PARENT–OFFSPRING RECOGNITION IN BANK SWALLOWS (*RIPARIA RIPARIA*): II. DEVELOPMENT AND ACOUSTIC BASIS

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Abstract. In study 1, bank swallow (*Riparia riparia*) chicks were exchanged with like-aged chicks from other broods. Parents accepted chicks that were transferred into their nests at age 15 days or younger; rejection began to occur at 16 to 17 days. In study 2, chicks' vocalizations were recorded in the burrow. We found that an immature begging call given by young chicks is replaced by a 'signature' call at 15 to 17 days of age. An acoustic analysis suggested that these calls are individually distinctive. Study 3 was a playback experiment designed to test whether the chicks' signature calls are a sufficient cue for parental recognition. We found that parents would approach a speaker broadcasting the calls of their chicks in preference to one simultaneously broadcasting the calls of alien chicks. The pattern of results suggests that parental recognition is based on the chicks' signature calls and that development of recognition is dependent on the development of the call.

The development of parent–offspring recognition is typically studied by experiments in which young of various ages are exchanged between like-aged broods. These exchange experiments have generally indicated that the onset of recognition is related to the ecology and natural history of the species. In colonial birds it has been found that brood exchanges are tolerated by parents until shortly before the chicks reach the stage of mobility. For example, recognition develops on about day 5 post-hatch in herring gulls (*Larus argentatus*) (Tinbergen 1953), and not until after about five weeks in kittiwake gulls (*Rissa tridactyla*) (Cullen 1957); in both cases these ages correspond approximately to the onset of intermingling of young.

Cue-isolation experiments, such as playback studies for acoustic cues, are useful to establish that parent–offspring recognition involves true recognition of individual characteristics, as opposed to purely indirect effects, e.g. recognition of a strange nest by the chick, or discrimination of the differences in comportment of a misplaced chick by the resident adult. The use of the playback method to demonstrate individual vocal recognition was championed by Beer (1970), who showed that laughing gull chicks (*Larus atricilla*) could discriminate the voices of their parents from those of other adults. The method has been used to demonstrate recognition of offspring by parents in five species; razorbilled auks (*Alca torda*) (Ingold 1973), elephant seals (*Mirounga angustirostris*) (Petrinovich 1974), domestic (Merino) sheep (Poindron & Carrick 1976),

squirrel monkeys (*Saimiri sciureus*) (Kaplan et al. 1978), and vervet monkeys (*Cercopithecus aethiops*) (Cheney & Seyfarth 1980).

If parental recognition of offspring does not appear until a particular age, and involves a single individually distinctive cue, then the critical age presumably depends upon the timing of both (1) the development of the cue in the chick, if it is not present at birth, and (2) the learning of that cue by the parent. In this paper we combine the approaches of developmental study and cue-analysis study, in order to separate, at least partially, the development of the processes of identification (the sender's providing the cue to its identity) and recognition (the receiver analysing and responding differentially to that cue). Our field observations on bank swallows (Beecher et al. 1981) suggest that (1) parent–offspring recognition is not essential before 14 days of age since chicks rarely fly into pre-14-day nests, and if they do, they are conspicuously older than the host's chicks; (2) recognition is required at 18 days, when the chicks begin to fly, and (3) a call given by the chick appears to be involved in recognition by the parent. Consequently, we expect recognition of chick by parent to develop between 14 and 18 days of age, and to be correlated with the development of some cue or cues, probably including the call.

This paper consists of three studies. The first of these was a transfer experiment in which chicks of various ages were exchanged between nests to determine if there is a critical offspring age for the development of parent–offspring recognition. The second study was a sonagraphic

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analysis of the individuality and ontogeny of the chick's 'signature' call. In the third study we carried out a playback experiment to determine whether the call is a sufficient cue for recognition of the chick by the parents.

Study 1: Chick Exchange Experiments
Methods

We exchanged chicks between broods that were approximately the same mean age (maximum discrepancy 2 days (one exchange only)). Since there is often a considerable range in the development of chicks within a brood, due in part to the asynchrony of hatching, we assigned each chick a developmental age based on the length of the ninth primary feather; this measure is a linear function of age through 19 days (Petersen 1955; Beecher & Beecher, unpublished.) All ages assigned to individual chicks on this basis were within the brood mean age post-hatch by ± 1 day.

