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## SOCIAL BEHAVIOR IN NESTING CLIFF SWALLOWS

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Gregarious behavior in birds may be regarded as the result of positive social responses. Such responses are generally, if not always, balanced by negative social responses. The social behavior exhibited by a bird in any particular situation may thus be regarded as reflecting a balance of the two responses.

The social and territorial behavior of nesting Cliff Swallows (*Petrochelidon pyrrhonota*), one of the most colonial of passerine birds, was studied from this point of view during the summer of 1950 at fourteen nesting colonies in northwestern Wyoming. Facilities were provided by the Jackson Hole Research Station of the New York Zoological Society; financial assistance was provided by a grant from the Society. I wish to acknowledge with gratitude the cooperation given by Mr. James Simon and other personnel of the Station and the aid of Mr. Arnold J. Petersen, Dr. J. Paul Scott, Dr. Nicholas Collias, Dr. Joseph Hickey and Mrs. Margaret Hickey in the critical reading of the manuscript.

The foraging area and nesting sites of the four colonies studied most intensively are shown on the map (fig. 1). Colony A, the largest (130 nests), was situated beneath a series of concrete spans above the Jackson Lake Dam. Colony B (36 nests), a subsidiary of Colony A a few hundred yards to the north, was under a seven-foot concrete culvert. Colony C (91 nests), also a subsidiary of A, occupied the eaves of the water tower and neighboring buildings in the village of Moran. Colony D (18 nests), one mile north of the others, was in a five-foot concrete culvert. Flood plains over which the swallows foraged from these colonies were formed by the geologically recent recession of lake or river waters that has left flat expanses of heavy soil covered with sedges, grasses and willow scrub, or with lush wet hay fields of timothy, blue grass and sedge (fig. 2). Behind these plains the terrain generally rises abruptly to benches or to foothills covered with sage brush and lodgepole pine.

Intensive observations were begun on July 1 at the height of the laying period in the four colonies near Moran and were continued until the end of August by which time all the local breeding birds had left the area.

### METHODS

All the 275 nests in the four colonies were numbered, and the history of each nest was followed and recorded in chart form. Experimental manipulation of nest contents was undertaken in one colony (C) which was early threatened by residents because it was considered a source of dirt and unpleasant odors. The colony ultimately was saved by the persuasions of the author. The results of these experiments are described in another paper (unpublished).

Studies of individual behavior were aided by observations on marked birds. Ninety-five adult birds were captured at their nests or netted at the entrances to the colonies for banding and marking. One hundred and forty-four nestlings were taken from their nests and marked. Marking consisted of a rather extensive spreading of acetone-base

lacquer paint, known commercially as airplane dope, on the remiges and rectrices as shown in figure 3. The objective in this type of marking was quick recognition of colony membership at considerable distances, and in this respect the technique proved highly successful. White, yellow and red painted birds from colonies A, B, and D and, to a lesser extent, green birds from colony C, could be quickly identified with the naked eye at 200 to 300 foot distances and often at much greater range. With seven-power binoculars, painted birds were often detected at distances where species identification was difficult. Paint was most clearly visible in birds flying against a dark background and could rarely be detected when they appeared as silhouettes against a light sky. Colors

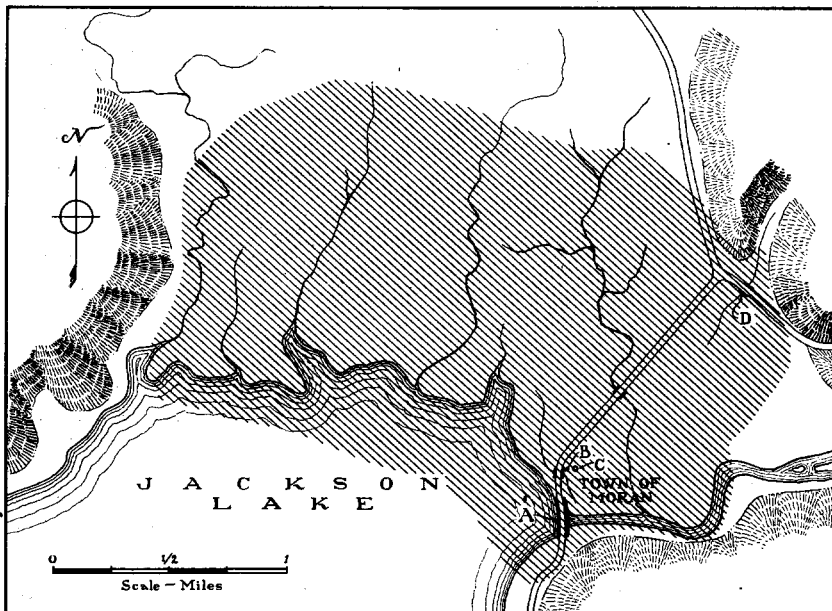


Fig. 1. Map of outlet region of Jackson Lake, Wyoming, showing the locations of the four Cliff Swallow colonies near Moran and the combined foraging range of the colony members (shaded areas).

on the alula, the outer primaries and the tertiaries were most conspicuous in perched birds although stains, made by acetone dilutions of the paint, on the underparts, rump and forehead were frequently of great help in the quick spotting of banded individuals among perched flocks. Forehead markings were most useful in nest observations. Special markings for individual identification were not attempted, but casual irregularities in painting were utilized in certain nest observations.

This extensive use of paint did not seem to hamper the birds in their flight, and the markings did not fade or deteriorate appreciably during the study period. Application of the paint was very time consuming, however. Each feather had to be painted individually with two coats and finally checked with a card or other separating tool to ascertain that it was free from neighboring feathers when dry. Even with the aid of a holding device, from 10 to 15 minutes was required to paint each bird.

Behavior was studied largely by direct observation with 7×50 binoculars. The birds were quite bold when the observer was quiet, and blinds were found to be unnecessary at the nesting colonies. A few planned experiments served to elucidate special aspects of territorial and flocking behavior.



Fig. 2. View of the foraging meadows of the Moran colonies from the northeast.



Fig. 3. An immature Cliff Swallow showing the pattern of paint used for distant recognition of colony origin.

#### CALL NOTES AND FLOCK INTEGRATION

Call notes feature importantly in the social integration of Cliff Swallow flocks, and a brief description of their characteristics is necessary background for discussions of social behavior. Three main types were observed: (a) "conversational" notes apparently functioning in general flock integration; (b) "defiance" calls, including the so-called "song," uttered in connection with territorial and aggressive displays between flock

members; and (c) "alarm" calls uttered at times of disturbance or threatened danger.

Conversational calls were given with considerable frequency by flock members in flight, at rest and particularly when approaching or leaving the nest, apparently in response to the social stimulus of flock companions. They consisted of harsh low chirping notes, given with a variety of inflexions and modulations, according to the situation. The most frequent form was a low *kersh*; when excited the pitch was raised and the calls repeated as *ash ash*. These calls appeared to have value in keeping the flock together during foraging and other activities. When used in the nest between members of a pair, the call was reduced to a soft short *kersh*.

The main "defiance" call or song was characteristically given by individuals sitting at the nest entrance or on an established perch, but it was occasionally uttered by a flying bird in a circling flock. It consisted of a series of high thin squeaks and low guttural gratings alternating in an extended song which often lasted for six or eight seconds. The head during utterances of this song was characteristically lowered, the bill slightly raised, and the throat feathers extended. When given by flying birds the tail was also spread and the wings dropped and moved with short quivering beats. Although generally given in response to the approach of other birds, this defiance song and display was also given by aroused territorial birds at their nest sites in the absence of other swallows, apparently as a type of possessional or territorial announcement. It almost invariably served to elicit aggressive responses from neighboring individuals and for this reason should probably not be regarded as a threat call; at least it failed to function in repelling intruders. A direct form of threat at close quarters consisted of stretching and snapping, or sometimes of bowing and gaping in a posture suggestive of the food begging behavior of fledglings.

The alarm call, given by colony members on the approach of an enemy or other disturbing factor at the colony or roost, consisted of a clear plaintive *zeoo* with a descending inflexion. This was uttered singly or, when the disturbance appeared suddenly, in a series of three or four calls. Loudness and pitch also seemed to vary with the degree and imminence of the potential danger. Birds in their nests responded promptly to this call by presenting their heads at the entrances. A whistled imitation of the call thus proved useful in checking the occupancy of nests. If given near a perching flock, the call typically precipitated a sudden departure of all but a few members. Soft low calls of this type were occasionally heard from foraging flocks, their function and significance at this time being obscure.

