

TERRITORY, NEST BUILDING, AND PAIR FORMATION
IN THE CLIFF SWALLOW

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COLONIAL nesting is a rather rare phenomenon among passerine birds, and there are few species in which it is more highly developed than the Cliff Swallow (*Petrochelidon pyrrhonota*). The social behavior of these birds as studied at a series of colonies in northwestern Wyoming in the summer of 1950 has been described in an earlier paper (Emlén, 1952). The present paper is concerned with problems of pair formation and related activities at the nesting site. It is based on observations made at the same colonies in Wyoming in 1950 and 1951, with supplementary data obtained at three colonies in southern Wisconsin in 1952.

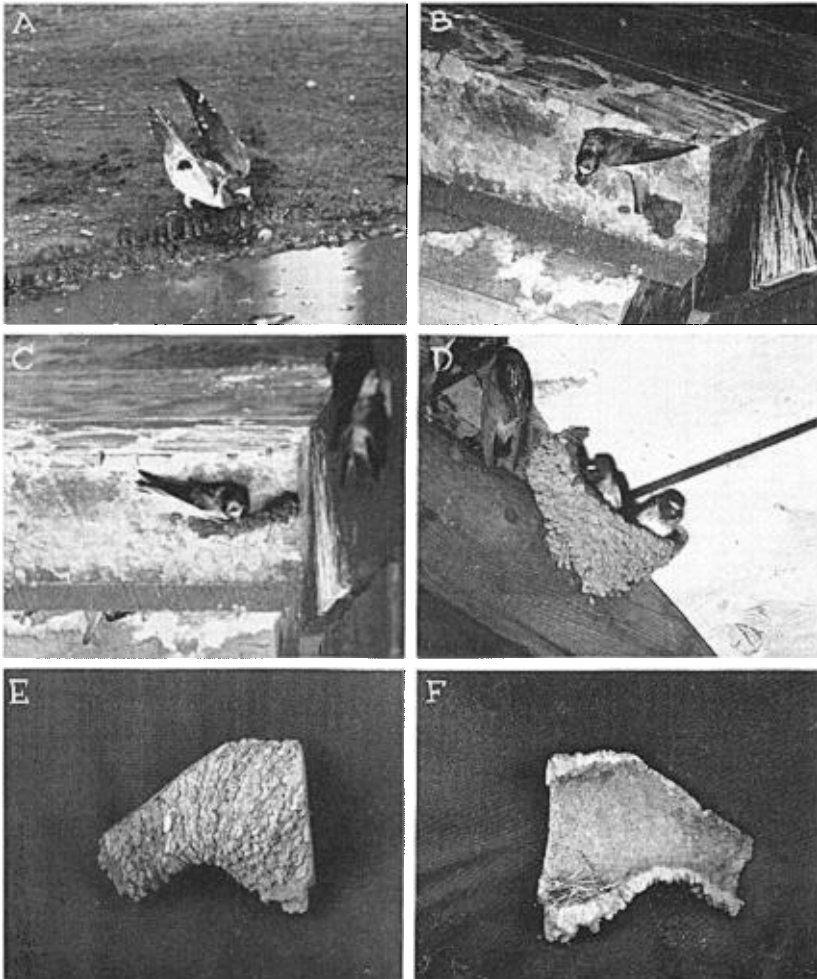
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MATERIALS AND METHODS

Observations were made with a 7 × 50 coated binocular. Large aluminum foil reflectors, 3 feet × 4 feet, were used extensively for illuminating heavily shaded colony sites and nest interiors, both for observation and for photography. Simple tent blinds were used in a few situations but were found to be unnecessary in most places. Many observations were made from a parked car.

Birds were marked for individual recognition by spraying them with fast-drying lacquer shot from a metal water pistol. By using this technique at the mud-gathering sites it was possible to mark birds at the very start of nest building. The random pattern of paint drops on the plumage (plate 4, A) was noted and recorded subsequently as the birds were being observed in their nesting activities. With about thirty birds so marked in two colors, no problems of confusion through duplication of markings arose. The lacquer on the wings and tail held up well through the breeding season; that on the body feathers was less permanent and occasionally caused bothersome clumping of the feathers.

Birds with completed or nearly complete nests were marked by suspending bits of string or small brushes dipped in enamel from the top of the nest openings. Most of the birds on entering thus received



NEST CONSTRUCTION. *A.* A marked (paint splattered) swallow collecting mud for nest building. *B.* Typical posture used in applying first mud pellets about $4\frac{1}{2}$ inches below the overhang. *C.* Horizontal posture assumed in nest building after initial ledge (stage I) has been completed. *D.* Placing mud on rim from position in nest cup in stage IV nest. *E.* Whole nest (stage VI) removed to show shape and structure. The angle of the top was determined by the slope of the roof under which this nest was built. Note the alignment of mud pellets in "growth rings." *F.* Median sagittal section of the same nest showing thickness of the shell, texture of the inner wall, and extent of nest lining.

a colored band or line across the white forehead. Color and chance variations in the width and form of this band served to identify individual birds as they stood in the nest entrance. Aluminum bands, presumably those placed on birds during the 1950 studies, served as additional markers on five birds observed for pairing behavior in 1951. Natural variations in plumage pattern and color supplemented these artificial markings and served to identify a number of birds which were never painted.

All behavior notes were made on the spot and each action described as it was performed. Observations were accordingly interrupted for note taking in preference to reliance on memory for more than a fraction of a minute. This procedure proved to be highly important in the fast action which often took place at the nest sites.

THE NESTING SITE

The essential features of the nesting habitat of the Cliff Swallow appear to be 1) an open foraging area, 2) a vertical substrate with an overhang for nest attachment, and 3) a supply of mud suitable for nest construction. All of these features must be contained within an area encompassed by the foraging range of the nesting birds.

The Foraging Range.—Foraging ranges at three colonies extended to two, two and one-half, and four miles, respectively, from the nesting sites. Colony membership could not be determined for most of the birds over the foraging range, but a nearly constant flow of individuals flying out from or back toward the nesting site showed the identity of the flock as a whole. The cruising speed of these birds over the inward or outward course was, in the absence of strong winds, about 100 yards in 10 seconds. A bird would thus require only from three to six minutes to reach an outpost in the foraging range. The extent of the range during pair formation and nest building was nearly if not just as great as in the period when food was being collected for the nestlings. During nest building and egg laying, however, the birds were more coordinated in their activities and visited outlying points in the range only at infrequent and irregular intervals. Later, the birds were less coordinated and tended to scatter or disperse in smaller subgroupings.

The shapes of the foraging areas were determined largely by topography and the distribution of grass and sedge meadows and, as a result, were highly irregular in shape. Intervening hills and wooded areas were generally circumvented where this was possible, but low sage-covered hills were frequently crossed and even used to a limited extent for foraging. Open water was no barrier, and shore lines were

avored as foraging areas. On several occasions the birds were encountered more than half a mile from shore over Jackson Lake. Flocks tended to circle high during mid-day and before storms, and at such times often drifted over the borders of timbered areas.

