ADVANTAGES AND DISADVANTAGES OF BANK SWALLOW
(*RIPARIA RIPARIA*) COLONIALITY[1]

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Abstract. We studied the advantages and disadvantages of Bank Swallow (*Riparia riparia*) coloniality in 1972 and 1973 by examining 54 colonies, ranging in size from 2 to 451 active nests, near Ann Arbor, Michigan USA. Four disadvantages were investigated: (1) increased competition for nest burrows and nest building materials, (2) increased competition for mates and matings, (3) increased possibilities of misdirected parental care because of either brood parasitism or the mixing up of unrelated young, and (4) increased transmission of ecto-parasites. Physical interference in reproductive functions and the possibility of intraspecific killing of offspring were also considered. The intensity of the various forms of competition increased with increasing colony size, though not always directly. Flea infestation also increased with increasing colony size. Intraspecific brood parasitism was not observed, and parent Bank Swallows began discriminating between their own and unrelated offspring at the time when the young first began to mix.

Three hypotheses to explain the maintenance of coloniality were tested: (1) shortage of suitable nesting habitats, (2) advantages associated with social foraging, and (3) reduced predation on adults, young, or eggs. Shortage of suitable habitat could not be demonstrated. Parents did not appear to feed in groups, and survivorship of nestlings during cold weather and weight of nestlings at 10 days of age both suggested that competition for food increased with increasing colony size. Although there was no relationship between colony size and amount of nocturnal predation, adult birds mobbed diurnal predators. Using a stuffed weasel, we studied such mobbing responses. Our data suggest that diurnal predators at larger colonies are (1) detected more quickly, (2) mobbed by greater numbers of birds, and (3) subjected to more vocal commotion than are predators at smaller colonies. Further, we demonstrated that mobbing is at least sometimes effective in deterring avian predators. We suggest that reduced predation on eggs and young, resulting from both group defense and "selfish herd" effects, is an important advantage of Bank Swallow coloniality.

Key words: Bank Swallow; coloniality; competition; nesting biology; Riparia riparia; *predation; social foraging.*

INTRODUCTION

Group living or coloniality is favored in animals only if the fitnesses of individuals within colonies are elevated above the fitnesses of noncolonial conspecifics. While no automatic or universal advantages are associated with group living, there are two automatic detriments (Alexander 1974): (1) increased competition for nest sites, nest materials, mates, and other resource, and (2) increased likelihood of ectoparasite and disease transmission. Other possible disadvantages, not necessarily automatic, include increased conspicuousness of groups to predators (Tinbergen 1952, Cullen 1960, Kruuk 1964); increased probability of indirect, deleterious consequences of nearby conspecific activity; increased chances of losing offspring because of intraspecific killing; and increased probability of rearing genetically unrelated offspring because of either cuckoldry, brood parasitism, or the mixing-up of young.

Alexander (1971, 1974) proposed that there may

be only three evolutionary reasons to explain why animals live in groups:

(1) susceptibility to predation may be lowered either because of aggressive group defense, as in savannah baboons, or because of the opportunity for individuals to use the group as cover (or to cause other individuals to be more available to predators), as with schooling fish and herds of small ungulates, (2) the nature of the food sources may make splintering off unprofitable, as with wolves dependent upon large game in certain regions, or with (hypothetical) groups dependent upon scattered large supplies of food that individuals locate too infrequently on their own, or (3) there may be an extreme localization of some resource, such as safe sleeping sites for hamadryas baboons or suitable breeding sites for some marine birds and mammals.

As Alexander (1974) further pointed out, grouped individuals gain because of the presence of others in the first two cases, while in the third they do not. It has been suggested that "social stimulation" or "social facilitation" of breeding has been important in the evolution of colonial birds in general (Darling 1938) and of Bank Swallows in particular (Emlen 1971). However, we agree with Orians (1961a) that such stimulatory effects probably evolved secondarily, and we suggest that these effects can
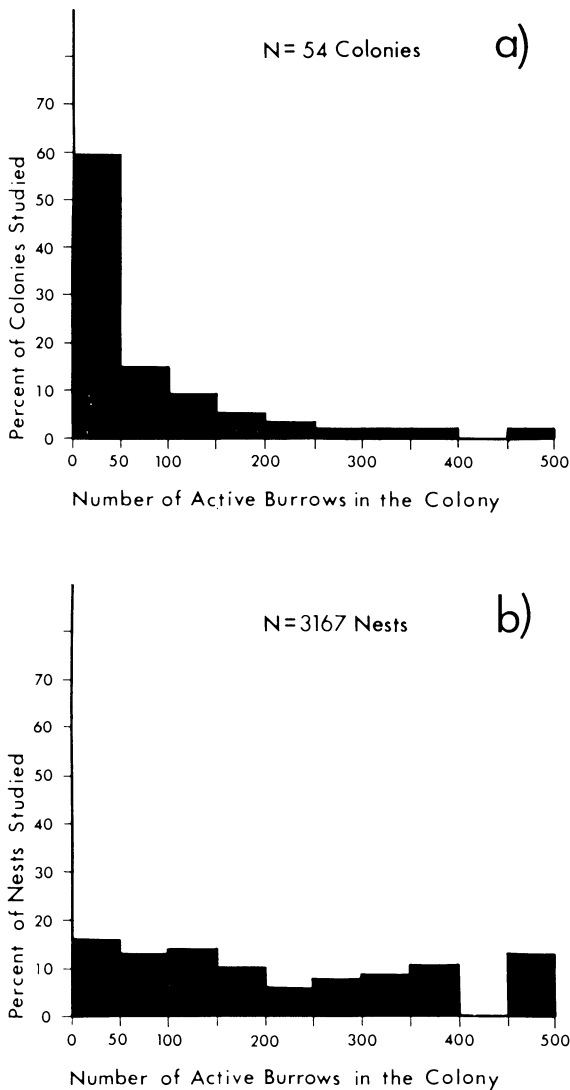
Fig. 1. a) Percent of Bank Swallow colonies observed in each 50-burrow size class during 1972–73 near Ann Arbor, Michigan USA. The 50-burrow classes are for illustrative purposes only. b) Percent of Bank Swallow nests in each 50-burrow colony size class during 1972–73. The 3,167 active burrows comprised the 54 colonies shown in a).

only be a result, never an evolutionary cause, of coloniality.

In each section of this paper we investigate one of the disadvantages or advantages of Bank Swallow coloniality. Colonies of various sizes, ranging from 2 to 451 nests, were studied and compared whenever possible; in 1973 we observed one Bank Swallow pair which nested alone. If coloniality is an evolutionarily ancient feature of Bank Swallow breeding biology, as Jósefik (1962) speculated, then the behaviors we observed probably evolved in the

context of group living rather than in response to recently disturbed habitats.

EXPERIMENTAL POPULATIONS AND TECHNIQUES

From May to August 1972 and 1973 we examined 54 Bank Swallow colonies of various sizes (Fig. 1a) in five counties near Ann Arbor, Michigan. Of these, approximately half were studied extensively. Bank Swallows nest along river banks (Jósefik 1962, Marian 1968) and lake shores (Stoner 1936) and in commercial gravel pits (Stoner 1936, Spencer 1962). Near Ann Arbor, most colonies are located in gravel pits, and all our data are from such colonies.

We determined the number of active nests in each colony by examining as many burrows individually as possible. We found varying numbers of apparently unused burrows in all colonies, and these were excluded for colony size determinations. Figure 1a shows that the final size of nearly 60% of the study colonies was 1–50 active nests (2–100 breeding adults). Similar percentages of "small" colonies were reported by Jósefik (1962), Marian (1968), and Oelke (1968). Such data misleadingly suggest that most Bank Swallows interact with relatively few conspecifics. However, as Fig. 1b shows, 71% of the Bank Swallows near Ann Arbor inhabited colonies containing 100 or more active nests, and 47% inhabited colonies of 200 or more.

Stoner (1936) reported that Bank Swallows sometimes raise two broods at a latitude similar to Ann Arbor's. We did not see clear cases of second nesting during our study.

All adult birds we studied individually were caught in mist nets or by hand at night in the nest burrows (as described by Bergstrom 1951) and were marked permanently with United States Fish and Wildlife Service numbered aluminum leg bands and temporarily with green, red, and yellow Magic Marker®, applied in various combinations to the birds' white breast feathers.

Svensson (1969) and Oring and Knudson (1973) apparently used a similar marking method. For color marking, the Bank Swallow's breast area was divided approximately in half, transversely, and different colors were applied to the anterior and posterior sections, or to both. Thus there were three individual patterns for each single color, plus various combinations of colors. The technique had no observable effects on the birds' behavior. Color-marked birds were easily identifiable, even at great distances, regardless of their wingbeat frequency. Young Bank Swallows used to determine parental recognition abilities were marked with U.S.F.W.S. leg bands, and, for visual observation, older nestlings were also marked with bits of brightly colored cloth fastened to the tops of their heads with nontoxic, water-soluble glue. In all transfer experiments, approximately 30 min elapsed from the time of nestling removal until each was placed in a foreign nest or was returned to its own nest. All experimental and control nests contained either four or five nestlings after transfers.

Burrows under observation were marked for identification at a distance by numbers or symbols scratched near them in the sand bank. We also marked certain burrows more permanently by attaching self-sticking, numbered circles of paper to nail heads, then driving the nails into the bank. These burrow marking methods had no observable effects on the swallows' behaviors. We observed nest contents using a dental mirror fastened at an oblique angle to the end of a 0.6-cm × 1-m dowel in tandem with either a concave shaving mirror

or, on overcast days, a flashlight. To mark nestlings, we dug out their burrows with a hand trowel, then repaired the burrows with the original sand or gravel. Parent birds readily returned to such burrows. We manipulated eggs for recognition experiments with as little disruption as possible to burrows and nests by using a plastic spoon fastened to the end of a thin dowel. Such eggs were marked with dots of Magic Marker® and placed into experimental nests within a few minutes after the time of their removal.

We recorded the birds' vocalizations with a Nagra-III™ tape recorder equipped with an American Microphone™ (Model D-33) microphone. All vocalization data were analyzed with this equipment or with a tape recorder (Uher™, Model 4000 Report-L). The simulated predator used in mobbing experiments was a long-tailed weasel (*Mustela frenata noveboracensis*), collected near Ann Arbor in 1933, and stuffed in a lifelike pose. Following the suggestion of Kruuk (1964), we introduced the weasel to a chosen burrow by hand, then departed quickly. We photographed mobs and burrow densities. For pictures of mobs, the camera was always placed 32 m from a central or edge burrow into which the stuffed weasel was placed. Observations were made with binoculars. The 11 adults collected during this study were killed with dust shot, and were sexed by dissection. Ten-day-old nestlings were restrained in small plastic bags and weighed to an accuracy of 0.1 g. Weighed nestlings were aged exactly by marking their home burrows on the day the eggs began hatching. We aged other nestlings approximately by comparing plumage characteristics with those of young of known ages.

All indicated significance levels are for two-tailed statistical tests.

THE DISADVANTAGES OF BANK SWALLOW COLONIALITY

Increased competition for nest sites and nest materials

Competition for nest sites and nest materials is a commonly reported disadvantage of bird coloniality. Among swallows, fighting for specific nest sites is apparently common, having been observed in Crag Martins (*Hirundo rupestris*) (Cramp 1970), House Martins (*Delichon urbica*) (Lind 1960), Purple Martins (*Progne subis*) (Allen and Nice 1952, Finlay 1971), Rough-winged Swallows (*Stelgidopteryx ruficollis*) (Lunk 1962), Tree Swallows (*Iridoprocne bicolor*) (Kuerzi 1941), and Bank Swallows (Petersen 1955, this study). That physical combat is sometimes exceedingly deleterious is suggested by Kuerzi's (1941) observation of a Tree Swallow death that resulted from a fight for a nest box. Competition for nest materials as manifested by stealing of these materials has been observed in many colonial species (Fisher and Lockley 1954, Cullen 1957, Sladen 1958, Crook 1964, Tenaza 1971). Siegfried's report (1972) that the major cause of nest and egg loss in a colony of Cattle Egrets (*Bubulcus ibis*) was intracolonial stick stealing suggests the potential seriousness of this disadvantage for individual parents. We investigated
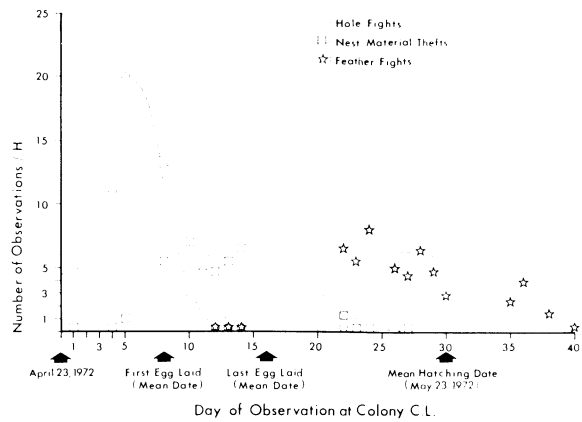

FIG. 2. Temporal sequence of the three types of intracolonial competition associated with Bank Swallow nesting activities. Data from a 289-nest colony in 1972.

the possibility of such competitive interactions among Bank Swallows by observing the behaviors associated with nest site location and nest construction at a colony of 289 active burrows in 1972 and, for comparative purposes, at three colonies of different sizes (5, 122, and 228 active burrows) in 1973. As the nesting season progressed, intracolonial conflicts over both nest sites and feathers (which are used to line nests) were observed, as was stealing of nest materials. The temporal progression of these behaviors at one colony is shown in Fig. 2.

