Kin Recognition Mechanisms: Phenotypic Matching or Recognition Alleles?
Author(s): Andrew R. Blaustein
Source: *The American Naturalist*, Vol. 121, No. 5 (May, 1983), pp. 749-754
Published by: The University of Chicago Press for The American Society of Naturalists
Stable URL: http://www.jstor.org/stable/2460878
Accessed: 11/04/2011 14:32

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/page/info/about/policies/terms.jsp. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/action/showPublisher?publisherCode=ucpress.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

The University of Chicago Press and *The American Society of Naturalists* are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist.*

http://www.jstor.org

KIN RECOGNITION MECHANISMS: PHENOTYPIC MATCHING OR RECOGNITION ALLELES?

Kin recognition in the absence of obvious opportunities to learn one's kin is an important biological phenomenon and elucidating the mechanism by which the recognition is achieved is a major challenge. Such recognition is important because it can facilitate preferential acts to kin if other factors such as proximity to or familiarity with other individuals are not correlated with kinship and if nepotism has been selected for. But precisely how is kin recognition achieved? It is critical to keep in mind that the essence of Hamilton's (1964) inclusive fitness model is that, all other things being equal, individuals should behave differently toward one another based on genetic relatedness, regardless of the mechanism by which individuals determine the degree of genetic relatedness among themselves.

There are four possible mechanisms proposed for kin recognition (reviewed by Alexander 1979; Bekoff 1983; Dawkins 1982; Holmes and Sherman 1982).

1. Recognition can be based on spatial distribution.—If relatives are distributed predictably in space, altruistic acts might be selected for if the acts are directed preferentially toward those individuals in a particular location. Such a location may be a home site or territory.

2. Recognition can be based on familiarity and prior association.—If relatives predictably occur in appropriate social circumstances, recognition could occur through social learning (Alexander 1979). Thus, individuals of the same litter within the same nest or those from one clutch may learn to recognize "familiar" individuals (see Bekoff 1981, 1983 for a detailed discussion of familiarity and recognition). Relatives might also recognize one another if they predictably meet in the presence of a third individual who is familiar to each of them. One example of this may be two maternally related half siblings from different litters that interact with their common mother (Holmes and Sherman 1982).

3. Recognition could occur through phenotypic matching.—In phenotypic matching an individual learns and recalls the phenotypes of relatives or of itself (assuming phenotypic similarity is correlated with genotypic similarity). The individual then assesses similarities and differences between its own phenotype and unfamiliar conspecifics. Thus, for example, if chemicals or odors are involved in kin recognition, they may have a genetic component, but must be learned for kin recognition to occur.

4. Recognition could be achieved by the action of recognition alleles.—Phenotypes could be used in recognition independent of learning if recognition alleles existed. In this system, the phenotypic marker (e.g., a particular chemical or odor) and the knowledge of that marker have genetic bases.

Mechanisms 1 and 2 are actually indirect means by which kin could be aided because kin per se are not actually recognized, rather those individuals most likely to be kin are the ones most likely to be aided and thus recognition errors may

Am. Nat. 1983. Vol. 121, pp. 749–754.

occur if these are the primary means of recognition. Recognition errors could also occur if mechanism 3 were utilized if individuals have a similar phenotypic marker but such a marker is coded by different genes or if the same genes coded for similar markers but the individuals were unrelated. The selective basis for mechanisms 1 and 2 is overall genetic relatedness, whereas for mechanism 4 it is the sharing of a particular gene (or small set of genes) that determines who will be aided. Mechanism 3 can depend on overall genetic relatedness or the particular gene(s) involved in producing the marker. Mechanisms 3 and 4 are the ones discussed in most detail when considering theoretical aspects of kin recognition (see discussion in Dawkins 1982). The problem is, the hypothesis invoking recognition alleles has generally been revoked in favor of the phenotypic matching hypothesis. The refutation of the recognition allele hypothesis is based primarily on theory although empirical evidence exists that is consistent with both the phenotypic matching and recognition allele hypotheses.

