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THE CAVE SWALLOW IN TEXAS

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Among the group of birds of tropical and subtropical distribution that reach their northern limits in the southwestern United States, the Cave Swallow (*Petrochelidon fulva*) is of special interest since it nests colonially in caves. It was first reported in the United States by Scott (1890), who collected two vagrants of the Cuban and Isle of Pines race, *P. f. "cavicola"* (= *coronata*, *fide* Hellmayr, 1934:34), on Garden Key, Dry Tortugas, Florida, on March 22 and 25, 1890. Twenty years later Bishop (1910:459) reported specimens obtained in Kerrville, Kerr County, Texas, which he referred to *P. f. pallida*, a race described by Nelson (1902:211) from Saltillo, Coahuila, México. That the Cave Swallow breeds in Texas was established in 1915 by Thayer's report of nests and eggs collected near Japonica, Kerr County. A year later the existence of "several isolated colonies" six miles west of Ingram, Kerr County, was announced by Smith (1916:191). Recently an extension of known breeding range to Eddy County, New Mexico, was reported (Kincaid and Prasil, 1956:452), and the existence of a colony in Edwards County, Texas, was briefly noted (Wolfe, 1956:50, and Pettingill, 1957:32). With the exception of these reports, a record of two individuals seen on the Tortugas in June, 1915 (Hull, 1939:24), and a description of a ceratophyllid flea from nests in Uvalde County, Texas (Eads, 1956:73-76), no further accounts of the Cave Swallow in the United States have been forthcoming in the 41 years since Smith's report. It therefore seems desirable to present additional information concerning variation, distribution, and ecology of this species in Texas.

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DISTRIBUTION

The Cave Swallow breeds in the Greater Antilles from Puerto Rico west to the Dominican Republic, Haiti, Jamaica, Cuba, and the Isle of Pines; the Cuban and Isle of Pines swallows are recognized as a separate race, *P. f. coronata*. On the continent the species breeds in Yucatán (*P. f. citata*) and in central Chiapas (subspecies?; see Amadon and Eckelberry, 1955:75) and, as *P. f. pallida*, in Eddy County, southeastern New Mexico, in central Texas, and in northeastern México, where it is known from three localities in Coahuila (Saltillo, Sabinas, Monclova) and one in Tamaulipas (Miqui-

huana). According to Hellmayr (1934:35) the Peruvian and Ecuadorian swallow *rufocollaris* is conspecific with *P. fulva*.

In Texas nesting of this colonial swallow is confined to limestone caves along the southern edge of the Edwards Plateau, a massive upland extending over much of the central and southwestern parts of the state. On the south and east the plateau descends to the low flatlands of Texas over the maturely eroded Balcones Escarpment, which decreases in height from 1500 feet at Del Rio near the Rio Grande to less than 100 feet north of Austin. Along the escarpment, where thick strata of limestone are exposed and highly dissected, numerous springs and caves occur, the latter ranging in size from small pits or shelters to gigantic cavern systems. Several of the larger springs are sources of rivers which flow to the lowlands.

The most widespread plant association of the dissected southern and southeastern parts of the plateau is a scrub forest of Mexican cedar (*Juniperus mexicana*), Texas oak (*Quercus texana*), and stunted live oak (*Quercus virginiana*). Extensive areas have been cleared and converted to grassland or savannah by cattle ranchers. The climate of this region is semiarid-mesothermal, with average annual potential evapotranspiration of 39.27 inches (Thornthwaite, 1948).

The distribution of breeding colonies of the Cave Swallow in Texas is shown in figure 1. Many, perhaps most, of the larger caves east of the Pecos River in western Val Verde County and west of Kerrville, Kerr County, are inhabited by these swallows.

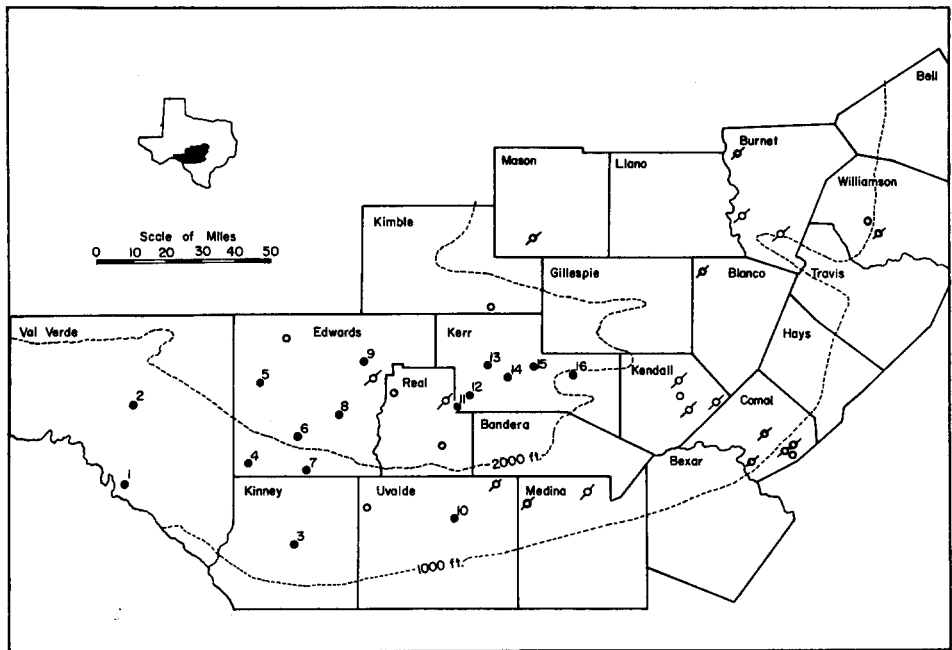


Fig. 1. Distribution of colonies of the Cave Swallow in Texas. Dots represent caves inhabited by swallows; circles with diagonal lines, seemingly suitable caves not occupied by swallows; circles, caves not investigated but judged as suitable from descriptions in the literature. 1. Abominable Sinkhole. 2. Fern Cave. 3. Webb Cave. 4. Rucker Bat Cave and Saltillo Cave. 5. Dunbar Cave. 6. Whitworth Ranch Cave. 7. Green and Hillcoate caves, Sergeant Ranch. 8. Thurman Cave. 9. Devil's Sinkhole. 10. Frio Cave. 11. Johnson Ranch Cave. 12. Wilson Cave. 13. Stover Cave. 14. Merritt Ranch caves. 15. 6 miles west of Ingram. 16. Kerrville.

South of the Balcones Escarpment, which follows a line drawn through central Kinney, Uvalde, and Medina counties, no caves of any size are found; and north of Val Verde, Edwards, and Kerr counties swallows have not been recorded although several caves are present in that part of the plateau. Undoubtedly other colonies will be discovered in Texas, but it seems rather unlikely that the breeding range extends much farther east or north than indicated by the distribution of colonies shown in figure 1. The most curious feature of the distribution of this swallow is that it occurs no farther east than Kerrville, since seemingly suitable caves are found in Bexar and other counties along the eastern margin of the Edwards Plateau east of Kerr County.