All chicks were removed from a nest, banded, and colour-marked (except that chicks younger than 12 days old could not be colour-marked at transfer and so were removed again and marked at 14 to 16 days). Marks consisted of left–right combinations of red, green, blue, and yellow made with broad-tipped felt marker pens. Two chicks from a brood were then exchanged with two from a like-aged brood. The remaining chicks in each brood (usually three) were then returned to their original nest. Since these chicks were treated similarly in all other respects, they are 'sham transfers' or controls. After these manipulations we did not inspect the burrows again, since disturbance can cause early fledging. We marked 41 experimental chicks and 52 controls; approximately equal numbers were marked at every age in the 9- to 19-day range. Parents were captured by mist-netting and marked in the same fashion as chicks. The experiment was carried out in five colonies over three years (1976–78). All burrows were observed for 4 to 8 h per day starting on day 14 post-hatch, when the chicks could generally be seen at the burrow mouth.

Results

All 52 sham transfers were re-accepted by their parents. (In 10 years of studying bank swallows, we have not had a single case of a parent rejecting its own chick after it was marked in the fashion described ($N = 503$).)

The fate of the 41 experimental birds depended on their age. Seven of the eight 18-day-old transfers flew from the burrow within 0.5 h

of the transfer; all seven were observed back at the home burrow by the next day. The only bird that remained in the nest 1.5 h was evicted by the resident adult. We have previously observed that birds 18 days old and older are highly likely to leave their own burrow after such handling. Since the chick normally flies at 18 to 19 days, flight from the burrow after a disturbance would be an adaptive response, allowing the chick to escape from predators (especially terrestrial ones). In any case, data on the response of resident adults to older birds cannot really be obtained through transfer experiments since the chicks do not remain in the 'foreign' burrow. Our natural observations (Beecher et al. 1981), however, indicate that the resident adult effectively discriminates 'visiting' chicks (usually 19 days or older) from its own, though mistakes do occur.

All 23 chicks 15 days old or younger were adopted by the resident adults, that is, they were seen at the burrow until it was vacated at 21 to 24 days post-hatch. The full range of behaviours normally seen between parent and chick were observed in these cases of adoption, including the parent feeding the chick at the powerlines and leading it back to the burrow. Three birds in this age group, from three different broods and transferred at 10, 11, and 12 days respectively, happened to fly back to their natural burrow when older (22, 21, and 22 days respectively). All three were evicted by their natal parent. This indicates that adoption was complete and symmetrical: the adoptive parent treated the chick as its own and the natural parent treated it as alien.

