CHAPTER 16

THE EVOLUTION OF PARENT–OFFSPRING RECOGNITION IN SWALLOWS

Michael D. Beecher

In this chapter, I discuss our research on the evolution of recognition in swallows, primarily in the context of parents recognizing offspring. There have been many demonstrations that parents recognize their offspring (for a recent summary, see Colgan, 1983), often under extraordinarily difficult conditions (for example, a free-tailed bat mother finds her pup in a maternity cave of a million bats; McCracken & Gustin, 1987). That this should be so is as about as straightforward a prediction as can be made from basic natural selection reasoning: in species where parents increase their reproductive success by providing parental care, they receive this benefit only if they direct the care to their own offspring rather than to unrelated young. It is a small step from this basic natural selection argument and the many empirical demonstrations of parent–offspring recognition to the hypothesis that parent–offspring recognition should be better developed in colonial species than in noncolonial species. After all, in noncolonial species, a parent may be able to restrict its parental care to its own offspring simply by keeping them in the nest, or in a particular place apart from other young. Pure recognition may not be needed, or at least not needed to the same extent. Put differently, it seems reasonable to suppose that colonial species would show adaptations for parent–offspring recognition that noncolonial species would not. The term "adaptation" refers to a trait that the species in question has which other closely related species do not have, and it carries the important theoretical implication that the ultimate cause of this species difference is a history of natural selection on the trait for the function specified: in this case, recognition (see Williams, 1966, for a general discussion of adaptation).

When my colleagues and I first began studying parent–offspring recognition in swallows, we supposed that there was already considerable evidence to support the idea that recognition is better developed in colonial species. We were surprised to discover, however, that there was not, despite generalizations to the contrary in textbooks and other secondary sources. The pattern of positive outcomes (demonstrations of parent–offspring recognition) and negative outcomes (failures to demonstrate it) was anything but consistent. Although most of the colonial species tested gave positive outcomes, not all did, and most of the noncolonial species tested also gave positive outcomes. Moreover, many of the studies were not adequate tests of recognition (I will discuss some of the problems in these tests later). Finally, rarely had a single investigator or group ever tested more than one species, which raises the question of comparability across different studies of different species. This confusing state of affairs is epitomized by the widely cited generalization that in herring gulls (which are colonial and where young intermingle at an early age) parents recognize their chicks, but in kittiwakes (which are also colonial but where the young cannot stray from their nests on narrow cliff ledges) parents fail to recognize their young. This generalization began with Cullen (1957), who compared her kittiwake studies to the herring gull studies of others. It turns out that this generalization is incorrect, and that in all gull species which have been adequately tested, parents fail to recognize their chicks in the early weeks (although chicks do recognize parents; Beer 1969, 1979; Holley, 1984; Knudsen & Evans, 1986; Miller & Emlen, 1975; Shugart, unpublished data).

All of this, taken together, led us to the conclusion that the pattern of positive and negative evidence might have more to do with the particular investigators than with the true state of affairs, and that in any case, there was no evidence that parent–offspring recognition differed in colonial and noncolonial species, or that it was affected by any ecological variable, for that matter. Thus, we began our work on parent–offspring recognition in swallows with three guidelines. First, we felt that the hypothesis that parent–offspring recognition is better developed in colonial species than in noncolonial species was plausible, but had not been confirmed for any group of animals. Second, we felt that the same research group had to look at both colonial and noncolonial species for an adequate test of the hypothesis. Thus, we decided to look in detail at both colonial and noncolonial swallows. Third, the major goal of our research—and this was predicated on the assumption that we would support the hypothesis that parent–offspring recognition is better developed in colonial swallows than noncolonial swallows—was to delineate the adaptations for recognition distinguishing these species.

SOME COMMENTS ON THE STUDY OF ADAPTATION IN ANIMAL BEHAVIOR

It is de rigueur these days to employ natural selection theory in the hypothetico-deductive fashion. While I agree that prediction should be central to the evolutionary approach to behavior, a purely predictive approach is often inappropriate. When the trait under study is complex—as is “recognition,” or “mating system,” or almost any of the composite traits we study in animal behavior—we may be able to predict general adaptive outcomes, but rarely will we be able to predict the particular adaptive solution which evolution has opportunistically selected from among the many possibilities.

Let me make this argument explicit. A prediction about the outcome of natural selection can be compelling, in the sense that if the argument has been correctly constructed, and if the supporting assumptions are correct, the prediction must be true. Indeed, if the prediction is not supported, we invariably reevaluate the argument and supporting assumptions. On the other hand, a prediction about the specific nature of the adaptations underlying the outcome—about the mechanisms—is inherently less compelling, and is often presumptuous. This is because natural selection is opportunistic. We can predict that animals will have evolved adaptive solutions to problems, but in any particular case, we generally cannot predict, on purely logical grounds, what opportunistic solution natural selection will have seized upon, nor what limitations (constraints on adaptation) this solution may have. In short, some solution to an ecological problem is necessary, but any particular solution is not.

The modern investigator of animal behavior should be a serious student of evolution, capable of constructing cogent natural selection arguments, eagle-eyed in detecting fallacious ones. The investigator, however, should not expect to be prescient, which is what correct “predictions” about mechanisms generally require. It is often rather easy to make an adaptive prediction about behavior, particularly when popular interpretation has set up a group selectionist or non-adaptive straw man. For example, consider the Mexican free-tailed bat mother who must find her pup amidst thousands or millions of other pups in the maternity cave. Several investigators were so impressed by the magnitude of this recognition problem that they concluded mothers must feed pups at random. McCracken, however, made, and subsequently confirmed, the contrary prediction that mothers do recognize their young in these circumstances (albeit imperfectly, see McCracken, 1984; McCracken & Gustin, 1987). It would generally be agreed that the McCracken prediction is a relatively easy, straightforward one by modern standards. Even its demonstration is relatively easy, given the modern technique of electrophoresis (and barring an aversion to bat caves). But the delineation of the actual adaptations which underlie this recognition, which must include evidence that they are absent (or less developed) in closely related bats not facing this recognition problem, is by no means easy. To delineate the adaptations, we are left with the time-honored empirical approach: we simply have get into the trenches and dig hard.

