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## THE EVOLUTION OF SELECTIVE AGGRESSION CONDITIONED ON ALLORECOGNITION SPECIFICITY

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**Abstract.**—Many sessile cnidarians deploy specialized structures while competing aggressively for living space. The initiation of aggression is often contingent on the relatedness of the interacting contestants; clonemates and close kin generally behave passively toward one another, whereas more distant relatives generally behave aggressively. Behavioral specificity of this sort requires that there be 1) an allorecognition system that can discriminate among subtle differences in cell-surface determinants and 2) a highly polymorphic genetic system that provides specific labels of relatedness (haplotypes or allotypes). The evolutionary models analyzed in this paper show that a population of individuals that behave aggressively only against haplotypically distinct individuals (discriminating phenotypes) will not be evolutionarily stable in the face of either unconditionally aggressive or unconditionally nonaggressive phenotypes. Furthermore, even if the discriminating trait were somehow fixed, the rare recognition alleles necessary to confer allotypic specificity could not become established through natural selection. Thus, allotypic specificity is unlikely to be maintained by individual selection acting directly through aggressive behavior.

Other selective mechanisms might account for the evolution of allorecognition specificity. Allotypic polymorphism could be maintained by pleiotropic mechanisms in which rare alleles are favored by natural selection acting either on gametic incompatibility, pathogen resistance, or somatic fusion, rather than aggressive behavior *per se*. However, these mechanisms do not explain the maintenance of selective aggression based on allotypic differences. Alternatively, if aggressive members of a clone indirectly enhance the reproductive output or survival of the entire clone (or close relatives), then kin selection acting directly through aggressive behavior could favor allorecognition specificity. Choosing among these alternatives will require the development of more sophisticated theory and empirical analyses of the costs and benefits of aggression.

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In many sessile cnidarians of the Classes Hydrozoa and Anthozoa, intraspecific spatial competition is mediated by aggressive behavior (Francis, 1973*a*, 1973*b*; Hildebrandt et al., 1979; Sebens, 1982*a*, 1982*b*; Ayre, 1983, 1987; Buss et al., 1984; Fujii, 1987). The initiation of aggression and the deployment of structures used primarily in aggression (e.g., acrorhagi, sweeper tentacles, mesenterial filaments) are often contingent on whether or not interacting contestants are clonemates or close relatives (reviewed in Grosberg [1988]). Allogeneic contestants (those with different self/nonsel markers) generally behave aggressively (or defensively), often injuring each other in the process of defending or acquiring space. In contrast, interactions between isogenic individuals (i.e., those bearing identical self/nonsel markers), which are likely to be clonemates or close kin, do not elicit agonistic behavior.

Behavioral specificity of this sort requires

the evolution of an allorecognition system that is capable of recognizing differences among genotypes as well as a highly polymorphic genetic system that provides unambiguous labels (allotypes) of relatedness or clonal identity. Crozier (1986) explored the conditions under which the costs and benefits of aggression alone should maintain polymorphism at allorecognition loci. He observed that an individual carrying a rare allotypic determinant would experience virtually universal aggression, whereas a carrier of a common allotype would suffer aggression much less frequently. If the costs of aggression were high relative to the benefits, then the rare alleles necessary to confer precise labels of self and nonself (or relatedness) would actually be selected against, rather than favored. Therefore, marker polymorphism would not arise or be maintained.

Even under conditions in which allotypic variability would be maintained, variability

alone does not explain the widespread evolution of allotype-specific aggression in clonal cnidarians. Mechanisms involved in recognition of allotypes and the modification of behavior must also be advantageous; otherwise allotypic polymorphism will not affect aggressive behavior. These considerations raise two interrelated questions. First, under what circumstances does the capability to distinguish self from nonself confer selective advantages? Second, given that there is some benefit to allorecognition, under what circumstances will novel allotypic variants increase in frequency? Although Crozier (1986) modelled the conditions favoring the evolution of allotypic polymorphism, little is known about the circumstances under which conditional aggression itself is advantageous (see Grosberg, 1988).

If most interactions between individuals involve pairwise contests, as is often the case with aggressive behavior between cnidarians, then both questions can be approached simply by analyzing the fitness costs and benefits of aggression. In this paper, we develop a mechanistic model of aggression incorporating three classes of behavior: 1) indiscriminate aggression; 2) conditional (or discriminating) aggression or nonaggression based upon allotype; and 3) unconditional passiveness. We analyze this model by determining the conditions under which a population composed primarily of one of the three behavioral phenotypes will have a higher mean fitness than all other rare phenotypes. Such a phenotype (one with highest fitness when common) is said to represent an evolutionarily stable strategy (ESS; Maynard Smith and Price, 1973). In game-theoretic studies of aggression such as the standard hawk-versus-dove game (Maynard Smith, 1982), mixed strategies often constitute an ESS. More specifically, individuals that fight conditionally (based on the phenotype of their opponent) can have higher average fitness than individuals that always fight or never fight. By analogy, selectively aggressive individuals, such as those that attack only different allotypes, could have higher relative fitnesses than both indiscriminate aggressors and nonfighters. For this to be the case, natural selection must favor rare allotypes to maintain polymorphism at allorecognition loci (Crozier,

1986). However, in the models presented in this paper, the costs and benefits of aggression to the individual always favor either indiscriminate aggression or obligately non-aggressive behavior. Based on individual selection alone, we find no case in which selective aggression toward allotypically dissimilar individuals will be favored.