A mixed response was seen with the 16- to 17-day-old transfers: four were adopted, four were immediately evicted, and two were not seen at any nest again (these latter two were the only birds of the 41 transfers to disappear). A post hoc analysis showed that all four of the adopted birds had been transferred into slightly younger nests, and the six that disappeared or were rejected had been transferred into same-age or slightly older nests. Four of the birds from the 16- to 17-day-old group returned to their home nest later. The two adopted 16-day-old transfers returned to their natal burrow five and four days later respectively (until that burrow was vacated). The two 16-day-old transfers that were evicted from the host burrow (this happened shortly after the transfer) made their way into other burrows, and back to the natal burrow after one and three days respectively. The chick
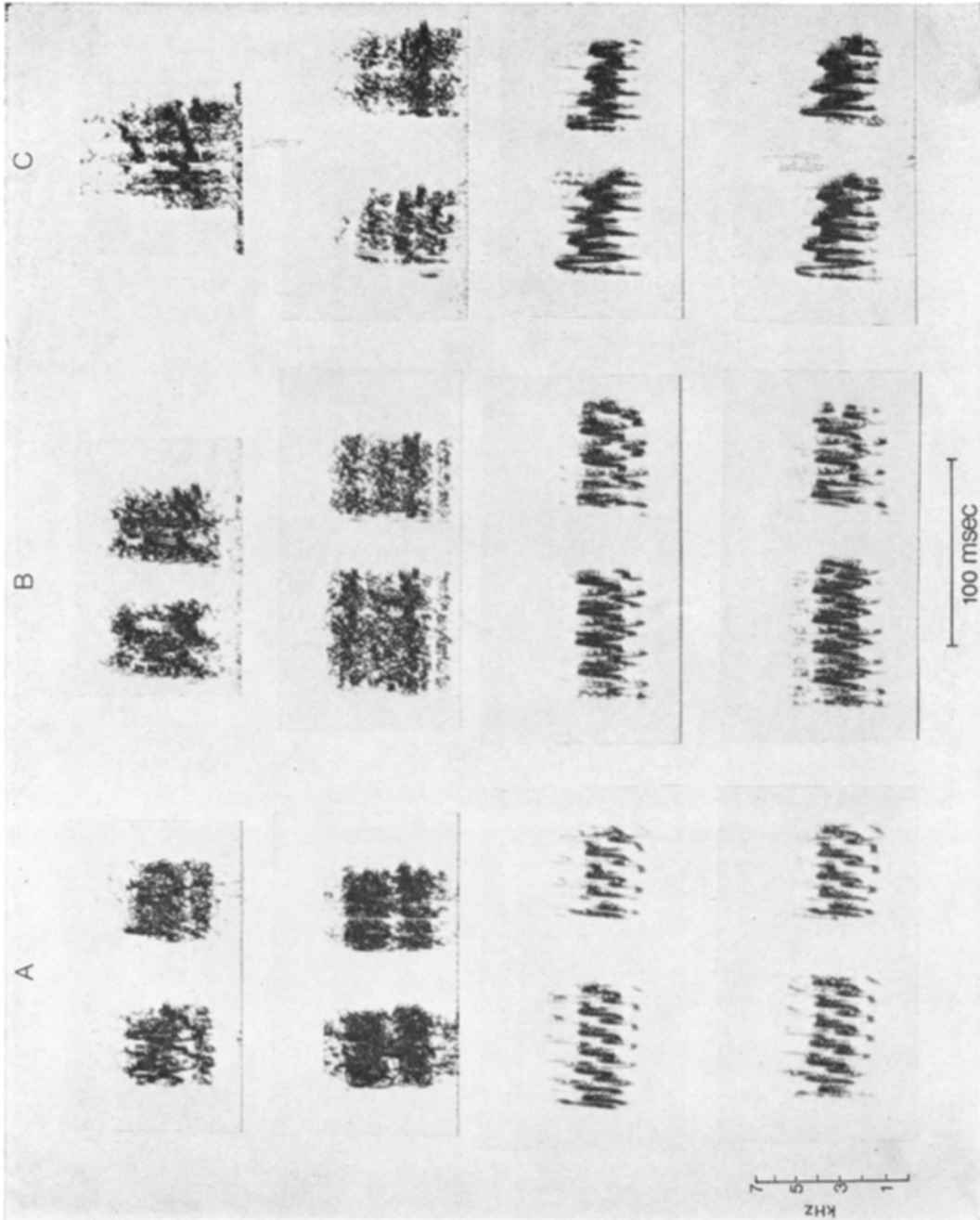
PLATE I

