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# Sex and the Evolution of Fair-Dealing\*

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Brian Skyrms has studied the evolutionary dynamics of a simple bargaining game. Fair-dealing is the strategy 'demand 1/2', competing with the more modest strategy 'demand 1/3' and the greedier strategy 'demand 2/3'. Individuals leave offspring in proportion to their accumulated payoffs. The rules for payoffs from encounters penalize low- and high-demanders. The result is a significant basin of attraction for fair-dealing as an evolutionarily stable strategy. From these considerations Skyrms concludes that a disposition to fair-dealing could have evolved. A very different picture emerges, however, when one considers genetic bases for the dispositions involved. A simple two-allele sexual model produces very different stable equilibria in the distribution of behavioral phenotypes. The equilibria for Skyrms's purely phenotypic selection process will not in general be attainable once one enters some simple genetic considerations.

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**1. Introduction.** This is an investigation in evolutionary game theory, with special attention paid to simple genetic mechanisms. It seeks to extend Brian Skyrms's modeling of the evolution of fair-dealing as a behavioral strategy in competition with strategies involving more modest or greedier demand levels (Skyrms 1996).

In a sense to be made clear below, Skyrms's model is purely phenotypic. It takes no account of possible genetic bases for the behavioral dispositions involved. The simplest possible extension of Skyrms's model to take account of genetic bases, however, forces one to draw very different qualitative conclusions about the likelihood of fair-dealing being favored by natural selection as an evolutionarily stable strategy. Conclusions at odds with those of Skyrms also force them-

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selves upon one when one considers realistic variations of his rule governing the division of spoils between competing parties with different demand levels. Both severally and jointly, sex and sub-draconian penalties on greed give fair-dealers short shrift.

*1.1. Evolutionary Game Theory.* Imagine the following. In a population of social individuals, there are finitely many behavioral types  $\beta_1, \dots, \beta_m$ . Every individual is of exactly one of these types. Individuals encounter one another randomly, two at a time. As a result of its encounters with others, each individual acquires a certain fitness value. This fitness value determines how many offspring it has. Offspring tend to resemble their parents in behavioral type.

Thus far we have a completely general account of [heritable] fitness-affecting phenotypic interactions. Since evolution requires only differential reproduction and heritable variation in fitness, we already know enough to be able to predict that there will be an evolutionary process, resulting possibly in changes in the population frequencies  $\phi(\beta_1), \dots, \phi(\beta_m)$  of the respective behavioral types. (Note that  $\sum \phi(\beta_i) = 1$ .) Moreover, the selection process could be frequency-dependent. For we have been told that encounters determine fitness. So, the relative proportions within the population of each behavioral type could be crucial in determining an individual's own eventual fitness—and that of those of the same type.

Let us now add some more detail about how interactions affect fitness. When two individuals encounter one another, they play a certain game. As a result of its various encounters (plays of the game), each individual garners resources. How much an individual garners in any encounter depends only on its behavioral type, and on that of the other party. This dependence is described by a prevailing payoff rule (call it  $\pi$ ). It is the individual's total accumulated resources, from plays of the game, that determine how many offspring it has.

We are now in the realm of evolutionary game theory. The importance of the game in question lies in how, via its associated payoff rule  $\pi$ , it affects the fitness of (individuals of) any given behavioral type. Let  $\varepsilon(i,j)$  be the probability that a given individual of type  $i$  will, on its next encounter, meet an individual of type  $j$ . Let  $\pi(i,j)$  be the payoff to an individual of type  $i$  from a sharing encounter with an individual of type  $j$ . The payoff matrix  $\pi(i,j)$  and the matrix  $\varepsilon(i,j)$  of encounter probabilities enable one to calculate the expected total resources  $\rho(i)$  garnered by an individual of type  $i$ . The defining equation is  $\rho(i) = \sum \varepsilon(i,j)\pi(i,j)$ .

Make the following further simplifying assumptions. At each bout of reproduction, all parents die. The number of offspring of any individual  $i$  is directly proportional to its accumulated resources  $\rho(i)$ . In-

dividuals encounter one another at random within the population at large. Thus  $\varepsilon(i,j) = \phi(j)$  and so  $\rho(i) = \sum_j \phi(j)\pi(i,j)$ .

Life has now become less interesting, but computationally more tractable. Given the payoff rule  $\pi$ , one can work out how any initial distribution  $\phi = (\phi_1, \dots, \phi_m)$  of population-frequencies of the behavioral types will change, from one generation to the next. One can examine whether the population will evolve to stable equilibria  $\psi$ —that is, constellations of frequencies (of behavioral types) on which evolutionary trajectories tend, from a surrounding neighbourhood, to converge. We shall write  $\phi \xrightarrow{[\pi]} \psi$  to express this. When the convergence is achieved within  $N$  generations we shall also write  $\phi \xrightarrow{[\pi]^N} \psi$ . When the frequency of any one behavioral type tends to unity, we say that the type in question *spreads to fixity*. But if more than one behavioral type enjoys a non-zero limiting frequency within the population, we say that the population has reached a *polymorphic equilibrium*. An equilibrium  $\psi$  will have a ‘basin of attraction’ in frequency-space: start the population off anywhere in this basin of attraction, and it will converge to the equilibrium  $\psi$  in question.<sup>1</sup>

Now enter the following further assumptions. Each offspring has only one parent. Breeding is true—that is, each offspring is of the same behavioral type as its (sole) parent. Finally, there are only three behavioral types.

