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Signals for Parent-Offspring Recognition: Strong Sib-Sib Call Similarity in Cliff Swallows but not Barn Swallows

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Abstract

We tested the prediction that the calls of sibling cliff swallow (*Hirundo pyrrhonota*) chicks are more similar than those of sibling barn swallow (*Hirundo rustica*) chicks. This prediction was derived from the hypothesis that the call of the colonial cliff swallow, but not the call of the noncolonial barn swallow, has been selected for signature function (i.e., for individual distinctiveness). In Study 1 we examined the calls of 22 cliff swallow sibling pairs and 23 barn swallow sibling pairs. The intraclass correlations for 4 of the 5 cliff swallow variables were significantly different from zero, and each of the 4 was approximately 0.5. Only one of the 4 barn swallow call variables was significantly different from zero. In a discriminant-function analysis of these data, cliff swallow chick calls were correctly identified as to sibship in 82 % of the cases, barn swallow chick calls in only 46 % of the cases. In Study 2 we cross-fostered eggs between cliff swallow nests to create foster sibships (all chicks in a nest were unrelated). We found no similarities among foster sib calls, and thus no evidence for call imitation of the calls of sibs or parents, suggesting that genetic differences are the main source of variance in cliff swallow chick calls.

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Introduction

The present study arises out of the general hypothesis that selection for parent-offspring recognition is more intense in the colonial cliff swallow (*Hirundo pyrrhonota*) than in the ecologically similar but more solitary barn swallow (*Hirundo rustica*). Cliff swallows typically nest in dense colonies and show numerous adaptations for colonial living, such as those related to foraging (Brown 1988). Barn swallows, on the other hand, nest solitarily or in small, loose colonies, and show few if any adaptations for colonial living (Shields et al. 1988).

Field studies have revealed large differences between these two species in the need for parent-offspring recognition; for example, cliff swallow parents must find their young in large creches (typically hundreds of chicks) whereas barn swallow parents, even those living in small colonies, keep their fledglings apart from other same-aged young (Stoddard & Beecher 1983; Medvin & Beecher 1986). These socioecological differences should favor adaptations for parent-offspring recognition in cliff swallows (adaptations sensu Williams 1966).

We focus here on one particular adaptation, a modification of the chick begging call, to increase its individual distinctiveness. Several lines of evidence suggest that the cliff swallow chick begging call is in fact adapted for this 'signature' function. First, chick calling is a conspicuous, consistent correlate of parent-offspring reunions in the creche (Stoddard & Beecher 1983). Second, playback studies have shown that cliff swallow parents discriminate between the calls of offspring and those of unrelated chicks, whereas barn swallow parents do not (Stoddard & Beecher 1983; Medvin & Beecher 1986). Third, an information analysis of the chick calls of the two species has shown that the cliff swallow call is more individually distinct: we estimate that the cliff swallow call could be recognized in groups 20 times larger than would be possible for the barn swallow call (Beecher et al. 1986; Medvin et al. in press). Fourth, in a laboratory conditioning study we found that cliff swallows, barn swallows and starlings all discriminated more readily among cliff swallow chick calls than barn swallow chick calls (Beecher et al. 1989; Loesche et al. 1991). Parallel evidence on the first three points comes from studies of the colonial bank swallow (*Riparia riparia*) and noncolonial Northern roughwinged swallow (*Stelgidopteryx serripennis*) (Beecher et al. 1981 a, b; Beecher 1990).

In the present study, we investigated another prediction of the hypothesis that the cliff swallow chick call is adapted for signature function. The prediction is that sibling calls will be more similar in cliff swallows than in barn swallows, and it follows from two distinct arguments.

