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PARENTAL RECOGNITION OF OFFSPRING IN THE CLIFF SWALLOW

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ABSTRACT.—We examined variation in the calls and facial patterns of Cliff Swallow (*Hirundo pyrrhonota*) chicks to test the prediction that, in species in which dependent young intermingle, coloniality necessitates parent-offspring recognition and thus favors the evolution of highly variable "signature" traits. The calls of Cliff Swallow chicks were found to be highly distinctive: interindividual variation was significantly greater than intraindividual variation for five measured parameters. Playback experiments indicated that parents could locate their chicks by these signature calls alone. We found that chick faces were individually distinctive as well. Chick faces could be readily distinguished by human observers, although we did not test whether or not Cliff Swallow parents actually use this information. Studies of several swallow species implicate coloniality as the variable in this family that separates species with distinctive chick signatures and strong parental recognition [Cliff Swallows and Bank Swallows (*Riparia riparia*)] from species in which these traits are weak or absent [Northern Rough-winged Swallows (*Stelgidopteryx serripennis*) and Barn Swallows (*Hirundo rustica*)]. *Received 9 December 1982, accepted 11 April 1983.*

IN most colonially breeding vertebrates with dependent young, there is a stage at which the newly mobile offspring intermingle while still receiving direct parental care. In this context, we should expect the evolution of individually recognizable characteristics in the young and the ability in the adults to distinguish their young by these characteristics. Moreover, we would predict higher phenotypic variability in offspring and a better-developed ability of parents to discriminate among offspring in such colonial species than in closely related solitary species. These predictions are borne out by the comparative study of the colonial Bank Swallow (*Riparia riparia*) and the solitary Northern Rough-winged Swallow (*Stelgidopteryx serripennis*) (Hoogland and Sherman 1976; Beecher et al. 1981; Beecher 1981, 1982). Rough-winged Swallow chicks show little interindividual variability in their calls, and parents fail to discriminate between their own chicks and unrelated chicks. Bank Swallow chicks, in contrast, show high interindividual call variability, and parents can recognize their chicks purely by voice. A similar correlation between coloniality and individual distinctiveness of vocalizations within a family of birds has been demonstrated in six species of penguins (Jouventin 1982).

The Cliff Swallow (*Hirundo pyrrhonota*), like the Bank Swallow, is a highly colonial species. On typical nesting sites, such as cliff faces, neighboring nests are often in contact, and nest densities can be as high as 50 nests/m². Colonies vary in size but seldom include fewer than 25 nests, often more than 50, and occasionally as many as 2,000 (Bent 1942). We therefore predicted extreme phenotypic variability in Cliff Swallow chicks and parental discrimination of such variability. On the basis of past results with the ecologically similar Bank Swallow, we decided to look for "signature" variation in the calls of chicks. In the first hour of observation in 1981, however, we saw that chicks possess

FRONTISPIECE. Faces of six fledging-aged Cliff Swallows. The three on the right are from the same nest.

individual facial patterns. We therefore examined facial patterns as well.

METHODS

Two study sites were selected in the high desert of north-central Washington. The Washburn Island colony consisted of about 50 active nests located on two T-shaped concrete support pillars of an elevated settling tank, 2 m from the bank of the Columbia River. A second colony under a bridge over Foster Creek also had about 50 active nests.

Parents were captured at night earlier in the season and were sexed by the extent of their brood patches. Each was fitted with a unique color-band permutation and was breast-dyed with the same color pattern. The dual marking greatly facilitated our recognition of the adults, both in flight and at the nest, and did not seem to alter their behavior.

To record calls, small microphones were mudded into the nest wall, barely protruding into the nest. Parents showed no reluctance to enter nests with microphones, providing the cords were secured against the concrete, but they would occasionally peck at a microphone from inside the nest and twice packed mud over the intruding portion. We chose Realistic 33-1056A omni-directional, 600 ohm condenser microphones because of their small size (12 mm diameter × 22 mm long) and flat response curve over the critical range of 1–8 kHz. Recordings were made on a Uher 4200 or 4400 Report Stereo IC recorder at 9.5 cm/s using Scotch 176 Audio recording tape. Tapes were scanned on a Unigon 4500 Real Time Spectrum Analyzer at a tape speed of 2.4 cm/s, and hard copy was produced on a Kay Sonagraph 6061E Spectrum Analyzer equipped with the 6083 Scale Magnifier.