Special environmental requirements for nesting of the Cave Swallow in Texas include (1) a cave providing rather extensive roughened or, preferably, pitted surfaces for attachment of nests *within the twilight zone* and at least four feet above the floor; and (2) a source of water for drinking and of mud or mud substitute (guano) for nest building either within the cave itself, in which case colonies may inhabit caves far removed from surface water, or within foraging range, which extends only a few miles from the cave. Water for mud may be provided either by seepage within the cave or by run-in surface water. Swallows regularly visit ranchers' open water tanks (ponds) to drink and in some instances to obtain mud. Undoubtedly these man-made water sources have been important in permitting the swallows to continue breeding in recent years within the drought-stricken central Texas region, where naturally occurring surface water was practically non-existent over extensive areas, except for a few days each year following rains. As a result of its ability to utilize cave walls for nesting and because in certain situations it may be independent of surface water, the Cave Swallow is able to maintain breeding colonies in arid regions which are uninhabitable to the Cliff Swallow (*Petrochelidon pyrrhonota*). The latter species requires for nesting a protected overhanging cliff or cliff substitute in close proximity to a source of mud (Emlen, 1952:196) and, at least in Texas, an extensive meadow, lake, or flood plain over which to forage.

Within the breeding range of the Cave Swallow in Texas the Cliff Swallow (*P. p. tachina*) also occurs, nesting on limestone cliffs along the major streams. Some of the largest colonies of the Cliff Swallow in Texas are in Kerr County along the North Fork of the Guadalupe River, for example at Camp Stewart (= Japonica) and at a lake along the river six miles west of Camp Stewart, and at Prade Ranch, in Real County along the Frio River. Contact between the two species of swallows in Texas is probably an uncommon occurrence as a result of their differing ecologic distributions. We have no record of the two species associating. The Cave Swallow also is sympatric with the race *P. p. melanogaster* of the Cliff Swallow in Coahuila, as at Saltillo (Burleigh and Lowery, 1942).

THE BREEDING COLONIES

The following is an account of all caves in Texas known by us to be inhabited by Cave Swallows. Several of the caves listed are also mentioned by White (1948) in his article on the caves of central Texas.

EDWARDS COUNTY. *Devil's Sinkhole, 10 miles northeast of Rocksprings.*—This giant cave, the largest of its type in the United States, has a sink-type opening 60 feet in diameter, which drops 110 feet vertically and widens into a large chamber partly filled by a conical mound of rock breakdown 100 feet in height. Swallows nest on the slanting roof of the lower chamber 110 or more feet below ground level and high above the sides of the rock mound.

A source of mud for nests is provided by water which seeps from the sides of the sink, wetting soil that has accumulated on the narrow limestone ledges and dripping to

the mound of rock and guano below. Brown Towhees (*Pipilo fuscus*) and Tufted Titmice (*Parus bicolor*) were seen to enter the sinkhole and forage over moss and lichens on the lower ledge of the sink about 100 feet below ground level. A Canyon Wren (*Catherpes mexicanus*), presumably a resident in the sink, foraged on ledges 70 feet down. Horned Owls (*Bubo virginianus*) also nest on ledges in the sink.

On the morning of September 21, 1956, first indication that swallows were preparing to leave the cave was a chorus of chattering calls at 6:10 a.m., given by birds in



Fig. 2. Entrance to Dunbar Cave, Edwards County. Xeric vegetation shown in background is typical of this part of the Edwards Plateau.

the lower chamber before they entered the sink but clearly audible from ground level. Shortly thereafter a compact flock of about 100 birds appeared at the base of the sink, executed three rapid ascending spirals, and emerged from the entrance in close formation, flying at high speed and calling continuously. Other groups of from 25 to 100 birds followed until an estimated total of 500 birds had emerged. Invariably flights were preceded by loud choruses of calls, which continued during ascent. In loose formation the flocks circled high in the air above the cave and flew toward the east. At 7:30 a.m. a loose flock of several hundred swallows appeared high above the cave and descended to the entrance in slow spirals. At one point in their descent the birds suddenly gathered together in a compact flock as a female Sparrow Hawk (*Falco sparverius*) passed below them, only to separate again when the hawk had passed. As the circling flock passed a few feet above the entrance, a few individuals dove into the sink; then suddenly the

whole flock dropped in. Some birds spiraled down the sink while others dove straight down. Many birds left the cave between 8:10 and 8:15 a.m. and again flew eastward. Emerging groups spiraled clockwise and counter-clockwise in the sink with about equal regularity; ascent of the sink always involved at least three full spirals, but some groups performed as many as 20.

Dunbar Cave, 21 miles west of Rocksprings.—The entrance of this cave is a vertical sink about seven feet in diameter (fig. 2), which penetrates 15 feet of limestone

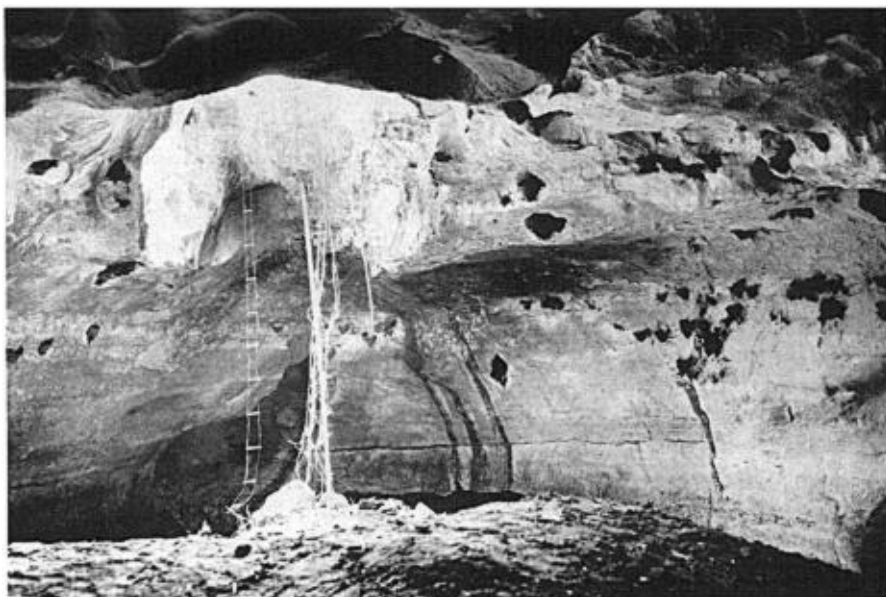


Fig. 3. First chamber of Dunbar Cave, Edwards County, taken from floor 30 feet below ground level. Note Cave Swallow nests in eroded pockets in the roof and on the walls.

before opening into an oval chamber approximately 70 feet in diameter and 15 feet in height. On the east and west sides of this chamber, passageways lead to other chambers of equal or larger size. About 400 swallows were present on September 29, 1956, perched on the 250-odd nests in the cave. All of these nests were located in the first chamber (see fig. 3). The greatest concentration of nests occurred on walls near the entrance sink, but a few were located up to 90 feet from the entrance. None was placed in the entrance shaft itself, which was exposed to direct sunlight.

In Dunbar Cave water seeping from the walls of the sink falls to the guano-covered floor of the first chamber, supplying a source of mud for the colony. Guano is produced by large numbers of cave bats (*Myotis velifer*) roosting in the cave, mainly in chambers other than the first, and by the swallows themselves.

At about 8 p.m. on September 29, all but 40 or 50 of an estimated population of 400 swallows left the cave when members of the University of Texas Speleological Society entered. The disturbed birds spent the night outside the cave, returning in a flock at 6:30 a.m. the next day. About 50 birds entered but after circling for an hour the majority was again driven away by our activities in and near the cave. Our presence in the cave greatly disturbed the birds, which began calling loudly and circled for several minutes in close formation and at high speed, just below the entrance, before flying out.