The signature-adaptation hypothesis presumes that the more certain the parent is of its relatedness to a begging young, the more likely it is to proffer parental care (Beecher 1982, 1988 a). If so, selection would shape suitable traits, such as a simple begging call, so that they are more complex and more individually distinctive, i.e., so that they would take on 'signature' function. The key point is that such selection would be frequency-dependent selection, because rarer phenotypes (signatures) are more distinctive and therefore more adaptive. Frequency-dependent selection will generally increase genetic variability, unlike the more typical cases of unidirectional selection or stabilizing selection which 'use up' genetic variability (Maynard Smith 1989). Thus selection for signature function should increase the proportion of phenotypic variation in the trait attributable to genetic variation (heritability), provided there is a genetic component to the trait to begin with and that environmental sources of variation remain the same throughout. Thus by this argument we would predict that the calls of cliff swallow sibs would be more similar (with respect to the total variation in the trait) than would the calls of barn swallow sibs.

There is a second possible route to increased call similarity among siblings. If selection for individual distinctiveness increases between-individual call variation, it will probably also (depending on the mechanism) increase between-sib call variation. For example, if call variation is heritable, then between-sib call variation should increase in proportion to between-individual variation (e.g., if heritability is near 1 and all the genetic variance is additive variance, then between-sib variance would be approximately half the between-individual variance). Thus an increase in between-chick variation has two opposite effects: a given chick becomes more different from unrelated chicks (making recognition easier) but also more different from its siblings (perhaps making recognition more difficult). No one has tested the hypothesis that increased between-sib (within-family) variation impedes recognition. Analogous tests of the hypothesis that increased within-individual song variation (i.e., within song repertoires) impedes individual recognition have provided conflicting evidence (FALLS 1982; BEECHER & STODDARD 1990; STODDARD et al. 1990). Nevertheless, if the assumption is true, chicks would be favored to imitate some common call model to reduce the between-sib call differences. The most likely model would be the calls of other sibs, or of their parents. Imitation must be considered a possible mechanism since imitation of bird songs is common in passerine birds, and has also been noted in some adult calls as well (MAMMEN & NOWICKI 1981; NOWICKI 1989; MUNDINGER 1970; 1979).

A second aspect of cliff swallow sociobiology that might favor call imitation is intraspecific brood parasitism. BROWN & BROWN (1989) have gathered data indicating that in a typical cliff swallow colony, about 10 % of the chicks may not be in their mother's nest. A foster (parasite) chick typically finds itself in a nest with 2—4 chicks who are biological siblings. Possibly the foster chick could enhance its chances by imitating the calls of its siblings. If call imitation were already present, intraspecific parasitism might provide a reinforcing selection pressure. It is not theoretically obvious, however, that call imitation would be favored in this case, given the opposing interests of the parasitized family (parents and chicks).

The genetic and imitation hypotheses of sib-sib call similarity are distinct but not mutually exclusive. Indeed, a likely scenario combines both hypotheses: selection first increasing allelic diversity at the call loci, and then favoring an imitation mechanism that reduces within-family call variation. The key point is that both hypotheses predict an increase in sib-sib call similarity associated with selection for parental recognition of offspring calls.

In this paper we describe two studies carried out to test the general signature adaptation hypothesis and the more specific genetic and imitation hypotheses. In the first, major study, we compared the calls of siblings in cliff swallows and barn swallows. The prediction by both hypotheses is that cliff swallow sibs will be more similar than barn swallow sibs. Since in this study we examined the calls of siblings raised together normally in the nest, we could not separate sib call similarity due to genetic relationship from that due to common environmental influences, and therefore could not distinguish between the genetic and imitation

hypotheses; even so, the study provides a direct test of the more general signature-adaptation hypothesis.

To distinguish between the two more specific hypotheses, we carried out a second, experimental study in which we cross-fostered eggs among nests to make up sibships composed entirely of unrelated chicks. Although we could not identify natal siblings in this design, the cross-fostering experiment opposes the two hypothesized mechanisms. Thus if environmental factors were primary, variation among foster sibships would be greater than variation within them, whereas if genetic factors were primary, the reverse would be true.

Study 1:
Comparison of Sib-Sib Similarity in Cliff Swallows vs. Barn Swallows

Methods

We recorded the calls of barn swallow chicks at nests in King County, Washington in 1982 and 1984, and those of cliff swallow chicks at nests in Okanogan County, Washington in 1981—1983. Recordings were made with small "tie-clip" condenser microphones affixed to the nest. These microphones provide an exellent signal/noise ratio when the vocalizer is close to the microphone (as birds in the nest are). Recordings were made with Uher 4000, 4200 and 4400 tape recorders.

