Behaviour 118 (1-2) 1991, E.J. Brill, Leiden

SIGNATURE VERSUS PERCEPTUAL ADAPTATIONS FOR INDIVIDUAL VOCAL RECOGNITION IN SWALLOWS

by

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(With 2 Figures)
(Acc. 7-II-199)

Introduction

Colonial living generally is associated with strong selection pressure for individual recognition (FALLS, 1982; JOUVENTIN, 1982; COLGAN, 1983; BEECHER, in press). For example, in most colonial species parents must find their offspring in large groups of like-aged young. A straightforward prediction concerning such species is that natural selection will have shaped adaptations for recognition (in the sense of WILLIAMS, 1966). This "bottom line" prediction does not suggest, however, what mechanisms may have been the target of selection nor how they might have been shaped. We have used statistical decision and signal detection theories to derive a model of the recognition process (GREEN & SWETS, 1966; BEECHER *et al.*, 1989; BEECHER, in press). In this model, the recognition process is analyzed into the following four components, described here in terms of parents attempting to discriminate between offspring and unrelated young.

1. The offspring must provide cues as to its relatedness to its parent ("signature" cues). Although we should not necessarily expect that the

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[2] This research was supported by grants from the National Science Foundation and the University of Washington Graduate School Research Fund. We thank our many undergraduate assistants and Inger BEECHER, DVM, for helping with bird care. Thanks also to Eliot BRENOWITZ, Warren HOLMES, Peter MARLER, Doug MOCK, Trish SCHWAGMEYER, Joan SINNOTT, Ken YASUKAWA, and an anonymous reviewer for their comments on earlier versions of this manuscript.

offspring will always signal "honestly", it is clear that the parent requires such cues if it is to have any basis for recognition (for a discussion of cases in which offspring might be selected to conceal their identity, see BEECHER, 1988a).

2. The parent must process these cues in order to perceive the difference between offspring and unrelated young. Presumably the parent compares the signal to some model contained in its memory.

3. The parent must decide whether the individual under scrutiny is in fact its offspring. In theory, the parent's decision rule should be based in part on the *a priori* probability of the young under scrutiny being offspring, the costs of the two types of error (*i.e.*, accepting unrelated young or rejecting true 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 small that selection would favor the decision rule, "always accept young you find in the nest".

4. The parent must take appropriate action. For example, if the encounter is in the home nest, and the parent decides that the young under scrutiny is an intruder, the parent could evict it, or not feed it.

The key point is that natural selection can shape the recognition process by acting on any of the signature, perception, decision and action components. Selection for recognition can (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; (3) modify the decision rule; (4) shape recognition behavior.

In this study we focus on signature and perceptual mechanisms, and attempt to separate them from one another and from the decision/action components. We chose two closely-related species for which there is an ecological basis for predicting differential selection on mechanisms for parental recognition of offspring. Cliff swallows (*Hirundo pyrrhonota*) typically live in large, dense colonies in which young intermingle extensively after fledging but while dependent on their parents (STODDARD & BEECHER, 1983). Barn swallows (*H. rustica*) usually nest solitarily or in small, loosely-associated groups; in either case, they tend to raise their young apart from other broods so that recognition is rarely a problem (MEDVIN & BEECHER, 1986). In colonial-nesting swallow chicks, a distinctive begging or 'signature' call develops between 14 and 18 days of age, just before the chick fledges from the nest at about 21 days of age (BEECHER, BEECHER & HAHN, 1981; STODDARD & BEECHER, 1983). In a field playback experiment, STODDARD & BEECHER (1983) found that cliff swallow parents discriminated between the calls of their offspring and unrelated young, and used this acoustic recognition system to find their young in creches of hundreds of fledglings. However, playback and cross-fostering experiments showed that barn swallow parents failed to respond to differences between the calls of their own and unrelated young, even though barn swallow chicks give begging calls similar to those of cliff swallow chicks in analogous circumstances; this lack of discrimination was observed in barn swallows nesting in small colonies as well as those nesting solitarily (MEDVIN & BEECHER, 1986). We attribute this species difference in discrimination to a history of strong selection for parent-offspring recognition in the colonial cliff swallow, and a lack of same in the noncolonial barn swallow. Comparable species differences in discrimination have been obtained for the colonial bank swallow (*Riparia riparia*) and the noncolonial northern roughwinged swallow (*Stelgidopteryx serripennis*) (HOOGLAND & SHERMAN, 1976; BEECHER *et al.*, 1981; BEECHER & BEECHER, unpubl.).

