EXTRA-PARENTAL COOPERATION IN THE NESTING OF CHIMNEY SWIFTS

BY RALPH W. DEXTER

Over a period of years, the interrelationships of individuals in a nesting colony of Chimney Swifts (*Chaetura pelagica*) are closely knit. In an effort to understand these relationships, I have carried on banding and life history studies of the breeding colony of this species inhabiting the campus of Kent State University in northeastern Ohio since 1944. The general methods, objectives, and some of the results of this study have already been published (Dexter, 1950a, 1950b, 1951, 1952).

The present paper is concerned with observations on nesting procedure in which one or two additional birds joined the parents for the nesting season. These visitors live in harmony with the family throughout the nesting period and share in the responsibilities of nesting. A few instances of such behavior have been mentioned previously in connection with life history studies of certain individuals (Dexter, 1951, 1952). The only other known references to such observations are two brief reports. Day (1899) wrote that (after hatching occurred in a nest she had under observation), "From this time forth a third Swift was seen to enter into the care of the nestlings, taking its turn at brooding and feeding." Sherman (1924:87) described the relationship, "Gentle and devoted to one another, they show similar amiability and courtesy to the adult stranger that comes into their home to share the work of feeding and brooding their young." She called the visiting bird a "nurse maid." Extra-parental coöperation in three other species of birds has been described by Skutch (1935).

In the preparation of this report, the assistance and encouragement of Mrs. Margaret M. Nice has been valuable.

During eight years of observations, I studied 22 threesomes and six foursomes. Ordinarily, only one pair of swifts occupies any one of the 88 air shafts available to the birds of this colony. Each year there has been an average of 13 pairs, the majority of them (91 per cent, on the average) having returned from past years' residence. There has been an average of three threesomes and one foursome each year. Altogether a total of 40 swifts (38 per cent of the breeding birds) have been involved in a threesome arrangement. Of these, two were involved five times, two others four times, five three times, and three involved twice. Eighteen swifts have lived in a foursome, one of them three times and four of them twice. Nine birds have been at one time or another in both a threesome and a foursome. Seven of these nine have been in multiple cases of one or the other. Not only is there

| | 1944 | 1945 | 1946 | 1947 | 1948 | 1949 | 1950 | 1951 |
|------------------------|------------------|----------------------------|-------------------|----------------------------|----------------------------|---------------------|---------------------|----------------|
| No. of pairs in colony | 13 | 11 | 11 | 17 | 14 | 14 | 13 | 12 |
| No. of threesomes | 2 | 2 | 5 | 1 | 3 | 4 | 2 | ŝ |
| No. of foursomes | 0 | 1 | 1 | 2 | 1 | 1 | 0 | 0 |
| Sex of threesomes | \$ \$ ¢ | & 4 4 | € ¢ ¢ † | \$ \$ \$ | \$ \$ \$ \$ | € \$ \$ \$ | ¢ ¢ ¢ ¢ ¢ † ` | €0 €0 0+ |
| and foursomes | € 5 5 5 | や さ さ | \$ 5 5 5 | 4 6 6 9 9 9 | €0 €0 0‡ | - \$ \$ \$ | 4 8 9 9 | ; |
| | | 4 3 3 3 3 3 | 9 3 3 ? | ¢ \$ \$ \$ | \$ \$ \$ | - \$ \$ \$ | ¢ \$ \$ | ; % ¢ |
| | | | | | 4 4 4 3 3 3 | 4 4 3 3 | €0 0+ 0+ | |
| | | | | | | 5 \$ \$ 5 t | ₽ \$ \$ | |
| Shafts of threesomes | D1; D4 | D1; D4 | D1; D4 | N9 | A1; Q2 | D1; P3 | D1; E1 | El; Sl |
| | | | | | 16 | 12; 21 | 02 Q2 | ۲۸ |
| Shafts of foursomes | | IH | HI | Q1; Q2 | P3 | El | | |

EXTRA-PARENTAL COMBINATIONS OF NESTING CHIMNEY SWIFTS

TABLE 1

THE WILSON BULLETIN

Ralph W. Dexter

a tendency on the part of certain individuals to participate in such a social organization, but they repeatedly choose the same air shafts for their coöperative nesting. One shaft has been thus occupied five times and another one four times. Three have been used three times and two twice. A total of thirteen shafts have been used. Males seem to be more inclined than females to take part in such behavior although both sexes participate. Since sex identification depends upon the dissection of dead birds and the indirect evidence of mating combinations, the sex of all individuals in the colony has not yet been determined. Fortunately, the sex of several key birds has been obtained through dissection, and one female was discovered which laid an egg after being abandoned by her mate (Dexter, 1950b). Knowing these facts, I could ascertain the sex of many individuals; 12 threesomes contained an extra male and five had an extra female. Five cases remain unsettled. Three of the foursomes had two extra males while the other contained one extra male and one of unknown sex. The data are summarized in Table 1.

