

VOCAL REPERTOIRES OF SYMPATRIC BARN AND CLIFF SWALLOWS

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THE Barn Swallow (*Hirundo rustica erythrogaster*) and Cliff Swallow (*Petrochelidon p. pyrrhonota*) often nest sympatrically. These ecologically similar species are insectivorous, build mud nests, may nest inside the same shed or barn, and have overlapping breeding cycles (Samuel, 1969). While conducting a study on the breeding biology of the two species, I noted that their songs and calls were different. These also play an integral role in pair formation and copulatory behavior and thus may aid in species recognition.

Songs often differ in closely related species (Marler, 1957), and several examples have been reported (Selander and Giller, 1959; Thielcke, 1962; Crowell, 1968). To maintain separation, vocalizations used as reproductive signals have to be distinct in sympatric species (Marler and Hamilton, 1966). Songs and calls help prevent interbreeding in wrens (Slud, 1958), flycatchers (McCabe, 1951; Stein, 1958), and meadowlarks (Lanyon, 1957), and may be important in the species discrimination of Crested Flycatchers (*Myiarchus crinitus*) (Lanyon, 1960). Marler (1957) suggests that colonial species have smaller vocabularies than their noncolonial relatives; analysis of the notes of these two swallows tests this hypothesis, for the Cliff Swallow is highly colonial, the Barn Swallow essentially noncolonial.

Emlen (1952, 1954) mentions a defiance song, a chur call, and an alarm call for the Cliff Swallow. Vietinghoff-Riesch (1964) discusses the song, twittering, attracting call, two alarm calls, and the utterances of the young for the European Barn Swallow (*H. r. rustica*).

I analyzed and compared the vocalizations of both these species. Conditions under which the notes were given are described, but their functions remain to be determined by future experimental studies.

METHODS

This study was made during the summers of 1967 and 1968 in barns and sheds in Preston County, West Virginia. Birds were sexed (Samuel, 1969) and paint marked (Samuel, 1970) for individual identification. Songs and calls were recorded in and around barns with a portable tape recorder (Norelco Carry-Corder). Descriptions of the behavioral context of each vocalization were noted. As a first step in determining the functional role of songs and calls, the clearest and most typical recordings were processed on a Kay Electronics Company Sona-graph machine, model 6061 B, at wide band settings. Mounts of two female Barn Swallows

TABLE 1
A SUMMARY OF SONGS AND CALLS OF BARN AND CLIFF SWALLOWS¹

Song or call	Given by	Connotation
Barn Swallow		
Twitter song	Male, female	Courtship
Whistle call	Male, female	Pair bond
Deep stutter call	Male (?), female	Low intensity threat
Plain stutter call	Male, female	High intensity threat
Whine call	Female	Precoital signal
Chirp call	Male, female	Contact
Plain sharp call	Male, female	Low intensity alarm
High-sharp call	Female	Alarm-attack
Rapid whine call	Male (?), female (?)	Nest site selection
Light chirp call	Nestlings	Given in nest
Cliff Swallow		
Defiance song	Male (?), female	Courtship, aggression
Chur call	Male, female	Flock integration
Purr call	Male, female	Alarm
Light chirp call	Nestlings	Given in nest

¹ Vocal response of the bird when hand-held, and the mobbing call of adults around a predator are not included.

and one female Cliff Swallow aided in the study of pair formation, copulatory behavior, and vocalizations.

VOCALIZATIONS

Long complex vocalizations used during courtship are termed songs, others are designated calls (Table 1). The Barn Swallow vocal repertoire is larger and also plays a greater role in precopulatory activity than that of the Cliff Swallow.

Copulatory behavior and vocalizations.—Pairing and copulation are distinct entities. Barn Swallow pair formation takes place on fences around the barn, and not in the nest area as with Cliff Swallows. A defended territory around the nest is necessary for Cliff Swallow pair formation (Emlen, 1954). Cliff Swallow females remain in the nest, using the defiance song and stimulus from other members of the colony (Emlen, 1954) to establish the pair bond. Barn Swallows do not use or defend the nest during pair formation.