Calls were analyzed on a Kay 6061B sonagraph. The filter was set to give an effective bandwidth of 180 Hz, the optimal setting for these signals (BEECHER 1988 b). This bandwidth value was obtained by setting the filter to "narrow-band" on the 16 kHz range, the plug-in scale magnifier to 25 % of full scale, and the tape recorder to half speed.
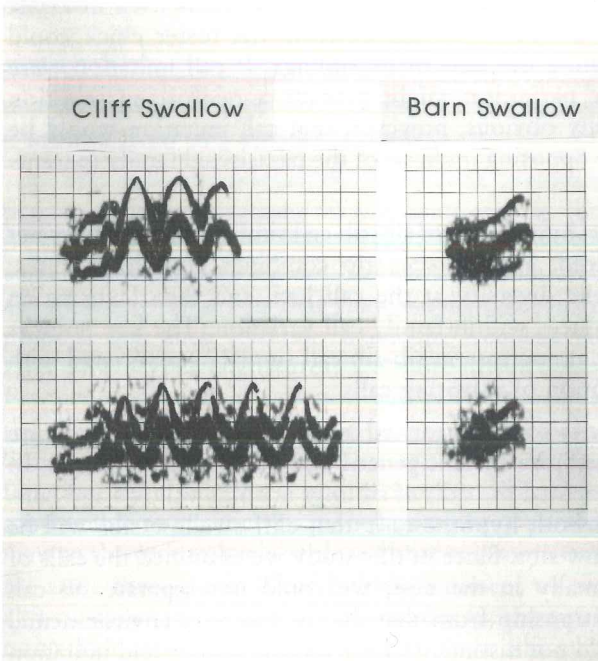

Fig. 1: Sonagrams of 2 cliff swallow chick calls and 2 barn swallow chick calls; not siblings. All calls are 'average' except that the second cliff swallow call is long. Sonagrams made on a Kay DSP-5500 sonagraph (analyzing bandwidth 247 Hz). Frequency scale 0—8 kHz, markers at 1-kHz intervals, time-scale markers at 100-ms intervals

The acoustic structure of the cliff swallow chick call is similar to that of the barn swallow chick call, as might be expected of congeneric species (Fig. 1). For both species, the call has the following features: (1) it is short, generally 50—100 ms in duration, (2) it is rapidly modulated, (3) most of the energy is in the range 2—6 kHz, and (4) it consists of two, nonharmonically related "voices" (typical for passerine vocalizations, GREENEWALT 1968; NOWICKI & CAPRANICA 1986). The major difference between the chick calls of the two species is that the frequency modulation is repetitive in cliff swallow calls, but not in barn swallow calls.

For quantitative analysis of these calls, we used the minimum number of variables required to describe a sonagram of a call (our rationale is explained in MEDVIN et al. subm.). This resulted in 4 variables for barn swallow calls and, because they involved an additional feature, 5 for cliff swallow calls. The variables were as follows. (1) DUR: Call duration. (2) FLV: Peak frequency of the lower voice. (3) RFM: Frequency range of one voice. (4) DVF: Frequency difference between the two voices, measured at the frequency peak. (5) PFM: Period of the frequency modulation, i.e., the average time between peaks. This last measure applies to the cliff swallow calls only. The calls and measurement procedures are described in detail in MEDVIN et al. (in press).

Design and Data Analysis

We selected 22 cliff swallow and 23 barn swallow sibling pairs for whom we had one good call from each sibling (total number of calls 44 for cliff swallows and 46 for barn swallows). A sibling pair was included only if we had positive identification of both chicks, and both calls were good recordings (low signal/noise). All calls were from the 'crystallized' stage, which occurs shortly before fledging (bird at least 17 days old): when this stage is reached, an individual's call varies minimally from one occasion to the next (MEDVIN et al. in press).

