

CLUTCH SIZE AND LAYING DATES IN CLIFF SWALLOW COLONIES

By M. T. MYRES

This is the first analysis of data recorded on British Columbia Nest Record Cards (Myres, Cowan, and Udvardy, Condor, 59, 1957:308). It concerns 79 nests of the Cliff Swallow (*Petrochelidon pyrrhonota*) which I studied in 1955 and 1956 at two colonies at the Sorensen Ranch, 12 miles southwest of Williams Lake in the Cariboo District of British Columbia. In addition, Dr. Arnold J. Petersen of St. Olaf College, Northfield, Minnesota, has kindly allowed me to use data collected by him in 1949 on 44 nests in a colony at Moran, Wyoming (colony B of Emlen, Condor, 54, 1952:177-199).

METHODS

The methods of analysis of the data provided on the nest record cards are those described by Myres and Snow (Bird Study, 2, 1955:2-24, 72-84, 169-178). Precise dates of the laying of the first egg in each clutch are either entirely accurate, or are correct at least to within two or three days. Either these clutches were studied while they were still being laid, or the date on which the first egg had been laid was calculated from the date of hatching, or from finding young in the nest and estimating their age. The incubation period has been taken as 14 days, although 13 days may be more accurate. The nestling period may last as long as 28 days. A few more broadly estimated first-egg dates are employed in addition in figure 2.

Myres and Snow (*op. cit.*) also discussed the question of accuracy of determinations of full clutch size. When the swallow nest was watched throughout the laying period, full clutch size was accurately determined. When a clutch was found seemingly complete, it had to be observed unchanged on two different days for full clutch size to be established. When only a single observation was made before hatching, full clutch size was established if there were not more than 13 days between the first visit and the day of hatching.

ACKNOWLEDGMENTS

I am grateful to Messrs. George Tucker, Clark Tucker, and Ward Herrick, who were living at the ranch in 1955 and 1956; they, and especially their wives, put up with considerable inconvenience until my observations were completed. I am especially indebted to Arnold J. Petersen for allowing me to publish with my own data the observations on clutch size which he made in Wyoming in 1949. I want to thank M. D. F. Udvardy and Robert B. Weeden for help in the preparation of this paper. C. S. Holling and Nancy McAllister contributed ideas, and the latter helped me in the field.

PROGRESS OF NEST BUILDING

The first colony studied (1955) was on the ranch house itself, under the eaves. The house is square with a roof that slopes to each side from a high point in the center. The nests were set against beams, under two feet of overlap by the roof. They were only 10 feet from the ground and could be reached with a short stepladder.

I am informed that up to 1952 the nests built by the Cliff Swallows here were more or less regularly knocked down. However, in 1953 and 1954, this was not done. Thus, in 1955, the central part of the colony on the east side was still intact when the birds returned. The nests were concentrated there, and most of the new nests were built on the north wall. On June 1, 1955, only five of the 18 nests eventually present on the north wall were completed. On the east side however 15 of the 35 nests which eventually had clutches were completed and a further three already had eggs. The south side had one

nest, the west none. Table 1 shows the state of completion of each nest by June 1 and clearly indicates the more advanced stage of nest preparation on the east wall.

The problem here is what determined the choice, in the first place, of the east side of the ranch for the initiation of a colony. M. D. F. Udvardy tells me that in Hungary he conducted some experiments on the positioning of nest boxes and found that those facing southeast were the first to warm up in the early morning, since they were the first to be flooded with direct sunshine. In June, on fine days, the sun rises high enough in the sky to keep the ranch house bathed all day in sunshine except in the late afternoon or evening. After the early morning, when nests on the east side of the house would receive direct sunlight, no nest would be thus lighted, since they are in the shadow of the eaves. Emlen (Auk, 71, 1954:16-35) shows that an essential feature of the nesting site of this species is that there be an overhang above the nest. This would be necessary if the mud

Table 1
Comparison of Stages of Nests According to Exposure on June 1, 1955

| | Total | Not yet begun | ¼ built | ½ built | ¾ built | Finished | Lined | Eggs |
|------------|-------|---------------|---------|---------|---------|----------|-------|------|
| East wall | 35 | | 2 | 1 | 14 | 10 | 5 | 3 |
| North wall | 18 | 2 | 4 | 3 | 4 | 5 | | |

nests were not to be washed away during summer thunder-storms. In the Cariboo District much the most common nesting site is at the apex of the roof inside barns or hay-lofts. However, I have seen a natural, cliff-nesting site at Leighton Lake utilized by swallows where the nests would not be protected from rain driving from the north.

