

Parent–offspring recognition in the barn swallow (*Hirundo rustica*)

MANDY B. MEDVIN & MICHAEL D. BEECHER

Department of Psychology, University of Washington, Seattle, WA 98195, U.S.A.

Abstract. Past research has shown that in the colonial bank swallow and cliff swallow, parents and offspring recognize one another by calls, enabling parents to locate and feed only their own chicks. To test the hypothesis that recognition traits are adaptations to coloniality, we examined parent–offspring recognition in the related but non-colonial species, the barn swallow. To allow cross-species comparisons, we used the same methods that had been used in the previous swallow studies. We carried out four studies. (1) Cross-fostering experiments done immediately before fledging gave no evidence of recognition. (2) In a playback experiment, parents gave no indication that they recognized the calls of their offspring. (3) In another playback experiment, chicks responded more strongly to the calls of their parents than to the calls of unrelated adults. The degree of recognition, however, was somewhat weaker than that seen in the two colonial swallow species. (4) Newly fledged young did not creche after fledging. Rather, family groups generally stayed apart from one another for almost 2 weeks, while parental care was still being given. The comparative data suggest that parent–offspring recognition via individually distinctive cues evolved in response to the intermingling of young associated with colonial living, and is thus weakly expressed in barn swallows compared to cliff swallows and bank swallows.

INTRODUCTION

We define parent–offspring recognition as the differential treatment of offspring by parents, or vice versa, based on individually distinctive cues. Numerous studies of colonial species have suggested that parent–offspring recognition is a key adaptation to colonial living, or more precisely, to the attendant intermingling of young usually found in colonial species (Beecher 1981; Falls 1982; Colgan 1983). Generalizations about the evolution of this trait, however, must be based on the comparative study of closely-related species with differing selection pressures for recognition, e.g. colonial versus non-colonial species. In particular, for recognition traits to be properly considered adaptations to coloniality, it must be shown that these traits are absent, or less developed, in related non-colonial species. The barn swallow (*Hirundo rustica*), a non-colonial species, represents an interesting case for the study of the evolution of parent–offspring recognition for several reasons.

First, the swallow family (Hirundinidae) is an ecologically homogenous group, varying primarily with respect to nesting habits and coloniality (Mayr & Bond 1943). This group is therefore ideal for the study of adaptations to coloniality. We feel that a comparison of the non-colonial barn swallow with colonial members of the family should

provide considerable insight into the evolution of parent–offspring recognition. Comparison of the barn swallow and the highly colonial cliff swallow (*Hirundo pyrrhonota*) is especially interesting as these two species are congeneric, and hybridize on occasion (Martin 1980).

Second, despite the importance of negative cases for a comparative analysis, the study of parent–offspring recognition has focused almost exclusively on species where recognition is highly developed, usually colonial species (this pattern can be inferred from reviews of the area, such as Falls 1982 or Colgan 1983). Swallows have been no exception in this regard: Research on two highly colonial species, the cliff swallow and the bank swallow (*Riparia riparia*) (Hoogland & Sherman 1976; Beecher et al. 1981a, b, 1985; Stoddard & Beecher 1983; Sieber 1985), is much more complete than that on the non-colonial barn swallow, rough-winged swallow (*Stelgidopteryx serripennis*), tree swallow (*Iridoprocne bicolor*) and purple martin (*Progne subis*) (Burt 1977; Brown 1978, 1979; Beecher et al. 1981b). For this reason, the study of the non-colonial barn swallow could provide critical information.

Third, while barn swallows are basically non-colonial, avoiding close nesting with conspecifics under most conditions, they are occasionally found in small, loose colonies (Bent 1942; Snapp 1976;

Barrentine 1978; Ball 1982; Shields 1984; Medvin & Beecher, unpublished data). Because of the barn swallow's proclivity for nesting on human-made structures, it is particularly hard to surmise whether colonial living was common enough in this species' evolutionary past to favour adaptations for parent-offspring recognition. Consequently, while we predict parent-offspring recognition to be less well-developed in barn swallows than in the colonial cliff swallows and bank swallows, it is not obvious where barn swallows should stand in relation to other non-colonial swallows. In addition, it is possible that parent-offspring recognition occurs in barn swallows nesting in groups, but not in those nesting solitarily. There is some evidence for such facultative expression of recognition in herring gulls *Larus argentatus* (von Rautenfeld 1978).

Fourth, an earlier set of studies by Burt (1977) has provided suggestive but conflicting evidence concerning parent-offspring recognition in barn swallows. Burt concluded that barn swallow parents can recognize their chicks, and that recognition develops very shortly before fledging. His conclusions are based on three lines of evidence. (1) He did cross-fostering experiments a day prior to fledging, and found no evidence for recognition. (2) In a variation on the cross-fostering experiment, he tethered both home and alien chicks next to the same nest. He found that while the parents at that nest fed both types of chicks, they were aggressive almost exclusively toward alien chicks. This difference, however, occurred primarily at only one of the three nests tested. Moreover, it may have occurred because alien chicks begged and struggled more than home chicks (which happened at all three nests). Therefore, the adult's behaviour towards its own versus alien chicks may have been a response to the chicks' reactions (caused by the chick's recognition of alien parents, siblings, or nest site), and not to differential, individually distinctive cues provided by the chick. (3) Burt watched post-fledging family groups, and observed that parents found and fed their own chicks, but not unrelated chicks, away from the nest. He concluded that recognition develops on the day of fledging, but is not used until the chicks actually leave the nest. He had little evidence, however, that parents use individually distinctive cues to locate their chicks away from the nest; as is the case earlier at the nest, circumstantial cues such as location may have been sufficient.

