RECOGNITION OF PARENTS' VOICES BY
YOUNG CLIFF SWALLOWS

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ABSTRACT.—Cliff Swallow (*Hirundo pyrrhonota*) chicks were played calls of parents and unrelated (control) adults at 9 and 18 days of age. Younger chicks showed no difference in the frequency of their antiphonal begging calls to parental vs. control calls. The older, near-fledging chicks, however, responded significantly more to parental calls than to control calls: 78% of their total antiphonal calls were in response to parental playback calls. In these older chicks, the degree of preference correlated with the measured acoustic differences between the parent and control calls. The results indicate that Cliff Swallow chicks are able to recognize their parents by voice before they leave the nest. Offspring recognition of parents is discussed as it relates to the evolution of parent-offspring recognition systems in general. *Received 12 September 1984, accepted 5 January 1985.*

SOME species live in socioecological circumstances requiring parents and dependent offspring to find one another among large numbers of conspecifics. In many colonial species, for example, a parent leaves its young in a creche while it forages at distant sites. To deliver food to its young on returning to the creche, the parent must recognize the offspring, or vice versa. In fact, parent-offspring recognition invariably has been found in such species. Theoretical discussions of this situation generally have emphasized the parents' need to recognize offspring but have ignored pressures for young to recognize parents (see Colgan 1983 and references therein). Indeed, it is sometimes argued that, far from being selective, offspring should actively seek parental care from nonparents. This emphasis derives from the straightforward argument that parents benefit only from care directed toward offspring, while young benefit from any parental care, whether received from parent or nonparent. In this view, misdirected parental care is a problem for parents but not for offspring.

The argument so far leads to the prediction that parents will recognize offspring but not vice versa. Field observations, however, have not supported this prediction. For example, when an Adélie Penguin (*Pygoscelis adeliae*) parent returns to the creche, only its own chicks respond to its calls and solicit feedings (Penney 1968, Thompson and Emlen 1968, Spurr 1975, Thompson 1981). This example is particularly instructive, since the creche often is portrayed

as the ideal situation for low-cost freeloading by young. What, then, is the shortcoming of the argument? It omits a key feature of the recognition process: parents can recognize offspring only if the latter provide individually distinctive cues ("signature" cues). Comparative evidence suggests that signature systems have been one of the key adaptations in the evolution of recognition (Beecher 1981, 1982; Jouventin 1982). Offspring signatures, however, have an additional consequence: not only do they enable the parents of the young to recognize them as offspring, but they allow other adults to recognize them as alien. Therefore, soliciting parental care from unrelated adults is not likely to be successful. Moreover, it will entail effort and perhaps some element of risk, such as attacks by unrelated adults. We thus arrive at the conclusion that the same variables that favor parents recognizing offspring must favor offspring recognizing parents.

This natural-selection argument suggests that offspring recognition of parents will coevolve with parental recognition of offspring. We examine a corollary of this argument in the present paper: Where parental recognition of offspring has been discovered in a species, we should expect to find offspring recognition of parents as well. Surprisingly, convincing demonstrations of both processes exist for only a few species (see Discussion). The present study examines whether young Cliff Swallows (*Hirundo pyrrhonota*) recognize their parents. We have shown in a previous study that Cliff Swal-

low parents recognize their young by voice (Stoddard and Beecher 1983). Because antiphonal calling between parents and chicks is so conspicuous both at the nest and after fledging, we chose to examine chicks' recognition of parents using a playback method. We recorded the calls of parents at the nest and later tested chicks on the calls of their parents vs. the calls of parents from another nest. We measured recognition by comparing the number of antiphonal calls chicks gave to parent calls vs. nonparent calls.

METHODS

Our study was conducted on Washburn Island in north-central Washington. The study colony of approximately 50 nests was located on two T-shaped concrete support pillars of an elevated fish holding tank. We have previously done a study of parental recognition of offspring at this site (Stoddard and Beecher 1983).

