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PARENT–OFFSPRING RECOGNITION IN BANK SWALLOWS (*RIPARIA RIPARIA*): I. NATURAL HISTORY

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Abstract. A field study of the highly colonial bank swallow (*Riparia riparia*) revealed several contexts in which parent–offspring recognition occurs. Parents find their young away from the bank when the young make spontaneous flights from the burrow, and also when the young, after such flights, have returned to incorrect burrows. The resident adult in the latter situation also shows recognition, by 'evicting' alien chicks. Resident adults also make mistakes, however, and feed alien chicks. An analysis of these mistakes revealed that (a) the majority of mistakes are made by the male parent, and (b) mistakes generally do not exceed 0.5% of the parent's total feeding bouts. Parents also feed young in a crèche away from the bank, both before and after the burrow is vacated.

In most species that have been carefully studied, parental care has been found to be selective, not communal. For example, feeding in the penguin (*Pygoscelis adeliae*) crèche was formerly considered to be non-selective (Kendeigh 1952), but study of marked individuals revealed that parents take care to feed only their own young (Thompson & Emlen 1968). The finding, confirmed in countless studies, that individuals restrict parental care to their own offspring, is consistent with the view that natural selection generally operates at the level of the individual, or that, as Williams puts it, individuals are 'designed to reproduce themselves, not their species' (Williams 1966, page 189).

There are a number of means by which parents can restrict parental care to their own offspring, including homing to the correct nest, shepherding of their young, and parent recognition of offspring. In species where young intermingle at some stage during which they still receive parental care, parent–offspring recognition is essential. In this paper we examine parent–offspring recognition in the bank swallow, *Riparia riparia*. We use the symmetrical term 'parent–offspring recognition' to refer to cases where the parent recognizes the young and/or vice-versa, with 'recognition' implying that the parent discriminates the young (or the young discriminates the parent) on some basis other than circumstantial evidence.

Bank swallows live in large colonies, which typically contain hundreds of nests, and exhibit clustering and high reproductive synchrony (Petersen 1955; Emlen & Demong 1975; Hoogland & Sherman 1976; Beecher & Beecher 1979). Though parent–offspring recognition might be expected in so colonial a species, coloniality does not always imply intermingling of young and consequent selection pressure for recognition. For example, while kittiwakes (*Rissa tridactyla*) live in dense colonies, the young cannot stray from their cliff-ledge nests. As one would predict, parent–offspring recognition is absent in kittiwakes, whereas it is present in other ground-nesting gulls (*Larus*) (Cullen 1957; but see also von Rautenfeld 1978). Parent–offspring recognition may also be absent in the colonial tricoloured redwing *Agelaius tricolor* (Emlen 1941). Thus any study of parent–offspring recognition should begin with a careful investigation of the ecology and natural history of the species in question to determine the contexts, if any, in which recognition occurs. In study 1 we describe the contexts for parent–offspring recognition in bank swallows, and in study 2 we evaluate the success of parents in restricting feeding to their own offspring.

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Study 1: Natural Contexts of Parent–Offspring Recognition

Methods

Our studies were carried out in the years 1970 to 1979 at colonies along the Connecticut and Deerfield Rivers in Massachusetts, and in sand quarries in Massachusetts, Michigan, and Washington. The colonies we studied ranged in size from 12 to over 1000 active nests; the typical colony had 100 or more active nests.

Capturing and marking. Adult birds were captured in two ways. Plastic bags (1.4-litre), punched with ventilation holes, were fastened to rolls of cardboard and inserted into the burrow mouth (Morris 1942). The birds were captured