Rucker Bat Cave and Saltillo Cave, 35 miles southwest of Rocksprings.—On September 30, 1956, we found nests in crevices and pits in the roof of Bat Cave on the Rucker Ranch. This cave receives its name from the large numbers of Mexican free-tailed bats (*Tadarida mexicana*) which roost in a chamber at the rear of the large main room. The main chamber is about 100 feet wide, several hundred feet long, and 50 to 60 feet in height. It opens to the surface through a large arched entrance; all of the main chamber is within the twilight zone and much of it is rather well illuminated. No birds were present on the day of our visit but to judge from numbers of nests seen, the colony is smaller than those at Dunbar Cave and the Devil's Sinkhole.

There is evidence that considerable volumes of water accumulate in the cave following rains; possibly the swallows obtain mud within the cave.

Saltillo Cave is on the Rucker Ranch a few miles from Bat Cave. It opens through a sink about 8 feet in diameter which penetrates limestone for about 5 feet to open in the ceiling of a large chamber having a floor 45 feet below ground level. Twilight zone illumination prevails throughout the cave. On December 2, 1956, Baker estimated that 1500 nests were located in the cave, mostly on the walls of three domes in the ceiling about 40 feet above the floor, and on April 7, 1957, between 2500 and 3000 swallows were present. In all probability this is the largest breeding colony of Cave Swallows in this country. On the cave floor beneath the domes, piles of bird guano up to 5 feet in height have accumulated. One row of about 10 nests apparently had been vandalized by a predator, possibly a ring-tailed cat (*Bassariscus astutus*), which had gained access to them by scaling the wall. The lowest nests in the cave were about 10 feet above the floor.

Whitworth Ranch Cave, 20 miles south-southwest of Rocksprings.—A colony of swallows is reported to inhabit a big shelter cave on the Whitworth Ranch, within 200 yards of Dragool Cave. Hettler found 400 birds there in August, 1956.

Thurman Ranch Cave, 15 to 20 miles south of Rocksprings.—On November 24, 1956, Kyser found approximately 50 nests in pits in the roof of this cave, which opens through three sinkholes measuring from 4 to 12 feet in diameter and penetrating 6 feet of limestone. Nests were located in the entrance room, a chamber 10 feet high and about 15 feet wide; the lowest nest was only 4 feet above the floor.

Hillcoate Cave and Green Cave, Sargeant Ranch on Rocksprings-Bracketville Road near Kinney-Edwards county line.—Hillcoate Cave opens through an arch 5 feet high and 15 feet wide in the side of a hill. The first chamber is 50 feet high, 100 feet wide, and about 500 feet long. About 50 Cave Swallow nests were seen by Baker on January 30, 1957, all of which were in the twilight zone within 100 feet of the entrance. The presence of nests of the Cave Swallow in Hillcoate Cave was first reported to us by Kyser, who explored the cave in November, 1956.

Green Cave is about one mile from Hillcoate Cave and is similar to it in dimensions. Baker noted about 50 nests there on January 30, 1957. Both caves on the Sargeant Ranch are within a mile of the ranch house, where windmill water tanks are located.

KINNEY COUNTY. *Webb Cave, Shahan Ranch, 7 miles north of Bracketville.*—This cave is entered by four sinks, the largest of which is 10 feet in diameter; these penetrate 20 feet of limestone to open into a chamber 30 feet in height. Kyser counted 150 nests in the cave on December 30, 1956. Water dripping from a hole in the ceiling near the entrance forms mud on the floor of the chamber, but several nests examined by Kyser were composed of mud which he judged to have been obtained outside the cave.

UVALDE COUNTY. *Frio Cave, Annendale Ranch, 7 miles south of Concan.*—This cave, one of the largest in Texas, consists of three large and two small chambers. Swallows nest on the pitted walls of the oval entrance room which is about 300 by 600 feet in

dimensions. Most of the entrance chamber is well lighted by way of two 20-foot chimneys and three arched entrances, total darkness being reached only in the inner 100 feet (White, 1948:61). Great hordes of Mexican free-tailed bats roost in the inner chambers.

VAL VERDE COUNTY. *The Abominable Sink, Ab Rose Ranch ("Old Mayfield Ranch"), 15 miles south of Comstock.*—A circular entrance sink about 35 feet in diameter penetrates 130 feet of conglomerate and shale to widen into an extensive chamber in limestone, which is in part filled with breakdown from the sinkhole. Apparently neither swallows nor bats inhabit the cave at the present time but on January 29, 1957, Baker found remnants of six or eight nests under a slab of shale about 120 feet down in the sink. There is evidence that the sink connecting the limestone chamber with the surface is still enlarging, as Mr. Rose reported that new breakdown had accumulated since his last visit. Possibly other nests were destroyed and the colony abandoned when this recent breakdown of the sink occurred.

Fern Cave, Martin Rose Ranch, 20 miles north of Comstock.—Fern Cave opens through a sink 25 feet in diameter and about 50 feet deep. In a chamber adjoining the entrance approximately 100 nests were found by Baker on January 29, 1957, most of which were on the sides of three large domes in the ceiling; a few nests were placed on walls about 20 feet above the floor of the cave. There is a water tank 200 feet from the cave entrance.

KERR COUNTY. *Cave near Japonica (= Camp Stewart).*—A nesting colony was found in June, 1914, by F. B. Armstrong (Thayer, 1915:102-103). Judging from the description quoted by Thayer, this cave is similar to the first chamber of Dunbar Cave described elsewhere. The entrance sink is about eight feet in diameter; ten feet down it widens into a "spacious chamber," the floor of which is 50 feet below ground level.

Six miles west of Ingram.—Smith (1916:191) reported "several isolated colonies" in this area, but unfortunately he failed to describe any of the caves or to fix their location more precisely.

Goat Shelter Cave and unnamed sinkhole, Johnson Ranch, 30 miles southwest of Hunt.—On October 9, 1956, we investigated two nesting sites at this locality reported to us by Eads. We found 80 nests in the Goat Shelter, a cave having an oval entrance 35 feet wide which opens obliquely down into a single chamber about 50 feet in diameter and 30 feet in height. Most of the nests were placed on the back wall and on the sides of large crevices and pockets in the roof. One nest was in an eroded pocket only 4½ feet above the cave floor. Another was only 15 feet in from the top of the entrance arch, in a well lighted part of the cave.

The second cave on the Johnson Ranch in which swallows nest is an unnamed sinkhole with a vertical entrance about 5 feet in diameter. A nest within the cave was visible from the ground surface. About 20 feet down the sink reportedly opens into a large chamber; we did not investigate the cave further.

A third cave on the ranch, a single dry chamber 10 feet in diameter and 9 feet in height, contained no nests. Apparently this cave is too small to furnish suitable nesting sites for a colony; also much of the wall surface is accessible to racoons (*Procyon lotor*) and other predators.

Wilson Cave, 20 miles southwest of Hunt.—This large shelter cave was visited on December 30, 1956. It contained perhaps 50 nests; all these were located in crevices and pockets in the walls and ceiling and so situated that direct sunlight did not fall on them. We were informed by the owners of the ranch that in the summer swallows regularly visit a water tank about two miles from the cave. Among specimens sent to us on loan from the U. S. National Museum is a female collected by B. E. Ludeman 20 miles southwest of Hunt on August 10, 1937.