Plan of the Study

We carried out four studies. (1) To test Burt's hypothesis that recognition develops in barn swallows just before fledging, we replicated the cross-fostering experiment with chicks at least a day older, during the period when chicks normally fledge. (2) To test Burt's hypothesis that parents recognize offspring by their calls, we carried out playback experiments during the period when chicks normally fledge. Parallel experiments, using the same playback methods, have shown that in the colonial bank swallow and cliff swallow, parents recognize their young by voice (Beecher et al. 1981a; Stoddard & Beecher 1983). In addition, to examine the hypothesis that parental recognition of offspring is a facultative trait, we did our tests on both colonial and non-colonial birds. (3) We also tested for chicks' recognition of parent calls, which has been clearly demonstrated in bank swallows and cliff swallows (Beecher et al. 1985; Sieber 1985). (4) In the final study, we followed fledgling barn swallows for 2 weeks after they left the nest to ascertain whether or not barn swallows creche. Bank swallow and cliff swallow parents often leave their fledgling young in a creche and return to feed them there (Emlen 1952; Beecher et al. 1981b, 1985), a strategy which demands well-developed recognition. If parent-offspring recognition is poorly developed in barn swallows, we might expect parents to avoid the intermingling of young that occurs in a creche.

GENERAL METHODS

Study Sites

Our two major study sites were in Seattle (King County) and Ellensburg (Kittitas County), in the state of Washington. In Seattle, we studied birds nesting either solitarily or in small, loose groups of 2-18 nests, on the outsides of buildings or similar structures; we termed these nests 'non-colonial'. The average nesting density of the groups was 0.1 nests per m². In Ellensburg, we studied birds nesting in denser groups of 40-50 nests, under bridges over irrigation canals; we termed these nests 'colonial'. The average nesting density of these colonies was 2.4 nests per m².

In the Ellensburg colonies, the birds placed their nests on eaves that were underneath the bridges. These nests were difficult to study, due to low bridge clearance, strong canal currents, and low water temperatures. To obtain nest access, we placed support ropes on the underside of each bridge, enabling a person in a small raft to work with individual nests. Nevertheless, the aforementioned difficulties precluded extended behavioural observations.

Capture and Marking Methods

We captured adults with mist nets. Birds were banded with U.S. Fish & Wildlife bands, and marked red, brown, green, blue, or combinations of two of these colours, with broad-tipped marker pens. The marks were placed on either the right and left sides or the upper and lower halves of the breast, below the gular patch. These marks lasted from 3 to 6 weeks (Beecher et al. 1981a, b).

We removed chicks from the nest directly, either by hand or with a small net. We removed them at 18–23 days, during the period when barn swallow chicks normally fledge (Burt 1977; Medvin & Beecher, personal observation); all of our experiments were conducted during the fledging period. Chicks were marked like the adults, except that only left/right combinations were used, and tail and wing underparts were also marked to facilitate observations at the nest.

Recording and Playbacks

All recordings were made using Realistic 33-1056A omni-directional 600-ohm condenser microphones, chosen for their small size and flat response curve over the critical range of 1–8 kHz. Recordings were made with Uher 4000, 4200 and 4400 tape recorders, on Scotch 176 Audio recording tape. Playbacks were made using Archer 5·7-cm miniature 8-ohm speakers.

Recordings were made of both parent and chick calls by placing the condenser microphones next to the nest. Parents were generally recorded on day 0–3 post-hatching because they vocalize frequently at that time. Chicks were recorded at 18–23 days of age; their calls crystallize at 17–18 days (Medvin & Beecher, unpublished data). Calls were analysed with a Unigon 4500 real-time spectrum analyser.

STUDY 1: CROSS-FOSTERING EXPERIMENTS

Problem and Methods

We replicated Burt's (1977) cross-fostering experiment with older chicks to determine if some form of parent–offspring recognition occurs at the age when young normally fledge (Beecher et al. 1981a). In our procedure, we exchanged one to three chicks from a brood with one to three chicks from a brood that was about the same age (maximum age discrepancy 1 day); these were the experimental chicks. The remaining chicks in each brood were handled similarly but returned to their original nest; they were 'sham' transfers, or controls. All exchanges were done at 18 days or older. All chicks remained in the nest for 1 h or more after the exchange took place. One transfer was carried out in the low density site in Seattle in 1982; the remainder took place in colonies in Ellensburg in 1983.

Young were transferred between 19 nests. These 19 transfers involved a total of 36 experimental chicks and 36 control chicks. For each nest, the median number of chicks per treatment was two, with a range of one to three. To ensure that both groups would be at a similar developmental age, controls and experimentals were matched for wing chord length (means = 87·0 mm and 87·3 mm respectively). Our dependent variables were (1) the number of experimental versus control chicks that we found in the nest the following day (12–24 h later), and (2) the number of nests with one or more experimental chicks remaining versus the number with one or more control chicks remaining.

We stress that absence from the nest the day following transfer does not in itself indicate recognition, because fledging sometimes begins on day 18, and undisturbed nests may be partially or completely empty on that day. If more experimental than control chicks are gone on the day following transfer, however, this finding indicates recognition, be it of chicks by parents, of parents by chicks, or of nest, nestmates or surroundings by chicks.

Results

Of the 72 control and experimental chicks, 36 (50%) were found in the nest the day following transfer, distributed among 13 (68%) of the 19

nests. Considered on a chick by chick basis, there was no significant difference between the number of remaining experimental chicks and control chicks (15, or 42%, versus 21, or 58%, respectively, $\chi^2 = 2.0$, one-tailed, $P < 0.10$, NS). Considered on a nest by nest basis, there was no significant difference between the number of nests containing experimental chicks and the number containing controls (10, or 53%, versus 13, or 68%, respectively, $\chi^2 = 0.99$, one-tailed, $P < 0.25$, NS).

Because of the nature of the Ellensburg colonies, extended post-transfer observations were not possible. Limited observations were made at a number of nests on the days following transfer, however, and parents were seen feeding both experimental and control chicks. In one instance, we noted that both experimental and control chicks left the nest by day, returned to the nest together in the evening, and were fed by the adults at the nest.