I thought at first that the extra birds residing with the mated pairs were either immature or too old for breeding. There is evidence, however, that Chimney Swifts can breed in their first year, and some of the multiple combinations remain intact for two consecutive years. Also, I have known combinations to dissolve after a year or two and all individuals take part in active breeding with one mate. Some, but not all, combinations are the result of the attachment of a yearling or an old bird in its last year of life to a mated pair.

Generally during the early stages of the nesting season mated birds of a pair roost for the night side by side on the wall of the air shaft; the extra bird roosts a few inches away or on an adjacent wall, but usually at the same level. After the nest has been completed, one bird may roost on the nest and two just below it, or two on the nest and one either below or beside it. Occasionally all three will roost side by side below the nest, especially just before the clutch of eggs is completed during which time the eggs are seldom incubated. After the nesting season is over and the juveniles have left, a threesome or foursome will sometimes remain roosting together nightly in the same shaft. At times all three or four will roost side by side. The mated pairs do not remain together any longer or in greater frequency than the multiple groups once the juveniles have left the home shaft. The combinations of three and four birds for nesting seem to be an agreeable arrangement, and all apparently assist with incubation of the eggs and care of the young. The histories of certain combinations follow. Observations were made with a flashlight at night and a mirror during the daytime. The birds were trapped for banding in the standard traps used for Chimney Swifts.

In 1944, a female (42-196912) nested with two birds of undetermined sex in shaft D1. The following year the female returned to the same place, but in the absence of the other two she nested with a young male (42-196934) which I had banded as a fledgling the previous year. They were joined by a female (42-196915) which had nested the previous year in shaft J1. In 1946, nos. 12 and 34 returned again to nest in D1 where they were joined by a male (42-184486). The latter was probably the functional male since no. 34 left the group before nesting was completed.

Late in September, 1946, when many of the swifts had already left the campus, no. 12 was recaptured from D1. She was roosting at that time, not with her mate of that year, but with the female visitor of the previous year (no. 15). No. 15 did not nest on the campus in 1946, and the mate of no. 12 that year was roosting alone in shaft D3 nearby. Nos. 12 and 86 nested together in D1 in 1947 and 1948. They had no regular visitor although in 1948 a yearling from the brood of 1947 (possibly an offspring of this pair) visited them briefly at the time nest-building began. In the spring of 1949, nos. 12 and 86 continued to nest in D1, but were joined by an all-season visiting male (42-188589). The following year all three returned to D1 and nested together again. Soon no. 12, the female, disappeared, and no. 89 deserted the other male and the four eggs on the nest, moved to shaft A1, and mated with the female there. After one week, the unattended eggs were destroyed. The remaining male, no. 86, then brought in a new mate (48-164508) who within a week laid a second clutch of eggs in the original nest. In 1951, this pair remained mated in D1 without visitors until after nesting was completed.

After having left the pair in D1 in 1946, no. 34 returned the next year to mate with no. 42-196984 in shaft S1. In 1948 these two returned there to nest again and were joined by a male (42-188552) for the season. The following year this latter male mated with a female in R1. Although nos. 34 and 84 were left to nest in S1 by themselves, he visited them briefly both before and after an unsuccessful attempt at nest building in R1.

When no. 89 parted from the other two birds inhabiting D1 in 1950, he completed nesting in shaft A1 with the female which had nested in that same place for the three preceding years. He returned the following year to shaft S1 where another threesome developed. This time he was mated with a female (42-196959) whose mate of the previous year (no. 52) did not return. The new pair was visited regularly by one swift and occasionally by several others throughout the nesting season.

After mating together in shaft H1 during the season of 1944, the female (42-196927) and the male (42-196928) returned to the same shaft the following year, but this time they were joined by two males (42-196941; 42-184425) that resided with them. No. 41 (captured as a juvenile the preceding year)

Ralph W. Dexter

is a possible offspring of nos. 27 and 28. In 1946 the original pair and this male (no. 41) returned together for another nesting season, while the second visitor (no. 25) moved into shaft G4 to nest with a female whose mate of the past two years did not return. No. 25 was replaced by another swift; thus, for the second consecutive year four birds nested together in shaft H1. In later years no. 41 nested with a single mate in G4 for three seasons. In the fourth and last year (1950) of the nesting of no. 41 and his mate in G4, another swift spent the season with them. The functional female that year was no. 42-196907; this female had been in another threesome in 1944, 1945, and 1946.

