To Thine Own Self be True? An Addendum to Feldgarden and Yund's Report on Fusion and the Evolution of Allorecognition in Colonial Marine Invertebrates

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Feldgarden and Yund (1) recently re-examined a question central to understanding the evolution of allorecognition systems in colonial and clonal marine invertebrates: "How does the genetic polymorphism necessary to restrict intergenotypic fusion to kin and clonemates accumulate in natural populations?" They argue that explanations invoking kin selection account fully for neither the extensive allelic polymorphism that characterizes the genetic systems that control allorecognition specificity, nor the apparent phenotypic instability of genetic chimeras. As a more parsimonious explanation than kin selection for these observations, they propose that frequency-dependent selection, acting at the level of the individual, promotes the accumulation of allotypic polymorphism by favoring fusion with self (and preventing fusion with nonself). To place this proposition into a conceptual framework, they cite two of my papers (2, 3) and assert that, "Several authors have noted that kin selection does not provide an obvious explanation for high allotype diversity." As far as it goes, this is an accurate statement, at least with respect to intergenotypic fusion in populations lacking kin structure. In these papers, however, J. F. Quinn and I developed a series of analytical models showing how individual selection could easily maintain allotypic polymorphism through the control of intergenotypic fusion.

So that there can be no misunderstanding about what we said, I quote a summary of our work on allotypic specificity and fusion from a paper published in 1988 (2, pp. 402–403; full references can be found in the original text):

It appears intuitively that individual selection acting to restrict allogeneic fusion could represent a general and potent selective force favoring the evolution of allorecognition and allotypic specificity (Burnet, 1971, 1973; Buss, 1982). In a theoretical analysis of this problem, Grosberg and Quinn (1988) defined the conditions necessary to favor rare allotypic variants in a single-locus, haploid model. Let c_f be the net per-capita fitness cost of fusion and b_f be the net fitness gain that is due to fusion. The expected fitness of an allorecognition allele, i, upon which fusion is conditioned, is then

$$W_i = 1 + P_i(b_f - c_f) \qquad (12)$$

where P_i is the frequency of allele i. Equation (12) shows that the fitness of an allorecognition allele depends upon both its frequency and the relative costs and benefits of fusion. If b_f is greater than c_f, then W_i will increase as P_i increases and the allele will become fixed in the population. However, if c_f is greater than b_f, then as P_i increases, W_i decreases. Consequently, rare alleles will be favored and allotypic polymorphism will accumulate only when the costs of fusion exceed the benefits. This raises the question of why individuals should ever fuse (Grosberg and Quinn, 1988).

One of the important effects of high levels of allotypic variation is the restriction of fusion to closely related individuals. Although the costs and benefits of genotype fusion should be adjusted according to the relatedness of the fused colonies (Hamilton, 1964; Buss and Green, 1985; Grosberg and Quinn, 1986), the effects of kin selection have not yet been incorporated into mathematical models of allotypic specificity.

I believe this passage leaves little room for misinterpretation, either of our approach to the problem, or of

the result that frequency-dependent selection, acting at the level of the individual, can favor rare alleles and promote the evolution of polymorphism at allorecognition loci through the restriction of intergenotypic fusion. Nevertheless, a number of biological complexities should temper the conclusion that individual selection is the primary force maintaining allotypic variation. First, as Feldgarden and Yund (1) mention, the theoretical prediction that individual selection can maintain allotypic polymorphism does not preclude the operation of kin selection. In fact, kin selection may be particularly effective in the many taxa of sedentary, clonal invertebrates in which sibling sexual propagules tend to remain spatially associated via restricted dispersal (4–8) or preferential settlement near kin (6, 9). Such a pattern of larval dispersal will, even after only a single generation, lead to kin structure, increased probabilities of fusion, and the opportunity for kin selection. Moreover, there is ample evidence that sexually produced propagules of some sponges, cnidarians, and ascidians can and do fuse soon after settlement (2). Thus, their claim [based on (6)] that, "Larval settlement as a function of future fusibility is the sole observation that we are aware of that is consistent with kin selection but not with the selective pressure of self fusion," could well apply to many clonal marine invertebrates.

Second, if the preservation of clonal integrity is the primary function of allorecognition systems, why should fusion ever be permitted between non-clonemates? In genetic terms, the overriding problem is: why, in many taxa, is only partial, rather than complete, genetic matching among alleles at allorecognition loci required for fusion to occur (2, 10)? After all, allorecognition systems requiring only partial allotypic matching, and based on self-recognition, are far less efficient at prohibiting fusion with nonself than systems requiring complete matching (in which any allelic discrepancy in allotype would lead to rejection and the preservation of genotypic integrity) (11). One answer [the one favored by Feldgarden and Yund (1)] is that intergenotypic fusion is simply a matter of imprecision in the recognition system and may be of little or no selective importance: "Although fusion between kin occurs, such events may simply represent mistakes in recognition due to the limitation of an imperfect system." It could be, as Feldgarden and Yund contend, that the genetics of invertebrate allorecognition are biochemically and phylogenetically constrained, so that partial genetic matching, and the recognition errors that it entails, is an evolutionary necessity, whatever the selective optimum.