### *The Structure of the Model*

*Assumptions and Definitions.*—Our approach to modeling agonistic interactions between conspecific individuals assumes that contests are pairwise and that an individual's fitness change in any one interaction depends upon its phenotype and that of the other contestant. We further assume that an individual's phenotype has two independent components: 1) its behavioral phenotype,  $X$ , and 2) its allorecognition phenotype,  $i$ . We use the term haplotype to refer to an individual's allorecognition genotype at the single allorecognition locus we consider. We use the term allotype more generally to refer to the net effects of all haplotypic determinants across loci (Klein, 1982).

We ask whether the ability to distinguish behaviorally among haplotypes is advantageous by considering three discrete behavioral phenotypes: 1) obligate aggressiveness independent of haplotype, 2) obligate passiveness, and 3) haplotype-specific aggressiveness, whereby aggression occurs only when contestants differ in haplotype. In genetic terms, these three characters are controlled by three alleles at a haploid locus. For notational convenience, we name the behavioral phenotypes belligerent (B), meek (M), and discriminating (D), respectively. Although the D phenotype is a conditional strategy, it is not analogous to the retaliator phenotype (*sensu* Maynard Smith, 1982) in a conventional hawk-dove-retaliator game model. This is because our discriminator behavior is conditional upon the phenotype of an independent character (i.e., haplotype), whereas retaliator behavior is conditioned directly by the behavior (hawk or dove) of the other contestant.

The other component of an individual's phenotype is its haplotype. Haplotype is determined by a haploid locus with a potentially infinite number of alleles. Clonemates

necessarily carry the same haplotype (barring somatic mutation); nonetheless, haplotypic matching need not imply clonal identity.

Because this is a two-locus model, linkage may affect the evolutionary outcomes. We therefore analyze the invadability criteria separately for populations in which behavioral and haplotypic traits are completely linked and in which they are free to recombine.

Three parameters in the model specify the fitness payoffs to individuals engaged in a contest:

- $d$  = the net fitness cost of possessing and maintaining structures used to contest resources;
- $c$  = the net fitness cost of engaging in a contest and behaving aggressively (this cost is fixed and does not vary according to the resistance offered by the other contestant);
- $v$  = the net fitness gain from acquiring the contested resource.

Both  $d$  and  $c$  are needed to specify costs completely because B phenotypes always pay both components of cost, whereas D phenotypes pay  $c$  only when interacting with a nonself haplotype. In this scheme, M phenotypes pay neither  $c$  nor  $d$ . We assume that all costs and benefits are positive (i.e.,  $d > 0$ ,  $c > 0$ , and  $v > 0$ ).

*The Payoff Matrix.*—We use these costs and benefits to define a matrix that specifies the fitness gains and losses associated with each class of interaction between all pairs of phenotypes (Table 1). The entries in the matrix are based on the following rules of interaction:

i) *Belligerent phenotypes (B).*—When belligerent phenotypes encounter any other individual, regardless of haplotype or behavioral phenotype, they engage in combat. Therefore, B phenotypes always pay costs  $c$  and  $d$ . If a B phenotype encounters another B individual, it wins the resource,  $v$ , with frequency 0.5 and fails to gain the resource with frequency 0.5 (or, equivalently, the contestants split the resource). Thus, the average per individual fitness gain in B versus B contests is  $v/2$ . (Our results do not require that the proportion of resource gained be exactly 0.5. Qualitatively, the same results

apply when the proportion gained is anywhere between 0 and 1.) The payoff to a B phenotype interacting with a D (discriminating) phenotype depends on whether the contestants carry the same haplotype. If a belligerent individual of haplotype  $i$  (denoted  $B,i$ ) interacts with a  $D,i$  individual, the  $B,i$  individual gains the full value of the resource,  $v$ , because the  $D,i$  individual does not counter with aggression. However, a  $B,i$ -versus- $D,j$  ( $j \neq i$ ) interaction is equivalent to a B-versus-B interaction, and the B phenotype gains, on average,  $v/2$  of the contested resource. Finally, because M phenotypes never contest a resource, B individuals always gain  $v$  in B-versus-M contests.

