

# GENETIC CLONAL RECOGNITION ABILITIES IN MARINE INVERTEBRATES MUST BE MAINTAINED BY SELECTION FOR SOMETHING ELSE

R. H. CROZIER

School of Zoology, University of New South Wales, P.O. Box 1, Kensington, NSW 2033, Australia

Received November 19, 1985. Accepted May 27, 1986

Various marine invertebrates form colonies or groups of genetically identical individuals. In many instances these animals show a very strong ability to distinguish between members of their own colony and those of other colonies, or at least between members of their own and of other clones (Ayre, 1982; Lubbock, 1980; Neigel and Avise, 1983a, 1983b, 1985). In anemones, individuals tolerate clonemates as neighbors, but attack members of other clones with which they come into contact (although habituation to repeatedly encountered foreigners occurs [Sebens, 1984; Stoddart et al., 1985]).

From the pattern of "mistakes," in which animals accept members of other clones, it is plausible to attribute this "clonal recognition" to the matching of genotypes at a single locus. The parallels between this system and the immune system of mammals are both obvious and previously noted (e.g., Lubbock, 1980), and are echoed by findings that the mouse immune system is itself associated with individual recognition (Boyse et al., 1983).

Two genetic models have been proposed for this recognition mechanism. Under the genetic-identity model, individuals would accept each other only if their genotypes at the recognition locus are identical (Lubbock, 1980; Neigel and Avise, 1983a). For example, if there are alleles *A* and *B* at this locus, *AA* individuals would only accept other *AA* individuals, and would reject *AB* and *BB* individuals. Under the allele-sharing model, individuals accept others if they share at least one allele in common (Scofield et al., 1982), so that *AA* individuals accept both *AA* and *AB* individuals, but reject *BB* ones.

It is worthwhile inquiring into the dynamics of these models, under the assumption that an animal imposes a cost on members of other clones that it encounters. This cost is certainly imposed in the case of the sea anemones studied, which possess special stinging organs (acrorhagi) used only against non-clonemates during fights. I will show below that polymorphism for the cues involved in recognition according to the above schemes is not maintainable if the only selection involved is that imposed by the recognition system itself.

## Analyses

The basic axiom is that the fitness of a genotype is proportional to the fraction of the population with which it can interact peaceably. For simplicity, I also assume that both mating and the resulting settlement of zygotes is at random.

Consider first the genetic-identity model applied to a single locus with two alleles, *A* and *B*, with frequencies *p* and *q*. The fitnesses at this locus are then:

$$\begin{array}{ccc} W_{AA} & W_{AB} & W_{BB} \\ p^2 & 2pq & q^2 \end{array}$$

The heterozygote is thus the genotype with the highest fitness over the range of allele frequencies of  $1/3-2/3$  (for which  $p^2 < 2pq > q^2$ ), so that one might expect that a stable polymorphism would occur, at least for populations with initial frequencies in this range. This is not the case. Let  $u = p/(1 - p)$ ,  $p = 0.5 + d$ , and let  $p'$  and  $u'$  be the values after a further generation. Then,

$$\begin{aligned} u' &= (p^4 + 2p^2q^2)/(q^4 + 2p^2q^2) \\ u'/u &= [0.375 + d(0.25 + d/2 + 3d^2)] / \\ &\quad [0.375 - d(0.25 - d/2 + 3d^2)]. \end{aligned}$$

So that, for positive *d* values, the population moves to fixation of *A*, and for negative ones to fixation of *B*. For the allele-sharing model, the fitness scheme is:

$$\begin{array}{ccc} W_{AA} & W_{AB} & W_{BB} \\ 1 - q^2 & 1 & 1 - p^2 \end{array}$$

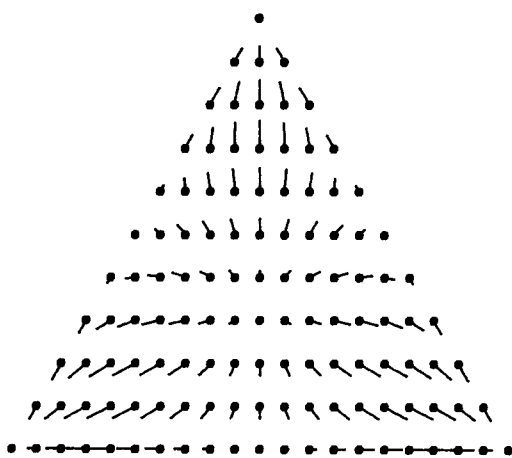


FIG. 1. Allele frequency changes for a three-allele system. The vertices of the triangle represent frequencies of one for one allele or the other. Each dot represents a starting position, and the line (if any) leading from it represents the direction of change of gene frequency in one subsequent generation. The lines shown here represent 0.4 times the frequency changes in one generation under the genetic-identity model, and a very similar picture results when the actual one-generation changes under the allele-sharing model are multiplied by two.