I saw apparently successful Barn Swallow copulations on two days (17 and 20 May 1968) approximately 8 days before the first eggs were laid. Previously singing males and/or females made many abortive copulation attempts. The male moved close to the female and she remained silent, gave a stutter call, or flew off. If she remained, the male flew behind her and tried to copulate, but repeated efforts did not result in successful union. Copulations that appeared successful were seen inside the barns on two occasions, both involving five pairs of birds. My notes for 17

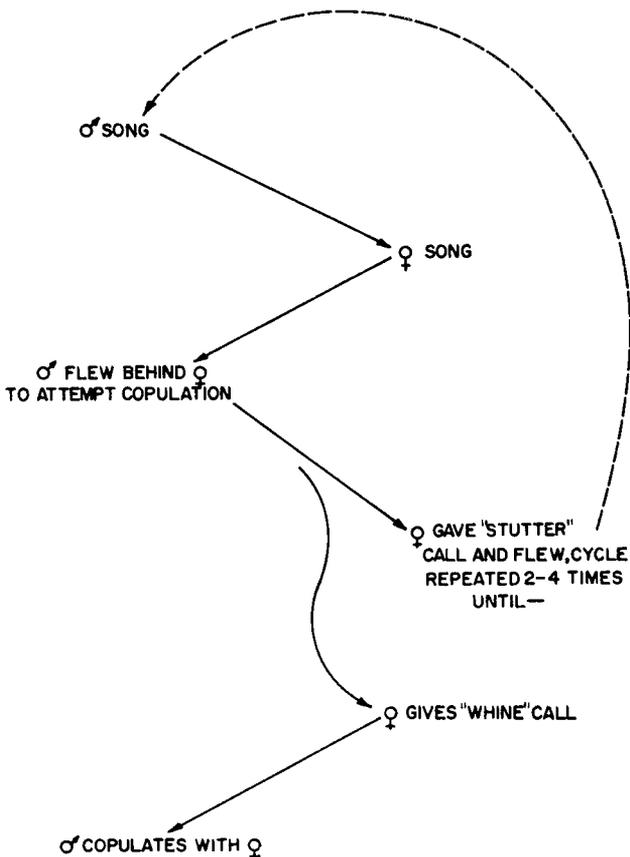


Figure 1. Behavior, songs, and calls leading to successful copulation in the Barn Swallow; diagram based on 21 copulations.

May 1968 describe the precopulatory and copulatory behavior (further summarized in Figure 1):

As I entered my blind, many birds were singing. Trying to watch all birds at once was confusing, so I concentrated on a pair of Barn Swallows, one of which was marked. The female perched near or in an old nest and sang. I could not tell whether the nest belonged to the marked pair, but the birds stayed in the general area of this nest. The male perched 10-20 feet away and sang or was silent. The female sang and the male flew behind as if to copulate. The female gave the plain stutter call, left the perch, and this cycle started again. After three such cycles, the female gave a whine call, and copulation occurred. Similar vocalizations and copulations took place simultaneously throughout the barn as a group activity. It is of interest that the birds showed no copulatory or vocal response to a model placed near the nest on the same day these copulations were seen.

I watched male Barn Swallows make 24 copulation attempts on the model Barn Swallow placed on the fence. During the actual copulation attempt, males gave the following vocal responses: song 16 times, silent 6 times, plain stutter call 2 times. Males usually perched beside the mount giving a whistle call or sang immediately before or after attempts. Attendant males drove off others with a stutter call. When the model was removed, the male returned to the same spot on the fence for as long as 30 minutes.

I saw four successful Cliff Swallow copulation attempts. A soft chur call accompanied three nest copulations. One unusual abortive copulation occurred within a flock of late arrivals. A male, perched on a wire in the opposite direction to a female, swung upside down and maneuvered under her in an effort to make cloacal contact. I noted no copulations at the mud-gathering areas.

Barn swallow twitter song.—The twitter was given by both sexes when perching or flying. It consists of a continuous, and sometimes repeated, series of notes approximately 6 seconds long, in the medium range frequencies of 2–5 KHz (Figures 2, 3). Each song is interspersed with grating notes given approximately every 6 seconds; thus a song 24 seconds long contains 4 grating notes. Song was sometimes preceded by a few repeated syllables (Figure 3B) before continuous song began.

Upon spring arrival at the barns, males perched and sang at all times of the day. Song intensity increased when any Barn Swallow flew close. Song was especially evident during pair formation and in the interim between broods. Perching males sang continually for 3–10 minutes, unless disturbed by other Barn Swallows. When birds were involved in a chase, the male sang while the female gave a deep stutter threat call. Song syllables also preceded and followed the whine call of the female.

Juvenile Barn Swallows sang within 1 month after leaving the nest. Flocks of first clutch juvenile birds gathered at the barns in August and gave a subsong. The basic notes of the subsong can be seen on Figure 2A and further song development involves expansion of this basic pattern. The grating notes of the song were present in the subsong (Figure 2).