Since we did not find a significant recognition effect, we examined the data for additional factors that influenced whether or not chicks stayed in the nest. First, we examined the hypothesis that older, or developmentally more advanced chicks, were more likely to leave the nest. The mean chord length of chicks that left the nest was not significantly different from that of chicks that stayed (87.6 mm versus 86.2 mm, $t = 0.8$, $P < 0.25$, NS). Second, we considered the hypothesis that leaving or staying is determined by factors that act similarly on all chicks in a nest, regardless of treatment, e.g. the parents may decide whether the chicks should all stay, or all leave. For nests of each size, we computed the expected probabilities of different numbers of chicks staying or leaving; our null hypothesis was that each chick's 'decision' was independent of those of the other chicks in the nest. To the contrary, we found that more nests were

mostly full (≥ 0.75 full) or mostly empty (≤ 0.25 full) than expected by chance (Table I, $\chi^2 = 9.97$, $df = 2$, $P < 0.01$).

Discussion

Our cross-fostering study provides little evidence for recognition at the nest: 10 of the 13 nests with chicks on the day following transfer contained foster chicks. These results contrast with those of comparable experiments on the colonial bank swallow: 18-day old chicks invariably either left or were chased from foster nests within a few hours of transfer (Beecher et al. 1981a, b). Since our barn swallow transfers were all carried out during the fledging period (day 18 or later), and all chicks were capable of flight (mean chord length was 87.1 mm, chicks can fly by 80 mm), it cannot be argued that our transfers were done too early. Thus if Burt (1977) is right about recognition developing 'shortly before' fledging, it is apparently not expressed while chicks are in the nest.

The strongest effect uncovered in this experiment was that chicks in a nest tended to act similarly, either staying or leaving in a group. Since we were not able to observe behaviour at the nest directly, we can only speculate on the nature of common influences. The simplest possibility is that chicks are directly influenced by the behaviour of other chicks in the nest. Alternatively, the parents at that nest may be the common influence; they may lead the chicks away as a group, or they may encourage the chicks to remain in the nest.

For those experimental chicks that remained in the foster nest, acceptance by the foster parent appeared immediate and complete. For example, in one 17-day cross-fostering done in a preliminary study, parents actually attempted to retrieve a foster chick which flew out of the nest at the time of the transfer. After chicks from this nest fledged, home and foster chicks were seen together with the adults, 7 days later, at a spot 2 miles from the nest site.

STUDY 2: PLAYBACK EXPERIMENT: DO PARENTS RECOGNIZE CHICK CALLS?

Problem

Burt (1977) suggested that barn swallow parents learn their chicks' calls while they are in the nest,

Table I. Number of nests in each category*

	Proportion of chicks gone from the nest		
	≤ 0.25	$0.25 < P < 0.75$	≥ 0.75
Observed	7	4	8
Expected	4.12	10.83	4.12

* Expected probabilities computed by binomial expansion for nest sizes of 5 ($N = 7$), 4 ($N = 5$), 3 ($N = 4$), and 2 ($N = 3$) where probability of chick leaving = 0.5.

but do not express this recognition until after the chicks leave the nest. This hypothesis would explain the failure of our cross-fostering experiment to give evidence of recognition. From this perspective, a more appropriate test would be a playback test, in which parents are induced to search for fledging-aged young that have been removed from the nest. In the present study, we carried out a playback experiment modelled on earlier studies which demonstrated parental recognition of chick calls in bank swallows (Beecher et al. 1981a, b) and cliff swallows (Stoddard & Beecher 1983). In addition, we examined the hypothesis that parent-offspring recognition might be expressed facultatively in barn swallows by testing both non-colonial and colonial individuals.

Methods

Our experiments were conducted at 12 non-colonial nests in Seattle in 1982, and seven colonial nests in Ellensburg in 1983. The experiments were carried out when the young in the nest were 19–22 days of age. On the day before or day of the test, we recorded chick calls at the nest to be tested. We then made tape loops which contained calls of two or three chicks at the nest. In 1982, these tape loops consisted of a natural string of six to eight chick calls lasting approximately 6 s, followed by 2 s of silence. In 1983, they contained three calls lasting 5 s, followed by 5 s of silence. In the playback test, speakers were placed on either side of the experimental nest, approximately 3–4 m apart; when possible, these speakers were placed by nearby empty nests (in some cases, we put up nests for this purpose). For the duration of the test, all young found in the experimental nest were removed, to stimulate searching by the parents. The number of young varied from two to five. A test consisted of four to six trials, with each tape played from each side an equal number of times. During each trial, calls were broadcast simultaneously from the two speakers: from one, the experimental tape previously recorded at the experimental nest, and from the other, a control tape recorded at another nest. The observer was blind as to which was which. Loudness at the two speakers was equalized by ear and matched to the loudness of normal calls. A trial began when a parent appeared and ended 2.5 min later. Approach responses of the parents were categorized as in the previous playback studies of swallows (Beecher et al. 1981a,b; Stoddard &

Beecher 1983): (1) hovers by the speaker, (2) looks at the speaker, (3) passes within 1 m of the speaker. We weighted these responses equally, and summed them to arrive at the total number of responses per nest.

Results

The results of the playback experiments are shown in Table II. Of the 12 non-colonial nests tested, parents responded to the speakers at only eight. For these eight, there was no significant difference in response to the experimental (home chicks) and control (alien chicks) tapes (Wilcoxon test, $T=25$, one-tailed, $P < 0.19$, NS). At four of the nests, adults totally ignored the playback speakers and spent all their time checking the home nest. Of the seven colonial nests, marked parents responded at only five. Again, there was no significant difference in response between experimental and control nests (parents actually responded more to alien chick calls).