THEORETICAL ARGUMENTS CONCERNING THE EXISTENCE OF RECOGNITION ALLELES

Alexander and Borgia (1978) suggest that the existence of recognition alleles is unlikely for two basic reasons. First, as pointed out originally by Hamilton (1964, p. 25), the actions of recognition alleles would be complex. Such alleles must (1) be expressed phenotypically, (2) cause the recognition of the phenotypic marker, and (3) enable those individuals carrying copies of these alleles to favor other individuals also carrying the alleles (for detailed discussions see Alexander 1979; Alexander and Borgia 1978; Holmes and Sherman 1982). This system is similar to the "green beard" altruistic system suggested by Dawkins (1976) in which he stated, for illustrative purposes, that one such phenotypic marker might be a green beard. Secondly, recognition alleles may be "outlaw" alleles (Alexander and Borgia 1978). Outlaws are alleles that favor themselves at the expense of all other alleles in the genome (including those at other gene loci) (Alexander and Borgia 1978). Segregation distorters or meiotic drive genes are examples of outlaws because such genes are favored at their own locus and appear in more than 50% of the gametes produced.

The theoretical arguments concerning the improbability of recognition alleles have been generally accepted (examples are Holmes and Sherman 1982; Kurland 1980; Sherman 1980; but see Rothstein 1980). This is interesting because Hamilton (1964, p. 25) was not so positive that recognition alleles are impossible. He suggested that the same a priori objections may be argued against the existence of assortative mating which has evolved "despite its obscure advantages." It is even questionable that recognition alleles would be outlaws (see Ridley and Grafen 1981; Rothstein and Barash 1982). Acceptance of the theoretical arguments may lead to premature rejection of the possibility of recognition alleles.

Phenotypic matching seems to be the favored mechanism for kin recognition even though empirical evidence consistent with both phenotypic matching and recognition alleles exists. The problem is, it is probably impossible to falsify the phenotypic matching hypothesis.

EMPIRICAL EVIDENCE CONSISTENT WITH BOTH PHENOTYPIC MATCHING AND RECOGNITION ALLELES

To illustrate the problem of differentiating between the phenotypic matching and recognition allele hypotheses I will describe the results of three recent kin recognition studies.

In their extremely important work on ground squirrels, Holmes and Sherman (1982) reported that Belding's ground squirrels (*Spermophilus beldingi*) that were electrophoretically identified as full sisters and maternal half sisters (within the same litter) seemed to treat each other differently as yearlings when aggressive and amicable behavior was quantified. Full sisters fought significantly less often than half sisters and chased each other significantly less often from territories than did half sisters. Both types of siblings shared a common nest and even a common uterus. Holmes and Sherman (1982, p. 506) suggest the data imply ". . . sibling recognition in *S. beldingi* is augmented by some mechanism in addition to simple association in the natal burrow." They also suggest that phenotypic matching may be involved in differentiating between maternal half siblings and full siblings (see p. 512). Individuals could learn their own phenotypic trait such as an odor and then assess the similarities and differences between themselves and other individuals they contact. Thus, full siblings may smell more similar than half-sibling ground squirrels.

Wu et al. (1980) showed that unfamiliar infant paternal half-sibling macaques (*Macaca nemestrina*) were preferred in association tests over unfamiliar nonrelatives. This study is particularly powerful because maternal learning effects are absent since only paternal and not maternal half siblings were used. Therefore maternal "labeling" or "imprinting" is unlikely (see Blaustein and O'Hara 1982 for discussion).

Phenotypic matching was invoked subtly by Wu et al. (1980) as the mechanism for macaque kin recognition. They suggest that an individual's experience of itself could be the basis for later social preferences. Dawkins (1982, p. 150) states "my bet is that the monkeys recognize resemblances of relatives to perceived features of themselves" (i.e., phenotypic matching). Bekoff (1983) correctly points out that the monkeys in the experiments of Wu et al. were allowed to interact with nonrelatives prior to testing and that later preference for relatives may be based on a model similar to the one proposed by Bateson (1978, 1980, 1982) to explain mate selection, whereby individuals choose mates who are slightly different from individuals with whom they were reared. Under Bekoff's (1983) interpretation the kin preference observed by Wu et al. (1980) may be an artifact and a preference for nonkin may have occurred had the macaques been reared with their half sibs.