This fitness scheme is one of selection for heterozygotes for all allele frequency values. Hence, the direction of the allele-frequency change for any frequency can be found by calculating the equilibrium frequency to which the population would move if these fitnesses remained constant:

$$\hat{u} = p^2/q^2$$

so that

$$\hat{u}/u = u$$

Hence, if  $p$  is greater than  $q$ ,  $p$  increases; and if  $p$  is less than  $q$ ,  $p$  decreases.

Extending the analysis to multiple alleles appears intractable without approximations for both models, but simulation for three alleles indicates that the same results follow (Fig. 1). Simulations also confirm that, as expected, changing the strength of selection by raising the fitness values used above to a power, or by adding a constant to them, does not alter the eventual outcome.

#### DISCUSSION

I have not shown that there is selection against recognition and discrimination by creatures such as sea anemones, only that there is selection against the cue system involved. Selection will favor anemones that are able to distinguish between clonemates and non-clonemates and to discriminate against the latter with acrorhagial attacks. But this form of selection leads to loss of the necessary polymorphism in the cues used for recognition.

If recognition imposes selection against the cue system necessary for it, how is it that such polymorphism persists? The simplest answer is that these polymorphisms are maintained by other forms of selection, and that the clone-recognition function observed by us imposes selection that is weak in comparison. It is tempting to suggest that these loci really are immune loci, and that the variation at them is maintained by host-parasite interactions.

The analysis of recognition systems presented here has general implications for recognition systems in other creatures, and it seems likely that many of these therefore also "piggy-back" on variation maintained by other forms of selection (Crozier, 1986).

The two models are unusual in that they involve selection for heterozygotes without this resulting in balancing selection, and appear to be little-known, although the genetic-identity model follows naturally from discussions by Wright (1959 pp. 123–124, 1969 pp. 131–136). There is also the parallel case that selection for an intermediate phenotype determined quantitatively does not necessarily yield polymorphism for the polygenes concerned (Robertson, 1956; Curnow, 1964), but this result follows because the heterozygote is not fitter than both other genotypes.

Finally, clones of marine invertebrates such as those discussed often show a markedly clumped distribution, so that inter-clone contact probably occurs much less frequently than under the random-settlement assumption made above. It is unlikely that this nonrandom population structure would materially affect the results, because its effect is to reduce the strength of selection which, as noted above, does not alter the eventual out-

come. Inbreeding, by lessening the frequency of heterozygotes, would essentially strengthen selection against rare alleles for the recognition cues.

#### ACKNOWLEDGMENTS

I thank J. Maynard Smith, A. Robertson, and J. James for bringing the quantitative inheritance case to my attention, W. S. Moore and an anonymous referee for helpful criticisms, and the Australian Research Grants Scheme for supporting my work on evolutionary genetics.

#### LITERATURE CITED

- AYRE, D. J. 1982. Inter-genotype aggression in the solitary sea anemone *Actinia tenebrosa*. Mar. Biol. 68:199–205.
- BOYSE, E. A., G. K. BEAUCHAMP, AND K. YAMAZAKI. 1983. The sensory perception of genotypic polymorphism of the major histocompatibility complex and other genes: Some physiological and phylogenetic implications. Hum. Immunol. 6:177–183.
- CROZIER, R. H. 1986. Genetic aspects of kin recognition: Concepts, models, and synthesis. In D. J. C. Fletcher and C. D. Michener (eds.), Kin Recognition in Animals. Wiley, N.Y. In press.
- CURNOW, R. N. 1964. The effect of continued selection of phenotypic intermediates on gene frequency. Genet. Res. 5:341–353.
- LUBBOCK, R. 1980. Clone-specific cellular recognition in a sea anemone. Proc. Nat. Acad. Sci. USA 77:6667–6669.
- NEIGEL, J. E., AND J. C. AVISE. 1983a. Clonal diversity and population structure in a reef-building coral, *Acropora cervicornis*: Self-recognition analysis and demographic interpretation. Evolution 37:436–453.
- . 1983b. Histocompatibility bioassays of population structure in marine sponges. Clonal structure in *Verongia longissima* and *Iotrochota birotulata*. J. Hered. 74:134–140.
- . 1985. The precision of histocompatibility response in clonal recognition in tropical marine sponges. Evolution 39:724–732.
- ROBERTSON, A. R. 1956. The effect of selection against extreme deviants based on deviation or on homozygosity. J. Genet. 54:236–248.
- SCOFIELD, V. L., J. M. SCHLUMPERGER, L. A. WEST, AND I. L. WEISMAN. 1982. Protochordate allorecognition is controlled by a MHC-like gene system. Nature 295:499–502.
- SEBENS, K. P. 1984. Agonistic behavior in the intertidal sea anemone *Anthopleura xanthogrammica*. Biol. Bull. 166:457–472.
- STODDART, J. A., D. J. AYRE, B. WILLIS, AND A. J. HEYWARD. 1985. Self-recognition in sponges and corals? Evolution 39:461–463.
- WRIGHT, S. 1959. Physiological genetics, ecology of populations, and natural selection. Perspec. Biol. Med. 3:107–151.
- . 1969. Evolution and the Genetics of Populations, Vol. 2. The Theory of Gene Frequencies. Univ. Chicago Press, Chicago, IL.

Corresponding Editor: R. C. Vrijenhoek