Signature Systems and Kin Recognition[1]

MICHAEL D. BEECHER

*Department of Psychology, University of Washington,
Seattle, Washington 98195*

SYNOPSIS. This paper examines mechanisms of individual identification in the kin recognition process. In type 1 kin recognition, the individual (*e.g.*, a parent) learns the identifying cues (the "signature") of particular kin (*e.g.*, offspring) at some stage when there are reliable contextual cues as to kinship (*e.g.*, the parent finds the young in its nest). These kin are subsequently recognized via their signatures in situations in which contextual evidence of kinship is lacking. The primary selection pressure in this case is for a mechanism that can generate a large number of distinctive signatures, and thus permit recognition in large groups. I develop a model that predicts the necessary information capacity of a signature system, and I test this prediction for the signature call of the bank swallow (*Riparia riparia*). The measured information capacity of 17 bits corresponds well to the prediction and, moreover, is substantially greater than that of the homologous call of the similar but non-colonial rough-winged swallow (*Stelgidopteryx ruficollis*). In type 2 kin recognition, reliable contextual evidence as to kinship is absent at all times, and kin must be recognized via a signature-matching process. For example, the individual might compare its own signature to that of the unknown individual, inferring kinship if their signatures are sufficiently similar. I describe a multi-locus genetic signature mechanism that would permit discrimination of kin from non-kin, and suggest how this model might be tested.

INTRODUCTION

A gene predisposing an individual to channel assistance to a relative (nepotism) will generally be favored over an alternative gene predisposing an individual to provide such assistance without regard to relatedness (non-selective altruism). For example, restricting parental care to one's offspring usually is favored over dispensing that care indiscriminately to any young in the group. This is because the conditions for the evolution of altruism are more favorable if the gene in question is in the beneficiary (where it receives the benefit) as well as in the donor (where it takes the cost). Since the donor shares more genes with a relative than with an unrelated individual, a gene for nepotism has a natural advantage over a gene for non-selective altruism (Hamilton, 1964).

In the most interesting circumstance, nepotism requires kin recognition. In this paper I focus on the mechanisms underlying kin recognition.

Kin recognition contains two distinct

components: One animal provides a signal as to its identity (identification) while a second animal decodes this signal (recognition proper). In theoretical considerations of the evolution of kin recognition, little attention has been paid to the identification side, perhaps reflecting the notion that this is merely a question of proximate mechanisms, and of no general significance. To the contrary, an important premise of this paper is that our understanding of kin recognition has been impeded by our tendency to focus on the recognition process and ignore the identification process.

To take an example, suppose we are considering a case like kittiwake gulls in which parents do not discriminate their own chicks from unrelated chicks in experimental tests (Cullen, 1957). We are apt to describe this situation by saying that kittiwake parents do not recognize their own chicks. Yet we could equally well say that kittiwake chicks do not reliably identify themselves. The fact is that in the absence of additional information both descriptions fit the experimental data equally well.

Our bias may arise from the basic asymmetry of the nepotism process: correct recognition is crucial to the aspiring nepotist, but not to the beneficiary, since the former

gains only if the beneficiary is indeed a relative, whereas the latter gains regardless of their relationship. Yet, while it is true that only the nepotist has a direct interest in the question of relatedness, the beneficiary will nevertheless be selected to participate in the recognition process; the reason is compelling, albeit indirect. In deciding whether or not to provide aid, the altruist must devalue the benefit of this aid by the probable relatedness of the two parties. The probable relatedness is the product of the appropriate coefficient of relatedness (say for parent-offspring) and the probability that the beneficiary is in fact a member of that kinship class (*e.g.*, offspring *vs.* unrelated). For example, suppose our nepotist is an adelie penguin parent arriving at a creche of several hundred like-aged chicks, one of which is her own. If she cannot determine with sufficient certainty which chick is hers, she will do better to swallow the food herself, thus using it toward the production of subsequent offspring (provided she can identify future offspring better than the present offspring). The general point is that, under these sorts of circumstances, the beneficiary is favored to decrease uncertainty about relatedness by reliably identifying itself.

In this paper I consider kin recognition from the perspective of the identification process. Specifically, I will focus on the mechanism of identification, which I refer to as a "signature" system, where a signature refers to a specific complex of phenotypic traits which is (to some degree) individually distinctive.

There are diverse routes by which kin recognition can be accomplished. As used in this paper, "kin recognition" is defined by its outcome: it applies to any case in which individuals recognize other individuals that in fact are kin. Yet there are (at least) three distinct cases.

Case I. The nepotist learns the signature of the critical relative during a period when there is reliable contextual (or "circumstantial") evidence as to kinship, and uses this signature for recognition in subsequent situations where contextual evidence is absent. Parent-offspring recognition typically occurs in this way. The parent learns the signature of its offspring while they are in the nest (den, etc.). Later, when young intermingle away from the nest, the parent locates its offspring on the basis of these learned signatures. This sort of kin recognition is revealed by experiments in which young can be successfully cross-fostered, but only prior to a critical age when the parents learn signatures. This mechanism of kin recognition is very common in group-living animals. Such a mechanism works equally well for recognition of kin or non-kin, insofar as it need provide direct information only as to individual identity, not genetic relationship.

Case II and Case III. In these two cases, the nepotist never has reliable contextual evidence of kinship. For example, non-littermate ground squirrel siblings have no circumstances in which to learn one another's identity. Baboon males are generally uncertain of paternity and may not be able to easily infer which infants in the troop are theirs. Yet ground squirrels can discriminate non-littermate siblings from unrelated individuals, as well as littermate full siblings from littermate half-siblings, despite no differential experience with the kinship classes in each case (Holmes and Sherman, 1982). And baboon males do preferentially assist their own infants over others (Packer, 1980; Klein, in preparation). Recent research, furthermore, has revealed several cases of kin recognition in the absence of prior contact between the individuals in question (Greenberg, 1979; Wu *et al.*, 1980; Blaustein and O'Hara, 1981; Waldman, 1981).

In both Case II and Case III, recognition occurs in the absence of prior contact between the related individuals. Both cases would seem to require some form of signature matching (or "phenotype matching," Holmes and Sherman, 1982). That is, you match the signature of the individual in question to some key model (*e.g.*, your own signature, your mother's, those of your littermate siblings). The expression "innate recognition" sometimes loosely applied to these cases is probably something of a misnomer, insofar as the *model* signature is probably learned. (However, if the model were a genetically-determined "in-

ternal expectation," the term might be reasonable.) Although Case II and Case III both refer to cases in which recognition occurs in the absence of prior contact (or of prior differential contact), and in both signature-matching is inevitably involved, the two cases differ in a very fundamental way.