Fig. 1. Vocalizations recorded at three nests. Each column (A, B, and C) is from a single individual. Top two rows are calls recorded at age 12 to 14 days. Bottom two rows are calls recorded on days 17 to 21.
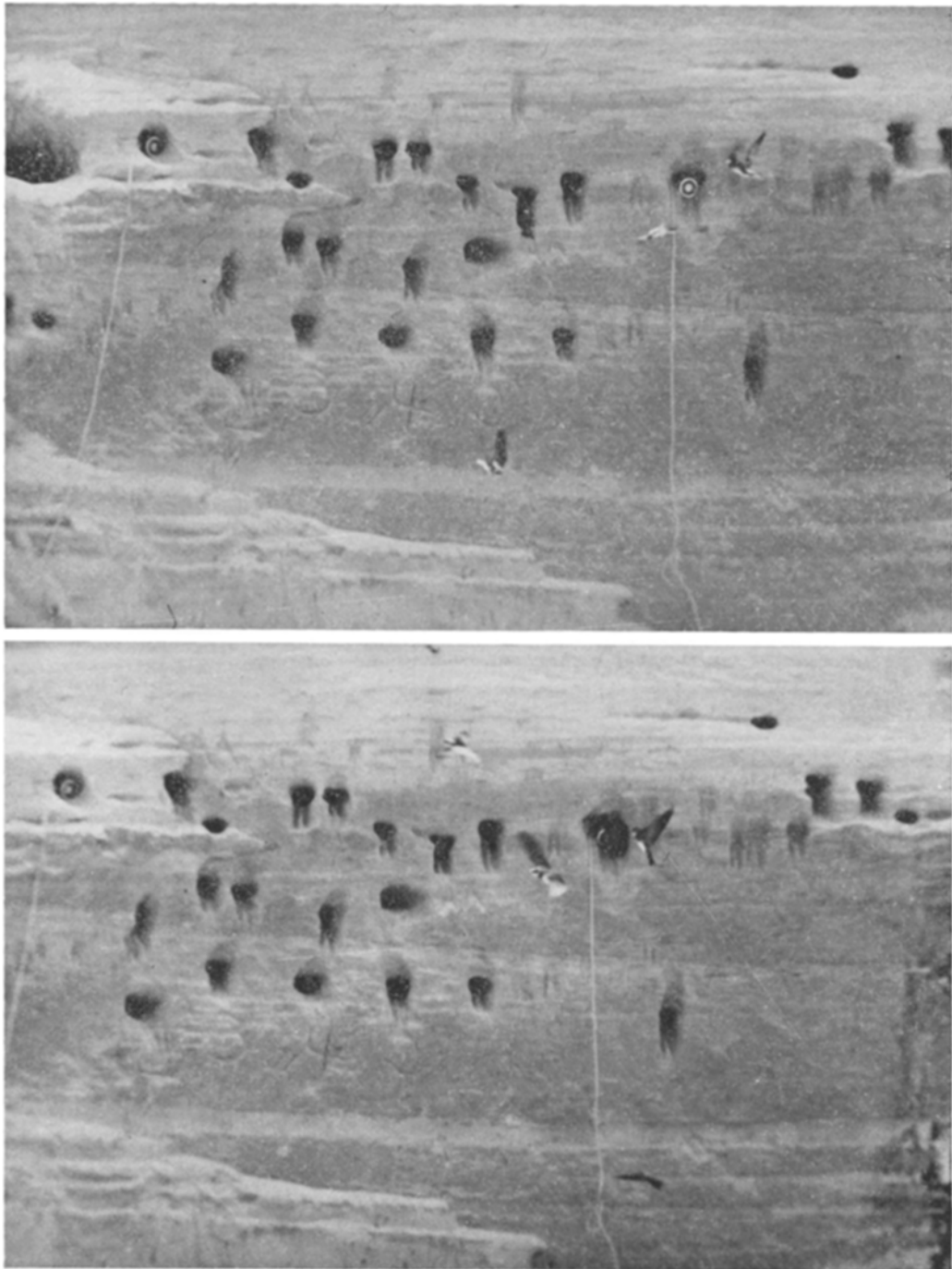
Fig. 3. Illustration of arrangement for playback experiment. Speakers set somewhat closer together than usual for purposes of photo. Photographed just after actual experiment for burrow R5A (burrow in centre of photo, above '5'). In bottom photo female parent is seen attempting to go around speaker into burrow (which she had done in the actual experiment, earlier, when the speaker was in a different burrow). Unmarked bird hovering in front of speaker in both photos may be male parent.

away one day was fed and remained at the natal burrow until day 23 (until that burrow was vacated). The chick that was away three days was evicted by its natural parent twice and not seen again after that day.