The possible factors involved in the distribution of nests on the ranch house are at least three: (a) Early morning warming of the nests on the east wall, facing the rising sun. Emlen (1954, *op. cit.*) writes that "the first period [of nest construction] each day was often the major one and generally started an hour or two after the sun had risen. During the rest of the day mud packing was intermittent and irregular." (b) Greater coolness on the north side and on the east side of the house after midday. In June temperatures on a fine day reach their maximum about mid-afternoon. East wall nests would be in shade. Under the eaves of the south and west sides, the microclimate would be exceedingly warm, and it may be for this reason that nests were not found there. However, other south-facing sites have been seen with nests. (c) Direction of flight from the mud source, which was located to the northeast of the ranch building. Young birds bringing mud to the ranch for the first time would arrive directed toward the north or the east wall. Finding no available space on the east wall, young birds would now find available space on the north wall. Emlen (1954, *op. cit.*) states that the male seems to select a site where he is visited by other birds. Before a state of mutual toleration with a female has been completely established, the male is already carrying mud pellets to the site, but the female soon joins in the same activity. Thus, males may arrive with mud at the colony before the pair-bond has been completely formed.

Whatever the reason for two-thirds of the nests being on the east side of the Sorensen Ranch, this was the older part of the colony, and more of the nests on the north side were begun from scratch in 1955.

CLUTCH SIZE

Ranch colony, 1955.—This was an ideal colony for study, for unlike colonies in hay-barns, the nests were easy to reach. Inspection was made by breaking away a little of the mud funnel of the nest until a hand could be inserted and the eggs or young counted with the tips of the fingers. As it was desirable not to disturb the birds too much, a small-

handed observer was an advantage; accordingly Mrs. Nancy McAllister made most of the actual counts for me on this colony. The birds repaired the funnels of the nests, within 24 hours, and no delay in the laying of the eggs was noticed. One egg was laid daily in most instances. Losses of eggs or young through disturbance are thought to have been minimal in 1955. Since we began inspections on the ranch colony while the birds were still building, we know the exact date on which the first egg was laid in all but two of the 54 nests for which we have knowledge of the full clutch size.

As mentioned, the construction of new nests was more frequent on the north side of the ranch (table 1). Partly for this reason clutches there were started later than on the east side. Analysis of clutch size (table 2) showed that only one of seven clutches that

Table 2
Distribution of Clutches of Three and Five Eggs in Relation to Number of Nests on Each Wall at the Ranch Colony in 1955*

| Clutch size | Wall | Number of nests with clutches as indicated | Total number of nests on walls | Per cent |
|-------------|-------|--|--------------------------------|----------|
| 5 | North | 1 | 18 | 6 |
| | East | 6 | 35 | 18 |
| 3 | North | 6 | 18 | 33 |
| | East | 9 | 35 | 23 |

* Differences shown here not statistically significant.

had five eggs was situated on the north side and that there were more clutches of three eggs on the north side. In terms of the total number of nests on each wall, the proportion of clutches of five eggs on the east wall was 12 per cent higher, and the percentage of clutches of three eggs on the north wall was 10 per cent higher. Average clutch size was lower on the north wall (3.6) than on the east wall (3.9). This difference is not significant statistically, but it may still be a biologically meaningful one.

It seems likely that there was some common factor acting toward late laying and low clutch size on the north side. Either this factor was differing microclimate or, more likely, nest building was being carried out by birds surplus to the colony of the year before and comprised of individuals breeding for the first time. Emlen (1952, *op. cit.*) states that "the position of a nest in a colony was correlated with the stage of the reproductive cycle of its owner. Twenty of the 32 nests classified as belonging to the late hatching group . . . were peripherally located while 86 of the 98 assigned to the early group were situated well back under the overhang . . . as in Darling's gulls . . . , the first birds tended to select central sites while later arrivals built peripherally . . . Centrally located nests may be more sheltered against winter damage and consequently in better condition for reoccupancy by dominant or aggressive birds . . ."