In sum, of the 19 nests tested, parents responded

Table II. Number of responses of parent to playback speaker

Expt. nest	Control nest	Total responses	
		Expt.	Control
Seattle: solitary nests			
A1	B1	9	8
B2	A2	10	24
A3	B3	4	17
A4	B4	40	25
B5	A5	28	8
A6	B6	15	6
A7	B7	14	12
A5	B5	18	15
Total		138	115
Percentage		55	45
Ellensburg: colonial nests			
C1	C2	1	5
C3	C1	7	10
C4	C3	15	13
C5	C4	29	37
C6	C5	19	17
Total		71	82
Percentage		46	54
Grand total		209	197
Overall percentage		52	48

to the playback calls in 13 cases. When the data from both nesting habitats were combined, there was no significant difference in the response to the experimental versus control tapes (Wilcoxon test, $T=49.5$, one-tailed, $P < 0.41$, ns).

Discussion

Barn swallow parents differ from cliff swallow and bank swallow parents in two ways. First, they give no evidence that they recognize their chicks' calls on the day of fledging. Cliff swallow and bank swallow parents in parallel experiments show strong recognition of their chicks' calls (Beecher et al. 1981a; Stoddard & Beecher 1983). Second, at six of the 19 nests studied, parents failed to respond at all to the playback calls, although they did search the empty home nest. In contrast, in our parallel experiments with bank swallows and cliff swallows, parents at every tested nest responded to the calls, and in every case preferred the calls of their offspring (Beecher et al. 1981a; Stoddard & Beecher 1983).

It is possible that barn swallow parents use visual characteristics of the chicks, and not calls, to distinguish them. We think this unlikely, however, for we can detect no individual variation in visual characteristics among barn swallow chicks, and we found no evidence for visual recognition from our cross-fostering experiments. In contrast, the congeneric cliff swallow shows conspicuous variation in facial coloration of chicks (Stoddard & Beecher 1983).

STUDY 3: PLAYBACK EXPERIMENT: DO CHICKS RECOGNIZE PARENTS' CALLS?

Problem

The conclusion of study 2 is contrary to Burt's (1977) suggestion that barn swallow parents recognize their chicks, probably by calls. As discussed in the Introduction, Burt based his conclusions primarily on his tethering experiment, which did not clearly distinguish between parental recognition of chicks and chick recognition of parents. It is possible that the trend in his data was due to chicks' recognition of parents, rather than vice versa. Chick recognition of parents by calls has been shown in several species of gulls (Beer 1969, 1970a, b, c; Evans 1970a, b), penguins (Penney 1962),

piñon jays, *Gymnorhinus cyanocephalus* (McArthur 1982) and colonial swallows (Beecher et al. 1985; Sieber 1985).

Methods

All experiments were done in 1982 at non-colonial nests in the Seattle area. The experiments were carried out when the chicks were 18 days of age. A tape loop was made consisting of two male parent calls spaced 1 s apart, 2 s of silence, two female parent calls spaced 1 s apart, and 2 s of silence; calls and silence totalled up to an 8 s tape loop. This tape design simulated the vocal exchanges of parents when changing positions at the nest. A speaker was placed 0.3 m to the right of the experimental nest, and chicks' responses were recorded with a condenser microphone placed on the left, immediately adjacent to the nest. The experiment consisted of nine 1-min trials per nest; three each of home parents' calls, alien parents' calls, and blank tape. The order of the trials was randomized with the restriction that all three types of trials occur before one type was repeated. The loudness of the calls was equalized by ear between trials, and matched to the loudness of the parents' natural calls. Each trial began after a feeding and when chicks had been quiet for 5 s. If a parent returned within 45 s of the beginning of a trial, the trial was discarded. If a parent returned before the end of 1 min, but after 45 s, the trial was counted and responses prorated. Intervals between trials varied according to parental feeding rates, with a mean of 8.4 min. Afterwards, we counted these calls at either half or quarter speed on the Unigon analyser.

Results

The results are summarized in Table III. The chicks showed a significant preference for the calls of their parents (Wilcoxon test, $N=13$, $W=61$, one-tailed test, $P < 0.02$). Ten of the 13 broods gave more responses to parent calls than to control calls. On a per nest basis, the mean percentage antiphonal responses to parent calls per nest was 55%.

Discussion

This study demonstrated that barn swallow chicks can recognize the calls of their parents. The study contrasts with study 2, which found no

Table III. Number of antiphonal responses by chicks during playback experiments*

Expt. nest	Control nest	Expt. responses	Control responses	Blank responses	P/(P+C)†
A8	B5	0	221	33	0.00
A6	B1	287	146	190	0.66
A3	B7	428	286	0	0.60
B1	A7	797	10	18	0.99
A4	A1	1388	901	21	0.61
A5	B4	912	881	0	0.51
A7	B1	120	20	2	0.85
B4	A5	1388	1118	157	0.55
A1	A4	26	82	2	0.24
A9	B8	711	232	1	0.75
A2	B10	17	110	1	0.13
A10	B10	750	747	5	0.50
B5	A8	771	285	3	0.73
Total responses		7595	5039	433	$\bar{X}=0.55$

* Responses are summed across nine 1-min trials at each experimental nest.

† P/(P+C)=the proportion of responses given to experimental (home) parents' calls divided by the total number of responses given to both experimental parents' and control (alien) parents' calls.

evidence that parents could recognize their offspring by voice. We must be cautious in making this comparison, however, since the two experiments used different methods, and methodological differences can influence the sensitivity of a test (Evans 1970a; Shugart 1977). It is possible that the antiphonal response procedure we used in study 3 is a more sensitive test of recognition than the speaker approach procedure we used in study 2. A convincing case, however, of a similar asymmetry in parent-offspring recognition has been demonstrated in laughing gulls (Beer 1979).

It should be noted that the average degree of parental recognition in non-colonial barn swallow chicks (55%) is not as great as in colonial cliff or bank swallows (78% and 75% respectively) (Beecher et al. 1985; Sieber 1985). This comparison indicates that while recognition of parents occurs in barn swallow chicks, it is somewhat weaker than in the two colonial species.