The food begging call of the young both before and after leaving the nest consisted of a rather high shrill *pleet* or *pleetcoet* and was a characteristic feature of postnesting flocks during August.

#### POSITIVE SOCIAL RESPONSES

All or nearly all the ordinary activities of Cliff Swallows were performed in groups, and positive social responses were readily seen on the loafing perches, at the foraging areas, at mud and grass-gathering areas, and at the nesting colonies.

*Gregariousness at the loafing perches.*—Large flocks of resting swallows lined up along telephone wires or on the branches of trees are a familiar sight to ornithologists (fig. 4). Loafing flocks are characteristic of the breeding season as well as of the post-breeding and migration periods. During the nesting season at Moran, groups were limited in size by the number of breeding birds in the local colonies. Late in July they increased rather suddenly as the local young fledged and joined their parents. A week or two later the flocks either left to join other colonies, or grew rapidly with the acquisition of foreign membership.

Starting about sunrise a large portion of the local adults accumulated in protected sunny situations near the colonies for an hour or so of sun-bathing and preening. Narrow ledges of trimming on the east face of a white painted house near colony C was the favorite site at Moran. Some birds came directly from their nests in colonies A, B, C and D (the latter one mile distant); others flew in from the lake or from nearby meadows apparently having made a flight first. The scarcity of fecal droppings on and below the wall suggested that little prior feeding had been done.

Telephone wires were the commonest perching sites for loafing swallows after seven o'clock in the morning. Habit seemed to be involved in the selection of loafing areas, for out of the many miles of wires accessible to the birds, a few limited regions, com-

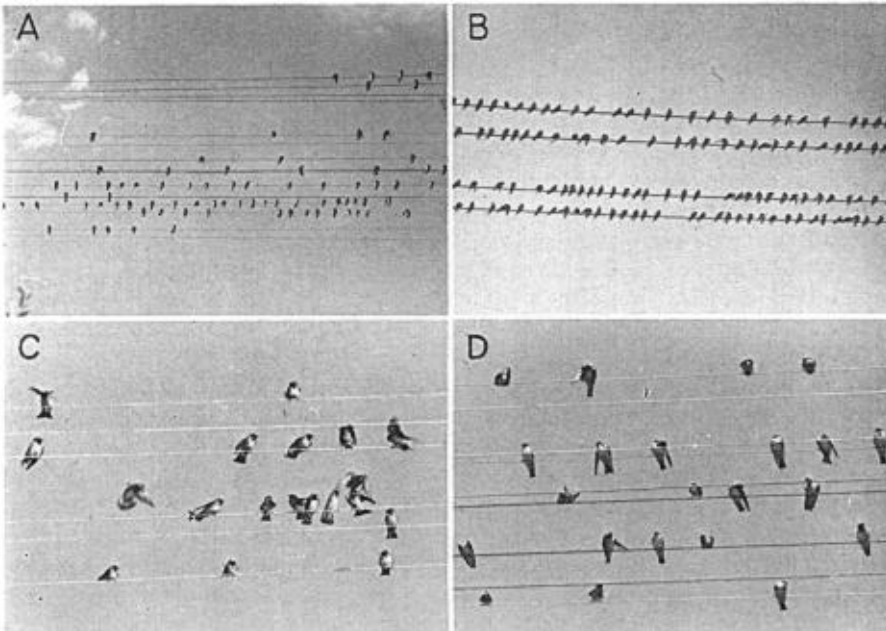


Fig. 4. Swallows on telephone wires. A, normal spacing of Cliff Swallows (Moran, Wyoming); B, normal spacing of Purple Martins (Madison, Wisconsin); C, group fighting of Cliff Swallows in response to singing on the wires; D, preening.

prising three or four sections of wire each, were characteristically used day after day. These were in relatively undisturbed areas affording clear vision for at least 100 feet. The observer was unable to detect any peculiar features of the favored sites over many unused sections of wire. Central location with respect to the main colonies was obviously involved, but birds from colony D, one mile distant, passed thousands of feet of good perching wires to join the group at Moran. Within the limited perching areas, the portions selected for use on any one occasion commonly varied from day to day and from hour to hour by as much as several hundred feet. On any single occasion the first bird or birds to alight seemed to form a focus of attraction for those that followed.

Birds of both sexes and from all of the four local colonies mingled freely in the loafing groups, coming either directly from their nests or straggling in from the foraging grounds. Cliff Swallows from distant colonies and swallows of other species also associated freely with the local birds in these groups. Most of the birds on the perches at

any one time were either resting, often with the bill turned back beneath the scapulars, or preening. Preening was usually vigorous and sometimes continued for as much as six or eight minutes without pause. Perhaps this preening was a type of displacement activity, a formalized behavior response to a tension resulting from the interplay of positive and negative drives as has been suggested for similar behavior in the Common Tern (*Sterna hirundo*) by Palmer (1941:100). It was often indulged in by isolated perchers, however, with nearly if not quite as much vigor as grouped birds. The activity seemed to spread through a flock by contagion so that the per cent actively preening at any one time was commonly either high or low (fig. 4). Single individuals seldom remained on a perch for more than five or ten minutes so that there was a continuous reshuffling of birds. In general the flock would tend to grow slowly for from 5 to 20 minutes as arrivals outnumbered departures. This might continue until one hundred or more birds were present. By this time an alarm call would be sounded by one of the birds and nearly all the flock would swing off, circling irregularly while the perching aggregation slowly reassembled.

The rate of accumulation of birds in the loafing flocks and the selection of perches with respect to the other birds was studied with the hope of learning more concerning the social forces involved. On arriving a bird would select a perch anywhere from 4 inches to 10 feet from the nearest percher. The 4-inch distance was commonly selected even when the flock was sparse, and the number of such close spacings seemed to be roughly proportional to the size of the perching flock until a high level of crowding had been reached when the filling of 8- to 10-inch spacings rapidly increased the ratio. Spaces up to about 30 inches were commonly filled centrally, the arriving bird choosing his central position with considerable accuracy.

In one place where a one-hundred-foot stretch of telephone wires and a half-dead aspen tree provided a perching area for a flock of about 140 swallows, the area was divided optically into five 20-foot sections and the numbers of birds on the three central and most heavily used sections counted at one minute intervals. Each time after being flushed the birds returned to the three central sections and occasionally to the terminal sections and the tree which lay within the west terminal section. The results of seven series of counts representing seven successive aggregations at this location on the morning of August 4 are shown in figure 5. In all these series the middle section attracted swallows most rapidly and eventually acquired the largest number. When the terminal sections were both used by birds, as in series 3 and 4, the center of balance of the group remained in the middle section. When the east terminal section was used, however, and not the west, as in series 5, the center of balance was shifted to the east. From these observations we may infer that central positions in an assembling flock were favored.

Although a perching flock clearly served to attract further members, density of grouping appeared to add an increasing element of instability into a resting assemblage and clearly had an inhibitory effect on perch selections at higher levels of density. A single bird or small group, as already noted, commonly served to decoy others of its own or related species. The first ten or twenty birds to arrive at a loafing site, however, generally dispersed themselves over most of the area eventually occupied by the whole assemblage. Growth then proceeded by intussusception rather than by accretion from a few focal points. In one observation on July 20, where a flock started to assemble at two points one hundred feet apart along a telephone line, the larger and denser group of 25 attracted 20 new recruits while the smaller group of 10 attracted 16. At higher density levels an inhibitory effect becomes apparent. In series 3 and 4, of figure 5, where accumulations at the perching area continued until the flock was largely settled, birds eventually stopped alighting in the densely populated central section and selected

perches in the peripheral areas. There was even a decline in the number of birds in the central section while the lateral sections continued to grow. That this decline occurred in series 4 at a level only about half that reached in series 3 suggests that this density response is to relative rather than to absolute crowding. An absolute crowding limit of approximately 50 birds in 20 feet, imposed by individual tolerance limits, is discussed in the next section of this paper.

Bank Swallows (*Riparia riparia*) and Tree Swallows (*Iridoprocne bicolor*) joined the Cliff Swallows on their roosts even before the young had hatched, and later the perching groups also included Barn Swallows (*Hirundo rustica*), Rough-wings (*Stelgidopteryx ruficollis*) and Violet-greens (*Tachycineta thalassina*). All species intermingled freely and each appeared to function in attracting others regardless of species. Immature birds tended to be dispersed peripherally in mixed flocks as did members of less numerous species.