Throughout excavation and nest-building individual swallows must often defend their burrows against conspecifics, and fights often develop. Fights usually begin at the edge of a burrow and the combatants then either fall from the bank face to the ground or, more often, continue battling in the air. Of 44 conflicts that began at the edge of a burrow, 31 (70%) ended in midair battles, and the remainder terminated only after the antagonists hit the ground. We did not determine whether trespassing birds had already begun excavations at other sites. Figure 3 shows the occurrence of nest site fighting at the three colonies studied in 1973. An analysis of these data, using observations from the 17 days following the appearance of the first burrow at each colony, shows that the number of fights per individual differed significantly between colonies ($p < .001$, Kruskal-Wallis analysis of variance by ranks) as a linear function of colony size ($p < .01$, Kendall rank order correlation). We used 17 days after the appearance of the first burrow because the mean time between hole initiation and deposition of the first egg is 18.0 ± 1.4 days ($N = 23$) and because we never observed fights at burrows with nests containing eggs or young. The data of Fig. 3 suggest that time, energy, and physical risk associated with
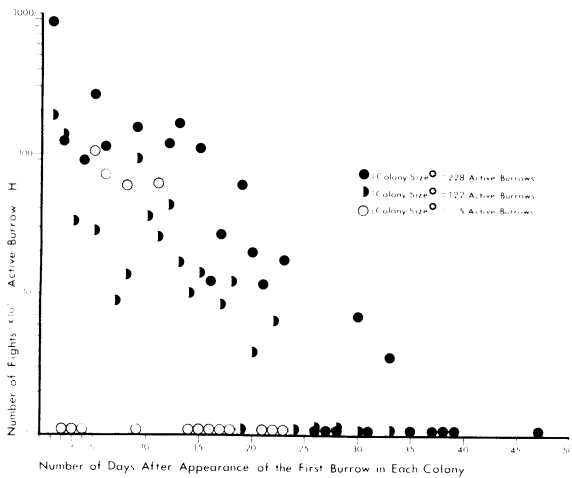
FIG. 3. Comparison of nest site conflicts (burrow fights and midair fights × 1,000; see text) at three colonies in 1973. Dates of Day 1 were 9 June for the 5-nest colony, 20 June for the 122-nest colony, 6 May for the 228-nest colony. * Colony sizes are the final number of active burrows observed in each. During the study period, colonies grew daily and such changes were taken into account for the per-bird analyses.

establishing and defending a nesting burrow increase directly with colony size.

When the burrow is deep enough, parent Bank Swallows hollow out a cavity at its distal end and begin to build a nest (Stoner 1936, Beyer 1938). In the Ann Arbor vicinity, nests usually contain a combination of grass stems, rootlets, straw, and twigs. As nests begin to appear, individuals steal nest materials from their neighbors. A thief usually visits burrows near its own until an untended one is found, enters this untended burrow, and emerges 5–60 s later with one or several nest material items, which it carries to its own burrow. Birds apparently do not steal from burrows containing owners: on nine separate occasions a bird ready to steal (as evidenced by the fact that it went on to steal from another burrow) stopped at the entrance of a burrow that was known to be occupied and flew off without attempting to enter. Of 67 separate instances of successful stealing, 58 (86%) occurred within a distance defined by the nearest five burrows in any

direction from the thief's home burrow. Successions of as many as seven thefts by one bird or mated pair were observed; the mean number of consecutive thefts was 1.8 ± 0.9 ($N = 18$). We did not determine if parents tend to steal in teams with one guarding the home burrow while the other robs. We recorded nest material stealing during the peak of this activity at the three colonies studied in 1973. For this analysis the peak of activity has been defined as the 20 days following its first observance, and each thief was scored only once, regardless of its number of consecutive robberies. The 20-day interval corresponds to the length of time that stealing was evident in the two colonies where it was observed in 1973. A similar time interval for nest material stealing was also observed at colony C.L., studied in 1972 (Fig. 2). Table 1 shows that the probability of nest material loss due to stealing did not differ significantly between the two larger colonies ($p > .35$, Student's t-test). However, it should be noted that stealing was never observed in the smallest colony, suggesting an advantage regarding nest material retention to members of smaller Bank Swallow colonies.

Shortly after the onset of incubation, Bank Swallow parents begin adding large quantities of chicken and duck feathers (Johnson 1958) to their nests (Stoner's 1936 photographs). That feathers are valuable to Bank Swallows is suggested by the many fights for them which we observed. Feather fights develop when colony members detect a bird winging toward its home burrow with a feather in its beak. Large swarms, sometimes consisting of more than 100 birds, quickly envelop the feather-bearer and in the melee the latter often loses its feather to a new bird. Sometimes the original finder is able to defend its feather successfully, but in one case a feather changed beaks seven times before it was finally taken into a burrow. Feather-fighting data from the three 1973 study colonies (Table 1) are from the 15 days following the first observed feather fight at the two large colonies and from a comparable time interval at the smallest colony. After 15 days there was a marked reduction in the frequency of feather fights at the two larger colonies. The per-

TABLE 1. Intercolonial comparison of the probability of a pair of Bank Swallows having nest materials stolen from them and of per bird involvement in a feather fight at three colonies in 1973. Text gives significance levels

| Colony size | Nest material stealing | | Feather fighting | |
	Separate days (h) of data	Thefts/burrow/h ($\bar{x} \pm$ SE)	Separate days (h) of data	Fights/bird/h ($\bar{x} \pm$ SE)
5	12 (19.5)	0.000 ± 0 ($N = 0$)	8 (12.6)	0.000 ± 0 ($N = 0$)
122	14 (18.3)	0.020 ± 0.008 ($N = 25$)	11 (11.4)	0.008 ± 0.005 ($N = 21$)
228	15 (16.2)	0.014 ± 0.005 ($N = 62$)	8 (12.6)	0.005 ± 0.004 ($N = 16$)

bird probability of feather fights was greatest in the intermediate-sized colony, but the differences between this colony and the 228-burrow colony were not significant at the $p < .05$ level ($.10 > p > .05$, Student's t-test). Feather fights were never observed in the smallest colony, even though feathers were brought to all nests. We observed birds stealing feathers from neighbors' nests as did Petersen (1955), but such robbery occurred too infrequently to permit intercolonial comparisons.

Increased physical interference with construction and maintenance of burrows

Indirect as well as direct consequences of nearby conspecific activity might deleteriously interfere with nesting. For example, Smith (1968) observed that hanging colonies of oropendolas (*Zarhynchus wagleri*) and caciques (*Cacicus cela*) sometimes cause the limb from which they are suspended to break. Groups of nests are presumably more likely than single nests to cause limbs to break, and increased likelihood of breakage is probably an indirect consequence of coloniality in these birds. For Bank Swallows, we observed three indirect disadvantages of this sort: physical interference, burrow coalescences, and bank cave-ins.

At various stages of the nesting cycle, adult Bank Swallows sometimes (apparently accidentally) flew into other adults while going to or from their home burrows. Since parents involved in such accidents probably sacrifice some time and energy, the occurrence of midair collisions (and attempts to avoid them) must constitute a disadvantage of Bank Swallow coloniality.

Sometimes two adjacent Bank Swallow burrows coalesce during the excavation of one or the other ($< 3\%$ of the 3,000+ burrows we studied). In every case, only one pair of swallows remained after the coalescence, which means that the other pair was forced to restart at another site (Petersen 1955 reported similar findings). Since only by breeding in a colony can an individual Bank Swallow lose a burrow because of coalescence, the probability of such loss must constitute another disadvantage of Bank Swallow coloniality.

Bank cave-ins occurred at 33 of the 54 colonies (61%) examined in 1972–73. These cave-ins are usually limited to one or a few burrows. Occasionally, however, scores of clustered burrows are destroyed by the collapse of a large part of a sand bank. Such collapses are caused by either erosion (Johnson 1958 gives an example) or instability of the bank's internal structure. At one colony we witnessed the destruction of 89 burrows by a single cave-in. Because the strength of any bank face must be some negative function of the number of

holes in it, increased probability of burrow loss via cave-in constitutes another disadvantage of coloniality for Bank Swallows. Stoner (1936) made a similar suggestion.

Increased competition for mates and matings

Male-male competition for mates and matings is a commonly observed phenomenon, even in monogamous species. While it is often selectively advantageous for a male and, under certain circumstances, for a female (Trivers 1972), to copulate with an individual other than its own mate, it is disadvantageous for any bird to allow its mate to copulate with a neighbor if such a copulation means either that the allowing bird risks the possibility of raising a genetically unrelated offspring or that the amount or quality of parental care dispensed by the promiscuous mate will be lowered. Because both male and female Bank Swallows participate in burrow excavation (Stoner 1936, Petersen 1955), nest building (Stoner 1936, Stoner and Stoner 1941, Petersen 1955), incubation (Stoner 1936, Moreau and Moreau 1939, Petersen 1955), and feeding of the young (Stoner 1936, Beyer 1938), a diminution of the parental investment of either parent might be detrimental to both parents.

Because of the proximity of conspecifics, the chances for males to increase their reproduction by mating with females other than their own mates are probably greater among colonial species than solitary species. However, males of colonial species probably also have a higher probability of being cuckolded. These considerations suggest that in colonial species (1) males should attempt to secure extra matings while at the same time guarding their mates against sexual assault, (2) females should guard their mates while occasionally accepting the advances of certain males, and (3) males should guard their females more than the reverse, since a male always risks rearing unrelated offspring when his mate copulates with an outsider but cuckolded females are at a disadvantage only if their mates give parental care to their offspring in other nests, thereby diminishing parental care at home. We attempted to test all of these predictions.

That male Bank Swallows sometimes attempt to mate with more than one female was suggested by Petersen (1955), who observed attempted copulations on dead birds near colony sites. We observed that, before clutches are completed, a stuffed female with outstretched wings typically elicits mounting by conspecifics when placed at a colony's base. Participating birds usually mount the decoy from the rear, vibrate their wings vigorously, then fly off. By collecting birds that made such attempts, we determined that only males participate ($N = 11$).
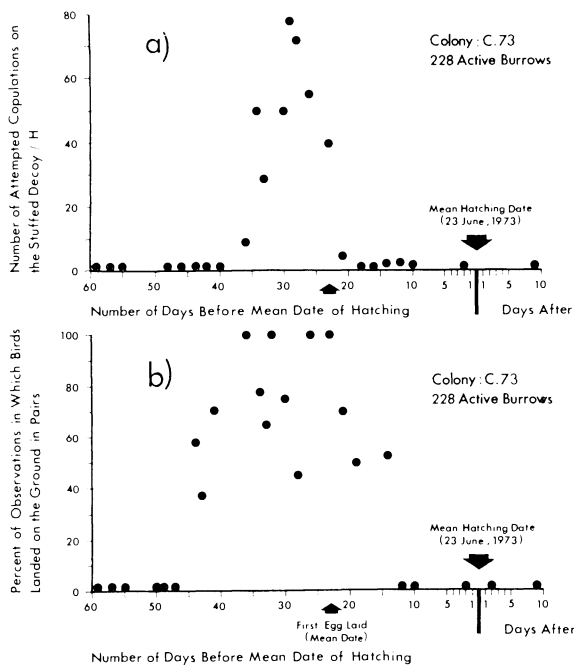
FIG. 4. a) Temporal progression of adult ♂ Bank Swallow copulation attempts on a stuffed ♀ conspecific observed at a colony of 228 nests in 1973. The mean hatch date was 23 June. b) Changes in the percent of observations in which two adult Bank Swallows landed on the ground in pairs, as opposed to singly, at the same colony.