*Discriminating phenotypes (D).*—Discriminators, like belligerent phenotypes, always pay the cost,  $d$ , of possessing and maintaining structures used in agonistic encounters. D phenotypes behave aggressively only when interacting with individuals with different haplotypes and, hence, pay the cost of engaging in combat,  $c$ , only when confronted by a haplotypically nonself individual. In a  $D,i$ -versus- $B,j$  ( $j \neq i$ ) contest, the D individual gains  $v$  with frequency 0.5 and fails to gain  $v$  with the same frequency. Similarly, in a  $D,i$ -versus- $D,j$  ( $j \neq i$ ) contest, D gains on average  $v/2$ , while paying  $c$ . A  $D,i$ -versus- $D,i$  contest results in a resource gain of  $v/2$  to both contestants; however, neither pays the cost of combat,  $c$ . The payoff to a  $D,i$  individual interacting with a  $M,i$  (meek) individual is the same as in a  $D,i$ -versus- $D,i$  contest. In comparison, when  $D,i$  encounters  $M,j$  ( $j \neq i$ ), the  $D,i$  individual pays  $c$  but always wins the contest and, hence, gains  $v$ .

iii) *Meek phenotypes (M).*—M phenotypes never behave aggressively; consequently, they pay neither  $c$  nor  $d$ . When interacting with B phenotypes, M phenotypes never gain any resource. The same result occurs when  $M,i$  phenotypes interact with  $D,j$  ( $j \neq i$ ) individuals. In contrast, when countering  $D,i$  phenotypes or other M individuals of any haplotype, the fitness gain is  $v/2$ .

#### *Random-Encounters Model*

*Calculation of Expected Fitnesses.*—The expected fitness,  $W$ , of each phenotypic class,

$X,i$  (behavioral type  $X$ , allotype  $i$ ), has two components: 1) the fitness payoffs from each class of encounter for all possible combinations of behavioral phenotypes and allotypes and 2) the probabilities that each class of encounter will occur. In this model, we assume that the probabilities of encounters between specific phenotypes are randomly determined (i.e., solely by the product of frequencies of the phenotypes in a population).

Based on the payoff matrix shown in Table 1, the expected fitnesses of each of the three behavioral phenotypes are specified by

$$\begin{aligned}
 W_{B,i} = & P_B \left( 1 - d - c + \frac{v}{2} \right) \\
 & + P_M (1 - d - c + v) \\
 & + P_{D,i} (1 - d - c + v) \\
 & + (P_D - P_{D,i}) \\
 & \cdot \left( 1 - d - c + \frac{v}{2} \right) \quad (1a)
 \end{aligned}$$

$$\begin{aligned}
 W_{D,i} = & P_{B,i} (1 - d) \\
 & + (P_B - P_{B,i}) \\
 & \cdot \left( 1 - d - c + \frac{v}{2} \right) \\
 & + P_{M,i} \left( 1 - d + \frac{v}{2} \right) \\
 & + (P_M - P_{M,i}) \\
 & \cdot (1 - d - c + v) \\
 & + P_{D,i} \left( 1 - d + \frac{v}{2} \right) \\
 & + (P_D - P_{D,i}) \\
 & \cdot \left( 1 - d - c + \frac{v}{2} \right) \quad (1b)
 \end{aligned}$$

$$\begin{aligned}
 W_{M,i} = & P_B + P_M \left( 1 + \frac{v}{2} \right) \\
 & + P_{D,i} \left( 1 + \frac{v}{2} \right) \\
 & + (P_D - P_{D,i}) \quad (1c)
 \end{aligned}$$

in which  $W_{X,i}$  is the fitness of behavioral phenotype  $X$  (which can take values of B, D, and M) with haplotype  $i$  and  $P_{X,i}$  is the frequency of behavioral phenotype  $X$  with haplotype  $i$ .  $P_B$  is the frequency of belligerent phenotypes summed over all haplo-

TABLE 1. The fitness payoffs to individuals with behavioral phenotype B (belligerent), D (discriminator), or M (meek) and allotype  $i$  interaction with B, D, or M phenotypes with the same ( $i$ ) or different ( $j$ ) allotypes ( $j \neq i$ ). For table entries,  $d$  is the fitness cost of producing and maintaining structures used for aggression,  $c$  is the cost of engaging in combat, and  $v$  is the value of the contested resource. See text for a complete explanation of the payoff matrix.

Payoff recipient	Opponent					
	B, $i$	B, $j$	D, $i$	D, $j$	M, $i$	M, $j$
B, $i$	$1 - d - c + v/2$	$1 - d - c + v/2$	$1 - d - c + v$	$1 - d - c + v/2$	$1 - d - c + v$	$1 - d - c + v$
D, $i$	$1 - d$	$1 - d - c + v/2$	$1 - d + v/2$	$1 - d - c + v/2$	$1 - d + v/2$	$1 - d - c + v$
M, $i$	$1$	$1$	$1 + v/2$	$1$	$1 + v/2$	$1 + v/2$

types (i.e.,  $P_B = \sum P_{B,i}$ ). Similarly,  $P_M$  is the overall frequency of meek phenotypes (i.e.,  $P_M = \sum P_{M,i}$ ), and  $P_D$  is the frequency of discriminating phenotypes (i.e.,  $P_D = \sum P_{D,i}$ ).