Stower Cave, 13 miles west of Hunt.—Davis visited Stower Cave in the fall of 1956, finding a few nests. The cave is a sinkhole with an entrance 8 feet in diameter. No swallows were present when Berner visited the cave at noon on April 14, 1957.

R. R. Merritt Ranch Cave No. 1, 6 miles southwest of Hunt.—This cave is a single chamber 25 feet in diameter opening by way of an 8-foot circular sink 35 feet above the floor. On December 29, 1956, three nests were found under an overhanging ledge below the sink. Two other smaller caves on the Merritt Ranch are not inhabited by swallows.

Kerrville.—It is probable that specimens reported by Bishop (1910:459) as having been obtained at Kerrville were collected elsewhere than in the immediate vicinity of the town.

SEASONAL STATUS AND ANNUAL CYCLE

In Texas the Cave Swallow is a summer resident. Available data suggest that time of arrival at the nesting colonies in the spring varies markedly from year to year. According to a report by Pettingill (1957:32) the species arrives in Edwards County in April; in 1955 Eads (personal communication) noted that none was seen at Frio Cave, Uvalde County, on March 30, but on April 20 many birds were present. In 1957 swallows were present in large numbers at the Devil's Sinkhole and Webb and Frio caves as early as February 9; in 1915 Armstrong collected specimens at "Kerrville" on February 6, and large series were taken by him in late February and March.

A fresh egg found on the floor of Frio Cave on April 5, 1957, indicated that laying was under way, although none of the nests which we were able to examine contained eggs. At Dunbar Cave on April 7, 1957, building and repair of nests was almost completed, and the gonads of several specimens collected were in or were approaching breeding condition. One female had an ovary measuring 8 mm. in diameter and an enlarged oviduct; the mate of this bird had testes 11 mm. in length and a conspicuous cloacal protuberance (Salt, 1954). The testes of another male were 10 mm. long. Two other males had testes 3 and 5 mm. in diameter; probably the latter two are first-year birds. Their wing lengths are 106 and 109 mm., whereas wings of the two males with enlarged testes measure 111 and 112 mm. Also the coloration of the presumed first-year birds is relatively pale. All specimens collected on April 7 were extremely fat; the heaviest bird, a male, weighed 25.1 grams.

In May, 1955, eggs had been laid and a few young were hatched at Frio Cave (Eads, 1956:73). Armstrong took 43 eggs from nests in Kerr County on June 7 and 8, 1914, including two sets of three, eight sets of four, and one set of five (Bent, 1942:489). These facts suggest that two broods are raised. The eggs are similar to those of the Cliff Swallow, except for slight differences in shape suggested by data given by Bent (*loc. cit.*).

In 1956 fall migration took place or at least was completed sometime between September 30, when hundreds of swallows were present at Dunbar Cave, Edwards County, and October 9, when none was found at two nesting sites visited in Kerr County. In this period there was a sharp drop in nightly temperatures at Kerrville and in central Texas generally. On December 29 and 30, 1956, and January 29 and 30, 1957, swallows were not found at several nesting sites visited in Kerr, Val Verde, and Edwards counties. Several ranchers expressed belief that the Cave Swallow may be present throughout the winter, at least in small numbers; but other than the impressions of these individuals, we have no evidence of the occurrence of the species in Texas during November, December, and January. The winter range of the Texas population is unknown; possibly the birds move south only as far as northeastern México, but no information seems to be available as to whether or not Cave Swallows are present there in the winter months.

Both adult and juvenal Cave Swallows have a complete molt in the fall. The post-

nuptial molt is completed or nearly so prior to migration of the adults. Molt was under way in an adult female collected on August 10; primary 1 is new and 2 is one-half grown. All 15 adult specimens taken at the Devil's Sinkhole on September 21, 1956, are in advanced stages of molt, as indicated in table 1. We interpret the unusual degree of uniformity of molt stage in this sample as an expression of close synchrony of the annual cycle in members of a colony. Synchrony of nest building and laying and hatching dates in colonies of the Cliff Swallow is discussed by Emlen (1952).

Table 1

Molt Stages of Specimens of *Petrochelidon fulva pallida* Collected at Devil's Sinkhole, Edwards County, on September 21, 1956

Sex and age	Number of primaries molted							Number of secondaries molted						
	2	3	4	5	6	7	1	2	3	4	5	6	7	
♂ ♂ adult				6	4	1					5	5	1	
♀ ♀ adult				3	1						3	1		
♂ juv.			1					1						
? juv.	1							1						

Unexpectedly, only two of 25 specimens collected on September 21 and 30 are immature, as indicated by an unpillared cranium as well as by the fact that they still bear some juvenal feathers. Both immatures are well behind the adults in stage of molt (table 1). The age ratio of the sample is subject to several tentative interpretations, one of which is that immatures normally migrate or at least desert the colonies before the adults. Another possibility is that in 1956 the nesting efforts of the population of the Devil's Sinkhole (from which 18 of the 25 specimens were collected) and, perhaps, of that at Dunbar Cave were largely unsuccessful.

NEST STRUCTURE AND LOCATION

The form of the nest shell is shown in figure 4. It is a rounded half-cup similar to stages III or IV in construction of the familiar retort-shaped nest of the Cliff Swallow described by Emlen (1954:23-24). Wetmore and Swales (1931:321) reported that nests of *P. f. fulva* are sometimes enclosed above, with a small entrance in the side; but in none of the thousands of nests of *P. f. pallida* that we have examined was there any evidence of an attempt to roof over the nest by extending the walls of the cup. The wide range of variation in nest size shown in figure 4 is characteristic of most colonies visited. In large part it results from the use of nests in successive breeding seasons, the nests becoming progressively longer and wider as additional layers of pellets are added to the rim. The composition of pellets may vary from year to year, with the result that older nests often show three or four layers of different colors and textures (see fig. 4A). A small nest was 5.1 inches wide at the rim and 3.6 inches long; one of the larger nests examined was 7.2 inches wide and 6.2 inches long. Dimensions of most nests fall between these extremes. When thoroughly dry the large nest, including shell, lining, and a large quantity of detritus in the nest cavity, weighed 970 grams; the small nest weighed 268 grams. Presumably nests are occupied until the combined weight of the shell and the detritus within causes them to fall from the cave walls.