We carried out a conventional sib-sib analysis (e.g., FALCONER 1981): a simple ANOVA with the data partitioned into between-family and within-family groups ('family' = 2 siblings). For each variable, we obtained estimates (Model II) of the between-family (σ^2_{BF}) and within-family (σ^2_{WF}) variances. We measured the degree of similarity between sibs for the the ith variable by the intraclass correlation

$$r' = \frac{\sigma^2_{BF}}{\sigma^2_{BF} + \sigma^2_{WF}} \tag{1}$$

The intraclass correlation is a conventional summary measure in sibship analyses (FALCONER 1981). It is conceptually similar to a Pearson correlation but avoids the arbitrary decision necessary with the Pearson r as to which sib goes into the 'X' category and which into the 'Y' category (with N sib pairs, there are 2^N possible splits and thus 2^N possible r's). For later analyses it is important to note that these variance estimates are based on the mean squares of the ANOVA as follows:

$$\sigma^2_{BF} = \frac{MS_{BF} - MS_{WF}}{n} \text{ and } \sigma^2_{WF} = MS_{WF} \tag{2}$$

where n is the number of individuals (siblings) per group (family) (SOKAL & ROHLF 1981; see also LESSELLS & BOAG 1987). The significance of the intraclass correlation is tested by the F-ratio of the ANOVA, i.e.,

$$F = \frac{MS_{BF}}{MS_{WF}} \tag{3}$$

The correlation analysis provides a test of the hypothesis that a particular acoustic variable for a particular species is significantly different from zero, as well as a quantitative description of the sib-sib relationship in each particular case. To test the hypothesis that the calls of cliff swallow sibs were more similar overall than were the calls of barn swallow sibs, we performed a discriminant function analysis (DFA) on each of the two chick data sets. This DFA produces a new set of variables, based on linear transformation of the original variables, which maximally discriminates among groups ('groups' = families or sibships here). Subsequently any call can be classified as to the group (sibship) to which it most likely belongs, i.e., the sibship centroid to which it is closest, and its distance from that centroid. We took two measures of sib-sib call similarity for each species. First, we calculated the percentage of calls correctly classified by the DFA as to sibship. Second, we calculated the difference between an individual's Mahalanobis distance from the sibship centroid and the individual's distance, on average, from all nonsibs; to avoid double counting, an individual was compared only to individuals in the same (arbitrary) half of the data set (i.e., N = 22 vs. 44).

All statistical analyses were done using the SYSTAT statistical package (WILKINSON 1986).

Results

Except for one variable, the sib-sib intraclass correlation coefficients (r') were higher for cliff swallows than barn swallows (Table 1). For the cliff swallows, 4 out of 5 r's were significant and these 4 were all about 0.5. For barn swallows only 1 out of 4 was significant, and it was also near 0.5. DUR, the sole variable that was significant for barn swallows, was the sole variable not significant for cliff swallows.

Table 1:   Intraclass correlations from ANOVAs

Variable	Cliff swallow		Barn swallow	
	r'	P	r'	P
DUR	.27	.102	.49	.006
FLV	.49	.008	.22	.143
DVF	.49	.008	.30	.075
RFM	.53	.004	.18	.197
PFM	.54	.003	—	—

r' = intraclass correlation (P 1-tailed)

We performed a similar analysis on the principal components of the PFM, FLV, RFM and DVF for the cliff swallows; this analysis removes the possible effects of variable intercorrelations. Each of the resulting 4 principal components gave a significant r'. The average of these r's, when each was weighted by the percent variance accounted for by its PC, was 0.51. Thus the analyses of the original data and PC-transformed data gave essentially identical results.

Calls were relatively more similar among sibs in cliff swallows than in barn swallows (Table 2). Calls of cliff swallow chicks were correctly identified as to sibship in 82 % of the cases, barn swallow chick calls in only 46 % of the cases (t = 3.87, p < 0.0005, n = 22, 23). The difference between the average distance to nonsibs and the distance to the sib was larger for cliff swallow calls than for barn swallow calls (2.90 vs. 1.58, t = 5.42, p < 0.0001, n = 22, 23).