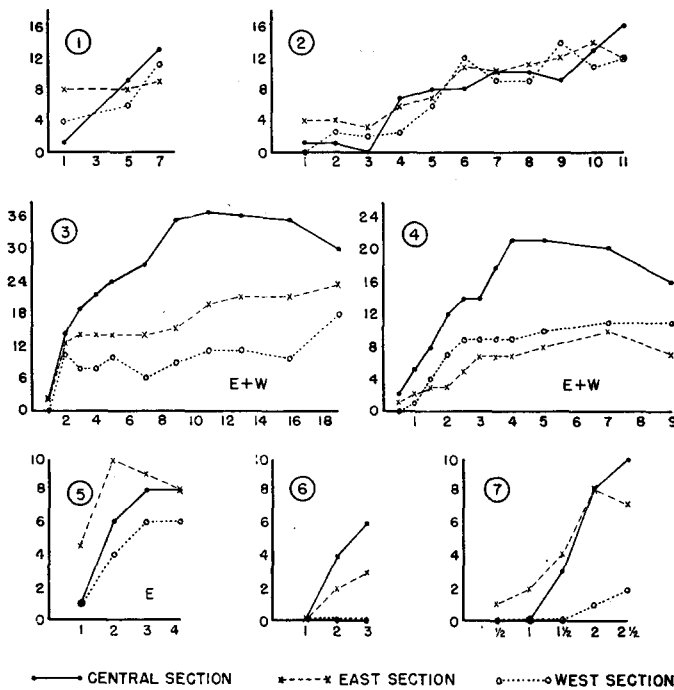


Fig. 5. Rate of accumulation of swallows in successive perching groups on telephone wires; August 4, 1950. The horizontal scale of each graph represents time in minutes, the verticle scale, numbers of birds on the wires.

*Gregariousness on the foraging areas.*—Throughout the nesting period the birds spend much of their time on the wing, feeding, gathering flying insects for the nestlings, drinking and bathing over the surface of a lake, or in activities which I tentatively interpreted as flight play. These activities in the vicinity of Moran were performed in July in loose flocks of from 25 to several hundred birds with members of the four local colonies all represented and freely interspersed. Later in the season the flocks increased in size as fledged young and swallows of other species, particularly Bank Swallows, joined the ranks and merged almost completely into the foraging groups.

Much of the foraging was done locally within a quarter mile of the nesting colonies,

but large elements of the population tended to drift away as a group, especially during the warmer parts of the day, to foraging grounds as much as four miles distant. Before the start of incubation these excursions, as noted by Buss (1942:158) and Pettingill (personal communication), often involved the entire nesting group, the colony site being completely deserted for as much as four or five hours at a time.

Later excursions were no less extensive, but many birds remained behind at the nests, and a nearly continuous stream of birds flowed back and forth between the colony and the foraging grounds of the moment, as mates exchanged duties at the nest or returned with food for the young. Birds flew directly in these shuttling flights, in so far as swallows ever fly a direct course, at speeds which averaged about 100 yards in 10 seconds or one mile in 3 minutes.

When on the foraging ground most of the birds at any given moment were aggregated in a single foraging unit. Storer (1927:107) noted this group-foraging phenomenon at a large colony in California, and Buss (1942:158) observed several manifestations of it at a colony in Wisconsin. Foraging flocks were loosely formed, each bird circling and darting about in an independent manner and showing none of the nice integration of movement to be seen in pigeon or shorebird flocks. A group would characteristically spread over from 2 to 5 acres when feeding low over the grass meadows. At times there seemed to be a pattern of circling either clockwise or counterclockwise, but within a few minutes this pattern would be lost in irregular maneuvers. The effect was usually a maelstrom of criss-crossing flights. Flock integrity was apparently maintained by the tendency for individual birds to turn and circle back as they found themselves pushing out beyond the main body of foraging birds. The nearly continuous flow of birds arriving from and departing to the colonies at times created a confusion which might have obscured the nature of these circumscribed foraging flocks had not the presence of color marked individuals revealed the identity and destination of birds which could otherwise have been interpreted as irregular stragglers.

A foraging flock rarely maintained a static position over a meadow for more than a few minutes. It would typically drift, sometimes so slowly that the movement would be noticed only with prolonged observation, occasionally quite rapidly, but never as a single directed flight participated in by all members.

This drifting of the flock as a unit over a varied terrain resulted in a progressive shifting of flock activity and a striking unanimity of behavior. Thus a large contingent of the local population became collectively engaged first in feeding, then in drinking over the lake, then in mud gathering, as noted in the next section, then in loafing, to produce a synchrony and unanimity of activity which was conspicuous whether the observer was located at a distant foraging ground or among the nests in the colony. Observing at the nesting colonies, the writer at first misinterpreted this behavioral conformity of the flock as the result of contagious responses to the activities of birds at neighboring nests.

During the warmer hours of the day, foraging flocks often operated high above the meadows, at heights estimated at 500 to 1500 feet, possibly in response to the diurnal movements of flying insects. A few soft call notes from the sky often called attention to these flocks, circling irregularly almost beyond the range of human vision. At such times flock unity seemed less developed, and the area or space occupied by a group at a given moment might be many times that used when the flock was near the ground. Looser organization and less regularity also seemed to obtain late in the season when the flocks had been augmented by immatures and by swallows of other species.

More tightly intergrated flocks sometimes formed for late evening maneuvers prior to night roosting and again in the early morning. Non-breeding birds and birds with



incompleted nests were active participants, moving off after the maneuvers to roost in a body at some distance from the colonies. Nesting birds were also involved, however, and the flights generally took place over or near the nesting places.

All participants, sometimes several hundred individuals, would unite to circle and wheel in a whirlpool of swirling birds suggestive of the pre-roosting flights of the Chimney Swift (*Chaetura pelagica*). It was impossible to determine whether the birds were feeding, but the whole procedure was suggestive of a social rather than a foraging activity. Occasionally a flock would split briefly, or a small group, leading off in a new maneuver, would fail to draw the main body of birds with it; but stragglers were few and the total effect was that of a cohesive aggregation.

*Gregariousness at mud- and grass-gathering areas.*—The gathering of mud and of grass for the nest was a major activity of Cliff Swallows during the nest building phase of the breeding cycle and irregularly thereafter as nests needed repairing. Mud for the nest shell was gathered at rain puddles or along open muddy banks of lakes, streams and sloughs and carried as small pellets in the bill to be added to the nest rim. Grass for the lining was collected in exposed dry spots where the stand was sparse and the grass texture fine.

Mud and grass gathering were highly social activities. All participating birds typically concentrated their activity on one or two areas of a few square yards regardless of the extent of suitable facilities in the neighborhood. From ten to thirty birds might be clustered together in this limited area while dozens more were shuttling back and forth to the nests. Each bird appeared to work independently, holding its wings high above the back and fluttering them as it pecked repeatedly until a large beakful had been secured (fig. 6A, B). Both members of a pair participated and characteristically exchanged places at the nest with each return. Collecting the mud usually required 15 to 40 seconds and placing it on the nest from 30 to 40 seconds. The time required to make the commuting flights was determined by the distance, being about 10 seconds for every 100 yards.

On the ground the group worked actively and often ignored the careful approach of an observer. All responded quickly, however, to an alarm call from one of their members and would frequently rise and wheel off even at imaginary disturbances. If the interruption was brief the birds returned, but if they were unable to return within half a minute or so, the sequence was broken and the birds shifted to another site or temporarily abandoned their mud gathering and moved on to other activities. A few sites were used repeatedly, but there was much irregularity in this respect, and it was impossible to predict where the group might gather the next time.

As in other social activities, members of all four local colonies at Moran mingled freely at the mud- and grass-gathering sites. The birds ordinarily worked side by side only a few inches apart regardless of colony membership and with little evidence of intolerance. Fights occasionally occurred, however, one bird deliberately alighting on another, grabbing it by the head or neck feathers and tenaciously holding on for 8 or 10 seconds (fig. 6C). Often these encounters resembled brief and incomplete copulations.