Discussion

The following hypothesis was developed on the basis of the foregoing results and tested in studies 2 and 3. We assume that the distinguishing cue, which for convenience we will call the chick's 'signature', develops between days 15 and 17 post-hatch. The parent learns this signature in what we suppose is an irreversible, imprinting-like process. The parental learning process must lag behind the chick's development of the signature, perhaps by a day or so. This hypothesis clearly pertains only to recognition of offspring by parents; though we believe recognition of parents by offspring also occurs, we suspect this becomes a significant factor only later, once the chick begins to fly (18 days and later). Our hypothesis accounts for the results of the transfer experiment in the following way: (1) in chicks aged 15 days and younger transferred into nests containing like-aged young, the signature has not developed and thus neither group of chicks elicits parental recognition. Contrariwise, birds older than 17 days cannot be transferred into like-aged burrows, for signatures are developed and have been learned by the parents. (2) Transfer of a 15- to 17-day-old chick, whose signature has developed, may succeed if it is into a nest containing slightly younger chicks, where the parents have not yet learned the signatures of their own chicks. Contrariwise, such a transfer may not succeed if it is into a same-age or older nest where the parents have learned the brood's signatures. (3) Young transferred into a like-aged nest during the 15- to 17-day critical period may find themselves in the position where neither or both their sets of parents recognize (accept) their signature, since the transfer may occur before or after the natural parents learn the chick's signature and before or after the host parents learn their own chicks' signatures (and presumably 'close' to further learning).

Study 2: Development of the Signature Call
Problems and Methods

Our field observations indicated that the two-note begging call given by chicks before being fed was the hypothesized 'signature'. As far as we can tell, this call precedes every feeding, whether in the burrow, in the air, or at the 'crèche'. When a recently fledged bird pursues an adult, the fledgling gives this call repeatedly. Our hypothesis suggests that (a) the call should have sufficient individuality to enable recognition and (b) the call's development should precede the development of parent–offspring recognition as demonstrated in the transfer experiments.

We made tape recordings from the burrow by placing Electrovoice Lavalier dynamic microphones directly in the burrow. We widened the mouth of the burrow and secured the microphone with clips to the side of the burrow, leaving enough room for the adults to enter and leave, and for older chicks to sit at the front of the burrow. It was possible to obtain good recordings from most burrows except those that turned sharply or were unusually deep. After the initial disturbance, the birds eventually ignored the microphone. We ran a 30-m cable from the microphone to our blind. There we monitored the recording and noted events occurring at the burrow, including where possible the identity of the chick that had made the call. Vocalizations were recorded on a Tandberg 11 tape recorder at 19 cm/s and analysed on a Kay Electric 7029 Sound Sonagraph with 6076 Scale Magnifier. The effective bandwidth was 180 Hz ('Narrow Band' setting, 16 kHz scale, tape at half speed).

Recordings were made at four different colonies in 1976, 1977, and 1978. To examine calls for individuality, we randomly selected 10 individuals (from 10 different nests) from those for which we had positive identification (i.e. each chick in the brood had been individually colour-marked, and we had seen and recorded who had given the call). To measure the ontogeny of the call, we recorded from each of 12 nests in one colony (Fox Quarry A, 1976) every second or third day and calculated the proportion of mature calls relative to immature begging calls (the immature/mature distinction is discussed below). Three observers independently classified each call as 'mature or 'immature'. There was complete agreement on 1242 of the 1258 calls (98.7%). The remaining 16 calls were classified according to the majority judgment.

Results

Young chicks give an immature begging call, beginning on about day 4 post-hatch. This call is a wide-band, formless call, typical of the early begging calls of many passerine nestlings (Fig. 1A, top, Plate I). In older birds, however, the call

sounds more distinct and Sonagrams of the call have a clear internal structure (Fig. 1, bottom, Plate I). Mature calls, but not immature calls, look individually distinctive. To check this impression, we had three naive observers attempt to match up two Sonagrams of an individual's calls, for both mature calls and immature calls. For both types, we took two calls each from 10 individuals. Twelve of these 40 calls, from three birds, are shown in Fig. 1. For each type, the observer successively matched one call from the first set to one from the 10 in the second set; the second set was reshuffled after each trial. All three observers matched the mature calls perfectly. For the immature calls, the percentage of correct matches was 20, 20, and 30 for the three observers, only slightly better than chance (10%).