Table 2:   Summary of discriminant function analysis

		Distance to other (DO)	Distance to sib (DS)	DO—DS	% correct classified
Barn swallow	$\overline{X}$	2.908	1.327	1.582	45.6
	SD	0.579	0.501	0.827	
Cliff swallow	$\overline{X}$	4.417	1.520	2.897	81.8
	SD	0.682	0.446	0.801	

Note: because cliff swallow analysis is based on 5 variables and the barn swallow analysis on 4 variables, other things being equal, distances will be larger for cliff swallows

Study 2:
Cliff Swallow Cross-Fostering Experiment

Design, Rationale and Analysis

In Study 1 the calls of sibs were more similar than those of unrelated chicks in cliff swallows. To be precise, the variance among cliff swallow sibs was approximately half the variance among unrelated individuals. The sibs compared in Study 1 were reared together, however, leaving unanswered the question of the relative importance of common genes vs. common environment. We addressed this question in Study 2 by separating cliff swallow sibs before hatching and rearing them apart in foster nests.

The basic design of the cross-fostering experiment was as follows. We chose a matched group of 4 cliff swallow nests in which laying had been initiated at about the same time (within ± 2 days), and which each contained 4 eggs (the modal clutch size in this colony). All 16 eggs were removed and switched among nests so that each reconstituted clutch contained 4 unrelated eggs. Switching eggs rather than chicks has the advantage that early learning is precluded (learning cannot occur in the egg as these altricial birds cannot hear until some time after hatching), and the disadvantage that related chicks cannot subsequently be identified. Although we attempted two replications of this experiment, natural disasters (nest collapses) eliminated one of the two. One chick was lost in each nest of our successful group, leaving us with 4 foster sibships of 3 chicks each.

Basic quantitative-genetics theory provides a prediction equation for our major dependent variable of Study 1, the intraclass correlation for natural sibships:

$$r' = \frac{\frac{1}{2}\sigma^2_A + \frac{1}{4}\sigma^2_D + \sigma^2_{EC}}{\sigma^2_P} \qquad (4)$$

where σ^2_A is the additive genetic variance, σ^2_D the dominance genetic variance, and σ^2_{EC}, the common environmental variance (FALCONER 1981). We compared two extreme hypotheses concerning these components of variance: Hypothesis 1 that the numerator contains only genetic variance (i.e., $\sigma^2_{EC} = 0$), and Hypothesis 2 that the numerator contains only environmental variance ($\sigma^2_A + \sigma^2_D = 0$). In the latter case, we assume that σ^2_{EC} results from some type of call imitation occurring in the first weeks after hatching. Thus if the foster sibships produced by cross-fostering are analyzed as were the natural sibships in Study 1, the genetic variance will be removed from Equation 2, so that $r' = \sigma^2_{EC}/\sigma^2_P$. Then by the genetic hypothesis (H1) the r' for foster families should equal 0.

By the imitation hypothesis (H2), on the other hand, cross-fostering does not affect the common environmental component, and r' for foster families should be the same as it was for natural families (= 0.5). We illustrate the imitation hypothesis with one particular plausible scenario. During

Table 3: Predicted outcome of cross-fostering experiment by the two hypotheses

	H2: Imitation	H1: Genetic
MS_B = MS between foster families	$\sigma^2_{WF} + n\,\sigma^2_{BF}$	σ^2_{WF}
MS_W = MS within foster families	σ^2_{WF}	$\sigma^2_{WF} + \sigma^2_{BF}$
F* = MS_B/MS_W	$1 + n = 4$	0.5

σ^2_{WF} and σ^2_{BF} are within- and between-family variance estimates from natural families of Study 1. These are families both in the sense of containing related chicks and in the sense of providing a common rearing environment. The two hypotheses of Study 2 attribute σ^2_{BF} to one or the other of these two features. According to H1 genetic differences are the sole origin of σ^2_{BF} and according to H2, nest differences are the sole origin of σ^2_{BF}

* Follows from Study 1, since $r' = 0.5$, i.e., $\sigma^2_B = \sigma^2_W$. Note: F actually should be somewhat larger than 0.5 because the loss of one chick from each foster nest produces some genetic differences among foster nests (unless all the chicks lost were from the same original nest)

their first week post hatching, parents call on most trips into the nest; the adult call is similar in many respects to the chick call, and it is individually distinctive (chicks recognize the parent call, Beecher et al. 1985). The chicks could use the parent calls as a model for their calls, which develop toward the end of their second week in the nest. The key point is that this hypothesized mechanism is totally unaffected by cross-fostering; by this hypothesis, the between-family and within-family variance estimates are properties of the nests (more precisely, the adults at the nests) rather than the genetic relationships of chicks within and between these nests.