To record parent calls, small (12-mm diameter) condenser microphones (Realistic 33-1056A) were mudded into the nest wall, barely protruding into the nest. Recordings were made on a Uher 4200 or 4400 stereo tape recorder at 9.5 cm/s, using Scotch 176 recording tape. Spectrograms of the calls were made with a Kay Sona-Graph 6061E Spectrum Analyzer with a 6083 Scale Magnifier. Calls for playback tests were dubbed onto 10-s tape loops. Each tape loop consisted of 2 calls from 1 parent, approximately 5 s apart. With a few exceptions due to nest losses, each tape was used in one playback test as an experimental (parental) tape and in a second as a control (nonparental) tape.

Playback tests were done when chicks were 9 days old and again when they were 18 days old (chicks begin to fly at 21–24 days). The nests tested had 2, 3, or 4 chicks. Due to nest losses and other reasons, all nests were not tested at both ages: 6 nests were tested at 9 days and 11 nests at 18 days, with 4 of the nests tested at both ages. A full-range playback speaker (Realistic 40-1285C) was hung about 0.5 m from the nest, facing the entrance. Parents adjusted to the presence of the speaker after about 10 min.

The sound level of the playback call was adjusted, before the beginning of the test, so that it matched the level of a call by a parent approaching the nest. This level remained constant throughout the test. Since all calls were recorded on the tape at a standard level, this procedure guaranteed equal loudness of parent and control calls.

A playback test consisted of 2 1-min trials each of the parental tape (P) and the nonparental tape (N), and a single 1-min trial of blank tape (B). The order of presentation was PNBNP or NPBPN. After a minimum intertrial interval of 5 min, a trial was begun

TABLE 1. Number of antiphonal responses by chicks to parent and control calls (2 min each of parent and control trials and 1 min of blank trial).

Home	Control	Parent	Control	Blank	P/ (P + C)[a]
9-day-old nests					
A1	B5	568	512	0	0.52
A17	B4	162	218	0	0.43
A22	A5	277	153	0	0.64
A12	A19	126	48	3	0.72
A19	B2	545	582	0	0.48
A24	A13	118	241	21	0.33
18-day-old nests					
B2	A1	235	180	0	0.57
B5	A1	315	119	14	0.72
A1	B5	364	146	11	0.71
A2	B5	313	86	0	0.78
C1	B6	82	16	3	0.84
B6	C1	237	11	0	0.96
A5	A22	297	76	0	0.80
A22	A5	105	59	0	0.64
A20	A11	112	2	0	0.98
A24	A13	269	193	0	0.58
A19	B2	143	0	0	1.00

[a] P/(P + C) = responses to parent call divided by responses to parent call plus responses to control call.

when the parents were away from the nest and the young were quiet. If a parent returned to the nest during a trial, the trial was terminated and the data discarded, since the chicks would call to the parent. For the same reason, trials also were terminated if a parent hovered or circled by the nest without entering. One observer was solely responsible for spotting parents; two others operated the playback and recording equipment. The length of an experiment was determined largely by the frequency with which the parents happened to be feeding at the nest, and took 0.5–2 h.

Antiphonal responses from chicks in the playback test were recorded with the nest microphone. The responses were taped and later counted by scanning the tape at quarter or half speed on a Unigon 4500 Real Time Spectrum Analyzer. Counts were done twice; all discrepancies were less than 1%.

RESULTS

Playback experiment.—For the 9-day-old chicks, there was no evidence for differential response to parental vs. nonparental calls: 3 of the nests responded more strongly to the parental calls, 3 more strongly to the nonparental calls (Table 1). The 18-day-old chicks, however, responded more strongly to the calls of their parents than to the control calls at all 11 nests tested ($P = 0.0005$, sign test). These older chicks gave an
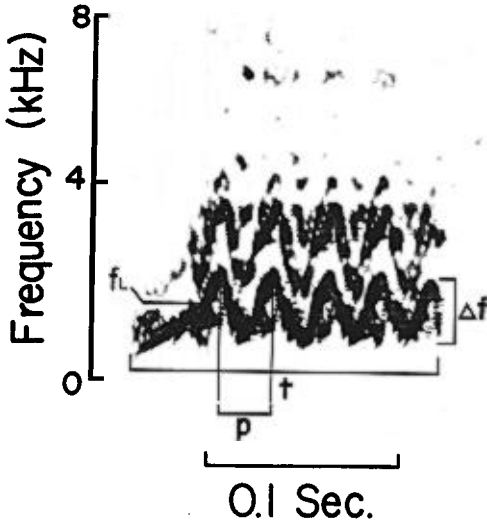
Fig. 1. Call of parent at nest C1, illustrating the 4 parameters analyzed: (1) fL, average frequency of the lower voice fundamental; (2) p, period of frequency modulation; (3) Δf, frequency difference between first modulation peak and valley of the lower voice; and (4) t, duration of call. A fifth parameter analyzed for chick but not adult calls is the frequency difference between the upper and lower voices. The call illustrated here is unusual for an adult call in having a strong upper voice (at the first frequency peak in this call the lower voice is 2.1 kHz, the upper voice is 3.5 kHz, and the weak second harmonic of the lower voice is 4.2 kHz).

