COLONIAL BREEDING IN THE BARN SWALLOW (*HIRUNDO RUSTICA*) AND ITS ADAPTIVE SIGNIFICANCE

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Social patterns in the swallow family (Hirundinidae) involve varying degrees of gregariousness during the breeding season. Some species, such as the Bank Swallow (*Riparia riparia*) and the Cliff Swallow (*Petrochelidon pyrrhonota*), breed in dense colonies of up to several hundred pairs. Other species, like the Tree Swallow (*Iridoprocne bicolor*) and the Rough-winged Swallow (*Stelgidopteryx ruficollis*), are solitary breeders. A third pattern of social behavior is that of breeding in small colonies of variable size. The Barn Swallow (*Hirundo rustica*) is such a species, found nesting alone and in aggregations of 2 to 40 or more pairs (Bent 1942).

This diversity of social breeding habits is the result of adaptation to a number of environmental pressures (Crook 1965). These pressures may involve habitat and food type, dispersion of food supplies, and availability and nature of nest sites. The latter is particularly important in elucidating the contrasting types of protection offered against predation, including both inaccessibility and crypticity of nest sites.

Mayr and Bond (1943) pointed out that the development of coloniality in the swallow family paralleled the development of the ability to build nests. Burrow-excavators of the genus *Riparia* and mud-nest builders of the genus *Petrochelidon* often breed in large colonies. On the other hand, the genera that utilize naturally-occurring cavities for nest sites, e.g., *Iridoprocne* and *Stelgidopteryx*, breed in a dispersed fashion, perhaps because of the erratic distribution of such cavities.

Why has coloniality developed in nest-building genera? At least 4 factors, singly or in combination, could have contributed to the evolution of colonial breeding habits: reduction in loss to predators, increased foraging efficiency, increased reproductive success through social stimultation, and increased utilization of available nest sites. In order to understand the phenomenon of coloniality in swallows and in Barn Swallows in particular, I undertook three analyses. First, I sought to determine how each of the 4 factors mentioned above varies with Barn Swallow colony size, utilizing data concerned with growth and survival of young and responses to predators and food supply. Second, I investigated

whether active interactions among the breeding pairs allow the development of a Barn Swallow colony, or whether such aggregations are the result of a passive congregation at a nesting site. The presence or absence of such interactions may be inferred from an examination of the variation in within-colony breeding synchrony and occurrence of second-brooding, as well as by direct observations of the social behavior involved in predator defense, foraging, and nest site selection. Last, I attempted to relate the observations for Barn Swallows to those for other swallow species in order to explain the rise of coloniality in the family as a whole.

METHODS

I conducted the present investigation in Tompkins County, New York during the breeding seasons of 1970 and 1971. The study included 34 colonies (table 1), most of them in barns or sheds. In all but one case the barns were abandoned. No persistent local insect populations could arise due to the presence of domestic animals, and all foraging had to take place away from the nest sites themselves.

The colonies ranged in number from 1 to 30 nests, and I arbitrarily distinguished 5 size categories: a) single: one pair, b) small: 2–5 pairs, c) medium: 6–9 pairs, d) large: 10–13 pairs, e) x-large: more than 13 pairs, in this study 17–30 pairs.

I visited all colonies 2 or 3 times per week, from mid-May to late August. I recorded date of hatch, clutch size, brood size, and number of fledglings for both first and second broods. I weighed nestlings with a 30-gram Pesola (Ruti-Zurich, Switzerland) spring balance (± 0.25 g) 3 times per week, from the first or second day after hatching in 1970 and from the 8th or 9th day in 1971 (day of hatching is defined here as day 1). As a rule, I did not weigh nestlings after the 16th day, since they were quite restless and often fledged prematurely.

Variances within and among colony sizes with respect to all data collected usually were not homogeneous and did not allow the use of parametric statistics. Therefore, I used nonparametric tests for most analyses. The Kruskal-Wallis test provided a method for comparing colony size means where ranking was possible. The Spearman rank correlation (r_s) test indicated the degree of correlation between two covarying variables. In cases where ranking was impractical, I used binomial and multinomial chi-square statistics.

RESULTS

SEASONAL REPRODUCTIVE OUTPUT

Some measure of the relative fitness of pairs breeding in colonies of different sizes is needed

TABLE 1. Distribution of Barn Swallow colony sizes studied in Tompkins County, New York, in 1970 and 1971.