The Nesting Substrate.—A variety of sites were used for nesting (plate 5). Of eighteen colonies observed in the Jackson Hole area, eight were under the eaves of buildings, four were under concrete culverts, three were under ledges in large concrete bridges or dams, one was on steel girders under a steel-wood bridge, one was on a natural limestone cliff, and one was on a sand bank. All of the three colonies under study in Wisconsin were on buildings. In all cases, the essential features of the site seemed to be: a) a vertical surface beneath a ledge or overhang and b) clearance below of at least three feet if over water and eight feet if over land. Almost any site possessing these features was explored by hovering flocks of swallows at the beginning of the nesting season. Sites used in previous years commonly had many old nests remaining in good condition, and these were quickly adopted. In other situations, the birds would alight and cluster wherever ledges, slight irregularities, or remnants of old nests provided toe holds. In one place where the birds were unable to secure a perch, the placement of narrow board strips five inches below the overhanging eave resulted in the prompt establishment of a nesting group. Low sites and sites without a protecting overhang seemed to hold no attractions for these hovering flocks. The first nests built at a site were located at the juncture of the vertical wall and the overhang, and if under a sloping eave of a roof, at the highest point or peak. Later builders would frequently utilize completed or partially built nests for either the vertical or the horizontal attachment surfaces. Nests would thus accumulate in masses, the colony extending downward under the primary series or horizontally outward under the overhang (plate 5, C). Nests built below the primary series were characteristically placed between two overlying nests, possibly as a response to the tendency to locate beneath a peak. Nests built outward on the horizontal overhang were most often placed at the end of the primary nest where the surface presented a vertical base. Occupants of the primary nests in such cases often extended their entrances downward to form a nearly vertical entrance tunnel. Old nests were used repeatedly in successive years until they fell into decay. In one obviously old colony, the primary nests at the juncture point persisted only as irregular broken walls of mud, largely untenable.

The height requirement of about eight feet over level ground was a valuable protection against predators, which could have made short

work of a breeding colony situated within their reach. Signs of predators were detected under several colonies. At Uhl Hill, where coyote signs were numerous, none of the 152 nests was within my reach when I wished to check nest contents.

Colonies situated over water did not show this height characteristic, and nests were often located within easy reach of an observer in a boat or wading. The apparent height requirement of at least three feet above the water level in such situations may be related to physical problems encountered by the birds in hovering and landing. In one colony where the birds were nesting under the eaves of a long shed, the nests were largely concentrated over two open doorways. The significance of this selection was not apparent.

Unusual Nesting Sites and Situations.—Some of the various types of nesting sites encountered are pictured in plate 6. Of these, the case of the nests located on a sand bank in a colony of Bank Swallows (*Riparia riparia*) (plate 5, D) appears to be unusual and of rather special interest. Finding an overhanging bank filling the basic requirements for a nesting site, these birds apparently had settled and started to build at the points where they could secure a toe-hold, viz., the entrances to the Bank Swallow burrows. The Cliff Swallows dominated at the burrows they had appropriated and proceeded to build, until complete retorts covered the entrances of the Bank Swallow burrows (plate 6, A). The Bank Swallows succeeded in gaining entrance only when the Cliff Swallows were away and, in several cases at least, finally abandoned the sites leaving their young to starve. No antagonism between the two species could be detected except at the jointly occupied sites, and here it was a clear case of dominance and subordination, the Bank Swallows rarely challenging the larger Cliff Swallows as they sat in the nest entrances.

Plate 6, B shows a group of nests on a barn, one of which was in the process of being appropriated by a male English Sparrow (*Passer domesticus*). This species was rare in the Jackson Hole area and was encountered only in this colony. Here, as at a colony observed in Wisconsin in May, 1951, English Sparrows were completely dominant over the swallows and readily replaced them in any nest they chose to enter. Birds in neighboring nests showed no particular response to the presence of the intruders.

A pair of Barn Swallows (*Hirundo rustica*) nested in one of the culvert colonies in 1950, apparently appropriating the base of an old Cliff Swallow nest as the starting point. This nest was six feet from the nearest Cliff Swallow nest, and, except for participation in the alarm displays when I entered the culvert, the birds apparently

remained quite independent of the Cliff Swallows which surrounded them. By contrast, a pair of Tree Swallows (*Iridoprocne bicolor*) feeding young in a nest thirty feet from an active colony in July, 1951, repeatedly attacked and chased the larger but less agile Cliff Swallows.