Barn Swallow whistle call.—The whistle (Figure 4A) given by both sexes, seems to be a pair bond call. The call is distinct and sounds like a whistle. It was usually loud when given by flying pairs or by single perched birds, and subdued when pairs were perched together. I heard it often during the nest building period when paired birds perched inside barns near the nest. A male gave light whistles after attempting copulation with the model. Whenever a singing male chased his mate, he gave

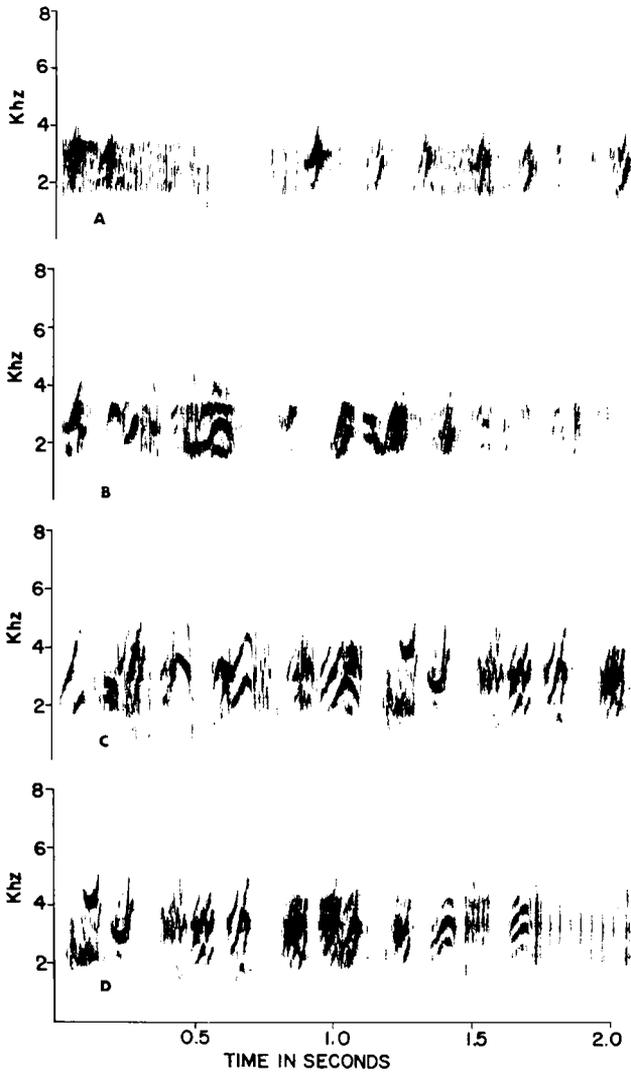


Figure 2. Juvenile Barn Swallow subsong and adult song. A and B, one juvenile subsong. Grating note located at 1.8 seconds of B. C and D, one adult song. Grating notes located at 1.7 seconds of D.

the whistle call. Flocks of adults flew 100–200 feet high during pair formation and between clutches, giving whistles (90 per cent), alarm calls (10 per cent), and an occasional song. Sometimes these flocks contained juvenile birds, but most often they were composed of adults from surrounding barns.

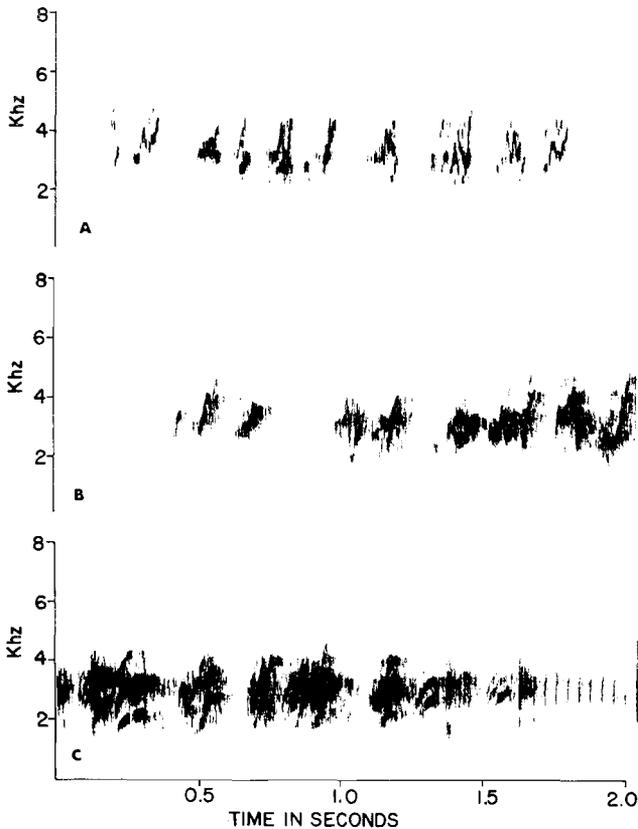


Figure 3. Adult Barn Swallow song. A, same basic note as in subsong. B and C, one song showing individual variation when compared to Figure 2C and 2D and A in this figure.