The accepted method for the objective analysis of individuality in Sonagrams of calls is to extract several features of the call and determine whether interindividual variability in these features is large relative to intraindividual variability (e.g. Epsmark 1975; Miller 1978; Cheney & Seyfarth 1980). While we were unable to extract any such features for immature calls, the task was relatively easy for the mature calls. The mature call is usually a two-note call; the second note is generally similar to the first and is sometimes dropped, so we have ignored it in the following analysis. A 'note' consists of paired figures, which are repeated (sometimes with modification) throughout the note. A 'figure' is a single, unbroken frequency sweep. The second figure in a pair is generally similar to the first, but is higher in average frequency. We suspect that the two figures represent the bird's two voices (Greenewalt 1968); we will present a detailed analysis of these calls elsewhere. Here we will discuss five measures that we extracted from the Sonagrams; the five are not exhaustive by any means, and they ignore in particular the important feature of figure shape: (1) Duration of first note of call. (2) Time Difference between

successive figure pairs, averaged over the whole first note. (3) Frequency Difference between the first major inflection in each figure, averaged over the whole first note. (4) 'Average' Frequency: the absolute frequency of the first inflection point of the first figure of the pair. Where there is a frequency drop throughout the call, as in C in Fig. 1, the measurement is taken at the midpoint of the first note. (5) Slope: the drop in Hz/ms measured over the duration of the first note.

Measurements of these five variables were taken on four calls each from 10 birds. Simple analyses of variance were performed for each variable. The five F-ratios are highly significant (Table I), indicating that intraindividual variability is very small relative to interindividual variability. Thus at least with respect to these five variables, it is correct to refer to these calls as 'signature' calls.

The development of the signature call is shown in Fig. 2. Ages are mean brood ages. Ages are plotted in two-day blocks to provide an N of 8 to 12 nests per point, and also because there is an error of ± 1 day in the assigned mean brood age.

It can be seen in Fig. 2 that the signature calls begin to appear on day 14 or 15 and by day 18 or 19 virtually all calls are signature calls. It appears that the major development takes place in the 16- to 17-day mean brood age range. We

Table I. Summary of Single Classification Analysis of Variance among Signature Calls of 10 Individuals for Five Acoustic Variables

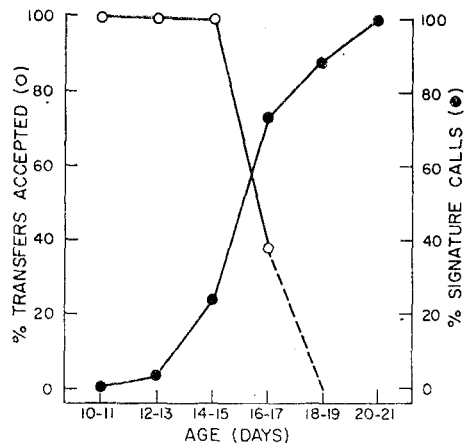| Variable	F
Duration	39*
Time Difference	185*
Frequency Difference	112*
Average Frequency	58*
Slope	11*

*$P < 0.001$.

Fig. 2. Percentage of signature calls (relative to immature calls), right axis (study 2). Percentage of transfers accepted, left axis (study 1). The curve for the latter is extrapolated to zero in the 18- to 19-day age range on the basis of natural observations in addition to the experimental results (see text).

believe the curve would be more stepwise if our data had been obtained from individual chicks of precisely known developmental age. In any case, it is likely that the few signature calls in the 14- to 15-day mean brood age range were given by older siblings in the brood (16 days old?), and the immature calls in the 16- to 17-day mean brood age range by younger siblings in the brood (15 days old?). Some broods have a runt, and it may be this sibling that gives the few immature calls seen on days 18 and 19.

Also plotted in Fig. 2 are the results of study 1. It should be stressed that these results of studies 1 and 2 were obtained independently, from different colonies at different times. The horizontal axis refers to the age of the transferred chicks. It can be seen that the curves describing the development of the signature call and the development of parent–offspring recognition both break at age 16 to 17 days. These data are consistent with the hypothesis that this call is a signature by which the parent recognizes its own young, and that the development of parental recognition depends upon the development of the call.