*ESS Conditions for the Indiscriminately Belligerent Phenotype (B).*—To determine whether a given phenotype represents an ESS immune to invasion by any new mutant, we first identify the general selection conditions under which a novel phenotype will outreproduce each of the other phenotypes in a model population. If a given phenotype is an ESS, it must have a higher fitness when common than all other alternative phenotypes (reviewed in Maynard Smith [1982]). The conditions for invasion will differ according to whether alleles at the behavioral and allorecognition loci assort independently between generations.

With complete linkage between the behavioral and allorecognition loci, progeny of a parent with a novel behavioral phenotype will have the same behavioral and allorecognition genotype as the parent (i.e., advantageous combinations of the two traits will not be broken down by recombination). Consequently, the "invadability" conditions must test whether any joint phenotype has higher fitness than that of a putative ESS. For the B behavioral phenotype to be an ESS, the following inequalities must be simultaneously satisfied:

$$\bar{W}_B > W_{D,i} \quad (\text{for any } i) \quad (2a)$$

$$\bar{W}_B > W_{M,i} \quad (\text{for any } i) \quad (2b)$$

$$\bar{W}_B > W_{B,j} \quad (\text{where } j \text{ is a novel mutant}). \quad (2c)$$

$\bar{W}_B$  is the mean fitness of a population composed entirely of belligerent phenotypes. The ESS conditions for a belligerent population are then determined by assuming that a population consists nearly entirely of B individuals (i.e.,  $P_B \approx 1$ ) and solving (2a)–(2c).

Regardless of allelic frequencies at the allorecognition locus,

$$\bar{W}_B = 1 - d - c + \frac{v}{2}. \quad (3)$$

Substitution of Equations (1a)–(1c) into the relevant inequalities (2a)–(2c) shows that, for a population of belligerent phenotypes

to be an ESS against discriminators of any haplotype,

$$v > 2c. \quad (4)$$

For a population of belligerent phenotypes to resist invasion by either self or nonself meek phenotypes

$$v > 2(d + c). \quad (5)$$

Without discriminators, invasion by a B phenotype with a novel haplotype would be evolutionarily neutral.

In contrast to the situation when the two loci are completely linked, independent assortment will break down associations between haplotype and behavioral phenotype in novel mutants. Therefore, mutants at either locus will increase in frequency only if their fitness, averaged over all alleles at the other locus, is greater than the fitness of the putative ESS. The following fitness inequalities must be satisfied for a population of belligerent phenotypes to be an ESS:

$$\bar{W}_B > \bar{W}_D \quad (6a)$$

$$\bar{W}_B > \bar{W}_M \quad (6b)$$

$$\bar{W}_B > \bar{W}_{B,j} \quad (\text{where } j \text{ is a novel mutant}). \quad (6c)$$

When D phenotypes are rare, we can assume that all interactions of discriminators are with belligerent phenotypes and that  $P_B \approx 1$ . Because of independent assortment,  $P_{B,i} = P_B P_i$  and  $P_{D,i} = P_D P_i$ . Therefore,

$$\begin{aligned} \bar{W}_D = \sum_i P_i \left[ P_i (1 - d) \right. \\ \left. + (1 - P_i) \right. \\ \left. \cdot \left( 1 - d - c + \frac{v}{2} \right) \right]. \quad (7a) \end{aligned}$$

Algebraic manipulation indicates that a population of belligerents cannot be invaded by discriminators [Expression (6a)] when

$$v > 2c, \quad (7b)$$

the same conditions found with complete linkage. Haplotype does not affect the behavior of M phenotypes; hence, introducing independent assortment into the model again does not change the ESS conditions for M-versus-B phenotypes. As before, nov-

el haplotypic mutants [Expression (6c)] are neutral.

*ESS Conditions for the Meek Phenotype (M).*—We identify the conditions under which a population composed primarily of meek phenotypes ( $P_{M,i} \approx 1$ ) would be an ESS by the same procedure used for belligerent phenotypes [see Expressions (2a)–(2c), (3a), and (3b)]. The mean fitness of a population of meek individuals is

$$\bar{W}_M = 1 + \frac{v}{2}. \tag{8}$$

The conditions that must be simultaneously satisfied for a meek phenotype to be an ESS are

$$\bar{W}_M > W_{B,i} \text{ (for any } i) \tag{9a}$$

$$\bar{W}_M > W_{D,i} \text{ (for any } i) \tag{9b}$$

$$\bar{W}_M > W_{M,j} \text{ (where } j \text{ is a novel mutant).} \tag{9c}$$

Substitution and algebraic simplification show that a meek population will be an ESS in contests with belligerent phenotypes of any haplotype, provided that

$$v < 2(d + c). \tag{10a}$$

If a population of meek phenotypes is to resist invasion by discriminators, then

$$v < 2 \left[ \frac{d}{1 - P_{M,i}} + c \right]. \tag{10b}$$

Finally, because haplotype does not affect the behavior of meek phenotypes, novel haplotypic mutants [Expression (9c)] are evolutionarily neutral.

Because the behavior of meek phenotypes is independent of the haplotype of an opponent, independent assortment will not affect the mean fitness of a nearly pure population of meek individuals. Similarly, the mean fitness of rare belligerent phenotypes will be the same as with complete linkage. Therefore, the condition for the invasion of a meek population by a belligerent mutant of any haplotype is the same as in (10a).