To take a broad example of the relative difficulty of predictions concerning outcomes compared with predictions concerning adaptations or mechanisms, consider research on the evolution of learning. There has been a tremendous interest in this area in recent years, and it has given us many demonstrations of adaptive *uses* of learning by animals. Nevertheless, it has not yet given us a single convincing demonstration of the action of natural selection on some aspect of learning, i.e., of adaptations of learning per se. (For a discussion of adaptive uses' of learning versus adaptations of learning, see Beecher 1988b; Sherry 1988.) To take a specific example which will be discussed below, bank swallow parents learn the calls of their young, while, so far as we can tell, rough-winged swallow parents do not. This is certainly an adaptive use of learning by bank swallows, but we have no evidence at this point that learning per se is in any way adapted for this function. Rather, as we shall see below, our evidence so far points to other sorts of adaptations. It would be interesting if we found that bank swallows imprint on chick calls while rough-winged swallows do not, but we have not yet shown that. These would be difficult experiments to do, in fact, and that is precisely my point. Unravelling the specific solutions (mechanisms) shaped by natural selection can be far harder than predicting (and confirming) that some sort of solution has been found.

A GENERAL PERSPECTIVE ON RECOGNITION

In this section, I provide a general perspective on recognition. We have used this perspective as a simple model which suggests the necessary observations and experiments. I use the term "parent–offspring recognition" to refer to discrimination of offspring from unrelated young by parents based on individually distinctive cues. This definition specifically excludes discrimination based on circumstantial evidence (e.g., the location of the young in the home nest). In this chapter I do not treat the reverse process of young recognizing parents (but see Beecher, Stoddard, & Loesche, 1985).

While some researchers in this area prefer not to distinguish between recognition and discrimination, I prefer to use "recognition" as a more general, theoretical term, for the simple reason that an animal capable of discriminating between two individuals (or classes of individuals) may do so in one circumstance but not in another. Furthermore, the "failure" of recognition may be just as adaptive as its "success." Thus, I prefer to use "discrimination" in reference to specific contexts and "recognition" in reference to an underlying ability which may be inferred from the occurrence of discrimination in at least some contexts.

Several examples of successes and failures of recognition in the same animal will be given below (for further discussion of this point, see Beecher, in press-b, and Beecher & Stoddard, in press).

While it is sometimes convenient to speak of "individual recognition" as if it were a simple trait, it is in fact an outcome or a composite of several separate traits. This is easily seen by considering the particular case of parent–offspring recognition as a generalized recognition problem. One animal (the receiver, parent) is seeking another individual (the target individual, offspring) and is confronted by an individual (the sender) that may or may not be the target individual. The recognition process consists of four logically independent components. First, the sender must provide *cues* to its identity ("signature" cues). Although we should not necessarily expect that the sender will always signal "honestly," it is clear that the receiver requires such cues if it is to have any basis for a decision (assuming circumstantial evidence is inadequate). (For a discussion of cases where offspring might be favored to conceal their identity, see Beecher, 1988a.) Second, the receiver must process these cues in order to *perceive* the difference between target and nontarget individuals. Presumably, the receiver compares the signal to some model contained in its memory. Third, the receiver must *decide* whether the sender is the target individual. In theory, the receiver's decision rule should be based in part on the a priori probability of the receiver being the target individual, the costs of the two types of error (i.e., accepting an unrelated chick or rejecting one's own offspring), and the benefits of the two types of correct decisions. For example, in a solitary species, the probability of finding unrelated young in the home nest might be so tiny that selection would have favored the decision rule "Always accept young you find in the nest." Finally, the receiver must take appropriate *action*. For example, if the encounter is in the home nest, and the parent decides that the sender is an intruder, it could evict it, or avoid feeding it. Another class of "recognition behaviors" includes paying attention to signature cues, careful inspection of young in the nest before feeding, and so on.

The key point is that natural selection can promote individual recognition by acting appropriately on any of these four components of recognition: signal, perception, decision, and behavior. (Note that the distinction between signal, perception, and decision rule is straight from signal detection theory; e.g., Green & Swets, 1966). Thus, there are four general ways in which natural selection could shape the recognition process. Selection favoring recognition could (1) increase signature variation among individuals and/or decrease it within individuals, thus making individuals more distinctive; (2) increase perceptual sensitivity or attention to the signature traits, thus allowing receivers to discriminate more readily among senders; (3) modify the receiver's decision rule; and (4) shape recognition behaviors. In the research described below we have tried to use particular studies to dissect out the particular adaptations underlying recognition.

SWALLOWS

My colleagues and I have studied four species of North American swallows: two colonial species of swallows (bank swallows, *Riparia riparia*, and cliff swallows, *Hirundo pyrrhonota*) and two noncolonial species of swallows (northern rough-winged swallows, *Stelgidopteryx serripennis*, and barn swallows, *Hirundo rustica*). The North American swallows are an excellent group for research on adaptations to coloniality, because they are a rather uniform group, with coloniality being one of the major dimensions distinguishing the species. Of the seven North American swallow species, only bank swallows and cliff swallows are unequivocally colonial. By "colonial," I mean that they generally nest in large groups, aggregate their nests, and show reproductive synchrony as well as social coordination of other activities such as nest material collection and foraging. The four study species we chose form two natural comparison pairs. Bank swallows and rough-winged swallows are physically quite similar and share the habit of nesting in burrows. Bank swallows dig their burrows in sandbanks along river cuts and (nowadays) in sand quarries, while rough-winged swallows opportunistically use burrows dug and abandoned by other animals as well as other similar cavities such as drainpipes. In Michigan, where we studied them, rough-winged swallows most often nest in bank swallow colonies, usually with one or two pairs being found at the edge of the colony. Cliff swallows and barn swallows are an even closer comparison, since they are congenerics and even hybridize on occasion (we have found one hybrid at our study sites, and see Martin, 1980).

