Vocalizations of the South African cliff swallow Hirundo spilodera

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The vocalizations of both adult and juvenile South African cliff swallows *Hirundo spilodera* are described. This swallow has a large vocal repertoire considering that it is a highly colonial species, and at least seven distinctive calls are recognized. In chicks there is a gradual change in the food soliciting call and it develops into the contact call. Contact calls of both chicks and adult birds were individually recognizable.

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Die roepe van beide volwassenes en kuikens van die familieswael *Hirundo spilodera* word beskryf. Hierdie swael broei in groot kolonies maar besit tog 'n verbasende groot repertoire wat uit ten minste sewe duidelik onderskeibare roepe bestaan. Die voedselbedelroep van kuikens verander geleidelik in 'n kontakroep en hierdie kontakroepe sowel as die van volwasse voëls is individueel herkenbaar.

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In testing the suggestion by Marler (1957) that colonial bird species have smaller vocabularies than their non-colonial relatives, Samuel (1971) found that where the barn (European) swallow *Hirundo rustica* and the American cliff swallow *H*. pyrrhonota occurred sympatrically, the non-colonial barn swallow had a larger vocal repertoire than the colonial American cliff swallow. From this one may conclude that colonially breeding swallows do not need a large vocal repertoire because vocal communication in dense colonies of birds is usually ineffective (Wiley 1976; Smith 1977). However, recently some colonial swallow species were found to rely heavily on vocalizations for individual recognition even though their total repertoire might not be large (Beecher, Beecher & Hahn 1981a; Beecher, Beecher & Lumpkin 1981b; Brown 1983; Stoddard & Beecher 1983). Although swallows are mostly poor singers compared to other passerines, it seems from the references cited and this study as if members of the Hirundinidae rely more on vocal communication than has been realized up to now.

This paper describes the vocalizations of the South African cliff swallow *Hirundo spilodera*, a highly colonial species breeding in colonies of up to 2 000 and even more birds (Earlé 1986).

Study area and Methods

Recordings of South African cliff swallow vocalizations were made at five breeding colonies around Bloemfontein, South Africa (29°06'S/26°13'E), during the summers of 1983/84 and 1984/85. A Uher 4000 Report Monitor tape recorder was used at a speed of 19 cm/s. Most of the recordings were made from a hide with a Canon unidirectional microphone and a parabolic reflector (0,9 m diameter). In the 1984/85 season, when twelve chicks were hand-reared, the calls of these chicks were recorded at two- or three-day intervals. Some calls were kindly supplied by the FitzPatrick Bird communication Library at the Transvaal Museum. Sonagrams of the calls were produced on a 400 Voice Identification Instrument, using the wide-band filter and flat shaping. Five terms will be used to describe the vocalizations of the cliff swallow. A note is a single element of a call and several calls containing similar or different notes constitute a song. A vocalization can either be a note, call or a song, depending on the situation. The term elements is used when the vocalization can not be described as a note, call or song (cf. Figure 2A).

The vocalizations of four hand-reared chicks were analysed and the vocalizations of at least two birds were analysed to describe the other calls. Because of the large numbers of swallows present when recordings were made, it was not possible to repeatedly record the vocalizations of specific individuals.

Results

Seven distinctive vocalizations were recognized in adult South African cliff swallows. No song of long duration occurred.

Adult vocalizations

Chatter call (Figure 1A)

The chatter call consisted of a series of warbles given by several individuals simultaneously and could be heard throughout the day. It probably advertised the presence of an individual at a specific site and may serve as a low-intensity territorial song. The duration of the calling sequence was about 0.4-0.5 s with elements ranging from 1-6 kHz.

Threat call (Figure 1B)

The threat call had very much the same structure as that of the chatter call with a delivery rate of about 10 notes per second. It was uttered when birds defended the nest or a site where nestbuilding was to start and might thus be interpreted as real territorial song. This call was given only in real threat situations and was usually accompanied by raising of the crown feathers and the open-bill display (Earlé 1985). The call was often repeated, each sequence lasting up to 1,2 s with notes and elements ranging from 1-4 kHz.

Nest-relief call (Figure 1C)

This call was given by both males and females on leaving the nest after being relieved by the mate. The call was usually given on the wing or, in a few cases, by a bird clinging to a nest entrance. The call comprised two sets of harmonics, the fundamental harmonics around 2 kHz and the other around 4 kHz. The call was repeated 5-10 times, each bout having a duration of 0.4-0.5 s.