TABLE 2. Intercolonial comparison of the number of copulation attempts by Bank Swallow adult ♂ ♂ on a ♀ decoy at three colonies of different sizes in 1973. These data differ significantly ($p < .01$, analysis of variance) but, when compared pairwise, only the 122- and 228-burrow colonies differed ($p < 0.5$, Student's t-tests)

Colony size	Separate days of data	Attempted copulations/burrow/h ($\bar{x} \pm SE$)
5	8	0.050 ± 0.019 ($N = 4$)
122	7	0.094 ± 0.014 ($N = 183$)
228	9	0.023 ± 0.016 ($N = 89$)

Our observation that semen is sometimes deposited on dead decoys suggests that the observed behaviors really were copulation attempts. Similar attempted copulations on dead birds have been reported in Brewer's Blackbirds (*Euphagus cyanocephalus*) (Howell and Bartholomew 1952) and Barn Swallows (*Hirundo rustica*) (Samuel 1971a). Copulation with nonmates has been observed in several colonial species: Little Blue Herons (*Florida caerulea*) (Meanley 1955), White Ibises (*Eudocimus albus*) (Kushlan 1973), Gray-headed Albatrosses (*Diomedea chrysostoma*) (Tickell and Pinder 1966), Laysan Albatrosses (*Diomedea immutabilis*) (Fisher 1971), and, among swallows, in Cliff Swallows (*Petrochelidon pyrrhonota*) (Emlen 1954), Tree Swallows (Chapman 1955), and House Martins (Lind 1960).

To study the probability of males being cuckolded, we placed a stuffed female at the bases of three different-sized colonies during the stages of burrow construction through incubation. Only during these stages do males attempt to copulate with a stuffed female (Fig. 4a). Table 2 shows that the per-bird number of attempted copulations on the decoy at the three colonies differed significantly ($p < .01$, analysis of variance). However, contrary to our

expectation, the greatest probability of males being cuckolded, as measured by the number of copulation attempts on the female decoy, was at the colony of 122 active burrows rather than at the 228-burrow colony.

To determine whether mates guard one another, we examined tendencies of adults to land on the ground and to enter burrows as pairs. Both of these tendencies change markedly with the progression of the nesting cycle. The percent of times that two birds landed synchronously rather than singly as a function of date is shown in Fig. 4b. The temporal similarity between attempted copulations on the decoy (Fig. 4a) and the mate accompaniment shown in Fig. 4b ($N = 96$ observations) suggests mate-guarding. The percent of times that adults enter their burrows in twos as a function of the individual pair's stage of reproduction was also investigated. The data from observations of 75 nests at one colony (colony size = 228) over one 3-day period are shown in Fig. 5. The obvious decrease in the tendency to enter burrows in twos coupled with the approach of incubation again suggests mate-guarding in Bank Swallows. Mate-guarding is further indicated by Stoner's (1936) daytime burrow examinations which suggest that mates tend to remain together during egg-laying and early incubation and to remain apart shortly after the onset of incubation. Although we did not determine with marked birds whether males guard females, females guard males, or both, sudden cessation of mate accompaniment with onset of incubation suggests that males guard females. If females guard males, then guarding should continue after a female finishes egg-laying since a male is apparently capable of insemination for several days after the termination of his mate's egg-laying (Petersen 1955). But if males guard females, then guarding should end with the termination of egg-laying (Fig. 5 and Stoner 1936), since sexual assault on the female after this time cannot lead to insemination. That males guard females is further suggested by Petersen's (1955) observation that it is always
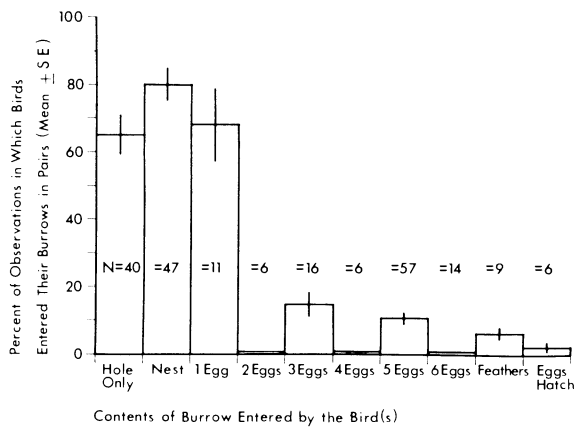
FIG. 5. Percent of observations ($\bar{x} \pm$ SE) in which two adult Bank Swallows entered a burrow in a pair, as opposed to singly, as a function of the stage of the nest within each burrow. These observations were made at a 228-burrow colony in 1973. N = sample size.

the male which follows the female during the time prior to incubation. Male guarding of females has also been observed in Brewer's Blackbirds (Horn 1968) and Barn Swallows (Samuel 1971*a*).

A comparison of Bank and Rough-winged Swallow roosting habits also suggests mate guarding in Bank Swallows. Both Bank Swallow parents commonly spend the night together in the home burrow, from the time of hole initiation until the young are about half grown (Petersen 1955, Lunk 1962, *but see* Stoner 1926). On the other hand, although females of the noncolonial Rough-winged Swallow often roost in the home burrow, males have never been observed to roost there with their mates (Blake 1953, Skutch 1960, Lunk 1962). We tried to determine if male Bank Swallows roost most often with their mates when inseminations are likely to be successful (before and during egg-laying), but we abandoned this attempt because of the extreme disturbance caused by our nighttime visits.

Increased intraspecific brood parasitism

Because of the potential attractiveness of a large group of breeding birds to interspecific brood parasites (Hamilton and Orians 1965), increased chances of caring for foreign eggs might constitute another disadvantage of coloniality. We found no evidence of interspecific brood parasitism. None of the 1,500+ nests we examined ever contained eggs or young of birds other than Bank Swallows.

Simultaneously laying conspecifics always represent a brood parasitic threat to parents (example in Weller 1959). In colonial species, the probability of caring for an unrelated conspecific because of this threat is presumably increased. Intracolonial brood parasitism has been observed in Lesser Snow

Geese (*Chen caerulesens*) (Cooch 1958, Cooke and Mirsky 1972) and has been suggested for Greater Flamingos (*Phoenicopterus ruber*) by Brown (1958). Species in which nests tended by one female commonly receive eggs produced by another (unrelated) conspecific may be expected to evolve egg-recognition abilities. Intraspecific egg discrimination has most often been reported in colonial sea birds (e.g., Johnson 1941, Tschanz 1959, Buckley and Buckley 1972*b*), although not all colonial sea birds recognize their own eggs (Davies and Carrick 1962). We investigated the possibility of intracolonial brood parasitism in Bank Swallows in several ways, including an examination of egg-recognition abilities.

In Lesser Snow Geese (Cooch 1958, Cooke and Mirsky 1972) and Red-headed Ducks (*Aythya americana*) (Weller 1959), both of which are parasitized intraspecifically, very large clutches ("dump nests") are sometimes observed. These are probably manifestations of intraspecific brood parasitism (Cooke and Mirsky 1972). We sought evidence of similar egg number variance in Bank Swallow clutches. We found that the $\bar{x} \pm$ SE final clutch size of 217 nests in one colony (in 1972) was 4.98 $\pm$ 0.05 eggs. No clutches of < three eggs were found. Although we observed one very large clutch of eight eggs, the small SE is indirect evidence that intracolonial brood parasitism does not occur in Bank Swallows. Petersen (1955) reported a $\bar{x} \pm$ SE Bank Swallow first clutch size of 5.03 $\pm$ 0.07.

Stoner (1936) and Petersen (1955) suggested that once a female Bank Swallow begins laying, the clutch increases at the rate of one egg/day until completion. One egg/day laying patterns have also been observed in Barn Swallows (Hosking and Newberry 1946, Purchon 1948, Samuel 1971*b*), Cliff Swallows (Samuel 1971*b*), Purple Martins (Allen and Nice 1952), and Tree Swallows (Austin and Low 1932, Paynter 1954). Variations in the one egg/day pattern might indicate intraspecific brood parasitism: zero eggs/day at an active nest might suggest that the owning female had parasitized a neighbor's nest, whereas two eggs/day might indicate parasitic exploitation of that nest. We looked for such variations by making intra-nest comparisons of clutch size on consecutive days. We examined nests between 0700 and 1100 h and recorded 347 comparisons from 140 nests. In 315 of these comparisons (90.8%), clutches increased by one egg during the 24 h between examinations. In 23 (6.6%), clutches did not increase, while in 9 (2.6%), they increased by two eggs. Some of the zero eggs/day observations might have represented parental responses to unfavorable weather. Such interruption of egg-laying sequences during inclement weather has been observed in Purple Martins by Allen and

Nice (1952) and in Tree Swallows by Kuerzi (1941). However, it is probable that the deviations from the one egg/day pattern were due to slight delays in the timing of egg deposition or to variations in our timing of nest examination. This interpretation is supported by the observation that of the nine clutches that increased by two eggs in one 24-h period, eight (89%) had not increased in size during the preceding 24 h. Absence of widespread variation from the one egg/day pattern suggests that there is little or no intracolonial brood parasitism in Bank Swallows.

The daily timing of egg deposition suggests the same. We counted eggs in 73 nests shortly after sunrise and shortly before sunset on 1 day, and shortly after sunrise the following day. Significantly more eggs ($p < .001$, chi-squared test) were laid during the night and early morning (91%) than during daylight hours (9%). Nighttime and early morning laying of eggs has also been observed in Barn Swallows (Brown 1924, Purchon 1948), House Martins (Brown 1924), Purple Martins (Allen and Nice 1952), Rough-winged Swallows (Lunk 1962), and Tree Swallows (Paynter 1954). On none of our many night visits to the colonies were the birds active, and individuals accidentally disturbed from their burrows seemed completely disoriented and unable to return home. These observations seem to rule out the possibility of nocturnal brood parasitism.

Adult Bank Swallows do not recognize their own eggs. We removed and marked the eggs from two active nests and added them singly to each of nine different nests. Recipient nests contained incomplete or recently completed clutches. In no case did the parents reject the foreign egg. Eight of the nine transferred eggs were hatched by their foster parents, and in the ninth case the nest was abandoned. We also transferred cracked eggs. Six times in six trials parents ejected a cracked egg that we introduced; in three of the six nests we had cracked the parents' own egg and replaced it. This indicates that parents are able to identify and reject at least some kinds of defective or unwanted eggs. That parents cannot recognize viable foreign eggs suggests again that Bank Swallow nests rarely, if ever, receive eggs laid by females other than the rightful owners.

Intracolonial killing of eggs or young has been observed in many colonial birds. Herring Gulls (*Larus argentatus*) (Paludan 1951, Tinbergen 1960, Brown 1967, Parsons 1971), Glaucous-winged Gulls (*Larus glaucescens*) (Vermeer 1963), Black-headed Gulls (*Larus ridibundus*) (Kirkman 1937, Weidmann 1956), Lesser Black-backed Gulls (*Larus fuscus*) (Paludan 1951, Brown 1967), Arctic Terns (*Sterna paradisaea*) (Pettingill 1939), Sooty Terns (*Sterna fuscata*) (Sprunt 1948), and Frigate Birds (*Fregata magnificens*) (Bent 1922) have all been reported to kill and cannibalize (unrelated) offspring. We found no evidence of either intraspecific killing or cannibalism during our 2-yr study.

Increased likelihood of misdirected parental care

The probability that young move between nests, with the possible result of losing an offspring or of mistakenly rearing an unrelated offspring is an obvious disadvantage of coloniality. Parents of solitary species rarely if ever encounter unrelated young in their nests, and local wandering of young of such species is unlikely to bring them into contact with unrelated conspecifics, although such mixing sometimes occurs after fledging (example in Burtt 1973). Furthermore, parents of solitary species seldom face the possibility of mistaking another nest for their own, as do parents among colonial species (Buckley and Buckley 1972a, b).

Available data suggest two general hypotheses about parent-offspring recognition in birds. First, among noncolonial species or species in which the mixing up of broods is rare, nest-site recognition may often be the only form of discrimination (Cullen 1957). Data on Noddy and Sooty Terns (Watson 1908, Watson and Laskey 1915) support this hypothesis. Noddy Terns (*Anous stolidus*), which are noncolonial tree nesters, recognize their own nest sites but apparently cannot recognize their own offspring regardless of the nestling's age. In contrast, Sooty Terns, which are ground-nesting colonial birds, begin to recognize their own young about 4 days after the chicks hatch. Second, among colonial species or species in which mixing up of broods occurs commonly, parent-offspring recognition should most often develop just prior to or coincident with the time when broods first start to mix. This latter hypothesis has been suggested previously (e.g., Cullen 1957, Davies and Carrick 1962, Snow 1963) and has recently been supported by Burtt (1973, *unpubl. data*) and by Miller and Emlen (1975).

