

Kin Recognition in Birds

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I develop the argument that for a true kin recognition system to evolve, selection must act on both parties: not only must recognition be favored in the donor of care, but reliable identification must be favored in the potential recipient of the care. This perspective suggests two complementary hypotheses, which I discuss and evaluate with data drawn from studies of birds. According to the signature adaptation hypothesis, when the sender benefits by reliably identifying itself, selection will act directly on phenotypic characters so as to enhance their signature properties. I summarize our studies on parent-offspring recognition in four species of swallows which are consistent with this hypothesis. In particular, acoustical and perceptual analyses of chick calls show that the calls of colonial swallows are more individually distinctive than are the chick calls of non-colonial swallows. According to the antirecognition hypothesis, when the sender does not benefit by reliably identifying itself, selection will act so as to minimize signature characteristics. I suggest two contexts for research on this hypothesis. The first context occurs when parentage is uncertain due to extrapair copulations and/or egg-dumping, and the second context occurs when there is a long period between the onset of chick mobility and chick fledging, as occurs typically in gulls. In both instances, parents will be favored to recognize genetic relatedness of offspring but offspring will be favored to conceal it. To date, data from bird studies are consistent with the prediction that the interests of chicks win out in this situation.

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INTRODUCTION

Since the seminal paper of Hamilton (1964), it has become apparent that care- and aid-giving behavior is usually predicated on kinship. Kin rec-

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ognition is one mechanism by which an individual can channel assistance to kin. I use kin recognition "in the broad sense" to refer to any case in which an animal discriminates between kin and nonkin on the basis of distinctive cues ("signatures," for short). These cues may be individually distinctive or distinctive of some larger group (say a sibling group). I use kin recognition "in the narrow sense" to refer to cases in which an animal makes such a discrimination despite no prior differential experience with the individuals discriminated (i.e., the kin and nonkin are equally unfamiliar or equally familiar).

Signatures are normally learned at a point when there is strong circumstantial evidence as to kinship and used in later circumstances where there is not. For example, bank swallow parents learn the signature calls of their young while they are in the nest (circumstantial evidence of kinship) and use them primarily to recognize these same young away from the nest later (Beecher *et al.*, 1981a,b). Although these calls do have a genetic component (Beecher *et al.*, unpublished observations), this is immaterial, for the parent's question, so to speak, is not whether the target bird is kin, but whether it is the same bird it cared for earlier at the nest (if it is, it must be kin). Bird song, although learned and thus not directly related to genotype, may still be used for kin recognition in some circumstances. Several workers have proposed that females optimally inbreed or outbreed by choosing males whose song resembles the song they heard as youngsters. Baker and Cunningham (1985) argue that female white-crowned sparrows select the most compatible genotype by choosing males of the same dialect type the females heard near the natal nest. McGregor and Krebs (1982) present evidence that a female great tit will choose a mate whose song resembles—but not too closely—the song of her father, which she learned early in life. They favor the "optimal outbreeding" hypothesis of Bateson that females are choosing genotypes similar, but not too similar, to their own (Bateson, 1980, 1983; discussed below). Note that the bird song example involves "phenotype matching" (Holmes and Sherman, 1982, 1983) or "signature matching" (Beecher, 1982), in which the target individual's signature is compared to the signature of a different individual (or individuals) learned earlier.

THE EVOLUTION OF RECOGNITION SYSTEMS

The general kin recognition process can be described as follows. One animal (the receiver) seeking another individual (the target individual) is confronted by an individual (the sender) that may or may not be the target individual. As a particularly clear example, consider a parent seeking its offspring in the crèche, where any chick taken at random would almost

certainly not be the target individual. The kin recognition process consists of four logically independent components.

(1) The sender must provide *cues* as to its identity and/or genotype (“signature” cues). Although we cannot 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 that circumstantial evidence is inadequate).

(2) The receiver must process these cues in order to *perceive* the difference between target and nontarget individuals. This is probably often a template-matching process in which the receiver compares the signal to some model contained in its memory.