Smith (1933) referred to the whistle when he wrote "sometimes the male would come through the window . . . to the nest, and, calling to his mate would approach. The female would answer, and, leaving the nest . . . the male meantime assuming the vacant place on the eggs. . . . Many times, however, the female would leave without any interposition of the male." I recorded similar behavior:

A marked male perched on a girder beside the nest gave a whistle call and the mate did not rise. He then fluttered in a circle under the nest, whistling continuously. The female left the barn while the male whistled and fluttered below the nest. The female returned almost immediately and sat on the nest. The male fluttered below the nest 11 times, whistling continuously. The female watched the male during this process, but she did not move from the nest. The male left the barn and whistled when he returned 15 minutes later. The female immediately

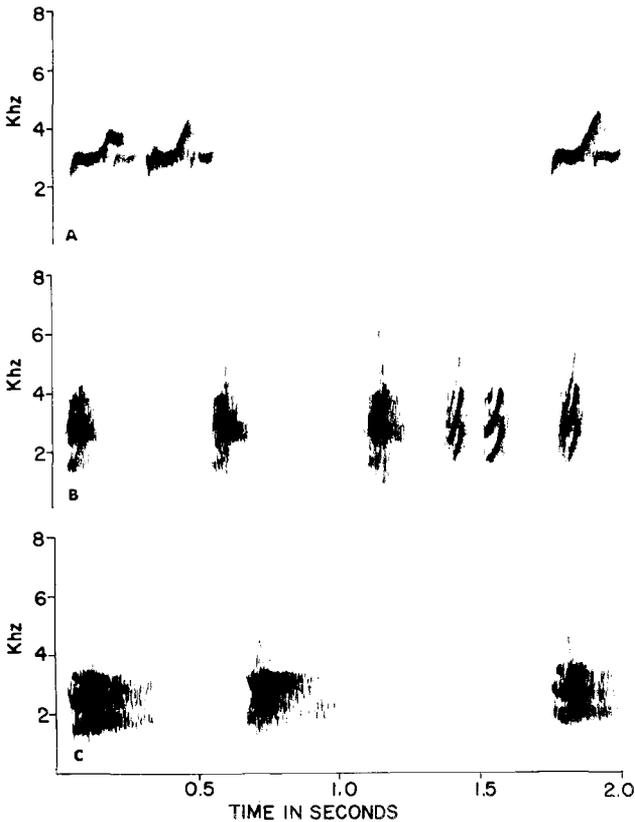


Figure 4. A, Barn Swallow whistle call. B and C, Barn Swallow chirp call. Note individual variation for three birds; the first 3 notes of B, the second 3 notes of B, and the 3 notes of C.

left the nest, and the male sat on the eggs; 30 seconds later the female returned to the nest.

Barn Swallow chirp call.—The function of this call is not fully understood, but it appears to be a contact call. The frequency is 1–6 KHz and individual differences in the sonograms occur (Figure 4B, 4C). Adults gave the chirplike call under various situations. Just previous to or during incubation they uttered it while flying inside the barn by the nest. Later, during brooding, adults occasionally chirped when coming to the nest area. Of 118 mist-netted adults, 33 chirped when released, followed immediately by an alarm call. Adults feeding over open fields always gave chirp calls whether with their mate or with a flock of swallows. Juveniles gave a call that sounded like the chirp