Evidence of parent-offspring recognition has been found in every colonially nesting species in which such recognition has been investigated. Herring and Laughing Gulls (*Larus atricilla*) (Tinbergen 1960, Beer 1969, 1970a, b), Ring-billed Gulls (*Larus delawarensis*) (Miller and Emlen 1975), Royal and Crested Terns (*Sterna maxima* and *S. bergii*) (Davies and Carrick 1962, Buckley and Buckley 1972b), Adelie Penguins (*Pygoscelis adeliae*) (Sladen 1958, Penny 1968), and Shags (*Phalacrocorax aristotelis*) (Snow 1963) clearly recognize their own offspring. In the Hirundinidae, parent-offspring recognition has been demonstrated in Barn and Tree Swallows

TABLE 3. a) Responses of parent Bank Swallows to non-offspring misplaced into the parent's home burrows, observed 5–14 July 1972. All data are from color-marked birds from one 11-burrow colony. On 31 occasions parents showed no response within 1 h to unrelated young at the home burrow. b) Responses of parent Bank Swallows to their own offspring when the latter became misplaced into burrows other than their own. Data are from the same colony as in a) 5–14 July 1972. On 44 occasions parents showed no apparent response within 1 h to their own misplaced offspring

a) Behavior of parents toward unrelated young at their own home burrows	Times this behavior was observed (N)	Different adults behaving this way (N)	Percent of total observations
Parent attempts to push or pull it out	18	7	22.5
Parent pecks at it	1	1	1.3
Parent feeds own offspring rather than unrelated young when presented with a choice	50	6	62.5
Parent feeds unrelated young rather than its own offspring when presented with a choice	11	2	13.7
Total	80		100.0
b) Behavior of parents toward their own offspring, misplaced into a burrow other than their own			
Parent "coaxes" its own offspring from the foreign burrow	2	1	2.7
Parent lands at and/or enters foreign burrow containing its own offspring	29	3	39.8
Parent feeds its own offspring at the mouth of the foreign burrow when there is no choice of whom to feed	38	5	52.0
Parent feeds its own offspring at the mouth of the foreign burrow when there is a choice of whom to feed	4	2	5.5
Total	73		100.0

(Burtt 1973, *unpubl. data*), and has been suggested for Crag Martins (Strahm 1956) and Bank Swallows (Petersen 1955). Petersen (1955) stated that parent Bank Swallows recognize and feed only their own fledged young, but he did not discuss the timing of recognition onset.

Young Bank Swallows occasionally get misplaced into foreign nests after coalescence of adjacent nest burrows. Nearly fledged young often walk across the bank face and into nearby burrows. Young which have recently learned how to fly commonly return to the wrong burrow. The rate at which such mixups can occur is indicated by the following observations: on 13 July 1972 at a colony of 11 active nests, 36 separate instances of mixup were seen during 4.5 h (27 times marked young walked into foreign burrows, 9 times they flew); on 15 July 1972 at the same colony, 15 instances of mixing up occurred in 4.0 h (8 walking "errors," 7 flying "errors"). Similar instances have also been reported by Stoner (1926, 1928a, b) and Petersen (1955).

To determine whether Bank Swallows discriminate between their own and unrelated offspring, we color marked parents and young of 10 broods at a colony of 17 nests in 1972. We recorded the responses of parents that encountered foreign young in their own

burrows and of parents whose own young were misplaced during 32.5 h of observation 5–14 July. Most of the observed responses were to natural mixups, but occasionally we deliberately mixed young to facilitate observations of particular parents. That our marking scheme was not causing or enabling parents to behave in certain ways was ascertained by color marking the young of one brood, observing parental recognition of these young, then changing the color of the marks, and again observing recognition. All cases of observed parent-offspring recognition involved young at least 17 days old.

Responses of parents whose young were misplaced into strange burrows are shown in Table 3a. We observed three forms of active discrimination against unrelated young at the home burrow: pecking, pushing out, and pulling out. We did not detect any cooperation between mates in the expulsion of strangers. We also observed more passive discrimination: parents preferentially fed their own young rather than unrelated young when there was a choice. Only two parents made any recognition errors at the home burrow, and these errors all involved feeding of unrelated young. Since both erring parents unequivocally recognized their own offspring on other occasions, these mistakes seem anomalous.

Responses of parents whose young were misplaced into foreign burrows are shown in Table 3b. Sometimes a parent fluttered in front of a strange burrow containing its offspring, as if it were trying to coax it out. When this apparent coaxing was successful, the two flew off together. At other times a parent landed at the edge of a strange burrow containing an offspring and sometimes even entered that burrow. The function of these behaviors is unclear to us, although feeding may have taken place within the foreign burrow, but they certainly represented offspring recognition. Moving to the edges of and entering foreign burrows was not observed in any other context at this stage of the nesting cycle. Parents sometimes went to the edges of strange burrows to feed their own offspring perched there. We observed such feeding under "choice" (when unrelated young were also at the edge of [their own] burrow) and "no choice" conditions. Regarding recognition of offspring misplaced into strange burrows, no errors were ever observed.

Parent Bank Swallows also recognize their own offspring when the latter are in flight. On five occasions, involving three different adults, we observed a parent meet (and sometimes feed) its own offspring in midair. On six other occasions, involving four different parents, an adult met its offspring in midair, then appeared to lead it back to the home burrow by flying straight toward the burrow while vocalizing, then swerving at the last moment so that the following young was able to enter. No aerial behaviors of these sorts were ever observed between adults and unrelated young.

We did not thoroughly investigate either whether the young can recognize their own parents, or the sensory mechanisms underlying parent-offspring recognition. However, on several occasions we observed a misplaced offspring remain deep within a strange burrow for long periods of time while both of its parents were absent from the colony, and then come to the burrow entrance only when one of its parents returned. Also, we often heard alternating vocalizations between parents and their offspring, even when it appeared to us that neither could see the other. These observations suggest that young Bank Swallows recognize their parents as well as vice versa, and that voice is probably important in this regard.

To determine the stage of nestling development at which parent Bank Swallows begin to recognize their own offspring, we transferred marked nestlings of ages 4–5, 8–10, and 13–15 days. For all transfers we placed single marked nestlings into nests containing unrelated young of the same age. Control transfers, in which nestlings were marked and returned to their own nests, were also performed. A

nestling was judged to be accepted by its own or foster parents if it remained in the nest where it was placed for at least 3 days and appeared healthy after the 3 days. Of 9 control and 12 experimental transfers, evenly distributed by nestling age classes, only 1 experimental transfer resulted in rejection of the introduced young. Parents were not observed to search out or feed their own 4–15 day offspring in foreign nests. As previously mentioned, rejection and searching-out were both frequently observed with older young. Since nestlings younger than 15 days rarely get misplaced into strange burrows under natural conditions, the prediction that parent-offspring recognition should develop just prior to or coincident with the time when broods first begin mixing is apparently realized in Bank Swallows.

To test whether noncolonial Rough-winged Swallows recognize their young, we transferred Rough-wing offspring. We transferred only young that were able or almost able to fly. Transferred young were placed into nests containing young of similar age. In none of 17 transfers was there any indication that parent Rough-wings can discriminate between their own and unrelated offspring. Since we have shown that Bank Swallow young at equivalent stages of development are recognized by their parents, these data suggest differences of the predicted sort regarding recognition abilities of Bank and Rough-winged Swallows.

Increased transmission of ectoparasites and diseases

Since most ectoparasites and diseases are commonly transferred from one individual to another by close association or by actual body contact (Rothschild and Clay 1957, Stefferud 1956), individuals of colonial species probably contract ectoparasites and diseases more often than do individuals of closely related noncolonial species. In a comparative study of several Ceylonese bats, Phillips (1924) suggested that infestation by at least one kind of ectoparasite increases with increasing coloniality. Jennings and Soulsby (1958) and Fisher (1952) have suggested that the incidence of disease increases with increasing coloniality in Black-headed Gulls and Fulmars (Fulmarus glacialis), respectively.

In the Hirundinidae, deleterious consequences of ectoparasitism have been convincingly demonstrated in South African Cliff Swallows (Petrochelidon spilodera) (Burgerjon 1964) and Purple Martins (Camin and Moss 1970), both colonial species. Camin and Moss (1970) observed that the presence of martin mites (1) increases parental tendencies to desert nests, (2) reduces average nestling weight, and (3) reduces the number of offspring fledged per nest. Stoner's remarks (1926, 1936) about Apaulina (= Protocalliphora) infestation suggest that
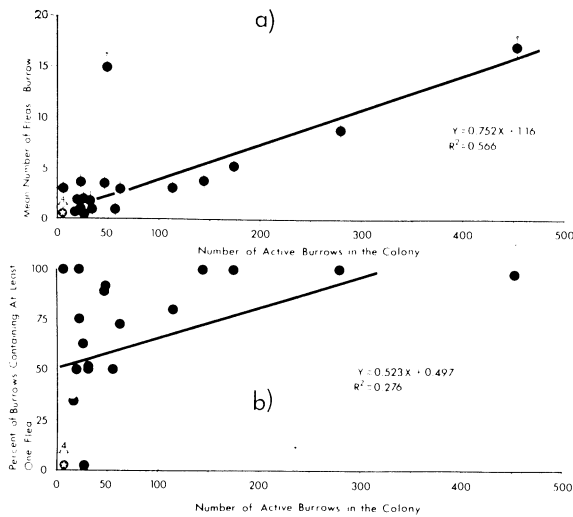
FIG. 6. a) Relationship between the number of fleas ($\bar{x} \pm$ SE) per Bank Swallow burrow and colony size in 1973. All data are from nests containing 10-day-old young. Significance: $p < .01$, regression. b) Relationship between percent of burrows with 10-day-old young containing at least one flea and colony size in 1973. Significance: $p < .01$, Kendall rank correlation test.

ectoparasitism at least sometimes depresses Bank Swallow fitness.

The bird flea *Ceratophyllus riparius* was the most commonly observed Bank Swallow ectoparasite in the Ann Arbor vicinity. These fleas were easily visible at the entrances of active burrows, where they were apparently waiting for a host to arrive. To assess the relationship between colony size and flea infestation, we recorded the number of fleas observed at the edges of 191 burrows from 22 colonies. All data are from burrows in which hatching started exactly 10 days previously, and counts were made between 0900 and 1700 h. We analyzed both the number of fleas per burrow (Fig. 6a) and the probability of having at least one flea (Fig. 6b) as functions of colony size. In each case there was a significant positive relationship (for both, $p < .01$, regression and Kendall rank correlation test). The observed relationships might be explained by the facts that large colonies (1) are more likely than smaller colonies to contain at least one flea-carrying bird, (2) are apparently characterized by more direct contact between individuals than are smaller colonies, and (3) have higher burrow densities than do smaller colonies (discussed later), but we did not thoroughly investigate the mechanisms involved. The positive slopes of Fig. 6a and 6b indicate that individuals in larger colonies experience more flea infestation than do individuals of smaller colonies. Büttiker (1969) counted ixodid ticks at several Bank Swallow

colonies of different sizes, but his data suggest no relationship between colony size and tick infestation.

Whereas Bank Swallows are commonly infested with one or more species of bird lice, dipteran larvae, fleas, mites, and ticks (Stoner 1936, Rothschild and Clay 1957, Büttiker 1969, this study), Rough-winged Swallows rarely harbor ectoparasites (Lunk 1962, *personal communication*). This suggests differences of the expected sort regarding ectoparasitism within colonial species and closely related solitary species.

We did not investigate disease transmission within Bank Swallow colonies, but we predict that such transmission increases with increasing colony size. That mortality resulting from disease can significantly reduce swallow populations has been documented by Lipaev et al. (1970) for three different species.

THE ADVANTAGES OF BANK SWALLOW COLONIALITY

Shortage of suitable nesting habitat?

Shortages of suitable nesting habitat could force individuals of any species to breed closer to conspecifics than would otherwise be most advantageous (Snapp 1973). That shortage of breeding space is a primary determinant of coloniality of island nesting marine birds has been suggested by Lack (1968). In the Hirundinidae, coloniality of Barn Swallows (Snapp 1973, *unpubl. data*), Bank Swallows (Emlen 1971), and Cliff Swallows (Emlen 1952) has been attributed, at least in part, to some sort of habitat limitation. However, only for Barn Swallows was the issue thoroughly investigated. We examined the possibility that Bank Swallow coloniality results from a shortage of suitable breeding habitat in four different ways.

The relationships between the disadvantages of group living for Bank Swallows and colony size already discussed suggest that pairs nesting alone might be at a selective advantage over colonial conspecifics. If colonies result mainly because of shortages of nesting habitat, then isolated Bank Swallow burrows are expected whenever suitable single-burrow habitats are available and there are areas of suitable habitat too large to be saturated by the local breeding population. We sought isolated, active burrows, but of the 3,000+ active nests observed, only 1 ($< 0.1\%$) was more than 100 m from another Bank Swallow burrow. Isolated Bank Swallow burrows have been observed by Hickling (1959) and Windsor (*personal communication*), but apparently very infrequently. On the other hand, we often saw Rough-winged nests > 100 m from the nearest conspecific's nest, as did Lunk (1962). That Bank Swallows are presumably more able, because of their excavating abilities, than Rough-winged to determine

the site of their burrows (Skutch 1960, Lunk 1962, Gaunt 1965) indicates that Bank Swallows could find isolated areas for breeding if it were advantageous to do so.