(3) 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, and the benefits of the two types of correct decisions. For example, in a solitary species the probability of finding an unrelated chick in the home nest might be so tiny that selection would have favored the decision rule, “always accept young you find in the nest” (cross-fostering experiments often suggest such a rule when parents accept clearly different foster young).

(4) 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 might evict it or avoid feeding it. Another class of “recognition behaviors” includes paying attention to signature cues, carefully inspecting young in the nest before feeding, and so on. Another example is the feeding chase of adelic penguin parents (Spurr, 1975; Thompson, 1981): before they will feed young, parents require them to leave the creche and follow them on a lengthy chase. This added cost gives the parent time in which both to assess the identity of the young (it calls throughout the entire chase) and, perhaps, to prevent unrelated young from trying to freeloader a meal (the lower the cost to soliciting a free meal, presumably the more common will be freeloading attempts).

The key point is that natural selection can promote recognition by acting appropriately on any of the *signal, perceptual, decision, and behavioral* components of recognition. Among the possible actions, five stand out. Selection can (1) increase signature variation among individuals and/or decrease it within individuals, thus increasing information about individual identity; (2) increase the signature/genotype correlation, thus increasing information about relatedness; (3) increase perceptual sensitivity or attention to the signature traits, thus allowing receivers to more readily discriminate among senders; (4) modify the receiver’s decision

rule; and (5) shape behaviors in sender and receiver facilitating identification and recognition.

In discussions of the evolution of recognition systems, it is often assumed that widespread genetically based phenotypic variation is present at the outset of the evolutionary process. Selection, then, is presumed to act primarily by directing the receiver's attention to the ubiquitous signature information already present and by shaping the receiver's decision rules and recognition behaviors. In this paper I argue from a different perspective, from the perspective of the sender. I argue that reliable identification signals (signatures) are a necessary condition for recognition and hence recognition is controlled as much by the sender as it is by the receiver/recognizer. This perspective suggests that whether or not recognition will evolve in a given situation depends on whether or not it benefits the *sender*. I believe that this perspective is a much more fruitful one for considering recognition generally, since recognition probably always benefits the recognizer but only sometimes benefits the sender. This perspective suggests two complementary hypotheses. First, in circumstances where the sender benefits by reliably identifying itself, selection will act directly on phenotypic characters so as to enhance their signature properties. I refer to this as the *signature adaptation* hypothesis. Conversely, in circumstances where the sender does *not* benefit by reliably identifying itself, selection will act so as to minimize signature characteristics. I refer to this as the *antirecognition* hypothesis. I consider recent research on kin recognition in birds from the perspective of these hypotheses. I then consider the signature adaptation hypothesis in some detail in the context of our research on swallows.

AN EXAMPLE OF NARROW-SENSE KIN RECOGNITION IN BIRDS

Despite the surprising plethora of cases of narrow-sense kin recognition discovered since approximately 1978 (see other papers in this issue), the only clear example discovered in birds to date is Bateson's (1982, 1983) demonstration of kin recognition in Japanese quail. Indeed, until Bateson's work, all well-documented examples of narrow-sense kin recognition in insects, anurans, and mammals appeared to involve olfactory signals. Bateson has shown that quail have quite refined kin recognition abilities; the cues, although not yet investigated, are probably visual, and possibly acoustic as well. Bateson (1982) found that female quail raised with siblings approached novel first cousins more frequently in a test apparatus than either novel third cousins, siblings, or unrelated individuals. Moreover, quail reared in mixed groups (kin and nonkin) preferentially associated with siblings over nonsiblings (Waldman and

Bateson, 1988). From these and other data, Bateson has argued that female quail may be pursuing a strategy of "optimal outbreeding." By favoring males that resemble known relatives, but do not resemble them too closely, females may be making an optimal compromise between the costs and the benefits of inbreeding and outbreeding (Bateson, 1980, 1982, 1983; see also Shields, 1983). As mentioned above, McGregor and Krebs (1982) have presented evidence suggesting that great tit females may choose their mates in a similar way, using song resemblance to their father as an indicator. The Bateson research shows that narrow-sense kin recognition can evolve in birds, at least in certain favorable circumstances. This demonstration is crucial for the ensuing discussion, for it provides a context in which we may judge failures of such recognition.