Year	Single	Small	Me-dium	Large	X-Large	Total
1970	6	3	3	3	1	16
1971						
Undisturbed	12	6	4	3	3	28
Experimental[a]				1	2	3
1970 & 1971[b]	4	3	2	3	1	13
Total	18	9	7	7	6	47

[a] Data from experimental colonies are considered only in analysis of timing of reproduction.
[b] Number of colonies included in the study during both seasons.

to assess the benefits or disadvantages of group nesting for the Barn Swallow. Seasonal reproductive output of an average pair in each colony is an appropriate measure of relative fitness and is expressed as the number of young fledged per breeding pair per year, the number of pairs being equal to the number that initiated a first brood. Reproductive output did not vary consistently or significantly with colony size over the 2 years of the study ($r_s = 0.226$). The reproductive output averaged 5.6 young (r = 2.7–8.0 young) corresponding to a seasonal reproductive success of 78.5% (r = 57–94%; 100% × number of young fledged/number of eggs laid) and was similar in both years.

The lack of consistent differences in reproductive output of different colony sizes suggests that Barn Swallows derive no benefits or disadvantages from nesting in colonies. However, the failure to discern dramatic differences in reproductive output does not preclude the existence of more subtle and perhaps conflicting effects of group nesting. In examining the data, I will consider two sources of variation in reproductive output. One deals with the relative importance of different sources of mortality, e.g., predation, failure to hatch, lack of food, and probability of post-fledging survival. The second concerns factors influencing

the potential number of young that can be produced in a season, such as variation in clutch size, occurrence of second-brooding and replacement-brooding, and date of hatch.

SOURCES OF MORTALITY

Whole-clutch mortality. The major source of mortality in both years consisted of whole-clutch loss of eggs and young due to suspected predation and abandonment (Table 2). This mortality represents a loss of 12.5% (218/1750) of the eggs laid over the two seasons, 17.2% (318/1850 eggs) if losses due to cats and humans are included. These figures correspond to an average loss of 0.6 and 0.8 young per pair, respectively.

The magnitude of losses due to suspected predation and abandonment was not affected in any consistent or significant manner by variation in colony size and ranged from 9.5% to 15.6% of the eggs laid (0.4 to 0.7 young per pair). Whole-clutch mortality in colonies of all sizes was equally distributed between loss of eggs (5.6%, 98/1750) and loss of young (6.9%, 120/1750). The size of the colony also had no effect on the ratio of abandoned to plundered nests. A total of 146 eggs and young (7.7%) in 33/376 nests were destroyed by unknown agents, probably birds or rodents. The remaining 76 eggs and young (4.1%) perished after abandonment of 17 nests. Abandonment accompanied or closely followed predation in the same colony in 10/17 cases, suggesting that the destructive agents also caused the abandonment.

Many colonial birds will mob potential predators, and the Barn Swallow is said to be an aggressive mobber in comparison to other colonial swallows (Bent 1942, Lind 1964). I have observed mobbing by Barn Swallows on several occasions. Two of the attacks involved prevention of Starling (*Sturnus vulgaris*) predation, and the swallows successfully drove off the Starlings. Three other occasions in-

TABLE 2. Barn Swallow mortality attributable to failure to hatch, whole-clutch loss, and partial-clutch loss for all colony sizes.

Colony size	Nests (eggs)	Whole-clutch mortality[a]	Failure to hatch	Partial-clutch mortality	Total Eggs	Total Young
Single	27(127)	9.5%[b]	13.4%	2.4%	19.7%	5.5%
Small	47(218)	13.3%	6.4%	1.8%	11.0%	10.6%
Medium	79(366)	15.6%	2.5%	3.3%	9.8%	11.5%
Large	107(498)	13.3%	3.8%	3.6%	9.8%	10.9%
X-large	116(541)	10.0%	5.9%	4.1%	12.4%	7.6%
Total	376(1750)	12.5%	5.2%	3.4%	11.5%	9.5%

[a] Nests destroyed by cats and humans not included.
[b] Percentages based on the total number of eggs laid in each colony size.

volved mammals (2 cats and a woodchuck), and the mobbing did not appear to disturb the mammals greatly. It is unlikely that mobbing is more effective in large Barn Swallow colonies than in small ones, although a conclusion on this matter must await further investigation. On the occasions that I observed mobbing, the only pairs that responded to the presence of the potential predator were those possessing nests in the immediate vicinity of the danger. I observed no colony-wide response other than an increase in alarm calls.

Failure to hatch. Failure of part of a clutch to hatch ranked second in importance as a source of mortality, accounting for the loss of 5.2% (91/1750) of the eggs laid (table 2). The proportion of eggs failing to hatch did not vary consistently or significantly with colony size in either year and ranged from 0.0% to 16.3% of the eggs laid. I did not attempt to determine the cause of the failure to hatch, so I do not know to what extent infertility, malformed embryos, or parental neglect contributed to the failure.

