be about 50 per cent. No estimate of mortality among young birds is available at present.

Some types of injuries apparently do not result in death of the injured birds.

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