PLATE I

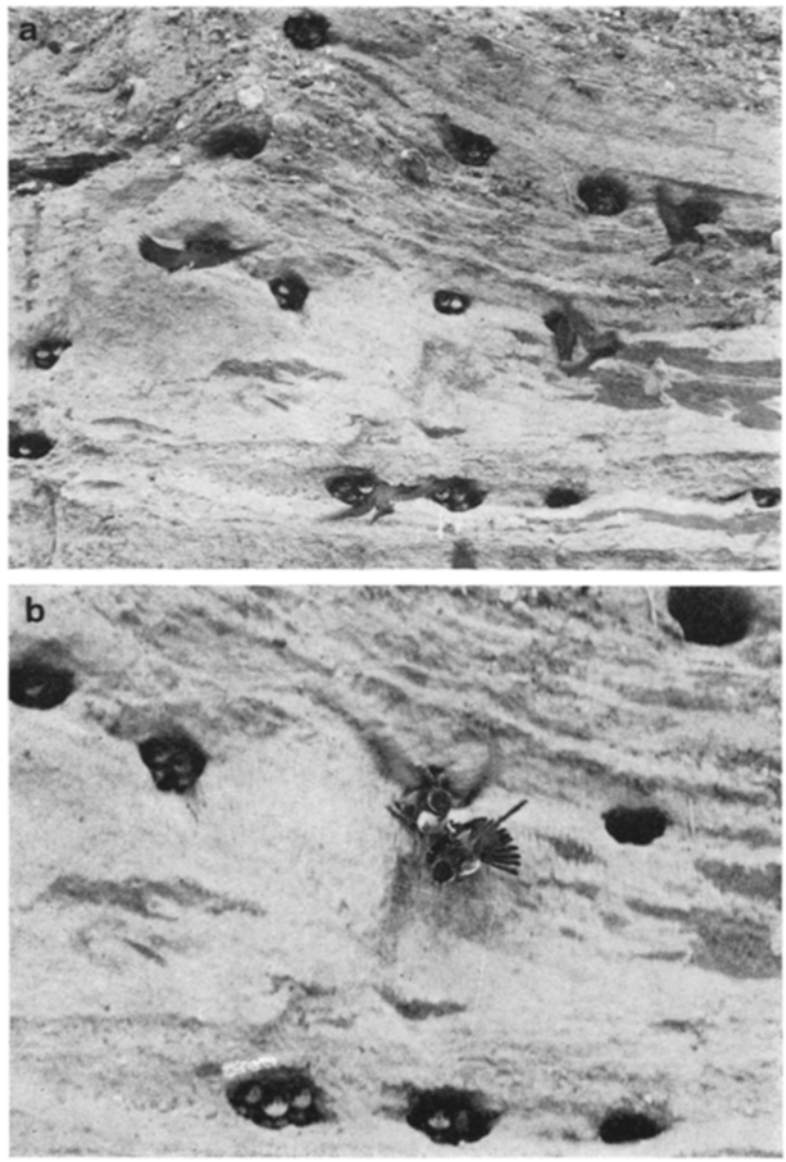

Fig. 1a, 1b.

PLATE II

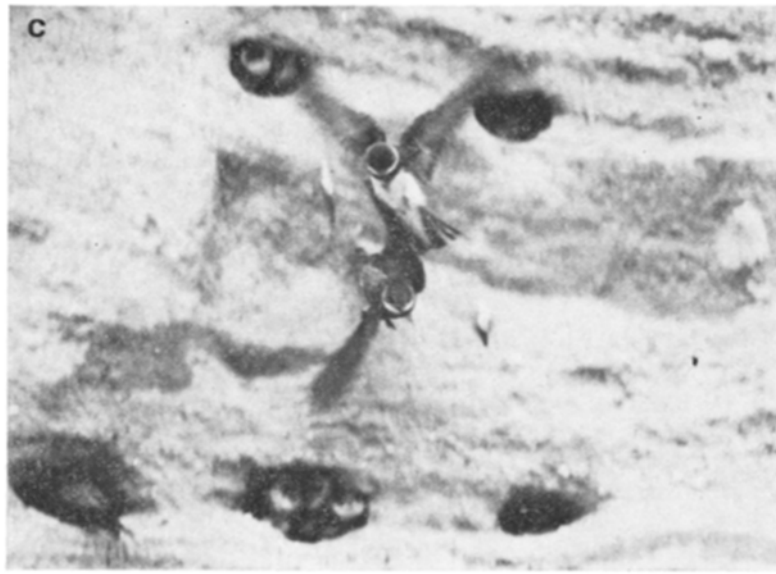

Fig. 1c.

Fig. 1(a). Typical view of bank swallow colony during the transitional period. (b and c) Adults evicting chicks from burrows.

as they left the nest at dawn. If the capture occurred early in the incubation period, both parents were often captured. The female can be sexed reliably by the presence of an incubation patch. Captures of exiting birds were also made by mist nets set close to the bank. Parents were banded and marked with broad-tipped felt marker pens; these markings lasted three to six weeks. Green, blue, red, and yellow were used, applied to the right and left sides or the top and bottom halves of the white underparts (below the breast band), giving 28 distinct combinations.