Partial-clutch mortality. The third component of mortality accounted for the loss of 3.4% (59/1750) of the eggs laid and included death due to starvation and accident (see table 2). The incidence of death to 1 or 2 members of a clutch was not linked significantly with colony size and varied from 0.0% to 8.5% of the eggs laid in a colony, usually contributing less to overall mortality than either predation or failure to hatch.

It was difficult to determine the causes of partial-clutch mortality of young. In some instances, the young died in the nest; in others, they disappeared without a trace or were found dead on the ground. The young that were found dead were never marked in any way that suggested predation as a cause of death, and I suspect that those young that disappeared were taken only after falling from the nest. In 76% of the cases (36/47), the young that perished had been retarded in weight and growth, and therefore starvation appears to have been an important factor in their deaths.

NESTLING WEIGHT AND GROWTH

The ultimate reproductive success of a pair of birds is represented by the number of offspring that reach reproductive maturity. The nestling stage is only the first period of exposure to selective pressures, and post-fledging mortality may be an extremely important part of natural selection of breeding habits. I was unable to measure post-fledging mortality per se, but I did collect data concerning the general health of older nestlings that might be of use in estimating the probability of post-fledging survival.

Differences in nestling growth curves among the colony sizes were slight. The curves reached peak weights of 20–23 g on the 13th or 14th day after hatching. Subsequent to this period, the weights began to taper off, as has been reported by other investigators (e.g., Stoner 1935, de Braey 1946, Nitecki 1964, Kuzniak 1967, Ricklefs 1967, 1968a, 1968b, George and Al-Rawy 1970). Variation in the growth curves did not begin to appear until after the 9th day in 1970, by which time the major portion of the increase in size and weight had already occurred. Therefore, it seems that factors of food supply and adult foraging efficiency may not be important until the latter half of the nestling period. Since young swallows must be able to forage on the wing at the time of fledging, deviations in the later portions of the growth curve could be significant in terms of post-fledging survival.

In order to investigate the significance of these deviations, I used the weights of nestlings on the 15th day as an indication of the general health of the young that would be fledging. This day occurs after peak weight has been attained and only a day or two before the young will fledge prematurely if disturbed. Variation among the colony sizes in 15-day nestling weight was significant in only 1 of 4 tests (the first brood of 1970: $P < 0.005$ for the Kruskal-Wallis test), and even this variation was not consistent with respect to colony size. Mean weights tended to be higher for solitary nesters and in medium-sized colonies (22.3 g). The lowest mean weight in 1970 was recorded in the x-large colony size (20.3 g). Standard deviation in mean 15-day weight, one indication of the degree of difficulty in obtaining sufficient food for all nestlings (Ricklefs 1968b), was not related significantly to colony size at any time during the two year investigation.

One variation in nestling weight with brood size is pertinent to this discussion of colonial nesting. In general, mean 15-day weight varied significantly with brood size only in the first brood of 1970, when weight was inversely related to brood size ($P < 0.005$, F = 9.33 for 1/70 df; see Snapp 1973). However, this pattern was not found in all colony sizes. Figure 1 shows that mean 15-day nestling weight decreased with increasing brood size only in large and x-large colonies ($P < 0.005$ for both
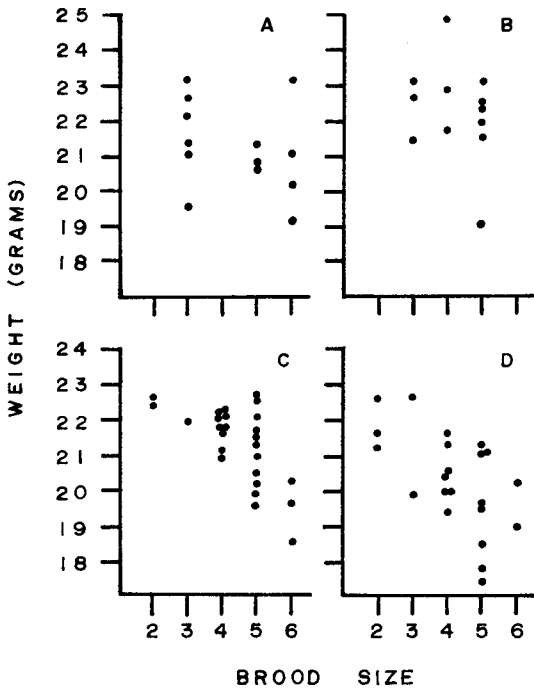
FIGURE 1.   Relationship between mean 15-day nest-ling weight and Barn Swallow colony size for different brood sizes. Each point represents one nest mean. Data are from the first brood of 1970 in singles and small colonies (A), medium colonies (B), large colonies (C), and x-large colonies (D).
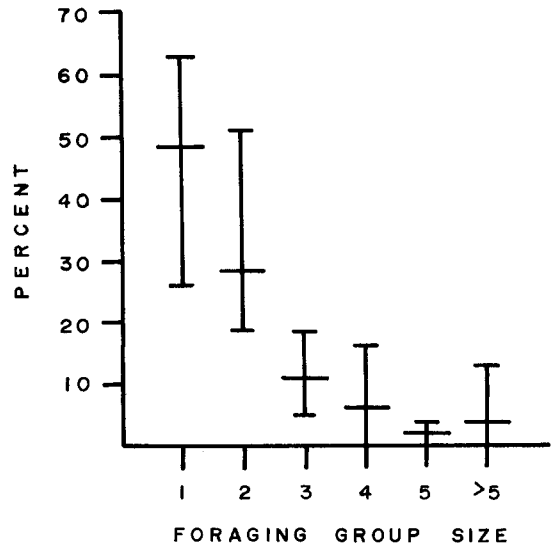