I think, however, that this response oversimplifies even the meager amount presently known about the cellular and genetic mechanisms that regulate allorecognition. In so doing, it begs several crucial observations pertinent to the evolution of allorecognition and intergenotypic fusion.

In particular, if there were no exceptions to the genetic rule of partial matching in the clades that Feldgarden and Yund cite, then their explanation retains substantial merit. However, in several of the invertebrate phyla that they mention, including some sponges, cnidarians, and ascidians, full allotypic matching appears to be required for fusion to occur (12–16). Similarly, recognition systems based on multiple independent loci are less prone to error than single locus systems with comparable levels of allelic variation (11). Although some well-studied taxa (e.g., the compound ascidian Botryllus) have primary allorecognition systems based on a single locus, other taxa appear to have allotypic markers encoded by several loci (17, 18). Finally, in the few systems that have been examined in any sort of detail, individual genotypes appear to distinguish among different classes of nonself (2, 10, 19). I do not know why there is such variation, but taken together, these observations suggest, at least, that more precise allorecognition systems can evolve, but often do not.

There are four other poorly characterized, but nonetheless crucial, aspects of allorecognition that further complicate our understanding of how allotypic specificity evolves. First, although some [but not all, e.g., (20)] genetic chimeras have been found to be **morphologically** unstable (21–23), little is known of the **genetic** stability of these chimeras (24) and thus the true costs and benefits of fusion. Moreover, in the colonial ascidian Botryllus schlosseri, the morphological stability of chimeras seems to depend on the relatedness, and perhaps allotypic similarity, of fusion partners (19–23).

Second, in the absence of clone-specific genetic probes, the frequency of chimera formation in natural populations of benthic invertebrates is notoriously difficult to estimate. In general, grafting assays imply that intergenotypic fusion should be rare, provided that there is little kin structure in a population (2). Thus, I am not surprised that taxa such as Hydractinia symbiologicarpus, which inhabit mobile substrata, spawn gametes, or have motile, free-swimming larvae, show little evidence of kin structure and consequently little evidence for natural chimeras (25). In contrast, other sessile species that live on fixed surfaces and brood low vagility, sexual offspring, ought to have much higher frequencies of intergenotypic fusion. This might be the case for other hydractiniids, such as Hydractinia milleri, and is known to be the case in Botryllus schlosseri (7).

Third, as Feldgarden and Yund acknowledge, it is essential to quantify the costs and benefits of fusion, and how these might vary with ontogenetic, genetic, and ecological circumstances. If the situation in a chimera is as simple as one genotype's fitness loss being exactly the other's fitness gain, then, over the long term, it is difficult to see why even the most closely related nonclonemates

should be allowed to fuse (except by recognition error). On the other hand, if costs and benefits depend on ontogenetic, genetic, or ecological factors, or if costs and benefits are not additive, then kin selection may be effective.

Finally, Feldgarden and Yund did not consider contexts other than intergenotypic fusion in which allotypic specificity regulates the nature and outcomes of interactions between conspecifics. For example, in many cnidarians, allotypic disparity leads to aggressive behavior, whereas similarity fails to elicit an aggressive response (2). For this set of alternative behaviors, both Crozier (26) and Grosberg and Quinn (3) showed that individual selection does not provide a straightforward explanation for the maintenance of allotypic variation; with kin structure, however, polymorphism can evolve (27). In still more complex situations, pure fusion or aggression models are unrealistic. For instance, in *Hydractinia symbiolongicarpus*, incompatible colonies usually behave aggressively, whereas compatible genotypes often somatically fuse (28). Theoretical analysis of these behavioral options predicts that allotypic variation can be maintained, but only if fusion is more costly than aggression (3).

The paper by Feldgarden and Yund does focus attention on the idea that the preservation of clonal integrity (which is an extreme form of kin selection) can be an important selective mechanism, an idea first articulated nearly a century ago by Bancroft (29), and echoed over a quarter century ago by Knight-Jones and Moyse (30) and Hamilton (31). The paper further helps to clarify how little we know about the genetics and fitness consequences of allorecognition and intergenotypic fusion. Until more of this sort of information is in hand for a variety of taxa, we should not consider recognition errors and their effects on inclusive fitness as being mere epiphenomena of imperfect allorecognition systems. Consequently, I am reluctant—even in the face of having shown how individual selection can maintain allotypic specificity in the context of fusion—to downplay the potential importance of kin selection.

Acknowledgments

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