A striking feature of mud-gathering activity was the simultaneity of its occurrence among the members of a colony. Nest building with mud is of necessity intermittent, extended interruptions being required for the fresh construction to harden before new increments can be added (Buss, 1942:156). A definite synchronization of mud-gathering activity was repeatedly noticed at the colonies under study, apparently attributable to the flock foraging behavior already described. This synchronization was most striking after the eggs had hatched and mud-packing behavior occurred only irregularly as nest repairing. Among the incessant flow of adults arriving with food for their young, one

bird would appear with a pellet of mud; a minute later others would be doing the same and within two or three minutes all birds would have switched from food gathering to mud packing. Nestlings gaping for food were ignored as the parent busily entered, then turned back to place its load of mud at the nest rim. For ten to twenty minutes nearly all the active birds would be packing mud, and then quite suddenly, this would stop and the birds would switch to another activity. The strength of the stimulus to pack

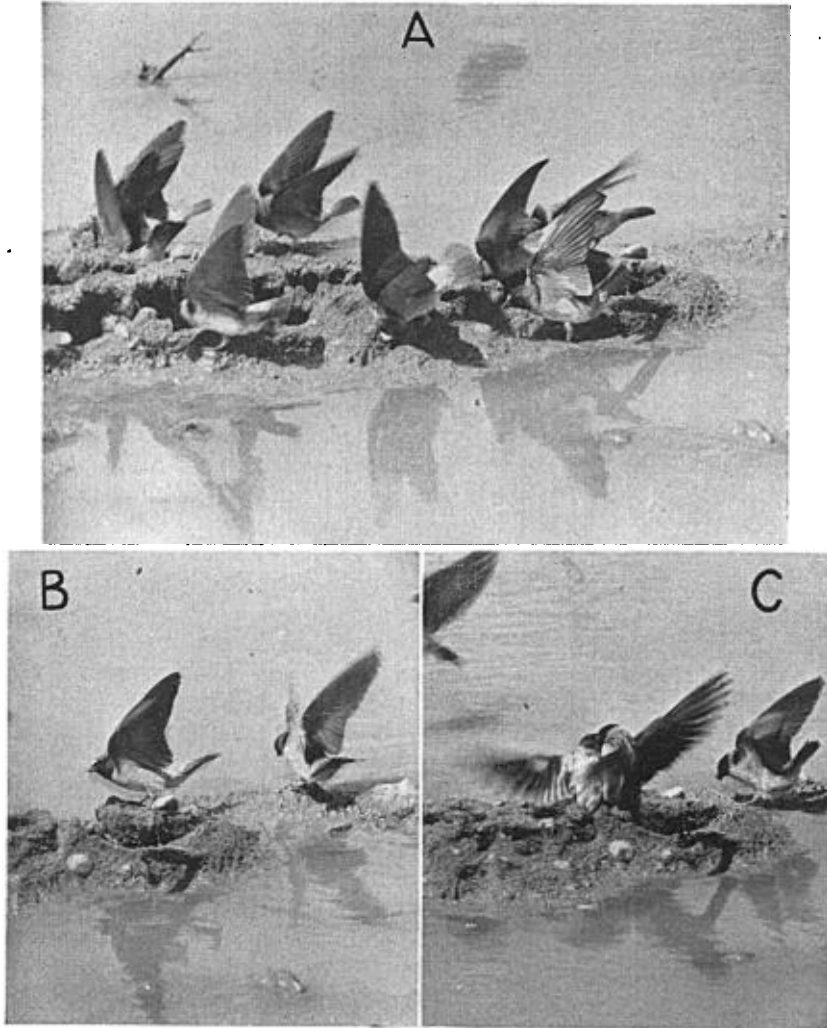


Fig. 6. Cliff Swallows gathering mud. A, B, typical grouping and postures; C, a fight.

mud, once the pattern had been set for the colony, is strikingly shown by the behavior of certain non-nesting birds and birds with completed nests that were repeatedly seen to pack mud to the colony and attempt to place it on nests other than their own. Before the writer was aware of this phenomenon he used the growth of nests as circumstantial evidence of their occupancy, but later he found that abandoned nests and even old shells from a previous year would occasionally have mud added to them during periods of mud-gathering activity in a colony.

*Gregariousness at the nest sites.*—Cliff Swallows are one of the most social passerine birds in their nesting activities. Nests are typically grouped in well defined colonies situated under overhanging cliffs, or, more commonly, under the protecting eaves of buildings, bridges and other man-made structures. They may be built as separate units in the larger spacings but often are merged into double nests, long rows or extensive masses (fig. 7A, B). The fourteen colonies under investigation at Moran varied in size from 18 to 178 nests. Colonies as large as 2000 nests have been described for the species (Buss, 1942). One cluster examined in a colony under a bridge at Elk Antler Creek in Yellowstone Park 76 miles north of Moran contained 900 nests merged into one mass.

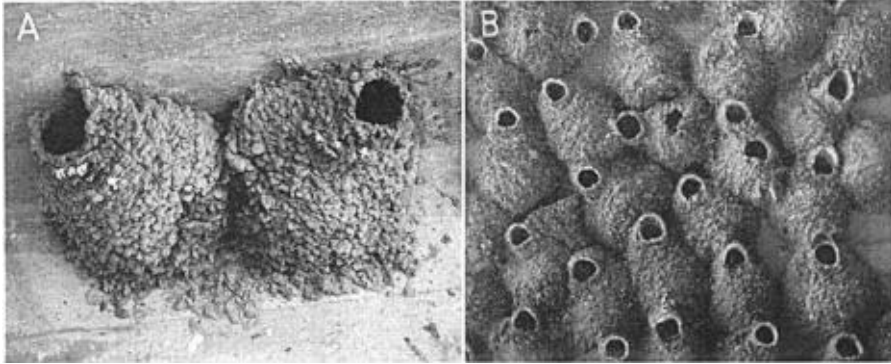


Fig. 7. Groups of nests of Cliff Swallows in a colony. A, contiguous nests showing flaring position of openings when nests are placed close together. B, a massed group attached to the ceiling of a concrete culvert, showing spacing of nest openings; two nests have breaks which should not be confused with natural openings.

When suitable sites are present, colonies commonly are subdivided or have scattered groups of nests at various points within a half mile or so of the main unit. Several of the colonies under observation had 4 or 5 semi-isolated subsections or peripheral subcolonies. The three nesting groups at Moran (A, B and C in fig. 1) and possibly also the fourth (D) should perhaps be considered as subgroups rather than as distinct units. In one case a single isolated nest was built late in the season nearly a mile from the nearest colony.

The members of these subdivisions and subcolonies apparently merge completely with birds from the parent colony as single social units. No intergroup antagonism was detected between the colonies at Moran (A, B, C and D in fig. 1) and one bird from colony A was observed perching peacefully among the members of the Elk Ranch Colony five miles away on August 4. Colonies would thus appear to be essentially open societies.

Although the start of nest building was not observed in this study, an examination of laying and hatching dates and of other signs of the stage of progress at individual nests revealed that there was a general synchrony of the cycle in the members of any single colony, more than would be expected to result from independent responses to seasonal and weather factors by the individuals (table 1). Thus all the birds in colony B in 1950 hatched their eggs between July 6 and 11. The bulk of the nests at the dam (colony A) hatched at the same time or perhaps a day earlier, but here there was a second, delayed, group which reached the same stage 10 to 12 days later. Most of the birds at the tower (C) and on the cabins nearby paralleled this second nesting group,

but a smaller number at the tower nested as a separate group about six days later. Observations by A. J. Petersen (personal communication) in 1949 (table 1) provide further evidence that each colony has an independent synchrony within itself. It would thus appear that social forces are involved in the determination of nesting dates and that each individual in a colony is influenced in its breeding schedule by its associates. This might be interpreted as an example of the "Darling effect" in which social forces acting through sensory channels influence the physiological mechanisms of flock members in such a way as to produce a parallel development of the reproductive tract and of reproductive processes (Darling, 1938). Further observations on pairing behavior at the nests (unpublished manuscript), however, indicate that the synchrony in some cases at least,

Table 1  
Hatching Dates at Cliff Swallow Colonies\*

		1949																													
Co'lony	July	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Total	
A					x	x	x	x	x	x																				118	
B						1			1	7	12	5	5	2	3	2				1									1	42	
C												x	x	x	x	x	x													50	
D																						x	x	x	x					22	
5 mi. E				x	x	x																								18	
6 mi. E			x	x	x	x																								125	
7 mi. E																				x	x	x	x							52	
22 mi. E										x	x																			150	
		1950																													
A				x	x	x	x	x	x	x					x		x	x	x			x		x						130	
B				3	9	8	5	4	3																					36	
C													1	1	1	7	7	6	10	2	2	3	8	5	3	1				91	
C'																x	x	x	x											30	
D						2	2	1	2						1	2	2	1												18	

\* Colonies as designated on map (fig. 1) or in miles from Moran. Numbers indicate number of nests examined which reached the stage on date indicated; an x indicates computed hatching dates in colonies with inaccessible nests. Bold face type denotes main hatching period for each colony. Totals indicate number of nests in co'lony. Data for 1949 from notes of A. J. Petersen.

was due to mass occupancy of a colony site followed, after about a week, by the withdrawal of those prospectors which had failed to establish territories and construct (or occupy) nests. Second attempts by these unsuccessful birds were subsequently made in similar mass clusterings at new sites peripheral to the established groups or at some distance from them.