We are now in the realm of Skyrmsian selection theory—of which more in a moment.

*1.2. Heritability and Innateness.* In quantitative genetics, a trait is said to be *heritable* if its variation among individuals is due at least in part to genetic differences among them. The concept of heritability is a statistical one, and finds its most useful application when the trait is polygenic and its variation is continuous. The concept of heritability is employed when one is concerned to factor out the relative contributions of nature and nurture to the interindividual variation of a given (polygenic) trait.

In developmental biology, a trait is said to be *innate* (for a given genotype) when it displays rigidity of development across the normal range of environmental influences (on that genotype).<sup>2</sup> With *asexual*

1. An equilibrium can be a small neighbourhood in frequency-space rather than just a point. In that case  $\psi$  will be a convenient point within that neighborhood, to which, after sufficiently many generations, the frequency vector remains appropriately close.

2. See von Schilcher and Tennant 1984, Ch. 1, §6, for a discussion of the connections and contrasts between the developmental biologist’s concept of innateness and the population geneticist’s concept of heritability.

reproduction, the form of an innate trait in the parent will be identical to its form in any of its offspring. But with *sexual* reproduction, simple Mendelian recombination can make matters different even for innate traits. Consider, for example, two alleles *a* and *b* for a single chromosomal locus. Suppose that the genotypes *aa*, *ab*, and *bb* give rise respectively to three distinct forms of the (monogenic, or single-locus) innate trait in question. Note that two parents whose genotypes are *aa* and *bb* will have only *ab* offspring—which resemble neither of the parents with respect to the trait in question. Similarly, two *ab* parents will have a brood one quarter *aa*, one half *ab* and one quarter *bb* (assuming no meiotic drive). So in this case one half of the brood will resemble neither parent with respect to the trait in question. Thus even with innate traits the parent-offspring correlation of trait-values need not be perfect.

All that natural selection needs is that traits be heritable (to at least some degree). Traits do not have to be innate, nor do they need to be 100% heritable, in order to be subject to natural selection. Natural selection can reshape the distribution of a heritable trait even if the trait is not innate. Indeed, natural selection can have a significant effect even if the environment makes a very important contribution to the expression of the trait in any individual. Moreover, a trait's heritability in the quantitative geneticist's sense can be established quite independently of any hypotheses as to the biological or psychological mechanisms whereby the trait is expressed.

These general considerations are worth bearing in mind when considering the likely sources of variability in behavioral traits such as resource-sharing strategies. Even if only a small amount of the variation is due to genetic differences (i.e., even if heritability is low), natural selection can nevertheless change the underlying distribution of alleles at the loci concerned. And certainly, in the *innate* case it will be of paramount importance to consider natural selection and its effects on the underlying genotypes.

**2. Skyrms's Use of Evolutionary Game Theory.** Skyrms believes that an appealing evolutionary story can be told about how, from among possible competing strategies in 'sharing encounters', the strategy of fair-dealing will probably evolve (Skyrms 1996). He imagines the encounters as involving two individuals at a time. In each encounter some resource-value is at stake, which is available to be divided between the two parties. It is their cooperation that make the resource available; it is assumed that the resource would not be available to any individual acting on its own. Each party brings a characteristic 'demand level' to the encounter. This is its 'strategy'—or, in our introductory terminol-

ogy, its ‘behavioral type’. The fair-dealer will demand 1/2 of what is at stake. There could also be more modest or greedier demand levels. Among these, Skyrms considers only ‘demand 1/3’ and ‘demand 2/3’ for his explanatory purposes. Playing the game consists in making one’s demand, and taking one’s resulting due, as prescribed by the payoff rule.

In an ideal world of share-and-share-alike, there would be no squabbling, and no squandering of resources. It would seem to be in everyone’s best interests to be fair-dealers. As everyone knows, however, greedier demanders might do better (especially against more modest parties). There must be some penalty, Skyrms thinks, to punish those who demand too much, especially in encounters among themselves. Those who demand too little will already be punishing themselves by garnering less than they otherwise might. The Skyrms payoff rule (henceforth: the rule  $\sigma$ ) penalizes high-demanders. The entry  $\sigma(i,j)$  in the  $i$ -th row and  $j$ -th column represents the payoff to an individual of type  $i$  from a sharing encounter with an individual of type  $j$ . The Skyrms matrix  $\sigma(i,j)$  is as follows:

	D1/3	D1/2	D2/3
D1/3	1/3	1/3	1/3
D1/2	1/2	1/2	0
D2/3	2/3	0	0

The leading idea is that, with suitable levels of punishment—represented by the zeros in the matrix above—deviations from fair-dealing would be held in check, and in due course eliminated, by natural selection. For it is assumed that individual’s demand levels are heritable, and that reproductive success correlates positively with what one gets as a result of what one demands. The most successful strategy, Skyrms believes, will prove to be ‘demand 1/2’—in the sense that it is ‘the unique evolutionarily stable equilibrium strategy of the symmetric bargaining game’ (Skyrms 1996, 11; note that the game in question is *defined* by the matrix just given).