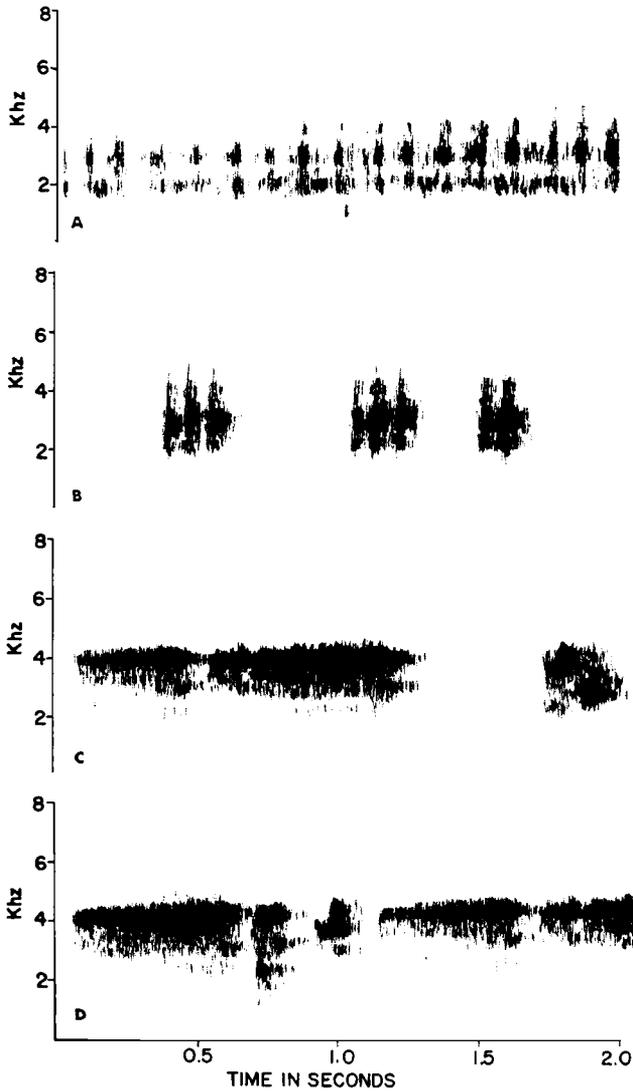


Figure 5. A, Barn Swallow deep stutter call. B, Barn Swallow plain stutter call. C and D, Barn Swallow whine call. Note a syllable of the song between calls at 1.0 seconds of D. C has two whine calls, one from 0.1–0.5 seconds, the second from 0.5–1.2 seconds. D has three calls, 0.1–0.7, 1.1–1.6, and the third is not completely graphed.

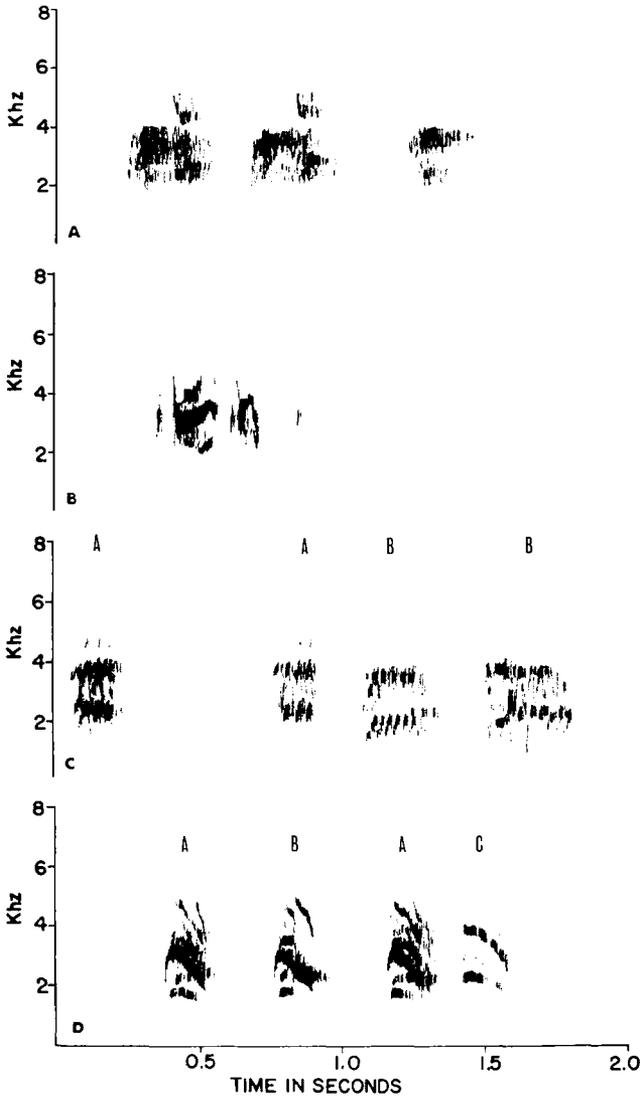


Figure 6. A, Barn Swallow plain sharp call. B, Barn Swallow high sharp call. C, Cliff Swallow chir call. D, Cliff Swallow purr call. Note individual variation for two and three birds in C and D, respectively.

call when disturbed in the nest. Juveniles chirped each of the 34 times that I watched them leave the nest.

The chirp call appears to be associated with adult-adult and adult-young contact; two instances support this. During fall migration, Barn

Swallows are sometimes seen in nests they had not occupied the previous summer. A pair disturbed from such a nest on 10 August 1968 flew continually under the nest chirping (Figure 4C) and giving plain sharp calls. Another instance occurred during late July, when a large migratory flock of some 500–800 mixed adult and juvenile Barn Swallows fed on insects drawn to spotlights on a golf driving range. The only call heard was the chirp call, and birds gave it continuously as the flock fed for 2–3 hours, possibly to maintain flock contact.

Barn Swallow stutter calls.—Two types were recorded: one appeared to be a low intensity threat deep stutter, the other a high intensity plain stutter call given as a strong threat (Figure 5A, 5B). Both had frequency ranges of 1–4 KHz. The deep stutter call was given only by the female when chased by a male during pair formation. The male was not known to use this call. The deep stutter was given as a single or double note while the plain stutter was given rapidly. The plain stutter was given by the male or female in perching situations, during copulation attempts with the model, in response to the model when placed in a nest with eggs, and by the female in absorptive copulation attempts.