Low-intensity alarm call (Figure 1D)

This alarm call was given by any individual first spotting danger, such as the observer moving closer to the colony. It was usually a double 'chik-chik' sound, each 'chik' of very short duration (0,05 s) and was sometimes followed by the high-intensity alarm call. The two notes had a frequency of 1,5-4 kHz and 2-3,5 kHz respectively.

High-intensity alarm call (Figure 2A)

This call, though only of about 0,1 s duration, consisted of three notes. A short high-pitched note extending from 3,5 – 5,5 kHz was preceded and followed by a lower note around 3 kHz. This call was given in intense alarm situations such as when an observer stood close to the colony. If a flying bird gave this call, all birds in nests immediately departed.

Distress call (Figure 2B)

The distress call was uttered by both adults and juvenile birds, although juvenile distress calls were not often heard. This call consisted of a broad band of sound with maximum energy concentration between 2 and 3,4 kHz, producing a harsh sound of about 0.12-0.15 s duration. The sounds were given at intervals of about 0.25 s. The call was uttered continuously by certain individuals when distressed such as when being handled during ringing operations. Each call had a duration of about 0.15 s with 0.25 s between successive calls.

Contact call (Figure 2C)

Contact calls consisted of two or three notes covering fre-

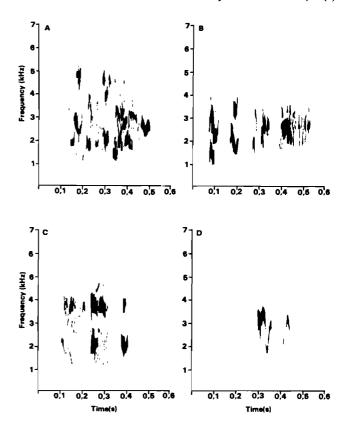
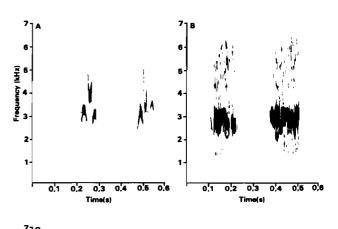


Figure 1 Sonagrams of South African cliff swallow calls. (A) Chatter call. (B) Threat call. (C) Nest-relief call. (D) Low-intensity alarm call.



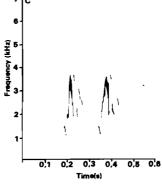


Figure 2 Sonagrams of South African cliff swallow calls. (A) Highintensity alarm call. (B) Distress call. (C) Contact call.

quencies from 1-3.8 kHz, with a brief introductory component at just above 1,0 kHz. Adult and chick contact calls were similar in structure. Two or three contact calls were usually given in quick succession, followed by a longer pause, then repeated. Each note lasted about 0,05 s with about 0,1 s

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between notes. Contact calls were often individually recognizable by the human ear, and certain behaviour patterns indicated that breeding mates could recognize each other by calls alone.

Vocalizations of the young

Begging call (Figure 3)

This call consisted of a broad band of sound lasting about 1.2 s between 1.5-4.5 kHz thus producing a harsh sound. Begging calls of young cliff swallows changed gradually throughout development. They appeared within the first 24 h after hatching but were weak at this stage when they were uttered with a characteristically open gape held vertically upward. At about day 8-10 the call was still harsh. After the chicks were 10 days old the call started losing its harshness and developed into the contact call (Figure 4).

Chick contact call

Although the chick contact calls all had a similar structure, each call was individually recognizable (Figure 4). The gradual development of the contact call from the begging call for two of the hand-reared chicks is shown in Figure 5. The harsh component gradually disappeared from the food-soliciting call but only in the adult contact calls were the calls free of any harshness. The contact call was given both by chicks in the nest and by young already on the wing. The call was probably well developed only when the chicks were 20 days old and more. Parent birds could find displaced (> 2 m) 21-day-old chicks in a very dense colony, thereby indicating that the calls

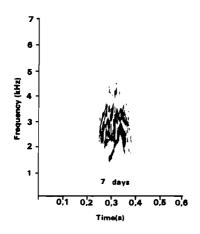


Figure 3 Sonagram of a South African cliff swallow chick food-soliciting call.