I should comment on the validity of the colonial–noncolonial distinction, for it is obviously crucial to interpretation of our comparative study. It is probably fair to refer to barn swallows and rough-winged swallows as "facultatively colonial," since in this country one occasionally does find them nesting in groups. Even when one does, however, the groups are typically small, with maximally dispersed nests and no reproductive synchrony. The key point is that all swallows are capable of coloniality because, unlike most passerines, they do not defend food territories, since they feed on unpredictable patches of insects. Thus, one sometimes finds the "noncolonial" swallow species in small groups, probably where suitable nesting sites are in short supply. Although this makes the colonial–noncolonial distinction less black and white, it does not blur the basic issue, which has to do with the evolutionary background of the species in question, not the size of the group in which our subject animals happen to be living. In fact, most of our research on both cliff swallows and barn swallows has actually been on birds living in colonies of about 30–50 nests. But all aspects of their behavior suggest that cliff swallows and bank swallows are adapted to colonial living, while barn swallows and rough-winged swallows are not. It is these adaptations to colonial living we are interested in. The intraspecific variation in group size that we find, however, does allow us to look at the *proximate* effects of group living on recognition.

NATURAL OBSERVATIONS OF RECOGNITION

The presence of colonial living in a species is almost a prima facie case for strong selection for recognition. In almost all colonial species, intermingling of young is inevitable and extensive, and there is great pressure on parents to recognize their young (the cliff-nesting kittiwake is an exception—Cullen, 1957). In the swallow species we have studied, intermingling of young is conspicuous in the two colonial species and rare in the two noncolonial species (Beecher & Beecher, unpublished data; Beecher, Beecher, & Lumpkin, 1981; Medvin & Beecher, 1986; Stoddard & Beecher, 1983).

In all four of the swallow species, parents continue to feed and care for young for some time after fledging. Young fledge after approximately 3 weeks in the nest, and their dependence on their parents wanes gradually over the next 2 weeks or so. Typically, there is a period ranging from a day to a week after fledging during which the young spend some of their time at the nest and some of their time away from the nest. From this point on, the situation diverges for the colonial and noncolonial species. In bank swallows and cliff swallows, this interim stage is usually longer than it is in noncolonial rough-winged swallows and barn swallows, in part because in the colonial species, parents often leave their just-fledged young in “creches” (“nursery” groups) near the colony. Chicks and parents frequently become separated and fly about looking for one another near the colony or nest site. Often lost young fly into the wrong nest. These errant flights present parents with a two-sided recognition problem: first, parents must search for their young in the colony, and second, parents must make sure that the young they find in their nest are actually their own. Interlopers are usually detected and ejected. The other major context for parent–offspring recognition in the colonial species occurs in the creche. We have found that creches are common in bank swallows and cliff swallows, and that parents can indeed locate their young in the creches.

In rough-winged swallows and barn swallows, on the other hand, recognition problems rarely arise because there are generally few or no similar-aged conspecific young nearby. Furthermore, even when the two noncolonial species are found in small groups, or when their nests are relatively clumped, parents avoid mixing their young with others in the early days after fledging. We have never observed creches in rough-winged swallows or barn swallows, although we occasionally see small groups of older fledglings, which are largely independent of their parents.

CROSS-FOSTERING EXPERIMENTS

In our cross-fostering experiments, we exchanged approximately half the chicks between two nests that each contained chicks of the same age. Control chicks were handled in the same way that experimental chicks were, but were returned to the home nest. In these experiments, we say that "recognition" has occurred when significantly more control chicks are accepted than experimental chicks. Field cross-fostering experiments generally provide only a first approximation to recognition, since the criterion of "recognition" is inevitably indirect. It is indirect because we generally cannot monitor the nest and our subjects exhaustively, and so must use "bottom-line" criteria of acceptance or rejection, such as whether the subject is present or absent in the nest 24 hours later.

The age at which the cross-fostering is done is crucial, since even when recognition occurs in a species, it typically does not appear until relatively late, usually shortly before fledging. The only case we will consider here, therefore, is cross-fostering carried out at about the time of first flights. The results are shown in Table 1. Of the three swallow species we tested, only the colonial bank swallow gave clear evidence of recognition (Beecher, Beecher, & Hahn, 1981). In comparable experiments with noncolonial rough-winged swallows and barn swallows, on the other hand, exchanged and sham-exchanged birds were accepted equally (Beecher & Beecher, unpublished data; Medvin & Beecher, 1986; see also Hoogland & Sherman, 1976).

Because bank swallows and rough-winged swallows nest together in sandbanks in Michigan, we were able to carry out interspecific cross-fostering experiments (Beecher 1981; Beecher & Beecher, unpublished data). Normally, such exchanges between species will fail because the chicks are poorly adapted to the heterospecific nest environment. In this case, however, both species are nesting in precisely the same habitat. Moreover, the diets of the two species are highly similar. In these exchanges, we would add a single bank swallow to

TABLE 1. Summary of Intraspecific Cross-Fostering Experiments

	Percentage of chicks accepted		Number of chicks [redacted]	
Species (Reference)	**Foster**	**Control**	**Foster**	**Control**
Bank swallow (1)	22	100	18	20
Rough-winged swallow (2)	100	100	12	14
Barn swallow (3)	42	58	36	41

Note. Data from: (1) Beecher, Beecher, & Hahn, 1981; (2) Beecher & Beecher, unpublished data; (3) Medvin & Beecher, 1986. In all experiments, chick exchanges were carried out on or shortly before first flights from the nest. Differing "acceptance" criteria were used in the different experiments. Thus, for example, in the case of the barn swallows, the criterion was that the chick be present at a nest check the following day. Many absent chicks, however, may have flown of their own accord, and thus may have been only temporarily absent from the nest. The bank swallow and rough-winged swallow nests were canvassed more closely.

a rough-winged swallow brood, or a single rough-winged swallow to a bank swallow brood.