tion, then, these measurements can be regarded as a fair characterization of a call.

We calculated an index of the difference between a parent call and a control call in the following way. (1) For each call, its measurement on a particular parameter (e.g. duration) was converted to a standard score (z = individual measurement minus mean, divided by standard deviation) based on the set of 13 calls. This was done for each of the 4 parameters in turn. (2) For each parent-control call pair, the parent-call standard score was subtracted from the control-call standard score, for each particular parameter in turn. (3) For each call pair, the absolute standard score differences for each call pair for all 4 parameters were summed. The two parent-control call pairs that were the most similar and most dissimilar are shown in Fig. 2. To illustrate the calculation of the difference index, the dissimilar call pair in Fig. 2 differs markedly with respect to the duration parameter (mean t = 105 ms, SD = 56 ms; A20 = 280 ms, z = +3.12; A11 = 90 ms, z = −0.26; z difference = 3.38). The absolute z differences for the 3 remaining parameters sum to 2.31, giving a total sum of 5.69. This is the difference index plotted in Fig. 3. The degree of preference for the parent call was strongly related to the degree of difference between parent and control calls (r = 0.82, P < 0.001, n = 11).

DISCUSSION

Development of recognition.—Clear evidence of recognition of parental calls was seen in 18-day-old chicks but not in 9-day-old chicks. This finding is interesting because most of the parental calls the chicks hear at the nest actually occur in the first week of life. In the first week, parents call at least once on every trip to the nest, usually as they enter. In the second and third weeks, however, parents call only occasionally. Thus, while 9-day-old chicks do not respond preferentially to parental calls, they already may have taken in all the information they need for the preference seen at 18 days. This hypothesis could be evaluated by testing 18-day-old chicks that have been prevented from hearing parental calls past day 9.

The difference in recognition shown by 9-day and 18-day-old chicks is consistent with the common finding that recognition does not develop as early as it could, but seems to appear only just before it is needed (e.g. shortly before fledging). This aspect of the development of

average of 78% of their responses to parent calls. At most nests, chicks did not respond at all during blank trials.

Analysis of parent calls.—The degree of preference of 18-day-old chicks for the parent calls varied from nest to nest, from 57 to 100% (Table 1). In a post hoc analysis, we examined the hypothesis that the degree of preference was related to the degree of difference between the parent call and the nonparental control call. To evaluate call differences, we made measurements on four parameters of each call, as illustrated in Fig. 1. We chose 4 of the 5 parameters used in our previous analysis of chick signature calls (Stoddard and Beecher 1983). As is the case with chick calls, the 4 parameters we analyzed were independent: all 6 intercorrelations were nonsignificant, r ranging from 0.07 to 0.31 (n = 13). Measurements of these 4 parameters were sufficient to reconstruct a reasonable replica of the original spectrogram. By these criteria of independence and reconstruc-
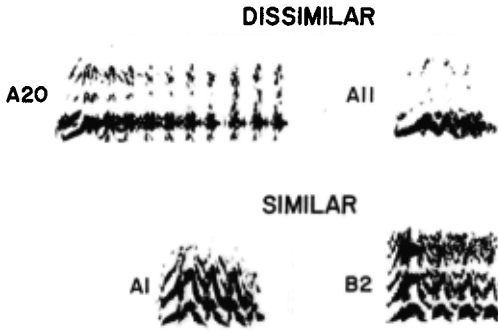
Fig. 2. A dissimilar experimental-control pair (A20 and A11, difference index = 5.69) and a similar pair (A1 and B2, difference index = 3.00). The upper voice is absent or weak (A11) in these calls, although harmonics are strong in all but A11.

