THE EVOLUTION OF ALLORECOGNITION SPECIFICITY

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ABSTRACT

Intraspecific aggression between clonal cnidarians is not random with respect to genotype; instead, agonistic behavior is modified according to the relatedness of contestants such that clonemates and close relatives behave passively, whereas more distant relatives behave aggressively. Aggression is often costly, with contestants suffering injury and losing space for attachment and growth. Similarly, intraspecific somatic fusion in many sponges, cnidarians, bryozoans, and ascidians is limited to interactions between close relatives and is thought to carry substantial fitness costs.

Such behavioral restriction requires the existence of both an allorecognition system and a set of cues that provides specific labels of relatedness. Several studies suggest that labels of identity (allotypes) are provided by one, or a few loci. Individual specificity therefore requires that the loci conferring allotypic specificity carry high levels of allelic variation. In the case of aggression, allotypic specificity directs aggression away from clonemates and close kin, and toward more distant relatives. In the context of fusion, allotypic specificity limits the potential for intraspecific fusion and its attendant costs.

Taken together, these considerations imply that rare allorecognition alleles, and the labels of individuality that they confer, should be favored by natural selection. However, the mechanistic models of aggression analyzed in this paper show that the individual costs and benefits of aggression alone will not favor the accumulation and maintenance of allotypic specificity. In contrast, allotypic polymorphism can be maintained directly by the individual costs and benefits of fusion provided fusion carries a net fitness cost. This raises the question of how fusion conditioned on relatedness can be evolutionarily stable. Our results suggest that selection acting at the level of clonal or kin-aggregations, rather than at the level of the individual, may provide an explanation for the evolution of allotypic specificity through aggression or fusion.

INTRODUCTION

One of the most striking aspects of self-nonself interactions among sessile, clonal invertebrates is the extraordinary precision with which clonemates and close relatives can be distinguished from nonclonemates and distant relatives (reviewed by Hildemann *et al.* 1979; Buss *et al.* 1984; Grosberg 1988). This precision requires that 1) an allorecognition system exists capable of detecting subtle differences among individuals and 2) there be sufficient genetic variation at loci conferring allotypic specificity so that relatedness can be reliably inferred from shared alleles. In the few cases where the formal genetics of allorecognition are known, allospecificity is controlled by the gene products of one, or at most a few loci (von Hauenschild 1954, 1956; Oka and Watanabe 1957, 1960; Sabbadin 1962; Scofield *et al.* 1982; reviewed in Grosberg 1988a). Therefore, to confer high levels of specificity, these loci must carry levels of variation approaching 100 alleles, a level of polymorphism which is nearly an order of magnitude greater than the levels recorded at other highly variable loci (reviewed in Grosberg 1988a). In this paper, we develop a formal evolutionary analysis of the question, "How are such high levels of genetic variation maintained at loci controlling allotypic specificity?"

There are a number of possible evolutionary mechanisms capable of maintaining genetic polymorphism at allorecognition loci. Theoretical considerations suggest that some selective mechanisms such as heterozygote advantage, and nonselective mechanisms such as a balance between mutation and genetic drift, are unlikely to promote the accumulation of the high levels of variation observed at allorecognition loci (Grosberg 1988a). However, frequency-dependent selection, in which the fitness of an allele increases when the allele is rare, is a plausible means by which high levels of allotypic variation can evolve (Bodmer 1972; Burnet 1973; Wakeland and Nadeau 1980; Hamilton 1982; Levin 1986). Frequency-dependent selection could act directly on the allorecognition systems of clonal invertebrates in at least two ecological contexts: 1) regulation of aggression and 2) restriction of fusion with neighboring colonies.

The acquisition and maintenance of living space in many sessile, clonal cnidarians of the Classes Anthozoa and Hydrozoa involves aggressive behavior, and the deployment of specialized fighting structures (Francis 1973a,b; Sebens 1982a,b; Ayre 1983, 1987; Buss *et al.* 1984; Fujii 1987). Such aggressive behavior is generally restricted to interactions between individuals belonging to different clones: contacts between clonemates (and often close kin) do not elicit aggression (reviewed in Buss *et al.* 1984). In this context, behavioral specificity conditioned on allotypic matching directs aggression away from clonemates and close kin, and toward more distantly related individuals. This suggests that the ability to discriminate self from nonself should be favored by natural selection on the costs and benefits of direct aggression.