The condition for the invasion of a population of meek individuals by a rare discriminator is  $\bar{W}_D > \bar{W}_M$  when  $P_M \approx 1$ . Because under independent assortment  $P_{D,i} = P_D P_i$  and  $P_{M,i} = P_M P_i$ ,

$$\bar{W}_D = \sum_i P_i \left[ P_i \left( 1 - d + \frac{v}{2} \right) + (1 - P_i) \cdot (1 - d - c + v) \right]. \tag{11}$$

Substitution and algebraic simplification show that discriminators can invade only when

$$v < 2 \left[ \frac{d}{1 - \sum_i P_i^2} + c \right]. \tag{12}$$

When there are many rare haplotypes, then Expression (12) simplifies to  $v < 2(d + c)$ . Therefore, the addition of independent assortment does not alter the conclusion that a population of meek phenotype will be an ESS only if the value of the contested resource is less than roughly twice the total cost [i.e.,  $2(d + c)$ ] of acquiring the resource.

*ESS Conditions for the Discriminating Phenotype (D).*—The mean fitness of a population composed entirely of discriminating phenotypes ( $P_D \approx 1$ ) is defined by

$$\bar{W}_D = \sum_i P_{D,i} \left[ P_{D,i} \left( 1 - d + \frac{v}{2} \right) + (1 - P_{D,i}) \cdot \left( 1 - d - c + \frac{v}{2} \right) \right]. \tag{13a}$$

This equation can be re-expressed as

$$\bar{W}_D = 1 - d - \left( 1 - \sum_i P_{D,i}^2 \right) c + \frac{v}{2}. \tag{13b}$$

The fitnesses of rare belligerent and meek phenotypes of any haplotype  $i$  are

$$W_{B,i} = P_{D,i} (1 - d - c + v) + (1 - P_{D,i}) \cdot \left( 1 - d - c + \frac{v}{2} \right) \tag{14}$$

$$W_{M,i} = 1 + P_{D,i} \left( \frac{v}{2} \right). \tag{15}$$

The fitness of a discriminating phenotype with a novel haplotype ( $j$ ) is

$$W_{D,j} = 1 - d - c + \frac{v}{2}. \quad (16)$$

For  $\bar{W}_D > W_{B,i}$ ,

$$v < 2 \left[ \frac{\sum_i P_{D,i}^2}{P_{D,i}} \right] c. \quad (17)$$

For  $\bar{W}_D > W_{M,i}$ ,

$$v > 2 \left[ \frac{d + c - c \sum_i P_{D,i}^2}{1 - P_{D,i}} \right]. \quad (18)$$

In general, for a population of discriminating phenotypes to be an ESS, Expressions (17) and (18) must be simultaneously satisfied. This would require that

$$d + \left[ 1 - \frac{\sum_i P_{D,i}^2}{P_{D,i}} \right] c < 0. \quad (19)$$

By assumption,  $d$  and  $c$  must be positive, and the term in the brackets must also be positive; therefore Expression (19) cannot be satisfied. Therefore, given that there are costs associated with aggressive behavior, a polymorphic population of discriminators will always be subject to invasion by either unconditionally nonaggressive or unconditionally aggressive phenotypes.

Finally, in order that  $\bar{W}_D > W_{D,j}$ , it must be true that

$$c \sum_i P_{D,i}^2 > 0 \quad (20)$$

which will always be the case. Consequently, haplotypic polymorphism will not accumulate, even if discriminator behavior is somehow fixed. However discriminator behavior is evolutionarily irrelevant without variability at an allorecognition locus (Crozier, 1986).

To analyze the conditions under which a discriminating phenotype will be an ESS with independent assortment, we once again define the mean fitness of a pure population of discriminators ( $P_D \approx 1$ ), as well as rare belligerent and meek invaders. As before, under independent assortment,  $P_{D,i} = P_D P_i$  ( $\approx P_i$ ). Similarly,  $P_{B,i} = P_B P_i$  and  $P_{M,i} = P_M P_i$ . Therefore, from Equation (1),

$$\begin{aligned} \bar{W}_D = \sum_i P_i & \left[ P_{D,i} \left( 1 - d + \frac{v}{2} \right) \right. \\ & \left. + (1 - P_{D,i}) \right. \\ & \left. \cdot \left( 1 - d - c + \frac{v}{2} \right) \right] \end{aligned} \quad (21a)$$

$$\begin{aligned} \bar{W}_B = \sum_i P_i & \left[ P_{D,i} (1 - d - c + v) \right. \\ & \left. + (1 - P_{D,i}) \right. \\ & \left. \cdot \left( 1 - d - c + \frac{v}{2} \right) \right] \end{aligned} \quad (21b)$$

$$\begin{aligned} \bar{W}_M = \sum_i P_i & \left[ P_{D,i} \left( 1 + \frac{v}{2} \right) \right. \\ & \left. + (1 - P_{D,i}) \right]. \end{aligned} \quad (21c)$$

Discriminators will resist invasion by rare belligerent phenotypes when  $\bar{W}_D > \bar{W}_B$ . Simplifying from equation (21), this will be true when

$$v < 2c. \quad (22)$$

Otherwise, as we know from Expression (7b), belligerence is an ESS. To resist invasion by the meek phenotype,  $\bar{W}_D$  must be greater than  $\bar{W}_M$ , or

$$v > 2 \left[ \frac{d}{1 - \sum_i P_i^2} + c \right]. \quad (23)$$

From Expression (12), we know that when this expression is not satisfied the meek phenotype is an ESS.