Barn Swallow whine call.—The whine call (Figure 5C, 5D) seemed to be a pre-coition signal of females. The call was 0.50 to 0.75 seconds long and repeated 2 to 6 times in succession. It was preceded and followed immediately by a few song syllables. The call preceded 21 of the 23 copulation attempts that took place inside barns, but was never heard during coition attempts outside the barns.

Barn Swallow sharp calls.—Barn Swallows gave sharp calls in two situations. The plain sharp call was an alarm call (Figure 6A), given in almost all situations in which the Barn Swallow was threatened: in 46 of 98 observed chases, on all my visits to the nests and barn, and by 101 of the 118 birds banded immediately after their release. The high sharp call appeared to be an alarm-attack call (Figure 6B) and was heard on three similar occasions. When I came near the barn, the birds, believed to be females, dived at my head giving the call until I left the area. I heard no juveniles giving the high sharp call, but they gave the plain sharp call near the end of their first summer.

Barn Swallow rapid whine call.—This call (Figure 7A, 7B) was given by birds perched in or near the nest soon after spring arrival. I don't know whether both sexes gave it, but the call varied in length and intensity. My notes for 24 April 1968 describe a typical behavior sequence involving its use:

Bird 1 perched 10 feet from a nest and chirped. The mate (bird 2) flew inside and gave a loud rapid whine call then perched beside bird 1. It continued to give very light rapid whines while bird 1 chirped. The rapid whine call was hardly

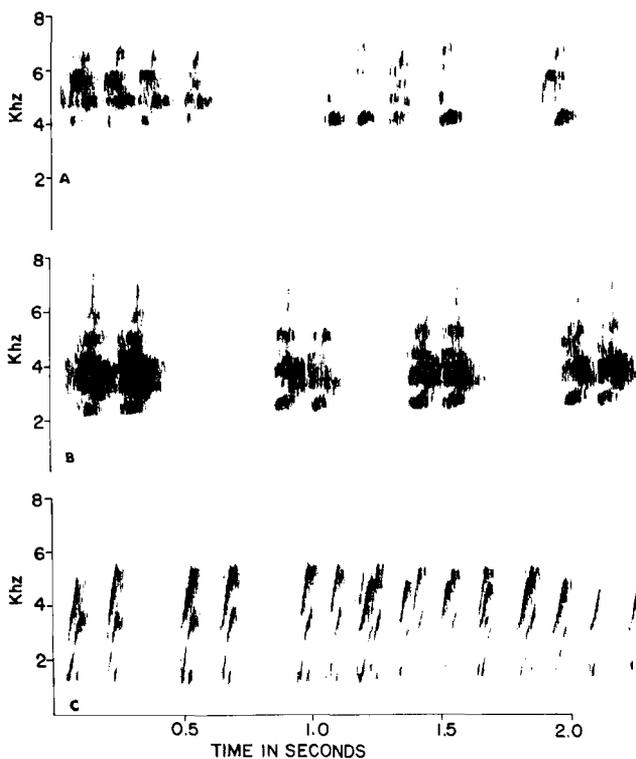


Figure 7. A and B, Barn Swallow rapid whine call. C, Barn Swallow light chirp call of nestlings being fed.

audible at 20 feet and was reduced to a few notes. Bird 2 left the barn and returned in 4 minutes. It flew into the nest and gave 10 rapid whines, each averaging 4.3 seconds.

Birds perched together gave low intensity calls of a few notes (Figure 7B) while birds flying by perched birds or flying by the nest gave loud rapid whines (Figure 7A).

Barn Swallow light chirp call.—Nestlings of both species gave light chirp calls when the parents arrived at the nest with food, but recordings were made only of Barn Swallows (Figure 7C). I did not note the age at which nestlings began to give this call.

Cliff Swallow defiance song.—This song consists of a series of high thin squeaks and low guttural gratings lasting as long as 6–8 seconds and has a frequency range of 1 to more than 8 KHz (Figure 8). Given both in the nest and in flight, it is almost totally limited to the courtship period. Late arriving birds give the song during pair formation activities.