FIGURE 2.   Percent of foraging events encountered for different foraging group sizes of Barn Swallows observed around 4 colonies with more than 8 pairs in 1971. Horizontal lines represent mean values and vertical lines indicate the range of values observed.

colony sizes, F = 21.4 and 12.6 respectively). This observation implies that adults might have had more difficulty finding food for nestlings in large colonies than in small ones. However, the variation did not appear at any other time during the study, so its validity requires substantiation.

FORAGING AND FEEDING RATE

The frequency with which adults visit the nest to bring food to nestlings is a crude measure of the availability of food in the immediate area. If feeding rates in any particular breeding location are lower than the average for the species, this could indicate local scarcity of food and/or the necessity to forage at greater distances than normal. One factor that could affect local availability of food for the Barn Swallow, an aerial insectivore, is the size of the colony that is exploiting food supplies in the immediate vicinity of the breeding site. No such effect was evident in 1970 when I observed feeding rates at 11 colonies. The variability in all colony sizes was great, and there was considerable overlap in feeding rates among the colony sizes. Mean rates did not vary significantly among the colony sizes, either on a per-nest or per-nestling basis. The

values fluctuated around mean rates of 29.1 visits per nest per hour and 6.9 visits per nestling per hour (ranges, 21.0–37.6 and 5.1–10.6 respectively).

A number of factors could have contributed to the large variability observed in the feeding rates and might have masked any differences attributable to colony size. It was impossible to insure that foraging conditions were identical at all colonies or in all observation periods. In an attempt to control some of the variability, I limited observations to the hours of 0700 to 1100, refrained from collecting data if any rain fell during observation hours, and restricted analysis of data to nests containing young between the ages of 8 and 13 days. A fourth factor affecting the feeding rate—brood size—was probably not an important source of variation in the colony size rates. Although feeding rate varied significantly with brood size (Snapp 1973), brood size itself did not vary with colony size.

Although colony size appeared to have no effect on feeding rates, it is possible that adults derived some benefit from foraging in groups in the larger colonies. In 1971, I observed adults in the field at 4 colonies of 8 or more pairs in an attempt to assess the role of social facilitation in feeding and location of food supplies. Observations on foraging patterns over a total of 7.5 hr support the conclusion that Barn Swallows forage as individuals and do not take advantage of the possibility of

group foraging and social facilitation offered by larger colonies. Most of the feeding appeared to take place within 400 m of the colony, and little clumping of feeders occurred. Figure 2 indicates that the majority of feeding adults foraged singly or in groups of 2 (360/476 cases).

TIMING OF REPRODUCTION

The data presented above indicate that losses due to actual mortality and to potential post-fledging mortality did not vary consistently with colony size. Next, it is important to examine whether any active interaction among the breeding birds might have contributed to variation in the reproductive output among the colony sizes. If social interactions occurred among breeding Barn Swallows, differences in date of hatch, synchrony, and/or second-brooding should be related to changes in the size of the colony.

Mean date of hatch. Clutch size showed a non-significant tendency to increase in the early stages of the first and second broods and to decrease thereafter (Snapp 1973). Comparison of the breeding biology of late breeders to that of other Barn Swallow pairs indicated that pairs which hatched young more than 5 days after the mean first-brood hatching date possessed clutches that averaged 0.8 eggs less than those of earlier breeders in 1970 and 0.45 eggs less in 1971 ($P < 0.025$ in 1970; non-significant in 1971 for multinomial chi-square test). In addition to laying a small first clutch, late breeders also produced fewer second broods. Only 18% (10/55) of those late breeders that should have been able to start a second brood actually did so, compared to 82% (144/176) of the earlier breeders.