Study 3: Playback Experiments
Problem and Methods

To obtain direct evidence that the 'signature' call is used by parents to recognize their young, we conducted a playback experiment in which the call was isolated from other possible cues given by a chick. Preliminary experiments were carried out in 1977, and the data reported here were gathered at the Dexter and Cherry Hill sites in 1978.

The experiments were carried out when the young in a nest were 18 to 21 days of age, a time when the young are likely to become misplaced in another burrow (Beecher et al. 1981). We included one 16-day-old nest among our nine experimental nests, for purposes of comparison; the previous data suggest that recognition should be weak or absent at this point, though some of the chicks in the brood may be beginning to give signature calls. On the day before a test, we recorded from the particular burrow to be tested. We then analysed these recordings on the Sonagraph, selected three different calls (when possible, of three different brood members), and prepared a tape loop. A long cassette tape in turn was made from this tape loop. In the playback test, speakers (Grason–Stadler TDH-49 earphones) were placed in each of two burrows immediately to either side of the experimental burrow, approximately 3 to 4 m apart (see Fig. 3, Plate II). For the duration of the test, all young from the experimental nest were removed, to stimulate searching by the parents. During a trial, calls were broadcast simultaneously from the two speakers: from one, the experimental tape previously recorded at the experimental burrow, and from the other, a control tape recorded at another burrow. The observer was 'blind' as to which was which. Loudness at the two speakers was equated by ear and set to match the perceived loudness of other young calling at the bank. With few exceptions, we used each tape loop once as an experimental tape and once as a control tape, thus ruling out spurious results due to the general effectiveness of a particular tape. A test consisted of four trials, with each tape played twice from each side. Trials were separated by approximately 10 min. We started the two recorders without regard to the presence or absence of the parents. The trial began when a parent appeared and terminated after 15 min, unless the parent was in the midst of responding to the speaker. Our minimum criterion for a positive response to a given speaker in a given trial was at least two 15-s bouts of hovering in front of the speaker. In theory a parent could respond positively to both playback speakers on a given trial (though in fact this never happened). In addition to this criterion measurement, we recorded the various behaviours of the parent, and summarized them according to a simple three point scale. Level 3: the parent pushed past the speaker into the burrow. A parent attempting to do so is shown in Fig. 3, Plate II. This is an exceptionally strong response, given that parents usually hesitate for quite some time before entering their own burrow after we place a strange object such as a microphone or speaker at the mouth. Level 2: the parent lands at the mouth of the burrow and 'listens' to the playback speaker; we also scored long-duration hovers ($\geq$ 1 min at a time) at the same level since they appeared equally persistent and since it was difficult in some cases for the bird to land at the burrow. Responses that met our two-15-s criterion but fell short of the above criteria were given the minimum Level 1 score.

Results

The results are given in Table II. The nest with 16-day old chicks was the only one at which both parents failed to respond. For the 18- to 21-day-old broods, 12 of the 13 parents preferred the experimental tape over the control tape (41 trials

to 0), that is, preferred the calls of their own chicks to those of alien chicks; the 13th parent failed to respond at all. A sign test on these data indicates that they are significant at $P = 0.004$ ($N = 8$ nests), or $P = 0.0002$ ($N = 12$ parents). Not indicated in Table II is the fact that all 12 birds responding positively (including those that responded on only two trials) responded to the speaker in both the left and right positions. We also observed that the females at nests 7R, R5A, and D3 responded to their tape again when it was the control tape, 1 or 2 days after it had been used as the experimental tape; in all three cases their burrows had been vacated and they had not been seen in the vicinity when the test began.

The female response was generally somewhat stronger than the male response (female median $= 2$, male median $= 1$). This finding parallels the stronger recognition shown by females in natural contexts (Beecher et al. 1981).

Discussion

Study 3 showed that the chick's signature call is a sufficient cue for a parent to discriminate between its own and alien chicks. Study 2 showed that this call develops at 15 to 17 days of age. Study 1 indicated that parents begin to recognize some cue (we believe it is the signature call) at about 17 days: this turns out to be a day or two after the chicks have begun to give the signature call, and a day or two before they ordinarily begin to fly.