Allorecognition systems also regulate fusion between contacting individuals in sponges (e.g., Van de Vyver 1970; Neigel and Avise 1983a; Wulff 1986) and colonial ascidians (Oka 1970; Tanaka 1975; Sabbadin 1982; Scofield *et al.* 1982), as well as some cnidarians (e.g., Ivker 1972; Hildemann *et al.* 1980; Neigel and Avise 1983b). Whereas allotypically distinct colonies (or individuals in the case of sponges) rarely fuse, allotypically identical or similar colonies can fuse and become somatically unified. There are several situations in which somatic fusion may provide fitness

benefits, especially if age at first reproduction or competitive ability are size-dependent (Buss 1982); however, many studies suggest that fusion entails substantial fitness costs to one, or both, members of a fused pair (Buss 1982; Grosberg 1987; Rinkevich and Weissman 1987). Because individuals with rare allotypic determinants are unlikely to fuse with other individuals and suffer the consequences of fusion, it seems intuitive that rare allotypes would have a substantial selective advantange over more common allotypes.

At first sight, it appears that the ability to discriminate self from nonself based on allotype would be favored by natural selection in the regulation of aggression and fusion. However, for an allorecognition system to be evolutionarily and ecologically important, the genetic polymorphism necessary to confer allotypic specificity must accumulate and be maintained. Simple models suggest that the selective conditions for maintenance of a polymorphic equilibrium are not obvious. Crozier (1986), implicitly assuming that the costs of aggression outweighed the benefits, showed that in a two-allele system in which aggressive behavior is conditioned on allotypic identity, rare or mutant allorecognition alleles will be eliminated, rather than favored, by selection. In this paper, we develop a general mechanistic analysis of the evolution of allotypic polymorphism by explicitly incorporating the costs and benefits of aggression and fusion into population genetic models.

THE AGGRESSION MODEL

Assumptions and Definitions

We first assume that all individuals possess the ability to discriminate self from nonself by a matching mechanism at a haploid allorecognition locus. The genotype of an individual at this locus is termed its allotype, and allotype is asexually inherited. This locus has a potentially infinite number of alleles, designated *i*, *j*, etc. Individuals which are clonemates will necessarily have the same allotype; however, allotypically identical individuals need not be clonemates. Thus, the allorecognition locus is not a clonal recognition locus.

We further assume that contests between individuals are pairwise, and that an individual's fitness change in any given interaction depends on whether it carries the same allorecognition allele as the other contestant. Two parameters in the model specify the fitness changes to individuals engaged in a contest:

c_a = the net fitness cost of engaging in an aggressive contest and behaving aggressively. This cost is fixed, and does not vary according to the resistance offered by the other contestant.

b_a = the net fitness gain from aggression, possibly due to acquiring the contested resource

These costs and benefits are used to construct a payoff matrix which defines the per capita fitness changes in contests between matched and unmatched allotypes (Table 1). In *i* versus *i* contests, neither individual behaves aggressively, hence neither pays the cost, c_a, of aggression. When contestants have matching allotypes, (e.g., *i* versus *i*), each individual gains half the value of the resource (*i.e.*, the per capita gain

Table 1. The fitness payoffs according to allotype for individuals engaged in potentially aggressive contests. i and j denote two allotypes; c_a is the cost of aggressive behavior; b_a is the value of the contested resource. See text for a complete explanation of the payoff matrix.

	Versus	
Payoff to:	i	j
i	$1 + b_a/2$	$1 - c_a + b_a/2$
j	$1 - c_a + b_a/2$	$1 + b_a/2$

is $b_a/2$). In i versus j contests ($j \neq i$), both individuals behave aggressively, and both pay the associated cost, c_a. We assume that contests between mutually aggressive contestants are symmetric, and each individual has a 50:50 chance of winning the full value of the resource. Alternatively, the contested resource could be evenly divided between the combatants. In either case, the average resource gain in self versus nonself contests is $b_a/2$, as in self versus self interactions. One could easily incorporate asymmetric contests into the model, such that a one of the contestants has either a greater probability than the other of winning a contest, or gains more than b_a of the contested resource (Grosberg and Quinn, unpublished results).