Studies on Cascades frog (*Rana cascadae*) tadpoles are particularly relevant to this discussion because of the various rearing regimes employed (Blaustein and O'Hara 1981, 1982; O'Hara and Blaustein 1981). In the first series of experiments animals reared with siblings and those reared in a mixed group of siblings and nonsiblings preferred to associate with siblings over nonsiblings (O'Hara and Blaustein 1981). In the second experimental series individuals reared in total isolation from an early embryonic stage preferred to associate with unfamiliar siblings over unfamiliar nonsiblings (Blaustein and O'Hara 1981). In the third experimental series, tadpoles reared with siblings or in isolation preferred to associate with full siblings over half siblings (either maternal half siblings or paternal half siblings) and half siblings over nonsiblings (either maternal or paternal; Blaustein and O'Hara 1982). Furthermore, in the latter series of experiments the jelly mass that surrounds each clutch and is produced by females was removed from two clutches. One clutch was reared with no jelly mass and tadpoles from this group preferred to associate with unfamilar full siblings over paternal half siblings. Tadpoles from a second clutch were reared with jelly from a paternal half-sibling clutch and tadpoles reared with this foreign jelly preferred to associate with unfamiliar full siblings over paternal half siblings from which their foreign jelly came. These jelly transplant experiments are important because it has been proposed that females may "label" their clutches through the jelly coats and thus tadpoles could learn to associate with individuals from the same clutch by learning characteristics contained within the jelly and "absorbed" by the tadpoles during development (see discussion in Blaustein and O'Hara 1982).

Results of these tadpole experiments reveal that tadpoles can differentiate between individuals of varying degrees of relatedness, even if they are reared in mixtures of siblings and nonsiblings, in isolation, or with full siblings. Holmes and Sherman (1982) interpret the results of the first two series of experiments (Blaustein and O'Hara 1981; O'Hara and Blaustein 1981) as a possible example of phenotypic matching. According to proponents of phenotypic matching, tadpoles reared in isolation could learn their own cues and later match their own phenotypes with other individuals, even totally unfamiliar ones, and then make their association choice. How does one explain the results of tadpoles choosing to associate with unfamiliar siblings over unfamiliar nonsiblings after these tadpoles were reared in mixed rearing regimes? It would be easy to invoke phenotypic matching for even these results. One could say that tadpoles reared with nonsiblings and siblings are still "closer to themselves," and thus an individual's own odor is the most pervasive one, so its choice could still be made by matching its own phenotype with other phenotypes.

Actually, isolation experiments, or those using paternal half siblings, will obviously yield equivocal results as far as differentiating between the phenotypic matching and recognition allele hypotheses is concerned. It may be impossible to falsify the phenotypic matching hypothesis. For example, if single tadpoles from one clutch were reared with numerous nonsiblings (as in O'Hara and Blaustein 1982) and still preferred to associate with siblings in association tests, one could still argue that the individual's own odor or phenotype was the most pervasive one. Therefore, phenotypic matching could be invoked but recognition alleles cannot be ruled out. If, however, the tadpole preferred those individuals they were reared with, in this case, nonsiblings, then the recognition allele hypothesis would not be supported (see Buckle and Greenberg 1981; Greenberg 1979). Unequivocal support for the recognition allele hypothesis could only be achieved by experimentally masking the ability of an individual to perceive the phenotypic marker in question throughout ontogeny. This seems difficult.

The results concerning ground squirrels (Holmes and Sherman 1982), macaques

(Wu et al. 1980), and tadpoles (Blaustein and O'Hara 1981, 1982; O'Hara and Blaustein 1981) are consistent with both phenotypic matching and recognition allele explanations. In fact, there may be essentially no difference between the two mechanisms. Phenotypic matching merely specifies a learned component whereby genetically encoded information is manifested. If the members of a population have identical genes enabling them to learn their individual phenotypic markers and to aid others with the same marker, then the difference between the two mechanisms is trivial. Proponents of phenotypic matching seem to require that there be no learning before recognition alleles are considered. However, virtually no complicated behavior is totally impervious to learning.