The spatial distribution of Bank Swallow burrows within a particular area also suggests that suitable habitat for breeding is not limiting. Often an entire sand bank appeared to us to be suitable, but birds nested only in a small portion. Stoner (1936) and Petersen (1955) reported similar findings. At nine different gravel pits we determined the linear amount of sand bank presumably available for nesting, as well as the linear amount actually used by the birds. Percent utilization of apparently suitable areas ranged from 5% to 50% (mean = 13%, SE = ± 5%). This suggests that the birds clump their burrows even when there is no apparent shortage of breeding space, but we realize that human observers probably cannot accurately discriminate between suitable and unsuitable areas for Bank Swallow nesting. Spencer (1962) found that no single soil type characterizes Bank Swallow colonies, and his results also suggest that clumping of burrows is unrelated to availability of suitable habitat.

If shortages of breeding habitat exist, then sand bank sites known to be suitable for Bank Swallow inhabitancy should be equally and maximally used each breeding season. Bergstrom (1951) reported considerable annual fluctuation (over a 7-yr period) in the number of Bank Swallows nesting at a specific river bank site. Stoner (1926, 1936:135) reported similar findings. At the only undisturbed sand bank for which we have information from successive breeding seasons, we observed a fluctuation in bank use apparently similar to that described by Bergstrom (1951) and Stoner (1936). It is possible that all of these observations can be accounted for by changes in habitat suitability between breeding seasons. However, they are more parsimoniously explained by the hypothesis that something other than shortage of breeding space is the principal reason for Bank Swallow coloniality.

Finally, the temporal pattern of formation of large Bank Swallow colonies suggests that the birds are not habitat limited. If large colonies are merely the result of a shortage of habitat, then individuals inhabiting these colonies should nest as far from conspecifics as they can and should remain as isolated as possible for as long as possible (Snapp 1973 argues similarly). Minimization of nearest-neighbor breeding synchrony and a heterogeneous mosaic of nest stages across the colony should result. To determine whether large colonies exhibit these characteristics, we examined as many nests as possible in colonies of 114, 279, 383, and 451 active burrows. All nest examinations at each colony were made in
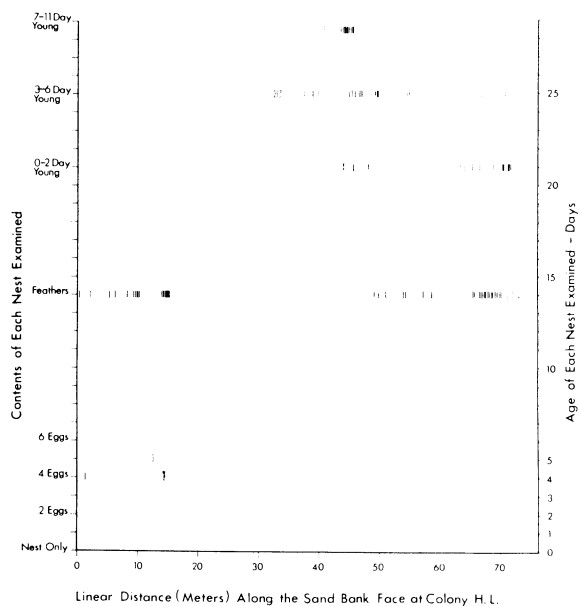

FIG. 7. Stages of 103 active Bank Swallow burrows on 14 June 1973 at a colony of 114 nests plotted against linear distance along the sand bank face. The chronological ordinate, indicating the mean number of days separating nests at each stage, was determined in 1972.

a single day. In all four colonies, consecutive nesters appeared to group their burrows, and there was an apparent maximization of nearest-neighbor synchrony, although each colony as a whole appeared asynchronous. Data from one of the colonies are shown in Fig. 7. Similar nonrandom patterns of large colony formation have been observed in Tricolored Blackbirds (*Agelaius tricolor*) (Tyler 1907, Orians 1961b, Payne 1969), Piñon Jays (*Gymnorhinus cyanocephala*) (Balda and Bateman 1972), Franklin's Gulls (*Larus pepixcan*) (Burger 1974b), White Pelicans (*Pelicanus o. roseus*) (Ward 1924), and Cliff Swallows (Emlen 1952). Since Bank Swallows of the colonies that we examined eventually utilized all parts of the colony sand banks, it is apparent that the entire bank constituted suitable breeding habitat in each case. Unless one postulates that the suitabilities of our four sand banks varied in a manner suggested by Fig. 7, our results further indicate that Bank Swallow coloniality cannot be explained in terms of a mere shortage of suitable breeding habitat. Although we examined only large Bank Swallow colonies in this regard, we believe that these arguments hold true for smaller colonies as well. However, both the variance in reproductive timing (Emlen and Demong 1975, this study) and the number of available nests are small within small colonies, and therefore we did not attempt to analyze nearest-neighbor synchrony in them.

Social foraging?

Social foraging, or group hunting for food, has been observed in many colonial species, including Brewer's Blackbirds (Horn 1968), Cliff Swallows (Emlen 1952), Oilbirds (*Steatornis caripensis*) (Snow 1961), Great Blue Herons (*Ardea herodias*) (Krebs 1974), Tricolored Blackbirds (Orians 1961*b*, Payne 1969), and White Pelicans (Behle 1944, 1958). Snapp (1973, *unpubl. data*) observed that Barn Swallows sometimes forage in groups of two or more. For both Cliff Swallows (Emlen 1952) and Bank Swallows (Emlen 1971, Emlen and Demong 1974, 1975), it has been suggested that social facilitation of foraging constitutes one of the principal advantages of coloniality.

Two independent considerations suggest that social foraging might be important to Bank Swallows: nature of their aerial prey and directional feeding patterns of adults. All arthropods preyed on by Bank Swallows are so small and of a nature that they can be easily captured by birds feeding alone (Beal 1918, Stoner 1926, 1936, Beyer 1938). Therefore, if social facilitation of foraging has evolved in these birds, it must be an evolutionary response to aggregated aerial prey that are widely and unpredictably scattered. These aggregations must consist of more food than can be easily consumed by one bird or mated pair, and must be difficult for solitary foragers to find (Ward 1965, Horn 1968, Alexander 1974, Krebs 1974). At least some prey meet these criteria, so it is possible that individuals which forage in groups will fare better than those which forage alone. We obtained indirect evidence that adults might sometimes feed in groups. At one colony of 17 active nests, we recorded the compass departure directions of six color-marked parents (from four different nests) on four different days during the time when young were being actively fed. We categorized each departure direction into one of twelve 30° circular segments. Because the six parents ranged far from the colony while foraging, we could not examine grouping tendencies during actual foraging. Therefore, we assume that the birds which left the colony heading in the same direction could have foraged together, while those which departed in different directions did not do so. We analyzed 8 h of directional data with the parametric two-sample (circular) test described by Batschelet (1965). With the exception of two parents from different nests during single hours of observation, the mean departure direction of each foraging parent overlapped significantly ($p < .05$) with that of at least one other parent during each hour of observation. The mean number of overlaps was 2.7 ± 0.2 (SE) out of a possible 5, and these data suggest that parents may not feed independently.

Conversely, several lines of evidence suggest that social facilitation of foraging is not an important feature of Bank Swallow coloniality. We investigated the clumping of burrows, the possibility of foraging signals, synchronization of feeding activities, foraging success during temporary food shortages, and nestling growth rate (as measured by weighing 10-day-old nestlings) as a function of colony size, and all of these investigations suggest that Bank Swallows do not feed in groups.

If social facilitation of foraging has been important in the evolution of coloniality, then the proximity of nests within a colony should represent a compromise between attempts to nest close enough to other parents so that information about foraging sites can be optimally gained and transferred, and attempts to nest as far as possible from other parents so as to reduce the disadvantages of coloniality. In Bank Swallows both the visual and auditory senses, at least, are probably well developed and it therefore seems that food signals between parents could be efficiently transferred even if nests were widely separated. Emlen (1952) observed that parents from four different Cliff Swallow colonies were "freely interspersed" at feeding sites, and that "on the foraging ground most of the birds at any given moment were aggregated in a single foraging unit." Unless members of each of these four colonies always found the food independently of members of the other three colonies, these observations suggest that group foraging in this swallow does not require that individuals group their nests within one colony. We believe that this argument is general: the social facilitation of foraging never requires coloniality. Therefore, this explanation is not likely to be sufficient for the tight clumping of Bank Swallow burrows.

Individuals that live in groups mainly because of advantages associated with social foraging are selected to be legitimately concerned about the food acquisition of others within the colony, one or more of which might be the finder of food on subsequent days. A system of reciprocity (Trivers 1971, Alexander 1974) involving food-finding signals is expected to evolve in this case. Alternatively, if coloniality is not based on social facilitation of foraging, then individuals are probably selected to maximize the capacity to "parasitize" the food-finding of other individuals and to minimize behaviors that might alert others to personal food-finding successes; no food-finding signals are expected in this case, but parasitism should be common. Great Blue Herons (Krebs 1974) apparently communicate information about food sources to conspecifics, as may Oilbirds (Snow 1961). Horn (1968) observed that Brewer's Blackbird parents

communicate information regarding foraging sites to other adults, but the transfer of information may represent parasitism since Horn concluded that the communication is "unintentional." Emlen (1971) noted that Bank Swallows sometimes "follow other individuals to the local, ephemeral concentrations of insects," but he never detected any food-finding signals (S. Emlen, *pers. comm.*). We also never detected any mechanism by which adult Bank Swallows inform other adults about food sources, but we realize that such signals might be so subtle as to render them practically undetectable to humans.

If social facilitation of foraging is of any significance, foraging parents are expected to at least sometimes synchronize their feeding activities with those of other parents. Such synchronization of feeding has been observed in several colonial species, including Great Blue Herons (Krebs 1974), Oilbirds (Snow 1961), and White Pelicans (Behle 1944, 1958, Low et al. 1950). There is dramatic synchronization of Bank Swallow arrivals at and departures from colony sites early in the breeding season, before any eggs are laid. At this time colonies are sometimes totally deserted for as long as 2–3 h, may fill with birds within a few minutes, then just as quickly become deserted again (Hickling 1959, S. Emlen, *pers. comm.*). This early season behavioral synchronization might be interpreted in several ways. However, unless such synchrony is also evident during the time when the young are being fed, there is no obvious support for the social foraging hypothesis.

It was our impression from observations at several colonies that parent Bank Swallows do not forage synchronously in either large or small groups when they are raising offspring. To test this, we recorded at one colony of five active nests the arrival times on 6 July and 9 July 1973 of all 10 color-marked parents to the colony site. On both days the distribution of arrival times was random (for both, $0.10 < p < 0.50$, analysis by testing for flatness of spectrum), indicating that parents do not feed in a unified group. With these data we further tested whether parents feed in smaller groups of two or three. We did this by examining the number of times that birds arrived in "reflexive pairs." Two parents constituted a "reflexive pair" when their arrival times were closer to each other than either one was to any other arrival time (Clark 1956, Clark and Evans 1955). A large number of reflexive pairs should have resulted if parents consistently fed in small groups. Assuming that individual parents feed independently, the expected numbers of reflexive pairs were 165 and 173 for 6 July and 9 July, respectively. We observed 176 and 182 reflexive pairs for these days, indicating no deviation from for-

aging independence ($p > .05$, E. D. Rothman, *personal communication*). These data suggest that, in addition to not feeding in large groups, parent Bank Swallows also do not feed in groups of two or three. Possibly, however parents that locate food sources somehow inform other parents of the existence and whereabouts of the sources, and continuous asynchronous feeding occurs until the food is exhausted. Once a bird learns from another bird about a foraging site, there may not be any advantage for the former to synchronize with the latter. In that case, there would be social facilitation of foraging with little or no feeding synchronization. Further, it is possible that Bank Swallows synchronize their feeding activities only temporarily under specific circumstances, and that our data are from times when such synchronization was not occurring. We suggest that similar data with marked individuals from large colonies and segments thereof would be valuable in deciding the issue.