We found that rough-winged swallows added to bank swallow nests were typically rejected (5 out of 6), whereas bank swallows added to roughwing nests were invariably accepted (6 out of 6). I should add that we also have seen rough-winged swallow parents feeding bank swallow chicks that had flown into their nest. What these interspecific transfers tell us that the intraspecific transfers cannot is that rough-winged swallow parents do not accept alien chicks purely because they cannot discriminate own from alien. Bank swallow chicks are clearly different from rough-winged swallow chicks (visually and acoustically), and we have seen roughwing parents do visible double-takes before feeding a bank swallow chick. The difference between bank swallows and rough-winged swallows in these interspecific fostering experiments parallels the difference between those passerine species that accept and those that reject cowbird eggs (Rothstein, 1982). The difference between cowbird and host eggs is quite conspicuous, and acceptance of cowbird eggs seems to reflect either a decision rule (possibly adaptive, see Rohwer & Spaw, 1988) or a lack of appropriate eviction behavior (Rothstein 1982), rather than a perceptual inability.

This inference is supported by a second type of cross-fostering experiment we carried out in which we exchanged rough-winged swallow and bank swallow broods from adjacent or close burrows (Beecher & Beecher, unpublished data). We observed that both sets of parents would shortly begin to feed their chicks at the new location. Although the behavior of the two sets of parents in this situation cannot be treated as independent (which is why we generally didn't use this very convenient design), rough-winged swallow parents were clearly attracted to the calls of their young. These experiments suggest that when forced to make a hard choice, rough-winged swallow parents can indeed discriminate conspecific from heterospecific chicks.

One interpretation of these interspecific cross-fostering experiments is that these two species normally employ different decision rules when confronted with the problem of discrimination between their own and alien young. In bank swallows, parents are often confronted with such a problem, and have been selected to base their decisions on individually distinctive cues. In rough-winged swallows, where such discriminations are almost never required, the criterion of "Feed any chick you find in your nest" has been a generally reliable, conservative rule. A chick's presence in the home nest is, of course, strictly circumstantial evidence as to its relatedness, but in rough-winged swallows it is a virtually fail-safe criterion. In bank swallows, however, it is an unreliable predictor of relatedness, at least for chicks near flying age. According to this hypothesis, in the chick substitution test, a rough-winged swallow parent that finds a bank swallow chick in its nest gives priority to the chick's location in the home nest over its unusual appearance and sound, and so accepts it. In the close interchange test, however, the rough-winged swallow parent is confronted not only with an entire brood of transplanted heterospecific chicks in its nest, but also with its own brood of chicks calling at the mouth of a nest close by. It cannot tend to both broods of chicks. In this case, the very large difference in calls and physical appearance is pitted against the very small difference in location, and the parent gives priority to calls and appearance. With regard to this hypothesis, I should point out that we have good evidence for a decision rule of this sort in a species where parent–offspring recognition normally occurs. Caspian tern parents will accept young substituted for their own in the first week of life, yet when given a choice between their own and alien young in nest scrapes on either side of the original nest, they will unfailingly choose their own (Shugart, 1977). Similar results are obtained with egg-fostering experiments in this species (Shugart, 1987).

PLAYBACK EXPERIMENTS

As noted earlier, during the interim period just after fledging, chicks and parents often become separated and fly about looking for one another near the colony or nest site. Reciprocal calling is a conspicuous feature of these events, and one forms the casual impression that these calls are critical to the reunion of chick and parent. The call given by the chick in these aerial reunions is the same begging call it gives before virtually every feeding at the nest, in the air, or (in the case of bank swallows and cliff swallows) at the creche. In the colonial context, many chicks will be calling at any one time. This is true at the creche and at the colony, where chicks sitting at the front of nests and chicks flying near the colony, presumably lost, create a cacophony. Despite the appearance of pandemonium, an observer tracking color-marked birds will discover that parent and chick usually get together. In the noncolonial context, there will usually be very few birds calling, and a parent searching for its young could assume that any chick flying about and calling is ipso facto its offspring. Thus, in barn swallows or rough-winged swallows, a begging call need only be a general "lost" call. In the colonial bank swallows and cliff swallows, however, the call ideally should have identifying or "signature" features as well, as a parent will typically be required to discriminate its calling young from other calling young.

In our playback experiments, we simulated the situation in which chick and parent become separated near the nest. Most often this will occur when the chick flies from, and tries to return to, the nest when the parent is away. On returning to the nest area, the parent must search for the lost chick, and will usually try to lure it back to the nest (although the strategies of parents of different species may differ somewhat; see below). Our procedures for all species were essentially the same, so as to enhance comparability (Beecher & Beecher, unpublished data; Beecher, Beecher, & Hahn, 1981; Medvin & Beecher, 1986; Stoddard & Beecher, 1983).

The experiment was done on nests where young were close to fledging. Some of the young had already taken some trips to and from the nest, or were on the verge of doing so. We began by temporarily removing the young from the nest and placing loudspeakers in or above two empty nests on either side of the empty home nest, 3–4 meters apart. (For barn swallows we sometimes had to install extra empty nests). When one of the parents returned to the home nest, it would begin to search for the missing young, i.e., calling from the nest or calling while flying about in the vicinity. At this point we turned on our playback tapes, and the parent heard calls coming from the two loudspeakers. From one loudspeaker, it heard the calls of its own chicks, recorded the previous day. From the other loudspeaker, it heard the calls of unrelated, similar-aged chicks. Our measure of recognition was the number of approaches the parent made to each playback speaker during a trial. Experimental and control calls were played an equal number of times on each side. Our question was, would parents respond more strongly to loudspeakers playing the calls of their own chicks—would they recognize their young by voice?

The results for all four species are summarized in Table 2. The first response measure is simply the percentage of tested parents that responded more strongly to the calls of their offspring than they did to the calls of the unrelated chicks. The second response measure is the percentage of the total approach responses to the two sets of calls that were approaches to the parent's own offspring. Both measures show that recognition is well developed in the colonial bank swallow and cliff swallow and absent (or at least weaker) in the noncolonial rough-winged swallow and barn swallow.