The position of a nest in a colony was correlated with the stage of the reproductive cycle of its owner. Twenty of the 32 nests classified as belonging to the late hatching group at the Moran Dam were peripherally located while 86 of the 98 assigned to the early group were situated well back under the overhang. Correlations between position of nest and stage of progress were vague at the other colonies because of the small size of the nesting groups and because of the close synchronization obtaining. It was clear at the tower colony and at Uhl Hill, however, that where double rows of nests occurred, or where single nests were placed below the main row, the lower nests lagged behind. Six late nests at the Elk Antler Creek colony in Yellowstone which still contained young on September 1 were all located in the lower tier or peripherally on the ceiling of the bridge. Thus, as in Darling's gulls (*op. cit.*), the first birds tended to select central sites while later arrivals built peripherally.

An important consideration in interpreting these data on the Cliff Swallow is that old nests in reasonable repair are patched up and re-used year after year. Thus, in a well protected site like the Moran Dam, centrally located nests may be more sheltered

against winter damage and consequently in better condition for reoccupancy by dominant or aggressive birds the following spring. Whether it be this or a straight matter of selection of centrally located sites by the first comers, the principle of peripheral lag applies and indirectly reflects a preference for central positions which may perhaps be compared with the preference for centrally located loafing perches noted earlier.

Darling (*op. cit.*) has noted that size of colony and position in the colony may affect nesting success. Unfortunately no comparable observations were made on the Cliff Swallows in the present study. It was noted repeatedly, however, that visits to the nests caused more disturbance in small than in large colonies. The owners of the isolated nest mentioned above were particularly perturbed by the observer's presence and gave the alarm call almost incessantly during his visits. The same excitability was conspicuous among late nesters after the majority of a colony had dispersed with their young. Such behavior suggests that flock association in nesting imparts a certain stability for the group members.

Unified group responses of a contagious nature leading to mass desertion of the colony, such as have been reported for the Tri-colored Blackbird, *Agelaius tricolor*, (Lack and Emlen, 1939:228) were not encountered. In none of the numerous cases of nest disturbance and nest abandonment did neighboring pairs respond; in two colonies where the majority of the nests were destroyed early in the season, the remaining pairs persisted. A temporary abandonment, en masse, of several colonies on the Buffalo Fork at the time of a cold, rainy spell on July 10 and 11 may have had an element of contagious behavior in it, but since all of the small minority of birds which had eggs at the time remained, the mass movement is interpreted as largely a summation of individual responses.

#### SOCIAL TOLERANCE LIMITATIONS

The negative social responses or expressions of individual independence which limit and regulate flocking behavior are clearly manifested yet spatially restricted in the Cliff Swallow. They can best be seen when the birds are at rest and are consequently considered in the following pages as they occur at (a) the loafing perches and (b) the nesting sites. Outbreaks of the grating song suggesting self assertion and defiance and instances of conflict were noted in foraging flocks and at mud- and grass-gathering sites (fig. 6C), but their significance at these times could not be interpreted.

*Intolerance at the loafing perches.*—Cliff Swallows when perched in linear arrangement along wires, ledges or branches, dispersed themselves so that there was a space of at least 4 inches between birds (fig. 4A). Allowing one inch as the breadth of a perching bird, this means a maximum of one bird per 5 inches of wire or 24 birds in 10 feet. This general rule of spacing also applies in the irregular branches of trees, on flat roofs or where a group of parallel wires adds a third dimension to the spatial arrangements of the flock.

Observations on the selection and maintenance of positions by birds in a loafing flock suggest that this spacing is a reflection of individual intolerance of crowding and that the size of the intervals between birds is related to the distance a bird can strike without shifting its feet. Swallows have weak feet and ordinarily do not walk or shift their position once they have settled. The defended zone is thus restricted by the size of the bird and the extent of its reach from a fixed position. Breeding Bank Swallows were observed to have similar restrictions to crowding on the loafing perches, commensurate with their slightly smaller size. The principle must be extended with caution, however, for other species including the Purple Martin (*Progne subis*) tolerate considerably closer spacing (fig. 4B).

New arrivals typically selected positions 4 inches or more from the nearest perching bird, and, as already noted, often chose perches midway between two resting swallows as though recognizing and respecting certain tolerance limitations. At such times no reaction was evinced unless the distance to the nearest bird approached the tolerance limit. When this occurred the incumbent might threaten with a brief grating squeak, or lower its head and snap before settling back to rest or preen. Occasionally a new arrival would attempt to squeeze into a 6- or 7-inch space, or would deliberately alight on or next to another bird (fig. 4C). Such situations were invariably followed by threats, scuffles and the retreat or departure of one of the birds. The aggressor in these encounters might be neither the new arrival or the incumbent. The new bird often withdrew even before alighting, to flutter off and try another place. At other times it would perch but remain in a tense upright posture with feathers compressed as one or both of the neighbors challenged its position. Occasionally it assumed a more aggressive attitude and attempted to dominate the neighbor either directly and aggressively (antisocial behavior) or hesitatingly and cautiously, taking advantage of the neighbor's preoccupation with preening or sunning. Such birds would often sidle clumsily along the wire, advancing and retreating as they challenged the incumbent. These approaches were successful in a few cases, but more often the challenger retired after 10 to 20 seconds.

Tolerance limits seemed to be the same for all individuals regardless of relationship or colony membership. Aggressive displays were repeatedly noted both between members of the same breeding colony and between members of different colonies. In one case the two contestants were apparently mates.

Young swallows after joining the adults on the loafing perches were still begging for food. The active gaping reactions of these birds toward their parents and at times toward other adult Cliff Swallows, other fledglings and even toward Bank Swallows, were difficult to distinguish from attitudes assumed in true aggressive behavior, indeed they may have had a considerable amount of the aggressive element in them. Parents generally responded by feeding, but when they had no food at hand, backed off and retreated before the aggressive advances of the young. Food begging by one young bird of another young sometimes resulted in a mutual display of gaping which subsided only after the birds had separated to a distance of 3 or 4 inches. Young swallows often approached others of their kind and even adults, pulling at wings, tails or head feathers. The victim of these advances either ignored them and waddled away, threatened with open bill, or even attacked. One such encounter was observed between a young Bank and a young Cliff Swallow, the former taking the initiative, the latter the successful defensive response.

*Intolerance at the nests (territorial behavior).*—Social tolerance limitations at the nest sites were similar to those observed at the loafing perches. Each individual defended the area within the reach of its bill against all intruders except the mate. The defended area at the nest, however, was fixed in position and thus assumed the characteristics of a breeding territory as generally defined.

An examination of the distribution of nest openings, in a colony even where nests were massed irregularly, revealed that neighboring nests rarely had their entrances closer than 4 inches unless the position and direction of the entrance tunnel was such as to shield the owner from birds perched at the entrances of neighboring nests. Two nests built together as a pair typically had the flaring form seen in figure 7A, and in larger groupings irregularities in form could often be correlated with the position of neighboring entrances as they existed or had existed during construction. "Growth" lines produced by the successive additions of mud to the nest rim during construction

were readily detectable in most finished nests and provided clues on irregularities in the course of construction.