Although the size of pellets used in construction of the nest shell is similar in *P. fulva* and *P. pyrrhonota*, the walls are thicker in nests of the former species. In *P. fulva* the thickness (measured between protruding pellets) varies from 1.35 inches (range in 7 nests, 0.9-1.7) at the rim to 0.86 inches (range, 0.8-1.0) at the base. In *P. pyrrhonota* the thickness varies in different parts of the nest from 0.24 to 0.66 inches, with an aver-

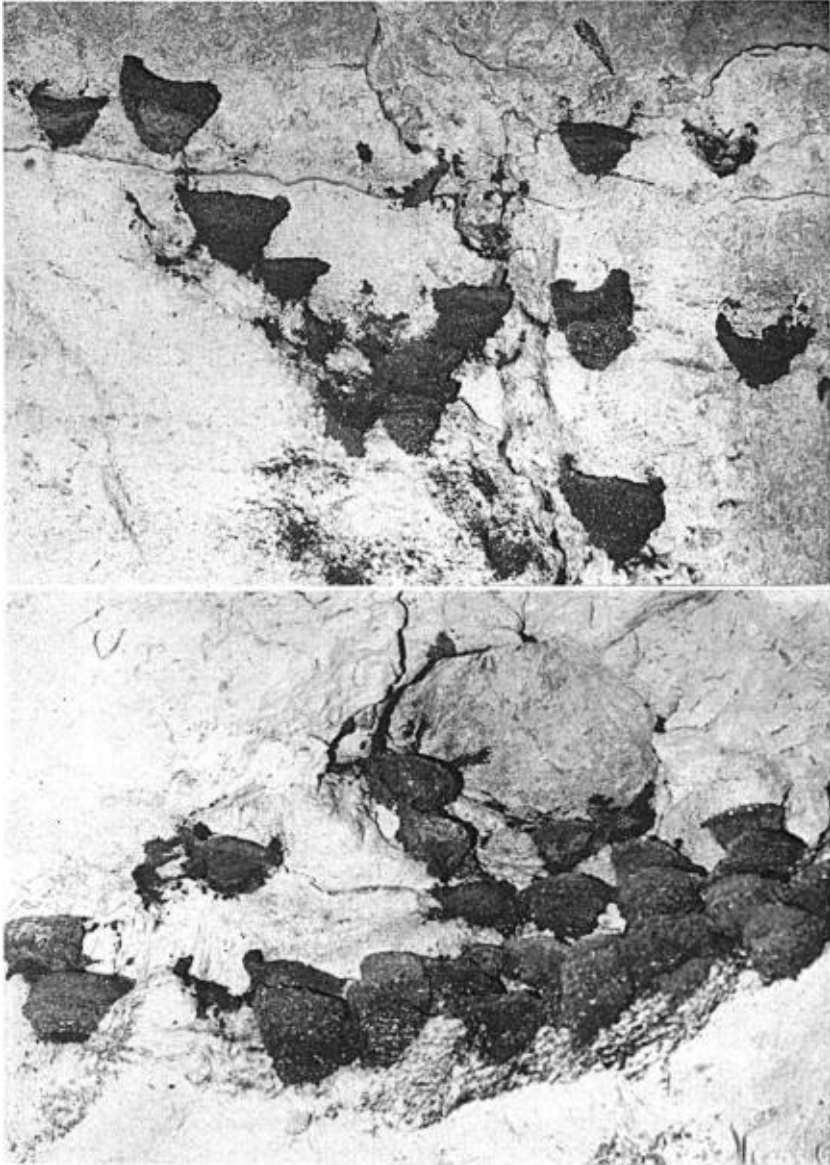


Fig. 4. Nesting sites of Cave Swallows in Dunbar Cave. Above, on vertical wall. Below, on sides of dome in roof; photograph taken looking up into dome.

age of about 0.44 inches (Emlen, 1954:21). Pellets from nests collected in Dunbar Cave are a mixture of weathered guano, soil, and limestone chips. Nest shells in some other colonies apparently are composed entirely of mud. The nest lining is a thin layer of cotton-like plant fibers of several types, thin strips of bark, fine grasses, and feathers. Much of the nest cup may be filled with a moist mixture of bat guano, old nest lining material, bits of eggshell, and fecal pellets of the myriads of insects and other arthropods

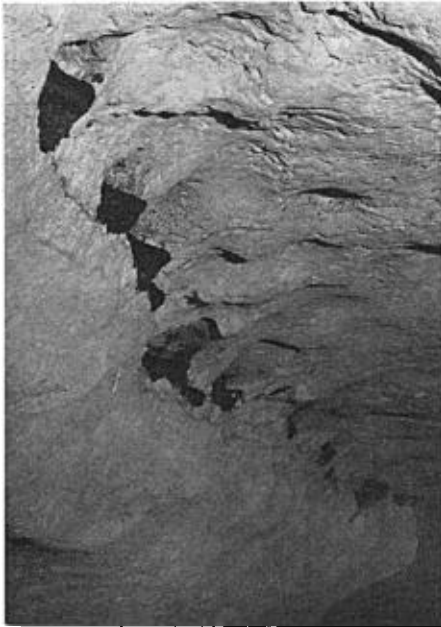


Fig. 5. Row of nests in eroded pockets up against ceiling in Dunbar Cave.



Fig. 6. Nest formed by partly sealing entrance of small pot-hole in limestone wall of Dunbar Cave.

which inhabit this mass of organic material; these include fleas, beetle larvae, and false scorpions. In Dunbar Cave, and presumably in other caves as well, the cave bat (*Myotis velifer*) frequently roosts on the roofs of pockets and crevices in which swallow nests are located and undoubtedly is a major contributor of guano. Probably it is the filling of the nest cup with guano and other organic material which necessitates extension of the rim by addition of new layers of pellets.

Emlen (1952:197) has presented considerable evidence to support his belief that the enclosed, retort-shaped nest of the Cliff Swallow "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." The enclosed top of the nest is regarded by Emlen as a late development in nest ontogeny in swallows, and, accordingly, he suggested that colonial nesting in *Petrochelidon* may have evolved recently.

The fact that the nest of the colonially nesting Cave Swallow is an unroofed structure can be reconciled with Emlen's views, provided location and spacing of nests in colonies are considered. It is certainly significant that in colonies of *P. fulva* we have never found large numbers of nests so closely grouped as in typical colonies of *P. pyrrhonota* (see for example, Emlen, *op. cit.*, fig. 7B). In most caves well over 50 per cent of the nests are located singly in small eroded pockets or crevices and are thereby effectively screened in all directions from neighboring nests. Irregularities in the surface of the cave walls determines spacing to some degree, preventing large concentration of nests in small areas, but the distribution of nests in all colonies visited clearly reflects a strong tendency for birds to build in isolated crevices and pockets or close up under an overhanging roof or ledge. Apparently flat vertical walls are used only when all other suitable

niches are occupied. Typical location of nests in eroded pockets is shown in figures 5 and 6; spacing of nests on a wall in Dunbar Cave is shown in figure 4. Figure 4 shows an unusually heavy concentration of nests on the sides of a large dome in the ceiling of this cave. Generally where two nests are in contact the upper one is a large nest that has been used for several years and the other, located below, is a small nest more recently built. It is unusual to find two nests in contact with the rims on the same level.

It is pertinent to this discussion of differences in nest structure in species of *Petrochelidon* to note that *P. fulva* nests in the twilight zone of caves, where illumination is relatively weak. From our observations, it seems probable that if *P. fulva* were to build nests having a roof and small tunnel entrance, it would have considerable difficulty in carrying out activities such as feeding the young within the nest and perhaps even in locating the nest entrance itself. Hence advantages resulting from the roofing of nests might well be outweighed by detrimental effects resulting from insufficient illumination in and about the nest.

Although in the United States the Cave Swallow nests only in caves, it is by no means so restricted in some other parts of its range. For example, in the Dominican Republic it has been found nesting not only in caves but also in clefts and crevices in cliffs, on ledges overhanging the sea, and on an iron bridge across a stream (Wetmore and Swales, 1931), situations typically selected by *P. pyrrhonota* in the United States. In Chiapas, México, Amadon and Eckelberry (1955:75-76) found *P. fulva* nesting beneath a portico along the plaza in Chiapa de Corzo and on the cathedral in Tuxtla Gutiérrez. We believe it is significant that both are regions in which *P. pyrrhonota* does not breed. The tentative inference is that where the two species are sympatric, as in Texas and New Mexico, nesting of *P. fulva* is restricted to caves by competition with *P. pyrrhonota*. Perhaps the superiority of the latter species stems in large part from its ability to establish larger colonies in limited areas of suitable nesting substrate, an ability dependent in turn, as suggested by Emlen, on the increased social stability resulting from the screening effect of the enclosed nests.