Evolutionary Analysis of the Aggression Model

To determine if allotypic polymorphism will accumulate, we first define the expected fitness, W, of an allotype, i, in terms of 1) the fitness payoffs from each class of encounter (self versus self and self versus nonself, with payoffs either $1 + b_a/2$ or $1 + c_a + b_a/2$, respectively) and 2) the frequencies of self-self (P_i) and self-nonself ($1 - P_i$) encounters. We assume that the frequencies of encounters are determined by the frequencies of allotypes in the population (*i.e.*, encounters are random). The expected fitness of an individual of allotype i is

$$W_i = P_i(1 + b_a/2) + (1 - P_i)(1 - c_a + b_a/2). \quad (1a)$$

This equation can be algebraically simplified to give

$$W_i = 1 - c_a + b_a/2 + c_a(P_i). \quad (1b)$$

The frequency of a novel allorecognition allele, j, will increase in a population only if W_j is greater than the mean fitness of the population, $\bar{W}$. The population mean fitness for the general multiallelic case at the allorecognition locus is

$$\bar{W} = \sum_i P_i[P_i(1 + b_a/2) + (1 - P_i)(1 - c_a + b_a/2)]. \quad (2)$$

Equation (1b) indicates that W_i increases linearly with P_i for all positive values of c; consequently, the most frequent allele in a population will have the greatest fitness,

and will tend to increase further in frequency until it is fixed. This result, in combination with equation (2), has four important implications regarding the accumulation of allorecognition polymorphism:

1. If there are two allorecognition alleles, then they will have equal fitness only when they are equally frequent. Thus, the only dimorphic equilibrium occurs when $P_i = P_j = 0.5$ ($j \neq i$). Any perturbation from this equilibrium will tend toward fixation of the allele with the higher initial frequency.

2. A population for which an allorecognition allele (i) is nearly fixed ($P_i \approx 1$) will have a higher mean fitness than any rare mutant allele ($P_j \approx 0$), so a rare mutant will always be selectively excluded.

3. For any non-equilibrium frequencies, the most common alleles will increase in frequency and the uncommon ones will decrease. Therefore, the equilibrium will not be approached from any starting point and will be globally unstable.

It is easily shown that the only internal equilibrium for k alleles occurs when all $P_i = 1/k$, and it is unstable.

In sum, the most common allorecognition allele in a population will tend to become fixed, and the polymorphic equilibrium that exists when all alelles are equally frequent will be both unstable and resistant to invasion by new mutants. Therefore frequency-dependent selection based on the individual costs and benefits of aggression is unlikely to favor the accumulation of allorecognition polymorphism.

THE FUSION MODEL

Assumptions and Definitions

We assume the same formal genetics of allorecognition as in the aggression model. We also assume that all interactions between separate colonies or individuals are pairwise, and that individual changes in fitness depend only on whether two contacting entities carry the same allotype. The fitness changes in any given intraction are specified by two parameters analogous to those used in the aggression model:

c_f = the net per capita fitness cost of fusing with another individual (or colony)

b_f = the net per capita fitness gain of fusing with another individual (or colony)

These two parameters are the elements of a fusion payoff matrix (Table 2) similar in form to the aggression payoff matrix (Table 1). There are, however, substantial differences between the fusion and aggression matrices. In the case of fusion, when allotypically matched individuals meet, they fuse somatically; each pays the cost of fusion, c_f, and gains some benefit, b_f. When allotypically distinct individuals meet, the colonies do not fuse, and neither individual gains or loses fitness.

Table 2. The per capita fitness payoffs according to allotype for the fusion model. i and j denote allotypes ($j \neq i$); c_f is the relative fitness cost of fusion; b_f is the relative fitness gain due to fusion.