Because of the effect of date of first brood hatching on clutch size and second-brooding, the number of young fledged from a colony could be influenced by the mean hatching date of that colony and by the percentage of late breeders present. However, variation in mean hatching date among the colony sizes was significant only in the first brood of 1970 when medium-sized colonies nested later than other colonies ($P < 0.025$ for Kruskal-Wallis test). The pooled mean dates were similar in both years: 13 June 1970 (±11.0 days) and 14 June 1971 (±8.8 days) for first broods, 23 July 1970 (±7.9 days) and 24 July 1971 (±4.5 days) for second broods. There was likewise no consistent relationship between colony size and percentage of late breeders in a colony (mean = 26% or 79/301 nests).

Within-colony synchrony. Synchrony of hatching dates within a colony was unrelated to colony size, 16 days being the mean duration of hatching over both broods of both years. First-brood hatching took place over a period of more than 16 days in 9/10 colonies in 1970 and in 11/16 colonies in 1971 ($r_s = -0.20$ and $+0.33$, respectively, for colony size analysis of standard deviations of hatching date). Within-colony synchrony was greater for the second brood in both years, only 2/8 of the 1970 colonies and 3/15 of the 1971 colonies taking more than 16 days to hatch out all nests ($r_s = -0.32$ and -0.27, respectively). The increase in synchrony from the first brood to the second is attributable to the lack of second broods among late breeders.

Colonies of all sizes were more synchronized in 1971 than in 1970, possibly the result of a long, cold spring in 1971 when mean temperatures in April and May were 2.8°C lower than those for the comparable period in 1970. This increase in synchrony in 1971 coupled with the similarity of the mean hatching dates in the two years suggest that the entire breeding season was not delayed by the cold weather. Rather, it appears that only early breeders were delayed, resulting in a clustering of hatching dates close to the mean for each colony. Therefore, it seems that only external conditions such as weather and not active interaction among breeding pairs can act to increase the synchrony of a colony.

Since the duration of first-brood hatching within most colonies was less than that of the population as a whole (-5.5 days average in 1970; -12.2 days in 1971), it is possible that within-colony synchrony, irrespective of colony size, could have had an impact on reproductive output in a colony. Such an impact might be expected if social stimulation played a role in determining the timing of breeding within a colony (Darling 1938). The critical timing parameter is the within-colony synchrony of the first brood, and this parameter bore no relationship to seasonal reproductive output ($r_s = -0.08$). Nor were there significant correlations in either first or second brood when each was considered separately ($r_s = -0.07$ and $+0.15$).

Occurrence of second broods. I examined second-brood occurrence in two ways: actual number present and potential number available. There was no significant correlation among colony sizes with respect to the proportion of pairs actually having a second brood ($r_s = -0.16$). An average of 49% (147/

301) of all first brood pairs and 57% (147/259) of the successful first brood pairs initiated second broods.

Three timing factors operate together to determine the potentiality of second-brooding: date of hatch of the first brood, date of fall migration (late August), and an inter-brood interval of approximately 45 days (R = 35–54 days). The combination of the latter two factors allows the determination of a date by which first-brood hatching would have to occur if a second brood were to be raised. This date is 23 June. An average of 77% of the Barn Swallow pairs successfully completing a first brood met the date restrictions and therefore were theoretically able to raise a second brood. However, only 65% (147/225) of all pairs with time to raise a second brood actually attempted to do so. Neither percentage varied significantly with colony size.

The lack of a consistent correlation between colony size and first-brood timing factors, inter-brood intervals, or percentage of late breeders suggests that the occurrence of second-brooding is not regulated by social interaction among breeding pairs and is probably unaffected by the density of breeding pairs. Similar observations hold true for the occurrence of replacement broods laid after destruction of previous clutches. Although abandoned nests and destroyed second-brood clutches were never replaced, 68% (25/37) of the nests destroyed in the first brood were replaced in the two seasons. The rate of replacement, interval between destruction and replacement, and the success of replacement broods were all unrelated to colony size, irrespective of the nature of the destructive agent.

DISCUSSION

Because of the scarcity of literature on many species of swallows, the following discussion will deal for the most part with northern temperate zone swallows and with species from other bird families.

EFFECT OF PREDATION

The impact of predation can be reduced by judicious placement of nests in inaccessible or cryptic locations and/or by behavioral activities on the part of breeding pairs, such as mobbing, increased alertness, and greater effectiveness of alarm systems.