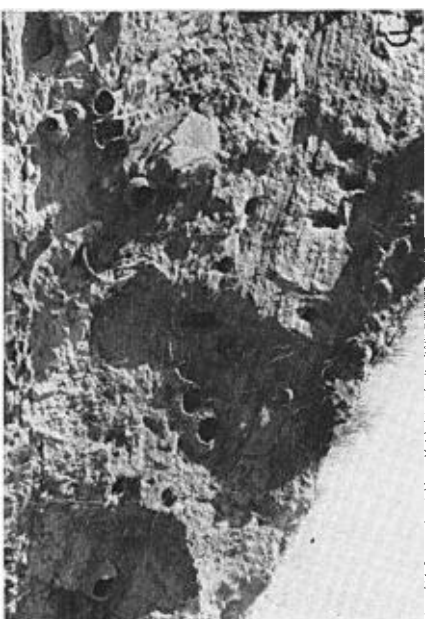
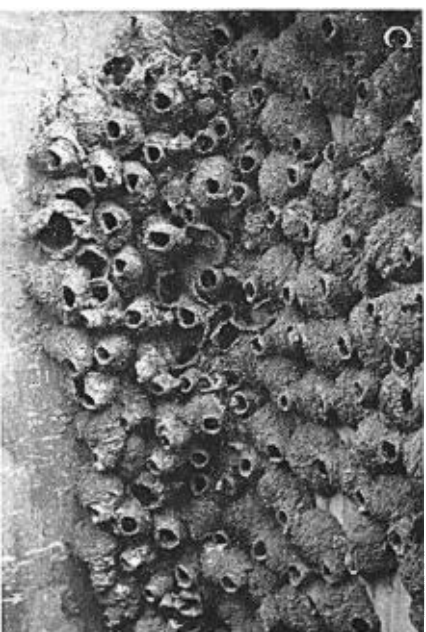
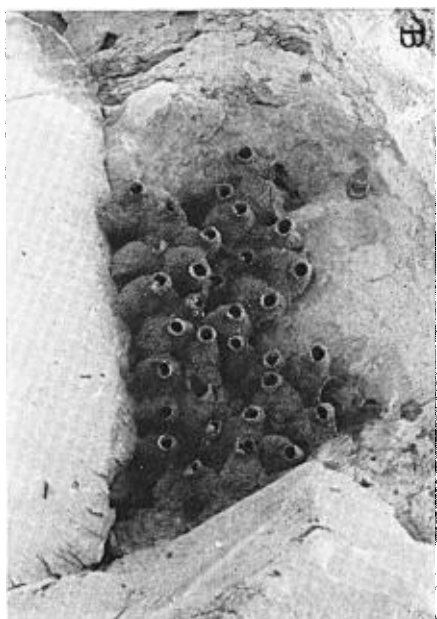
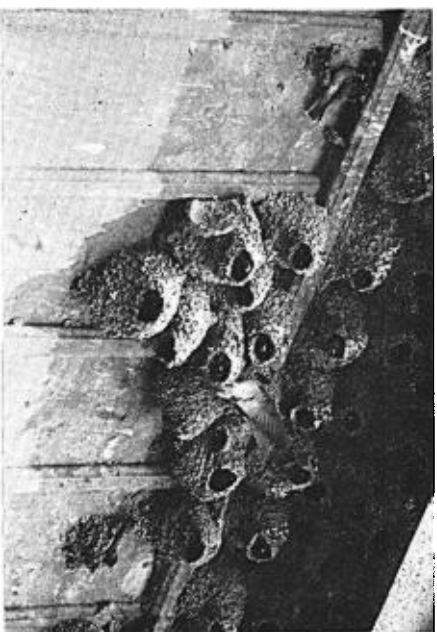
Nesting Materials.—Mud for nest construction was gathered at sites from twenty feet to at least one-half mile from the nesting colony. After rains, almost any puddles close to the nests were utilized, but at other times the birds went farther afield. The availability of mud thus affected the rate of construction. Mud collecting was an intermittent activity in which nearly all members of a flock participated as a group. One or two birds would start the activity by descending to a particular mud site, others would follow, and soon the entire flock would be gathering mud and carrying it back to their nests. At Moran, where members of five subcolonies commonly foraged as a group, the individuals from the more remote subcolonies persistently returned to the mud site selected by the combined flock, even though this meant travelling long distances and passing numerous good sources of mud en route. For instance, birds from one subcolony established late in the 1951 season at a point half a mile east of Moran, started by bringing their mud all the way from Moran. Later they adopted a local source of supply, and their foraging associates from the Moran subcolonies had a turn at traversing the half-mile span.

At the mud sources, the birds typically circled for several minutes, hesitating repeatedly over the site. As soon as one had landed, others followed, and within ten or twenty seconds, up to twenty or thirty birds might be clustered on the wet mud, each working independently with wings partly or fully extended over the back and fluttering lightly. Mud was gathered by a series of vigorous jabs until a large bill-full had been amassed, when the bird would take off and head directly for its nest.

The quality of the mud varied considerably from colony to colony according to local conditions. Nests in some colonies contained much sandy silt and were clearly more friable than nests in other colonies. Several types of mud were often found in a single nest indicating that various sources had been utilized in its construction.

Nests built too rapidly or in humid weather often collapsed before they were completed. In early August of 1951, a prolonged wet spell resulted in the crumbling of many nests which had stood for over a month and contained advanced young nearly ready to fledge.

Dried grass for the nest lining was commonly collected near the nesting site. Transporting of grass from distant sites was not noted but might have occurred undetected. The collecting of this material



NESTING SITES OF CLIFF SWALLOWS. *A.* Under the eaves of a barn, Deerfield, Wisconsin. *B.* On a limestone cliff, Moran, Wyoming. *C.* Under a concrete culvert, Yellowstone Park, Wyoming. *D.* On a dirt bank, superimposed on a Bank Swallow colony, Yellowstone Park, Wyoming.

was, as with the mud, a social activity in which many birds from a flock participated as a group. The period of greatest grass gathering activity was in the early morning before mud gathering had started.

FORM AND CONSTRUCTION OF THE NEST

Form of the Nest.—The form of the typical nest shell of the Cliff Swallow is depicted in plate 4, E and F. It consists of a globular nesting chamber extended forward into a short tubular entrance tunnel with the mouth directed downward. Dimensions of 15 sample nests varied from 5.5 to 10.5 (mean, 7.7) inches in overall length and from 5.5 to 8 (mean, 6.3) inches in basal width. The opening in completed nests was from 1.3 to 2.0 (mean, 1.7) inches in height and from 1.5 to 2.7 (mean, 2.0) inches wide. The height at the back (outside measurement) was almost invariably between 4 and 4.5 inches. The thickness of the floor and side walls varied from 0.24 inches in depressions between protruding pellets to 0.66 inches at the centers of large pellets and averaged about 0.44 inches. Walls were slightly thinner toward the roof and entrance. Two average-sized nests weighed 578 and 816 grams when thoroughly dry.

Variations in size and shape were due in part to the nature of the site and to the fact that many birds never completed the entrance tunnels of their nests. The typical nest placed close under an overhanging ledge had no mud roof while the occasional nest placed in the clear (see plate 6, A) was completely roofed. Nests placed in natural crevices at the Uhl Hill cliff had nothing more than short projections of mud extending and narrowing the natural entrance opening (plate 6, D).

The nest proper (or nest lining) was a sparse collection of fine grasses with occasionally a few sticks, hairs, and feathers. Many nests were nearly devoid of any such materials, a few had considerable amounts, but never as much as is commonly found in nests of the Barn Swallow.

Reoccupation of Old Nests.—Nests built in sheltered places generally stood essentially undamaged from year to year and were used repeatedly by the birds. Good nests were used as they were found; partially broken nests were rebuilt. Breaks in the walls or entrance tunnels were neatly repaired so that it was often difficult to distinguish between old and new construction after the mud had dried. Holes in the floor, however, were sometimes overlooked or only crudely covered with nesting material. Three reoccupied nests at the Elk Antler colony in Yellowstone Park had eggs partly protruding through holes in the floor. Small holes experimentally drilled through the floors of two

nests containing young were never repaired whereas similar holes in the walls and entrance tunnel were neatly patched from the inside.

Old broken nests were occasionally occupied and rebuilt. In one such nest, which had a large break in the side, the occupants built a new entrance tunnel at the site of the break and nearly closed the old entrance by additions of mud from the inside. Several nests were found with two complete tunnels and openings. While the history of these nests was not known, their structure in two cases suggested that they were broken nests which had been rebuilt in this peculiar form. In a third case (plate 6, C), the even structure suggested complete new construction along atypical lines.

Nest Construction.—As noted by Buss (1942) nest construction must proceed at a relatively slow rate so that each fresh addition may dry and harden to form a firm base for further construction. Nest building as observed in this study required about one week. The work was intermittent; periods of building activity rarely lasted more than two hours and were separated by interruptions of from a half-hour to four or five hours or occasionally several days. The first period each day was often the major one and generally started an hour or two after the sun had risen. During the rest of the day mud packing was intermittent and irregular.