It is possible that barn swallows and rough-winged swallows normally use visual cues for recognition. Our failure to find parental recognition in the cross-

TABLE 2. Summary of Playback Experiments

Species (Reference)	Number of parents tested	Percentage of parents choosing offspring	Percentage of parental responses to offspring
Bank swallow (1)[a]	12	100	100
Rough-winged swallow (2)	5	40	47
Cliff swallow (3)[a]	7	100	86
Barn swallow (4)	13	61	52

Note. Data from: (1) Beecher, Beecher, & Hahn, 1981; (2) Beecher & Beecher, unpublished data; (3) Stoddard & Beecher, 1983; (4) Medvin & Beecher, 1986.

[a] Colonial species.

fostering experiments with these two noncolonial species argues against this interpretation. In addition, of the four species, only cliff swallow chicks show marked individual variation in face color pattern (see Stoddard & Beecher, 1983). Although we have not investigated whether cliff swallow parents use this visual variation for recognition, this species difference is opposite that expected if the noncolonial swallow species use the visual modality rather than the acoustic modality; additionally, we know of no case in which visual recognition has been shown in birds where the visual variation is not conspicuous to the eye of the human observer.

I should emphasize that in all four species, parents searched for their lost young and were attracted to loudspeaker calls. The difference is that in the colonial species, parents always chose the calls of their young, while in the noncolonial species, parents appeared to choose the calls randomly. Nevertheless, I should note some differences between the searching behavior of parents in these species. Of the two noncolonial species, we made our most detailed observations on barn swallows. Compared to either of the colonial species, barn swallow parents were more likely to stay at the nest and call, less likely to actively search away from the nest, and less strongly attracted to the playback speakers. This difference suggests that barn swallow parents may recognize the calls of their chicks, at least to some degree, but that their normal style of dealing with lost chicks is to call them back home rather than to go out and try to find them via their calls. Or possibly, lost chicks that do not respond to the parental call (as happened in our experiment) represent such an unusual event for barn swallows that selection has not shaped the call-directed searching behavior we see in bank swallows and cliff swallows. These behavioral differences suggest a conclusion similar to the one I drew from our interspecific fostering experiments with rough-winged swallows. The noncolonial swallow species may "fail" our recognition tests (cross-fostering experiments, playback experiments) not simply because they have difficulty discriminating between their own and alien chicks, but also because in their evolutionary background they have not had to make such discriminations. That is, in the normal field context, barn swallows and rough-winged swallows do not normally have to evict alien chicks from their nests, do not have to select their young out of a crowd away from the nest, and so forth, and so natural selection has not equipped them with the necessary behaviors and decision rules that we see in bank swallows and cliff swallows.

SUMMARY OF FIELD STUDIES

The evidence from our field studies (observational, cross-fostering, and playback) supports the generic natural selection prediction that recognition will be better developed in colonial species than in related noncolonial species. Moreover, since the cliff swallow versus barn swallow comparison studies were mostly done on colonies of similar size, this species difference must be traced to the ultimate effects rather than the proximate effects of colonial living, i.e., to the group sizes which were experienced by ancestral cliff swallows and barn swallows, rather than to those experienced by the birds we happened to study.

Our major goal has been to go beyond simple confirmation of the generic natural selection prediction to an analysis of the actual adaptations underlying the coloniality–recognition correlation. To do this, we must look closely at our observational, cross-fostering, and playback studies. Although no one of these rather conventional tools of analyzing recognition permits dissection of the components of recognition (signal, perception, decision rule, and behavior), taken together they provide some strong hints that decision-rule and/or behavioral adaptations are part of the story. For example, rough-winged swallow parents fail to discriminate between bank swallow and rough-winged swallow young when both are present in the home nest, yet they do make the correct choice when forced to do so (when their young and alien young are placed in adjacent nests). Barn swallow parents seem to follow a somewhat different "roundup" strategy than do the colonial swallows, tending to return to the home nest and calling lost young to them, rather than actively searching for and retrieving them. Thus, it would be misleading to summarize the studies described above by saying, "Colonial swallows recognize their young, while noncolonial swallows do not." This statement places all the emphasis on capacity, suggesting that the adaptations are exclusively signal and/or perceptual. We decided, therefore, to examine signal and perceptual adaptations directly via two additional types of study. First, we carried out a signal analysis of the calls used by bank swallows and cliff swallows in recognition and of the homologous calls of rough-winged swallows and barn swallows. We were looking for evidence of adaptation of these calls for "signature" function in the colonial species. Second, we brought cliff swallows and barn swallows into the laboratory to carry out a perceptual analysis of their calls. In the laboratory, we could analyze the birds' perception of conspecific and heterospecific calls, and potentially separate out signal and perceptual adaptations.

INFORMATION ANALYSIS OF SWALLOW CHICK CALLS

Perhaps the simplest hypothesis concerning adaptations for recognition (and thus the first one to occur to me) is that the signals used in recognition have been modified so as to be more individually distinctive in the colonial species. As mentioned earlier, chick calls are a key part of recognition in natural circumstances. Inspection of sonagrams of the calls used by swallows strongly suggested this hypothesis, since the calls of the colonial species appeared more individually distinctive than the homologous calls in the noncolonial species (see Figure 1). Clearly, a method was needed to objectify and quantify these visual impressions.

To evaluate this "signature adaptation" hypothesis, therefore, I developed a model for analyzing the relative information capacities of signals (a preliminary version is described in Beecher, 1982, and the final version is in Beecher, in press-a). The model combines the Shannon information measure (Shannon & Weaver, 1949) and the Model II (Random Effects) of Analysis of Variance (e.g., Sokal & Rohlf, 1981). I provide a brief outline of the model here.