STUDY 4: PARENT-OFFSPRING INTERACTIONS AFTER FLEDGING

Problem

Parent-offspring recognition is most important

when young leave the nest and can mix with other similar-aged fledglings. We have found no evidence that barn swallow parents recognize their young by calls or, so far as we can tell, any other cue. If parents do not recognize their young by individually distinctive cues, they should attempt to keep them apart from other fledglings (Colgan 1983). So, unlike bank swallows and cliff swallows which creche, we might expect barn swallows to do just the opposite, and keep their young in separate family groups. This study examines grouping patterns of barn swallow young for the first 2 weeks after fledging.

Methods

Our observations were conducted primarily in Seattle, at the Woodland Park Zoological Gardens and surrounding neighbourhoods in 1979. In total, we followed 11 family groups. The young were colour-marked prior to fledging, as in the other experiments. Nests were checked daily to see if the young had fledged. Fledging was considered to have occurred when at least half of the young from a family group had flown out of the nest, and this day was designated day 1. We searched for fledglings daily, from 0700 hours to 1900 hours, either

on the zoo grounds or in the neighbourhood within 0.80 km of the zoo. Out of the total number of observation periods that fledglings were observed, 71% occurred in the neighbourhoods, 25% in the nest area, 3% in the nest, and 1% on the zoo grounds. In the neighbourhoods, fledglings were most often found on power lines. A standard effort was made to locate each of the family groups through the first 2 weeks of the post-fledging period. Locating family groups was facilitated by the fact that families often returned to the same location for several days. Once located, we watched the group for approximately 45 min, or less if the birds flew off before the observation period was over.

When we found fledglings from a focal family, we made 5-min scans of the following items: (1) the distance each family member was from the other nearest family member; (2) whether or not alien fledglings were present, and if so, the age and spatial relationship of the alien fledgling(s) to the focal family group; (3) the behaviour of both focal and alien chicks; and (4) the type and duration of parental care, e.g. feedings. All distance measurements were accurate to within 0.3 m. We then divided our spatial data into four mutually exclusive categories.

(1) Fledgling alone: a single fledgling was found greater than 10 m from another fledgling of a different family group.

(2) Family alone: two or more fledglings from a focal family group were closer to each other than to an alien fledgling(s) of a different family group; if an alien fledgling(s) was present, it was greater than

10 m away from the focal group. In fact, for the majority of the scans in this category there were no other families within view.

(3) Family clumped: an alien fledgling was seen within 10 m of a family group of two or more fledglings, but the fledglings from the focal family group were closer to each other than to the alien fledgling.

(4) Family interspersed: alien fledglings were present, and one or more fledglings from the focal family group were closer to an alien fledgling than to a fledgling of their own family group.

We coded these categories without regard to the presence or absence of a parent. Scans of fledglings who returned to the nest at night were not included in our analysis.

Additional data on post-fledging behaviour were collected at the Ellensburg colonies in 1983. The young were marked in a similar fashion, and we searched a 5 km area around each of the two colonies. Since the search for fledglings was not as intensive as for the Seattle data, these results are presented separately.

Results

On fledging, parents typically took their fledglings off the zoo grounds, to a location in the surrounding neighbourhood. This location was an average of 0.48 km away from the nest. The family usually remained in that same area for the first few days. Typically, the 11 families frequented different areas.

The major finding was that the young were rarely

Table IV. Spatial patterns of fledgling groups

Days	Nests		Scans		Categories*			
	No. found	No. used	Total no.	Average per nest	Fledgling alone	Family alone	Family clumped	Family interspersed
1-2	17	15	166	11.1	8(0.05)	157(0.94)	—	1(0.01)
3-4	15	15	176	11.7	11(0.06)	124(0.71)	25(0.14)	16(0.09)
5-6	14	14	123	8.8	6(0.05)	105(0.86)	9(0.07)	3(0.02)
7-8	13	11	70	6.4	27(0.39)	36(0.51)	2(0.03)	5(0.07)
9-10	8	7	46	6.6	8(0.17)	35(0.76)	3(0.07)	—
11-12	9	9	44	4.9	14(0.32)	27(0.61)	—	3(0.07)
13-14	2	2	6	3.0	6(1.00)	—	—	—
15	1	1	2	2.0	—	—	—	2(1.00)
Total			633	6.8	80(0.13)	484(0.76)	39(0.06)	30(0.05)

* a(b); a = the number of scans, (b) = the proportion of scans observed on that day.

near (within 10 m of) other young: only 11% of the overall time, and virtually never in the first 2 days post-fledging (Table IV). Over time, there was a change in the frequency with which each of the spatial patterns was seen. First, some mixing of fledglings from different nests began on days 3–4. Second, by 1 week of age there was an increase in the proportion of single fledglings seen. Third, the duration of an observation period also decreased with increasing fledgling age, as fledglings became more mobile, and flew off before an observation period had ended. Fourth, by approximately 2 weeks post-fledging, no family groups were found.

When clumped and interspersed fledgling groups occurred, in all but one instance we saw no aggression by parents towards alien chicks. We also noted that for virtually all fledglings, arrival to and departure from a particular location occurred only when accompanied by a parent. For both first and second clutches from our sample, day 10 was the last day that parents were seen feeding fledglings. Fledglings were, however, difficult to locate after day 10, and may simply have moved out of our census area. Parents and fledglings from the first clutch were occasionally seen together at the nest site, after the second clutch had been initiated.

In Ellensburg, we rarely located fledglings within 5 km of a colony, probably because it was impossible to thoroughly canvas the area near the colony. When fledglings were located, however, they were found in separate family groups within 0.4 km of the colony, at a distance from the other birds.