Because the hypotheses we are testing are mutually exclusive, they make an additional, testable prediction concerning the variance estimates obtained in the cross-fostering experiment. The argument is as follows (and see Table 3). According to Hypothesis 1 (genes only), our cross-fostering scheme removes σ^2_{BF} from the mean square between families and adds it to the mean square within families (these families are now genetically heterogeneous). That is, whereas for natural families we expected r's greater than zero and F's greater than one (see equations 1—3), by the genetic hypothesis we should expect the reverse for foster families (although r' cannot be < 0, F can be < 1). Moreover, since for natural families r's $\approx$ 0.5 (Study 1, all variables except DUR), we take as given that $\sigma^2_{BF} = \sigma^2_{WF}$, and calculate a predicted value for F: by H1 F should be 0.5, and by H2 it should be 4 (see Table 3). Because we cross-fostered eggs rather than chicks we cannot identify natal families (i.e., the sib groups dispersed amongst the foster nests). The major consequence for the analysis is that we cannot obtain separate estimates of the between-natal-family and between-foster-family variances, and thus we cannot evaluate hypotheses that sib-sib call similarity is due to *both* genetic covariance and imitation. Nevertheless, we can still test our two mutually exclusive hypotheses, because they dictate that one of these variances is zero.

Methods

The experiment was performed in 1983 in our Okanogan County cliff swallow colony. The data from this study were not statistically analyzed until after the complete analysis of Study 1, and we treat Study 1 as logically prior to Study 2. Recording and call analysis were as in Study 1. We analyzed only the 4 variables for which r' was approx. 0.5 in Study 1 (i.e., PFM, FLV, RFM and DVF).

For each of the 12 chicks, we obtained 8 calls. Measurements on each of the 5 variables were obtained as in Study 1; the analysis is based on the means of these 8 observations for each chick for each variable.

Results

Considered with respect to the strongly contrasting Hypothesis 1 (similarity due entirely to genes in common) and Hypothesis 2 (similarity due entirely to common environment), the results are more consistent with the first hypothesis (Table 4). The r' for foster families is 0 for three of the four variables and the fourth r' is not significantly different from 0. As predicted by Hypothesis 1, the

Table 4: Intraclass correlations, Study 2

Variable	r'	F*
FLV	0	0.272
RFM	0	0.543
DVF	0	0.965
PFM	.18**	1.682

* By Hypothesis 1, F should = 0.5, by Hypothesis 2, F should = 4

** Note: When $MS_{BF} < MS_{WF}$, F < 1 and a negative value is obtained for the variance estimate σ_{BF}. In this case, r' is entered as 0

mean square within foster families was typically greater than the mean square between foster families: F was < 1 for 3 of the 4 variables. The geometric mean was 0.70. In all 4 cases it was closer to the predicted value by H1 of 0.5 than to that of H2 of 4.

To address the question of redundancies among these variables, we repeated the analysis on the first two principal components of PFM, FLV, RFM and DVF (the first two accounted for 82 % of the total variance). They, too, give F's of less than 1 ($\overline{X}$ = 0.66).

Discussion

In summary, the calls of cliff swallow sibs were more similar than those of barn swallow sibs. This difference was predicted by the hypothesis that the call of the colonial cliff swallow but not the call of the noncolonial barn swallow has been selected for signature function. The intraclass correlations for 4 of the 5 cliff swallow variables were significantly different from zero, and these 4 were each approximately 0.5. The single nonsignificant variable, DUR, we have previously shown to be the least individually distinctive of the 5 variables, i.e., to have the smallest between-individual to within-individual variance ratio (BEECHER et al. 1986; MEDVIN et al. in press). This, too, is consistent with the signature-adaptation hypothesis which regards both the increase in the between-individual to within-individual variance ratio and the increase in sib-sib similarity as outcomes of selection for individual distinctiveness.