Suppose we are measuring a single variable trait, such as the duration of a call, and have *n* observations each on *k* individuals. Then by the model a particular observation, X_{ij}, is assumed to be composed of two independent components: a component B_i, reflecting true differences between individuals, and a "within-individual" or "error" component, W_{ij}, i.e.,

$$X_{ij} = B_i + W_{ij}$$

assuming that the means are zero. Because B_i and W_{ij} are independent, the variances have the simple relationship

$$\sigma^2_T = \sigma^2_B + \sigma^2_W$$

where σ^2_T is the total variance in X and σ^2_B and σ^2_W are the variances in *B* and W respectively.

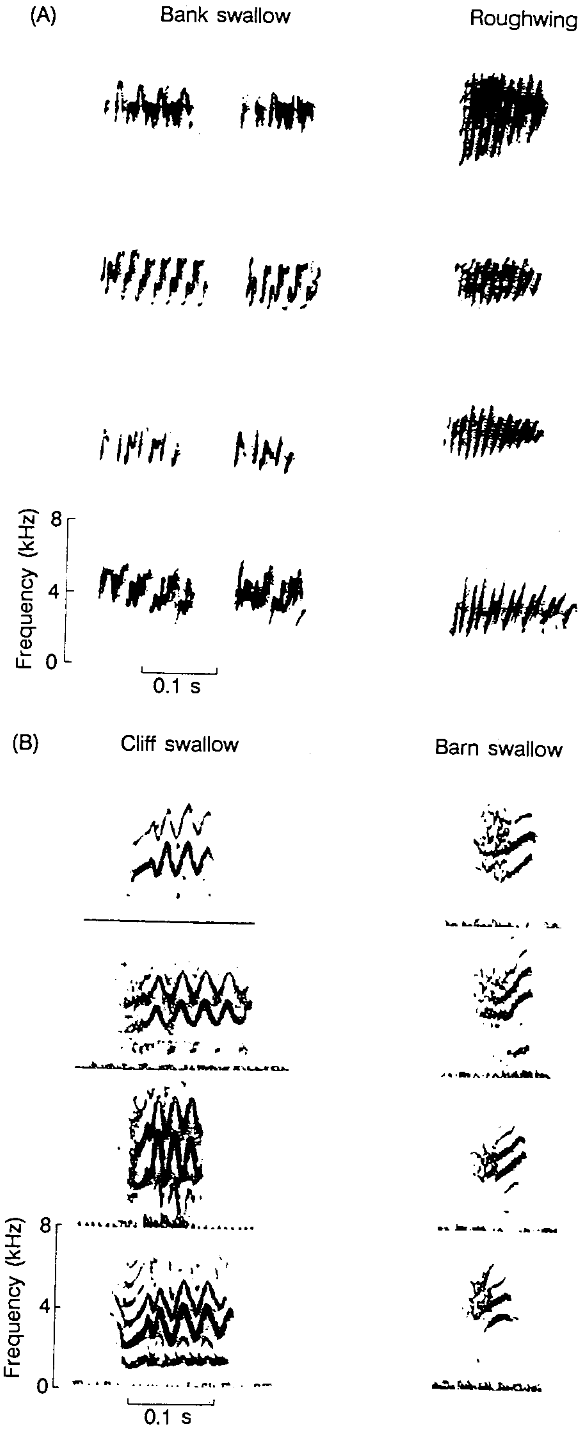
H is then defined as the amount of information needed to reduce the total uncertainty to the within-individual uncertainty, which turns out to be

$$H = \log \frac{\sigma_T}{\sigma_W}$$

H so defined has all the properties an information measure should have (see Shannon & Weaver 1949), including the following: (1) Signature information increases directly with σ_B and inversely with σ_W; (2) $H = 0$ when $\sigma_B = 0$; (3) *H* is an absolute measure with a nonarbitrary zero, the unit of measure being the within-individual uncertainty. The original units of measurement are immaterial. We can compare, say, the amount of signature information conveyed by the amount of dark feathering on the face with that conveyed by the average frequency of a call.

The signature traits typically measured by investigators, however, are inherently multivariate. That is, they can be analyzed into a number of intercorrelated variables. This is certainly true of the calls we are considering here. Studies in this area have generally overlooked the intercorrelations, doing a separate ANOVA on each variable. It is sometimes assumed that the larger the number of significant *F*s obtained in such an analysis, the greater the potential signature information. Such an assumption is incorrect, of course, since much of the information may be shared by variables, i.e. may be redundant.

The problem of variable intercorrelations is circumvented by doing a principal components transformation of the original data. The information analysis is


(A)
Bank swallow
Roughwing
Frequency (kHz)
8
4
0
0.1 s
(B)
Cliff swallow
Barn swallow
Frequency (kHz)
8
4
0
0.1 s

then done on the principal components, which are uncorrelated and preserve the total nonredundant variance (generalized variance) of the original data set. Then the total information H_S is simply the sum of the information H_i in each of the principal components, and

$$H_S = \Sigma\, H_i = \Sigma \log \frac{\sigma_{Ti}}{\sigma_{Wi}}$$

where σ_i is the standard deviation of the *i*th trait.

The analysis of swallow calls begins with extraction of measurements from sonagrams of calls. We have done the complete analysis only on the cliff swallow and barn swallow chick calls (Medvin, Stoddard, & Beecher, unpublished data). An analysis of a small data set of bank swallow and rough-winged swallow chick calls was done using an earlier, preliminary version of this method (Beecher, 1982); analysis of larger data sets using the final method is in progress (Beecher & Beecher, unpublished data).

The call parameters are chosen so as to describe the call as completely as possible with the smallest number of parameters. We used five parameters for the cliff swallows and four for the barn swallows. With the exception of the fifth parameter (cliff swallows but not barn swallows have a periodic frequency modulation of the call), the parameters were comparable for the two species. This comparability condition is essentially irrelevant for our analysis, for the method allows us to compare apples and oranges, or calls and odors, or whatever signature sets we choose. The key condition is that we extract all of the information in the signatures of the two species being compared, or that if we do not, that we err on the conservative side. We have met the second part of this condition. We evaluated our success in extracting most of the information in the calls with this parameter set by reconstructing the original calls from our measurements. While the replicas we got were somewhat crude, they were better for the barn swallow calls than for the cliff swallow calls. Thus, our error is conservative, given our hypothesis, since it means that our method underestimates the information capacity of the cliff swallow calls more than that of the barn swallow calls.