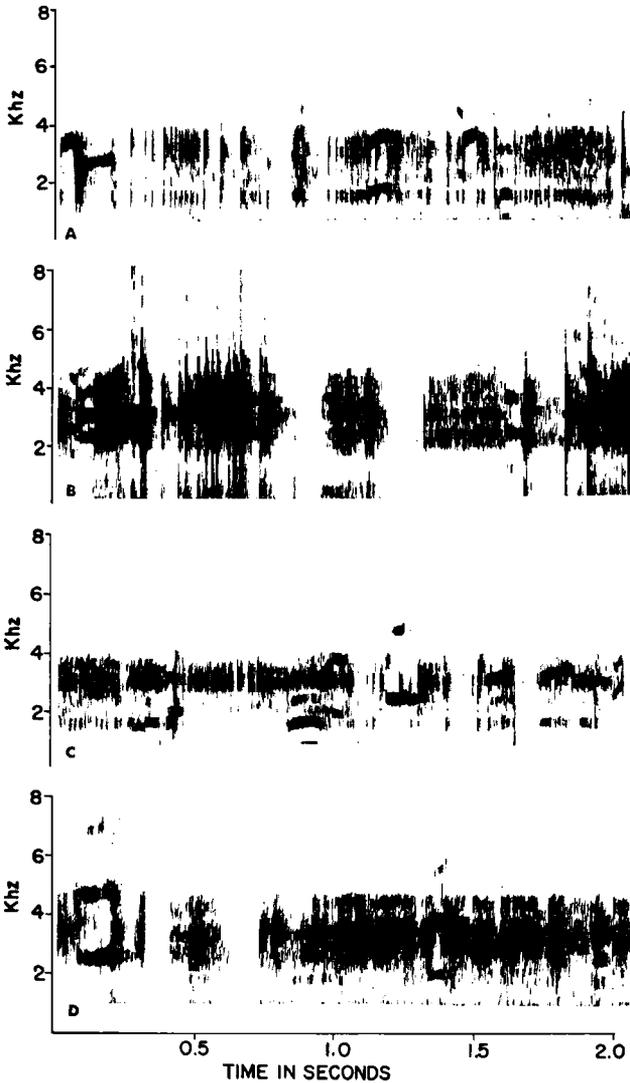


Figure 8. Cliff Swallow defiance song. Each is a portion of the song of four different individuals.

It plays the major role in establishment of the pair bond (Emlen, 1954). A nest occupant occasionally gave a few syllables of the song when no other birds were present.

The song is complex, and comparisons with other individual sonograms

TABLE 2
 OCCURRENCE OF THE CHUR OF ONE PAIR WHEN ENTERING OR LEAVING
 THE CLIFF SWALLOW NEST DURING BROODING¹

Times entering nest	Calls	Times leaving	Calls
36	17	37	15 ²
30	14	30	24 ²

¹ Data collected during 184 minutes of observations.

² Significant at 0.001 level (*t*-test).

indicate individual differences (Figure 8). I never heard juveniles give it during their first summer.

Cliff Swallow chur call.—All birds gave this chur continually while flocking outside barn entrances immediately after they arrived in the spring. The call (Figure 6C) was also used when birds approached or left the nest. The frequency was 2–5 Khz. From observations of a marked pair, the male and female gave the chur about 50 per cent of the time when entering the nest. The female gave more calls (24 calls during 30 departures) than the male (15/37) when leaving the nest (Table 2). The female repeated the call twice quickly 9 of the 30 times she left the nest; the male gave no double calls. This call may govern the synchrony of arrival and departure in a colony. When one bird gave the call as it left the nest, others immediately left. Birds arriving to the nest gave it, whether or not the nest was empty; both adults and juveniles gave it when arriving and leaving perching lines. Occasionally individuals could be identified by the slight variations in this call (Figure 6C).

Cliff Swallow purr call.—Any alarming event, such as the presence of man at the colony, elicited this call. The frequency was 2–5 Khz and individual differences occurred (Figure 6D). When given, all birds left their nests, flew around the barn entrance, and continued to give the purr until the disturbance ceased.

Interspecific recognition of songs and calls.—The only calls to which both species responded were the alarm calls. When I approached the nests, an alarm call by either species brought a response from both species if they were within hearing.

DISCUSSION

Copulations.—Stimuli preceding coitus differed between these two species. Barn Swallow coition took place following a sequence of behaviors terminated by a female whine call. Copulations were a synchronous group activity by Barn Swallows at individual barns. Thus, the synchrony of egg laying (Samuel, 1969) results from most pairs in the barn having simultaneously participated in copulatory behavior.

Cliff Swallow copulations were more spontaneous between individual pairs within the nest and were not a group activity. Precopulatory behavior occurred in the nest (also noted by Emlen, 1954) and had little stimulatory effect on other colony members. Egg laying synchrony may be related to simultaneous arrival, pair formation, and nest building for all birds in a colony.

Size of vocal repertoire.—The greater portion of this paper deals with Barn Swallows because of their larger repertoire. Three songs and calls were recognized in adult Cliff Swallows as a colonial species, while nine calls were recognized in the noncolonial Barn Swallow. Cliff Swallows may not need calls equivalent to all those of Barn Swallows because they use visual signals instead. Excessive calling under colonial conditions might be confusing and thus serve no real function.