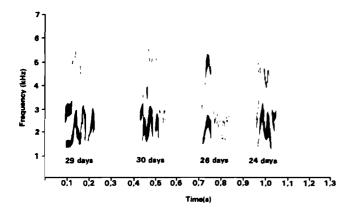
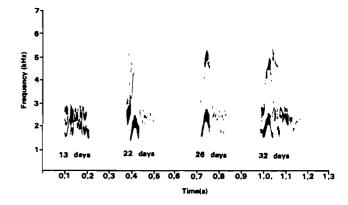


Figure 4 Sonagrams of the contact call of four unrelated South African cliff swallow chicks. The ages of the chicks are given in days. Note the inter-individual variation.



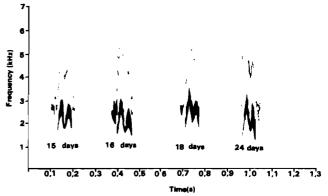


Figure 5 Sonagrams of a series of calls from two individual South African cliff swallow chicks showing the development of the contact call.

were individually recognizable. The contact call consisted of whistled notes at 1,5 kHz with a duration of about 0,12 s each and the entire contact call sequence consisted of 3-7 of these whistles repeated in less than 1 s before a pause of a few seconds.

Discussion

I believe the most striking feature of the behaviour of the South African cliff swallow is the unexpectedly large vocal repertoire for a colonial bird. Marler (1957), Wiley (1976) and Smith (1977) all mentioned that vocal communication may be inefficient in colonies of birds because too many signals from different individuals impinge on the receiver at any given time, creating confusion (the 'cocktail party effect'). Brown (1983) suggests that directional visual displays, which can be orientated towards specific individuals, may be favoured in colonial birds. This is not the case in the cliff swallow with its relatively large repertoire and individual recognition of chick contact calls by parent birds and vocal recognition by breeding partners. In the cliff swallow a territorial song of long duration is absent because the territory consists of only a nest opening and must be 'defended' so often that a song of long duration would be inappropriate as the nest would have to be defended again before a long call sequence is complete. A brief threat call at the nest has the dual function of a territorial 'song' and of keeping intruders away from the nest by combining the call with threatening postures. The American cliff swallow H. pyrrhonota which shows a number of behaviour patterns very similar to those of the South African cliff swallow has a very much smaller vocal repertoire (Table 1) while the more solitary-nesting European swallow and purple martin Progne subis has a larger repertoire (Samuel 1971; Burtt 1977; Brown 1984). It thus seems as if the American cliff swallow and even some solitary-nesting American swallows such as the violetgreen swallow Tachycineta thalassina (Brown 1983) may not

Table 1 The size of the vocal repertoire of some members of the Hirundinidae

Species	Size of the repertoire	Breeding colonial/solitary	Reference
Hirundo rustica	8-10	solitary	Samuel 1971
Progne subis	10	solitary in natural state	Brown 1984
Tachycineta thalassina	3	semi-colonial	Brown 1983
Hirundo pyrrhonota	4	colonial	Samuel 1971
Hirundo spilodera	7	colonial	This study

rely as heavily on vocal communication as the South African cliff swallow does.

With vocal communication in the cliff swallow so well developed it is not surprising that voices are individually recognizable to promote social organization in the colony. The individuality of the chick contact calls ensures that parental care is not misdirected and that parents can find fledglings after they have left the nest, but still need some parental care. Individual chick recognition is also a feature of communication in both American cliff swallows (Stoddard & Beecher 1983) and bank swallows *Riparia riparia* (Beecher et al. 1981a). However, the chicks of some solitary-nesting swallows such as the rough-winged swallow *Stelgidopteryx serripennis* show little inter-individual variability in their calls, and parents fail to discriminate between their own chicks and unrelated chicks (Beecher 1982).

Although it was suggested by Stoddard & Beecher (1983) that the white facial markings of the American cliff swallow might also aid identification of chicks, in addition to the voice, it seems unlikely that this is very common. These authors gave the impression that all chicks had these facial markings but never actually stated the number that really had these markings. In the South African swallow less than 25% of all chicks examined had any white markings, probably too few for facial recognition of chicks to be universal in a South African cliff swallow colony.

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