In the introduction we outlined two plausible, independent mechanisms which would produce stronger sib-sib call similarity in cliff swallows. (1) Selection for rare signatures is frequency-dependent selection and should increase genetic variance in signature traits. On the other hand, selection for a species-typical begging call, presumably the primary selection pressure in barn swallows, should reduce genetic variance. If environmental sources of variance remained constant, an increase in genetic variance would increase the heritability of signature traits and the similarity of sib signatures. (2) Selection for increased between-individual variance may incidentally increase within-family signature variance: this correlated effect might work against the selected effect, i.e., it might impede recognition. If so, mechanisms decreasing within-family signature variation would be favored: since the signature here is vocal and the species is a passerine bird, the obvious candidate is imitation of the calls of family members.

The cross-fostering design of Study 2 separates the genetic and environmental components. The results of this cross-fostering experiment rule out the extreme possibility that normal sib-sib resemblance is due entirely to some common environmental factor such as call imitation in the nest. Moreover, the results are consistent with the pure genetic hypothesis. Nevertheless, as pointed out in the Introduction, if selection has in fact increased allelic diversity at call loci, imitation might arise to reduce within-family diversity. Although our cross-fostering experiment clearly favors the pure genetic hypothesis over the pure imitation hypothesis, it is not powerful enough to distinguish these extreme

hypotheses from more subtle mixed hypotheses. A more powerful design would keep track of natal sibships and provide separate estimates of the between-natal family and between-foster family variances. Cross-fostering would have to be done after hatching to accomplish this. Unfortunately, because of the difficulty of getting into cliff swallow nests, and the probability that imitation, if it occurs, does so in the first week post-hatch, this design would be difficult to accomplish.

A final piece of evidence against imitation is the failure of sib-sib resemblances to exceed approximately 50 % (r' = 0.5); for all four of the major cliff swallow variables, r' reaches but does not exceed 0.5. There is ample evidence in songbirds of song and call sharing in the 90 % or better range. Although song sharing is rarely quantified, examples abound in the literature of close song matches between neighbors (e.g., KROODSMA 1974; PAYNE et al. 1981). NOWICKI (1989) measured one key parameter of the chickadee call and found that the variance among birds in an experimentally created flock dropped to less than 10 % of the starting value (i.e., r' ≈ 0.9) one week after flock formation (NOWICKI 1989, see his Fig. 2). If chicks imitate their nestmates or the adults at the nest, it is not at all clear why imitation should stop at 50 %.

If we assume that σ^2_{EC} in equation 4 is equal to zero, then the estimated narrow-sense heritability (σ^2_A/σ^2_P) of the cliff swallow call would be about 1 if σ^2_D is 0, and less than 1 if there is appreciable dominance variance. It would be nice to have half-sib covariances because they lack the dominance-variance component, but this is not possible in field studies. We have considered parent-offspring correlations (which also lack the dominance-variance component) but the prediction equations are applicable only if the calls have been obtained at the same developmental stage. For cliff swallows in particular, significant changes occur in the call between chicks and adults (in particular, the upper voice and thus DVF disappears in most adults and FLV drops significantly). This change in the voice will inevitably reduce the parent-offspring covariance.

BAKER & BAILEY (1987 a, b) obtained results similar to ours in a study of the separation call of the northern bobwhite (*Colinus virginianus*). First, they showed via playback experiments that the bobwhite separation call is used for individual recognition. Second, they showed, via a cross-fostering experiment, that genetic variation is the major source of phenotypic variation in the call. They found no evidence for call imitation.

Finally, as noted earlier, BROWN & BROWN (1989) showed that intraspecific brood parasitism is common in their cliff swallow colonies in Nebraska. If it occurred in our colony, its effect on call similarity would depend on the nature of the mechanism producing this similarity. With regard to genetic factors, the occurrence of brood parasitism would cause us to underestimate heritability. With regard to call imitation, it should not affect the data in any way.

Acknowledgments

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