If the number of haplotypes in the population is large, then Expression (23) becomes approximately  $v > 2(d + c)$ . In any case, Expressions (22) and (23) cannot be simultaneously true if  $d > 0$  (which it is by assumption). Consequently, with independent assortment, a polymorphic population of discriminating phenotypes cannot be an ESS against both meek and belligerent phenotypes. The conditions for invasion of novel haplotypes are the same as before, so polymorphism at the allorecognition locus will not accumulate.

#### Aggregation Model

*Calculation of Expected Fitnesses.*—A growing body of data indicates that dispersal of asexual propagules (and often sex-



ual propagules as well) can be spatially restricted in many clonal invertebrates (reviewed in Jackson [1985, 1986] and Grosberg [1987]). Such philopatric dispersal can lead to spatial association of similar allorecognition phenotypes. Under these circumstances, contests between matching haplotypes should occur more often than if haplotypic frequencies alone determined encounter frequencies (the random-encounters model). In this section, we ask whether this type of bias can provide a selective advantage to a discriminating population such that the discriminator phenotype can be an ESS.

We model this situation by introducing an aggregation parameter,  $\delta$  ( $0 < \delta < 1$ ), where  $\delta = 0$  is the random-encounters case and the probability that encounters are between identical haplotypes increases toward unity proportionally to  $\delta$ . Consequently, for an individual of type  $i$ , the relative frequency ( $\alpha_i$ ) of encounters with its own haplotype is

$$\alpha_i = \frac{(1 + \delta)P_i}{(1 + \delta)P_i + (1 - \delta)(1 - P_i)} \quad (24a)$$

where  $P_i$  is the frequency of haplotype  $i$  summed over all behavioral genotypes. The relative frequency ( $\beta_i$ ) of encounters with nonidentical haplotypes is

$$\beta_i = \frac{(1 - \delta)(1 - P_i)}{(1 + \delta)P_i + (1 - \delta)(1 - P_i)} \quad (24b)$$

Note that  $\alpha_i + \beta_i = 1$ .

Substituting the encounter frequencies specified by Equations (24a) and (24b) for those assumed in the random-encounters models does not change the qualitative conclusions in any of the cases we have analyzed. For some parameter values, either belligerent or meek phenotypes prove to be evolutionarily stable strategies. However discriminating populations can always be invaded by either meek or belligerent mutants.

We illustrate this with the case of greatest biological interest: a discriminating population that is polymorphic at the allorecognition locus, with independent assortment between loci. The expected fitness of each phenotype in a nearly pure population of discriminating phenotypes is defined by a set of expressions analogous to (21a)–(21c):

$$\bar{W}_D = \sum_i P_i \left[ \alpha_i \left( 1 - d + \frac{v}{2} \right) + \beta_i \left( 1 - d - c + \frac{v}{2} \right) \right] \quad (25a)$$

$$= 1 - d + \frac{v}{2} - c \sum_i P_i \beta_i$$

$$\bar{W}_B = \sum_i P_i \left[ \alpha_i (1 - d - c + v) \right] \quad (25b)$$

$$+ \beta_i \left( 1 - d - c + \frac{v}{2} \right) \Bigg]$$

$$= 1 - d - c + \frac{v}{2}$$

$$+ \left( 1 + \sum_i P_i \alpha_i \right) \frac{v}{2}$$

$$\bar{W}_M = \sum_i P_i \left[ \alpha_i \left( 1 + \frac{v}{2} \right) + \beta_i \right] \quad (25c)$$

$$= 1 + \frac{v}{2} \sum_i P_i \alpha_i$$

$$W_j = \alpha_j \left( 1 - d + \frac{v}{2} \right) + \beta_j \left( 1 - d - c + \frac{v}{2} \right) \quad (25d)$$

$$= 1 - d - c + \frac{v}{2}.$$

Substitution and algebraic simplification yield that, for  $\bar{W}_D > \bar{W}_B$ ,

$$v < 2c \left[ \frac{1 - \sum_i P_i \beta_i}{\sum_i P_i \alpha_i} \right] \quad (26)$$

In order that  $\bar{W}_D > \bar{W}_M$ , it must be true that

$$v > 2 \left[ \frac{d + c \sum_i P_i \beta_i}{1 - \sum_i P_i \alpha_i} \right] \quad (27)$$

For D to be an ESS, Expressions (26) and (27) must both be satisfied; that is,

$$2 \left[ \frac{d + c \sum_i P_i \beta_i}{1 - \sum_i P_i \alpha_i} \right] < 2c \left[ \frac{1 - \sum_i P_i \beta_i}{\sum_i P_i \alpha_i} \right] \quad (28a)$$

Since  $\alpha_i + \beta_i = 1$ ,  $\sum_i P_i \alpha_i + \sum_i P_i \beta_i = 1$ ,

Expression (28a) simplifies to

$$d < 0 \quad (28b)$$

which, by assumption, cannot be true. Therefore, aggregation of similar haplotypes leads to a state of affairs similar to the random encounters model: a discriminating phenotype cannot be an ESS against both unconditionally aggressive and nonaggressive mutant behavioral phenotypes.