The Skyrmsian selection process has, as stressed above, a special feature: *every individual is (in the relevant phenotypic respect) exactly like its (sole) parent*. This is what makes Skyrmsian selection *purely phenotypic*. This special feature could be realized in two distinct ways. And both these ways tolerate complete omission of any genetic considerations in the modeling.

The first way for the selection process to be purely phenotypic is for the parent-offspring influence to be completely environmental. Imagine that either (i) the parent has complete power to indoctrinate its off-

spring; or (ii) the offspring's desire to imitate the parent's example is overriding; or (iii) there is a happy confluence of parental concern and juvenile diligence. Whatever the psychological mechanism, at this environmental extreme the 'breeding true' would be achieved in a 'purely cultural' fashion. Acquiring one's behavioral type (adopting a strategy) would be a matter of imitation and learning—like learning to play the piano, rather than growing five toes on each foot. Indeed, at this level of cultural abstraction, one could conceive of the *strategies*, rather than the biological individuals, being the replicators. It is clear that at this environmental extreme (that of *nurture* as opposed to *nature*) genetic considerations become irrelevant for the modeling.

The second way for the selection process to be purely phenotypic is for an exact parent-offspring resemblance to be wholly due to their exact similarity in some relevant genotypic respect, and to the innateness of the associated phenotypic trait. The 'purely genetic' extreme described here (that of *nature* as opposed to *nurture*) could arise when offspring were asexual clones of the parent. If the phenotypic trait were innate, then every individual would be (in the relevant phenotypic respect) exactly like its (sole) parent. Ironically, with such genetic determination, genetic considerations once again become irrelevant for the evolutionary dynamics. Because the genotype-phenotype correspondence is rigidly one-to-one, the modeling can be purely phenotypic, and the genotypes ignored altogether.

So we see that Skyrmsian selection can be realized at two very different extremes, one purely environmental and the other purely genetic. Both of these extremes allow one to ignore genetic considerations altogether when studying the evolutionary dynamics of the trait in question, and to deal directly and only with the phenotypes. And that is why we call Skyrms's model *purely phenotypic*.

Real-world populations of social individuals, however, tend to be found at neither of these extremes. Social individuals are not usually asexual; and, while important phenotypic traits are heritable, offspring in sexually reproducing species often fail *exactly* to resemble, in those important phenotypic respects, either one of their parents. Instead, we have to contend with the reality of genetic recombination. This means that even when certain traits are wholly innate, the offspring might not, in the relevant phenotypic respect, be exactly like either of its parents. Parent-offspring correlation of phenotypic traits need not be random; but it need not be *perfect* either.

For the three sharing strategies in Skyrms's model to be innate, there would have to be three genotypes corresponding respectively to 'demand 1/3', 'demand 1/2', and 'demand 2/3'. Every individual would breed true, all its offspring having the same genotype, and hence ex-

hibiting the same strategy, as their (sole) parent. But with sexual reproduction, matters are different: as soon as there is genetic variability individuals do not always breed true, even when the phenotypic traits in question are innate. This is because of sex.

Skyrms's assumption that offspring exactly resemble their (sole) parents is adopted also in the account of Batterman, D'Arms, and Górný 1998 (henceforth, BDG). The BDG-model, like the Skyrms model, does not take sexual reproduction into account.

The Skyrms-BDG purely phenotypic modeling is our acknowledged departure point. We shall maintain the following points of simplifying agreement with purely phenotypic modeling: parents die immediately after reproducing; the number of any individual's offspring is directly proportional to its accumulated resources; there are just three strategies or behavioral types (demand 1/3, demand 1/2, and demand 2/3); and individuals encounter one another randomly for plays of the game, two at a time.<sup>3</sup>

Our guiding question is: *Can the selection process reliably vouchsafe that fair-dealing will always be an evolutionarily stable strategy?* Holding at least the points of methodological agreement just mentioned will allow us to focus on two other, more important, features of the modeling in which developments might be desirable in pursuit of an answer to this question. These features are: (1) the nature of the genotype-phenotype relation; and (2) the fitness-affecting phenotypic interactions (i.e., the payoff rule). We shall make our first modeling innovation (or extension) with regard to feature (1). Then we shall make a second innovation with regard to feature (2). We shall examine the effects of each innovation in isolation, and then see what results from combining them.

**3. The Dialectical Situation.** We shall find, on making the foreshadowed innovations or extensions in the modeling with respect to features (1) and (2), that many of the qualitative conclusions from purely phenotypic modeling are undermined. That is, the evolutionary processes whose study is made possible by the innovations to be described result in very different kinds of equilibria than those produced by purely phenotypic modeling. In particular, *the strategy of fair-dealing does not emerge as evolution's favorite choice.*

3. Both Skyrms and BDG examine different relaxations of this last randomness assumption, by introducing so-called correlation coefficients; and we can follow them in that regard. The question of correlation coefficients, however, is orthogonal to the main concerns of this paper; and limitations of space prevent us from considering it. Suffice it to say that in our two-allele model positive correlation coefficients improve the fortunes of the allele for low demanding.