PARENTAL UNCERTAINTY: A CONTEXT FOR KIN RECOGNITION

There is now a great deal of evidence to suggest that in many birds, parents cannot necessarily use location in the home nest as a completely reliable predictor of relatedness. A number of electrophoresis studies on passerine birds have shown that a fairly high fraction of offspring is unrelated to one or both of the putative parents (Gowaty and Karlin, 1984; Gavin and Bollinger, 1985; Westneat, 1987). There are two sources of parental uncertainty. First, extrapair copulations are evidently much more common than was once realized. Second, "egg-dumping" is likewise much more widespread than had been realized and may even be a relatively common parental strategy in some colonial species (Brown, 1984).

The parental uncertainty resulting from extrapair copulations and egg-dumping would certainly seem to favor kin recognition by parents based on self-matching. Self-matching would seem to be virtually the only mechanism available to the parent for distinguishing offspring from unrelated young within a brood. The antirecognition hypothesis, however, suggests that we should not expect to find such a mechanism in this situation. Let us assume that in the ancestral condition parents cared for young in the nest and there was certainty of paternity. As conditions promoting uncertainty of paternity evolved (e.g., coloniality), so too did selection for parental certainty mechanisms, such as mate-guarding, nest-guarding, and narrow-sense kin recognition. The last mechanism, however, requires that offspring signal their genetic identity. While we now know that this is possible and that many (perhaps most) signature cues have a genetic component, the catch is that such identification would not benefit the young. Clearly a chick in a nest would not benefit by signaling that it is unrelated to the parent at that nest. A chick that *is* related would benefit by so signaling *only* if it were in a brood in which some other

chick signaled that it is not related (in which case the parent could redirect care from the latter to the former). The conditions here are not favorable for the evolution of such a kin recognition mechanism, and we should expect to find such a mechanism only if signatures are not under the control of the sender, e.g., if genetic information is incidentally present in the signature.

Negative predictions are always difficult, since one is forced to look for lack of evidence to prove the point. We begin with the positive context that kin recognition by self-matching is certainly possible. There is evidence for self-matching in a number of species [for reviews see Holmes and Sherman (1983) and other papers in this issue]. Additionally, the kin recognition seen in Japanese quail may involve self-matching, although this point cannot yet be conclusively made (Waldman and Bateson, 1988). To date, however, there is no evidence for kin recognition by self-matching in any bird where parental uncertainty is a potential problem. In fact, many cross-fostering experiments have shown that parents learn the signatures of the young while they are in the nest, usually shortly before fledging, and that parents will evidently learn those of unrelated foster chicks as readily as those of offspring. For example, we have done such cross-fostering experiments with bank swallows, a good candidate species for parental uncertainty [extensive egg-dumping has been demonstrated in the other North American colonial swallow, the cliff swallow (Brown, 1984)]. We have found that not only are foster chicks accepted and cared for after fledging (if fostered before signatures develop), but also offspring that are fostered to another nest and happen to return to the home nest are rejected by their true parents! In further experiments in which we carried out more sensitive tests, we found no evidence for kin recognition by self-matching (Beecher *et al.*, unpublished observations).

As mentioned above, there are a number of cases of kin recognition discovered to date that are thought to involve self-matching. For example, Holmes and Sherman (1982, 1983) so interpret their finding that Belding's ground squirrels behave more altruistically toward littermate full sisters than toward littermate half-sisters. The essential difference between these cases and the parental uncertainty case we have just considered is that in the former the sender can benefit by a reliable signal (when it interacts with a more closely related kin) as well as lose by the signal (when it interacts with a less closely related kin). In the parental uncertainty case, as just indicated, the major effect of the signal for the sender (the unrelated chick) is a cost. In conclusion, the antirecognition hypothesis predicts that kin recognition by self-matching should occur only in those situations where a reliable signal of genotypic identity benefits the sender as well as the recognizer. The parental uncertainty situation is one where it does

not, and thus I predict that we will not find cases of kin recognition by self-matching in this situation.