In Case II, kin recognition occurs via a common, acquired signature. For example, the mother may "label" her offspring, as may occur via the milk in goats (Gubernick, 1980) or in spiny rats (Doane and Porter, 1978). Waldman's (1981) experiments suggest that this may be the mechanism by which sibling tadpoles reared in isolation recognize one another: the common signature may be a chemical transmitted from the mother to each of them via the egg mass jelly. Thus, in terms of the mechanisms involved, Case II is essentially the same as Case I: When the tadpole is learning its own signature, it is also learning its siblings' signatures, since they are one and the same.

In Case III, kin recognition occurs via the similarity of *different,* inherited signatures. As yet, this hypothesized mechanism has not been shown to operate in any particular example of kin recognition (though it would appear to be a good candidate for some cases, such as in sweat bees; Greenberg, 1979; Buckle and Greenberg, 1981). In this case, the signature is the direct outcome of a genetic mechanism within the individual, and thus directly reflects the individual's genotype. Therefore the degree of similarity of the signatures of two individuals will be correlated with their degree of relatedness.

Thus the basic distinction arising from a consideration of the mechanism of kin recognition is quite different from our original distinction based on differential experience. Case I is distinguished from Case II and Case III in that differential experience occurs in the former case but not in the latter two. The more interesting distinction, I would suggest, is between Case I and Case II on the one hand and Case III on the other. I will dub these Type 1 and Type 2 kin recognition, respectively. In Type 1, one recognizes kinship when the presumptive relative's signature

matches a model signature learned earlier (which model could have been the signature of that very relative, Case I, or the identical signature of oneself or another, common relative, Case II). In Type 2, one recognizes kinship when the presumptive relative's signature is sufficiently similar to a model signature learned earlier, where the two signatures are distinctly different but the degree of similarity of the two is predictive of genetic similarity.

In this paper I will consider the characteristics required of a signature system which functions in one of two general contexts. (1) *Case I/Type 1*. Direct learning of the signature is possible, and the primary selective pressure is for many unique signatures. (2) *Case III/Type 2*. Learning of the signature (directly or indirectly) is not possible, and the primary selective pressure is for signatures that directly reflect relatedness.

KIN RECOGNITION TYPE 1:
FINDING KNOWN KIN IN A CROWD

The prototypical example of this case is parent-offspring recognition in a colonial species. Typically the parent can learn the offspring's signature before recognition is required. For example, the offspring may remain in close proximity to the parent (as in many ungulates, *e.g.,* Epsmark, 1971) or remain in the nest (*e.g.,* royal terns, Buckley and Buckley, 1972). At some later stage the still dependent young mix; at this stage the parent must use its knowledge of its offspring's signature to distinguish it from unrelated young. I will take as my primary example the creche, or nursery group, common among colonial bird species, for it has two convenient features for the analysis of identification systems. First, the young in the creche intermingle more or less completely. Second, one can usually specify the typical creche size for a species. Taken together those two features enable us to state quantitatively what the identification system must accomplish. Although my analysis is couched in terms of colonial birds and the creche situation, it is generalizable to a wide variety of other situations involving individual recognition in large groups.

We can see at once that the critical feature of such an identification (signature) system is that it must pack a lot of information. While having to learn the identity of a few offspring seems a simple enough task, the difficulty lies in the fact that the parent must subsequently distinguish these chicks from hundreds of other similar-aged chicks. To get individual distinctiveness on a large scale, a single graded variable is not sufficient. For example, the color variation seen in Harris's sparrow (Rohwer, 1975) does not allow one to distinguish more than 10 or so birds. While this is probably adequate for sorting out a dominance hierarchy, it does not uniquely identify very many individuals. Preferable would be a pattern system, one in which we have several independent dimensions. For example, royal terns, colonial waterbirds with a creche system, appear to use color variation in the down and soft parts for individual identification of chicks. Buckley and Buckley (1970) measured color variation in a large number of royal tern chicks and broke the variation down into six components: bill color, bill tip, leg color, leg blotching, down color, and degree of down spotting. The finding most germane to the present discussion is that variation on these dimensions was uncorrelated. With six independent dimensions and say five levels of each, we generate 5^6, or over 15,000, distinct chick color patterns, or signatures.

I begin with the very simple prediction, then, that a signature system functioning in this sort of context will be of the pattern type, i.e., will consist of a number of independent dimensions. The advantage of the pattern type of signature system over a uni-dimensional system, is that it can generate a large number of distinctive signatures without taxing the discriminative memory capacities of the animal on a particular dimension. To appreciate this point, imagine having to recognize your chick in the creche on the basis of its particular shade of grey, where there are 15,000 possible shades.

It is not possible to calculate the number of possible royal tern signatures on the basis of the data given in Buckley and Buckley (1970). The list given above, however, is a conservative one, neglecting some of the variation in the visual modality as well as all of the variation in the chick's call, which Buckley and Buckley elsewhere (1972) suggest also functions in chick recognition. The 15,000 number given above is purely a pedagogical figure and is probably an order of magnitude too low. I will now develop an argument for predicting how many possible distinct signatures a species will need given its typical creche size. I will then turn to data we have gathered to test this prediction in one particular colonial bird, the bank swallow.

Creche model

Consider a creche of 256 similar-aged, unrelated chicks. For the parent of each chick to locate its offspring in this group, a necessary condition is that each of the 256 chicks possess a unique signature. A number of signature systems would permit this; for example, four dimensions of four levels each would give $4^4 = 256$ signatures. Thus the minimum information capacity of a signature system which would allow perfect recognition in a 256-chick creche is $H = \log_2 256 = 8$ bits (that is, a parent could narrow the search down to its chick with a minimum of eight binary decisions). The problem here is that we cannot simply assign each chick a distinctive signature, in the same way we could assign each member of an athletic team a unique jersey number. A more realistic biological assumption is that each chick gets its signature independently of every other chick. Thus two individuals could get the same signature. It is obvious, then, that the number of distinct signatures, M, must be considerably larger than the creche size, S. How much larger M is than S determines the probability, p, of an error, i.e., of two or more chicks getting the same signature. This probability is easily computed given the assumptions that signatures are equiprobable and are drawn at random (with replacement):