Now it is important to appreciate exactly what we take the dialectical situation to be, given how the modeling innovation to be described yields results at odds with those of Skyrms. There are two considerations to be distinguished. First, one could ask

- (I) Are the likely evolutionary circumstances of our own past better modeled by a purely phenotypic selection process or by one of the processes afforded by one of our modeling innovations?

This is an empirical question, one best answered by the extent to which the predictions of the respective models might match our pre-theoretical observations of the social phenomena. This is where the models are applied, or tested. Any pre-theoretical evidence, for example, that stable economic stratification in many a human society is the outcome of much *unfair* dealing could well be taken to support something like our genetically-minded modeling extension rather than the purely phenotypic model. For in a wide range of circumstances our model predicts a *stable* three-way polymorphism; whereas the purely phenotypic model does not predict it under any circumstances. (The only three-way polymorphism of the purely phenotypic model is unstable.) Purely phenotypic models tend in general to provide poor explanations of heritable behavioral traits in sexually reproducing organisms.

Secondly, one could require that the modeling address the question

- (II) Is fair-dealing likely to spread to fixity independently of whatever the genotype-phenotype relation might be?

This is a more a priori question, to be answered by examining the consequences of the modeling. We do this by implementing the model and exploring its computational results. In this regard, our investigations yield a negative answer to question (II). Fair-dealing is *not* likely to spread to fixity independently of whatever the genotype-phenotype relation might be. We demonstrate this with our main modeling extension: *a single-locus two-allele model for the innate case*.

Now admittedly this is a very specialized genetic scenario; but it is not to be neglected by any theorist aspiring to allege a general tendency of fair-dealing to spread to fixity, regardless of the nature of the genotype-phenotype relation. There are two feeding strategies in *Drosophila* larvae, which behavioral geneticists call *rover* and *sitter*. Rovers stay on the surface and forage widely. Sitters stay put and dig deep. This is quite a radical difference in behavior—not just in degree or intensity, but in *kind*. Yet the difference is known to be due to two alleles for a single locus (see Sokolowski 1980). If such a difference—even if only on the part of a fruit fly—can be due to variation at a single chromosomal locus, then one has to keep an open mind about

the possibility that organisms such as primates might likewise display variations in the *degree* or *intensity* of a certain kind of behavior as a result of variations at but a single locus.

The specialized nature of our chosen genetic scenario should kindle interest in the further question:

(III) When the genetic model is developed further, to a multiple-locus, multiple-allele model allowing for gene linkage, dominance-recessiveness and other genetic effects, and when the genotype-phenotype relation is conceived more generally so as to allow the phenotypic traits to be not wholly innate, will the qualitative results resemble those of purely phenotypic selection or those of the single-locus two-allele model of the innate case?

The reader is cautioned against too hasty a judgment call on this last question. The Mendelian combinatorics of evolutionary game theory even in the case of a single-locus *three*-allele model allowing for dominance-recessiveness are so complicated, notwithstanding the simplifying effects of our points of methodological agreement above, that qualitative predictions would at this stage be premature.<sup>4</sup> A great deal of further computer-aided intellectual effort is needed in order to settle question (III). It is only to be hoped that the current investigations will be a spur to this even more ambitious extension of genetic modeling in evolutionary game theory.

**4. A First Move Towards Greater Generality: Introducing Sex.** We want to introduce sex into the theoretical picture. This is the single major extension we envisage in order to move towards a model capable of finding application in the real world regardless of what its Mendelian secrets may turn out to be. The position here is that variations in social behavior in some sexually reproducing (diploid) species might, in an interesting range of cases, be the result of genetic variation at a single chromosomal locus. So we look first at the most obvious and most modest *genetic extension* of the purely phenotypic model. We take off from Skyrms's model, and introduce the minimum that it takes to get sex into the picture. Our discussion will focus on 'sharing strategies' as the phenotypic trait of interest; and these traits will be assumed to be

4. Templeton (1982) discusses significant differences between what would be predicted by a naive adaptationist (or purely phenotypic) model, and what is predicted by a particular single-locus, three-allele model. The latter model postulated various orderings of fitnesses of the six possible genotypes, as well as a dominant-recessive pair among the three alleles. The real-world phenotypic traits being modeled were two different levels of malarial resistance, one level of malarial susceptibility, and two levels of sickle-cell anemia.

innate. But the considerations to be advanced subsequently are perfectly general, applying to any innate trait admitting genetic variation of the kind here bruited.

*4.1. Intermediate Inheritance and Over-Dominance.* Consider the sexual case where two alleles—say,  $a$  and  $b$ —account for the phenotypic variety of ‘demand 1/3’, ‘demand 1/2’ and ‘demand 2/3’. If we assume intermediate inheritance (IH), then we could assign the phenotypic demand levels to genotypes as follows:

1/3	1/2	2/3	
			—IH
$aa$	$ab$	$bb$	

But the correspondence might be different. It might be the heterozygote that demands the most. Such a situation is one of so-called ‘over-dominance’, and is well-known to geneticists:

1/3	1/2	2/3	
			—OD
$aa$	$bb$	$ab$	

Note that we are adopting a convention to the effect that the homozygote  $aa$  demands less than the homozygote  $bb$ . Thus we shall speak of  $a$  as the allele for low demanding, and of  $b$  as the allele for high demanding. This holds regardless of the heterozygote’s demand level. We shall also assume in our displays that demand-levels increase from left to right: (1/3,1/2,2/3). Thus intermediate inheritance is evident in the triple ( $aa,ab,bb$ ); and over-dominance obtains when the triple is ( $aa,bb,ab$ ).