Although these studies indicate the important role of the chick's signature call in parent–offspring recognition, they do not of course preclude other sorts of recognition, in particular recognition of parent by chick and of home burrow by chick. Further studies are underway to evaluate the chick's ability to recognize its parent.

Hoogland & Sherman (1976), as part of a larger study on bank swallows, report carrying out a transfer experiment similar to our own. They transferred 12 chicks 4 to 15 days old into like-aged nests. All but one (age not given) were accepted (still present and healthy at least three days later). These results correspond to our own with young chicks.

Burtt (1977) performed brood-exchange studies on barn swallows (*Hirundo rustica*) and tree swallows (*Iridoprocne bicolor*), but these experiments are difficult to compare with ours because of differences in methodology. Burtt exchanged broods (intraspecifically) at 3, 7, 12, and 17 days post-hatch. For both species there was no difference in subsequent weight gain between exchanged and sham-exchanged birds, nor were any rejection behaviours on the part of the host parents reported. Chicks exchanged at 17 days fledged sooner than sham-exchanged chicks in tree swallows but not in barn swallows, though for both species fledging occurred earlier than in unhandled chicks, and on the same day (on the average) as the transfers. It was not observed whether these early-fledged chicks stayed with the host parents or returned to their natural parents. In another experiment, Burtt found that barn swallow parents directed more aggressive actions toward 17-day-old alien chicks than toward their own chicks, when the chicks were tethered near the parents' nest. Burtt also observed that barn swallow chicks are

Table II. Playback Experiment: Number of Responses to Experimental and Control Tapes

Tapes*			Female				Male†			
Age‡	Exp.	Control	E.	C.	Neither	Strength	E.	C.	Neither	Strength
21	7R	5R	4	0	0	3	—	—	—	—
16	10B	7R	0	0	4	0	0	0	4	0
21	R5A	R2	4	0	0	3	—	—	—	—
18	R2	R5A	2	0	2	1	0	0	4	0
21	D3	R5A	4	0	0	3	—	—	—	—
20	D18	D3	2	0	2	1	3	0	1	1
19	D1	D18	4	0	0	2	2	0	2	1
19	D10	D1	4	0	0	2	4	0	0	2
18	D8	D10	2	0	2	1	2	0	2	1

*The nest tested is that designated by 'Exp. Tape'.
†Male unmarked at three nests.
‡Days post-hatch (mean).
3: Parent goes past speaker into burrow (on one or more trials).
2: Parent lands at burrow or hovers in front of burrow mouth for $\geq$ 1 min (on one or more trials).
1: Parent hovers in front of burrow mouth for $\geq$ 15 s at least twice on given trial (minimum response criterion).
0: No discernible response to playback speaker.

fed by their parents at a roost away from the nest after fledging.

One of the more consistent findings of studies of parent–offspring recognition, noted in the introduction, is that the timing of its development is closely tied to the onset of the intermingling of young. Our study suggests a proximate cause for such timing in bank swallows, namely that a critical cue (signature call) does not develop in chicks until about 15 to 17 days post-hatch, and some time is required for the parents to learn this call. In some species, undoubtedly, this explanation will be inapplicable or insufficient. Though the proximate cause of the onset of parent–offspring recognition may vary from species to species, there may be a more general ultimate cause. We should ask, why does parent–offspring recognition not develop until very shortly before it is required? For example, why do bank swallows not develop the signature call at, for example, 10 days of age, allowing the parents more time to learn it, and leaving a greater margin for error? We believe that the general explanation is that parent–offspring recognition carries with it a potential cost which prevents its occurrence in species where intermingling does not occur, or delays its occurrence until intermingling does occur in those species in which it does. A mistake in recognition can be costly: a parent may evict its own chick. Thus it may be advantageous to delay recognition by individual characteristics until it is truly needed, since an alien chick may be recognizable prior to then purely by its older age. Recognition of individual characteristics at an earlier age would be superfluous for the purpose of rejecting alien chicks and might possibly lead to rejecting one's own chick. Though such mistakes could occur at any age, at the later age their low probability would be offset by the high probability of rejecting alien chicks.

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