Playback experiments were conducted to determine whether parents could identify their own offspring by voice alone. The playback procedure was based on our observation that parents will search the colony for lost chicks (see below). Around the onset of chick mobility, we recorded chick signature calls in nests at which we had color-marked at least one parent. Three calls from two or three chicks in the experimental nest were transferred to one track of a 3.5-s tape loop, spaced 1 s apart. Three calls from another nest were placed on the other track of the tape loop in a similar arrangement to serve as a control. When possible, an experimental tape track was used as a control in the subsequent test. Grason-Stadler TDH-49 earphone speakers were mounted above the mouths of two nests, one at each end of the horizontal pillar section, 3 m apart. Cords were secured and run down to the Uher 4200 in our observation blind. During a trial, chick calls from the nest being tested were broadcast from one of the two speakers (designated the experimental speaker), and calls from the control nest were simultaneously played from the other (control) speaker. As the playback equipment was installed, all remaining chicks were removed from the nest to elicit searching behavior by the parents.

To extract the chicks, a small hole was cut in the side of the nest. The chicks were flushed out the mouth of the nest and into a waiting bag by a gently prodding finger. The hole was then patched with mud. Detailed instructions for this delicate operation may be obtained by writing to the authors.

A playback trial was begun and at least two observers recorded approach behavior to the experimental and control speakers. At the termination of a 5-min trial, the speaker cords were interchanged at the tape player to switch the experimental and control calls between the two speakers. After a silence of about 3 min, or as soon as the parent reappeared, another trial was begun. Four such trials were conducted for each experimental nest. The observers were uninformed of whether their assigned speaker was playing the experimental or control calls on a given trial.

Facial variation was examined by extracting and photographing chicks at least 18 days old from nests at both colonies. At least two color photographs were taken of each chick's face using a macro lens, and a strobe if ambient light was low. The chicks were banded and replaced in their nests. Unlike Bank and Barn swallows, fledging-aged Cliff Swallows will generally stay in the nest when replaced after handling. Preliminary observations of color-marked birds at the Washburn Island colony showed that Cliff Swallow chicks become mobile between 21 and 24 days of age, when they leave the nests for increasingly extended periods during which they improve their flight capabilities and learn to forage. During this phase, which lasts 1–3 days, the chicks are still fed in their nest by the parents. When they discover their chicks' initial departure, the parent Cliff Swallows search for them in the air and in other nests in the colony, eventually finding them and leading them back to the home nest. Parents and chicks call frequently throughout such sequences.

RESULTS

Chick voices.—Chick vocalizations begin to acquire an individually unique pattern when chicks are around 15 days of age, although the call does not become pure and consistent until the chicks are between 18 and 21 days of age. Examples of chick signature calls are shown in Figs. 1 and 2. The call is comprised of two simultaneous whistles. The non-harmonic relationship between the two whistles suggests that they are produced by opposite sides of the bird's syrinx. The call is modulated over the frequen-
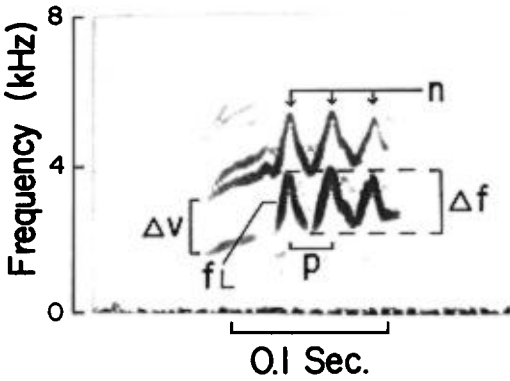
Fig. 1. Signature call of a Cliff Swallow chick showing the parameters evaluated. F-ratios (see text) are given after each parameter description. Δv = frequency difference between upper and lower voices ($F = 41.5$). f_L = average frequency of the lower voice (74.0). p = period of frequency modulation (226). Δf = frequency difference between first modulation peak and valley of the lower voice (22.4). n = number of modulation cycles (51.7).

Fig. 2. Two signature calls each from three unrelated Cliff Swallow chicks (A, B, and C). Note the intraindividual consistency.

cy range of approximately 1–6.5 kHz with a duration of approximately 100 ms (see Fig. 1). Often there are family resemblances among the signature calls of sibs. We are presently analyzing sibling resemblances and are attempting to disentangle genetic and imitative components by cross-fostering experiments.