$$p = 1 - (1 - 1/M)^{S-1}. \qquad (1)$$

For $S/M < 0.1$, this simplifies to

$$p \cong S/M. \qquad (2)$$

The quantity we want to predict is M, and

$$M \cong S/p. \tag{3}$$

Given our assumption that signatures are equiprobable, this can be expressed in terms of the information measure

$$H = \log M \cong \log S/p. \tag{4}$$

Predicting the information capacity of the bank swallow signature call

I use the above argument to predict the information capacity of one particular signature system. Bank swallows (*Riparia riparia*) are highly colonial birds that nest in sand banks found along rivers and streams, and nowadays, in man-made gravel pits. Because these nesting sites are scarce, and perhaps for other reasons as well, bank swallows nest in large, dense, highly synchronous colonies (Petersen, 1955; Emlen and Demong, 1975; Hoogland and Sherman, 1976; Beecher and Beecher, 1979). There are several contexts in which parent-offspring recognition is required, the most demanding being a creche situation occurring after fledging on powerlines near the colony site (Beecher *et al.*, 1981*b*). We have found that parents do indeed recognize their young in this situation, and have shown by playback experiment that they do so on the basis of a call made by the chick (Beecher *et al.*, 1981*a*).

The typical bank swallow creche size (S) at our study sites is 100–1,000. We cannot easily derive an estimate of p, but it must be quite small, as we have never seen a parent make an error at the creche (*i.e.*, feed the wrong chick). A reasonable estimate would be 0.01 to 0.001, which is small enough to gibe with the good recognition we observe, but not so small as to be unrealistic. By equations 3 and 4, then, the predicted values are $M = 10^4$–10^6 signatures and $H = 13.3$–19.9 bits. The information measure H has several advantages over M. First, H is still applicable when the signature dimensions are not discrete but continuous, a fact I make use of below. Second, a given value of H, unlike a given value of M, has the same meaning regardless of the probability distribution of signatures. Third, the M measure can be

somewhat misleading, for it may suggest that the parent's task is more demanding than it really is. The parent's task is not to recognize all 10^4–10^6 signatures, only to differentiate those of its own offspring from all the rest. In any case, should the number of signatures seem unrealistically large, consider our own recognition of human faces. Given the phenomenal number of distinct faces, it is instructive that normally we have no difficulty recognizing offspring, parents, mates and the other significant people in our lives.

To measure the information capacity of the bank swallow signature call we have measured six parameters of these calls (Beecher and Beecher, in preparation). Examples of these calls are given in Figure 1, and the measured parameters are described in the caption. We first determined whether each parameter was individually distinctive, that is, whether inter-individual variability was greater than intra-individual variability. Results of simple analyses of variance are given in Table 1: each of the F-ratios was highly significant ($P \ll 0.001$).

Variance measurements are directly translatable into information measurements (Shannon and Weaver, 1949; Attneave, 1959):

$$H = \log k\sigma \tag{5}$$

where k is a constant associated with the particular form of the distribution. In the present case the net information is that attributable to the between-individual variance less that attributable to the within-individual variance, *i.e.*,

$$H \text{ (net)} = H \text{ (between)} - H \text{ (within)}$$
$$H = \log(k\sigma_B) - \log(k\sigma_W)$$
$$H = \log(\sigma_B/\sigma_W). \tag{6}$$

Here I have assumed that the between-individuals and within-individuals measurements are similarly distributed. (Most reasonable violations of this assumption do not materially change the argument; Beecher and Beecher, in preparation.) Since σ_B is an estimate of the standard deviation derived from the between-individuals sum of squares and σ_W is an estimate of the same standard deviation derived from the with-
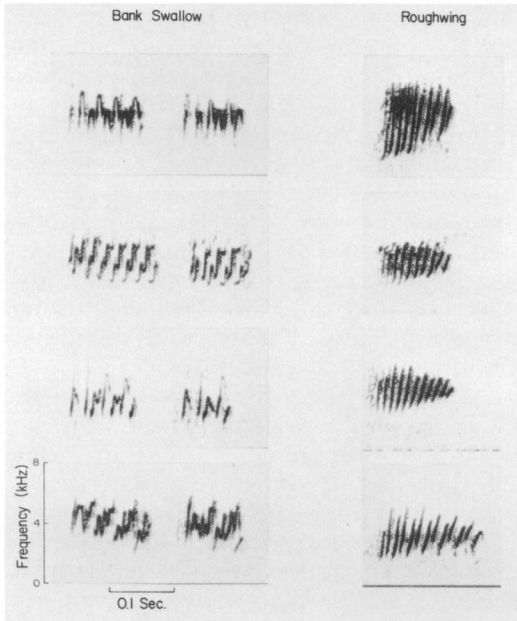
FIG. 1. Left: Calls from four individual bank swallow chicks. Right: Calls from four individual roughwinged swallow chicks. Roughwing calls can be described simply as a series of upward frequency sweeps (figures). The figures in a bank swallow call, on the other hand, come in a variety of forms, usually containing several increases, decreases and usually reversals of slope of the frequency sweep. Additionally, bank swallow figures are paired, and the pair is repeated, sometimes with modification, throughout the call. The shape of the figures in the pair may be identical or dissimilar in varying degrees. We suspect that the two figures of a pair may represent the bird's two voices. Effective bandwidth of the sonagrams is 180 Hz. The following parameters were extracted from sonagrams of the bank swallow calls. (1) *Call duration.* (2) *Slope,* in Hz/msec, of the call. (3) *Figure duration,* averaged over all figures in the call. (4) *Figure frequency:* The absolute frequency of the first inflection point of the first figure. (5) *Figure shape:* Percentage of positive slope in each figure, averaged over all figures in the call. (6) *Frequency difference* between the first major inflection point of each figure in the pair, averaged over all figure pairs in the call.

in-individuals sum of squares, equation 6 is approximately equal to

$$H \cong \log\sqrt{F}. \qquad (7)$$

Note that when there is no inter-individual variation beyond that accountable from intra-individual variation, F is near 1 and H is near 0.