In 1947 no. 27 nested with three males (42.196995; 42.188523; -24) in shaft Q1. This group scattered the following year, but three of them continued to live in other groups of three and four birds. No. 27 joined two males in Q2; nos. 95 and 23 joined the pair which had nested during the preceding year in P3 and which continued to nest there in 1948. The female of that pair (42.196910) returned in 1949 with males 95 and 23, her former mate having disappeared, and they continued as a threesome. In 1950, however, no. 23 soon left the other two and made an unsuccessful attempt to nest in R2. The other two remained as mates in P3 for that year and had no visitor.

Female no. 42-196909 nested in shaft E1 for six consecutive years (1944-49). During that time her mate was no. 42-196921 each year except 1945, and each year she nested with a single bird until 1949. In 1949, two other swifts, one of them a male (42-188588), joined the pair in E1 for the season when their nest was about three-fourths completed. In 1950, male no. 21 returned to the same shaft but with a new mate (42-188595), a visitor in El at the end of the previous nesting season. In addition to the new female mate, male no. 88 returned as a regular visitor again. Soon after nesting was underway, no. 88 left the group to replace a male (42-188655) which had died in shaft G3. No. 88 then mated with the female there; together they constructed a nest ten days following the new union (see Dexter, 1951). In 1951, no. 21 and his new mate again nested in E1 with an occasional male visitor, but this time with a different male--no. 48-164570. This visitor did not stay consistently in E1, and once I found soot in the band, indicating that some nights he had roosted in a chimney. This bird was removed for experimental purposes before the end of the season and died, apparently from fright, in a respirometer.

In addition to the observations of threesome and foursome combinations described and tabulated here, there were a number of instances discovered in which a visitor joined a pair for a brief time but soon left to nest with a mate of its own or to roost elsewhere. Some of these visitors apparently left the campus colony.

There were seven cases discovered where an extra swift roosted with a pair over varying lengths of time before nesting began. For example, the same pair residing in E1 was visited by an individual for one evening two weeks before nest construction began in 1946. This bird was not found again until the fall migration of 1947, when it again roosted in E1 with five other swifts, including the breeding male of E1. I never again saw the visitor in question.

The pair which nested in shaft M7 in 1946 had a different visitor roost with them on two occasions during the month preceding nest construction. These two visitors, one a female (42-196902) and one a male (42-196954), later mated with each other in shaft N9. The male had previously nested in that shaft for two years and continued to do so for another three years, but only in 1946 was he mated with no. 02. In 1947, he and his new mate had an all-season visitor. In 1948, this pair nested by themselves.

A pair which nested in A1 (42-196987; 42-188656) for three years had two visitors in 1948. One on May 20, just three days before the nest foundation was built, was a male (42-188540) which failed to mate that season but returned to nest in following years and formed a threesome in 1950 in shaft M7, as mentioned earlier. The other visitor, also a male (42-188546), joined the pair during egg-laying and remained for the balance of the season. The next year, 1949, this male nested in shaft A5, not far from the pair it resided with in 1948. Just before nos. 87 and 56 nested in A1 in 1949, they had for a brief time a male visitor (42-188655) which had nested in the colony for two years and which soon left to nest again with its own mate.

There is a possibility that some of the early visitors mentioned above might have remained with the mated birds throughout the season if they had not been disturbed by trapping and handling. Mated birds are fairly tolerant of trapping, but unmated individuals sometimes leave if they are disturbed too much. Further, on some occasions when a bird left a threesome or foursome group, it did so to obtain a mate and establish its own nest. It would appear that some visitors are simply waiting for an opportunity to secure a mate of their own. Mrs. Margaret Nice has suggested to me that multiple nesting in this colony may be the result of a shortage of females; my data do not permit a conclusive answer to this possibility.

SUMMARY

1. During eight years of observations on the nesting behavior of Chimney Swifts living in a colony on the campus of Kent State University, I found 22 Ralph W. Dexter

cases where three birds nested together and six cases where four birds nested together.

2. Certain individuals were often involved in, and seemed to prefer, threesome and foursome combinations. Of 40 individuals which participated in threesomes, 12 were involved more than once. Of 18 participating in foursomes, five were involved more than once. Nine birds have been part of both a threesome and a foursome at one time or another.

3. Thirteen air shafts have been used by these combinations; eight of them have been used more than once.

4. Males seem to be involved more often than females in extra-parental coöperation. Twelve threesomes had an extra male, five had an extra female, and five remain with sex undetermined. Three foursomes had two extra males and three others had one extra male and one of unknown sex.

5. Some of the visitors are known to be birds in their first year and some are old birds in, apparently, their last year, but many are intermediate in age and engage in active reproduction in later years.

6. The parents and visitors often remain as a unit throughout the nesting season and share the work of incubation, brooding, and feeding of the nestlings.

7. Seven cases of brief visits by an additional bird just before nesting began were discovered. Some of these might have developed into continuing threesomes if they had not been disturbed by trapping, but in other cases the birds left after finding mates of their own. Probably some visitors are just waiting for an opportunity to obtain a mate.

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