Young bank swallows were captured by removing them from the nest before 14 days of age. Young of this age are still fed at the back of the burrow and are unable to fly; thus we are assured that they are true residents of the nest. A flashlight device, based on one described by Lunk (1962), was used both for inspecting nest contents and for extricating chicks. A 1.2-m length of copper tubing carried wires from a 6-V battery, attached to the operator's belt, to a flashlight bulb and dental mirror mounted at the far end. To extricate a chick from the burrow (typically about 1 m deep), the mirror–bulb attachment was carefully hooked behind the bird, who was then coaxed toward the burrow mouth. Occasionally, one or more chicks were inaccessible and could not be marked. We marked young of a brood identically in most cases, and assigned all siblings the mean age of the brood, as determined by known hatching dates. Since the typical bank swallow clutch of five eggs (rarely four or six) hatches out over one to three days, the actual age of any individual differs from the mean by a maximum of $\pm$ one day. In cases where we wished to distinguish the behaviour of younger and older siblings, or to keep track of all members of a brood individually, siblings were marked differently.

Chicks were marked similarly to the adults except that (a) only left/right colour combinations were used and (b) marks were extended to the lower margin of the gular region. Marks are apparently ignored by the parents, unless they are too dark (black, brown, dark blue) or cover the entire gular region. Capturing and marking of the young was generally done before dawn, to minimize disturbance to the colony.

Our results are based on observations of 238 marked adults and 503 marked young from 124 broods. Observation-hours totalled approximately 1350 h.

Observational methods. The observer watched from a blind or car, with 7 × 35 field glasses or the naked eye. Our early observations were ad lib (Altmann 1974), as we wished to determine the major contexts of parent–offspring recognition. Later we generally used one of two sampling methods. Where the event was relatively infrequent (e.g. the 'eviction' of a chick from a burrow by an adult), we watched a number of burrows in a subcolony simultaneously. We then characterized the event in terms of either rate (e.g. number of evictions per hour per burrow) or percentage of burrows for which the event occurred on a given day. Where the event was frequent, complicated or required us to follow it away from the bank, we focused on a single burrow, or occasionally a few adjacent burrows.

Results

Young come to the burrow entrance, where some brood members can be seen most of the time after 14 days post-hatch. Typically a chick will retreat from the entrance after being fed several times, to be replaced by a hungrier chick. From about 15 to 16 days on, virtually all feedings take place at the entrance, thus permitting positive identification of adult and chick.

Figure 1a (Plate I) is a typical picture of a small section of a colony during the period when young are at the front of their burrows. Clearly, though many young are clustered together, parent–offspring recognition will not be required if (a) the parents correctly identify their nest and (b) the young remain in their nest. We have never seen a parent mistakenly feed at another nest (except in cases where recent cave-ins have radically changed the face of the bank). Chicks, however, do not stay in their nests. There is a four- to five-day period when chicks leave and return to the nest; we refer to this period as the Transitional Period: the brood is no longer nest-bound (Nestling Period) nor completely fledged from the nest (Fledgling Period). The Transitional Period arises in part because of the asynchrony of hatching—older sibs are ready to fly before younger sibs—and in part because of a period of at least several days during which young birds remain dependent upon their parents while developing their flying and foraging skills. We define the Transitional Period for a burrow as beginning with the first flight of a chick and ending when the burrow is vacated.

We usually see the first flights from a burrow on day 18 or 19. For a sample of 50 nests, the median first observed flight day was 18 (mean

18.7, SD = 0.99). The true date can only be earlier, since we typically sampled only 3 to 5 h per day and so probably missed some first flights. Eighteen-day-old chicks are capable of strong flight. The median final day at the burrow was day 21 (mean 21.2, SD = 1.30).

Early flights. There are three major circumstances for flights by chicks during the Transitional Period. (1) The chick chases the parent out of the burrow. (2) The chick spontaneously leaves, perhaps stimulated by hunger. (3) The parent attempts to lure the chick out by refraining from feeding the chick and hovering in front of the burrow. These flights are an obvious context requiring parent–offspring recognition. Our observations in the first years of our study revealed that a reliable indicator of a bank swallow colony in the Transitional Period is the cacophony of young birds flying about giving the two-note 'lost' call. Though they may chase after any adult that appears, only their parents will respond with a single-note, lower-pitched call. These reunions end with the parents perhaps feeding the chick in the air and/or leading it to the burrow, out to the colony Loafing Area (see below), or out of sight.