The sequence of laying of the various clutches on the two walls is given in figure 1. It shows that the c/5's were all started before June 7 and that all but one of the 15 c/3's were begun on June 7 or later. In figure 2 the main part of the laying period is broken up into three-day periods, and the numbers of each clutch size laid in each period are compared as percentages of the total for each three-day interval. This is done for the Ranch colony (1955), the Barn colony (1956), and Colony B at Moran, Wyoming (1949). It shows quite clearly that in the colonies as a whole there was during the laying period a complete switch from the laying of clutches of five eggs to the laying of clutches of four or three eggs. In the first three days of the laying period at the ranch in 1955

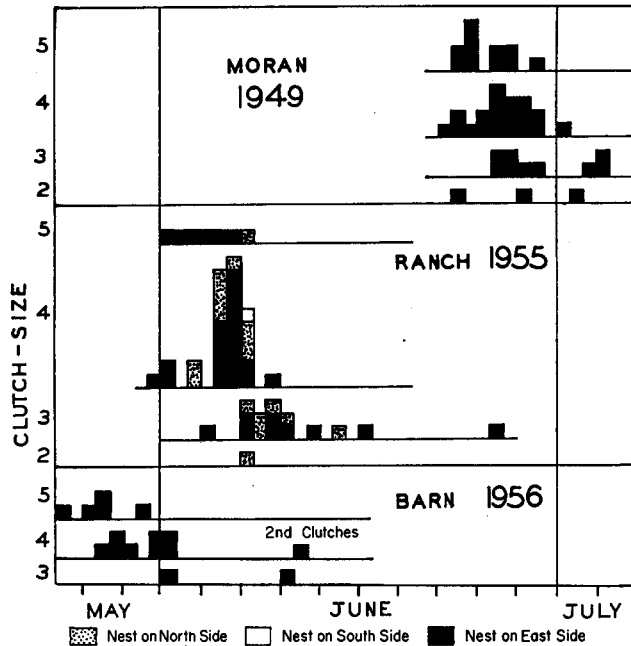


Fig. 1. Dates of laying of first egg in each clutch at three colonies of Cliff Swallows. Height of each small square represents one clutch and width represents one day. Variable shading applies to colony at Ranch in 1955 only.

(June 1–3) birds started to lay clutches of five and four nearly in the proportion of 1:1 (the actual figures on the graphs are the result merely of the selection of June 1 as the starting date for the first three-day period). A week later the likelihood of finding a newly laid clutch of c/3 is as great as that of finding a fresh clutch of c/4. In figure 1 it can be seen that the peak of c/3 layings lies 3 to 4 days after that of the c/4 layings.

The most remarkable finding is that all the birds in the colony laid their eggs in an extremely short period. In the case of the ranch group, 21 of the 54 clutches were begun on June 5 and 6 (fig. 1) and 32 of the 54 clutches were begun between June 5 and 7. As many as 50 clutches were begun within the twelve days between June 1 and June 12. The four late clutches were all of three eggs.

Barn colony, 1956.—The ranch colony was no longer available in 1956 because the nests had been destroyed and the beams greased to prevent rebuilding. Instead I studied a colony of 35 nests in the apex of the nearby hay-loft. First clutches were begun on May 24 and May 26 (fig. 1) and laying was complete by June 1, except for two second clutches in nests that lost their eggs. In this year breeding began earlier than in 1955. Only six clutches were studied while laying was still in progress, but 10 other clutches are precisely dated since hatching dates were carefully observed. Two of these were the replacement clutches mentioned earlier. Figure 1 includes only these 16 clutches, but in figure 2 nine additional clutches have been included.

The proportion of c/3's is considerably less than in the ranch colony the year before (4 per cent of the total as against 26 per cent; see table 3). This smaller number of c/3's was balanced by a higher proportion of c/5's (40 per cent as against 14 per cent). The proportion of c/4's did not change appreciably. Laying took place over a nine-day period only, excluding replacement clutches.