During periods of activity when both members of the pair were participating, pellets were added at the rate of between 0.2 and 2.0 per minute varying with the distance of the mud source. One active pair brought forty-four pellets to their nest in a half-hour, thus adding more than half an inch to its rim. Nests, however, rarely advanced more than an inch and a half in a day and generally required a minimum of a week for completion (average one inch per day). Progress was slowed at the Moran colonies during the drought period of mid-July, 1951, presumably as a result of mud shortage, and many nests built at this time were smaller than average. Mud-packing was also retarded on damp rainy days; it was greatest during sunny weather following rains.

The number of pellets incorporated in a nest is difficult to determine, but between 8 and 12 distinct pellets are usually visible per square inch of outer surface. Additional pellets not visible on the nest surface number about 5 per square inch, bringing the total to approximately 15. On this basis an average nest with 60 to 80 square inches of surface would contain from 900 to 1200 pellets, and one inch of new construction, an average day's work, would contain about 80 pellets at early stages, about 200 at middle stages, and about 120 at late stages of construction.

The progress of construction of new nests can be conveniently divided into seven stages. The attainment of each stage marks a change in the behavior of the birds and is apparently of considerable importance in the onset of copulation and egg laying. These stages are pictured in plate 7 and described below.

Stage I—a narrow line or crescent. Before starting to build, birds cling to the surface at the prospective site and inspect their surroundings. They repeatedly stretch upward to the overhanging ledge, apparently seeking a toe-hold within comfortable reach. The first pellets are placed by a lateral twist of the body at the level of the feet (plate 4, B), almost invariably between 4 and 4½ inches below the sheltering overhang. Subsequent pellets are often scattered rather widely in an irregular line at the same level. By the time the stage is completed, the location is pretty well fixed and the line has become a narrow but solid crescent of mud with the ends turned upward. The males do most or all of this early construction. Dry grass is often brought and dropped loosely on the mud ridge, where, lacking sufficient support, it quickly falls off unless parts are caught in the wet mud and worked into position with new pellets. The grass and straw to be seen in most completed nests are apparently incorporated, for the most part, in this manner, rather than by being brought in with the pellets.

Stage II—a shallow crescent-shaped ledge projecting from 1 to 3 inches. By the time the nest is an inch wide, the birds can rest on it and defend it more effectively against intruders. Upon alighting, the bird characteristically takes a semi-crouched position in the floor of the crescent and reaching laterally or, with a twist of the head, to the front, explores along the rim for a place to affix the pellet (plate 4, C). Pellets are placed on the outer edge and then worked into position with a vibrating inward movement of the head. Placement generally requires twenty or thirty seconds although rearranging of this and other fresh pellets on the rim often prolongs the process to over a minute. The form and curvature of the nest as it advances seems to be determined by the extent of the bird's reach from the crouched building position. The front or outer rim often slopes downward at this stage. Dry grass is commonly brought and dropped into the cup but is generally kicked out within a few minutes.

Stage III—a rounded half-cup projecting 2 to 4 inches. From stage II, construction proceeds by extension and upturning of the lateral and ventral walls to form a broad cup. The birds are now fairly well screened from view when in the interior, and dry grass when brought may remain for some time. The first egg is occasionally laid at this

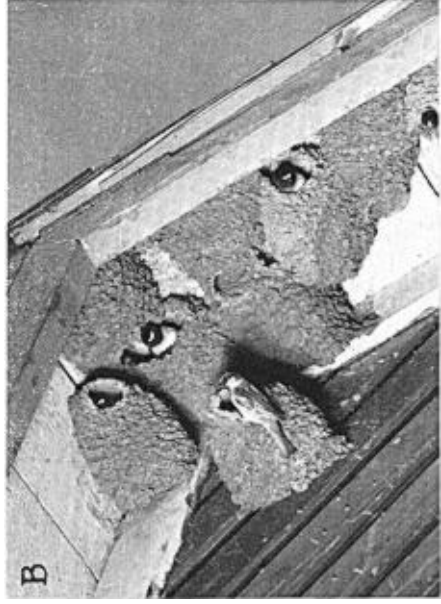
stage, but generally not until later. In building, the birds still perch with their feet in the center, reaching laterally or forward to place their pellets at the rim. This stage and the next are the periods of most rapid nest building.

Stage IV—a bowl with complete side walls projecting 3 to 6 inches. Progress to stage IV involves especially the extension of the lateral walls toward the sheltering overhang above. When the overhang is irregular in form or absent (as in the nest secondarily occupied by the English Sparrow in plate 6, B) the lateral walls are extended upward until they finally meet to form a roof. The forward edge is advanced at a similar rate. Pellets are still placed by reaching from a position with the feet in the bottom of the nest cup (plate 4, D). Nest lining material when brought is now generally retained. Egg laying is commonly started.

Stage V—a wide mouthed retort projecting 4 to 8 inches. From stage IV the walls and floor rim are extended forward and the opening somewhat narrowed. In placing mud the birds enter the nest cup but may then crawl forward to reach the rim which is now leveling off to form a sill. Many nests advance no farther than this stage and thus retain a wide though low-roofed entrance.

Stage VI—a narrow mouthed retort projecting 5 to 10 inches with unroofed entrance tunnel. Nest construction is retarded after stage V. Pellets may be added to the rim, however, extending the ventral lip outward and the lateral edges inward so as to narrow the opening to a circle about $1\frac{1}{4}$ to $1\frac{3}{4}$ inches in diameter. The first egg has generally been laid by this time, and varying amounts of nest lining material have accumulated. The birds, now well shielded from intruders except at the small entrance opening, are relatively immune from attack and spend most of their time quietly sitting at the entrance and looking out. The nest shown in plate 8, E and F had progressed no farther than stage VI.

Stage VII—a complete retort projecting 6 to 10 inches, with entrance tunnel. Most nests are completed with the turning down of the ventral lip and the roofing of the opening to form a complete entrance tunnel. The form and direction of this entrance tunnel varies according to the position of the nest in relation to exit and entrance routes and particularly in relation to neighboring nests. Almost without exception, the tunnel is directed away from the nearest neighboring entrance; this may be downward or abruptly to the right or left. The completion of stage VII is generally accomplished after egg laying has started. Nest extension or modification was not noted after incubation had started, although nest repairs, sometimes ex-



UNUSUAL NESTING SITES AND SITUATIONS. *A.* Nest built over the opening of a Bank Swallow tunnel. *B.* Nest being usurped by a House Sparrow. *C.* Nest with two entrances. Fragment below is the remains of an old nest. *D.* Nests in pot-holes in a limestone cliff.

tensive and involving changes in shape, were made at any time until the young fledged.