Song and threat displays were repeatedly in evidence at the nest site especially during nest construction. A bird, when it was not actually packing or adding mud to the structure, sat on the ledge of the incomplected nest following the movements of each

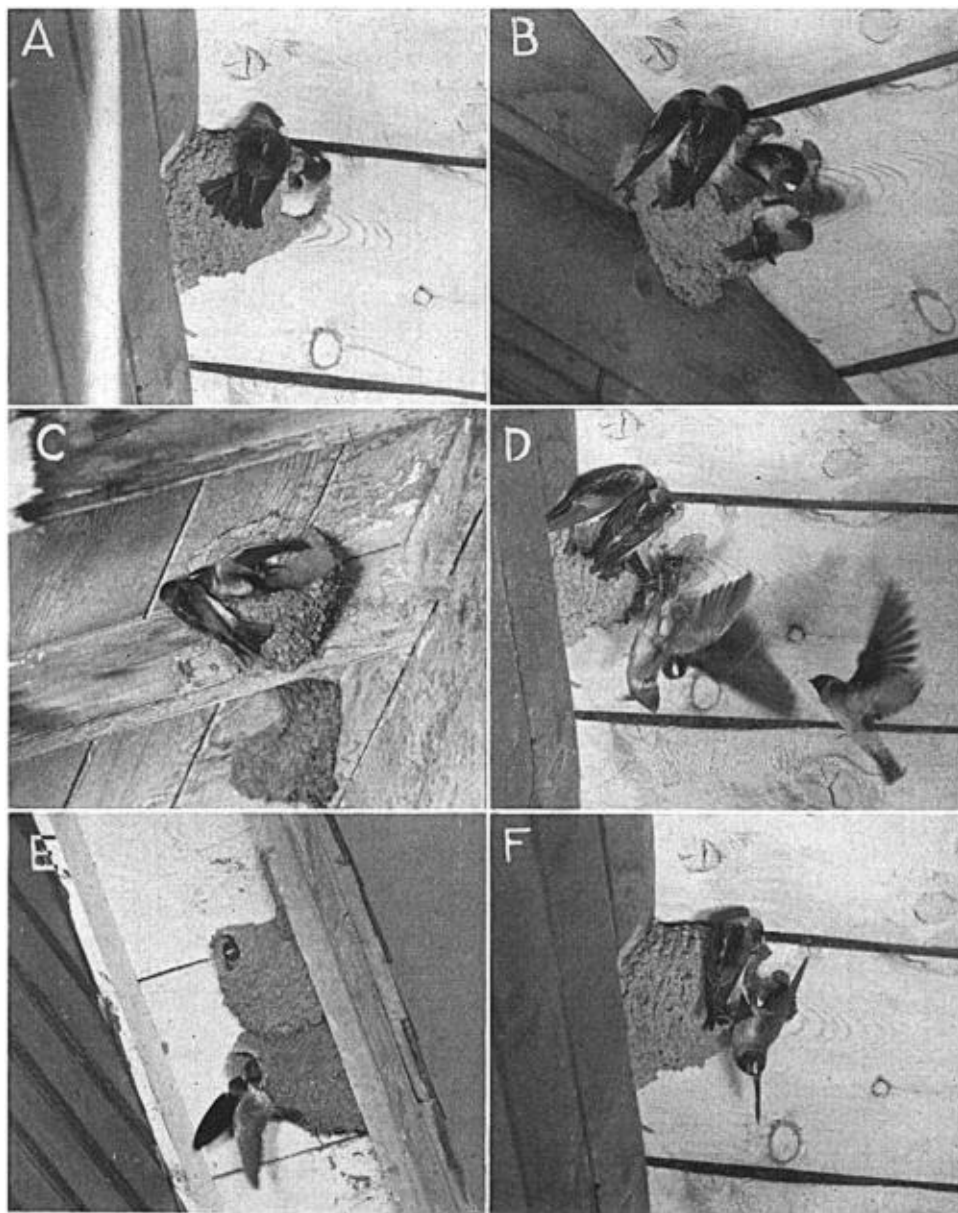


Fig. 8. Defense of the nest (for interpretations of actions, see text). The birds on the side of the nest in A, B, D and F were a pair starting a new nest at that point; residents of the nearly completed nest threatened and attacked these encroachers whenever their heads came within reach.

passing swallow and threatening those that came close (fig. 8A). Song attracted rather than repelled intruders and it was not uncommon to see from one to three or four birds hovering and alighting at the nest entrance of a singing defender. The usual sequence was: (1) a bird would approach and deliberately alight at the nest rim, leaning far back so as to avoid the blows of the resident (fig. 8B). (2) The resident, singing continuously and vibrating half-closed wings, would threaten and jab at the intruder's head which was kept just out of reach. (3) The intruder would give up and fly off after a few minutes. Any bird which came within reach was vigorously evicted (fig. 8C, D). Intruders apparently never took the aggressive in these fights but often showed great per-

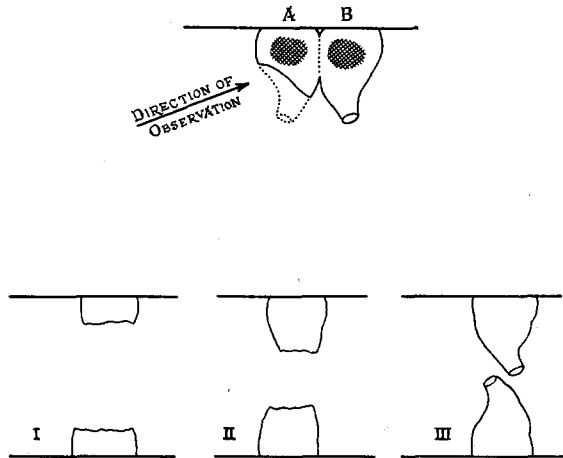


Fig. 9. A, B. Twin nests experimentally interconnected by breaking the intervening partition. The outer part of nest A was broken away to permit observation of nest interiors. Outlines of original structures indicated by dotted lines.  
I, II, III. Three stages of growth in a pair of opposing swallow nests.

sistence (fig. 8E). Occasionally an intruder would succeed in actually entering a nest whereupon the defender would grab it and the two would scuffle and twirl in the nest for up to a minute before tumbling from the entrance still locked in combat. Usually they parted after falling a few feet but on one occasion they were seen to drop together into the water four feet below and then separate and fly off. Not infrequently one bird, presumably the resident, would be seen leaning from the nest entrance, suspending another bird from its bill by the head, neck or body feathers (fig. 8F). The latter, on release, would fly swiftly away uttering the conversational chirping note, or occasionally a subdued cry suggestive of the alarm call. At times the fighting would continue after the intruder had been evicted, taking the form of a chase, especially if the intruder persisted in returning to the nest for repeated assaults.

Territorial threat and fighting were most frequent at partially built nests where a wide entrance meant a relatively large area to defend or close approximation of neighboring entrances and many avenues of approach for intruders. That it was this that occasioned the fighting rather than the attainment of a particular stage in the breeding cycle is indicated by the prompt reappearance of intrusion and fighting at nests which had been broken back by the observer. The completion of a narrow tunnel entrance apparently served to reduce the occasion for quarrelling at the nest.



At one colony the formation of the eaves structure on a barn roof created a situation which led to increased rather than decreased conflict as nest construction advanced (fig. 9, I-III). Vertical surfaces on both borders of an 11-inch eave provided support for two facing rows of nests. At early stages of nest construction the space between the rows was adequate (fig. 9I), but as the building progressed the openings inevitably approached each other (fig. 9II). Fighting at this time became frequent and intense and, when the opponents were absent, the birds were repeatedly observed to lean from their own nests and peck fragments from the rim of the opposing nest. When the space between pairs of opposing nests had been narrowed to about two or three inches, alighting at the entrances invariably led to fighting. Both members of each pair sang almost without interruption, and irregular visiting contributed to a picture of general confusion. On one occasion a bird from one nest was seen to reach across and grab a bird from the opposite nest; a struggle ensued in the first nest followed by a tumbling fall as the two, locked in combat, dropped between the nests. The following day the quarrel had been largely resolved with the completion of entrance tunnels which turned to right and left so as to effect the necessary separation of the openings (fig. 9III).

The various observations lead to the hypothesis that the peculiar form of the Cliff Swallow's nest is a special adaptation for the intense localized type of territorial behavior associated with colonial nesting in the species. The walls of the structure apparently serve as a protecting shield against interference by other birds and thus reduce the occasion for fighting and contribute to the tranquility and stability of the colony. By completely surrounding the nest cup on all but one side, these walls may be regarded as enclosing the territory with a solid screen, leaving only the region around the opening to be defended.