	Versus	
Payoff to:	i	j
i	$1 - c_f + b_f$	1
j	1	$1 - c_f + b_f$

Evolutionary Analysis of the Fusion Model

In parallel with the aggression model, the expected fitness of given fusibility allotype, W_i, is the product of the fitness payoffs from each class of encounter and the frequencies of each class of encounter. Thus, the expected fitness of allotype i is

$$W_i = P_i(1 - c_f + b_f) + (1 - P_i), \tag{3a}$$

which simplifies to

$$W_i = 1 + P_i(b_f - c_f). \tag{3b}$$

As was the case with the aggression model, a novel allorecognition allele, j, arising in a population will be favored only if $W_j > \bar{W}$. The mean population fitness for the general multiallelic case at the allorecognition locus is defined by

$$\bar{W} = \sum_i P_i[P_i(1 - c_f + b_f/2) + (1 - P_i)]. \tag{4}$$

In contrast to the results of the aggression model (in which the fitness of an allotype was directly proportional to its frequency), equation (3) shows that the relationship between the fitness of an allotype and its frequency can be either positive or negative, depending upon the respective values of b_f and c_f. If $b_f > c_f$, then as P_i increases, so, too, does W_i. If $b_f < c_f$, then as P_i increases, W_i decreases; therefore, the frequency of allele i will increase until $W_i = \bar{W}$. In the unlikely event that $b_f = c_f$, W_i is independent of P_i.

In biological terms, if the benefits of fusion exceed the costs, then novel allorecognition alleles will be selected against, and polymorphism will not accumulate via frequency-dependent selection. However, if fusion is costly, then an allorecognition allele will have maximum fitness when rare; consequently, rare allotypes will be favored by natural selection and allotypic polymorphism can accumulate.

THE COMBINED AGGRESSION AND FUSION MODEL

Assumptions and Definitions

This analysis modifies the fusion and aggression models by assuming that allotypic matching leads to fusion and mismatching leads to aggression. The best known example of this kind of model is the behavior of the athecate hydroid *Hydractinia echinata*. In this species, allotypically matched colonies fuse somatically by stoloniferous extensions of their gastrovascular systems; mismatched colonies do not fuse, and additionally produce hyperplastic stolons which are used aggressively (reviewed in Buss *et al.* 1984).

We make the same genetic assumptions as before. Specification of the payoff matrix requires four parameters, which are defined in the aggression and fusion models. Two of the parameters account for fitness gains (*i.e.*, b_a and b_f), and two denote fitness losses (*i.e.*, c_a and c_f).

The payoff matrix for this model is shown in Table 3. When matching allotypes interact, they fuse and have the same net per capita fitness change as in the fusion model. When different allotypes contact, they behave aggressively, and the payoff is identical to that in an *i* versus *j* interaction in the aggression model.

Evolutionary Analysis of the Combined Model

The expected fitness of an allotype, *i*, is

$$W_i = P_i(1 - c_f + b_f) + (1 - P_i)(1 - c_a + b_a/2). \qquad (5)$$

This equation has the same general form as equations (1a) and (3a), and shows that if $b_f - c_f > b_a/2 - c_a$, then as P_i increases, W_i increases. As in the case of the fusion model and the aggression model (when $b_f > c_f$), there is no stable polymorphic equilibrium, and allotypic polymorphism cannot increase. However, if $b_a/2 - c_a > b_f - c_f$, then the frequency of *i* will increase until $W_i = \bar{W}$. In other words, if the net fitness benefit of fusion exceeds the net benefit of aggression, then allotypic polymorphism will not accumulate; however, if the opposite is true, then polymorphism can accumulate. It is easily shown that the only polymorphic equilibrium occurs when all extant alleles are equally abundant.

Table 3. The fitness payoffs according to allotype under the combined fusion and aggression model. *i* and *j* denote two allotypes; c_a is the cost of aggressive behavior; c_f is the cost of fusion; b_a is the value of the contested resource; b_f is the fitness gain due to fusion.

	Versus	
Payoff to:	*i*	*j*
i	$1 - c_f + b_f$	$1 - c_a + b_a/2$
j	$1 - c_a + b_a/2$	$1 - c_f + b_f$

DISCUSSION

The phylogenetically widespread evolution of allorecognition specificity, and the requisite accumulation of allotypic polymorphism, are commonly accounted for in terms of the individual fitness advantages of either minimizing the likelihood of somatic fusion, or restricting aggressive behavior to non-kin (reviewed in Grosberg 1988a). Given the conspicuousness and apparent ecological importance of intercolony aggression in cnidarians (reviewed in Buss *et al.* 1984), such explanations are intuitively appealing. However, Crozier (1986) showed that under the simplest model of the evolution of allotypic polymorphism, allorecognition specificity will not evolve through its effects on agonistic behavior. His diploid model, which assumes that the fitness costs of aggression exceed the benefits, demonstrates that a two-allele polymorphism is unstable; once the frequency of one allorecognition allele exceeds the frequency of the other, the more common allele evolves to fixation.