Discussion

We have shown that unlike bank or cliff swallows, barn swallow fledglings do not creche, but remain for the most part in separate family groups. These data complement our finding that barn swallow parents do not recognize their offspring by individually distinctive cues. Brown (1978) found that purple martins similarly maintain separate post-fledging family groups. He also mentions 'frequent' adoptions of alien young. He did not, however, quantify his data, so that we can make no direct comparison between the two studies. The maintenance of separate post-fledgling family groups has been seen in other species (e.g. ring-billed gulls, *Larus delawarensis*, Evans 1970a; song sparrows, *Melospiza melodia*, Smith 1980). Few studies, however, have been conducted which examine, within the same species, both parent-off-

spring recognition and the spatial patterns of post-fledgling young (but see Balda & Balda 1978; McArthur 1982).

Circumstantial cues may aid barn swallow parents in locating and feeding only their own young. First, the repeated use of the same location by barn swallow post-fledging groups may establish the location as a rendezvous point for parents and chicks that have been separated. Young of other species are known to use the home territory in this way (Noseworthy et al. 1973; Noseworthy & Lien 1976). Second, as barn swallow fledglings recognize their parents, their behaviour may be different when with their own parents versus alien parents. For example, when we found both focal and alien fledglings together, typically fledglings from only one family group vocalized as parents flew in to feed, while fledglings from the other family group were quiet.

Burt (1977) observed barn swallow parents and young post-fledging, and noted several instances of aggression by parents toward alien young. He regarded these instances as evidence that parents could tell their own from alien young. During our more extensive observations, in those cases when alien fledglings were near a family group, we saw little evidence of selective aggression towards alien young.

GENERAL DISCUSSION

Parent-offspring Recognition in Barn Swallows

We summarize our comparisons of parent-offspring recognition in non-colonial barn swallows with recognition in colonial bank and cliff swallows as follows. First, both cross-fostering and playback experiments gave no evidence that barn swallow parents, whether nesting in colonial or non-colonial situations, can recognize their young by individually distinctive cues. Comparable experiments with colonial bank swallows and cliff swallows have provided strong evidence of vocal recognition by parents. Second, playback experiments showed that barn swallow chicks, like colonial bank and cliff swallow chicks, can recognize their parents by voice. For barn swallow chicks, however, this recognition is somewhat weaker than that shown by the other two species. Third, unlike parents of the two colonial swallow species, barn swallow parents did not leave newly

fledged young in creches. Rather, family groups generally stayed apart from other similar family groups, especially in the first few days after leaving the nest.

Our first conclusion is that in this group of swallows, the adaptations permitting parent-offspring recognition in cliff and bank swallows may have evolved as a result of colonial living and the attendant extensive intermingling of young. Our findings implicate coloniality as an ultimate, but not a proximate, correlate of well-developed parent-offspring recognition in swallows. That is, whether the bird being tested for recognition is nesting colonially or solitarily in a particular area is far less important than its species' history of coloniality (cliff swallows and bank swallows) or non-coloniality (barn swallows and rough-winged swallows). This point is made particularly well by a comparison of the recognition tests of colonial barn swallow parents in this study and the comparable tests of cliff swallow parents by Stoddard & Beecher (1983). The colonies of both species were quite similar, consisting of about 50 active nests on human-made structures in Eastern Washington, yet evidence for recognition was strongly demonstrated in the cliff swallows, but not in the barn swallows.

Adaptations for Recognition

In birds, recognition often occurs via calls (see Falls 1982; Colgan 1983). For calls to serve as individually distinctive cues, there must be sufficient variation among individuals in their calls (Beecher 1982; Falls 1982; Jouventin 1982). Our analyses of the calls of four swallow species indicate that chick calls are more individually distinctive in colonial cliff swallows and bank swallows than in non-colonial barn swallows and rough-winged swallows (Beecher 1982; M.B. Medvin, P.K. Stoddard & M.D. Beecher, unpublished data). This difference corresponds to our pattern of positive results for colonial species and negative results for non-colonial species in tests of parental recognition of offspring (Beecher et al. 1981a; this paper).

While barn swallow parents do not appear to recognize the calls of their young, the young do recognize the parents' calls. This asymmetry is possibly due to a difference in the individual distinctiveness of parent calls versus chick calls, i.e. parent calls may be more individually distinctive than chick calls. Alternatively, the asymmetry may

be related to a difference between parents and chicks in their perceptual ability to recognize calls, i.e. chick calls may contain sufficient cues, but parents lack the perceptual ability to process this information. It seems unlikely, however, that parents would be poorer than chicks in regard to this perceptual ability.

Some of the species differences we have observed may be due not to signal or perceptual adaptations, but to differences in post-fledging parental strategies. Specifically, in the playback experiments, barn swallow parents appeared to be less inclined to search for their chicks in other nests (as indicated by the lack of response to the playback speakers) than are bank swallows and cliff swallows. In comparison with chicks of the colonial species, however, barn swallow chicks rarely return to the nest during the day post-fledging (Beecher et al. 1981b; Stoddard & Beecher 1983; M.B. Medvin, M.D. Beecher & S.J. Andelman, unpublished data). The difference we find in the strength of response may occur simply because barn swallow parents have different chick retrieval strategies than colonial bank swallow or cliff swallow parents. For example, if a barn swallow parent loses track of a chick, it may wait at the location where the family group is typically found, or return to the home nest, rather than search for its chick elsewhere, e.g. in an alien nest. It is thus possible that barn swallow parents are better at recognition than our playback experiments indicate. It seems unlikely that this difference could entirely account for the results, however, for the fact remains that in most of the experiments (13 out of 19), barn swallow parents did respond to the playback speakers, but did not respond differentially to offspring versus alien calls.