The H's according to equation 6 for the bank swallow call parameters are given in Table 1. If the six dimensions were truly independent, we could simply add these H's to get the total information. However, the dimensions are not completely independent, as can be seen from the intercorrelation matrix in Table 1. Since our only two significant correlations are between two different pairs of variables, the solution is straightforward. (Where there are multiple intercorrelations, an approach based on principal components analysis is most appropriate, *e.g.*, Kaya and Kabayashi, 1972.) Where two dimensions X and Y are not orthogonal, the total information is

$$H(X,Y) = H(X) + H(Y) - T(X,Y)$$

where T is the information shared by X and Y. T can be expressed in terms of the correlation between X and Y when these are continuous variables (Shannon and Weaver, 1949; Attneave, 1959):

$$T = \log(1/\sqrt{1 - r^2}). \qquad (8)$$

When we add the H's for our six dimensions and subtract the two significant T's, we get an estimate of the information capacity of the bank swallow signature call of 17.0 bits. This is within our predicted range of 13–20 bits.

Comparative predictions

The route to our quantitative prediction and its ultimate test are fraught with some perils, the main one being the ballpark guess of the parameter p. A comparative approach, however, allows us to test these ideas in a more general way. If we were to examine several closely related species that differ with respect to the typical creche size, the information capacity of their signature systems should vary accordingly. We are testing this prediction at present in several species of swallows. So far we have completed the story for two species. In addition to the bank swallow, we have done a similar analysis on the calls of the roughwinged swallow (*Stelgidopteryx ruficollis*). Roughwings are very similar to bank swallows but are probably the least social of all North American swallows. Where we have

TABLE 1. Analysis of variance and information measurements.

Variable	F**	σ_B/σ_W[a]	H	Correlation matrix[b]					
				D	t	f	F	b	s
Call duration (D)	47.6	7.55	2.92		−0.01	−0.43	+0.16	+0.48*	−0.12
Figure duration (t)	164	14.0	3.80	0		−0.41	+0.71*	−0.25	+0.04
Frequency difference (f)	109	11.4	3.51	0.15	0.13		−0.28	+0.11	−0.41
Figure frequency (F)	55.8	8.18	3.03	0.02	0.50	0.06		+0.17	+0.39
Call slope (b)	10.4	3.53	1.82	0.19	0.05	0.01	0.02		+0.25
Figure shape (s)	30.2	6.02	2.59	0.01	0	0.13	0.12	0.05	

[a] Note: The ratio σ_B/σ_W would precisely equal the square root of the F-ratio, except that in the former each sum of squares is divided by its appropriate sample size (k = 10 individuals, n = 40 calls), whereas in the latter each sum of squares is divided by its appropriate degrees of freedom (k − 1 and n − k). Thus $\sigma_B/\sigma_W = \sqrt{[n(k-1)/k(n-k)]F} = \sqrt{1.2F}$ in this instance.

[b] r's above the diagonal; T's below the diagonal.

* $P < 0.05$.

** All $P \ll 0.001$.

studied them in Massachusetts, Michigan, and Washington, we usually have found just one or a few pairs at a site.

A variety of parallel experiments with roughwings and bank swallows have shown that roughwings fail to show parent-offspring recognition in situations where bank swallows do (Hoogland and Sherman, 1975; Beecher, 1981; Beecher et al., 1981a, b; Beecher and Beecher, in preparation). This is as would be predicted, since roughwings have no real need for this capacity. We then proceeded to analyze the roughwing call that is homologous to the bank swallow call, the chick food-begging call. This vocalization is given in all of the same circumstances as the bank swallow call. Examples are shown in Figure 1. We performed an analysis on the roughwing call similar to the one described above, and obtained a total H of 3.2 bits. Working backwards, we find that this would not be sufficient (for a reasonable p) even for a creche size of 2. Roughwings, of course, do not have creches and it probably suffices for parents to "recognize" their offspring simply on the basis of location cues.

How might a signature system be generated?

There are three general classes of mechanisms by which a signature could develop within an individual. While they are not mutually exclusive, it is convenient to discuss them separately.

(1) *Acquisition/Imitation.* Offspring may acquire their signatures from parents or some other individual. For example, bank swallow young could imitate the calls of their parents, or, since there is asynchrony of hatching, younger sibs could imitate older sibs. Obviously some other mechanism is required to explain the origin of the signature of the parent (in the first case) or of the oldest sib (in the second case). The term "imitation" is quite appropriate for vocal signatures, but not for certain other instances, such as maternal "labelling" of offspring (as probably occurs in the olfactory modality for goats, Gubernick, 1980; and perhaps tadpoles of the species *Bufo americanus,* Waldman, 1981).

(2) *Random Generator.* Here any individual has the ability to develop any signature. That is, it has the neural and productive equipment to produce a signal that has particular values along the N dimensions. At some critical point in development, the neural/productive system is activated in some random way with a characteristic signature ultimately developing. It is easy to conceive of the first two mechanisms operating in concert.

(3) *Multi-Locus Mechanism.* This mechanism is perhaps the simplest genetic mechanism that could generate a pattern signature. Suppose we have several independent loci with several alleles at each locus. If each locus affects a distinct phenotypic character, we would have as many dimensions to the signature as we have loci,

and the extent of variation on each dimension would be related to the number of alleles at the corresponding locus. I consider this mechanism in more detail in the next section.

These relatively general hypotheses are readily distinguishable by test. We are presently analyzing the bank swallow signature call using a method traditionally associated with human behavior genetics, specifically, comparison of siblings raised together and apart. We do this by experimental reconstitution of broods in the field and in the laboratory. Among the various comparisons possible, the most basic are groups of foster siblings and broods of siblings raised apart. Again assuming for convenience that only one of the mechanisms is operating in any particular case, the basic predictions of the three hypotheses are the following. (1) The Imitation hypothesis predicts that the similarity of the signatures of foster sibs will be the same as that of true sibs and greater than that of sibs raised apart. (2) The Random Generator hypothesis predicts that variation among the signatures of all three groups will be the same. (3) The Multi-Locus hypothesis predicts that the signatures of sibs, whether raised together or apart, will be more similar than those of unrelated individuals (raised together or apart). Needless to say, if more than one of these mechanisms is operating, intermediate predictions would be in order.

A genetic mechanism

In this section I elaborate on the multilocus genetic mechanism just discussed. It should be clear that this mechanism is *not* demanded for the type of kin recognition I have been discussing so far. The point I wish to make, however, is that both the mechanism itself and its presumed evolution are quite plausible. An interesting aspect of this genetic mechanism is that it also permits type 2 kin recognition; I discuss this feature in a later section. My presentation is again couched in terms of the selective pressure of parent-offspring recognition in a colonial bird creche. It is assumed that (a) the signature system is a closed, genetic system, and (b) the parent

learns to recognize the signatures of its offspring. The signatures in question can be visual, auditory, olfactory or combinations of two or more modalities.