To evaluate the individual distinctiveness of these calls, we performed a simple analysis of variance on each of five parameters. This is the standard method of evaluating whether or not interindividual variability is large relative to intraindividual variability (e.g. Cheney and Seyfarth 1980, Beecher et al. 1981). The parameters we derived are illustrated in Fig. 1 and are described in its caption. These parameters do not exhaust the potential information in these calls; we are undertaking a more detailed analysis. The present analysis is based on six calls each from nine unrelated chicks (each from a different nest). For all five parameters, interindividual variance was significantly greater than intraindividual variance; each of the F-ratios was highly significant ($P \ll 0.001$; values given in Fig. 1 legend).

Playback experiment.—Observations at an experimental nest began when a marked parent returned to feed its chicks. Upon discovery of the empty nest, the parent usually flew in loops
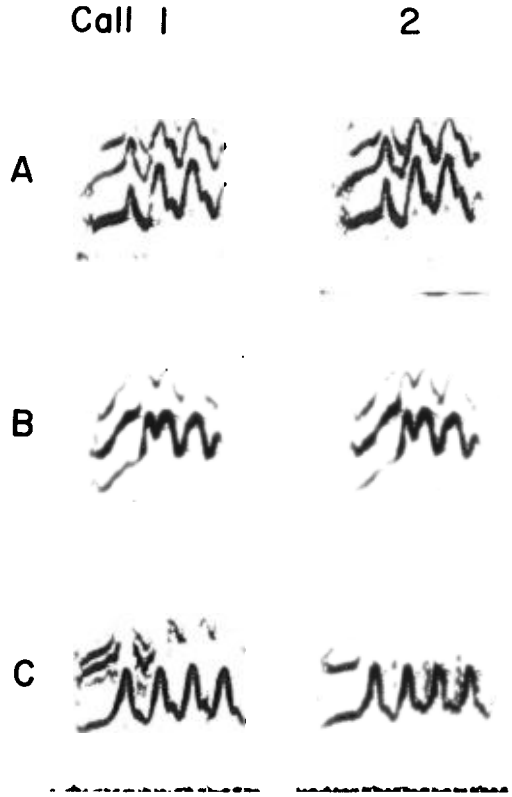
out and back to the nest several times while giving a search call. While clinging to the mouth of its nest, the parent would orient to the experimental speaker. It would then fly to a nest in the vicinity of the speaker. Parental responses to the nest underneath the experimental speaker or the control speaker or an immediately adjacent nest were regarded as positive responses and were categorized from weakest to strongest: aerial speaker check (pass within 0.3 m of, look at, or hover in front of speaker) = 1; external contact with speaker nest (touch briefly, perch at nest mouth, peer inside) = 2; and enter nest with speaker = 3. The results of the tests are shown in Table 1. For all response categories, the seven parents tested responded more strongly to the calls of their own chicks than to control calls (summed score for each parent; sign test, $P < 0.01$). While it is not indicated in Table 1, all birds responded only to the experimental speaker on the first

TABLE 1. Number of speaker responses during playback experiments. Responses are summed across four 5-min trials at each experimental nest. E = experimental call speaker, C = control call speaker.

Experimental nest	Control nest	Sex of observed parent	Aerial check E:C	External contact E:C	Enter E:C
A20	A4	M	2:0	5:0	
A8	A11	M	6:1	9:1	
A11	A8	M	40:4	11:1	
B1	B13	F	32:11		
B9	B1	M	6:0	1:0	
B13	B9	M	17:6	13:0	5:2
B13	B9	F	1:0	2:0	

trial. Responses to the control speaker occurred only on later trials.

On one occasion, the father from nest B9 hovered twice in front of a speaker playing calls of his chicks as a control for a different experimental nest, despite the presence of his chicks in his own nest. The father at nest A20 made repeated passes at the observation blind when his sequestered chicks began calling from within their holding bag inside the blind. On several occasions we also saw the unmarked second parent fly from the vacant nest to the experimental speaker. These latter cases are not included in our analysis, as we do not have positive identifications of the unmarked birds.

Chick faces.—The facial patterns of Cliff Swallow chicks become distinctive around 13 days of age, when the feathers on their chins and foreheads break from their quills. We presume that the distinctive pattern remains constant for each individual beyond the duration of our observation period, because the pattern is made up of facial contour feathers, which are retained at least until late summer. The quantity and distribution of white feathers provides the most discernible variation among chicks, but background coloration also varies considerably and includes black, slate, chocolate, rufous, and tan (see Frontispiece).