To evaluate the consequences of chick mobility during the Transitional Period we watched six burrows on days 18 to 20, for approximately 4 h each day (67 burrow-h). All chicks in a brood were individually marked. We observed 63 flights by chicks: in 40 cases the chick left 'spontaneously', in 21 it chased the parent from the burrow, and in 2 it was lured out by the parent. Of the 40 spontaneous-flight cases, in 13 the chick was eventually led back to the burrow by the parent, in 12 the chick returned to a burrow unaided (10 of these were to the correct burrow), and in 15 it did not return before the conclusion of the observation period. Of the 23 cases in which chick and parent left together, in 11 the parent eventually led the chick back, in 6 the chick returned unaided (5 times to the correct burrow), and in 6 it did not return before we left. It is evident, then, that parent and chick can find one another, or stay together, in a large colony away from the home burrow. We suspect that in many of the 21 cases whose outcomes we did not witness, the parent led the chick to the colony Loafing Area away from the bank (see below).

Searching and leading by parents. Parents appear to have some ability to keep tally of their young, since they are often seen searching the bank when some of their brood are still in the burrow. For example, at one colony of marked birds, we stimulated searching by the parents in all 8 cases where we temporarily removed the entire brood, and in 7 of the 10 cases where we temporarily removed two chicks. Searching consists of looking into burrows other than the home burrow. If the burrow is vacant, the parent typically enters it; if it is active, the parent typically hovers or perches near the entrance. The parent may also fly about in the vicinity of the bank while giving its one-note call.

As indicated above, a parent is often seen leading its young back to the nest during the Transitional Period. The parent either flies into the burrow pursued by its chicks, or veers off at the last possible moment, repeating this behaviour several times if the young do not enter.

The mobility of chicks during the Transitional Period is reflected in the correlated increases in parents searching, parents leading young back to the burrow, and young lost in foreign burrows, seen in Fig. 2.

Young in alien burrows: response of resident adult and natural parent. When they fly back to the bank, young often return to burrows other than their own ('visits' by 'alien' chicks to 'foreign' burrows). Since visits almost invariably occur into active burrows containing similar-aged young, they create 'experiments of nature': when the resident adult arrives to feed its young,

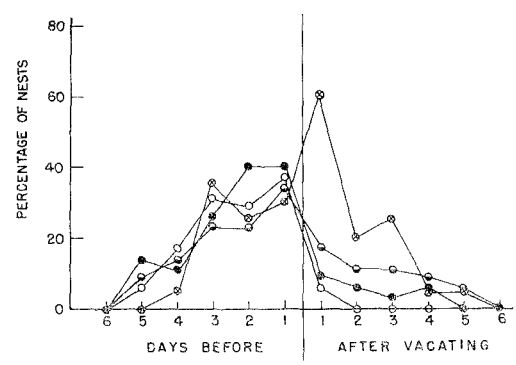

Fig. 2. Percentage of broods for which the following events were seen on the six days before and the six days after vacating the burrow: ●, a chick was lost in a foreign burrow within the subcolony; ◒, the parents were searching the subcolony; O, the parents led the chick(s) back into the home burrow; ⊗, the chicks were seen in an aggregation on the powerlines ('in crèche'). Based on 35 nests (20 nests for ⊗) from five subcolonies (1973, 1975, 1976, 1977).

it finds an alien chick amongst its own. The adult responds in one of three ways. It may 'evict' the alien chick, it may feed it (a 'misfeeding'), or it may ignore it.

Figure 1b and c (Plates I and II) show two examples of an adult evicting a young bird: the adult grips the chick by the feathers with its beak and pulls or shoves it out of the nest, often chasing it away from the bank. We have seen 83 evictions involving colour-marked individuals (where we knew the young and the adult to be unrelated); we have seen many more involving unmarked individuals. We have never seen a bank swallow parent evict its own young from its burrow. Parents do make mistakes and feed alien chicks. We evaluated the frequency and significance of these mistakes, and the overall effectiveness of the recognition system, in study 2. In some cases an alien chick may remain in a burrow for an hour or more without being fed and ultimately leave of its own accord. Though the failure to feed may be an example of passive rejection by the resident adults, the connection between the chick's departure and the parent's behaviour is not as clear as it is in the case of an eviction.