We will consider two evolutionary hypotheses. According to the signature adaptation hypothesis, natural selection makes the signals themselves more individually distinctive, by increasing inter-individual variation and/or decreasing intra-individual variation in signal parameters (BEECHER, 1982, 1988a). According to the perceptual adaptation hypothesis, natural selection acts on the receiver's perception of the signals used for individual recognition. These two hypotheses are not mutually exclusive.

The present study was designed to test possible perceptual and signature adaptations for acoustic individual recognition in cliff swallows. Using the methods of animal psychophysics, we compared the perception of cliff swallow and barn swallow chick calls by adults of both species. Signature adaptations would be suggested if we found that the calls of different cliff swallows are more readily discriminated than those of different barn swallows, by listeners of either species; this outcome would imply selection on cliff swallow calls for greater individual distinctiveness. Perceptual adaptations would be suggested if we found that cliff swallow listeners discriminate among calls more readily than do barn swallow listeners; this outcome would imply selection on cliff swallow listeners for acute discrimination of call differences.

By the perceptual adaptation hypothesis, cliff swallow listeners should be better than barn swallow listeners at discriminating among cliff swallow calls and other similar stimuli. Other similar stimuli would include barn swallow calls, because the two species are closely related,

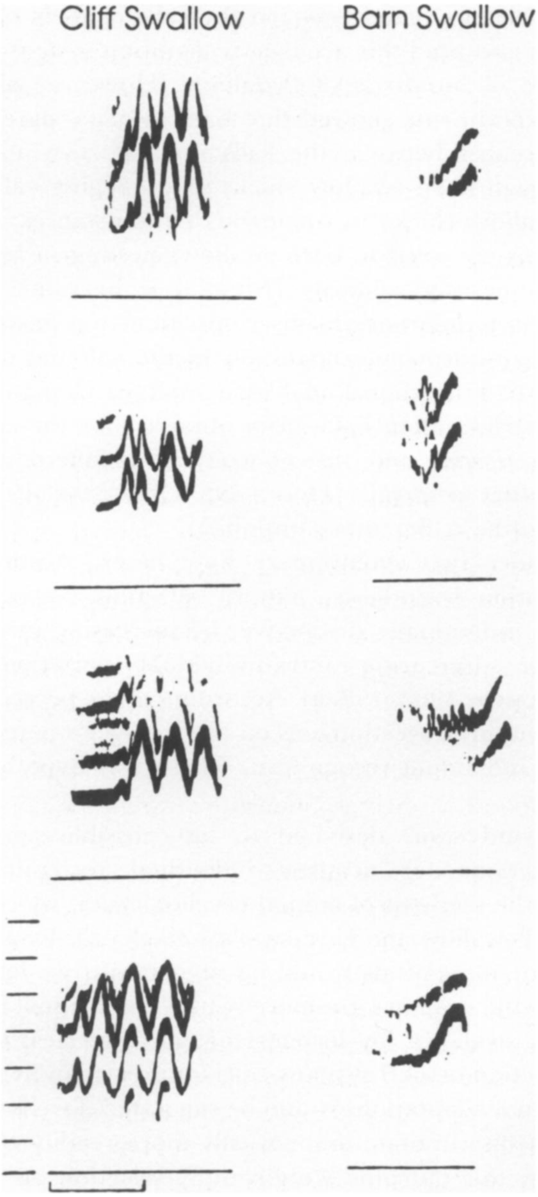

Fig. 1. Sonagrams of eight of the 26 begging calls of barn swallow and cliff swallow chicks used in the present study. Calibration markers for frequency = 0-8 kHz, time marker = 0.05 sec.

and the chick call has the same basic acoustic structure in both (Fig. 1). The major structural difference between cliff swallow and barn swallow calls is a periodic frequency modulation present only in the cliff swallow call. Thus a perceptual adaptation that facilitates the discrimination of cliff swallow calls may well also facilitate the discrimination of barn swallow calls. The perceptual adaptation hypothesis therefore predicts that cliff swallows will be better than barn swallow listeners at discriminating among swallow calls in general, regardless of whether they are cliff swallow calls or barn swallow calls.

The signature adaptation hypothesis has received support from an analysis of the sonagrams of swallow chick begging calls (BEECHER *et al.*, 1986; BEECHER, 1989; MEDVIN *et al.*, unpubl.). This analysis showed that cliff swallow signature calls are more variable among individuals and less variable within individuals than are the analogous calls of barn swallow chicks, such that the estimated information capacity of the former was about 20 times greater than that of the latter. Nevertheless, such objective measures may extract different information than the birds actually use, and the ideal test of the signature adaptation hypothesis is a perceptual one, where the animals themselves analyze the calls.