The genetic mechanism consists of several independent loci with several alleles at each locus, generating N distinct genotypes and M ($\leq$N) distinct phenotypes (signatures). I assume that the signature traits are essentially neutral with respect to all other aspects of fitness; in any case, these are precisely the types of traits that would be selected for the signature function.

The signature system would arise in the following way. Assume a selection pressure for recognition of chick by parent, as occurs in the creche situation. Imagine a mutant allele which is more or less selectively neutral, and which has an identifiable effect on the phenotype of the chick. This allele will be favored, then, because it facilitates recognition of the chick by the parent. Since the rarest phenotype is the most easily recognized (least often confused with others) by the parent, the selective advantage of such an "identifier" allele will be negatively correlated with its relative frequency. This "rare-type" advantage for mutant alleles will lead to multiallelic "identifier" loci. Since these loci will occur throughout the genome, the basic effect will be magnified through the multiplicative combination of these different polymorphic traits; in general, a particular combination of these phenotypic traits will be rarer than any particular allele. The number of distinct combinations (signatures) M is related to the number of phenotypes per locus, m, for L loci. by

$$M = \bar{m}^L \qquad (9)$$

where $\bar{m}$ is the geometric mean of the m's at each locus. Thus the number of loci and number of phenotypes per locus needed to produce M signatures is

$$L = \log_{\bar{m}}M. \qquad (10)$$

In Table 2, I give the number of loci required for several values of m and three selected values of M. These three values of M cover the range, 10^4–10^6, described as reasonable for bank swallows earlier; they probably describe the range of the creches

of most colonial species. Note that when m = 2, the number of loci equals the information capacity of the system in bits (assuming equiprobability of signatures). It can be seen that for M = 10⁵ (H = 17 bits, our estimate for bank swallows), 6–10 loci with 3–6 phenotypes per locus are sufficient to generate the requisite number of signatures (the requisite information capacity). This is an entirely feasible genetic mechanism.

This hypothesized mechanism bears formal resemblance to the histocompatibility antigen loci. It is worth noting Burnet's (1973) remark concerning the latter: "It is likely that in all species of vertebrate there are so many distinguishable histocompatibility antigens that they can serve to differentiate every individual in a natural population of the species from any other" (p. 360).

KIN RECOGNITION TYPE 2: RECOGNIZING UNKNOWN KIN

In type 2 kin recognition, contextual evidence of kinship is weak or absent and the kin in question have *different*, genetically-determined signatures. The key feature is the second, for as suggested earlier, if the kin in question are "labelled" alike with identical signatures, then an individual in effect has learned its unknown kin's signature earlier when it learned its own (or its parents' or its siblings', etc.); thus we have only a slight variation on type 1, where the kin's signature is learned directly. As in my discussion of type 1 kin recognition, I will couch the argument in terms of parent-offspring recognition. As before, however, the argument is generalizable to numerous other cases, including sibling recognition in particular. For illustration, consider two examples. In some baboons and in a number of other primates, males live in groups which include their offspring, but because of a promiscuous mating system, they are uncertain of paternity. A male can probably infer paternity with some accuracy by noting who the infant's mother is and remembering with whom he mated (which is basically how the observing scientist infers probable paternity in these animals; Packer, 1980; Klein, in

TABLE 2. *Number of loci (L) required as a function of various numbers of phenotypes per locus (m) and three plausible combinations of creche size (S) and acceptable probability of signature duplication (p).*

m*	Example*	M = S/p		
		10⁴	10⁵	10⁶
2	2 alleles, dominance	13.3	16.6	19.9
3	2 alleles, additivity	8.4	10.5	12.6
5	3 alleles, additivity	5.7	7.2	8.6
6	3 alleles, co-dominance	5.1	6.4	7.7
10	4 alleles, co-dominance	4.0	5.0	6.0
12	6 alleles, additivity	3.7	4.6	5.6

* For simplicity, the table assumes that m is the same at each locus. "Example" is one particular situation that would give that m. More generally, one would expect m to be different at each locus, in which case we substitute the geometric mean m̄ for m. Note that in this table, entries for m = 2 are equivalent to the information capacity (H) in bits of the signature system (where all signatures are equiprobable).

preparation). However, an alternative or additional means to this end would be for the male to compare the infant's signature (olfactory?) with his own, inferring kinship if they are sufficiently similar. In a number of communally-breeding animals, parental care has been shown to be somewhat more selective than was originally thought (*e.g.*, Vehrencamp, 1977; Bertram, 1979). For example, an ostrich hen, who incubates the eggs of other hens along with her own, will push from her nest some fraction of the eggs when the number is large. When she does so, she apparently recognizes her own and evicts only the eggs of the other (non-incubating) hens (Bertram, 1979). It is possible that she recognizes distinctive characteristics (signatures) of her eggs, though it is as yet unknown if she actually does so. As I suggested in the Introduction, the best candidates for type 2 kin recognition at present are cases where siblings recognize one another in the absence of prior differential experience and where "labelling" seems unlikely (Buckle and Greenberg, 1981; Holmes and Sherman, 1982). Finally, it seems reasonable to suppose that additional cases will be described in which ecological circumstances favor this sort of kin recognition.

What sort of genetic mechanism would permit individuals to directly recognize kinship? To do so they must be able to es-

timate the proportion of genes they share, so it would seem necessary that some portion of the genome be "visible" (the signature). By judging the similarity of their signatures, they could make inferences about the similarity of their genomes as a whole. The genetic signature model described in the previous section would fulfill this function, provided we add one feature. Namely, the phenotypic effect of each allele at a signature locus must be independent of that of other possible alleles at the locus, for dominance or blending allelic interactions would lead to a confusing phenotypic identity of distinct allelic combinations. For example, for a classical quantitative trait, the distinctive genotypes 1,4 and 2,3 give identical phenotypes (5). Conversely, the similarity of the genotypes 1,2 and 2,4 is not apparent in their corresonding phenotypes (3 and 6, respectively). While such blending is of no concern for type 1 kin recognition, where it is only necessary that there be a large number of possible signatures, it does clearly interfere with the recognition of genetic similarity (type 2 kin recognition), for it leads to the misclassification of unrelated individuals as relatives, and vice versa.