Over-dominance has been found quite frequently with polygenic traits in very inbred populations. But it is perfectly feasible for monogenic traits as well. Indeed, there is now even an explanation on offer as to the molecular mechanism that produces over-dominance in the single-locus case (Kacser and Burns 1981). We shall investigate only the kind of over-dominance just indicated. There is of course also the possibility that it is the heterozygote that demands the *least*.

The disadvantage in the two-allele case for three expressed values of a trait is that the trait-values are not completely independent genetic competitors. The situation is made more complex by heterozygosity. (In real life the strategies might not be independent competitors; it is an empirical question whether they are so.) Note that if the two alleles were dominant-recessive, then only two values for the trait would ever

be expressed. So, since we are assuming three expressed trait-values, it follows that in the two-allele case we have to rule out dominance-recessiveness. That leaves us, then, with intermediate inheritance and over-dominance as the only possibilities in the two-allele model. Only when we examine a three-allele model shall we be able, and obliged, to consider dominance-recessiveness as a genuine—and indeed rather likely—option.

It is not unrealistic to hypothesize that three behavioral types might arise from the action of just two alleles, with intermediate inheritance or over-dominance for the heterozygous case. Increasing demand levels could well be the result of, say, increasing concentrations of certain chemicals in the brain. These increased concentrations could have the effect of either stimulating or inhibiting certain kinds of neural activity. Nor is it unrealistic to assume that regimes of intermediate inheritance or of over-dominance (of either of the two possible kinds) could result from the neurochemical effects of the different alleles in homozygous and heterozygous combination. After all, it has been seriously hypothesized, even if not conclusively established, that even such a complicated psychological disorder as manic depression might be a single-gene defect (see Egeland et al. 1987 and Berrettini 1997, 262, 264; for a more skeptical assessment of the single-gene hypothesis for psychiatric disorders, and alternative explanatory—but still *genetic*—models, see Comings 1997). In light of the seriousness with which psychiatric geneticists are prepared to consider single-gene hypotheses, there is no *prima facie* reason why we should not consider as plausible the hypothesis that variations in sharing behavior might be due to variation at but a single genetic locus. The model we have suggested is adequate to just such a situation, where the variation is confined to one critical locus and is moreover absolutely minimal.

If the truth remains more complicated, then at the very least our model approximates it more closely than the purely phenotypic model, which does not enter any genetic considerations at all. Moreover, our model would lend itself to whatever further complications might be needed in order to save it from the charge of oversimplification.

*4.2. A Simple Disagreement with Purely Phenotypic Modeling.* Reflection on the two-allele case yields an important and almost a priori disagreement with purely phenotypic modeling. Take the case of intermediate inheritance. First, the combination *ab* (1/2-er) could not drive out the other two (the 1/3-er *aa* and the 2/3-er *bb*) to extinction. Even with every individual at a given time being of type *ab*, random meiosis, matings, and fertilizations would ensure, by Mendel's laws, that in the next generation about one quarter of the offspring would be *aa* and

one quarter  $bb$ . Thus in this ‘two-allele’ genetic set-up, one could not attain the purely phenotypic result of fixity for ‘demand 1/2’. (Here we have to assume meiosis is random, that is, that there is no meiotic drive. This assumption is justified by citing the need to isolate just the effects of the game-playing strategies on reproductive fitness.)

Second, there could be no polymorphic equilibrium, of the kind predicted by purely phenotypic modeling and confirmed in our non-stochastic replication of Skyrms’s model, of homozygous 1/3-ers (genotype  $aa$ ) and homozygous 2/3-ers (genotype  $bb$ ), unless matings took place strictly between the same genotypes. For, if any  $aa$  individual were to mate with any  $bb$  individual, all their offspring would be heterozygous 1/2-ers ( $ab$ )!

*4.3. Evolutionarily Stable Strategies and Invading Alleles.* *Evolutionarily stable strategies* are strategies that, once followed by almost all members of a population, prevent invasion by any other mutant strategy (see Maynard Smith 1982, 10, 24). Any mutant strategy would naturally be exhibited, initially, by only a very small proportion of the population. In the purely phenotypic case one could consider any one of ‘demand 1/3’, ‘demand 1/2’ and ‘demand 2/3’ as a candidate for ESS status, and try to ‘invade’ the population with one of the others. In the two-allele case, however, this kind of thought experiment is compromised by the genotype-phenotype relation. For, if almost all individuals were heterozygotes  $ab$ , then the very next generation would be about one quarter  $aa$ , one half  $ab$ , and one quarter  $bb$ ; and that would be a successful invasion (by  $aa$  and  $bb$ ). Thus any candidate for ESS would have to be homozygous (say  $aa$ ). Any imagined invasion would have to involve a new allele  $b$ —probably, therefore, in a new heterozygote  $ab$ . If the first  $ab$  individual manages to leave any offspring, half of them will be  $ab$ . Any interbreeding among these will produce a brood one quarter  $bb$ —and thus a third strategy would pop into the scene. Thus invasions would not be ‘single strategy’ invasions for very long.