We also know that barn swallow young, in comparison to the other two species, are rarely found in alien nests. Since one cost for a parent of rejecting an alien chick is that the parent may mistakenly reject its own chick (Beecher 1981), selection might favour a conservative strategy for the parent of accepting all young in the nest, or all young which 'act as if they belonged to that nest'. Therefore, it is possible that barn swallow parents are better at recognition than the cross-fostering experiments indicate. A more sensitive experimental method, e.g. a dual nest choice (Shugart 1977), might enable us to test this hypothesis.

Alternatively, circumstantial cues may be sufficient to enable parents to locate their chicks, e.g.

the comportment of the chick or the location of the family group. In barn swallows, the probability of locating your chick is high, particularly as (1) barn swallow young do not creche, but maintain family groups in separate locations; (2) the family group location remains stable over time; and (3) when fledglings leave an area, they are virtually always accompanied by a parent (M.B. Medvin, M.D. Beecher & S.J. Andelman, unpublished data).

The Asymmetry in Recognition

Our experiments reveal an asymmetry in barn swallow parent-offspring recognition: barn swallow parents do not appear to recognize their young by individually distinctive cues, but young do recognize their parents. The question arises as to why selection would favour offspring recognizing parents, but not vice versa. In considering this question, we must examine the costs and benefits of recognition, for both the parents and their young.

(1) Parents: the benefit to a parent of recognizing its own chick is that the parent is thus able to restrict its care to that chick, thus promoting the parent's fitness. However, there are also costs for the parent in attempting to discriminate between its own and alien chicks. In particular, the parent may accidentally reject its own young (Beecher 1981; Beecher et al. 1981b). The potentially high cost of recognition is supported by the fact that in many species parental recognition does not occur until just prior to the onset of mobility (for a review, see Evans 1970a, b; Shugart 1977; Colgan 1983). In situations where the cost of recognition may exceed the benefit, e.g. the probability of young intermingling is low, or there are clearcut circumstantial cues available, there would be no selection for parents to recognize their chicks by individually distinctive cues.

In addition, if parents identify themselves with individually distinctive cues, such that the young can recognize the parents, then chick behaviour becomes a potential identification cue for the parent as well. For instance, one such indirect cue would be chicks who act differently based on whether or not they recognize the adult as their parent. A clear example is provided by Beer's studies of the laughing gull (*Larus atrilla*, Beer 1979). In a simultaneous playback experiment, parents given a choice of chick calls responded equally to those of both their own and the alien chick. Beer then placed one alien and one home

chick in separate boxes equidistant from the parents, so that parents could hear the chicks but not see them. When the parent called, looking for its chick, only its own chick responded; the alien chick remained silent. The parent then went to the box where the chick was calling. It appears that in laughing gulls, 'the chick that responds to its parent's call' is a sufficient cue for parental acceptance, and may substitute for true recognition.

(2) Young: the traditional argument against offspring recognition of parents is that young should try to solicit parental care, e.g. feedings, from any adult (Beecher 1981; Falls 1982). Recognition of the parent would not only be unnecessary, but might hinder such solicitation, perhaps by altering the chick's behaviour toward parental versus non-parental adults. When parents recognize their offspring by individually distinctive cues, however, offspring may not benefit by begging from non-parents, as the probability of obtaining a feeding is low (Beecher et al. 1985). In certain instances such begging may be dangerous (Evans 1980; Beecher 1982). Therefore, in this circumstance it is to a chick's advantage to recognize its parent.

In the case where parents do not recognize offspring, however, it is not clear why offspring need to recognize parents. A chick could take advantage of the situation, and solicit care from any adult that it sees. As barn swallows do not creche, however, soliciting non-parental care may not be an optimal strategy, as it would usually require leaving the guaranteed care of the family group. In addition, it might also subject the chick to attacks from adults without young (e.g. Harper 1985). It is notable that in virtually all the species which have been studied, young have been found to recognize their parents (for a review see Colgan 1983; but see Brooke 1978). In many of these same species parental recognition of offspring has not been examined (or negative results have not been reported), so that we do not know whether or not asymmetries in recognition are common.

There may also be alternative selection pressures acting on offspring to recognize parents. For example, siblings may compete for feedings or attention from the parents. The sibling that is quickest to respond to the parent upon its arrival is most likely to get the first feeding. Young that recognize the parent's calls would probably be quicker to respond to the calls. While chicks could vocalize to every parent that came by, indiscrimi-

nate responding would take energy, and could increase the probability of predation (McArthur 1982).

ACKNOWLEDGMENTS

We would like to thank Sandy Andelman, Virginia Bound, Connie Nosbich, Jim Schwartz, and Sally Zeylmaker for their help in the field. John Cleary provided technical assistance in setting up the rope system at the Ellensburg bridges. Les Beletsky, Robin Foster, and Gary Shugart made valuable comments on the manuscript in its earlier stages. This research was funded by an NSF grant to Michael D. Beecher through the University of Washington, and a Frank Chapman Fund award to Mandy B. Medvin.