It is also of interest that in Trans-Pecos Texas, where the Cave Swallow apparently is absent, the Cliff Swallow occasionally nests in caves along rivers.

TAXONOMIC COMMENTS

There are no differences in color and pattern among specimens from Coahuila, Texas, and New Mexico that cannot be accounted for on the basis of individual or seasonal variation. Measurements of samples from these regions are presented in table 2; for comparison size data for *P. f. fulva* and *P. p. tachina* have been included. The large size claimed for *P. f. pallida* by Nelson (1902:211) and Ridgway (1904:56) on the basis of six specimens is confirmed by our large series. In color *P. f. pallida* differs from *P. f. fulva* in having the rufous pigments yellower (less reddish) and paler (less intense), especially on the rump, anterior under parts, flanks, and under tail coverts; centrally the under tail coverts are brownish gray rather than brown. Nelson (*loc. cit.*) probably got the erroneous impression that the reddish wash "is usually absent along sides of breast and body" in *P. f. pallida* from comparing his worn breeding specimens with fresher-plumaged material of *P. f. fulva*. In the fresh fall series from Texas all specimens show a conspicuous cinnamon wash in these areas, although the color is paler (near 7.5 YR 6/5, Munsell Book of Color) and less extensively distributed on the flanks than in *P. f. fulva*. With wear this wash is lost and the gray and dusky brown bases of the feathers of the flanks and breast are exposed, as in Nelson's material from Coahuila and Tamaulipas and in March and June specimens from Texas.

Weights of *P. f. pallida* derived from extremely fat specimens taken on September 21

were: ♂♂ 20.32 (18.4–22.3); ♀♀ 20.55 (20.0–21.1). On September 30 seven specimens were captured and held in captivity without food and water for 36 hours. When sacrificed, they showed little or no subcutaneous fat and averaged 17.1 grams (range, 17.4–18.4), showing an average weight loss of 2.7 grams.

Remnants of dark throat patch in P. fulva.—In 17 (34 per cent) of the 50 specimens of *P. f. pallida* examined, from one to seven feathers of the throat and/or anterior part of the breast have a terminal blackish brown mark, duplicating in shape and posi-

Table 2

Average and Extreme Measurements of <i>Petrochelidon</i> in Millimeters							
	Sex	No.	Wing	Tail	Bill from base	Tarsus	
<i>P. f. pallida</i>							
	Texas	♂	13–23 ¹	109.0 (106–112)	48.42 (47.0–49.9)	8.25 (7.6–8.7)	12.46 (12.1–13.0)
		♀	9	108.7 (104–113)	48.94 (47.8–50.7)	8.19 (7.5–8.5)	12.79 (12.3–13.6)
	New Mexico	♂ + ?	3	110.9 (109–112)	49.57 (48.9–50.8)	8.60 (8.5–8.7)	12.57 (12.0–12.8)
Coahuila ²	♂	1	107	48	12	
	♀	5	107.9 (106–110)	48.6 (47.0–49.5)	12.1 (12.0–12.5)	
<i>P. f. fulva</i> ³							
	Hispaniola	♂	8	99.5 (97–103)	41.6 (37.0–44.2)	7.9 (7.4–8.3)	12.5 (11.3–14.7)
	♀	2	100.5 (100–101)	43.4 (41.5–45.3)	7.9 (7.4–8.3)	12.5 (11.3–14.7)	
<i>P. p. tachina</i>							
	Texas	♂	18	104.0 (100–107)	46.89 (44.6–49.3)	7.55 (7.2–8.2)	11.81 (11.4–12.4)
	♀	9	102.9 (100–105)	46.39 (44.8–49.2)	7.61 (7.0–8.1)	11.60 (11.2–12.1)	

¹ 13 specimens for wing and tail.

² Measurements from Ridgway (1904).

³ Measurements from Wetmore and Swales (1931).

tion those which form the posterior part of the conspicuous metallic black throat and breast patch in *P. pyrrhonota*. In one female (Texas Nat. Hist. Collection 1264) these markings are very prominent, forming a patch 8 millimeters in diameter centrally on the breast and throat. In the majority of specimens of *P. f. pallida* these markings are entirely absent.

Because neither Ridgway (1904) nor other authors have noted the presence of throat markings in *P. fulva*, it was at first thought that their presence in specimens of *P. f. pallida* indicated hybridization with *P. p. tachina*. However, after examining large series of both *P. f. pallida* and *P. p. tachina* from central Texas and a small series of *P. fulva* from the Greater Antilles, we now favor a different interpretation.

Both in *P. f. pallida* and, to a lesser degree, in *P. p. tachina*, the size of the throat patch varies individually. By arranging four selected reference specimens of each of the two species in order of increasing size and conspicuousness of the throat patch, it was possible to demonstrate a gradual transition from the typical unmarked condition in *P. f. pallida* (class 0) to the extreme condition in *P. p. tachina* (class 7), in which the throat and anterior breast are almost solid glossy black (see fig. 7). Individual variation in *P. p. tachina* and in samples of *P. f. pallida* is shown in table 2, based on class scores assigned to adult and first-year specimens. There appears to be no sexual variation in this character, although larger samples might reveal slight but statistically significant differences. That relatively more specimens of *P. f. pallida* show throat markings in the sample of September, 1956, than in the sample taken in March and June, 1914, is doubtless attributable to the fact that the September birds are in very fresh plumage, whereas the others are in moderately worn plumage, which is, in most cases, badly

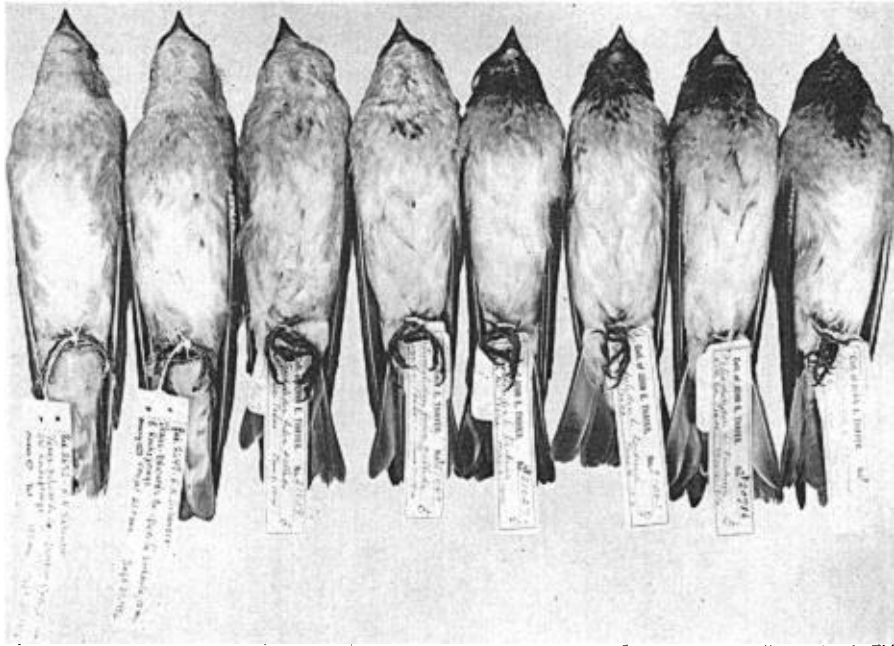


Fig. 7. Variation in throat pattern in Cave Swallows and Cliff Swallows. From left to right, four specimens of *Petrochelidon fulva pallida* (classes 0 to 3) and four of *Petrochelidon pyrrhonota tachina* (classes 4 to 7).

grease-stained and discolored. For this reason, in specimens collected in 1914, the markings are less conspicuous, especially in those having only a few small ones.