Fig. 3. Scatterplot of degree of chick preference for parental call [P/(P + C)] vs. degree of difference between the parent-control call pair the chicks in each nest were exposed to, as measured by the difference index (see text).

recognition has been much discussed (e.g. see reviews by Miller and Emlen 1975, Beecher 1981, Falls 1982, Colgan 1983). It should be cautioned, however, that the relatively late appearance of recognition could be the consequence of an insensitive test situation. For example, Shugart (1977) found that, in standard chick substitution tests, Caspian Tern (*Sterna caspia*) parents did not consistently reject alien chicks until day 9, shortly before the period of chick mobility. When tested in choice trials, however, the parents correctly chose their chick on day 2 or 3.

Natural contexts for parent-offspring recognition in Cliff Swallows.—Antiphonal calling appears to play a key role in the maintenance of family integrity once Cliff Swallow chicks begin to fly. We have seen parent and chick calling back and forth when the chick has flown into the wrong nest, is flying about the colony, or is away from the colony in the creche (at our study site these temporary creches form in bushes several hundred meters from the colony). These antiphonal calling bouts typically end with the reunion of parent and chick. Our experiments (Stoddard and Beecher 1983, this study) have confirmed our impression from field observations that these calls form the basis for mutual recognition.

Mutual parent-offspring recognition may well be a prerequisite for family integrity in highly colonial, creche-forming species. Parental recognition of chicks alone probably is insufficient in such cases because finding a particular chick in a large creche is a needle-in-a-haystack proposition. Indeed, a parent's ability
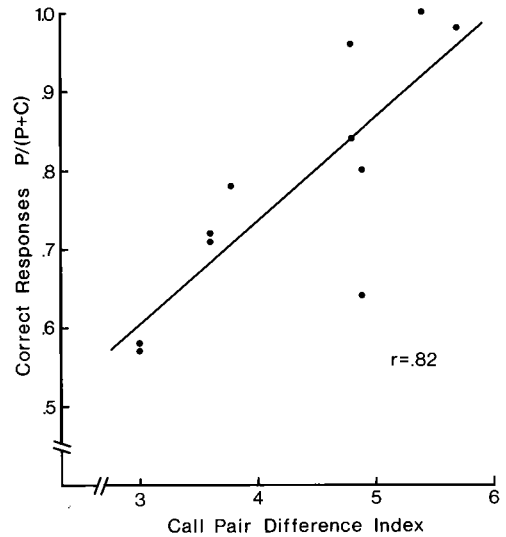
to locate its chick may hinge on the chick's acting as a "first filter," i.e. responding only to the calls of parents. Even if this first filter is imperfect and the chick also responds to the calls of some adults whose calls sound similar to the parents' calls, the chick's selectivity would still simplify the parent's task. For example, suppose a chick typically calls back to 5% of the returning adults (its own parents and some similar-sounding adults) and that the creche size is 500 chicks; on average, the parent would have to choose among only 25 chicks rather than the full 500.

Mutual recognition.—The Cliff Swallow is only the third avian species for which mutual recognition between parent and offspring has been demonstrated. Mutual recognition by calls also has been demonstrated in the Bank Swallow (*Riparia riparia*, Beecher et al. 1981, Sieber 1985) and the Pinyon Jay (*Gymnorhinus cyanocephalus*, McArthur 1982). It sometimes is stated in literature summaries that mutual recognition occurs in Ring-billed Gulls (*Larus delawarensis*). However, while Evans (1970, 1980) showed that chicks recognize the calls of their parents, the reciprocal experiment has not been done. In fact, Miller and Emlen (1975) found that parents accepted both muted chicks and visually altered chicks (in the latter case rejection re-

sponses sometimes occurred for a few hours, but dissipated as chicks continued to approach parents).