FAILURES OF PARENTAL RECOGNITION IN COLONIAL GULLS

As more studies look at parental recognition of offspring and offspring recognition of parents, a number of cases have been found where young recognize parents, but not vice versa. Although there are alternative interpretations (and we consider two below), the phenomenon appears to be robust and widespread in gulls. In several gull species, parents fail to recognize their young until the young begin to fly, despite the fact that such recognition would appear to be useful: from a few days after hatching, young are mobile and may stray from nest to nest in the colony. Moreover, we know that recognition is possible since young recognize their parents by voice shortly after hatching and parents do learn the calls of their young eventually, shortly before the young begin to fly at about a month of age (reviews given by Beer, 1979; Shugart, 1988). The oft-stated but incorrect generalization that herring gull parents recognize their chicks a few days after hatching is based on cross-fostering experiments in which recognition was expressed primarily by the chicks and only secondarily by the parents. This asymmetry in recognition is surprising given the conventional argument that the onus of recognition is on the parent: parental care benefits a parent only if the recipient young is related, but it benefits the young no matter what their relationship (Beecher, 1981, 1982; Holmes and Sherman, 1983).

Clearly any theory of kin recognition should suggest why parental recognition does not evolve in a situation where it is clearly possible and apparently would be desirable for the parent. Our sender's perspective is again helpful in explaining this outcome in gulls and, in fact, revealing that it is not that different from what has been seen in other colonial species. It has been noted for quite some time—the generalization may have been made first by Davies and Carrick (1962)—that in those species where parental recognition occurs, it develops just shortly before chick mobility. In ground-nesting gulls, there are essentially two such periods: first, when the young begin to move about on the ground a few days after hatching, and, second, when the young begin to fly at about a month. The key point is that the chick does not need the parent to recognize it in order to feed it before fledging, for it will be fed merely by being in the nest. While a recognizable call might benefit the chick when lost away from the nest by facilitating the parental searching, it may not be necessary if the parent calls and searches on finding a missing chick at the nest; if the chick recognizes the calling parent, it can home to the parent and

nest. Moreover, when away from the nest there is a danger to having a reliable signature, namely, that unrelated parents may reject or attack you. Gull adults can easily injure or kill a chick. Moreover, an abandoned chick may be adopted by foster gulls if it makes it to another nest and acts as if it belongs there (e.g., Holley, 1984). Thus reliable signatures would appear to have a net cost to gull chicks, and we again have the conditions for the antirecognition hypothesis. It is only when the young fledge, and the nest is abandoned, that a reliable signature is required, for the young can no longer expect to receive parental care simply by being in a particular place.

SIGNATURE ADAPTATIONS: A COMPARATIVE, QUANTITATIVE APPROACH

In this section I turn to an explicit test of the signature adaptation hypothesis. The hypothesis predicts that, if we compare several closely related species which vary with respect to selection pressure for recognition, (1) the variation in the degree of recognition will correspond to the variation in the degree of selection for recognition, and (2) signature variation will be greater in the species requiring recognition. The second prediction, the key one for this hypothesis, requires a quantitative method for comparing two species with respect to the degree of signature complexity, the amount of information about identity conveyed by a signature.

The presence of colonial living in a species is almost a *prima facie* case for strong selection for recognition. Typically intermingling of young is inevitable and extensive in a colonial species, and there is great pressure on parents to recognize their young (for an exception see Cullen, 1957). With this in mind we turned to the North American swallows. They make an excellent group for research on adaptations to coloniality since they are a rather uniform group, with coloniality being one of the major dimensions distinguishing among the species. Of the seven major North American swallow species, two are fully colonial, the bank swallow and cliff swallow. By "colonial," I mean that they generally nest in large groups, aggregate their nests, and show reproductive synchrony as well as social coordination of some other activities, such as nest material collection and foraging [see Medvin and Beecher (1986) and Beecher and Stoddard (1988) for a discussion of this issue]. We have studied two colonial–noncolonial pairs of these species. The first pair is the colonial bank swallow (*Riparia riparia*) and noncolonial northern rough-winged swallow (*Stelgidopteryx serripennis*). I reported on these results in my earlier review of kin recognition (Beecher, 1982). Since I developed the signature adaptation hypothesis in the course of this study, I felt that a