The genetic approach therefore provides reason to re-conceive the process by means of which equilibria might be achieved. The point is clearest in the innate case, where each genotype determines a unique demand level. Invasion by a mutant strategy requires a new allele to enter the gene pool. This means that the new strategy thereby arising will enjoy some miniscule initial representation in the population, the allele responsible for it having arisen by mutation. With our single-locus, two-allele model we can think of these invasions as effecting a transition from an earlier stage where there is only one allele for that locus, to a later stage where we now have the two alleles of the model, the new one having arisen by mutation. Thus the new allele will in all

probability find itself initially within a new heterozygote, in a population of individuals otherwise homozygous in the old allele. This means that evolutionary stability is best judged in terms of what happens with initial positions such as the following, whose evolutionary trajectories we shall study below:

$$\begin{pmatrix} aa & ab & bb \\ 0 & 10^{-7} & 1 - 10^{-7} \end{pmatrix} \text{ -- allele } a \text{ for low demanding invading; IH}$$

$$\begin{pmatrix} aa & ab & bb \\ 1 - 10^{-7} & 10^{-7} & 0 \end{pmatrix} \text{ -- allele } b \text{ for high demanding invading; IH}$$

$$\begin{pmatrix} aa & bb & ab \\ 0 & 1 - 10^{-7} & 10^{-7} \end{pmatrix} \text{ -- allele } a \text{ for low demanding invading; OD}$$

$$\begin{pmatrix} aa & bb & ab \\ 1 - 10^{-7} & 0 & 10^{-7} \end{pmatrix} \text{ -- allele } b \text{ for high demanding invading; OD}$$

In the genetic case, then, it becomes less important to consider (as purely phenotypic models invite one to do) the *size* of any basin of attraction for a stable polymorphism or for fixity of a given strategy. For, when the new alleles arise by mutation, much of the area of each such basin of attraction (considered as providing starting points for an evolutionary process) is rendered irrelevant. This is because points in the irrelevant areas correspond to frequency vectors with non-trivial components for all behavioral types involving the invading allele. When a new allele invades, however, at least one of the behavioral types based on it will be *ex hypothesi* in a miniscule initial proportion within the population. Thus the sheer size of any basin of attraction can no longer feature in a probabilistic argument (as in Skyrms 1996, 16, and BDG 81) to the effect that evolution would be likely to produce the result in question (that is, the attractor within that basin). Instead, one should look at what successive invasions, one allele at a time, would do.

**5. Qualitative Results from the First Innovation (Introducing Sex).** We shall not lay out the mathematical details of the two-allele model; suffice it to say that they represent a smooth and direct generalization of the details of the purely phenotypic model, and are easy to implement computationally. We are concerned here rather to report the results.

The first remarkable result is the following:

*Example 1.* With over-dominance (with the heterozygote as the highest demander) and the Skyrms matrix  $\sigma$  in effect, a tiny 1-in-10,000,000 proportion of *ab* heterozygotes in an otherwise wholly *aa* homozygous population will see the new allele *b* for high de-

manding spread within about 60 generations to high representation in a stable polymorphism:

$$\begin{pmatrix} aa & bb & ab \\ 1 - 10^{-7} & 0 & 10^{-7} \end{pmatrix} \xrightarrow{[\sigma]^{60}} \begin{pmatrix} aa & bb & ab \\ .5286 & .3969 & .0745 \end{pmatrix}$$

This equilibrium will be achieved only when allele  $b$  is the invader.

*Example 2.* If the roles are reversed, so that allele  $a$  for low demanding is trying to invade an otherwise wholly homozygous  $bb$  population, then allele  $a$  simply never gets a look-in:

$$\begin{pmatrix} aa & bb & ab \\ 0 & 1 - 10^{-7} & 10^{-7} \end{pmatrix} \xrightarrow{[\sigma]} \begin{pmatrix} aa & bb & ab \\ 0 & 1 & 0 \end{pmatrix}$$

So, we see that over-dominance favors the allele  $b$  over the allele  $a$ .

By contrast, intermediate inheritance favors both:

*Example 3.* With the Skyrms payoff rule  $\sigma$ , there is a remarkably stable evolutionary equilibrium, which is achieved quite rapidly, and from both extremes for the initial proportion of allele  $a$  in the gene pool. The rarer allele in each case is introduced once again only via heterozygotes:

$$\begin{pmatrix} aa & ab & bb \\ 0 & 10^{-7} & 1 - 10^{-7} \end{pmatrix} \xrightarrow{[\sigma]^{40}} \begin{pmatrix} aa & ab & bb \\ .3967 & .4663 & .1370 \end{pmatrix}$$

$$\begin{pmatrix} aa & ab & bb \\ 1 - 10^{-7} & 10^{-7} & 0 \end{pmatrix} \xrightarrow{[\sigma]^{100}} \begin{pmatrix} aa & ab & bb \\ .3967 & .4663 & .1370 \end{pmatrix}$$

The Skyrms rule is severe on high-demanders, leaving them empty-handed when the combined demand level in an encounter exceeds 1. This accounts for the genotype  $bb$  (demand 2/3) making up less than 15% of the population in this last equilibrium, while  $aa$  (demand 1/3) makes up almost 40%.