FORMATION OF THE PAIRING BOND

The process of pair formation was observed *in toto* in four cases and in part in many others. The general procedure can be outlined in a series of steps which follow each other in sequence. On some occasions these steps apparently followed each other in rapid succession and overlapped. On other occasions they developed slowly or were never completed. As observed at Madison, Wisconsin, in the spring of 1952, they started immediately upon the arrival of the birds from the South.

From the beginning, the general behavior of the birds on the nesting area was marked by aggressiveness and intolerance of close association (Emlen 1952). This was seen particularly at the nesting sites. It was also conspicuous in the mixed flocks on the loafing perches and in flying groups as they maneuvered near to or at considerable distances from the nesting site. Flying individuals, particularly those slightly apart from the denser clusters, suddenly broke into a prolonged flight song with throat feathers extended and wings stiffened and fluttering. Immediately all birds within 8 or 10 feet turned and gave chase, driving the singing bird downward until it ceased to sing. Paired and unpaired birds of both sexes took part in these flight songs and chases. The performances appeared to be expressions of excitement, perhaps sexual excitement, but bore no detectable relation to pair formation. All steps of pair formation took place within a small defended territory at the nesting site.

Step 1. Birds hover at colony site. Starting with their arrival on the breeding grounds, non-breeding birds hovered in clusters around prospective nesting sites. Scores of birds would converge and cluster with much singing and fighting, then swerve off and circle for another approach. False approaches were frequent, but as soon as a few individuals succeeded in alighting beneath the overhang, a swarm followed, clinging, often precariously to any available ledges and even to the backs of the first arrivals. A toe-hold secured, the first arrivals assumed a crouched vertical posture with neck drawn in, bill stiffly raised, and wings quivering. Here they sang for twenty or thirty seconds, tensely rigid or occasionally snapping back at one of their aggressive neighbors. Then, either quite suddenly or after a gradual decline in the excitement, the clamor ceased and all birds flew off as a group, with or without the sounding of alarm calls, to circle and again return. The frequent interruptions occasioned by these outflights had

the effect of maintaining a high level of excitement among birds clustering at the site.

Hovering at nest sites occurred most frequently during the two or three hours after sunrise and again during the half-hour preceding sunset, but was observed occasionally throughout the day. It continued from the inception of breeding activity until pioneering nests were nearly completed, and thereafter in lesser amounts as "raiding" behavior (Emlen, 1952: 195). Raiding groups, like the early clustering flocks, were thought to be composed entirely of non-breeders. Marked breeding birds from neighboring colonies were never detected, whereas birds rendered non-breeding by the destruction of their nest in a neighboring colony were seen in the raiding parties on several occasions.

Step 2. Certain individuals persistently return to perch at the same spots. As a flock hovered and clustered at the prospective nesting site, certain individuals, recognized by their paint splatter pattern or by natural variations in plumage, were observed to alight repeatedly within a few inches of the same spot. In one case, this localization was detected during the first five or six visits, and it seems likely that individual site selection typically started within the first few minutes of hovering at a new colony site. Where old nests were present returns were accurately pinpointed; where there were no nests or prominent landmarks, localization was less precise and often extended over a foot or more of space.

In all of three cases where subsequent observations of copulation revealed the sex of the birds, the consistently returning individuals were found to be males. In several other cases, they were strongly suspected of being males. Females also tended to localize their attentions during the early clustering flights, but were apparently slower to alight and less regular in returning to the same spot. Birds which consistently returned to a site in these early clusterings will hereafter be referred to as primary squatters.

Step 3. Singing of primary squatters attracts swarm of secondary visitors. The singing of the primary squatters served to attract a swarm of from 1 to 8 or 10 secondary visitors which hovered over, alighted close by, and even perched on top of them. In contrast with the crouched singing posture of the primary squatter, these secondary visitors perched erect, their heads characteristically turned out, their wings often partially opened so as to cover a part or all of the back of the squatter. In this position they often sang, and, if undisturbed, would enter a sort of song duel with the squatter, turning their heads toward his and lightly pecking his bill (plate 8, B and C). The squatter's typical response after a short delay was a vicious snap, or occasionally, a chase.

The main focus of attraction for these secondary visitors appeared to be the primary squatter rather than the site, but this is not clear, for the visitors commonly alighted in the absence of the squatter. Excitement was clearly centered around the squatter when he was present, however, and the visitors, when they alighted in the squatter's absence, showed little defensive behavior and were easily displaced.

Step 4. Certain secondary visitors repeatedly return to the same primary squatters. With continued observation at a site it became apparent that the same secondary visitors were repeatedly returning to the same primary squatters. During the first few days an established squatter might have 3 or 4 regular visitors plus an indefinite number of irregular visitors. Generally only one visitor appeared at a time, but occasionally they clustered around or above him fighting amongst themselves (plate 8, A).

Step 5. Repetition of visits leads to mutual tolerance (pairing bond). After from one to four or five days, one visitor generally became conspicuous as the consistent repeater at the site. This repetition of visits seemed to lower the level of intolerance between this bird and the primary squatter, fighting subsided, and eventually a relationship of mutual tolerance developed, which was the pairing bond (plate 8, D). Visitors included birds of both sexes and differences between the sexes in behavior or posture were not sharp. In all three cases where a pairing bond was completed between birds subsequently sexed, however, the persistent visitor was a female.

The time required for pair formation from step 1 to step 5 varied greatly. In some cases the steps overlapped and the whole procedure appeared to be completed in five or ten minutes. At other times including two cases under close study, the primary squatter never succeeded in obtaining a partner and after about a week gave up and disappeared. It is actually impossible to assign a definite time span for the establishment of a pairing bond, since the relationship, being little more than simple intra-individual tolerance, may occur in varying degrees and may be gradually intensified after the essential elements are established.

The principal differences in behavior which assured a heterosexual bond appeared to be, first, the greater persistence and speed of males in repeatedly returning to specific sites at the onset of clustering (territory establishment), and secondly, the greater persistence of females in returning to established squatters in the face of territorial aggressiveness.