REFERENCES

- Balda, R. P. & Balda, J. H. 1978. The care of young piñon jays and their integration into the flock. *J. Ornithol.*, **119**, 146–171.
- Ball, G. 1982. Barn swallow fledgling successfully elicits feeding at a non-parental nest. *Wilson Bull.*, **94**, 362–363.
- Barrentine, C. D. 1978. The biology of bridge nesting barn and cliff swallows in Central Washington. M. S. thesis, University of Washington.
- Beecher, M. D. 1981. Development of parent-offspring recognition in birds. In: *Development of Perception, Vol. 1* (Ed. by R. K. Aslin, J. R. Alberts & M. R. Petersen), pp. 45–66. New York: Academic Press.
- Beecher, M. D. 1982. Signature systems and kin recognition. *Am. Zool.*, **22**, 477–490.
- Beecher, M. D., Beecher, I. M. & Hahn, S. 1981a. Parent-offspring recognition in bank swallows (*Riparia riparia*): II. development and acoustic basis. *Anim. Behav.*, **29**, 95–101.
- Beecher, M. D., Beecher, I. M. & Lumpkin, S. 1981b. Parent-offspring recognition in bank swallows (*Riparia riparia*): natural history. *Anim. Behav.*, **29**, 86–94.
- Beecher, M. D., Stoddard, P. K. & Loesche, P. 1985. Recognition of parents' voices by young cliff swallows. *Auk*, **102**, 600–605.
- Beer, C. G. 1969. Laughing gull chicks: recognition of their parents' voices. *Science, N.Y.*, **166**, 1030–1032.
- Beer, C. G. 1970a. Individual recognition of voice in the social behaviour of birds. In: *Advances in the Study of Behavior, Vol. 3* (Ed. by D. S. Lehrman, R. A. Hinde & E. Shaw), pp. 27–34. New York: Academic Press.
- Beer, C. G. 1970b. On the responses of laughing gull chicks (*Larus atricilla*) to the calls of adults. I. Recognition of the voices of the parents. *Anim. Behav.*, **18**, 652–660.
- Beer, C. G. 1970c. On the responses of laughing gull chicks to the calls of adults. II. Age changes and responses to different types of calls. *Anim. Behav.*, **18**, 661–677.
- Beer, C. G. 1979. Vocal communication between laughing gull parents and chicks. *Behaviour*, **70**, 118–146.
- Bent, A. C. 1942. Life histories of North American flycatchers, larks, swallows, and their allies. *U. S. Nat. Mus. Bull.*, No. 179.
- Brooke, M. de L. 1978. Sexual differences in the voice and individual vocal recognition in the manx shearwater (*Puffinus puffinus*). *Anim. Behav.*, **26**, 622–629.
- Brown, C. R. 1978. Post-fledging behaviour of purple martins. *Wilson Bull.*, **90**, 376–385.
- Brown, C. R. 1979. Chick recognition in purple martins (*Progne subis*). *The Southwestern Natur.*, **24**, 683–714.
- Burt, E. H., Jr. 1977. Some factors in the timing of parent-chick recognition in swallows. *Anim. Behav.*, **25**, 231–239.
- Colgan, P. 1983. *Comparative Social Recognition*. New York: Wiley.
- Emlen, J. T., Jr. 1952. Social behaviour in nesting cliff swallows. *Condor*, **54**, 177–191.
- Evans, R. M. 1970a. Imprinting and the control of mobility in ring-billed gulls (*Larus delawarensis*). *Anim. Behav. Monogr.*, **3**, 193–248.
- Evans, R. M. 1970b. Parental recognition and the 'mew call' in black-billed gulls (*Larus bulleri*). *Auk*, **87**, 503–513.
- Evans, R. M. 1980. Development of behaviour in seabirds: an ecological perspective. In: *Behaviour of Marine Animals, Vol. 4, Marine Birds* (Ed. by J. Burger), pp. 271–322. New York: Plenum.
- Falls, J. B. 1982. Individual recognition by sounds in birds. In: *Acoustic Communication in Birds, Vol. 2* (Ed. by D. H. Kroodsma & E. H. Miller), pp. 237–278. New York: Academic Press.
- Harper, D. G. C. 1985. Interactions between adult robins and chicks belonging to other pairs. *Anim. Behav.*, **33**, 876–884.
- Hoogland, J. L. & Sherman, P. W. 1976. Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. *Ecol. Monogr.*, **46**, 33–58.
- Jouventin, P. 1982. *Visual and Vocal Signals in Penguins, Their Evolution and Adaptive Characters*. Berlin: Verlag.
- McArthur, P. D. 1982. Mechanisms and development of parent-young recognition in the piñon jay (*Gymnorhinus cyanocephalus*). *Anim. Behav.*, **30**, 62–74.
- Martin, R. F. 1980. Analyses of hybridization between the Hirundinid genera *Hirundo* and *Petrochelidon* in Texas. *Auk*, **97**, 148–159.
- Mayr, E. & Bond, J. 1943. Notes on the generic classification of the swallows, Hirundinidae. *Ibis*, **85**, 335–341.
- Noseworthy, C. M. & Lien, J. 1976. Ontogeny of nesting habitat recognition and preference in neonatal herring gull chicks, *Larus argentatus pontoppidan*. *Anim. Behav.*, **24**, 637–651.
- Noseworthy, C., Lien, J. & Stoker, S. 1973. Habitat preferences in neonatal herring gulls. *Auk*, **90**, 193–194.
- Penny, R. L. 1962. Breeding behaviour is influenced by vocal recognition of the voices of the adelic. *Nat. Hist.*, **71**, 16–25.
- von Rautenfeld, P. B. 1978. Bemerkungen zur Austauschbarkeit von Kücken der Silbermöwe (*Larus argentatus*)

- tus) nach der ersten Lebenswoche. *Z. Tierpsychol.*, **47**, 180–181.
- Shields, W. M. 1984. Factors affecting nest and site fidelity in Adirondack barn swallows (*Hirundo rustica*). *Auk*, **101**, 780–789.
- Shugart, G. W. 1977. The development of chick recognition by adult caspian terns. *Proc. Colonial Waterbird Group*, **1**, 110–117.
- Sieber, O. J. 1985. Individual recognition of parental calls by bank swallow chicks (*Riparia riparia*). *Anim. Behav.*, **33**, 107–116.
- Smith, J. N. & Merkt, J. R. 1980. Development and stability of single-parent family units in the song sparrow. *Can. J. Zool.*, **58**, 1869–1875.
- Snapp, B. D. 1976. Colonial breeding in the barn swallow (*Hirundo rustica*) and its adaptive significance. *Condor*, **78**, 471–480.
- Stoddard, P. K. & Beecher, M. D. 1983. Parental recognition of offspring in the cliff swallow. *Auk*, **100**, 795–799.

(Received 15 May 1985; revised 17 October 1985; MS. number: A4545)