second, independent test of the hypothesis was required, and I turned to a second colonial–noncolonial pair, the colonial cliff swallow (*Hirundo pyrrhonata*) and noncolonial barn swallow (*Hirundo rustica*). This second pair is particularly interesting, as the two species are especially closely related—they are congeners and hybridize on occasion (Martin, 1980). I review here our work on swallows, focusing mainly on parental recognition of young and emphasizing our newer work on the cliff swallow–barn swallow pair (Beecher *et al.*, 1981a,b, 1985, 1986; Beecher and Beecher, 1983, 1988; Stoddard and Beecher, 1983; Medvin and Beecher, 1986; Medvin *et al.*, 1988).

Observational and Experimental Evidence

In all four of the swallow species we have studied, 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. In all four species, there is a period ranging from a day to a week in which the young will spend some of the time at the nest and some of the time away from the nest. In the colonial bank swallow and cliff swallow this interim stage is usually longer than it is in the noncolonial rough-winged swallow and barn swallow, in part because in the colonial species parents often leave their just-fledged young in creches quite near the colony; the two noncolonial species, even when they are found in small groups or when their nests are relatively clumped, avoid mixing their young with others in the early days after fledging. In any case, during the interim period chicks and parents may become separated and may fly about looking for one another near the colony or nest site. This is particularly noticeable in bank swallow and cliff swallow colonies, because of the numbers of birds and because newly fledged young may actually fly into the wrong nest. Reciprocal calling is a conspicuous feature of these events, and one forms the casual impression that calls are critical to 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 or away. This call is therefore ideally suited to be an identifying or “signature” call.

We hypothesized that the begging call of bank swallows and cliff swallows has been elaborated for signature function, specifically that it is more individually distinctive than the homologous call in rough-winged swallows and barn swallows. We assumed in this analysis that coloniality has evolved relatively recently in the two colonial swallows (Mayr and Bond, 1942). Particularly in the case of the cliff swallow–barn swallow pair, it is likely that the noncolonial species resembles the presumed non-

colonial common ancestor of the two species. We carried out two types of field experiments to evaluate parent–offspring recognition in these species. In our cross-fostering experiments, we exchanged approximately half the young between two same-aged nests. 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 (as mentioned earlier, usually shortly before fledging). The only case we consider below, therefore, is cross-fostering carried out just before fledging. The cross-fostering experiment is rather crude, however, in that even if recognition is found, it is generally not possible to ascertain who recognizes whom or what. In the playback experiment, on the other hand, we can separate parental recognition of chicks from chick recognition of parents. We consider only our experiments on parental recognition here.

We did parallel playback studies on all four species using the same basic procedure. As in the cross-fostering experiments, the playback experiments were 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. The experiment began with us removing the young from the nest, temporarily, and placing loudspeakers in each of two nests, on either side of the empty home nest. When one of the parents returned to the nest, it would begin to search for the missing young. 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 chicks. We took various measures of recognition, such as approaching a loudspeaker, hovering in front of it, or trying to get into the nest.

The results of the cross-fostering and playback experiments are summarized in Table I. The results of both sets of experiments suggest that

Table I. Summary of Field Tests of Parental Recognition in Swallows

Species	Cross-fostering	Playback	Conclusion
Bank swallow ^{a,b}	Yes	Yes	Yes
Rough-winged swallow ^c	No	No	No
Cliff swallow ^{a,d}	—	Yes	Yes
Barn swallow ^e	No	No	No

^a Colonial species.

^b Beecher *et al.* (1981b).

^c Hoogland and Sherman (1976); Beecher and Beecher (1988).

^d Stoddard and Beecher (1983).

^e Medvin and Beecher (1986).

parent–offspring recognition is well developed in the colonial bank swallow and cliff swallow but absent or weak in the noncolonial rough-winged swallow and barn swallow. Our failure to find parental recognition in cross-fostering experiments on barn swallows and rough-winged swallows counters the argument that their failure to recognize in the playback experiment is due to their normal use of nonvocal cues. In addition, circumstantial evidence suggests that barn swallows do not use visual cues (essentially the only other source of cues for individual recognition in birds). Cliff swallow chicks show marked individual variation in face color pattern, while barn swallow chicks show no such variation. Although we have not investigated whether cliff swallow parents use this visual variation for recognition, this species difference is opposite that expected if barn swallows 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 (the same cannot be said for the acoustic modality).