If social facilitation of foraging is an important aspect of Bank Swallow coloniality, foraging success might increase with increasing colony size, since larger colonies presumably contain more food-searching parents that inform other parents (accidentally or otherwise) of the existence and whereabouts of new food sources. Conversely, if social foraging is not important, intracolonial competition for food should be detectable, at least at larger colony sizes. Comparing foraging success with colony size proved difficult. At first we considered intercolonial comparison of feeding rates. However such a comparison would be meaningful only if parents from different colonies brought the same quantities of the same prey to their offspring on each feeding trip (Nettleship 1972). In a preliminary 2-day investigation, we examined variation of average weight gained per feeding trip per clutch within and between colonies. We manipulated compared clutches so that they contained the same number of young (five) of approximately the same size and age, all younger than 10–11 days. We recorded feeding rates and weight changes at no less than two nests from each of two different colonies during the same hours of the same days. Compared colonies were at least 8 km apart. On both days that we recorded feeding rates and weight changes (8 and 9 June 1973), intercolonial variation in weight gain per feeding trip per clutch was greater than intracolonial variation, but on only one of the days were the differences statistically significant at the $p < .05$ level (Student's *t*-tests). From these data we conclude (1) that parents from different colonies apparently capture either different prey or different quantities of the same prey, and (2)

that intercolonial comparisons of feeding rates alone would be meaningless.

At a time in 1972 when most of the Bank Swallow colonies in the Ann Arbor vicinity contained unfledged young, there were four consecutive days (21–24 June) of unusually cold, damp weather. This cold spell provided us with an unexpected opportunity to compare foraging success with colony size. On 25 and 26 June we visited 10 of our study colonies and discovered dead, unmutilated young below burrows at all of them. Since no alternate explanation (such as disease) for the widespread mortality was evident, we assume that the juvenile deaths resulted from the inability of parents to adequately feed their offspring during a time of food scarcity; similar widespread Bank Swallow juvenile mortality occurred again near Ann Arbor in 1974 following a period of cold, damp weather (R. L. Marsh, *personal communication*). That the number of aerial arthropods decreases dramatically with decreasing temperature or increasing precipitation has been demonstrated by a variety of methods (Hardy and Milne 1938, McClure 1938, Glick 1939, Freeman 1945). Further, extensive mortality of adults and young of species dependent on aerial arthropods for food has often been observed following periods of cold, damp weather (Koskimies 1950, Lack and Lack 1951, Haigh 1968), especially among swallows (Chapman 1935, Bergstrom 1951, MacLeod et al. 1953, Mason 1953, Benton and Tucker 1968, Skead and Skead 1970). If social facilitation of foraging is an important feature of Bank Swallow coloniality, then associated benefits should be most obvious during times of prey scarcity. We recorded juvenile survivorship, measured as the percent of nests with at least one surviving nestling, at each of the 10 colonies that we examined after the 1972 cold spell (Fig. 8). A significant negative relationship exists between juvenile survivorship and colony size ($p < .05$, regression). These data suggest that during times of aerial prey scarcity, when help with food-finding would presumably be most valuable, social facilitation of foraging, if it occurs, seems to be of minor effectiveness for Bank Swallow parents.

If social facilitation of foraging constitutes one of the primary advantages of Bank Swallow coloniality, then nestlings in large colonies might be expected to grow faster than nestlings in smaller colonies. Parents of the former are presumably better able than parents of the latter (because of the presence of more food-finding, signaling conspecifics) to find aerial prey. If, on the other hand, social facilitation of foraging has not evolved in these birds, there should be no relationship or a negative relationship between nestling growth rate and colony size. For Barn Swallows, Snapp's data
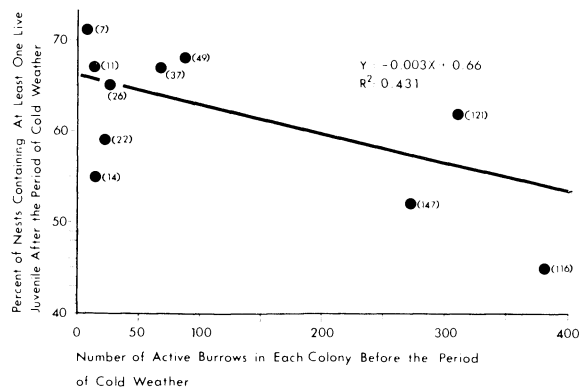

FIG. 8. Relationship between survivorship of nestling Bank Swallows after 4 days of cold weather (21–24 June 1972) and colony size. Significance: $p < .05$, regression. Numbers in parentheses are the number of nests examined in each colony. Survivorship of nestlings during this period was age-dependent, older young dying first ($p < .05$, chi-squared; data from 98 nests at one colony), but the age of nestlings and colony size were unrelated ($p > .50$, regression).

(1973, *pers. comm.*) suggest a negative relationship between nestling growth rate and colony size. To estimate nestling growth rate, we weighed 199 clutches from 21 different colonies on the 10th day after the initiation of hatching. Whenever possible, weighings were made before noon. We chose the 10th day because the growth curve for nestling Bank Swallows does not become asymptotic until more than 10 days after hatching (Petersen 1955, R. L. Marsh, *unpublished data*). Therefore, recorded weights provide indirect information about parental foraging success during the 10 days following hatching. Our results (Fig. 9) show no relationship between colony size and the number of young in the nest on the 10th day after the initiation of hatching. After the removal of the effects of clutch size on 10-day nestling weight by multiple regression analysis, we conclude that there is a significant negative relationship ($p = .052$) between 10-day nestling weight and colony size. Three assumptions inherent in the interpretation of our data are (1) that no relationship exists between weight at hatching and colony size, (2) that either all clutches were fed by two parents or that no relationship exists between the presence of two feeding parents at each nest and colony size, and (3) that no relationship exists between time elapsed before the completion of intra-nest hatching, which usually extends 2–3 days (Petersen 1955, S. Emlen, *personal communication*), and colony size. The relationship in Fig. 9 suggests that benefits from social foraging do not constitute an important advantage of Bank Swallow coloniality. In fact, these data, along with the cold weather death data (Fig. 8), suggest that increased competition for
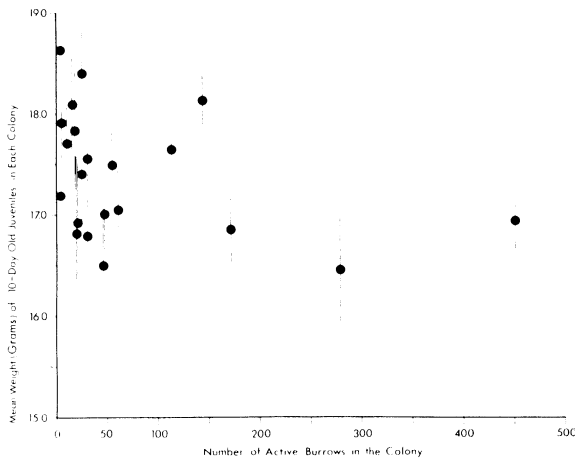
FIG. 9. Relationship between weight (mean ± SE) in grams of 10-day-old Bank Swallows and colony size. Significance: $p = .052$, multiple linear regression, with clutch size and colony size as independent variables and mean weight as the dependent variable. Mean weight of 10-day nestlings varied inversely with clutch size ($p < .01$, regression), but clutch size on the 10th day after the initiation of hatching and colony size were unrelated ($p > .50$, regression).

food might be another disadvantage of Bank Swallow coloniality.

Decreased predation?

It is possible that individuals might gain by breeding in colonies because of decreased predation on themselves or their eggs and offspring. Discrimination is difficult between those advantages or characteristics of coloniality resulting from social facilitation of foraging and those resulting from decreased predation. For example, using similar evidence, Gadgil (1972) reached essentially opposite conclusions from those of Ward (1965), Zahavi (1971), and Ward and Zahavi (1973) regarding whether social facilitation of foraging or decreased predation is more important in the evolution of communal roosting (another form of group living).

Among colonial birds, the most commonly observed form of group defense against predators is mobbing, although decreased predation could theoretically result without mobbing (or any other form of group defense) because of "selfish herd" effects (Hamilton 1971). Mobbing may involve physical assault or the creation of auditory or visual chaos. That avian mobs are at least sometimes successful in deterring predators has been repeatedly demonstrated (e.g., Burton and Thurston 1959, Kruuk 1964, Horn 1968, Burger 1974b). Among swallows, predator mobbing has been observed in Barn Swallows (Smith and Graves 1973, personal communication, Snapp 1973), Crag Martins (Strahm 1956),

House Martins (Lind 1962), and Tree Swallows (Kuerzi 1941). Bank Swallows also mob predators (D. Windsor and S. Emlen, personal communication, this study), and we investigated the possibility that an important advantage of Bank Swallow coloniality is reduced predation on eggs, young, or adults.

When a predator approaches a Bank Swallow colony, a mobbing response quickly develops, involving many or most of the colony parents. If the predator gets close to one or more burrows, mobbing birds begin flying in a horizontally oriented, doughnut-shaped vortex which at any given instant is several bird layers thick. Individual birds fly within the vortex, hover in front of the predator for a few seconds, then fly within the vortex again. From observations with color-marked birds we determined that (1) only adults mob (i.e., recently fledged juveniles do not), (2) individual parents mob predators that are attacking burrows very distant from their own, and (3) the mobbing response is usually initiated by one or more adults whose burrows are in the immediate vicinity of the predator's first approach. Mobbing occurs during all stages of the nesting cycle and typically there is no physical contact between predator and mobbing birds. We did not investigate whether mobbing varies with different predators, but such variation probably exists (Kruuk 1964).

As we have noted, individual Bank Swallows often mob a predator that is attacking burrows very distant from the home burrow. Since mobbing Bank Swallows are sometimes captured and killed by predators (similar killings have been observed in other species by Hartley 1950 and Smith 1969), mobbing obviously entails certain reproductive risks, and the advantage for parents of mobbing predators far from the home burrow is not clear. Banding studies by Stoner (1937, 1941) and Bergstrom (1951) suggest that close relatives only rarely nest in the same colony, so kin selection (Hamilton 1964, Maynard-Smith 1964) seems unlikely. The question of why a parent Bank Swallow mobs a predator when its own home burrow is not in apparent danger is similar to the question, analyzed by Trivers (1971) of why individuals of some species utter alarm calls when their own phenotypes are not in apparent danger. We believe that parent Bank Swallows probably minimize their own mobbing and maximally parasitize the mobbing of other parents, and that the probability of such cheating increases with increasing colony size.

If decreased predation is an important advantage of Bank Swallow coloniality, then the following are appropriate expectations:

1) Animals eliciting mobbing should prey on Bank Swallows.

2) Mobs should at least sometimes successfully deter predators.

3) Effectiveness of mobbing should increase with increasing colony size.

4) Spatial arrangement of burrows within a colony should reflect attempts by individuals to maximize selfish herd effects (Hamilton 1971).

5) Intracolonial breeding synchrony should be greater than intercolonial breeding synchrony.

6) Large colonies should experience less predation per adult or per nest than smaller colonies.

We tested each of these hypotheses with the following results.

1) *Do Bank Swallows mob only "real" predators?* —The following animals at least sometimes elicit Bank Swallow mobbing under natural conditions: long-tailed weasels (Lunk 1962), Common Crows (*Corvus brachyrhynchos*) (this study), Belted Kingfishers (*Megaceryle alcyon*) (this study), Blue Jays (*Cyanocitta cristata*) (this study), House Sparrows (*Passer domesticus*) (this study), and Sparrow Hawks (*Falco sparverius*) (D. Windsor and S. Emlen, *personal communication*, this study). All of these are known or suspected predators or destroyers of Bank Swallow adults or clutches (Lunk 1962, Freer 1973, D. Windsor and S. Emlen, *personal communication*, this study). The following birds, repeatedly observed near Bank Swallow colonies but not known or suspected Bank Swallow predators, were never seen to elicit mobbing: Rough-winged Swallows, Barn Swallows, Cliff Swallows, Mourning Doves (*Zenaidura macroura*), and Song Sparrows (*Melospiza melodia*).