The laboratory conditioning procedure we used in this study provides a major advantage over field tests. In a field experiment, we cannot induce swallows to respond to heterospecific signals, or to the calls of unrelated conspecifics, much less test their discrimination of such calls. In a field playback test, a bird responds differentially to signals according to their biological significance, rather than their perceptual (*i.e.*, discriminable) differences. Given two calls that are perceptually different, a bird will respond differentially to them in the field only if one is more biologically significant than the other (*e.g.*, calls from an offspring and an unrelated chick); it will respond equally to them if they are of equivalent biological significance (*e.g.*, calls of two related chicks, two unrelated chicks, or two heterospecific individuals). In the laboratory, however, we can test a bird's ability to discriminate between biologically equivalent test calls, by making food reward contingent upon differential responses to the stimuli. Note in this context the distinction between the terms recognition and discrimination as we use them here. Recognition typically (but not always) refers to an internal, unobservable process that may or may not result in differential responses, depending on the biological relevance of a stimulus. Discrimination refers to observable, differential responses to stimuli. Thus, as noted above, an animal may recognize differences between related and unrelated young, but not necessarily respond differentially to them. Only in the laboratory can we distinguish between the processes of recognition and discrimination.

Methods

Subjects.

Our subjects were two barn swallows, three cliff swallows, and one European starling (*Sturnus vulgaris*). We included a non-swallow because the logic of the signature adaptation hypothesis suggests that any bird should find cliff swallow calls more discriminable than barn swallow calls. We took birds from the nest at 5-8 days of age, thus eliminating species differences in vocal experience with swallow chick begging calls, which develop at 14-18 days of age. Birds were hand-reared in a shared aviary and trained as first- and second-year adults.

Stimuli.

The stimulus set consisted of one call each from 14 different cliff swallow chicks and 12 different barn swallow chicks, randomly selected from a master file of about 1000 field recordings. Four examples from each set are shown in Fig. 1. Calls were analyzed on a Kay 6061 B Sonagraph. The filter was set to give an effective bandwidth of 180 Hz, the optimal setting for these signals (BEECHER, 1988b). This bandwidth value was obtained by setting the "narrow-band" filter on the 16 kHz range, the plug-in scale magnifier to 25% of full scale, and the tape recorder to half speed. The measured acoustic parameters were: (1) duration of the call, (2) peak frequency of the lower voice, (3) frequency difference between the upper and lower voices, (4) range of frequency modulation of the lower voice, and (5) period of frequency modulation. The different voices in the calls were identified as such if they occurred simultaneously and were not harmonically related to each other. The frequency modulation parameter pertains to cliff swallow calls only, as the frequency modulation in the barn swallow chick call is a simple unidirectional sweep. There were no significant differences between sample and master call sets on the mean or variance of any parameter, so we consider the sample sets representative. All calls were digitized at 45 ksamples/sec, low-pass filtered on an 8-pole Butterworth with a corner frequency of 7 kHz, and high-pass filtered on a 4-pole Butterworth with a corner frequency of 1 kHz. Stimuli were presented to the birds using a micro PDP-11 computer (STODDARD, 1990).

Procedure.

We used a food-reinforced keypeck procedure to train the adult birds to discriminate among calls of different chicks of each swallow species. All experimental contingencies were controlled by computer. A bird received two calls per test session, each from a different individual of the same species. For each pair, one call was designated the positive (GO) stimulus and the other the negative (NOGO) stimulus. We tested each bird in its home cage, placed in a sound-isolated test chamber and attached to a panel containing a feeder apparatus with two illuminated keys. A peck on the first (observing) key produced one or the other call (equal probability of GO or NOGO). If the call was a GO, a peck within 1 sec on the second (response) key was reinforced with an opportunity to feed (mealworm bits for the swallows, turkey starter for the starling). If the call was a NOGO, and the bird withheld responding for 1 sec, it could then initiate the next trial by pecking the observing key. If a bird keypecked within 1 sec of a NOGO, or failed to respond to a GO, a 5-sec blackout of the houselights occurred. Test sessions consisted of 40-100 trials.

Our measure of the discriminability of a given call pair was the number of sessions required to reach a criterion performance of 85% correct responses (peck if GO stimulus, wait if NOGO stimulus). Each bird was trained on unique pairings of the 14 cliff swallow and 12 barn swallow calls. A bird was trained to this criterion on one particular call pair of one species, then trained to criterion on a second pair from the other species, and so on until it had learned at least 5 barn swallow and 5 cliff swallow call pairs (barn swallow B and the starling learned 10 of each). Each bird received preliminary training on one barn swallow pair and one cliff swallow pair, which were not included in data analysis. Once past these two preliminary pairs (which were both learned slowly), the number of sessions to reach criterion did not systematically decrease further.