NATURE OF THE PAIR RELATIONSHIP

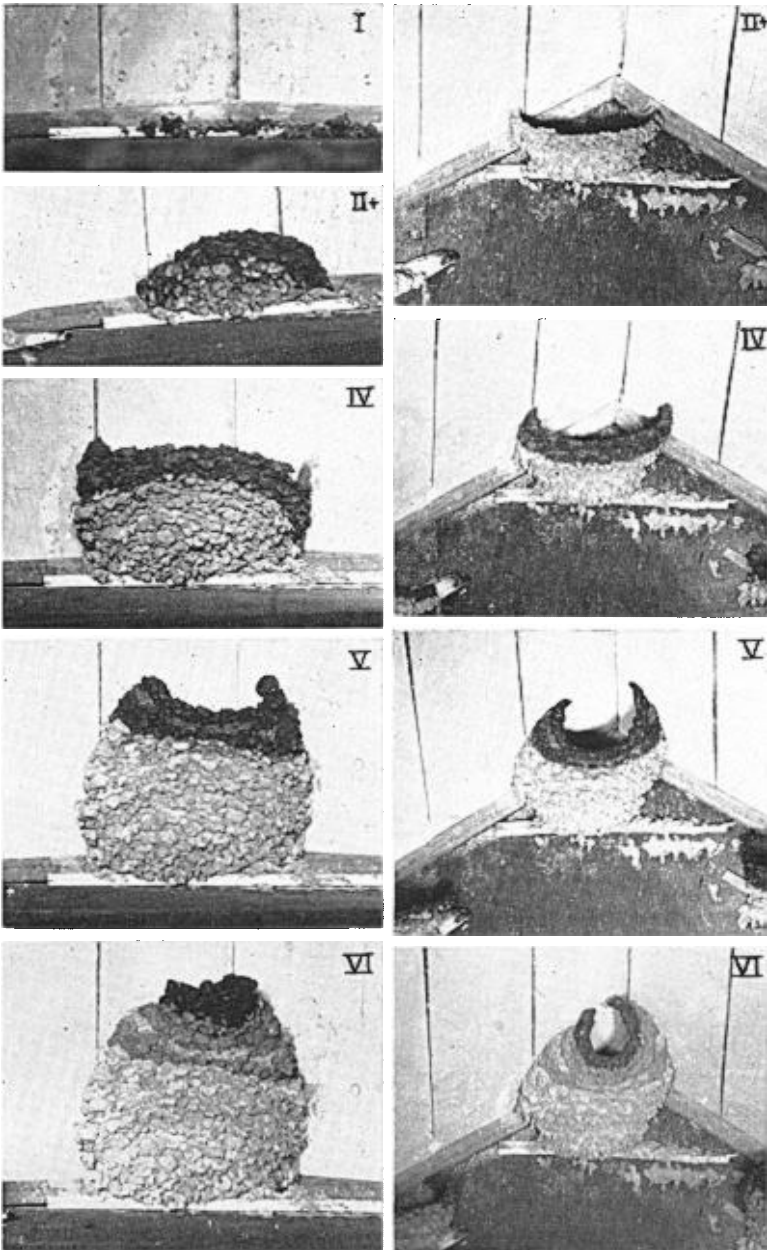
The pairing bond appeared to be largely, if not entirely, a relationship of mutual tolerance at the nesting site. Evidence of more complex interactions, such as has been described for various other species was not detected. From its nest entrance, a bird would quickly and accurately distinguish its mate from others approaching the colony, yet would make no special response when its mate was attacked as it visited a neighboring nest only a few feet away.

Pair relationships were not detected away from the nest. Mates were never seen to occupy neighboring perches on the community loafing sites, and could rarely be found together in the same perching group. They were never noted to associate closely at the mud gathering puddles. In the few cases where individually marked birds were recognized in song clusters or in promiscuous copulatory activities at the mud puddles, mated birds were never noted to be associated.

The pairing bond, although pretty well established before nest-building had started, was strengthened by joint participation in the activities of nest construction and the defense of the territory or nest site. The nature of the relationship may best be seen in observations of these two activities.

Cooperation in Nest Building.—The carrying of mud pellets to the site of pair formation generally started before the pairing bond had been completely established (step 3 or 4). The male seemed to initiate the work, but the female soon joined in and, in some cases, took as active a part as he did. The usual procedure was for the birds to take turns, one remaining at the site while its mate was away collecting mud. The exchange at the nest site was typically rapid and unceremonious. The arrival of one was the signal for departure of the other. When this occurred before the incumbent had finished working its last pellet into the nest rim, however, the newcomer would crowd in behind and then push forward. In early stages of construction when the ledge was still narrow, this frequently led to the displacement of one or the other bird. Each bird seemed intent on its work and paid no noticeable attention to its mate except for a soft note of greeting as it landed and a harsher double note as it left.

Although building activity was started in a new colony well before the clustering behavior of pair formation had subsided, the two activities remained very distinct. The early morning hours were largely filled with pair formation activities, raiding, and nest defense. Then, often quite abruptly, the birds would shift their whole activity to nest building. One bird would appear with mud and, ignoring the pairing



PROGRESSIVE STAGES IN NEST CONSTRUCTION, VERTICAL AND DIAGONAL VIEWS. Roman numerals indicate stage of development as described in the text. Fresh wet mud added during the day appears dark.

activity around him, busily work his pellet into place on the nest rim. Within a few minutes nearly all the others in the colony or colony section would shift their activities in the same way, changing the whole tenor of activity in the flock (Emlen, 1952: 186). Individuals engaged in building dropped completely all traces of pairing behavior. Each bird appeared to give its full time and attention to the task even, at times, to the extent of ignoring trespassers stealing mud from another part of its nest. After a half hour or so of intensive building activity, the entire flock might revert to clustering and territorial defense or to loafing until, quite unpredictably, another session of nest building would be initiated. As nest construction advanced, the distinctness of these periods waned, and birds would frequently interperse nest building with defensive behavior.

Primary squatters, presumably males, that failed to secure partners by the time nest building was under way in the colony joined in the mud carrying under the stimulus of their more successful colony associates. Two nests built by such single individuals advanced to stages II or III before the bird gave up and disappeared. In another case the builder finally secured a mate when his nest was at stage III. One unpaired bird became so occupied with nest building that he consistently ignored potential mates that came to the site; his nest fell on the fifth day suggesting that it was of inferior construction. Another bird late in the season acquired a mate which failed to assist him in nest building. The nest, as a consequence, advanced slowly, the mate became less and less regular in its appearance, and the pairing bond was gradually dissolved before the nest was completed.

Nests started by single birds were narrower than the typical nest. Incomplete, generally undersized shells are often found near the edge of advanced colonies and may represent the efforts of such unmated individuals.

Defense of the Nest Site.—Defense of the nest site was essentially no different from the intolerance of close association demonstrated by birds wherever they congregated. Its only unique characteristic was its localization. Aggressiveness exhibited at the first clusterings at the colony site (step 1 of pair formation) appeared the same both qualitatively and quantitatively as that seen after the bond and the nesting territory had been thoroughly established. From the beginning, the extent of the defended territory around the nest was apparently determined by the reach of the bill from the nest rim, a distance of about four inches (Emlen, 1952: 190). Nesting birds spent much time watching colony mates fly past and flutter up to neighboring nests. They occasionally made threatening gestures

toward those that came close, but rarely attacked except as an intruder actually alighted within reach. No essential changes were noted as the nesting cycle progressed except that the occasion for defense was reduced with the completion of the nest and the reduction of the opening from a broad ledge to a narrow hole.