Though parents are typically seen searching burrows when their young are lost, they rarely enter active foreign burrows or feed their young there. We recorded 17 instances of parents feeding young in foreign burrows: in 12 cases, the burrow was an inactive one (no other chicks); in 2 cases it was a rough-winged swallow's (*Stelgidopteryx ruficollis*) burrow; and in 3 cases, it was connected by a ledge to the home burrow (thus in fact there was an element of ambiguity as to which was which). Twice we have seen parents evict their own young from a foreign burrow.

Parents feeding young away from the burrow. The final context requiring parent–offspring recognition occurs away from the bank, during and following the Transitional Period. Fledglings often form large aggregations on powerlines near the bank while the parents forage. When an adult returns, it flies down the line, 'finds' a particular chick, and then feeds it. The feeding is preceded by the chick and adult calls described earlier. These groups of young bank swallows are thus similar to the crèches described for some colonial waterbirds (e.g. Thompson & Emlen 1968). We watched one such aggregation, specifically looking for feeding interactions involving marked young and marked parents. We observed 18 feedings of marked young by marked adults: in every case the feeding adult was the parent of the young. In no case did we see a marked adult feed an unrelated chick.

Study 2: Evaluation of Recognition at the Burrow

'Visits' are one of the most interesting aspects of chick mobility during and after the Transitional Period. Initially we were unsure how they should be regarded. Are they simply incidental consequences of a stage in which young develop their flying and foraging skills (i.e. accidents)? Or are they attempts by a chick to garner additional feedings at little cost? From the point of view of the resident adult: do visits constitute a serious drain on its energy? How effective is the recognition system? To answer these questions, we conducted a study in which we focused on visiting young and attempted to quantify the relative frequency of visits and their various outcomes.

Methods

We chose for our primary study a subcolony (Dexter B 1973) that was small enough that we could keep track of all visitors; rarely was there more than one visitor at any one time. There were 12 bank swallow burrows, one rough-winged swallow burrow, and 17 inactive burrows. We marked 45 young from 10 bank swallow broods and 14 of the 24 parents. Chicks of nine of these marked broods were capable of flight during the nine days of the study (one brood was considerably behind the rest). The site was observed for 50 h over 11 days, most intensively for the first 9 days (47 h).

The focus of observation (Altmann 1974) was any chick in a foreign burrow. Once a visitor was noted, the observer kept track of it and noted whether it was fed, was evicted, or flew from the nest. In addition, the observer scanned the burrows each half-hour and recorded what birds were visible in each burrow. Similar observations, but without the time information, were made at three additional sites: Dexter A 1973 (we marked 22 burrows, 24 parents, and 40 young from 10 broods); Pleasant Lake 1974 (13 burrows, 16 parents, 39 young from 10 broods): and Dexter 1975 (14 burrows, 14 parents, 33 young from 9 broods).

Results

The results of the major study (Dexter B 1973) are given in Table I. We observed 46 separate instances of a chick appearing in an active

foreign burrow, and only four instances of a chick visiting a vacant burrow. This suggests that visitors prefer active burrows, since in fact there were more vacant burrows (17) than active ones (13) in this subcolony. The 46 visits inside active burrows were made by young from eight of the nine marked broods capable of flight, and occurred into all 13 active burrows. Consistent with the data presented earlier (Fig. 2), most of these visits occurred in the three days previous to the visiting chick's vacating its home burrow.

The most common outcome of the 41 visits inside active bank swallow burrows (Table I) was that the chick simply left (19 instances, or 46%). The departure may reflect the chick's recognition of its error or, as we indicated earlier, the resident adult's passive rejection. In 12 cases (29%), the bird was fed at least once by the resident adult (a 'misfeeding') and later left on its own accord. The maximum number of misfeedings before the bird left was 4; the mean was 2.0. In the remaining 10 cases (24%), the bird was evicted. Two of these evictions occurred after a misfeeding on a previous visit.