A few simple experiments were performed at one colony to test this concept and to throw further light on the extent and nature of territorial defense. In the first experiment the partition between two adjacent nests, each containing half grown young, was broken so as to form a large hole or window through which the birds could freely pass back and forth (fig. 9A, B). The entrance hole of nest A, facing the observer, was then enlarged so as to permit a clear view of the interior of each nest. Within a few minutes after the observer had retired to the observation point, an adult returned to nest A and fed the young without showing detectable signs of alarm or disturbance. A minute later, and while the A bird was still in its nest, one of the owners of nest B returned with food, but on noticing the adult bird in nest A through the window, flew off uttering loud alarm calls. The second member of the A pair then arrived as its mate flew off. This bird hesitated briefly over its own nestlings, then reached through the opening into nest B and fed the vigorously gaping young in that nest. An owner of nest B again lit at the opening during this procedure but promptly flew off in alarm. Possibly because of these initial circumstances the B birds remained in an alarmed state during the ensuing 20 minutes while the A birds continued a nearly normal routine of feeding, delivering food to their own young five times and to those of their neighbors through the window four times. The first successful entrance of its nest by a B bird occurred 26 minutes after the A birds had started feeding. The second member of the pair followed shortly and after delivering its beakful of food to the young was suddenly confronted by an A bird through the window. A short scuffle ensued after which both birds left by the B entrance. But within a few seconds they and their mates had returned, and a round of fighting started which the observer was unable to follow in detail. One of the A birds which was marked was seen to enter its own nest repeatedly and leave or be thrown out of its own entrance and that of the B nest with equal frequency, but aside from this, individual identification of the contestants was followed with difficulty. Fighting con-

tinued without interruption during the ensuing ten minutes, then subsided with occasional flurries as the birds returned to feeding and nest repair activities. Behavior appeared to be quite normal except for brief but violent scuffles when a returning bird chanced to meet one of the neighbors in the combined nest interior. By the end of an hour enough observations had been made to formulate several generalizations which were substantiated by further observations the following day: (a) Fighting occurred only when a bird upon entering its nest encountered a neighbor in the combined nest interior. (b) Both members of each pair participated vigorously in the fighting. (c) Each bird was aggressive in both nests and attacked as frequently and as viciously in one as in the other. (d) Birds frequently left by the opening of the other nest but invariably entered through the opening of their own nest.

Nest repair was started during the first half hour, and by the next morning the entrance of nest A had been largely repaired and the window between the two nests had been nearly closed. A rebreaking at this time precipitated a performance similar to that of the preceding day and a second closing of the hole.

These few observations suggest that the birds of each pair initially accepted the entire combined interior of the two nests as their own possession, indiscriminately feeding the young of either nest and vigorously defending both cavities against intrusion. They also support the concept of a fixed defense zone or territory surrounding the natural nest opening, for while birds left the combined interior freely by either exit, they invariably entered by their own opening and defended only that opening.

As a further check on the significance of the natural opening, the partition between two other nests was perforated when one nest, C, was active and contained half-grown young, and the other, D, was abandoned and empty. As in the first experiment the birds in nest C accepted the disturbance and continued to feed their young, invariably entering through their own normal opening but leaving by either route. The following day, after it was clear that the birds were adjusted to the new situation, the normal opening of nest C was plugged with mud so that the only approach to the nestlings was by way of nest D. The confusion created by this act was great. During the first eight minutes 19 approaches were made to the nest. The birds simply hovered before the closed entrance for a few seconds, then flew on to return again after a brief circling flight. Once a bird lit at the site of the opening and pecked lightly at the plug, and once one flew on after hesitating at its own nest and entered another nest six feet away, apparently delivering its beakful of food there. In the ensuing two hours the owners of nest C continued to flutter up to their plugged nest openings but at less frequent intervals. Each visit was now brief, and the birds often moved on to other nest entrances as though seeking some suitable place to rest and deliver their loads of food. Neighboring nest owners vigorously repulsed these advances, however, sitting in the mouths of their nests and singing threateningly as the birds from C hovered near. Several times in these hovering flights a bird alighted on the rim of nest D as though by accident, and once one proceeded to enter and may possibly have delivered food through the window. But the new approach through nest D was never adopted, and the young in nest C died of starvation several days later before the experimenter realized that the closure of the natural opening had effectively excluded the parents from their brood.

There was no evidence of a defended flock territory around a breeding colony. Marked birds of other membership were repeatedly seen mingling with the local birds at colony entrances and without signs of antagonism. Furthermore, the birds which circled a colony giving alarm calls when the observer intruded were noted on several occasions to include marked individuals from neighboring colonies.

## ANTISOCIAL AGGRESSIVE BEHAVIOR

Quite distinct from the defensive behavior of birds holding perches on the loafing wires or at the nest was an aggressive type of behavior indulged in by isolated individuals or by gangs of mixed colony composition. To all appearances many of the attacks of these raiders were deliberate and unprovoked and had no relation to nest or perch defense.

The status of these raiders and the situations which provoked their aggressive displays were not clear. Birds of both sexes were apparently involved, but young birds were never noted in raids at the nests. The similarity of the behavior of nest raiders to that of birds in the process of establishing a new colony site (unpublished observations) suggests that many may have been non-nesting birds prospecting for sites. The proportionately large representation of marked birds among them (usually 20-30 per cent) lends further support to this hypothesis, for the writer was guilty of causing a considerable number of desertions when he netted birds at their nests for marking. Specifically, two marked birds at the tower colony (C) were known to have taken up the raiding behavior immediately after they had been released from nesting duties by the destruction of their nests. Birds with nests were also known to participate in raids from time to time and it is likely that the composition of raiding parties was highly variable.

Raiders were strongly attracted to singing birds and to birds in distress following a nest disturbance. They were also much in evidence at the time the young were leaving the nests, concentrating at points where parent and fledgling activity was greatest.

Single raiders were noticed early in the season, but by mid-July they commonly joined forces into transitory groups of 3 or 4, and by mid-August into gangs of up to 10 or 15 with representatives from 2 or 3 of the local colonies. At this time they often moved from one site to another, spending from 10 to 20 minutes at each place before moving on. Although aggressive in their advances, these raiders generally if not invariably assumed a subordinate attitude in actual conflicts at nests. They would typically fly up to a nest entrance to hover briefly and circle off or to alight at the rim and lean far back so as to avoid the defense of the inmate. Usually the raider got no farther, but occasionally it gained entrance whereupon a fight ensued. On eviction the raider characteristically circled out and back. The nest defender might remain in the entrance or, if the raider was persistent, might make chase as the raider dodged and twisted and attempted to return. Often more than one nest was involved, and the nest owner found relief as its tormenter shifted to a neighbor's nest. At times, however, 3 or 4 raiders would work on a single nest at one time, giving the owner no rest for many minutes.

The motivation behind this raiding is not clear. Nests with defending owners were generally selected in preference to unattended nests, but numerous instances of successful entry suggest that the nest rather than the bird held the attraction. Unattended nests, and particularly empty nests, were commonly used as perches by the raiders, and when so occupied were defended as territorial possessions against all comers with vigorous singing and threat. In one case an old abandoned and empty nest was defended repeatedly although interruptedly by a single marked raider for two days on July 20 and 21, during which time it added nearly an inch of new mud to the rim. This was interpreted as an abortive attempt at territorial establishment which, although only irregularly contested by other raiders, failed to materialize. Perhaps it would have been successful had the season not been so far advanced.

Unattended nests containing eggs or small young held little attraction for raiders, but were briefly entered on occasion. Not uncommonly, however, the young or eggs of a nest were found on the ground below following a disturbance, and it is suspected

although not proven that raiders were responsible. Advanced young which had made their first flights and returned would, by food-begging actions, successfully protect their nests against raiders in the absence of their parents; in many instances a raider veered off or leaned back and left in response to the gapings of advanced nestlings. Interpretation of these gaping reactions as defensive is, however, unwarranted; they did not differ visibly from those directed to parents returning with food.

Aggressive attacks were not confined to the nest sites. Local spats involving from 2 to 10 birds occurred in loafing flocks on telephone wires every few minutes (fig. 4C). Some of these were merely adjustments of spacing, but others, especially late in the season, were caused by direct assaults. As at the nest, most of the attacks were perpetrated by a relatively few individuals, and, in certain instances at least, these were the same individuals that were currently raiding nests. In many of these encounters the attacker struck suddenly, either hitting the perching bird in passing flight or alighting briefly on its back. The victim, apparently surprised by the attack and generally knocked off balance, either flew off or quietly righted itself and continued its dozing or preening. In other cases, perhaps those in which the perching bird was alerted, the aggressor approached hesitatingly, hovering overhead or alighting on the wire a few inches away. This type of approach was generally greeted with threatening gapes and song which, with or without actual conflict, soon led to the displacement of one or the other contestant. Song given at such times often precipitated a local squabble involving from 5 to 10 birds clustering about and hovering over the singer (fig. 4C). Even in flight a singing bird was often approached or attacked by from one to 4 or 5 swallows.