Defense by the members of a pair was apparently entirely independent; an attack by one member rarely being joined by the mate. Exceptions in which both members took part occurred when the two were together at the nest opening. At such times, however, the birds showed nothing that could not be most readily interpreted as coincident independent attacks. After construction was completed and the eggs laid, males were perhaps a bit more aggressive at the nest than females, but this difference was not clear. In three nests, males started roosting on their nests at night when construction had proceeded to about stage V. Females started at the same time or a few nights later, but it was the male that generally came to the entrance first when a flashlight was turned on the nest. In one nest, the male regularly perched in the nest entrance during the early hours of the night.

No defense was used against English Sparrows in the two colonies where these birds were usurping nests. The swallows quickly stepped aside with or without alarm notes and allowed the sparrows to take over. No instances were seen in which sparrows attempted to enter a nest containing young. Mr. Bodeman, on whose barn the large Deerfield, Wisconsin, colony was located, informs me, however, that the swallows fly about in great alarm but make no move to interfere.

The alarm evoked by human interference was exhibited by all colony members and appeared to be a general alarm, although some nest owners showed increased excitement when their particular nests were being examined. Attacks on the human intruder, such as is characteristic of the Tree Swallow did not occur. Isolated pairs and birds in small nesting groups showed more alarm (called longer and more frequently) than those in the large colonies.

COPULATORY BEHAVIOR

Copulatory behavior of an abortive nature occurred on the loafing perches, at the mud gathering sites, and possibly also on the wing in the chases precipitated by flight singing. Resting or mud gathering individuals of either sex were suddenly pounced upon by a bird from above, and seized by the crown or nape feathers. A tussle ensued in which the aggressor characteristically spread its tail and apparently tried to establish cloacal contact. Interpretation of these perfor-

mances was difficult, however, and often they seemed no more than aggressive attacks. In the two instances observed where individual identities were determined, the bird selected by the aggressor was not its mate. The conditions under which they most often occurred suggest that they were typically promiscuous and independent of mate- or sex-recognition.

Complete copulations regularly occurred on the nest and were never observed elsewhere. They characteristically occurred between the two members of a pair after a period of quiet perching together in the nest. On two occasions, however, they were performed in a hurried manner by visiting males from neighboring nests during the absence of the owner. The females showed no reluctance in accepting these males, but in one case the female joined her mate a few seconds later in a violent pursuit of the intruder.

In a mated pair in the copulatory phase of the nesting cycle (immediately preceding and during egg laying), the male characteristically initiated copulatory activity by repeatedly leaving his mate at the nest entrance to retire to the nest cup and crouch in a posture suggestive of the squatting of a receptive female (plate 8, E). Each time he did this he would utter the soft "ksh-ksh" call commonly used between members of a pair at the nest. In most cases, the female made no detectable response to this behavior but sat passively at the nest entrance, looking out. At other times she raised her bill and turned her head slightly as though looking back over her shoulder and sang softly. To this the male responded by retreating farther into the nest and crouching. Such performances were repeated at irregular intervals for as much as 15 or 20 minutes without any particular display of excitement. Finally the female followed the male back into the interior of the nest. Here she crouched and permitted the male to mount with violently flapping wings (plate 8, F).

Nest construction had in all cases progressed to the shallow cup stage (III) or beyond before copulatory behavior started. A nest of at least this size would seem necessary for the copulation preliminaries described above, and may feature in the onset of the behavior. Copulating birds generally tumbled from the rim in cup stage nests, apparently before the act had been completed. In more advanced nests, however, copulation was completed within the nest. The female then shook herself and resumed her post at the entrance. The male likewise returned to the entrance but frequently returned to the nest cup three or four times as though inviting a repetition of the procedure.

As many as five copulations were observed between the members of a pair in one morning; three occurred within one seven-minute period, and the shortest interval recorded between copulations was about two minutes.

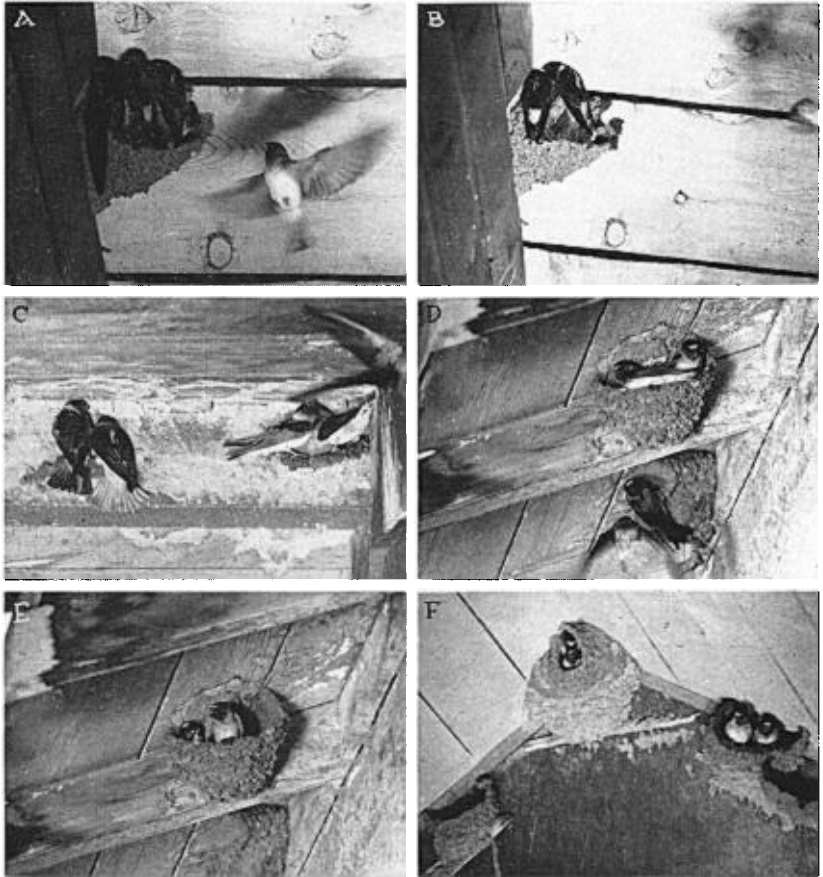
Precopulatory behavior in a nest, although relatively quiet, frequently aroused excitement among the birds in neighboring nests. There was no evidence of contagious behavior at these times, but visiting was increased, and the nest of the mating pair often became the center of considerable clustering and chasing. In wide-open nests in stage III or IV of construction, the resulting confusion was considerable, and outside birds repeatedly gained entrance and apparently attempted copulation. Defense against these intruders was largely, if not entirely, conducted by the male, who at times was left panting by the frenzied activity. Intruders at these times were persistent but rarely put up more than a brief defense against the resident male. In advanced nests with smaller entrances (stages V, VI, or VII), defense of the nest was far simpler, but intruders still persisted and occasionally gained entrance. A rough-and-tumble scramble followed during which additional birds sometimes crowded in to add to the confusion. After from 10 to as much as 30 or 40 seconds the intruders would tumble from the opening, frequently dragging one or both of the residents with them in a squirming, flapping mass.