As is obvious in the 'misfeed + evict' cases, the resident adults may respond in a mixed fashion to the alien chick. This may be true of the 12 'pure misfeed' episodes, too, for the resident adults may have refrained from feeding the chick on unobserved visits before or after those in which they did in fact feed it. We can evaluate the extent of 'passive rejection' by comparing feeding rates of own versus alien chicks. Our sampling method precluded simultaneously measuring feeding rates at these burrows, but typically these rates are approximately 25 per burrow per hour (unpublished observations; Petersen 1955). Thus in the absence of any discrimination on the part of the host parent, an alien chick could expect to receive about 4 feedings per hour. In fact, in the 42 visits the birds were fed 26 times in 35 bird-hours, for a feeding rate of 0.74/h. If the eight 'pure eviction' cases are deleted, the misfeeding rate is 26 times per 29 bird-hours or 0.89 per hour. Perhaps, then, the resident adults were displaying some degree of recognition (discrimination) even in those cases where they did not evict the alien chick. Alternatively, the lack of feeding may have been due to a lack of begging by the alien chick, which recognized the strangeness of the burrow and the other chicks and/or adults. The remaining cases in Table I are consistent with data described earlier: parents may feed their chicks in vacant burrows, or in a rough-wing burrow, but they will not feed them in an active bank swallow burrow.

The significance of the resident adults' errors can be evaluated by calculating the average number of misfeedings per hour during the period covered in the major study. We observed 26 misfeedings of marked birds over 476 active burrow-hours. We must add to this number misfeedings of unmarked birds, which we have to estimate, since we could not be sure, in most cases, whether unmarked young belonged to that burrow or not. These unmarked visitors came from the 20% of the chicks at this subcolony we did not mark, and from chicks at other nearby subcolonies. We can derive a crude estimate of the number of misfeedings of unmarked birds from the number of evictions of unmarked birds (unlike the former, the latter are unambiguous since parents never evict their own chicks from their own burrows). This method assumes that misfeeding and eviction rates are positively correlated and proportional to the visitation rate. We saw 12 evictions of unmarked birds as compared to 10 of marked birds, so we can estimate that there were 1.2 times as many misfeedings of unmarked birds as there were of marked birds (26), or roughly 31. This gives an

Table I. Outcome of Each Instance of Chick Appearing in a Foreign Burrow*

		Outcomes					
Visit inside:	No. episodes	Leaves	Resident misfeeds	Resident evicts	Resident misfeeds, later evicts	Own parent feeds	Hours
12 Bank swallow burrows	41	19	12(24)	8	2	0	35
Roughwing burrow	5	2	2(7)	0	0	1(3)	4.5
17 Vacant burrows	3	2	—	—	—	1(12)	2.5

* Total number of feedings in parentheses.

estimated total misfeeding rate of 0.12 per hour, or 0.5% of the parents' total feeding rate. This figure applies roughly to the last week of the nesting period; nests get virtually no visitors prior to about 15 days post-hatch. We determined misfeeding rates similarly for three additional subcolonies (Nos 1, 3, 4 in Table II): all three were lower. At four additional subcolonies we measured only eviction rates. Of the eight total subcolonies, Dexter B 1973 had the second-highest eviction rate observed. Thus our data suggest that our 0.5% misfeeding rate, the cost to the resident adults, is close to a 'worst-case' estimate.

Table II also contains information concerning some of the factors determining visitation rates. From these data, and other unquantified observations, we have tentatively identified three of the factors that determine visitation rate. (1) When the powerlines are close to the bank, young birds are more apt to fly back and forth. This was the situation at the Dexter colony each year through 1976 (Nos 1, 2, 4, 5): the bank can easily be seen from the powerlines, approximately 50 m away. Interestingly, in 1977 and 1978, the powerlines were not used, apparently because of heavy predation at the colony by blue jays (*Cyanocitta cristata*) (who were not present in the previous years): this was correlated with a drop in the eviction rate (Nos 7, 8) compared with that rate in previous years. (2) The earliest subcolonies will have only intra-colony visitors (but these may be attracted elsewhere), while the latest subcolonies can get visitors from earlier subcolonies (and their own chicks can visit only within their own subcolony). This was probably a critical factor in the high misfeeding and eviction rates at No 1 and No 2, both late subcolonies. (3) As indicated earlier (Table I), visitors clearly prefer active burrows with other chicks at the front: they rarely fly into empty burrows or into pre-14-day burrows. Furthermore, we have noted a tendency for birds to be attracted to larger subcolonies containing many burrows with young at the mouths. The relatively low eviction rate at No 4 in Table II, for example, was correlated with a high visitation rate simultaneously at another, much larger and slightly later subcolony.