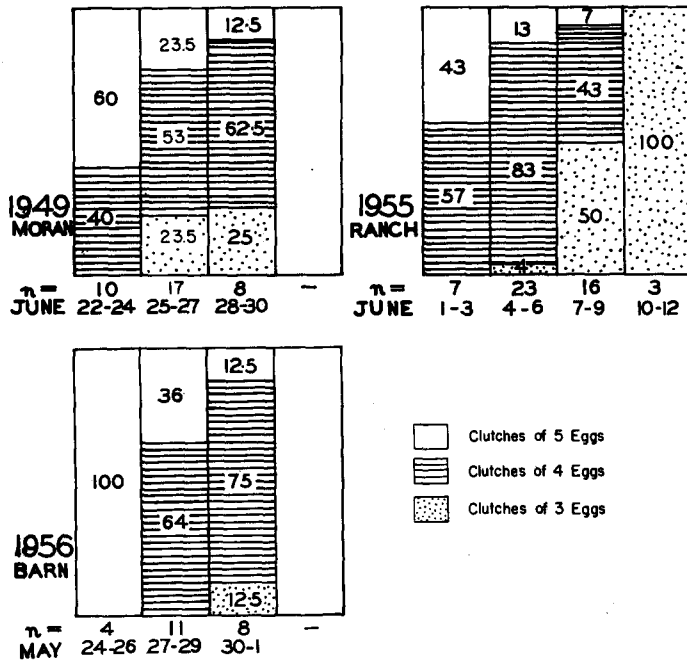


Fig. 2. Percentages of different clutch sizes during the main part of the laying season grouped in three-day periods. Clutches of two eggs omitted; n = number of clutches in each period. The trend in clutch size is statistically significant at $P < .01$ for the Ranch colony in 1955, and at $P < .05$ in the Barn colony in 1956.

Table 3
Percentage of each Clutch Size in the Main Laying Periods of 1955 and 1956

| Clutch size | 1955 (Ranch) June 1-12 | 1956 (Barn) May 24-June 1 |
|-------------|---------------------------|------------------------------|
| 5 | 14 | 40 |
| 4 | 60 | 56 |
| 3 (and 2) | 26 | 4 |
| | 100 | 100 |
| Total nests | 50 | 23 |

Colony B at Moran, Wyoming, 1949.—The nests at this colony which were under a culvert were found to be a subsidiary of the much larger Colony A, which had 118 nests and was situated under a bridge nearby. The nests in Colony B were all built anew in 1949. It will be noticed that the season was a late one, by the standards of the Cariboo area, which is exactly eight degrees latitude farther north (about 550 miles) and at 3000 feet elevation instead of 6500 feet. In the Cariboo area snow melts by early May, but at Moran it lasts until June 1 and thus as table 1 of Emlen (1952, *op. cit.*) indicates it was a usual time for laying at Moran. Although it was a late June-early July laying colony, it did not have a lower than average mean clutch size, and figure 2 indicates exactly the same progressive trend in clutches laid from c/5's to c/3's as was found in British Columbia. In this respect it lies midway between the two British Columbian seasons of 1955 and 1956.

DISCUSSION

One possible reason for the low number of c/5's in the ranch colony is that the weather in the week preceding laying in 1955 was extremely cold and wet. However, the main reason for the trend in the size of clutches laid is believed to be that birds breeding for the first time do so late and lay smaller clutches than older birds. Thus, the mean clutch size will, in any one year, be a reflection of the age-structure of the colony. A banding program at a number of colonies is greatly to be desired to prove this point.

SUMMARY

Two medium-sized colonies of the Cliff Swallow were studied in the Cariboo District of British Columbia in 1955 and 1956. Data were gathered on 54 nests at the first in 1955 and on 35 nests at the second in 1956. Data on 44 nests of one colony at Moran, Wyoming, in 1949 have been added to this analysis.

At the first colony, nests were confined to the east and north walls of a low ranch house. There were more newly built nests on the north side. Factors in the selection of nesting sites are discussed.

Clutches of three eggs were more frequent on the north side of this house than on the east side. Clutches of five were concentrated on the east side. Laying is highly synchronised within any one colony. The first clutches begun are of five or four eggs, but a few days later there is a considerable number of threes. This significant trend was found in all three colonies.

Although proof from banded birds is still unavailable, it is believed that a greater number of birds breeding for the first time were doing so on the north side of the ranch, that such birds have to build nests completely anew, and that they lay most of the clutches of three eggs.

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