Information Analysis of Swallow Chick Calls

To analyze the relative information capacities of chick calls for colonial and noncolonial swallow species, I developed a model for applying the Shannon information measure (Shannon and Weaver, 1949; Beecher, 1988). The model is essentially identical to the Model II (random effects) analysis of variance (e.g., Sokal and Rohlf, 1981). Using an earlier version of this model, I have shown that the information capacity of the bank swallow signature call is considerably greater than that of the homologous begging call in the rough-winged swallow (Beecher, 1982). As indicated above, however, the signature adaptation hypothesis was developed in the course of (not proposed before) the bank swallow study; in fact, it was my first comparisons of the sonagrams of bank swallow and rough-winged swallow chick calls that first gave me the idea for this information analysis. I thus felt that an independent test was required, and we turned to the cliff swallow–barn swallow pair for this analysis. The results of this study are described in detail by Medvin *et al.* (1988).

The analysis begins with extraction of measurements from sonagrams of calls. We choose parameters so as to describe the call as completely as possible with the fewest 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, we err on the conservative side. We have met the second 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 get are 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. This analysis conserves the total nonredundant variance in the original set of measurements. Simple ANOVAs are carried out on the principal components, and between-individual, within-individual, and total variance estimates are obtained according to Model II (random effects). The total information is

$$H = \sum \log \sqrt{S_{Ti}^2/S_{Wi}^2}$$

where S_{Ti}^2 and S_{Wi}^2 are the total and within-individual variance estimates for the i th principle component.

The analyses of cliff swallow and barn swallow chick calls are summarized in Table II, in terms of the original measurements (means, standard deviations based on the variance estimates, and among-individual parameter intercorrelations), not the principal components. Table II also provides a brief description of these measurements. The total information capacity, based on the ANOVA of the principal components (not shown in Table II), 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 a greater information capacity for the colonial species parallels the difference found between the colonial bank swallow and the noncolonial rough-winged swallow in an earlier study using a preliminary version of this method (Beecher, 1982). The difference between cliff swallows and barn swallows of 4.17 bits 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.

Jouventin (1982) has done a similar analysis using a less-sophisticated quantitative approach. Comparing several species of penguins varying in degree of coloniality, he has shown that the signature calls of the more

Table II. Means, Standard Deviations (Based on Variance Estimates), and Correlation Coefficients for Information Analysis (Original Measurements, Not Principal Components)^a

	Cliff swallows					Barn Swallows				
	<i>T</i>	<i>f</i>	Δv	Δf	<i>P</i>	<i>T</i>	<i>f</i>	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	
<i>T</i>	—	-0.42	-0.39	-0.16	+0.37	—	-0.28	-0.53	+0.04	
<i>f</i>	—	—	+0.23	+0.58	-0.32	—	—	-0.44	+0.02	
Δv	—	—	—	-0.23	+0.50	—	—	—	-0.30	
Δf	—	—	—	—	+0.20	—	—	—	—	

^a Parameters are as follows: (*T*) duration of the call; (*f*) peak frequency of the lower voice; (Δv) frequency difference between the upper and the lower voices; (Δf) frequency modulation range of the lower voice; (*P*) the period of frequency modulation. This last parameter pertains to cliff swallows only. Numbers in the bottom half of the table are correlation coefficients based on the between-individual data.

colonial species are more complex. Thus his results parallel ours and support the signature adaptation hypothesis.

Perceptual Studies of Swallow Calls

Returning to our comparison of the information capacity of cliff swallow and barn swallow chick calls, several assumptions are implicit in this analysis. 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. 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 describe briefly here.