In two nests under intensive daily observation, the first egg was laid 4 and 6 days, respectively, after the first observed copulation at the nest. Copulations were seen nearly every day thereafter until the middle of the laying period. The latest observed occurrence was on the afternoon preceding the laying of the last (fourth) egg.

DISCUSSION

Territory plays an important role in pair formation in a large number of birds. The male, arriving first, establishes himself and drives off all others of his kind until a female invader, recognized through appearance or through behavior, is accepted as the mate (Lack, 1940). This is essentially the procedure followed by the Cliff Swallows here described except that the whole procedure has been greatly intensified by the small size of the territories, the simultaneity of activities and the strong gregariousness of the birds.

Territory.—In most birds the procedure of territory establishment seems to involve two changes of behavior: a) localization of activity and b) increased intolerance of associates. In the Cliff Swallow only the first of these two changes is apparent. The universal intolerance of close crowding observable wherever swallows are congregated simply



PAIR FORMATION AND COPULATION POSTURES. *A.* Clustering of non-breeding birds at a potential nest site on the side of an old nest. *B.* Typical postures assumed by the primary squatter (*left*) and secondary visitor (*right*) in early stages of pair formation. *C.* A squatter and visitor in early stage of pair formation (*left*) and a partially mated pair in a song duel (*right*). *D.* A pair completely tolerant of each other (pairing bond completed). *E.* Male retiring into nest cup preparatory to copulation. *F.* Copulation in a stage VI nest.

becomes associated with a specific site through repeated visits. The degree of intolerance and its extent apparently change but little with this locality fixation except as the enforced position of the bird may handicap or aid his activities. Thus, a bird alighting on a vertical nesting surface before the nest has been started is obliged to cling facing inward in a position ill suited to defensive activity, while later, facing outward on a nest rim he can readily watch for and fend off invaders.

Pairing and mating functions are considered by Mayr (1935) to be at the root of all territorial behavior, the other functions such as food allotment and population control having appeared incidentally as secondary attributes. Such reasoning applies well to the Cliff Swallow where territorial behavior and pair formation are inextricably linked. The male selects a site or territory and repeatedly returns to it, aggressively repelling all who cluster around him. Through aggressive persistence, one of these visitors, a female, finally succeeds in penetrating the territorial barrier to establish a pair relationship of mutual tolerance with the male. Territory performs a further function in strengthening or fixing this bond by serving as a refuge from the social strife outside in which the pair may associate intimately in nesting activities.

Another basic function of territory which has been emphasized by Nice (1941, 1943) is the prevention of interference in raising the young. This function is particularly clear in the Cliff Swallow where territories are small and closely packed. Experiments with the breaking of nest walls (Emlen, 1952: 193) suggest that without such physical supplements to territorial boundaries successful nesting might be quite impossible in the Cliff Swallow. Protection against interference in nesting is accomplished by a combination of mud walls on five sides and defensive behavior on the sixth.

Song.—Modern interpretations of bird song generally suggest a dual function of a) repelling territorial intruders and b) attracting potential mates. In the Cliff Swallow singing is associated with displays of aggressiveness and, around the nesting colony, appears to be a direct response to intruders on or near the territory. This suggests that song might properly be interpreted as a threat or, perhaps, a symbolized "intensionsbewegung" or incipient form of attack. Song, however, serves as an attractant rather than a repellent to other birds, which swarm in and cluster around the singer. It thus fails completely as threat if the function of threat is to repel.

A function of attraction in a context of aggressiveness suggests motivational interpretations implied in the words challenge or defiance. Such terms have no objective meaning, however, and add

nothing to our understanding of the behavior except as they suggest subjective experience. The same criticism applies to such common interpretations of bird song as proclamation, self-assertion, advertising, satisfaction, eagerness, or longing. They may suggest attractive parallels with human behavior which are recognized in subjective experience, but such analogies are unprovable and potentially misleading. The only objective way to interpret bird song is in terms of its causes and effects; the situations which induce it and the responses which it elicits.

The environmental situations associated with singing in the Cliff Swallow have already been reviewed. Song was most prominent at the colony sites during pair formation but occurred wherever birds congregated on loafing perches, at mud sites or in foraging flocks. It was used both by aggressors and defenders and was employed as a prelude to as well as an accompaniment of actual conflict. Less commonly, singing occurred in lone birds left behind at the colony site or in relatively isolated birds at the edge of a foraging flock. In such cases it presumably reflected physiological disturbances similar to those which occurred in the conflict situations.

The effect of singing was to elicit attack or more singing by neighboring swallows. In dense flocks it often led to a confused chorus or a maelstrom of fighting involving half a dozen or more birds. Song thus served to create and maintain a condition of intense excitement at the scenes of territorial establishment and pair formation. One of its primary functions may well be that of a stimulating agent in advancing these essential activities of the reproductive cycle.

Song also functioned to attract other birds, including females, to the territories. While the behavior of both the attractor and the responding visitor was aggressive, we have seen how such aggressiveness is gradually suppressed and eventually replaced by tolerance in the process of pair formation. No repelling effects of song were detected.

The use of song away from the nest site may be interpreted in terms of causation as described in the preceding paragraph and need not raise questions of additional functions.

Sex Recognition.—Tinbergen (1939) has noted that in species where sex is not readily detected by morphological or vocal characters, sex recognition is generally slow and is accomplished in a series of behavioral interactions between the two birds. The Cliff Swallow seems to follow this pattern.

Differences in behavior during the period of pair formation were subtle and to all appearances merely quantitative variations of

characters common to both sexes. They seemed to consist primarily in the amount of initiative and of persistence shown in clustering at the prospective nesting sites. Males showed more initiative in selecting sites and squatted on them more tenaciously than did females. Females were slower and more hesitant in selecting sites, but more persistent in withstanding the repelling actions of birds already on a site.

These differences, it should be noted, are of a social rather than a sexual or epigamic nature. The absence of epigamic elements in the process of pair formation is, in fact, quite striking and emphasizes the distinctness of pairing and mating activities. True sexual behavior in the form of precopulatory and copulatory activities was conspicuously absent during the process of pair formation. Away from the colony sites it persisted, may even have increased, in the form of promiscuous matings at the mud gathering sites and on the loafing perches. At the nesting sites, however, it was conspicuously absent until after the intense activity of clustering and nest establishment had subsided.

The question often raised in discussions of pair formation as to whether sex, per se, is recognized seems quite meaningless in this case. The birds apparently established recognition of a specific individual after a period of intense interaction in which differences in social behavior favored a bond between opposite types.

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