The acoustical measurements derived from the sonagrams are next subjected to a principal components analysis. Simple ANOVAs are carried out on the principal components and between-individual, within-individual, and total variance estimates are obtained according to the Model II (Random Effects) model. The total information is then computed by the formula given above.

The analyses of cliff swallow and barn swallow chick calls are summarized in Table 3, in terms of the original measurements (means, standard deviations based

◄**FIGURE 1.** (A) Sonagrams of the calls of four bank swallow chicks and four rough-winged swallow chicks. (B) Sonagrams of the calls of four cliff swallow chicks and four barn swallow chicks.

TABLE 3. Acoustical Measurements of Cliff Swallow and Barn Swallow Chick Calls

	Cliff swallows					Barn swallows			
	T	f	Δv	Δf	P[a]	T	f	Δv	Δf
Mean	74.4	3.71	1.53	1.25	29.0	67.0	3.84	1.14	0.797
SD Total	31.8	0.395	0.404	0.304	5.12	7.76	0.359	0.183	0.261
SD Within	8.88	0.084	0.142	0.141	0.662	3.62	0.083	0.107	0.151
T	—	−0.42	−0.39	−0.16	+0.37	—	−0.28	−0.53	+0.04
f	—	—	+0.23	+0.58	−0.32	—	—	−0.44	+0.02
Δv	—	—	—	−0.23	+0.50	—	—	—	−0.30
Δf	—	—	—	—	+0.20	—	—	—	—

Note. T = duration of the call (ms); f = peak frequency of the lower voice (kHz); Δv = frequency difference between the upper and lower voices (kHz); Δf = frequency modulation range of the lower voice; P = the period of frequency modulation (ms). Numbers in the bottom half of the table are correlation coefficients based on the between-individual data.

[a] This parameter pertains to cliff swallows only.

on the variance estimates, and the among-individual parameter intercorrelations), not the principal components. Table 3 also provides a brief description of these measurements. The total information capacity, based on the ANOVA of the principal components (not shown in Table 3), is 8.74 bits for cliff swallow calls and 4.57 bits for barn swallow calls. Thus ,as predicted, the information capacity of the signature calls of the colonial cliff swallow is greater than that of the noncolonial barn swallow. This finding of greater information capacity for the colonial species parallels the difference found between the colonial bank swallow and noncolonial rough-winged swallow in an earlier study using the preliminary version of this method (Beecher, 1982). The difference of 4.17 bits between cliff swallow calls and barn swallow calls can be roughly translated to say that approximately 20 times more individuals can be identified, to the same degree of precision, with the cliff swallow signature system.

PERCEPTUAL STUDIES OF SWALLOW CALLS

Several assumptions are implicit in our comparison of the information capacity of cliff swallow and barn swallow chick calls. First, we assume that we have extracted all (or most of) the relevant information from the calls. Second, our method weights all extracted parameters equally (or more precisely, by σ_{Ti}/σ_{Wi}). Third, the method provides a measure of the information capacity of the calls, not of the information extracted by the receiver; in a sense, it presumes an ideal receiver. It should be clear that all of these assumptions relate to a single issue: does our call analysis parallel the birds' perception of the calls? To answer this question, we have carried out a study of the perception of cliff swallow and barn swallow chick calls by cliff swallows and barn swallows, which I will describe briefly here (Beecher, Loesche, Stoddard, & Medvin, 1989; Loesche, Stoddard, Higgins, & Beecher, unpublished data).

We tested the hypothesis that cliff swallow calls are more discriminable than barn swallow calls by training laboratory-reared birds of both species to discriminate among the calls of different individuals of each species. We used the methods of "animal psychophysics" (Stebbins, 1970), training birds to discriminate among calls for a food reward. The reward contingencies (for example, responses to the call of cliff swallow A are rewarded, and responses to the call of cliff swallow B are not) allowed us to circumvent confounding natural contexts and natural decision rules and focus in on signal and perceptual adaptations. On the basis of the call analysis just described, we predicted that cliff swallow calls would be more distinctive, or discriminable, than barn swallow calls.

Our birds were trained as adults to discriminate among chick calls. Birds were trained in a soundproof booth equipped with a loudspeaker, a light, a feeder, and two pecking keys. Pecks on the left, "observing" key turned on a call. In each pair of calls, one was arbitrarily designated the positive (GO) stimulus and the other the negative (NOGO) stimulus. Pecks on the right, "report" key within 1 second of the GO call were reinforced with an opportunity to feed. Pecks within 1 second of a NOGO call, or a failure to respond to a GO call, produced a time-out period during which the houselight was out. A bird received only one pair of calls in a given session, with the two calls always being from different individuals of the same species. The bird was trained on the same pair of calls until it reached a criterion of 85 percent correct responses in a session. Thus, our measure of the discriminability of a call pair was the number of sessions it took to reach this criterion. Training on a new pair of calls began in the next session. The experiment was terminated when a bird had learned five or ten pairs each of cliff swallow and barn swallow calls. We tested two cliff swallows, two barn swallows, and one European starling (*Sturnus vulgaris*), all hand raised. Each of the five birds received unique pairings of calls, and the calls were chosen to be representative of our larger data base for the two species.