Mobbing activity in the Barn Swallow is not as highly developed as that observed for other swallow species, notably the solitary-nesting swallows, although Barn Swallows were able to drive Starlings away from their nests when the latter attempted to enter. By contrast, a solitary natural-cavity nesting species, the Tree Swallow, is reported to be very aggressive in defending its nest against nest-site competitors from other species (Kuerzi 1941, Chapman 1955).

The Barn Swallow is not alone among colonial swallows with respect to the ineffectiveness of predator defense. In fact, the Bank Swallow, Cliff Swallow, and House Martin (*Delichon urbica*) are reported to be even less aggressive and less effective in mobbing predators and nest-site competitors (Windsor and Emlen 1975, J. T. Emlen 1952, 1954, Lind 1962, 1964, respectively; but see also Hoogland and Sherman 1976, on Bank Swallow mobbing behavior). One reason for the ineffectiveness of mobbing in colonial swallows may be the lack of crypticity of the nest site. Horn (1968, 1970) found that mobbing by Brewer's Blackbirds (*Euphagus cyanocephalus*) was effective only against flying birds, and not against mammals, snakes, or perching birds; crypticity of the nest site was the main deterrent to predation by the latter. Likewise, Kruuk (1964) found that the mobbing behavior of Black-headed Gulls (*Larus ridibundus*) served primarily to distract potential predators and thereby enhanced the effectiveness of nest crypticity and diminished the ability of the predator to locate eggs or young. A similar distraction effect might occur as a result of the aggressive activity of the solitary-nesting Tree Swallow. However, there is no evidence to indicate that predator defense is enhanced by increases in breeding density among colonial swallows, in contrast to the situation in Black-headed Gull colonies (Kruuk 1964). Hoogland and Sherman (1976) provided some data to indicate a potential enhancement of predator defense in Bank Swallow colonies but have yet to demonstrate an actual decrease in predation with increasing colony size.

The observations of Barn Swallow mobbing behavior lead one to the conclusion that aggregation has not conferred any benefit from the standpoint of decreasing mortality due to predation. On the other hand, colonial breeding does not appear to have been detrimental with respect to predation loss. Although the large number of birds increased the conspicuousness of the nesting site, the level of predation in Barn Swallow colonies was not greater than that suffered by solitary nesting pairs of the same species.

EFFECT OF FOOD SUPPLY

In his examination of the breeding of Brewer's Blackbirds, Horn (1968) suggested that uniform dispersal of food would result in a similar dispersal of nests, while temporal and spatial uncertainty of food supply would result in a clumping of nests. Brown (1964) had previously related territoriality with defendability of a uniformly dispersed food supply. Aerial insect populations are often spatially and temporally variable (e.g., MacLeod and Donnelly 1957, 1958, Johnson 1969) and hence not defendable. Since these animals provide almost all of the swallow diet (Beal 1918), one would not expect to find swallows defending feeding territories and therefore colonial breeding would not be prohibited by this type of aggression.

Horn's hypothesis of nest distribution does not imply or require the existence of social facilitation in foraging. However, if a colony becomes very large, it is reasonable to expect that local food supplies might become depleted to an extent that would compel the birds to forage at greater distances and make social facilitation invaluable in reducing the time spent searching for food (see also Ward and Zahavi 1973, Krebs 1974). Several colonial swallow species have been observed feeding in large flocks during the breeding season (Bank Swallows, Stoner 1936, S. T. Emlen and Demong 1975; Cliff Swallows, J. T. Emlen 1952, 1954; House Martins, Knopfli 1971; Purple Martins [Progne subis], Johnston and Hardy 1962). The absence of social foraging patterns in Barn Swallow colonies may indicate that the colonies have not reached the size at which foraging distance becomes so great that nestling growth suffers unless social feeding enhances foraging efficiency. Barn Swallow colonies are smaller than those of the Bank Swallow, Cliff Swallow, and House Martin.

In fact, most of the evidence presented in the section on nestling weight and growth indicates that food supply is not always a critical factor in determining Barn Swallow colony size. For example, nestling death due to suspected starvation was very low in all colony sizes (1.8% to 4.1% of eggs laid), and was less important as a mortality source than predation or failure to hatch. Nestling weight varied significantly among the colony sizes only in the first brood of 1970, but in a manner that was unrelated to the density of nesting pairs. On the other hand, mean weights of 15-day-old nestlings varied inversely with brood size in large and x-large colonies at this time, and not in smaller colonies, indicating that adults might have had some difficulty finding sufficient food.