In order to investigate further the possibility that variation in throat pattern results from introgressive hybridization, we drew scatter diagrams to test for correlations between throat pattern and some other characters in which the two species differ. If recent hybridization were involved, correlation of intermediacy of characters would be expected in the presumed hybrids (Anderson, 1949). Evidence of correlation with throat pattern was found only for wing length in *P. f. pallida*; it was absent in both species in our comparisons of throat pattern versus (1) color of the forehead, (2) width of the forehead crescent, (3) color of the sides of the throat and chin, (4) color of the rump, (5) bill length, and (6) tarsal length. No intergradation between the species was noted in characters 1 through 3, but some overlap in color of the rump and in size occurs. The scatter diagram in figure 8 shows a weak correlation between wing length and throat pattern in male specimens of *P. f. pallida*, but not in *P. p. tachina*, and the absence of correlation in specimens of either species as regards throat pattern and tarsal length.

In *P. f. pallida* correlation between throat pattern and wing length shown in figure 8 would be expected if throat markings were more prevalent and the wing averaged slightly smaller in first-year than in adult individuals. It may be noted that the two immature specimens taken in September have newly grown feathers of the throat and anterior breast that are conspicuously marked; the male (TNHC 1269) falls in class 2 and the female (TNHC 1263) in class 1. Also a juvenal-plumaged specimen from Tamaulipas (USNM 158851) has pale dusky brown markings on the throat (class 1). Thus all known immature specimens in our series show remnants of a throat patch.

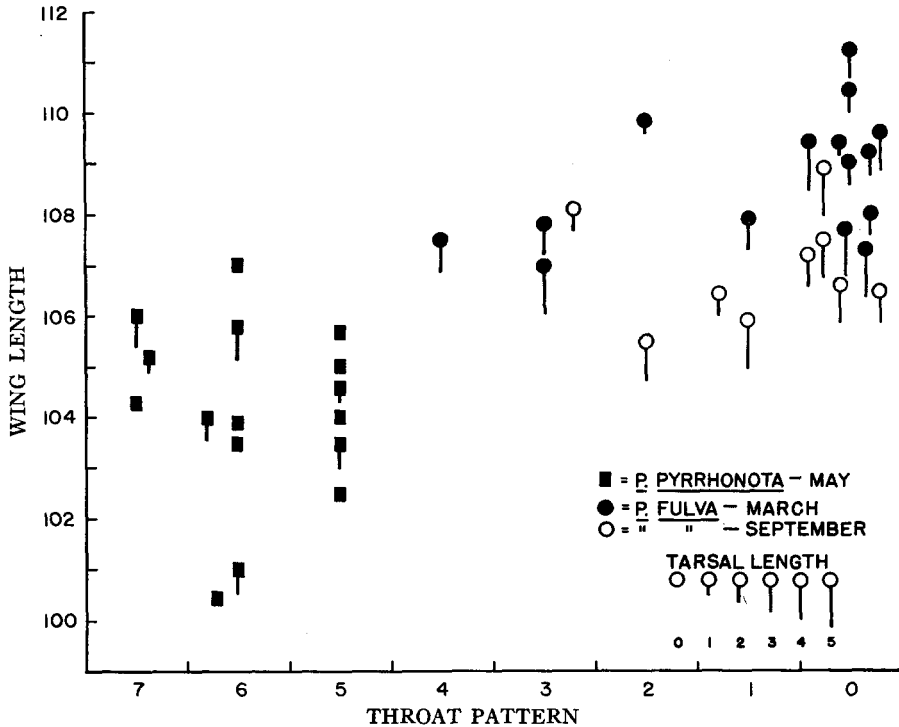


Fig. 8. Scatter diagram of males of *Petrochelidon* from central Texas showing wing and tarsal length and throat pattern. Six categories of tarsal length are used; length of line is proportional to actual tarsal length. See text for further explanation.

Wing length might be expected to average slightly smaller in first-year than in adult individuals even though the postjuvinal molt is complete. Presumably the March and June sample of *P. f. pallida* includes both adult and first-year birds and the September sample includes some birds which are undergoing their first postnuptial molt and are thus in the process of losing their first-year status. Since wing length in the latter sample represents length of old primaries acquired in the previous annual molt (see page 353), any differences in length between adult and first-year wings would be as apparent as in the March and June sample. The important point is the absence of correlation between throat pattern and length of two skeletal parts which are subject to continuous growth until adult size is reached, namely bill and tarsal length. Measurements of bill and tarsal length of two specimens undergoing postjuvinal molt indicate that these structures reach adult size before the molt is completed. In nestling Cliff Swallows studied by Stoner (1945:211) in New York, the tarsus reached adult size 12 to 13 days after hatching.

Considering the evidence presented, we conclude that variation in throat pattern in populations of the two species does not result from present-day hybridization. The possibility remains that genes determining throat pattern were exchanged through hybridization at some time in the past, perhaps when *P. pyrrethota* and *P. fulva* first came into secondary contact and before reproductive isolation was complete. But as an alternative explanation we suggest that the remnants of the throat patch present in *P. fulva* may represent vestiges of a character possessed by the common ancestor of the two species, which has been retained or further developed in *P. pyrrethota* and largely lost

Table 3

Variation in Throat Pattern in Adult and First-year Birds

Form	Date	Sex	No.	Classes of Throat Pattern								Per cent with throat marks
				0	1	2	3	4	5	6	7	
<i>P. p. tachina</i> (Texas)	May, June, 1914	♂	17						6	8	3	100.0
		♀	9					1	3	3	2	100.0
<i>P. f. pallida</i> (Texas)	March, June, 1914	♂	15	10	1	1	2	1				33.3
		♀	9	6	3							33.3
<i>P. f. pallida</i> (Texas)	September, 1956	♂	10	5	2	1	2					50.0
		♀	11	7	1	1	1	1				36.4
<i>P. f. pallida</i> (Mexico)	April, May, 1902	♀	4	4								00.0
<i>P. f. subsp.</i> (Antilles)	♂	4	4								00.0
		♀	6	4	2							33.3

in *P. fulva*. In any event, they are present, although very weakly indicated, in two of the 10 specimens of *P. fulva* from the Greater Antilles which we have at hand and are thus not unique to populations sympatric with *P. pyrrhonota* (table 3).