As with voices, faces show noticeable family resemblances. Chicks from the same brood generally have the same background coloration and, to a lesser extent, similar distributions of white. The three chicks on the right side of the Frontispiece are siblings. The three chicks on the left side are from different nests.

We presented human subjects with a set of eight color photographs of the faces of 18- to 24-day-old chicks. Subjects were then given a different, randomly chosen photograph of one of those chicks to match up with a photo from the original eight. People made very few mistakes and scored significantly higher than random on their matches ($P \ll 0.001$). Parent Cliff Swallows probably possess discriminatory abilities equal to or better than humans, but this remains to be demonstrated.

DISCUSSION

The present study demonstrates that both the calls and faces of Cliff Swallow chicks are individually distinctive. We have also shown that parents use the individual distinctiveness of the chicks' calls to identify and locate lost chicks. A goal for future research will be to determine how chick facial variation is used by the parents.

Results of studies of parent-offspring recognition to date have been consistent with the hypothesis that parent-offspring recognition should be well developed in colonially breeding species in which young intermingle and absent from or poorly developed in species in which offspring mixing rarely occurs before independence. In the colonial Bank Swallow and Cliff Swallow, there is extensive variation in the signature calls of the chicks, and parents can recognize their chicks by their calls alone. In the solitary or facultatively colonial Rough-winged Swallow and Barn Swallow (*Hirundo rustica*), cross-fostering experiments give no evidence of parent-offspring recognition, and variation in chick calls and plumage is minimal (Hoogland and Sherman 1976, Burtt 1977, Beecher et al. 1981, Beecher 1982, Medvin and Beecher unpubl. obs.). These findings suggest that the large-scale intermingling of chicks that occurs in colonial swallows has favored the evolution of signature traits in chicks and discrimination of these traits by their parents.

We were surprised by the existence of two potential modes for chick recognition in Cliff Swallows, as the equally colonial Bank Swallows show no individually distinctive plumage traits. Although we have not yet done the parallel experiment on Cliff Swallow face recognition, we were able to recognize different chicks on this basis ourselves, in the field as

well as in the lab test described earlier. Thus, we consider it likely that parents use facial patterns in some way, and we shall briefly discuss the significance of dual modes of recognition. Multiple recognition modes have not yet been demonstrated in birds, though Buckley and Buckley (1970, 1972) describe extensive variation in the down coloration of Royal Tern (*Sterna maxima*) chicks and believe that chick calls may also be used for recognition. Two or three modes are probably common in mammals—olfactory, visual, and/or auditory—although only in the case of humans and domestic sheep have all three modes been confirmed (e.g. Porter and Moore 1981, Shallito Walser et al. 1981).

We propose three explanations for why the Cliff Swallow might need to recognize its chicks both auditorily and visually, while the ecologically similar Bank Swallow employs only the acoustic mode.

1. A Cliff Swallow parent can find its strayed chick at another nest by its voice. Once there, however, the parent may have difficulty discriminating among five screaming voices in the highly reverberant mud nest. Our recordings indicate that signature calls degrade severely when a parent returns and all chicks are present and eager to be fed. Faces can be distinguished no matter where the chicks are sitting, thereby providing a distortion-free second basis for discrimination. Bank Swallow burrows are not nearly so reverberant, so this problem is not as critical for Bank Swallow parents.

2. Related to the previous hypothesis, Bank Swallow burrows are acoustically isolated by the absorptive properties of the sand bank, and Bank Swallow parents are therefore generally exposed only to the loud signature calls of their own chicks. Parent Cliff Swallows are exposed on all sides to the calls of neighboring chicks, and they may inadvertently learn these calls too. Facial recognition may allow secondary parental discrimination of offspring from among a larger set of chicks whose calls are familiar to the parents.

3. Undoubtedly there is a limit to the amount of signature information that can be carried by a brief 100-ms call. Cliff Swallows may have circumvented this problem by exploiting an additional recognition mode. If this hypothesis is correct, Cliff Swallow parents' recognition of young away from the nest should be partially impeded by experimental alteration of chick facial patterns. This hypothesis should be distinguished from hypotheses such as the first two, which propose that visual and acoustic cues are used under different circumstances.

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