It is a curious fact that parent-offspring recognition usually has been studied piecemeal. Investigators have tended to examine parental recognition or offspring recognition, but not both. For example, it has been shown that mothers recognize pups by voice in elephant seals (Petrinovich 1974) and that pups recognize mothers by voice in Galapagos fur seals and sea lions (Trillmich 1981), but in none of these species has the reciprocal process been studied. The paucity of reciprocal studies is accentuated when strict criteria for recognition are required. It is fairly common to find rigorous demonstrations of one sort of recognition by a cue-isolation experiment but only weak evidence for the reciprocal process (e.g. naturalistic observations, cross-fostering experiments, analyses of calls or visual features for individuality). It should be emphasized that cross-fostering experiments (the most common vehicle for the investigation of parent-offspring recognition) do not reveal the direction of recognition. Although they sometimes are presumed to measure mainly parental recognition of offspring (the outcome often is expressed in words such as "parents rejected cross-fostered young"), the procedure confounds several kinds of recognition. For example, it often is said of cross-fostering experiments with gull species that parents may reject alien young on the basis of the transplanted chick's frightened behavior, i.e. the chick may recognize nest, surroundings, or parent as unfamiliar and in its reactions provide the cues the parent uses to reject it (e.g. Miller and Emlen 1975). Nor is demonstration of the existence of individually distinctive (signature) traits sufficient evidence for recognition; it must be shown that this information actually is used by one party to recognize the other. Cue-isolation experiments, on the other hand, permit strong demonstrations of recognition. Cues are easily isolated in the acoustic mode (playback experiment) or olfactory mode. Although visual cues cannot so readily be isolated, in theory recognition could be evaluated by tests before and after subtle visual alteration (rejection after gross visual alteration is difficult to interpret, although acceptance would seem clearly to argue against recognition in the visual mode).

We suggest that research is needed to explicitly examine the hypothesis that offspring recognition of parents is a necessary correlate of parental recognition of offspring. Beer's (1969, 1979) studies on Laughing Gulls (*Larus atricilla*) demonstrate that we cannot assume recognition is necessarily mutual. He showed by playback experiments that offspring recognize parents by voice but that parents do not recognize chicks by voice. Additional experiments indicated that parents depend on chicks to recognize them. The evidence to date from other gull species, though not so complete as Beer's work on Laughing Gulls, is consistent with the hypothesis that recognition is primarily by offspring (e.g. Holley 1984). Clearly, this outcome is not suggested by the natural-selection argument advanced in the introduction. The only point we wish to make here, however, is that mutual recognition cannot be assumed to exist given only evidence of parental recognition or of offspring recognition.

Signature traits.—Individual recognition often is assumed to be a simple consequence of two characteristics of a species: the inevitable existence of phenotypic variability in individuals and the possession of well-developed sensoriperceptual systems that permit detection of this variation. Considerable evidence, however, suggests that the phenotypic variability used for recognition (signature traits) should be regarded as an adaptation for recognition. For example, in two bird families, swallows and penguins, it has been shown that both the occurrence of recognition and the complexity of signature traits are correlated with the degree of coloniality (Beecher 1981, 1982; Jouventin 1982). For example, the Bank Swallow recognizes its young and the young have individually distinctive calls, while the closely related but noncolonial Northern Rough-winged Swallow (*Selgidopteryx serripennis*) does not recognize its young and the homologous chick call is not individually distinctive (Hoogland and Sherman 1976, Beecher et al. 1981, Beecher 1982). Parallel results have been found for the Cliff Swallow and the noncolonial, congeneric Barn Swallow (*Hirundo rustica,* Stoddard and Beecher 1983, Medvin and Beecher MS).

Parent signature calls.—The present study provides additional evidence for the hypothesis that signature traits evolve in response to selection pressure for recognition. Our data allow us to compare parent signature calls of the

colonial Cliff Swallow and Bank Swallow and the noncolonial Barn Swallow. Comparable playback studies of all three species have shown that offspring respond more strongly to the calls of their parents than to calls of unrelated adults. The magnitude of the preference, however, is as predicted by the colonial-noncolonial distinction: Banks 75%, Cliffs 78%, Barns 55% (Sieber 1985, this study, Medvin and Beecher MS). This difference in turn is correlated with our preliminary measurements of the complexity of adult calls in these three species. That is, we suggest that the stronger discrimination between parental and alien calls shown by Bank Swallow and Cliff Swallow chicks compared to Barn Swallow chicks may be due, at least in part, to the larger differences among calls in the two colonial species. This interpretation is supported by the intraspecific difference noted in the present experiment: Cliff Swallow chicks made clearer discriminations between parental and alien calls (i.e. stronger preferences for the parental call) when the difference between the calls was greater.

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