In color and pattern, although apparently not in size, *P. p. melanogaster* of the central plateau of México and Oaxaca more nearly resembles *P. f. pallida* than does *P. p. tachina*. In *P. p. melanogaster* the forehead is chestnut or cinnamon rufous and the throat patch is often indistinct and only slightly glossy. The chin, throat, and sides of the head are rich chestnut, however, as in other races of *P. pyrrhonota* (Ridgway, 1904: 51). Measurements of *P. p. melanogaster* given by Ridgway (*op. cit.*: 52) and van Rossem and Hachisuka (1938) indicate that it is about the same size as *P. p. tachina*.

In two male specimens of *P. pyrrhonota* in the Texas Natural History Collection from the Big Bend region of western Texas, the throat patch is very small (class 3), and in one (TNHC 1073 from Black Gap, Brewster County) the forehead is cinnamon brown. The throat patch is somewhat larger in three other breeding specimens from Presidio County, but the skins are prepared in such a fashion that the extent of the patch cannot be determined accurately. Both *P. p. tachina* and *P. p. melanogaster* have been reported breeding in Brewster County (Van Tyne and Sutton, 1937: 58-59; Thompson, 1953: 171; and Phillips and Thornton, 1949: 119), and Van Tyne and Sutton noted that individuals closely resembling *P. p. melanogaster* of western México are present in small numbers in breeding colonies of *P. p. tachina*. These authors concluded that four of their 31 breeding birds from Brewster County "are actually representatives of *melanogaster*," rejecting the hypothesis that they are variants of a population most of whose members are referable to *P. p. tachina* and raising the question of whether or not *melanogaster* and *tachina* are conspecific. Material at our disposal is inadequate to solve this problem, but it may be noted that the forehead of a specimen of undetermined sex collected on June 27, 1948, in Presidio County (TNHC 221) is intermediate in color between the two forms, thus suggesting intergradation.

VOCALIZATIONS

As adequate accounts of the vocalizations of the Cave Swallow are not available, the following brief descriptions, taken from tape recordings made at the Dunbar Cave colony, may be of some interest.

Typically the song consists of a series of squeaks blending into a complex melodic warble and ending in a series of double-toned notes in which a *gua* sound and a very low *nock* sound are given simultaneously. Often a sharp *eeep* note terminates the song.

In some instances the elements of the song do not follow the usual sequence or are given separately. A complete song lasts 3 seconds. At Dunbar Cave on April 6 birds were singing from their nests, and on several occasions birds sang in flight as they circled above the cave entrance. Conflict between birds for nests was much in evidence, accompanied by high-pitched, nasal *che* notes. The song was occasionally given in late September by birds perched on their nests in Dunbar Cave.

The song of *P. fulva* clearly corresponds to the "defiance" song of *P. pyrrhonota* given in connection with territorial and aggressive displays and described by Emlen (1952:180) as "a series of high thin squeaks and low guttural gratings alternating in an extended song . . ." In Texas at least, the song of *P. pyrrhonota* is much shorter than that of *P. fulva* and lacks the melodic warbling phrase.

In flight while leaving or returning to the cave, Cave Swallows keep up chattering choruses of short calls, which seem to consist of a great variety of different notes. However, repeated listening to recordings of these choruses revealed that only three basic types of calls are given. By far the most frequent of these is a short, clear *weet* or *chewweet* given at medium pitch with either a rapidly ascending or, less commonly, descending inflection. The next most frequent call is a very loud, sharply accented, and high pitched *che* or *chu* note, usually given in series of two to four. This became the dominant call of individuals which were disturbed by our presence in the cave and which were circling rapidly in a compact flock preparatory to leaving the cave. The third call is somewhat similar to the second but is a lower pitched, clearer *choo* and has a descending inflection. This was rarely given and then only by disturbed birds.

The *weet* and *chewweet* calls of *P. fulva*, which apparently function in maintaining flock integration, are similar to calls given by *P. pyrrhonota*. Perhaps the high pitched *che* or *chu* call corresponds to those "conversational" notes of *P. pyrrhonota* described by Emlen (1952:180) as a low *kersh*, modified under excitement to a higher pitched *ash ash*. The third call of *P. fulva* noted previously is similar to the alarm call of *P. pyrrhonota* described by Emlen (*loc. cit.*) as a "clear plaintive *zeoo* with a descending inflection," but from our limited experience we are not prepared to state that it has a warning function in *P. fulva*.

Navigation in the caves.—Since Cave Swallows do not penetrate into caves beyond the twilight zone it is improbable that they have need of a special acoustic orientation system such as that possessed by *Steatornis*, a bird which roosts and flies in totally dark parts of caves (Griffin, 1955). To test this possibility, however, we captured a dozen individuals in Dunbar Cave and released them singly in totally dark chambers and large passageways of the cave well in beyond their nesting chamber. Some birds were released in the center of large chambers, while others were released a foot or two from the cave wall. Almost invariably the birds fluttered to the top of the cave and hovered against the ceiling, often circling slowly around the chamber or passageway. None gave audible vocalizations at any time. As the birds circled, their wings almost continuously brushed against the roof and walls of the cave, producing a clearly audible swishing sound. It was apparent that the swallows detect surfaces by brushing their wings against them as they move about with hovering flight. Possibly at close range they also detect air currents reflected from surfaces but this remains to be tested experimentally. If a bird happened on to a large crevice, ledge, or eroded depression it would perch and some individuals managed to cling to roughened areas on the wall, but some birds finally fluttered to the floor exhausted after several minutes of hovering flight. We noted that none undertook straight-line flight along the passageways or attempted to leave the immediate region of the cave in which they were released, behavior which might be expected if the birds were able to navigate by echolocation.

To test further the possibility that echolocation was being used, however, we tightly plugged the ears of five birds with balls of moist cotton and released them in total darkness after making certain that they had been given no opportunity to see the walls of the chamber in which they were released. The behavior of these birds did not differ in any way from that of birds which we had previously tested or from that of five controls released at the same time.

SUMMARY

In Texas the Cave Swallow (*Petrochelidon fulva*) nests colonially in the twilight zone of limestone caves along the southern edge of the Edwards Plateau from Val Verde County east to Kerr County; all caves known to be inhabited are described. Ecologic isolation limits contact between the Cave Swallow and its sympatric congener, the Cliff Swallow. It is suggested that in Texas and New Mexico nesting of the Cave Swallow is restricted to caves by competition with the Cliff Swallow.

The Cave Swallow is resident in Texas from early February to late September or, possibly, early October; laying begins in early April. Adults undergo postnuptial molt prior to fall migration.

The nest is an unroofed half-cup shell composed of pellets of mud and/or guano and lined with feathers and plant fibers. Nests are re-used year after year, becoming progressively larger as additional layers of pellets are added to the rims. Cave Swallows show a strong tendency to build their nests in isolated crevices and pockets or close up under overhanging ledges, in positions well screened in all directions from neighboring nests. Apparently this behavior achieves the same end as does the roof of the nest of the Cliff Swallow, namely that of increasing social stability by reducing territorial conflict.

Thirty-four per cent of specimens of Cave Swallows from Texas show remnants of a dark throat or breast patch, resembling in shape and position the posterior part of the metallic throat and breast patch present in the Cliff Swallow. The hypothesis that this condition results from present-day hybridization with the Cliff Swallow is examined and rejected. Instead it is suggested that it represents a vestige of a character possessed by the common ancestor of the two species.

The vocalizations of the Cave Swallow are compared with those of the Cliff Swallow. The songs of the two species are rather distinctive, the other calls less so.

The possibility that Cave Swallows have a special acoustic orientation system for navigating in caves was tested experimentally, with negative results.

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