Let us consider, then, a parent attempting to determine if a particular young is its offspring by comparing their signatures. Could our hypothetical genetic mechanism permit this discrimination with some reasonable degree of accuracy? To answer this question, we note that the probability of two individuals sharing an allele at a signature locus has two components. First is the probability that an allele is identical by descent (IBD). Second is the probability that it is not IBD but is "identical by chance" (IBC). For unrelated individuals, of course, only the latter component applies. Note that when there is only one allele at the locus, relatives and non-relatives alike must be identical at this locus, and the locus is useless for the kin recognition function. When the number of alleles is infinitely large, the probabilities for alleles IBD and IBC are r and 0 respectively, *i.e.*, the traditional coefficient of relatedness.

I have derived probability distributions for the proportion of alleles shared at a locus for different classes of relationship
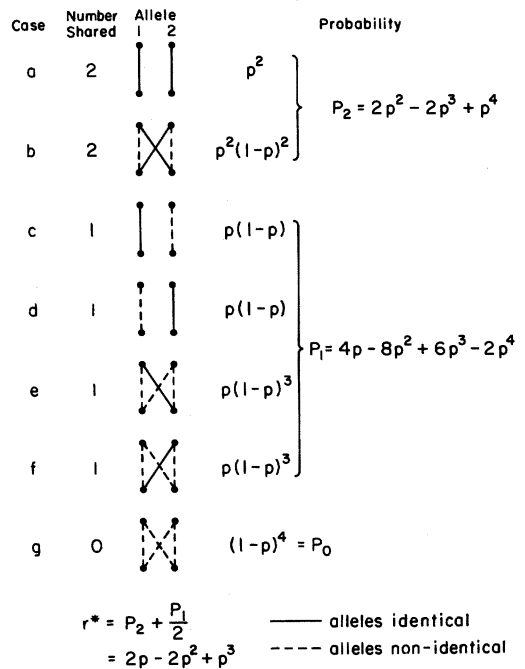

FIG. 2. Computation of alleles shared for unrelated individuals. In each case, the two alleles of one individual are shown at the top, and the two alleles of the other, unrelated, individual are shown at the bottom. Solid lines between allele pairs indicate they are identical, dotted lines between allele pairs indicate they are non-identical. P_2, P_1 and P_0 are the derived probabilities that two unrelated individuals share 2, 1 and 0 alleles, respectively.

(Beecher, in preparation). The derivations follow directly given the simplifying assumption that all alleles at a locus are equiprobable. This assumption allows us to say that the probability (gene frequency) of any allele at a locus is simply $1/n$, where n is the number of alleles at a locus. This is a reasonable assumption, since it is the expected equilibrium condition for the "rare-allele" advantage discussed earlier. The expected (mean) value of the proportion of alleles shared at a locus I call r^* because of its relationship to the coefficient of relatedness, r. For the parent-offspring relationship, the probability of sharing both alleles is simply $p = 1/n$ (one IBD, the other IBC = p), while the probability of sharing only the one IBD is $1 - p$. Hence for the parent-offspring case

$$r^*_0 = \tfrac{1}{2}(1 + p). \qquad (11)$$
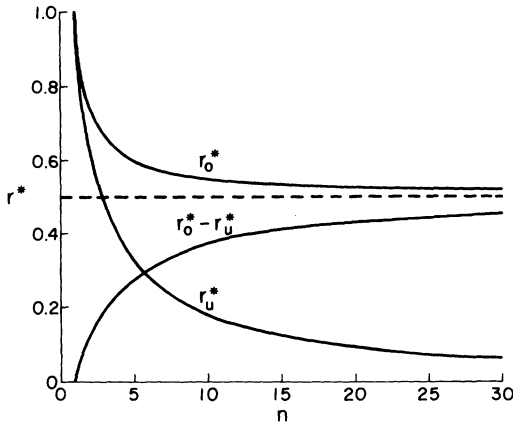
FIG. 3. Expected proportion of signature alleles shared (r*) as a function of number of alleles at the locus (n), for parent-offspring (r*$_o$) and unrelated individuals (r*$_u$), and the difference between the two. Note that r*$_o$ = 1 when n = 1 and approaches 0.5 (r$_o$) as n gets large, while r*$_u$ = 1 when n = 1 and approaches 0 (r$_u$) as n gets large. Their difference thus approaches 0.

For unrelated individuals, an allele can be IBC only, and the calculations shown in Figure 2 give

$$r^*_u = 2p - 2p^2 + p^3. \qquad (12)$$

Figure 3 shows that both r*$_o$ and r*$_u$ equal 1 when n = 1, and approach r (½ and 0, respectively) as n gets very large (p gets very small). Thus the effect of increasing n is to increase the difference r*$_o$ − r*$_u$ (Fig. 3) and so to enhance discrimination of kin from non-kin. Increasing the number of loci (L) does not affect r*, but it does decrease the variance of the sampling distribution of this proportion, and decreases misclassification errors thereby. The effect of increasing L is shown in Figure 4 for the case where n = 6 at all loci. The probability that parent and offspring will share a particular number of signature alleles will be the binomial distribution on [L, 2L] where p = 1/n. The probability for parent and unrelated individual will be the trinomial distribution on [0, 2L], with P$_2$, P$_1$ and P$_0$, as given in Figure 2. From Figure 4 it can be seen that the chance of our parent and a non-relative sharing a large proportion of genes IBC decreases as L increases.
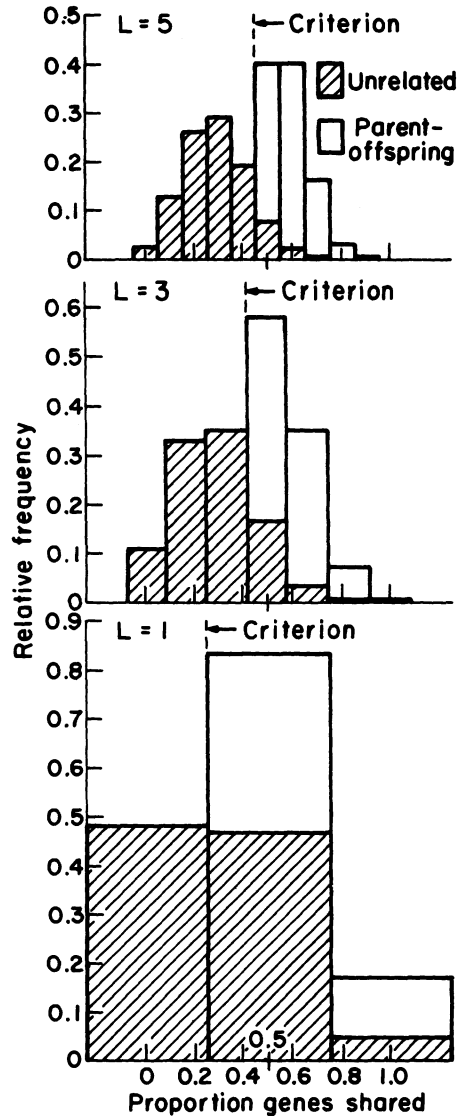
For reasonable (small) values of n and L,