2) *Does Bank Swallow mobbing deter predators?* —On 28 June 1972 at a colony of 172 active nests, we saw a Blue Jay attack, kill, and then eat a young Bank Swallow that had fallen from its home burrow. After witnessing this natural predation, we set up a mobbing experiment at the same colony. We removed three young Bank Swallows from their home burrows and with 15-cm pieces of string tethered one at each of three different distances from the main group of burrows (Table 4). On 17 occasions, one of at least two different Blue Jays entered the colony area and attempted to attack one of the tethered young. We replaced nestlings that were killed or injured in these attacks with uninjured young. On each of the 17 attempts, the attacking Blue Jay was mobbed to some extent, but the mobs near the main cluster of burrows were more often effective at jay deterrence than those at the other two positions (Table 4). The data in Table 4 demonstrate that Bank Swallow mobs are at least sometimes effective in deterring a predator, and that Blue Jays, and presumably other predators, are more

TABLE 4. Deterrence of wild Blue Jays by Bank Swallow mobs at a 172-burrow colony in 1972

Behavior of Blue Jays	Distance from burrows to tethered young Bank Swallow		
	0–1 m (bank face)	9–11 m (bank base)	18–20 m (Center of gravel pit)
Times jays attack and kill the young bird (N)	0	2	7
Times jays attack but are unsuccessful in killing the young bird (N)	0	2	1
Times jays are deterred from attacking the young bird (N)	5	0	0
Successful attacks at each distance (%)	0	50	88

often effectively deterred from areas immediately adjacent to large clusters of burrows than from more distant areas. Isolated Bank Swallow nests may therefore be especially susceptible to predation. We also observed several successful deterrences of Sparrow Hawks by Bank Swallow mobs under natural conditions. At Bank Swallow colonies near Ithaca, New York, D. Windsor and S. Emlen (*personal communication*) observed numerous attempts by Sparrow Hawks to capture adults and young, and they suggested that mobbing Bank Swallows "seem to be almost totally ignored" by attacking Sparrow Hawks. However D. Windsor and S. Emlen (*personal communication*) also observed that 16 of 25 attempted predations by Sparrow Hawks (64%) were unsuccessful. Perhaps some of the 16 failures resulted, at least in part, from Bank Swallow mobbing.

3) *Does the effectiveness of Bank Swallow mobbing increase with increasing colony size?*—For Arctic Terns and Arctic Skuas (*Catharacta skua*), Williamson (1949) suggested that the "aggressiveness" of mobbing directed toward humans, at least, increases with increasing colony size. We observed few cases of attempted predation under natural conditions during our 2-yr study, and we were therefore unable to make direct comparisons of Bank Swallow mobbing success with colony size. We could, however, make indirect comparisons. We examined three aspects of mobbing (mob size, quickness of initiation, and vocal commotion), each of which probably affects predator deterrence. Mobbings for these comparisons were always elicited by placing the stuffed long-tailed weasel in a central burrow.

If Bank Swallow mobbing has evolved in the context of predator deterrence, then increases in the number of mobbing parents should favorably affect the probability of repelling predators. Because it is impossible to count accurately the number of
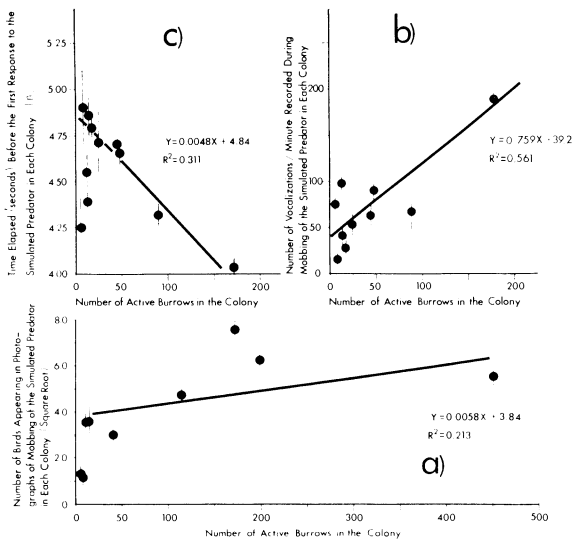
Fig. 10. (c) Relationship between time elapsed (natural logarithm) before the first response to the stuffed weasel ($\bar{x} \pm$ SE) and Bank Swallow colony size. Significance: $p < .001$, regression. (b) Relationship between vocal commotion associated with Bank Swallow mobbing and colony size. Each mean $\pm$ SE represents 3 min of tape-recording during a single mob at each colony, analyzed in 1-min increments. Significance: $p < .05$, regression. (a) Relationship between number of Bank Swallows (square root) appearing in photographs of mobs ($\bar{x} \pm$ SE) and colony size. Significance: $p < .001$, regression.

birds in a mob, we photographed mobs at approximately 1-min intervals at nine different colonies after the mobbing response to the centrally placed, stuffed weasel had fully developed. At the four largest colonies, we photographed mobs at two or three different central burrows. We assume that there is no relationship or a negative relationship between colony size and (1) percent of mobbing birds captured within the photographs, and (2) the effect of the presence of nearby human observers on the mobbing response. Since entire mobs did not fit into the camera's field, the actual number of mobbing birds at all colonies was larger than our data indicate. Our data are shown in Fig. 10a. To stabilize variances, we analyzed the square root of observed mob sizes. The positive relationship between the square roots of photographed mob sizes and colony size is highly significant ($p < .001$, regression), and this suggests that predators invading large colonies are mobbed by more adult Bank Swallows than are predators invading smaller colonies.

Because large colonies contain more pairs of eyes than do smaller colonies, predators should be more quickly detected in the former (similar arguments were made by Lack 1954, Crook 1964, and Pulliam

1973). Further, approaching predators that are quickly detected and subsequently mobbed are probably more likely to be deterred than are predators not so quickly detected. Therefore, individuals of large colonies should be at an advantage over individuals of smaller colonies in this regard. To determine the relevance of these arguments to Bank Swallows, we examined the relationship between colony size and time elapsed between introduction of the stuffed weasel and the initiation of mobbing. Initiation was scored when one or more adults first began to flutter in front of the weasel; in all cases, the full mobbing response developed soon after initiation. We recorded elapsed time intervals before mobbing initiation 3–6 times at each of 11 colonies. After each trial we removed the weasel for at least 15 min to allow the birds to resume normal activity. The data are shown in Fig. 10c. To stabilize variances we analyzed the natural logarithms of elapsed times before mob initiation. Figure 10c shows a significant negative relationship between the natural logarithms of mob initiation times and colony size ($p < .001$, regression), and this suggests that predators are more quickly detected in larger colonies. To determine whether elapsed times before initiation of mobbing vary significantly within the same colony on different days, we collected a second series of these data at five colonies within a week of the first series. At four of these five colonies, there was no significant difference at the $p < .05$ level (Student's t-tests) between the first and second series of elapsed times. Why adults from larger colonies apparently respond more quickly to predators than do adults from smaller colonies is not obvious. Possibly parents from the former feel relatively safe within a large collection of birds, and return quickly to the colony site after any disturbance. There is another possibility: as noted earlier, it was usually a parent whose home burrow was near the stuffed weasel that initiated mobbing, even though a large number of parents of the colony eventually participated. Consequently the relationship shown in Fig. 10c might be generated if (a) parents tend to watch closely only some critical area around their own home burrows for the first approach of predators, and (b) burrow density increases with increasing colony size. We have no data bearing on (a), but we were able to demonstrate (b) by counting the number of burrows within three concentric circles of different radii (0.4 m, 1.0 m, and 2.4 m) at 26 different colonies. At each colony we chose the area with the greatest apparent burrow density, and then designated a burrow within that area as the center for all three concentric circles. At each radius, burrow density increased directly with colony size (for all three, $p < .01$, regression), suggesting that

each area of burrows in large colonies may be watched by more parents than are areas of similar sizes in small colonies.

Finally, we investigated the vocal commotion associated with mobbing. Just before and shortly after fledging, young Bank Swallows usually remain at the edges of burrows where they are fed by parents. When such young hear mobbing adults' alarm notes, they retreat into their nest chambers (D. Windsor and S. Emlen, *pers. comm.*). This retreat ensures safety from most avian predators and probably from some nonavian predators, and increases in the number or frequency of alarm notes probably enhance the likelihood that each young Bank Swallow will hear one or more alarm notes in time to respond appropriately. Further, the collection of different sounds made by mobbing Bank Swallows may help deter predators, although we have no data bearing directly on this issue. If the vocal commotion annoys, distracts, or confuses some predators so that they are induced to move on in search of different prey, increases in vocal commotion should favorably influence deterrence of predators. To examine the relationship between vocal commotion and colony size, we tape-recorded mobbing vocalizations for 3 min after mob initiation at 10 different colonies. When possible, we placed the recording microphone and the stuffed weasel into the same burrow. We did not record vocal commotion during normal activity (i.e., no mobbing) for comparison, and so we are unable to compare colonies independent of "background" vocalizations. We analyzed the data by dividing the single recording from each colony into 1-min segments and counting the number of vocalizations within each segment. We made no attempt to separate vocalizations into "predator-related" and "predator-unrelated" categories, but we agree with D. Windsor and S. Emlen (*pers. comm.*) that some sounds are heard only during mobbing. The data (Fig. 10b) show a significant positive relationship between vocal commotion generated during mobbing and colony size ($p < .05$, regression), suggesting an advantage to individuals of larger colonies in this regard.

4) *Does the spatial arrangement of burrows within Bank Swallow colonies reflect attempts by individuals to maximize selfish herd effects?*— Hamilton (1971) and Vine (1971) suggested that individuals might gain by breeding near conspecifics because of increased opportunities to cause others or their offspring to be more available to predators than themselves or their own offspring. In this way, colonial breeding could be selectively advantageous even in the absence of any form of group defense. Advantages of breeding in such "selfish herds" (Hamilton 1971) should be most evident at greatest colony densities. Therefore, if decreased predation is an important benefit of coloniality, parents should compete to nest within clusters of maximal density. Further, assuming only that predators approach from outside the colony, there should be identifiable differences between the breeding success of central and peripheral nests, resulting either directly or indirectly from differences in predation. This effect will be enhanced, moreover, by tendencies of older, more experienced, or more powerful pairs to acquire the safest nesting sites. That central nests within colonies experience less predation than peripheral nests has been demonstrated in several species, including Adelie Penguins (Eklund 1961, Taylor 1962, Reid 1964, Penney 1968), Black-headed Gulls (Kruuk 1964, Patterson 1965), Piñon Jays (Balda and Bateman 1972), and White Pelicans (Schaller 1964). In addition, that central nests within a colony are more successful than peripheral nests in one or more ways which might be at least indirectly related to decreased predation has been demonstrated in Brewer's Blackbirds (Horn 1968), Cattle Egrets (Siegfried 1972), Kittiwakes (*Rissa tridactyla*) (Coulson 1968), Cliff Swallows (Emlen 1952), and Bank Swallows (Emlen 1971).

Bank Swallows within a colony typically group their burrows in dense clusters. As discussed previously, this tight clumping is not satisfactorily explained by either limitation of suitable breeding habitat or social facilitation of foraging. On the other hand, maximization of nest densities is expected when there is heavy predation on adults or clutches (Hamilton 1971). The apparent ubiquity of tight clumping of burrows within colonies provides indirect evidence that Bank Swallow coloniality may have evolved in the context of decreased predation.

Emlen (1971) reported that central nests of Bank Swallow colonies are more successful than peripheral nests, and he suggested that the differences were the result of increased abandonment of peripheral nests rather than to differential predation. However, Emlen's (1971) findings may indicate effects of selfish herd life. The absence of increased predation at peripheral sites might be the result of excessive abandonment of these sites by younger, less experienced, less powerful parents and by parents that have been selected to recognize situations unfavorable for rearing clutches to completion.

For Bank Swallows it is particularly difficult to distinguish between center-edge differences resulting from selfish herd life and those resulting from differences in group defense. To determine whether peripheral nests have as much protection from predators via mobbing as central nests, we photographed central and peripheral mobbing responses

TABLE 5. Number ($\bar{x} \pm$ SE) of Bank Swallows counted in photographs of central and edge mobs at various colonies. Mobs were elicited by the stuffed weasel. All data were compared by Student's t-tests. *To stabilize variances, we analyzed the natural logarithms of photographed mob sizes at this colony

Colony size	No. birds in central mobs $\bar{x}$	No. birds in edge mobs $\bar{x}$	Significance of center-edge differences
114	23.15 ± 1.17 ($N = 3$)	16.42 ± 1.50 ($N = 2$)	$p < .01$
172	61.50 ± 4.63 ($N = 2$)	45.10 ± 2.07 ($N = 2$)	$p < .01*$
198	41.20 ± 3.49 ($N = 2$)	26.83 ± 3.75 ($N = 1$)	$p < .05$
451	29.13 ± 2.12 ($N = 2$)	22.57 ± 2.17 ($N = 3$)	$p < .05$

to the stuffed weasel at four large colonies. At each colony we took several pictures of each mob. We assume that (a) the percent of the mobbing birds captured within the photographs and (b) the effect of the presence of human observers on the mobbing response did not vary between centers and edges of the same colony. Our data are shown in Table 5. At each colony, photographs of central mobs contained more birds than did those of peripheral mobs (for all four, $p < .05$, Student's t-tests). Selfish herd effects must certainly be considered in any investigation of center-edge differences, but the data of Table 5 suggest that differences between center and edge mobs might also be important, at least for Bank Swallows.