Although I do not necessarily endorse their existence, I recommend that we keep an open mind as to the existence of recognition alleles. Certainly the empirical evidence presented is consistent with either explanation. Both mechanisms function similarly and lead to the same evolutionary predictions. Both mechanisms allow an individual to recognize others they have never had contact with. Perhaps parsimony should prevail in the final consideration. Given the theoretical arguments against the existence of recognition alleles it may be suggested that phenotypic matching is the more parsimonious explanation. However, according to the empirical evidence, recognition alleles provide an explanation that is at least as parsimonious and perhaps more so. Should theory outweigh empirical evidence when parsimony is to be invoked? It is important to evaluate such questions carefully.

ACKNOWLEDGMENTS

I wish to thank Kathy Lumas, Rick O'Hara, and especially Steve Rothstein for critically reviewing the manuscript and providing many valuable suggestions for improving it. Kathy Moore provided valuable discussion. Two anonymous reviewers offered extremely valuable suggestions for improving the manuscript. Financial support was provided by NIH Biomedical Research Support Grant RR07079, the O.S.U. Research Council, and NSF grant BNS 8120203.

LITERATURE CITED

Alexander, R. D. 1979. Darwinism and human affairs. University of Washington Press, Seattle.

Alexander, R. D., and G. Borgia. 1978. Group selection, altruism, and the levels of organization of life. Annu. Rev. Ecol. Syst. 9:449–474.

Bateson, P. 1978. Sexual imprinting and optimal outbreeding. Nature 273:659–660.

———. 1980. Optimal outbreeding and the development of sexual preferences in Japanese quail. Z. Tierpsychol. 53:231–244.

———. 1982. Preferences for cousins in Japanese quail. Nature 295:236–237.

Bekoff, M. 1981. Mammalian sibling interactions: genes, facilitative environments, and the coefficient of familiarity. Pages 307–346 *in* D. Gubernick and P. H. Klopfer, eds. Parental care in mammals. Plenum, New York.

———. 1983. The development of behavior from evolutionary and ecological perspectives: towards a generic social biology. *In* E. S. Gollen, ed. The evolution of adaptive skills: comparative and ontogenetic approaches. Academic Press, New York.

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

———. 1982. Kin recognition in *Rana cascadae* tadpoles: maternal and paternal effects. Anim. Behav. 30:1151–1157.

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

Dawkins, R. 1976. The selfish gene. Oxford University Press, New York.

———. 1982. The extended phenotype. Freeman, San Francisco.

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

Hamilton, W. D. 1964. The genetical evolution of social behavior. I, II. J. Theor. Biol. 7:1–52.

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

Kurland, J. A. 1980. Kin selection theory: a review and selective bibliography. Ethol. Sociobiol. 1:255–274.

O'Hara, R. K., and A. R. Blaustein. 1981. An investigation of sibling recognition in *Rana cascadae* tadpoles. Anim. Behav. 29:1121–1126.

———. 1982. Kin preference behavior in *Bufo boreas* tadpoles. Behav. Ecol. Sociobiol. 11:43–49.

Ridley, M., and A. Grafen. 1981. Are green beard genes outlaws? Anim. Behav. 29:954–955.

Rothstein, S. I. 1980. Reciprocal altruism and kin selection are not clearly separable phenomena. J. Theor. Biol. 87:255–261.

Rothstein, S. I., and D. P. Barash. 1982. Gene conflicts and the concepts of outlaw and sheriff alleles. J. Social Biol. Struct. (in press).

Sherman, P. W. 1980. The limits of ground squirrel nepotism. Pages 505–544 *in* G. W. Barlow and J. Silverberg, eds. Sociobiology: beyond nature/nurture? Westview Press, Boulder, Colo.

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.

ANDREW R. BLAUSTEIN

DEPARTMENT OF ZOOLOGY
OREGON STATE UNIVERSITY
CORVALLIS, OREGON 97331

Submitted May 27, 1982; Revised October 5, 1982; Accepted October 22, 1982