Our analysis of the evolution of conditional aggression extends Crozier's analysis in two fundamental ways. First, equation (1b) indicates that the fitness of an allorecognition allele which mediates aggression will increase linearly according to the frequency of that allele in a population. In our haploid model, this relationship holds for any number of alleles, and is not limited to the two-allele case examined by Crozier (1986). Second, even if the benefits of aggression outweigh the costs, as long as there is some cost to aggressive behavior, frequency-dependent selection will act to remove rare allotypes from a population. Thus, allotypic polymorphism should not be maintained by simple individual selection acting through aggression conditioned on allotype.

This theoretical prediction is at odds with the empirical reality that most clonal cnidarians restrict aggression to non-clonemates and non-relatives: somehow, allotypic polymorphism is maintained in nature. The cost/benefit model of colony fusion conditioned on allotypic matching provides one apparent escape from this dilemma: allotypic polymorphism can accumulate and be maintained through natural selection acting directly on the fitness costs and benefits of somatic fusion. By this logic, the allotypic polymorphism necessary for aggressive specificity is maintained pleiotropically via the fitness costs of somatic fusion, rather than directly via aggressive behavior. There is some empirical support for this hypothesis: in the hydroid *Hydractinia echinata*, colonies that are reciprocally aggressive are somatically incompatible, whereas passive interactions generally lead to fusion (Buss *et al.* 1984). This pleiotropic mechanism has the peculiar feature that fusion dynamics will only maintain polymorphism (1) if the costs of fusion exceed the benefits; or (2) if the net fitness cost of fusion exceeds the net cost of aggression. In both cases, fusion must lower overall fitness if it is to maintain polymorphism; thus, a conditionally fusing phenotype would seem to be evolutionarily unstable against a mutant phenotype that simply did not fuse. Indeed, in many cnidarians, somatic fusion is unknown, even between colonies that behave passively toward each other (reviewed in Grosberg 1988b).

There are other pleiotropic mechanisms which could indirectly maintain allotypic variation. These include host-pathogen defense systems (see Crozier 1986, this volume) and gametic incompatibility systems analogous to those found in several families of angiosperms (see Oka 1970; Scofield *et al.* 1982). Even if it were possible to maintain allotypic polymorphism pleiotropically, it must be advantageous to

condition behavior on allotype. In the case of conditional aggression, Grosberg and Quinn (unpublished results) developed an individual cost/benefit model which showed that no matter how large or small the apparent benefits of allotypic discrimination, a population of conditionally aggressive individuals will have a lower mean fitness than a mutant individual that is either unconditionally aggressive or unconditionally passive. Therefore, aggressive behavior conditioned on allotypic identity will not be evolutionarily stable in the face of alternative phenotypes that are either unconditionally aggressive or passive. The fact that fusion must be costly in order for allotypic polymorphism to evolve indicates that conditional fusion is unlikely to be sufficiently evolutionarily stable to maintain allorecognition specificity.

Because the individual costs and benefits of fusion and aggression cannot readily account for why these behaviors are conditioned on allotypic identity, other explanations must be sought. Studies on clonal aggregations of sea anemones (e.g., Francis 1973a,b, 1976; Sebens 1982a,b) and aggregations of clonemates or kin in other clonal taxa of benthic marine invertebrates (e.g., Olson 1985; Grosberg and Quinn 1986; Grosberg 1987; reviewed in Jackson 1985, 1986) indicate that plausible explanations are likely to be found in terms selection acting at levels such as kin groups or demes, rather than at the level of selection on the individual. Indeed, other theoretical studies (e.g., Mirmirani and Oster 1978; Grafen 1979) suggest that the incorporation of kinship into models of competition and aggression can produce outcomes substantially different than models ignoring kin selection.

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INVERTEBRATE HISTORECOGNITION

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