**6. Qualitative Results from the Second Innovation: Allowing More Versatile Payoff Rules.** It would be sensible to investigate the effects of other payoff rules than that represented by the Skyrms matrix  $\sigma$ . For it does not strike one as wholly realistic to assume that neither party to an encounter receives *any* resource-value at all if the sum of their demand levels exceeds unity. Why should the penalty on high demanding be so severe? In order to justify the zeros in his payoff matrix, Skyrms resorts to the expository fiction of a referee who confiscates the whole cake. But a more realistic assumption, not calling for such expository fictions, would be that the result of such 'greedy' encounters

would be some division (in proportion to demand levels) of at least *some* portion of the disputed resource. The resource may, to be sure, be diminished or forfeited as a result of conflict over its (even only prospective) division. But even two hyenas each of which wants more than half of the carcass usually manage to munch a few morsels.

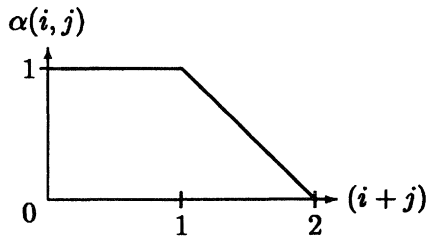
There is a useful role to be played, then, by a function that we shall call  $\alpha(i, j)$ . This represents the *available intact value* of a resource (whose initial value is normalized to unity) left over for division between two contesting claimants with demand levels  $i$  and  $j$  respectively. Clearly  $0 \leq \alpha(i, j) \leq 1$  and  $\alpha(i, j) = \pi(i, j) + \pi(j, i)$  (whence  $\alpha(i, j) = \alpha(j, i)$ ). When  $\alpha(i, j) < 1$ , the 'forfeited value'  $1 - \alpha(i, j)$  has been forfeited by the two claimants because of the contest between them.

Whatever payoff rule is in effect, the residual value  $\alpha(i, j)$  is always shared in proportion to the respective demand levels  $i$  and  $j$ . Thus we always have what may be called the *sub-rule of proportional division*:

$$j \cdot \pi(i, j) = i \cdot \pi(j, i)$$

This sub-rule says that the more one demands, the more one gets—of what is available to both parties (namely,  $\alpha(i, j)$ ). This makes good sense of the operational meaning of a 'demand' level. Different payoff rules, since they all embody the sub-rule of proportional division, will then differ from each other only in how they determine the 'available value'  $\alpha(i, j)$  from the demand levels  $i$  and  $j$ .

In general, the greater the sum of the two demand levels  $i$  and  $j$ , the greater the ensuing conflict, and the lower will be the available intact value  $\alpha(i, j)$  of the acquired resource with initial value 1. We would approximate this thought by saying that  $\alpha(i, j)$  is  $\min(1, 2 - (i + j))$ :

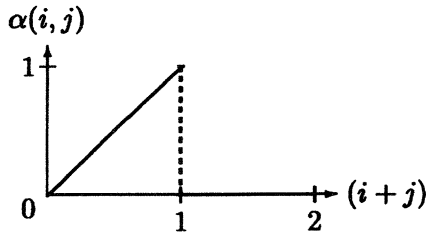


Available intact resource value  $\alpha(i, j)$  in encounters between demand  $i$  and demand  $j$  (a continuous case)

Notice that  $\alpha(i, j)$  is a continuous function of the sum  $(i + j)$  of demand levels. We shall call a payoff rule *continuous* just in case its associated residue function  $\alpha(i, j)$  is continuous, like the one (call it  $\gamma$ ) depicted in the graph above. Skyrms's payoff rule  $\sigma$ , by contrast, is *discontinuous*



because its associated residue function  $\alpha(i,j)$  is  $i + j$  if  $0 \leq i + j \leq 1$ , 0 if  $i + j > 1$ , which jumps discontinuously from 1 to 0 when  $(i + j)$  reaches 1:



Available intact resource value  $\alpha(i,j)$  in encounters between demand  $i$  and demand  $j$  (Skyrms's discontinuous case)

The question now arises whether  $\alpha(i,j)$  should be able to take non-zero values when  $i + j > 1$ . When the two demand levels match one another, for example, the division should be 50-50. But 50-50 of how much?—the whole resource (whose value is unity)? Or only some fraction thereof?

The discontinuous rule  $\sigma$  is extremely gloomy on this score. It sets the fraction in question to *zero*. It envisages total destruction (or forfeiture) of the resource as soon as  $i + j$  exceeds unity, no matter by how little. According to the rule  $\sigma$ ,  $\alpha(i,j) = i + j$  if  $0 \leq i + j \leq 1$ , 0 if  $i + j > 1$ , as depicted in the last graph. This may be excessive, and biologically unrealistic.

For, consider the case where the resource in question does *not* spoil with time. When  $i + j \leq 1$ , proportional shares could be enjoyed, and any (non-spoiled) left-overs could be made available for another 'encounter'. Iterating, two low-demanders could eventually achieve a proportional division of the *whole* initial value of the resource. When  $i + j > 1$ , however, the ensuing conflict could well spoil or destroy the resource—but in a way that worsened only *gradually*. We could imagine destruction being total when both parties wanted the whole hog. But there could be a gradual slide to this fractious extreme. Thus we could have, say,  $\alpha(i,j) = \min(1, 2 - (i + j))$ , as depicted in the first graph above.