Informational content.—Peterson and Bartholomew (1969) note that "overt responses of animals to vocal signals can be objectively described, but the information transferred from emitter to receiver can only be inferred." Thus, any connotations of these vocalizations must be verified through experiment. Emlen (1952, 1954) describes the defiance song and a conversational call as functioning in flock integration for Cliff Swallows. The song is both a courtship and territorial song, but is not given prior to copulation within the nest as is the chur. The chur has individual variations that may assist in identification before copulations or when birds arrive at the nest. The defiance song is given occasionally by a bird in the nest during incubation and brooding, but is probably not used to maintain the pair bond. More likely such songs are a threat call to the returning, not immediately recognized mate.

The Barn Swallow courtship song is complex, variable, and has individual differences that probably attract females, but it is occasionally given by the female. Many of the functional differences in the calls of the two species may be a result of one species being colonial and the other not. Barn Swallows give different calls for contact or location (chirp), for pair bond maintenance (whistle), for threatening situations (stutter), during precopulation (whine), and while selecting the nest site (rapid whine). The whistle call usually takes the form of duetting, which is defined as alternation of calling between members of a pair of potential mates (Stokes and Williams, 1968). Cliff Swallows use only the chur call for contact or location, precopulation, and nest arrival and departure. Cliff Swallow groups feed together, and a call announcing the arrival or departure to the colony is important. Barn Swallows feed in flocks, often in pairs, and the whistle call is important in maintaining contact.

Cliff Swallows use only one alarm call while the Barn Swallow has

high and low intensity alarm calls. The high-sharp call may have evolved in females protecting the nest to summon other Barn Swallows when confronted by a predator. The three females that gave this call all had nestlings at the time. The occurrences of a vocabulary of alarm calls of several grades is shown for other species (Petrides, 1938; Armstrong, 1963). Calls of different intensity may have different meanings.

Physical structure.—Many European passerines have uniform high-pitched alarm calls of long duration (Marler, 1957), but none of the three swallow alarm calls are of this pattern.

Five swallow vocalizations fit the vocal classification proposed by Collias (1960). The low intensity sharp call of Barn Swallows is harsh and relatively high-pitched as are alarm calls (Collias, 1960), while threat calls of Barn Swallows are low-pitched and harsh as Collias describes. Very harsh notes may be used in threat situations, and this is true for the Cliff Swallow song. The chirp of Barn Swallows is brief and repetitive and may fit Collias's classification of attracting notes to small young. The whistle of Barn Swallows is identical to the classification of pleasure notes, but I doubt if the connotation is the same.

The physical structure of the chirp, stutter, deep stutter, sharp, and rapid whine of Barn Swallows is similar. All contain notes of short duration with a wide frequency spread, but the ontogeny of these calls is not known.

Barn Swallow subsong.—Armstrong (1963) suggests that juvenile songs are really subsongs. A subsong has the following characteristics: 1) it consists of random subdued warbling of greater duration than primary song; 2) it usually contains recognizable call notes interspersed within the framework of warbling notes, but it is typically without any phrases suggestive of definitive primary song; 3) it is often composed of a greater range of frequencies than later developmental stages; and 4) it shows greater similarity between species than does primary song (Lanyon, 1960). The Barn Swallow subsong meets most of these qualifications. These songs are subdued and contain notes found in the adult song.

In summary, complex songs may vary greatly in closely related species (Marler, 1957), and they do in Barn and Cliff Swallows. The exact roles and functions of all their various songs and call is still unknown. The differences in pair formation and copulatory behavior and their associated vocalizations in the two species probably help maintain reproductive isolation.

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SUMMARY

Both species use songs and calls during pair formation and during precopulatory behavior. Cliff Swallow pair formation takes place around the nest, while Barn Swallow pair formation occurs as birds feed and perch outside the barns. Barn Swallow copulation occurs only after the female gives a whine call, while perched in or near the nest. Cliff Swallow copulations take place within the nest, and they are fairly synchronized in each colony.

Males and females of both species give the song. Juvenile Barn Swallows use this song within 1 month after leaving the nest. Grating notes in the subsong are also found in adult song. Adult Barn Swallows use a pair bond call and Barn Swallow adults and juveniles utilize a contact call. Barn Swallows also have two stutter calls when threatened, while Cliff Swallows use the song in threat situations. Cliff Swallows use one chur call during pair formation, group feeding, during arrival at and departure from the nest, and prior to copulation. Barn Swallows have two alarm calls of varying intensity, while Cliff Swallows have only one.

Separation may be maintained by the differences in the vocalizations and by basic differences in pair formation and copulatory behavior.

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