5) *Is intracolonial breeding synchrony greater than intercolonial breeding synchrony?*—If decreased predation on adults, eggs, or young constitutes an important advantage of coloniality, then parents are expected to synchronize their reproductive activities with those of other parents within the colony (Elgood and Ward 1963, Kruuk 1964, Patterson 1965). Parents that start clutches before any other parents are at a disadvantage because (a) early in the nesting cycle their eggs are extremely attractive and vulnerable to predators since all other nests contain no or fewer eggs, and (b) later in the nesting cycle, since they are closer to successfully rearing offspring, they may work harder than more synchronous birds to defend their broods. Parents that start clutches after all other parents may during much of the nesting cycle be able to exploit the predator defenses of other, earlier breeding parents. However, these late breeders will be at a disadvantage later in the nesting cycle when all or most of the other parents have departed with their offspring and when, therefore, their own offspring will be especially attractive and vulnerable to predators. That asynchronous

breeders within a colony experience reduced reproductive success has been demonstrated in many colonial species, including Puffins (*Fratercula arctica*) (Nettleship 1972), Red-winged Blackbirds (*Agelaius phoeniceus*) (Robertson 1973), Shags (Snow 1960), Storm Petrels (*Oceanodroma castro* and *O. tethys*) (Harris 1969), Black-headed Gulls (Weidmann 1956, Patterson 1965), Herring Gulls (Paludan 1951, Brown 1967, Parsons 1971), and Lesser Black-backed Gulls (Brown 1967). Within the latter three gull species, at least, the reduced breeding success of asynchronous breeders apparently results mainly from increased predation, some of which is intraspecific.

To determine to what degree Bank Swallows synchronize their reproductive activities, we examined as many nests as possible from nine different colonies (containing from 4 to 61 active nests) on 14–15 June 1973. We classified nests into 1 of 12 categories based on their contents. Each category represented a different known or estimated age of the nest. We considered empty nests to be zero days old, nests containing one egg, 1 day old, nests with young that had just hatched, 21 days old, etc. Our data are shown in Fig. 11. For colonies containing fewer than about 60 active nests, intracolonial breeding synchrony is greater than intercolonial breeding synchrony ($p < .001$, Kruskal-Wallis analysis of variance by ranks), a conclusion also reached by Emlen (1971) and Emlen and Demong (1975). Intracolonial breeding synchrony has also been shown to exceed intercolonial synchrony in Black-faced Diochs (*Quelea quelea*) (Ward 1965), Black-headed Weavers (*Ploceus cucullatus*) (Hall 1970), Brown-hooded Gulls (*Larus maculipennis*) (Burger 1974a), Cliff Swallows (Emlen 1952), Swallow-tailed Gulls (*Creagrus furcatus*) (Hailman 1964), Tricolored Blackbirds (Lack and Emlen 1939, Orians 1961b), and White Pelicans (Behle 1944, Schaller 1964). Even when two small, distinct Bank Swallow colonies are close together and thus are presumably subjected to similar selective pressures, intracolonial breeding synchrony is greater than intercolonial synchrony in nearly every case. As previously discussed, nesting in large Bank Swallow colonies usually starts at some middle and radiates toward the ends of the bank (Fig. 7). Although each large colony as a whole appears asynchronous, there is a maximization of nearest-neighbor breeding synchrony.

We did not compare reproductive successes of synchronous and asynchronous breeders within Bank Swallow colonies. However Emlen and Demong (1974, 1975) have made such a comparison. By following individual nests from the initiation of egg-laying until the 16th day after hatching began, they
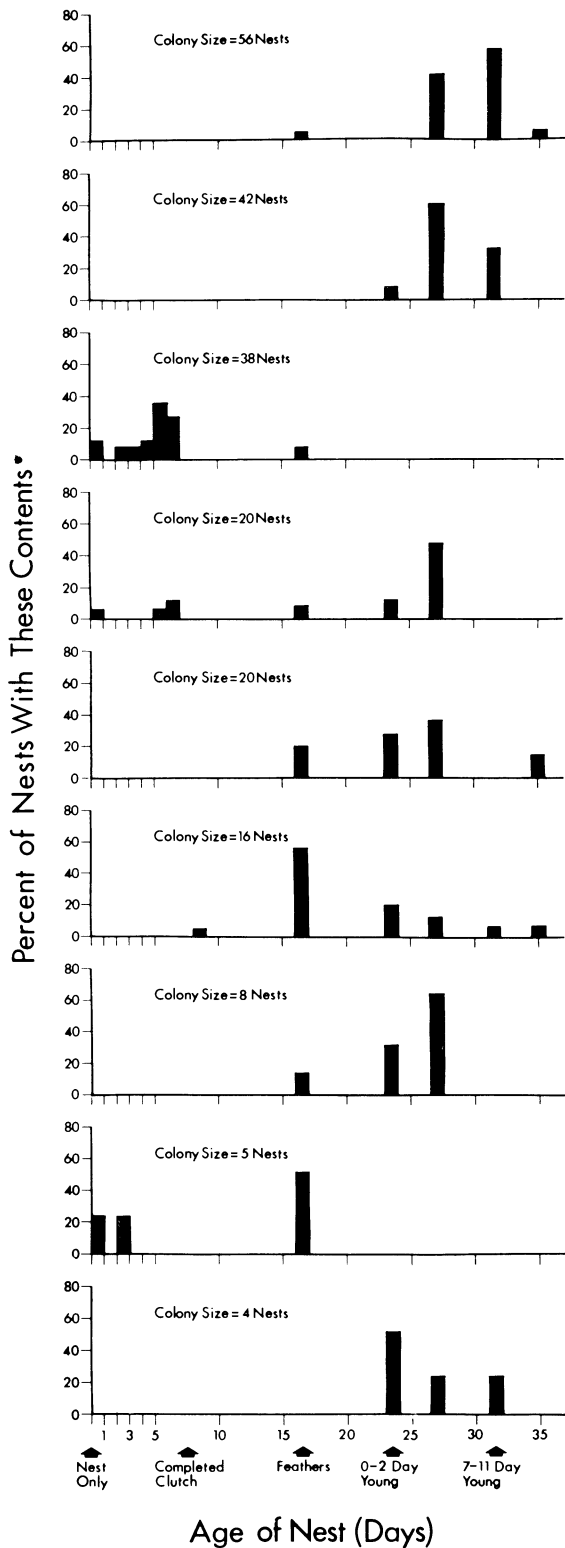
Age of Nest (Days)

FIG. 11. Percent of Bank Swallow nests at each stage in nine colonies examined 14–15 June 1973. The examined colonies contained from 4–61 active nests. Intracolonial breeding synchrony was significantly greater than intercolonial synchrony ($p < .001$, Kruskal-Wallis analysis of variance by ranks.).

showed that, as predicted, asynchronous breeders reared fewer offspring than did more synchronous birds. A significant part of this difference resulted from differential predation (Emlen and Demong 1975) but Emlen and Demong (1974, 1975) suggested that most of the difference resulted because asynchronous breeders had fewer opportunities to benefit from social facilitation of foraging.

As offspring near fledging, individual parents within a colony might be expected to take greater risks during mobbing, as apparently Barn Swallow parents do with the first clutch at least (J. M. Smith and H. B. Graves, *pers. comm.*). Increased intensity of mobbing in response to humans (and, presumably, other predators) as the nesting cycle progressed has been observed in Black-headed Gulls and suggested for Herring Gulls (Tinbergen 1960). From our own daily observations at Bank Swallow colonies we learned that mobbing of predators occurs at all stages of the breeding cycle, even before any eggs are laid, and we were unable to detect any changes in mobbing with progression of the cycle, although we predict that such changes occur.

We have assumed that reproductive synchrony within Bank Swallow colonies is an evolved response to predation, and the presence of such intracolonial synchrony is consistent with the hypothesis that Bank Swallow coloniality evolved in the context of decreased predation. However, breeding synchrony is also expected if coloniality has evolved in the context of social foraging (Horn 1970, Ward and Zahavi 1973, Emlen and Demong, 1974, 1975). The mere presence or absence of reproductive synchrony within colonies cannot be used to distinguish between coloniality dependent on decreased predation and that dependent on benefits from social foraging.

6) *Does predation per nest vary with Bank Swallow colony size?*—If decreased predation is an important advantage of coloniality, there should be less predation per nest in large colonies than in smaller ones. That breeding success is a positive function of colony size has been demonstrated in Black-headed Gulls (Patterson 1965), Fulmars (Fisher 1952), Gannets (*Sula bassana*) (Fisher and Vevers 1944, Nelson 1966), Herring Gulls (Darling 1938, *but see* Haartman 1945), Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) (Fautin 1941), Red-winged Blackbirds (Robertson 1973), and Tricolored Blackbirds (Orians 1961*a*, Payne 1969). Within larger Black-headed Gull colonies (Patterson 1965) and Red-winged Blackbird colonies (Robertson 1973), at least, it is apparent that much of the increased breeding success results from decreased predation per nest. Zahavi (1971) suggested that White Wagtails (*Motacilla alba*) in large com-

munal roosts experience less predation than birds in smaller roosts.

For Bank Swallows, we compared the amount of predation with colony size by investigating predation on clutches. We were unable to investigate predation on adults. Empty undisturbed nests were not scored since we could not determine whether predation by nondigging predators, such as weasels or avian predators, had occurred or whether the young had successfully fledged. For the 65 cases of apparent digging predation that we located at 22 of 46 colonies, there was no significant relationship between amount or percent of predation and colony size.

This lack of statistically significant correlation is not necessarily fatal to our predation hypothesis. Evidence from tracks, scent, and our arrival times at certain colonies suggested that practically all predations we observed were by nocturnal digging predators such as foxes, dogs, raccoons, or skunks. Although nighttime mobbing of predators occurs in one colonial species (Kruuk 1964), it does not occur in Bank Swallows. Coloniality based on decreased predation does not necessarily reduce predation by all predators (Hamilton 1971). In fact, evolved defenses against one predator might actually increase susceptibility to another (Kruuk 1964).

Unfortunately, many diurnal nonavian predators and most diurnal avian predators leave behind no tell-tale signs of their successes or failures at Bank Swallow colonies. Although mobbing by adult Bank Swallows is at least sometimes successful in deterring some diurnal predators (Table 4), there is no simple way to compare diurnal predation on adults or young with colony size. If such a comparison is ever made, we predict that large Bank Swallow colonies will prove to be more effective than smaller colonies in deterring diurnal predators and that individuals in large colonies experience less predation than those in smaller colonies.

CONCLUSIONS

We conclude that there are five major disadvantages of Bank Swallow coloniality:

1) *Increased competition for nest sites and nest materials*: That such increased competition occurred in the studied Bank Swallow colonies is indicated by (a) the positive relationship between the per-bird number of fights for nest burrows and colony size, (b) the higher per-bird probability in larger colonies of having nest materials stolen, and (c) the higher per-bird probability in larger colonies of being forced to fight for feathers (used to line nests).

2) *Increased physical interference*: We observed three types of physical interference within Bank Swallow colonies, each of which probably increases with increasing colony size.

3) *Increased competition for mates*: We observed competition for mates just prior to and during egg-laying. Bank Swallow males attempted to protect their mates from sexual assault and at the same time apparently attempted to copulate with other females.

4) *Increased likelihood of misdirected parental care*: Mixing up of unrelated Bank Swallow young began when they were older than 15 days. The development of parent-offspring recognition coincided with the time when young from different broods first started to mix.

5) *Increased transmission of ectoparasites*: Both the absolute number of Bank Swallow fleas per burrow and the per-burrow probability of being infested with at least one flea increased with increasing colony size.

Two other possible disadvantages were investigated, but they probably do not affect Bank Swallows:

6) *Increased intraspecific brood parasitism*: Although ample opportunities for intraspecific brood parasitism seemingly existed, Bank Swallows apparently laid eggs only in their own nests.

7) *Increased intraspecific killing of young*: Although numerous opportunities for intraspecific murder apparently existed, there was no evidence that adult Bank Swallows ever injured or killed either their own or unrelated young.

Regarding the advantages of Bank Swallow coloniality, we conclude the following:

1) Bank Swallow coloniality apparently does not result merely because of a shortage of suitable space for breeding, as indicated by (a) the rarity of isolated burrows, (b) the clumped distribution of burrows within large sand banks, and (c) the nearest-neighbor breeding synchronization within large colonies.

2) Bank Swallow coloniality seemingly has not evolved in the context of social facilitation of foraging, as suggested by (a) the absence of either large or small foraging groups, (b) the fact that young of large colonies do not survive so well as young of smaller colonies when food is in short supply, and (c) the fact that weights of 10-day-old young are inversely related to colony size.

3) The hypothesis that decreased predation is important in maintaining Bank Swallow coloniality is supported by (a) the success of mobs in deterring predators, at least sometimes, (b) the apparent increase in mobbing effectiveness with increasing colony size, (c) the fact that, within a colony, central nests are better protected than peripheral nests from predators, and (d) the presence of intracolonial breeding synchrony.

ACKNOWLEDGMENTS

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