Finally, we analyse another factor relating to the misfeeding and eviction rates. We noted during the main study of 1973 that evictions were most often made by females and misfeedings were most often made by males. In Table III, we have collected data from this study and studies of several other subcolonies. We have classified an individual as an 'evictor' or 'feeder', since this prevents the data from being overly influenced by particular individuals for whom we had many observations of one or the other; also each datum in the table is thus an independent observation. We can see a clear trend for evictions to be made by females and mistakes to be made by males ($P = 0.0006$, Fisher exact probability test).

Discussion

Contexts of Parent–Offspring Recognition

In summary, there appear to be three primary contexts requiring parent–offspring recognition. (1) Beginning on about day 18 post-hatch, young fly from the burrow with or without their parents. We observe that following these flights parents and young are able to keep or get together. (2) During the Transitional Period, young frequently fly into the wrong burrow. Their own parents often search for them and sometimes find them there. More commonly the alien chick leaves 'of its own accord', which may reflect recognition by the resident adult (who did not feed it) and/or belated recognition by the chick that it is in the wrong burrow. Frequently we see the resident adult mistakenly feed the alien chick (recognition failure) or evict it (recognition). (3) Parents locate their young in crèche-like assemblages on powerlines away from the bank, both before and after the burrow is vacated. In this situation, and in aerial reunions, recognition appears to involve calls given by both offspring and parent.

Mix-up of Young at the Burrow

Petersen (1955) and Stoner (1926) previously reported observing young bank swallows in the wrong burrow, but the only detailed description of such events prior to the present study is by Hoogland & Sherman (1976). They report an apparently very high visitation rate at a subcolony they observed in Michigan (we cannot arrive at a quantitative estimate since they do not supply all the necessary data and since an unspecified proportion of the visits were not natural but arranged by the investigators). The critical condition for the high visitation rate appears to have been that the chicks were able to walk from their burrow to adjacent burrows (the majority of visits followed walks, not flights). This situation is unusual (see Fig. 1a); generally we see it only in banks with very fine sand. Even so, there were only 11 misfeedings at

Table II. Evictions and Misfeedings at Eight Subcolonies

No.	Subcolony	Active burrow hours	No. marked chicks	No. misfeedings, marked chicks	Est. total misfeedings*	Est. misfeeding rate	No. evictions marked, unmarked	Eviction rate	Powerlines in sight of bank?	Comments
1	Dexter A 1973	361	40	9	24	0.066	3, 5	0.022	yes	Second-to-last subcolony
2	Dexter B 1973	476	45	26	57	0.120	10, 12	0.046	yes	Last subcolony
3	Pleasant Lake 1974	156	39	0	~0	~0	0, 4	0.025	no	
4	Dexter 1975	130	33	0	~0	~0	0, 2	0.015	yes	Chicks attracted to another subcolony
5	Dexter 1976	115	32	**	—	—	12, 0	0.104	yes	
6	Fox Quarry C 1976	129	38	**	—	—	2, 1	0.023	no	
7	Dexter A 1977	56	22	**	—	—	0, 0	0	***	
8	Dexter 1978	84	30	**	—	—	0, 0	0	***	First subcolony

*Calculated as described in text.
**Not sampled.
***Yes, but not used because of predation (see text).

Table III. Number of Individual Adults of Each Sex Feeding or Evicting Alien Young at the Adult's Burrow (Number of Instances of Each Per Individual Disregarded)

Site	'Feeder'*		'Evictor'*	
	Male	Female	Male	Female
Dexter B 1973	6	1	0	3
Dexter A 1973	3	0	1	3
Pleasant Lake 1974	0	0	1	3
Dexter 1975	0	0	0	2
Total	9	1	2	11

*Two females and one male at Dexter B 1973 who both misfed and evicted are classified as 'feeders'. Otherwise all 'feeders' were seen only to misfeed and 'evictors' only to evict. $P = 0.0006$, Fisher exact probability.