Finally, for  $\bar{W}_D > W_{D,j}$ ,

$$\sum_i P_i \beta_i < 1 \quad (29)$$

which will always be the case if  $1 > \delta > 0$ . However, as  $\delta$  approaches 1, there will be little contact between differing haplotypes, and the  $D,j$  phenotype will be almost neutral.

#### DISCUSSION

Numerous studies have documented the existence of allotype-specific conditional aggression in cnidarians (reviewed in Buss et al. [1984], Francis [1988], and Grosberg [1988]); however, few of these studies have analyzed the conditions under which conditional aggression should evolve. Both Purcell (1977) and Francis (1973b) accounted for the evolution of conditional aggression in anemones in terms of the costs and benefits of such behavior to individuals. By this argument, restriction of aggression to allotypically distinct individuals should lower the average costs of aggression below that expected if aggression were unrestricted. Allotypic restriction of aggressive behavior appears to be especially advantageous where limited dispersal of asexual and sexual propagules leads to spatial association of clonemates and kin (Jackson, 1985, 1986; Grosberg, 1987; Francis, 1988). Yet even in loosely structured invertebrate populations, there appear to be substantial advantages to recognition of clonemates or close kin. For example, Gilbert (1976, 1977) showed that females of the rotifer *Asplanchna sieboldi* often cannibalize non-clonemates but rarely prey upon clonemates.

The models in this paper confirm and extend the dilemma first raised by Crozier (1986): assuming that allotypic discrimination is established in a population, when the costs of aggression outweigh the benefits, the rare alleles conferring allotypic specificity cannot increase in frequency. As is usual in ESS analyses, we considered a haploid model with and without tight linkage. Although it remains to be seen whether the same results hold in a full diploid model, Crozier (1986) found identical results in an analysis of diploid models for some of the cases we considered.

In our formulation, the fitness of a haplotype increases linearly with haplotype frequency precluding the accumulation of allotypic polymorphism. However, our analysis of the evolution of self/nonself discrimination indicates a more general problem: no matter what the apparent benefits of discrimination, a phenotype that restricts aggressive behavior to haplotypically distinct individuals (the discriminator phenotype) cannot be an ESS against both unconditionally aggressive (B) and unconditionally passive (M) phenotypes. Even if the modeled population is spatially structured and contests are biased toward haplotypically matched interactions, a polymorphic population of discriminators will always be subject to invasion by either belligerent or meek phenotypes.

This conclusion presupposes that belligerent individuals have some mechanism to prevent damaging their own tissues while behaving aggressively toward other individuals. Otherwise, unconditional aggression is biologically impossible. In the absence of belligerent phenotypes, there exist conditions [e.g., those defined by Expressions (18), (23), and (27)] in which a haplotypically polymorphic population of discriminating phenotypes would be an ESS against the only possible invader, a meek phenotype. If other loci are used by belligerent individuals to distinguish their own tissue from that of other individuals, then the evolution of variation at these loci could be subject to the same constraints as at the allorecognition locus analyzed in this paper. Therefore, some sort of nongenetic induced tolerance, such as that known from the anemone *Me-*

*tridium senile* (Purcell and Kitting, 1982), may be necessary to account for the existence of apparently unconditionally belligerent clonal species (e.g., the anemone *Anthopleura elegantissima* [Francis, 1973a, 1973b; Sebens, 1982b]).

The widespread occurrence of selective aggression based on allotypic similarity (or identity) requires both an advantage to selective aggression and variability in the recognition cue. Our analyses suggest that an advantage to conditional discrimination does not easily arise out of simple individual cost/benefit models. Even assuming that discrimination were somehow fixed (as does Crozier [1986]), the maintenance of allotypic variation is still problematical. Both with and without linkage, discriminating phenotypes with novel haplotypes cannot invade a population of discriminators. How, then, is it possible to account for the widespread evolution of aggressive behavior conditioned on allotype and for the accumulation of the requisite polymorphism at allorecognition loci?