Data analysis.

Our procedure, typical of an experiment in animal psychophysics, required thousands of test trials per subject. We used six subjects, which is one more than the minimum necessary to statistically evaluate the hypothesis that cliff swallow chick calls are more discriminable than barn swallow chick calls. If all six subjects responded in this direction, the outcome would be significant at p = .0156 by a sign test. With respect to the hypothesis that cliff swallows will learn calls faster than other species, three subjects of each species is the minimum necessary for statistical validity: if the three cliff swallows were all faster than the other three birds, the outcome would be significant at p = .05 by a sign test.

Results

Fig. 2 shows the mean sessions to criterion for each subject for, respectively, barn swallow and cliff swallow call discriminations. All six birds discriminated more easily among cliffs swallow calls than among barn swallow calls (p = 0.016, sign test; p = .014, t test; barn swallow calls: 6.67 ± 2.18 (S.D.) mean sessions to criterion; cliff swallow calls: 4.23 ± 2.07). Note that the difference is also significant if we consider only the swallow subjects (p = .03, sign test). These results support the signature adaptation hypothesis.

The general perceptual adaptation hypothesis predicted that cliff swallow listeners would learn call discriminations more quickly on average than would the other birds. The mean sessions to criterion for all call pairs for the three cliff swallows was 2.5, 4.5 and 5.3 sessions, for the starling 6.6 sessions, and for the two barn swallows, 5.5 and 8.4 sessions. This result is in the predicted direction and significant (p = .05, sign test).

Discussion

In summary, all birds found cliff swallow calls more discriminable than barn swallow calls. Thus three converging lines of evidence support the signature adaptation hypothesis: (1) the results of this laboratory study,

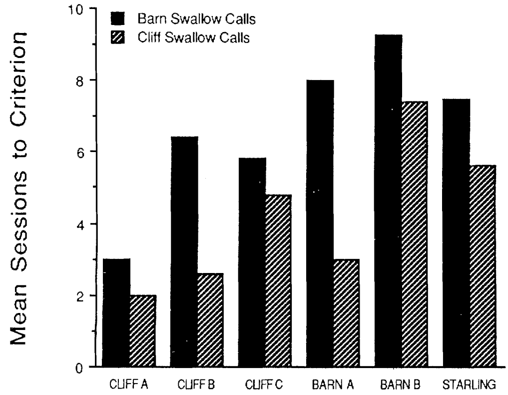

Fig. 2. Mean sessions to criterion for each subject for discrimination of barn swallow and cliff swallow calls.

(2) sonagraphic analysis of swallow calls showing greater information content for cliff swallow calls (Beecher *et al.*, 1986; Medvin *et al.*, unpubl.), and (3) field playback studies showing that cliff swallow parents but not barn swallow parents discriminated between the calls of offspring and unrelated young (Stoddard & Beecher, 1983; Medvin & Beecher, 1986). We suggest that cliff swallow chick calls are adapted for recognition by increasing inter-individual variation, and that this signature adaptation contributes to the superior discrimination abilities shown by cliff swallow parents in the field.

Although the design of our experiment was ideal for testing the signature adaptation hypothesis, it was not ideal for testing the perceptual adaptation hypothesis. The cliff swallows did learn the calls of both species more quickly, on average, than did the barn swallows and the starling. We cannot rule out the possibility, however, that cliff swallows are simply better at this sort of learning task, independent of the particular stimuli, than are barn swallows and starlings. To rule it out, we would need to demonstrate that barn swallows and starlings do as well as cliff swallows on some suitable control discrimination, *e.g.*, a visual task. Thus our results are consistent with, but do not provide strong support for, the perceptual adaptation hypothesis.