11 marked burrows in 32.5 h; there were 18 eviction attempts (how many succeeded was not stated). Their observed misfeeding rate appears to be slightly lower than that which we observed at the Dexter B 1973 colony (26 misfeedings of marked birds from 10 broods over 50 h). That their misfeeding rate is somewhat lower despite their artificial inflation of the visitation rate suggests again that our 0.5% figure is a worst-case estimate. Hoogland & Sherman also noted many feedings by parents of their young at foreign burrows: 38 when the chick was alone at the mouth (inactive burrows?) and 4 when it was at the mouth along with the resident chicks; the latter cases were apparently distinctive in that they are described as occurring at the edge of the foreign burrow. Though we have rarely seen feedings at foreign burrows, these are precisely the circumstances under which we have observed them: when a chick is by itself at the burrow and/or when it has walked along a ledge to an adjacent burrow; typically parents feeding chicks at active foreign burrows appear somewhat hesitant.

Why Do Chicks Make Mistakes?

We have never seen a chick succeed in being fed at a foreign burrow for any length of time. For example, at the Dexter B 1973 subcolony, the maximum number of misfeedings at the same burrow was four. We are reluctant, therefore, to consider 'visiting' an adaptive strategy for chicks. Unless acceptance by the resident adult is complete ('adoption'), it may well be that the best strategy for the chick, at least before complete independence from the parents normally occurs, is to stay with its parents. The most commonly observed outcome of a visit is that the alien chick leaves. It may do so because it belatedly recognizes that it is in the wrong burrow, or hears its parents or siblings outside. We cannot, of course, distinguish this possibility from that of passive rejection by the resident adult; and both may in fact occur. In any case, though selection on the visiting chick is indirect (a feeding by the resident adult is as good as a feeding by the natural parent), the chick will be selected to avoid or terminate visits if the resident adults eventually recognize it, and if its natural parents are still present in the subcolony.

We suggest that the most plausible explanation of visits is that they are an incidental consequence of the Transitional Period combined with colonial life; visits would not occur if fledging were all-or-none (as it is in many birds) and/or if the birds were not colonial. Visiting can be exacerbated by certain other factors, including proximity of the 'crèche' site to the colony, ledges between burrows, the presence nearby of other subcolonies, and doubtless other unknown factors.

Why Do Parents Make Mistakes?

Parental discrimination of their own from alien chicks at the burrow, while not perfect, appears to be good enough that visits by alien chicks do not extract a significant cost. Our data suggest that in the last week at the nest, misfeedings probably make up no more than 0.5% of the total feedings, and perhaps much less. We suggest that there are several factors which may contribute to the occurrence of misfeedings. (1) It may not be efficient for parents to attend carefully to the relevant cues on every trip to the nest. Rather, on most trips the parent may simply home to the nest, feed as quickly as possible, and leave. This situation should be contrasted with feeding in the crèche, where the parent has no cue for recognition other than that provided by the chick. (2) Parents should be favoured to

follow a 'conservative' strategy with respect to evicting, since the cost of misfeeding is much less than the cost of evicting their own chick. The fact that we have witnessed no accidental evictions of chicks by their parents from their own burrow is consistent with the hypothesis of a conservative criterion for eviction. (3) Most of the mistakes are by the male parent (whatever the reason may be). A few mistakes by the male will be inconsequential so long as he can count on the female evicting the alien chick at some point.

Sex Differences in Recognition

In piñon jays (*Gymnorhinus cyanocephalus*), Balda & Balda (1978) also found that males are more likely to feed alien young than are females. They suggest two possible explanations. First, since apparently it is primarily females that emigrate in piñon jays, a male will on average share more genes with an alien chick than will a female. This explanation probably does not apply to bank swallows, since they are a migratory species and banding return data (e.g. Stoner 1937) strongly suggest that bank swallow colonies do not have the kinship structure found in piñon jays and other sedentary species. Second, Balda & Balda indicate that dominant males in the group succeed in copulating with females other than their mates, and they hypothesize that it is these males that are feeding 'alien' young, which in fact may actually be their own. Again this explanation does not seem to apply to bank swallows. Although we have observed that males routinely attempt to copulate with females other than their mates (Beecher & Beecher 1979), our observations suggest that their success rate must be very low. Considering this fact and the size of bank swallow colonies, the probability that a visitor to a bank swallow male's burrow is in fact his own offspring must be very low.

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