FIG. 4. The distribution of proportion genes shared for L (the number of loci) = 1, 3 or 5 and n (the number of alleles at a locus) = 6 for each locus. The criterion for classifying an individual as "unrelated" is 0.5, and is held constant for the three different distributions shown. The percentage of unrelated individuals that fall above this criterion (unrelated individuals misclassified as offspring) for L = 1, 3 and 5 is 52%, 21% and 10%, respectively. The means of these distributions are r* = 0.58 (parent-offspring) and 0.28 (unrelated) (see formulae in text). Note that the difference between the means of the distributions is unaffected by L (but does increase as n increases) while the variances of the distributions decrease as L increases (they are only slightly affected by changes in n).

could our parent accurately determine whether a young was indeed its offspring? Inspection of Figure 4 shows that when $n = 6$ and $L = 5$, the parent could do quite well if it adopted the following criterion. "If this individual shares 50% or more of its signature alleles with me, I will treat it as an offspring. Otherwise I will treat it as a non-relative." This decision rule would lead to no errors of the first kind (treating kin as non-kin) and (when $L = 5$) only 10% errors of the second kind (treating non-kin as kin). Thus, especially if combined with independent contextual evidence, this mechanism would permit quite good determination of kinship. Note that discrimination is considerably poorer for $L = 3$ (0 and 21% errors) and $L = 1$ (0 and 52% errors).

I conclude, as in the previous section, that a rather modest genetic mechanism could accomplish a rather sophisticated function. The next step, clearly, is to see if such mechanisms exist in nature. As a final note, a recent study by Yamazaki *et al.* (1976) suggests that histocompatibility loci could function as signature loci. This study found that congenic mice chose females in mating preference tests that differed from them at only the histocompatibility locus H-2 over females that were genetically identical.

CONCLUSIONS

The main theme of this paper has been that to understand the varieties of kin recognition we must carefully examine the mechanisms underlying individual identification. For simplicity I have ignored the complementary process by which identifying signals are decoded (recognition proper); without question, a complete analysis ultimately will require examination of both sides of the recognition process. I have focused on two particular sorts of kin recognition: type 1, where the primary problem is finding your kin in a large group and where there is opportunity earlier to learn their signatures, and type 2, where there is no opportunity for such learning and the problem is to determine kinship directly by matching your own

unique signature (or those of known kin) to that of the unknown kin.

For type 1 kin recognition, I have suggested that identification (signature) systems can be analyzed in terms of their information capacity. Among the advantages of this approach is that it provides a basis for (a) comparing this communication system with others, such as the bee dance language (Haldane and Spurway, 1954; Gould, 1975), and (b) comparing the signature systems of many disparate species.

I have proposed two very similar genetic mechanisms which could generate signature systems for each of the two types of kin recognition. In both cases, signatures are generated by several independent loci with several alleles at each locus. In the second case, the additional feature is required of independence of effects of alleles at a locus. Since the second genetic mechanism could fulfill both types of signature function, an interesting implication follows: if such a mechanism evolved in the selective context of type 1 kin recognition, then given the appropriate opportunities, it could allow type 2 kin recognition, which could then become a secondary selective context. For example, perhaps the primary selective pressure on the Belding's ground squirrel signature system (Holmes and Sherman, 1982) was recognition of nestmates; the ability to discriminate full- from half-sibling nestmates could be a secondary, adaptive consequence of the evolved mechanism. A corollary of this point is that type 2 kin recognition must be validated in a natural field context (or at least a valid approximation thereof), for the laboratory demonstration of an "unlearned" preference for kin might only indicate that the animals incidentally *can* make such discriminations; it says nothing about whether they normally *do* so in the real world.

A second, related implication is that a signature system fulfilling both type 1 and type 2 functions might be adaptive for animals that have to deal with "mixed" cases, where context is a good, but not completely reliable, predictor of kinship. For example, in bank swallows the young the parent finds in its nest are probably, but not

definitely, its own. Unrelated young occasionally fly or (more rarely) walk into the nest (Beecher *et al.,* 1981*b*; Beecher and Beecher, unpublished observations). Intraspecific nest parasitism is an unconfirmed but real possibility in this highly colonial species. Males have some uncertainty of paternity (Beecher and Beecher, 1979). While at present we cannot say if the sum of these uncertainties is significant, let us suppose for the moment that it is. Then given our genetic signature mechanism, a parent could (a) learn the signatures of the young in its nest, but, (b) applying some conservative criterion, reject, or disfavor, any chick in the nest whose signature is a poor match to its own. Our cross-fostering experiments with bank swallows are consistent with the common finding that foster young are accepted provided they are fostered prior to a point very close to independence (fledging) of the young (Beecher *et al.,* 1981*a*). Yet more subtle measures (*e.g.,* weight gain) might reveal a preference for true offspring over foster young. We are presently carrying out such experiments in bank swallows. I believe this comment applies to virtually all cross-fostering experiments to date. It is significant that the first-observed and strongest effect in cross-fostering experiments with ground squirrels is that nestmates are preferred over non-nestmates, regardless of genetic relationship. The preference for more closely-related individuals (whether the comparison is made among nestmates, or among non-nestmates) is a more subtle one, and requires sensitive tests (Sherman, 1980; Holmes and Sherman, 1982).