The absence of a consistent effect of colony size on weight in Barn Swallows does not rule out the possibility that these birds are food-limited in some situations. Considering the general impression of the instability of insect populations and the extreme influence of food supply on success in other aerial insectivores (Common Swift [Apus apus], Lack and Lack 1951; House Martin, Bryant 1975), it would be surprising if food supply did not exert a selective pressure on Barn Swallows at some point during some breeding seasons (see Snapp 1973).

EFFECT OF SOCIAL STIMULATION

Darling (1938) hypothesized that the size of a colony of breeding birds has a direct influence on the development and synchronization of the reproductive condition of the individual members of the colony. He suggested that larger colonies should be both more synchronized and more successful. "Social stimulation" is a term that encompasses a wide variety of possible colony-size effects, including the enhancement of breeding success through increase of sexual motivation and parental care as well as through increase in breeding synchrony.

At this point, it appears that social stimulation plays a small role, if any at all, in the establishment of Barn Swallow colonies. Synchrony of breeding was not strong, and it was not correlated with colony size. Each pair appeared to operate independently of others with respect to the initiation of breeding and the timing of second broods. Although I did not observe pre-copulatory behavior in detail, breeding behavior did not appear to be contagious as in Brewer's Blackbirds (Horn 1968) and some other swallow species (e.g., Cliff Swallows, J. T. Emlen 1952, 1954; Bank Swallows, Petersen 1955, S. T. Emlen and Demong 1975; Purple Martin, Allen and Nice 1952).

Possibly the mere presence of birds at a colony resulted in the recruitment of additional pairs by drawing attention to the existence of suitable breeding sites. However, there was no indication that the recruited individuals responded physiologically to the established pairs, or that recruitment occurred differentially with respect to the degree of similarity in reproductive condition between the established pairs and the newcomers. Any effect of recruitment on synchrony appeared to operate independently of Barn Swallow col-

ony size. In addition to this lack of correlation between colony size and synchrony, there was no influence of synchrony or colony size on breeding success in the Barn Swallow.

The absence of data for many colonial species of swallows makes it difficult to compare the role of social stimulation in the Barn Swallow with its role in the family as a whole. Strong synchrony of activities has been reported for the Cliff Swallow (J. T. Emlen, 1952, 1954) and Bank Swallow (Stoner 1936, Petersen, 1955, S. T. Emlen and Demong, 1975). However, the literature is by no means in agreement on this point. Myres' (1957) data indicate no effect of colony size on synchrony of egg laying within Cliff Swallow colonies, but his study involved a different colony each year, and he did not investigate breeding success at all. A similar lack of correlation between colony size and breeding synchrony was found by Lind (1964) in his study of the House Martin. S. T. Emlen and Demong (1975) reported that breeding success is significantly related to the degree of synchrony within Bank Swallow colonies, but there is no relationship between colony size and synchrony.

EFFECT OF NEST-SITE AVAILABILITY

Availability of nest sites may be a critical factor influencing colony formation for many bird groups, notably offshore seabirds (Lack 1967), herons (Lack 1968), nomadic blackbirds (Orians 1961), and savannah weaverbirds (Crook 1962, 1964). The Barn Swallow also has nesting requirements that may result in a scarcity of suitable nest sites.

Barn Swallows prefer to nest inside structures such as barns, sheds, and the undersides of bridges and culverts. Before the development of human settlements, they probably used shallow caves and crevices in cliffs and are occasionally reported to do so today (Bent 1942, Murray 1962). Since Barn Swallows do not inhabit the darker recesses of the areas they use for colonies (Davis 1937, pers. observ.), most natural caves do not provide much room for nesting. This situation contrasts markedly with the situation for other colonial swallows. Numerous nest sites are available on the exposed vertical surfaces occupied by Cliff Swallows, Bank Swallows, and House Martins, as well as in the inner recesses of large caves inhabited by Cave Swallows (*Petrochelidon fulva*). Therefore, the actual number of suitable nest sites available to Barn Swallows may be few, and it may be that the shortage of nest sites explains the fact that

Barn Swallows defend the approaches to the nest as well as the area immediately surrounding the nest site itself (Davis 1937, pers. observ.).