#### DISCUSSION

The evolution of colonial nesting as a specialized form of social organization should properly be considered from the point of view of survival values which can be demonstrated in the colonial system. This has been ably done by Darling (1938) for various sea birds where he showed an increased stability, a mutual stimulation of reproductive activity, and an increased nesting success in large as compared with small colonies.

Also of importance in the evolution of colonial nesting are the spatial restrictions which narrowly specialized behavioral characteristics impose on a species. The specialization, whether inherent or traditional, which restricts nesting gulls and alcids to small islands so limits the number of usable breeding sites that procreation of the species depends on maximum utilization of the available space. A similar situation applies in the Cliff Swallow. The special environmental requirements for nesting in this bird include importantly a protected overhanging cliff, or cliff substitute, a source of mud of suitable quality for nest building, and an open foraging area. Sites containing all these essential features in close proximity were decidedly rare in North America before European settlement, and if each adequate site because of extensive territorial requirements could support only one pair of swallows, the dispersion would have been dangerously sparse for procreation and survival of the species. Any behavioral mutations which served to reduce the size of the defended territory around the nest and thus permit colonialism would, under such conditions, have survival value and be perpetuated.

The special behavioral and social patterns associated with colonial nesting conceivably have the same basic elements as the more familiar types of territorialism and dominance found in noncolonial species and probably evolved along with colonialism itself from a primitive noncolonial pattern. In all birds the beginning of the nesting season is marked by an increasing aggressiveness which, depending on the substrate of specific morphological and behavioral characteristics, leads to one or another of the many rec-

ognized types of territorial or hierarchical organization. Each species has its own pattern, relatively constant among its members, but clearly distinct from that of other species. The general pattern in the Cliff Swallow is similar in many respects to that of various colonial sea birds, suggesting a parallel evolution in diverse phylogenetic groups under similar restrictive pressures created by narrow specialization of nesting requirements.

Social coordination as seen in synchronized nesting and group foraging may likewise be interpreted as an evolutionary development or specialization in a colonial species of a basic behavioral characteristic. Such coordination has, to be sure, rarely been described for any but colonial species, but observations of this type are difficult to make, and the phenomenon may simply have been overlooked. Darling (1952) has recently summarized several studies which show or suggest that even in non-colonial species a powerful and important stimulus to reproductive processes is imparted by boundary contacts with the residents of neighboring territories. Coordinated behavior is apparently favored by the high frequency of boundary contacts which occur in colonial species.

The construction of an enclosed mud shell surrounding the nest proper is a behavioral specialization of considerable theoretical interest. This characteristic, as already suggested, appears to be related to the intense localized territorialism of the species, the shell screening the nesting bird from its numerous close neighbors and thus enhancing social stability in the group. In connection with this hypothesis it is interesting to examine the isolationist tendencies of other colonial birds. Colonial seabirds nesting in the open on a solid horizontal substrate characteristically space their nests so as to prevent neighbor interference and apparently never construct screening partitions. Where vegetational screening occurs, however, the nests may be more closely spaced and territorial fighting reduced (Austin, 1940:163). Colonial nesting on an elevated substrate imposes different problems of potential interference, and maximum utilization of space in a limited sphere is often associated with some form of screening. Species which utilize natural cavities on vertical substrates, such as those found on some sea cliffs, are naturally screened. Birds which excavate in dirt banks, as the Bank Swallow and the Bee-eater (*Merops*), are separated from each other by the walls of their burrows. The sociable Weaver Finch (*Philetaerus*), the Palm Chat (*Dulus dominicus*) and the Green Parakeet (*Myopsittacus monachus*) which, as a flock; construct massive nesting stacks with numerous cavities, are similarly screened individually from their neighbors.

The special construction of screening walls appears as a common characteristic of colonial birds which do not utilize or excavate nesting cavities. Among tree nesters many colonial weaver finches (Ploceidae), oropendolas and caciques (Cassicinae) typically construct globular or gourd-shaped nests with small and often downward projecting openings. The mud shell of the Cliff Swallow may perhaps be considered as an analogous case in a species using a vertical cliff rather than the branches of trees as the nesting substrate.

Although this trait of constructing enclosed nests is strongly developed in colonial species, it is by no means confined to them. Occurrences of it in non-colonial forms may have their explanations in completely unrelated factors. But since many are encountered among close relatives of the colonial swallows, orioles and weaver finches, it is possible that nest form may, at times, be a conservative inherited characteristic reflecting the habits of ancestral forms.

A comparison of the mud nests of cliff- and ledge-nesting swallows reveals a series ranging in complexity from a simple cup as found in the Barn Swallow to an elongate

retort with entrance tunnel such as that built by the Cliff Swallow. Homologous relationships seem to exist through the series: the mud frame or cup has merely been extended upward and outward until the retort form is achieved. Construction in the Barn Swallow and the Cliff Swallow proceeds in a closely similar manner up to the time of egg laying. At this point the Barn Swallow stops while the Cliff Swallow continues to complete its retort and to maintain it in repair. The special peculiarities of the Cliff Swallow's structure associated with the screening function are thus late developments in the nest ontogeny. One is tempted to interpret this in terms of Haeckel's law of recapitulation as evidence for a recent evolution of colonial nesting in the genus *Petrochelidon*.

#### SUMMARY

The social and territorial behavior of Cliff Swallows was studied at four colonies near Moran, Wyoming. Special attention was given to manifestations of positive and negative social responses and the balance of these in foraging, loafing and nesting activities. Adults and advanced nestlings were conspicuously marked with paints for individual identification.

Loafing aggregations on telephone wires and other suitable perches comprised members of all four colonies in close association. New arrivals at these roosts generally selected central perches at first, but later chose peripheral perches as crowding in the central portion became great. Limitations on crowding were imposed by individual intolerance of neighbors. A space of approximately four inches on all sides, about the reach of a perched bird, was defended against all comers. Encroachment on this defended space was resolved by threat displays and/or fighting.

Foraging aggregations comprised members of all four of the colonies. Usually nearly all foraging birds at a given time were grouped together into one unit which kept its unity by the consistent turning back of individuals as their independent forays brought them to the periphery of the aggregation. A foraging group, covering from 5 to 15 or 20 acres at a given moment, typically drifted as a unit, moving as much as two miles from the nesting sites. Arriving and departing birds from the nesting sites tended to confuse the picture of flock unity.

The gathering of mud for nest construction and repair was a social activity appearing and disappearing in irregular rhythm as the foraging aggregate shifted its scene of activity. The force of contagion originating in the foraging group occasionally induced individuals with completed nests to pack mud uselessly to other nests or to old broken nest shells.

Nesting aggregations or colonies showed no clear-cut independence or exclusiveness; flocks circling or resting close to a colony frequently contained marked birds from other colonies. Positive social responses were manifested by the close spacing of nests and the infrequency of isolated nests. Coordination of nesting activity was evidenced by a synchrony of reproductive cycles within groups as compared with other groups in the same colony or in other colonies. Interruptions of nesting activity by cold weather involved all members of colonies except those that had advanced to the incubation stage.

Displays of intolerance at the nesting colonies were similar to those observed at the loafing perches. Being fixed in location and semipermanent, the defended zone around a nest may be regarded as a true territory with a radial dimension determined by the reach of the occupant from the nest sill. Threat displays, song and territorial fighting were frequent and influenced the form of the nest and the eventual position of the opening. Experiments with interconnecting nests revealed that defense extends to the immediate surroundings of the entrance and to all that lies behind the entrance, and that,

while any convenient exit is used, only the proper opening of the nest is used as an entrance and center of defense.

Small groups composed at least in part of non-breeding individuals moved about from nest to nest and from colony to colony, molesting breeding birds at their nests and on the loafing perches.

The evolution of colonial nesting in the Cliff Swallow is thought to be related to the rather exacting requirements of the species for nesting sites and the scarcity of suitable situations before the construction of bridges and other artificial sites by white man.

Behavior patterns associated with colonial nesting differ from those of noncolonial nesters only in superficial features and may be considered as of the same phylogenetic origin. Similarities in behavior patterns of phylogenetically unrelated colonial birds are interpreted as instances of parallel evolution.

A positive correlation of screened nests with colonial nesting in birds is noted, and a hypothesis for the evolution of the mud retort from a simple mud nest of a noncolonial ancestral type is proposed.

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