The details of our perceptual studies are given by Beecher *et al.* (1988) and Loesche *et al.* (1988). We tested the hypothesis that cliff swallow calls are more discriminable than barn swallow calls by training lab-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 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) allow us to circumvent confounding natural contexts and natural decision rules and focus 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 loudspeaker, light, feeder, and two pecking keys. Responses on the left, "observing" key turned on a call. For each pair of calls, one was arbitrarily designated the positive (GO) stimulus, and the other the negative (NOGO) stimulus. Keypecks on the right, "report" key within 1 s of the GO call were reinforced with an opportunity to feed. A keypeck within 1 s of a NOGO call, or a failure to respond to a GO call, produced a timeout 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 remained on a particular call discrimination until it reached a criterion of 85% correct responses in a session. Our measure of the discriminability of a call pair was thus the number of

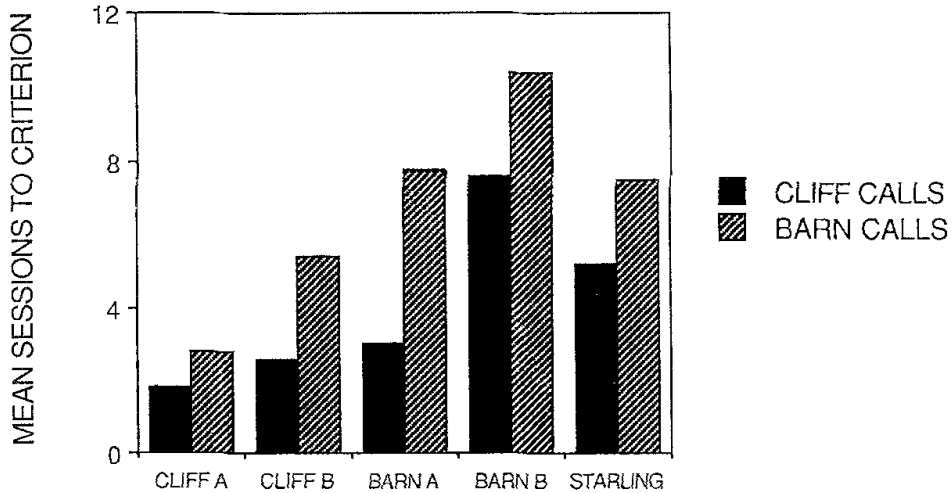


Fig. 1. Mean sessions to criterion for five birds. For cliff A, cliff B, and barn A, the data represent five pairs each of cliff swallow calls and barn swallow calls (10 pairs total); and for barn B and the starling, 10 pairs each (20 pairs total).

sessions to reach this criterion. Training on a new pair began in the next session. The experiment was terminated when a bird had learned five 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 Fig. 1. 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 biggest 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 support the hypothesis that natural selection has acted on the chick's begging 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.

CONCLUSIONS

I have argued that for a true recognition system to evolve, selection must act on both parties: not only must recognition be favored in the donor of care (which should always be the case), but reliable identification

must be favored in the potential recipient of the care (and this will not always be the case). The costs and benefits to the two parties in a recognition system should be evaluated in terms of the baseline or ancestral condition. Specifically, a kin recognition system will evolve only if both parties fare better with it than they did without it. Many previous arguments [including my own (Beecher 1981, 1982)] have suffered by attempting to frame the argument in absolute adaptationist terms rather than as a true evolutionary scenario, with kin recognition evolving (or failing to evolve) from some earlier condition. In circumstances where the benefits of being recognized exceed its costs, selection will act to increase signature information (as to identity and/or genotype). Our swallow research provides support for this signature adaptation hypothesis, indicating that colonial swallows have responded to strong selection for more individually distinctive calls. In circumstances where the costs of being recognized exceed its benefits, selection will act to minimize signature information. I have suggested two possible areas for investigating this antirecognition hypothesis. First, in species where there is uncertainty of paternity or maternity due to extrapair copulations and/or egg-dumping, parents will be favored to recognize genetic relatedness of offspring but offspring will be favored to conceal it. Second, in species where the ancestral condition is parents feeding young at the nest, chicks will be favored to conceal relatedness until fledging. I suggest that this condition may be widespread in birds but especially conspicuous in gulls because of the long period during which young are mobile but have not yet left the nest area.

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