Demonstrating perceptual adaptations on the basis of behavioral experiments is a less straightforward task than it appears at first. The design used in the present experiment, where each species is reciprocally tested on the vocal signals of each species, yields clear evidence for or against perceptual adaptations provided two conditions obtain: (1) The hypothesis is that both species have adaptations for their respective signals, and (2) the signals of the two species are reasonably different from each other. Some would add a third condition, that the individuals tested have not had differential experience with conspecific *vs* heterospecific signals (this usually requires that the subjects be lab-raised). When the first two conditions are met, the prediction is that species A will discriminate more easily among species A signals than among species B signals, and vice-versa for species B. We are aware of only one previous behavioral study using this reciprocal design. Using conditioning procedures like ours, SINNOTT (1980) tested red-winged blackbirds and cowbirds on the song of both species and found that, as predicted, each species was superior at discriminating its own song. The only limitation of this study was that the birds had been caught as adults, and so were experienced with conspecific but not heterospecific signals. In the present study we used this reciprocal design, and lab-raised animals in the same acoustic environment. The characteristics of our study species did not, however, satisfy the first two conditions given above. Rather, (1) we hypothesized that cliff swallows but not barn swallows would have perceptual adaptations for chick calls (or, if both species had such adaptations, they would be more elaborated in cliff swallows), and (2) the chick calls of each species were very similar to each other, as might be expected for congeneric species. Consequently, any adaptation in cliff swallows that facilitated the perception of cliff swallow calls would be likely to facilitate the perception of barn swallow calls as well. Thus we predicted that cliff swallows would be better at discriminating among cliff swallow calls and barn swallow calls (and, presumably, some larger range of similar acoustic stimuli). This is a less powerful prediction, for a variety of species differences unrelated to perceptual adaptations would lead to this same outcome. For example, cliff swallows might simply be particularly proficient at this sort of laboratory task, in which case a perceptual superiority would show up for a wide range of stimuli, including non-acoustic stimuli. Cliff swallows might also be more motivated or more behaviorally flexible under the test conditions. We have no reason to argue for these (or any other) alternative hypotheses, but they remain viable hypotheses in the absence of suitable control experiments. In short, strong interpretation of our data with regard to the perceptual adaptation hypothesis requires an appropriate control task, which in turn requires a more detailed hypothesis concerning the nature of the adaptation. An experiment such as ours is only the first step in the test of the perceptual adaptation hypothesis. In the next step, alternative perceptual adaptation hypotheses are delineated and these suggest additional tests involving other sorts of stimuli. We do not intend to carry this line of research forward with swallows because of the extreme difficulty of keeping these birds in captivity, but we do offer the general suggestion for workers in this area.

As a final point, the present lab study contrasts with our field studies in suggesting that the difference between cliff swallows and barn swallows in call discrimination may only be a quantitative one, at least insofar as signal and perception are concerned. In the lab, both barn swallow adults and cliff swallow adults discriminated among calls of different conspecific chicks. In the analogous field experiments, on the other hand, cliff swallow parents reliably responded to differences between the calls of their own and unrelated chicks, but barn swallow parents did not (STODDARD & BEECHER, 1983; MEDVIN & BEECHER, 1986).

We consider two possible explanations for the lab-field difference. First, of course, the laboratory experiment is different in a number of ways from the field experiments; in many (but not all) of these ways, the lab task is easier. For example, in the lab discrimination task, birds had to choose between only two calls at a time. Further, discriminations were presented without the blurring effect of within-individual variability. The lack of evidence of call recognition by barn swallow parents in the field, then, may be due in part to a lack of statistical power, because the effect would necessarily be smaller in barn swallows (barn swallow chick calls are inherently less discriminable than cliff swallow chick calls, and possibly the perception of barn swallow adults is less acute for these sorts of acoustic stimuli).

A second explanation for our failure to find evidence of call recognition by barn swallow parents in the field is suggested by the argument that natural selection may shape different decision rules in cliff swallows and barn swallows. In particular, barn swallow parents may be selected to ignore call differences and to accept any chick found in the nest. In species that do not breed colonially, an unrelated chick in the nest will be an extremely rare event. In such circumstances, natural selection may favor very conservative decision rules because of the potential cost to a parent of rejecting its own chick. The decision rule hypothesis predicts that barn swallows may well discriminate among conspecific calls in the lab, where the payoff contingencies are quite different, even though they fail to respond to these differences in the field (BEECHER, in press).

Summary

Field experiments have shown that parents in the colonially-nesting cliff swallow (*Hirundo pyrrhonota*) discriminate between their offspring and unrelated young whereas parents in the closely-related but noncolonial barn swallow (*H. rustica*) do not, and that discrimination is based on the chick begging call. In a laboratory experiment, we trained three cliff swallows, two barn swallows and a European starling (*Sturnus vulgaris*) to discriminate among chick begging calls of the two swallow species. All birds discriminated more easily among the calls of different cliff swallows than among the calls of different barn swallows, suggesting that cliff swallow calls are more individually distinctive, and may be adapted for a signature function. Moreover, cliff swallows discriminated among both cliff swallow and barn swallow calls faster than did the other birds, which is consistent with a perceptual adaptation for conspecific calls that incidentally facilitates the discrimination of similarly-structured heterospecific calls.

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