These nest-site characteristics, in combination with the defense of an area around the nest, result in dispersal of nests within a building, and Barn Swallows are seldom found nesting less than 3 m apart. Although nests on different beams may be closer, they almost always have different approaches. Small buildings, therefore, have only 1 to 3 pairs nesting in them, as do larger barns that are tightly shuttered and do not provide the wide entrances attractive to Barn Swallows. In Scandinavia the Barn Swallow is not known as a colonial breeder (Curry-Lindahl 1961, Lind 1964, von Haartmann 1969), although groups of 2 to 3 pairs are not uncommon. The well-kept nature of the barns and sheds may contribute to the solitary nature of the breeding habits there (pers. observ.). In the United States the large number of abandoned barns and the wide-open nature of most cow sheds has greatly increased the number of nest sites available in any one place. A similar situation occurs in Germany (pers. observ.), where the Barn Swallow is also known to nest in large groups (von Vietinghoff-Riesch 1955).

Nest-site limitation occurs in other species of swallows as well. The high degree of aggressiveness displayed by at least 4 species of natural-cavity nesters (Tree Swallow, Kuerzi 1941, Chapman 1955; Rough-winged Swallow, Lunk 1962; Purple Martin, Allen and Nice 1952, Johnston and Hardy 1962; and Blue Swallow, *Hirundo atrocaerulea*, Snell 1969) may be connected with the need to defend a limited resource, namely a suitable site for nesting. All of these species, except the Blue Swallow, readily use artificial nest sites, suggesting that their breeding density may be limited by the availability of natural cavities. The Blue Swallow builds its mud nests in potholes in the shallow valleys of Rhodesia and vigorously defends these limited nest sites (Snell 1969).

In conclusion, the Barn Swallow seems to have evolved mechanisms that permit pairs to nest near one another but at well-spaced intervals, a condition that allows groups of 2 or 3 pairs to nest together in most natural breeding sites. It appears that the larger colonies now are a passive extension of the natural occurrence of small nesting groups, and that the nature of the buildings available has had a profound influence on the development of colonial breeding in the Barn Swallow.

SOCIALITY IN THE SWALLOW FAMILY

Evidence suggests that nest-site availability may have played an important role in the evolution of both social patterns and nest-building behavior in swallows (Mayr and Bond 1943). Geographical distribution of swallow species is such that an area contains at most one species in each of the following nesting categories: burrow-excavator, exposed-surface mud-nester, recessed-surface mud-nester, tree cavity-nester, substrate cavity-nester (Snapp 1973). However, the presence of a high degree of synchrony within the colonies of certain swallow species indicates that nest-site availability alone is not sufficient to account for the high degree of sociality observed in the breeding season. It is perhaps significant that those species which are most synchronized are also found in the largest colonies (Bank and Cliff swallows).

Evidence that synchrony in colonial swallows is a response to predation pressure is scanty, and behavioral defense mechanisms have not developed to a great degree. Observations of the foraging behavior of some species indicate that difficulty in locating food sources may play a role in producing within-colony synchrony. The fact that there is less synchrony between colonies than within colonies in these species (J. T. Emlen 1952, 1954, and Myres 1957, on Cliff Swallow; Stoner 1935, Petersen 1955, S. T. Emlen and Demong 1975, Hoogland and Sherman 1976, on Bank Swallow; Snapp 1973, on Barn Swallow) suggests that there may not be a severe temporal concentration of food abundance that would impose breeding synchrony on the birds.

In addition, House Martins and Barn Swallows both produce two broods each year, indicating that synchrony is not solely the result of an intense concentration of food in the early part of the summer. Although all swallow species feed on the same insect orders (Beal 1918), highly synchronized and colonial species do not have two broods, whereas those nesting in smaller less synchronized colonies do. There is no reason, from timing considerations, why Cliff Swallows and Bank Swallows could not produce a second brood throughout most of their ranges. It is possible that food supplies in the latter half of the summer are low enough to prohibit successful nesting in large aggregations. Changes in insect quantity or quality may also explain why some Barn Swallows with time to raise a second brood do not always attempt to do so (see also Bryant 1975 on the House Martin).

SUMMARY

Four factors could account for the presence of coloniality in the Barn Swallow: predation, starvation, social stimulation, nest-site availability. Neither the number of pairs that collected in a colony nor the degree of within-colony synchrony affected reproductive success by consistently increasing or decreasing losses due to predation or food shortage. Colony size also did not influence the degree of synchrony, occurrence of second broods or replacement of destroyed clutches, as might have been expected if social stimulation were important. However, the number of pairs in a colony rose in parallel with the increase in the size of the building and/or the number of entrances to the building. Therefore, the implication is that Barn Swallow colonies represent passive aggregations of breeding birds and do not actively recruit additional pairs. The lack of close synchrony and the absence of colony-size effects on reproductive success indicate that coloniality in the Barn Swallow has not reached the level of breeding density where pressures other than nest-site availability begin to exert an influence on the development of social breeding patterns.

ACKNOWLEDGEMENTS

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