The simplest individual-selection hypothesis is that rare allorecognition alleles are advantageous because of their effects on traits other than aggression. This hypothesis implies that aggression is keyed on a pleiotropic (and perhaps beneficial) effect and not directly favored by selection. There are three mechanisms invoking pleiotropy that have some empirical foundation. First, the fundamental role of allorecognition may be the control of gametic compatibility, whereby fertilization occurs only when sperm and maternal allotypes differ (Oka, 1970; Scofield et al., 1982; Scofield, 1988). Consequently, rare allotypes have greater mating success. Comparable systems are known in several families of angiosperms (reviewed in de Nettancourt [1977], and Mulcahy and Mulcahy [1983]). The second mechanism supposes that pathogens gain access to their hosts by mimicking host allotypes, thereby evading the host's immune system. This will lead to frequency-dependent selection that favors rare host allotypes until they become so common that pathogens capable of infecting such allotypes have a selective advantage (Bodmer and Bodmer, 1978; Hamilton, 1982; Levin, 1986; Crozier, 1988).

The third mechanism involves restriction of somatic fusion between individuals (Buss, 1982; Buss et al., 1984). Elsewhere (Grosberg and Quinn, 1988), we have shown that fusion conditioned on allotypic identity is not evolutionarily stable. Moreover, in most anemones, somatic fusion is not known to occur (Grosberg, 1988).

Any of these pleiotropic mechanisms could explain the accumulation of polymorphism at allorecognition loci in some species. But none of them addresses the more general problem of how aggressive behavior conditioned on allotype should evolve. In the models in this paper, populations of allotypically polymorphic discriminators are always subject to invasion by either unconditionally belligerent or unconditionally meek phenotypes. It is not obvious why maintenance of allotypic polymorphism by some other mechanism should change this outcome. In other words, maintenance of a polymorphic cue to clonal identity and kinship cannot alone explain the evolution of aggression conditioned on such a cue.

Allorecognition specificity could also be maintained by kin selection acting directly on the regulation of aggression. The simple models analyzed in this paper assume that the cost : benefit ratio of aggressive behavior depends only on the phenotypes of the individuals engaged in a contest. In general, if the costs of aggression outweigh the benefits, then passive behavior will be favored by natural selection. Conversely, if the benefits of aggression outweigh the costs, then indiscriminate aggression should evolve.

This model, however, considers selection only at the individual level. If aggressive members of a clone lose per capita fitness but, in the process, indirectly enhance the reproductive output or survival of the entire clone, then the costs of aggression will be offset to some degree by the fitness gains of nonaggressive clonemates (Hamilton, 1964a, 1964b; Brace, 1981; Francis, 1988). For example, sea anemones often aggregate into clonal groups, with isolated genotypes among such groups being rare (Francis, 1976; Hoffmann, 1976; Sebens, 1982a, 1982b; Ayre, 1984; but see Purcell and Kitting [1982]). In the clonal anemone *Anthopleura elegantissima*, peripheral individuals

in a clonal group have highly developed defensive structures called acrorhagi; these individuals contribute little to the asexual growth and gametic output of a clone, and central individuals do the bulk of sexual reproduction and asexual growth (Francis, 1976). This division of labor among members of a clone suggests that the direct fitness costs of aggressive behavior by peripheral individuals are offset by an indirect fitness gain via increased fecundity or survival probabilities of central individuals. If the indirect benefits of aggression exceed costs only when aggressive behavior is directed away from clonemates (or close kin), then a discriminating phenotype could be selectively favored over both belligerent and meek phenotypes. Under these circumstances, the ESS could be influenced by kinship, much as are the outcomes of other games (e.g., Grafen, 1979; Queller, 1984).

Our models do not incorporate the further complication that the costs and benefits of aggressive behavior are likely to be size-dependent. Size-dependence may prove to be an important component of understanding the evolution of allorecognition specificity, because many demographic parameters are strongly size-dependent in clonal invertebrates (Hughes, 1984; Kirkpatrick, 1984; Hughes and Connell, 1987) and the strength of kin selection may be size-dependent. For example, in cnidarians that form clonal groups or colonies, fitness could increase disproportionately with clonal size, because 1) size (hence, competitive ability) of defensive individuals increase with clone size (Francis 1976, 1988), 2) the absolute number of individuals available to replace injured peripheral aggressors increases (Sebens, 1982a), 3) the ratio of perimeters to central area decreases (hence, proportionately fewer individuals would be required to defend the clone), and 4) the onset of reproductive maturity is often size-dependent (Buss, 1982; Wahle, 1983; reviewed in Harvell and Grosberg [1988]). The utility of our models may therefore be limited to comparisons among small, or similarly sized, clones or individuals.

The evolutionary processes analyzed in this paper give clear answers to both of the questions posed in the Introduction. Given fixed cost : benefit ratios, size-indepen-

dence, and no division of labor, allotype-specific aggressive discrimination is unlikely to evolve. Even if such discrimination existed, it is improbable that selection could favor the rare alleles necessary to confer specificity. Taken together, these results suggest that allotypic specificity is not simply maintained by individual selection acting directly on agonistic behavior. However, if 1) the cost : benefit ratio of aggression changes according to the relatedness of neighbors, 2) there is division of labor, or 3) fitness depends on the size of a clone or kin-group, then the answers are not so obvious. The existence of such biological complications implies that complete answers to the questions await the development of more sophisticated theoretical models and empirical analyses of the costs and benefits of aggression.

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