While this paper clearly is advocating examination of the genetics of signature systems, it is a fact that few of these systems have yet been studied thoroughly enough to permit genetic analysis. For example, the olfactory signatures that undoubtedly are common in mammals and insects essentially are known only by inference (*e.g.,* Buckle and Greenberg, 1981). I predict that examination of olfactory signatures will play a particularly important role in our understanding of individual and kin recognition. While the acoustic signatures of birds and mammals have received more explicit attention, they have not been subject to very sophisticated analysis to date. For neither olfactory nor acoustic signatures do we yet have any data pertaining to underlying genetic mechanisms. The well-described visual signatures of royal tern chicks and eggs (Buckley and Buckley, 1970, 1972) undoubtedly have a strong genetic component, and visual signatures of this sort may prove quite amenable to conventional genetic analysis. Parent-offspring and sibling-sibling comparisons, where appropriate controls are taken to evaluate experiential influences, should enable us to test explicit genetic models of the sort described in this paper. Furthermore, these models can also predict the outcome of kin recognition studies such as that of Greenberg (1979). He found that sweat bees guarding the nest accepted unfamiliar kin roughly in proportion to their degree of relatedness. It seems clear that probability distributions of the sort in Figure 4 predict what these numbers should be, given particular L/n combinations and particular decision rules. An attempt by Crozier and Dix (1979) to account for data on recognition via "colony odors" in hymenopterans produced a genetic model very similar to the one I have given in this paper.

Finally, I believe that the study of kin recognition is like so many other problem areas in behavioral biology. It is becoming increasingly clear that ultimate and proximate causes, while perhaps logically independent, are inevitably intertwined in the evolution of the behavior. Thus we will not unravel the evolution of a behavioral process such as kin recognition unless we consider both selective forces and underlying mechanisms.

REFERENCES

Attneave, F. 1959. *Applications of information theory to psychology.* Holt, New York.

Beecher, M. D. 1981. Development of parent-offspring recognition in birds. *In* R. Aslin, J. Alberts, and M. Petersen (eds.), *Development of perception,* Vol. 1, pp. 45–65. Academic Press, New York.

Beecher, M. D. and I. M. Beecher. 1979. Sociobiology of bank swallows: Reproductive strategy of the male. Science 205:1282–1285.

Beecher, M. D., I. M. Beecher, and S. Hahn. 1981a. Parent-offspring recognition in bank swallows (*Riparia riparia*): II. Development and acoustic basis. Anim. Behav. 29:95–101.

Beecher, M. D., I. M. Beecher, and S. Lumpkin. 1981b. Parent-offspring recognition in bank swallows (*Riparia riparia*): I. Natural history. Anim. Behav. 29:86–94.

Bertram, B. C. R. 1979. Ostriches recognise their own eggs and discard others. Nature 279:233–234.

Blaustein, A. R. and R. K. O'Hara. 1981. Genetic control for sibling recognition? Nature 290:246–248.

Buckle, G. R. and L. Greenberg. 1981. Nestmate recognition in sweat bees (*Lasioglossum zephrum*): Does an individual recognize its own odour or only odours of its nestmates? Anim. Behav. 29:802–809.

Buckley, P. A. and F. G. Buckley. 1970. Color variation in the soft parts and down of royal tern chicks. Auk 87:1–13.

Buckley, P. A. and F. G. Buckley. 1972. Individual egg and chick recognition by adult royal terns (*Sterna maxima maxima*). Anim. Behav. 20:457–462.

Burnet, F. M. 1981. Multiple polymorphism in relation to histocompatibility antigens. Nature 245:359–361.

Crozier, R. H. and M. W. Dix. 1979. Analysis of two genetic models for the innate component of colony odor in social Hymenoptera. Behav. Ecol. Sociobiol. 4:217–224.

Cullen, E. 1957. Adaptations in the kittiwake to cliff-nesting. Ibis 99:275–303.

Doane, H. M. and R. H. Porter. 1978. The role of diet in mother-infant reciprocity in the spiny mouse. Devel. Psychobiol. 11:271–277.

Emlen, S. T. and N. J. Demong. 1975. Synchronized breeding in a colonial swallow: A new hypothesis. Science 188:1029–1031.

Epsmark, Y. 1971. Individual recognition by voice in reindeer mother-young relationship. Field experiments and playback experiments. Behaviour 41:295–301.

Gould, J. L. 1975. Honey bee recruitment: The dance-language controversy. Science 189:685–693.

Greenberg, L. 1979. Genetic component of bee odor in kin recognition. Science 206:1095–1097.

Gubernick, D. J. 1980. Maternal "imprinting" or maternal "labelling" in goats? Anim. Behav. 18:124–129.

Haldane, J. B. S. and H. Spurway. 1954. A statistical analysis of communication in *Apis mellifera* and a comparison with communication in other animals. Insectes Sociaux 1:247–283.

Hamilton, W. D. 1964. The genetical evolution of social behaviour, I and II. J. Theoret. Biol. 7:1–51.

Hanken, J. and P. W. Sherman. 1981. Multiple paternity in Belding's ground squirrel litters. Science 212:351–353.

Holmes, W. G. and P. W. Sherman. 1982. The ontogeny of kin recognition in two species of ground squirrels. Amer. Zool. 22:491–517.

Hoogland, J. L. and P. W. Sherman. 1976. Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. Ecol. Monogr. 46:33–58.

Kaya, Y. and K. Kobayashi. 1972. A basic study of human face recognition. *In* S. Watanabe (ed.), *Frontiers of pattern recognition,* pp. 265–290. Academic Press, New York.

Packer, C. 1980. Male care and exploitation of infants in *Papio anubis.* Anim. Behav. 28:512–520.

Petersen, A. J. 1955. The breeding cycle in the bank swallow. Wilson Bull. 97:235–286.

Rohwer, S. 1975. The social significance of avian winter plumage variability. Evolution 29:593–610.

Shannon, C. E. and W. Weaver. 1949. *The mathematical theory of communication.* Univ. of Illinois Press, Urbana.

Sherman, P. W. 1980. The limits of ground squirrel nepotism. *In* G. W. Barlow and J. Silverberg (eds.), *Sociobiology: Beyond nature/nurture?,* pp. 505–544. Westview Press, Boulder, Colorado.

Vehrencamp, S. L. 1977. Relative fecundity and parental effort in communally nesting anis, *Crotophaga sulcirastris.* Science 197:403–405.

Waldman, B. 1981. Sibling recognition in tadpoles: The role of experience. Z. Tierpsych. 56:341–358.

Wu, H. M. H., W. G. Holmes, S. R. Medina, and G. P. Sackett. 1980. Kin preference in infant *Macaca nemestrina.* Nature 285:225–227.

Yamazaki, K., E. A. Boyse, V. Mike, H. T. Thaler, B. J. Mathieson, J. Abbott, J. Boyse, Z. A. Zayas, and L. Thomas. 1976. Control of mating preferences in mice by genes in the major histocompatibility complex. J. Exper. Med. 144:1324–1335.