The results of the perceptual study are shown in Figure 2. It can be seen that all five birds learned cliff swallow call discriminations more readily on average than they learned barn swallow call discriminations. There is no hint of an advantage for conspecific calls; in fact, the greatest preference for cliff swallow call pairs was shown by one of the barn swallows. These perceptual experiments are consistent with the results of our information analysis of the calls, and they support the hypothesis that natural selection has acted on the chick's begging

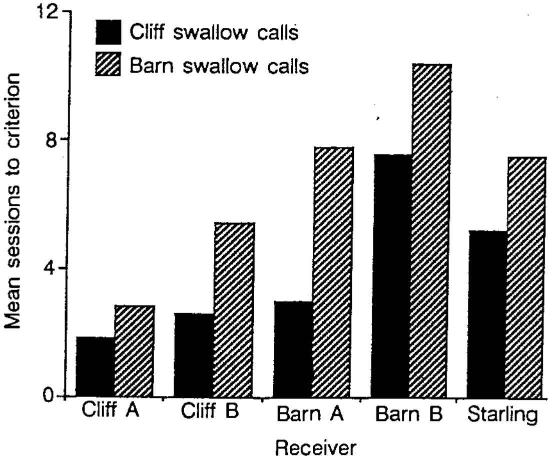


FIGURE 2. Mean sessions to criterion of 85 percent correct responses for discrimination between pairs of cliff swallow calls (dark) and pairs of barn swallow calls (stippled) by two cliff swallows (Cliff A and Cliff B), two barn swallows (Barn A and Barn B), and a starling. Results are based on 10 pairs of calls for the cliff swallow subjects and barn swallow A, and 20 pairs of calls for barn swallow B and the starling.

call in cliff swallows and bank swallows so as to enhance the call's individual distinctiveness. Thus, in these colonial species, this "signature call" is properly considered an *adaptation* for parent–offspring recognition.

At the same time, these studies also show that the difference in discriminability between barn swallow and cliff swallow calls is purely a quantitative one. All birds could in fact discriminate between two calls from different barn swallows. Although these discriminations were presented without the blurring effect of within-individual variability, we believe they show that barn swallow calls can be discriminated, though not so easily as cliff swallow calls.

The one thing we have no evidence for in any of these studies is perceptual adaptations. Our sample size here is too small to rule out such adaptations, and the difficulty of these laboratory experiments, at least with swallows, precludes further attempts to get at such adaptations. Nevertheless, the acoustic sense of passerines is generally highly developed, and it is not clear that there is a great deal of need or room for further perceptual adaptations for this single purpose of better perceiving signature calls. Elsewhere we have argued against the likelihood of perceptual adaptations specifically for analyzing swallow calls (Beecher, et al., 1989; Beecher, Medvin, Stoddard, & Loesche, 1986).

CONCLUSIONS

By combining our various approaches, we have put together a preliminary characterization of the differences among these four species of swallows with respect to the four components of parent–offspring recognition. First, signals are more distinctive in colonial species. The calls of cliff swallow and bank swallow chicks show more individual variation than those of barn swallow and rough-winged swallow chicks. Also, there is face plumage variation in cliff swallow chicks but not in the other species. Second, so far as we can tell, perception of these signals does not differ among the four species. Third, the decision rule used by the noncolonial species appears to be more conservative, giving priority to the location of chicks over signature cues. Fourth, the colonial and noncolonial species use different searching strategies, and eviction and other actions that might be thought of as "recognition" behaviors are seen only in the colonial species. If we imagine that the noncolonial swallows resemble more closely the common ancestors of all four species, then these conclusions form a rudimentary evolutionary scenario as well.

I hope readers will agree that we have gone beyond a simple test of the prediction that colonial swallows should show better parent–offspring recognition than noncolonial swallows and that we have begun to delineate the actual adaptations shaped by natural selection in response to the pressures for recognition. We feel that our summary characterization is charitable, and that we have clearly demonstrated only the "signature" call adaptation. We have just sketched out what I have called "decision rule" or "behavioral" adaptations, and admittedly, the evidence is skimpy. We have argued against "perceptual" adaptations, but again, on the basis of admittedly limited evidence. And of course there are other possible adaptations, such as learning adaptations (discussed in the introduction), which we have not yet investigated.

Finally, I would like to return to the discussion of the relative difficulty of predictions concerning adaptive outcomes as compared to the delineation of actual adaptations or mechanisms. It was straightforward to predict a higher level of parent–offspring recognition in colonial swallow species than in noncolonial swallow species. Had we not found it, we would have suspected that we had some of our basic facts wrong, or that our thinking was muddled in some way. On the other hand, it has not been particularly easy to predict the actual mechanisms—the adaptations—by which colonial swallows solve these recognition problems. I did "predict" signature adaptations, but the point is that this is merely one mechanism by which recognition could be improved, and there are alternatives. If we had failed to find evidence of signature adaptations, the correct course of action would have been to note that such an adaptation is not a *necessary* solution to the problem of recognition, that it might have been *constrained* in some way, and that alternative adaptations (e.g., perceptual) might achieve the same end. The better one's sense of the animals under study, the more likely one may be to correctly "predict" which of several alternative solutions is more likely. For example, elsewhere we have argued that signature adaptations are much more likely than perceptual adaptations in the case of swallow acoustical recognition, essentially on the grounds that there is much more room for elaboration of the calls than for elaboration of the perceptual system (Beecher et al., 1989). But these are hardly predictions of the sort one derives from rigorous theory. Indeed, in these cases it is often hard to disentangle prediction from observation, especially since we tend to shift things into the logical (predictive) format when writing up the research. Did I predict signature adaptations, or did the idea originate in my casual observation that sonagrams of bank swallow calls looked more individually distinctive than those of rough-winged swallow calls? I did decide that the cliff swallow versus barn swallow test was needed as an independent test of this prediction. In the end, however, it makes no difference whether this "prediction" originated in a lucky observation or in good theory. For the value of the results lies not in how we arrived at them, but in whether they ultimately advance our understanding of the evolution of animal behavior.

SUMMARY

I have described a series of studies which tested and confirmed the prediction that parent–offspring recognition is better developed in colonial swallows (bank swallows and cliff swallows) than in noncolonial swallows (northern rough-winged swallows and barn swallows). The primary goal of the studies, however, was to characterize the adaptations underlying the difference. The studies have suggested that elaboration of a chick "signature" call, so that it is more individually distinctive, is one such mechanism. We also provided evidence for adaptations of specific behaviors ("eviction" behavior and searching strategies) and perhaps for adaptations of "decision rules." We provided evidence against perceptual adaptations.