This continuous rule with  $\alpha(i,j) = \min(1, 2 - (i + j))$  (which we have called  $\gamma$ ) would entail that low-demanders would obtain a little more than they actually demand in encounters with each other; and that high demanders, though still punished in encounters with each other, would not be so strictly punished. In accordance with the sub-rule of proportional division, the payoff matrix for the rule  $\gamma$  would be as follows:

	D1/3	D1/2	D2/3
D1/3	1/2	2/5	1/3
D1/2	3/5	1/2	5/14
D2/3	2/3	10/21	1/3

To appreciate the difference that the continuous rule  $\gamma$  can make, we shall consider in this section only the effect of that rule, not the effect of introducing sex. The qualitative results on the purely phenotypic model are extremely sensitive to initial conditions and the payoff rule. Switching from the discontinuous payoff rule  $\sigma$  to the continuous rule  $\gamma$  just suggested dramatically alters the nature of the equilibria attained in the purely phenotypic case.

*Example 4.* One can test the prospects of 1/3 and/or 1/2 spreading within the population when the initial frequencies are (.005,.005,.99). With Skyrms's discontinuous rule  $\sigma$ , 1/2 is wiped out, and 1/3 and 2/3 establish an evenly divided equilibrium within 10 generations. Yet with the continuous rule  $\gamma$ , 1/2 not only survives, but spreads to fixity within 200 generations:

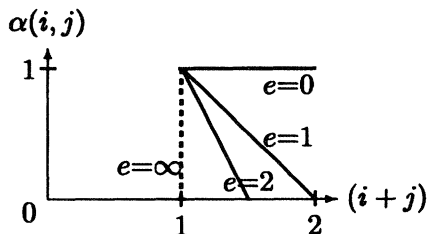
$$\begin{aligned} (.005,.005,.99) &\xrightarrow{[\sigma]^{10}} (.5,0,.5) \\ (.005,.005,.99) &\xrightarrow{[\gamma]^{200}} (0,1,0). \end{aligned}$$

Such dramatic differences are to be had even with very slight variations in a single parameter that could be introduced to calibrate the 'penalty' on high-demanders. The continuous rule  $\gamma$  above says that the total available resource value (which we are normalizing to unity) is proportionally divided between the two individuals when their combined demand level ( $i + j$ ) does not exceed 1; but diminishes when ( $i + j$ ) exceeds 1. At present a straightforwardly proportional diminution is envisaged:

$$\alpha(i,j) = 2 - (i + j) \quad (\text{when } i + j > 1)$$

Thus when ( $i + j$ ) = 2, the available value is 0. We could modify this effect by introducing a 'penalty' factor  $e > 0$  (yielding the preceding equation when  $e$  takes value 1):

$$\alpha(i,j) = 1 + e(1 - (i + j)) \quad (\text{when } i + j > 1)$$



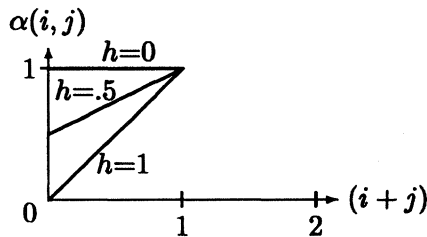
Available intact resource value  $\alpha(i,j)$  (when  $i + j > 1$ ) resulting from varying values of the penalty factor  $e$  on high-demanding

We find that variation in this penalty factor  $e$  can induce dramatic phase transitions.

It is not only high-demanders who are ‘punished’ by the discontinuous rule; for the low-demanders also suffer when they encounter each other, by virtue of forfeiting some part of the total resources available. When the sum of the demand levels  $i$  and  $j$  is less than 1, the discontinuous rule allows only  $(i + j)$  of the resource value to be available for (proportional) distribution. Thus if a 1/3-er encounters a 1/3-er, they each get 1/3, and 1/3 is forfeited by both sides; if a 1/3-er encounters a 1/2-er, the 1/3-er gets 1/3, the 1/2-er gets 1/2, and 1/6 is forfeited by both sides. So with the discontinuous rule  $\sigma$  we have

$$\alpha(i, j) = (i + j) \text{ (when } i + j \leq 1)$$

In order to relax this imposed forfeiture on low-demanders, we introduce the forfeiture factor  $h$ , taking values between 0 and 1; and we recast the foregoing part of the discontinuous rule so that it reads, more realistically, as  $\alpha(i, j) = h(i + j - 1) + 1$  (when  $i + j \leq 1$ ):



Available intact resource value  $\alpha(i, j)$  (when  $i + j < 1$ ) resulting from varying values of the forfeiture factor  $h$  on low-demanding

When  $h = 0$  we have complete generosity towards low demanders. They get to divide the whole resource in proportion to their demand levels. When  $h = 1$  we have Skyrms’s treatment of low demanders. For values of  $h$  between 0 and 1, we have varying levels of generosity towards low-demanders (the more generous the lower the value of  $h$ ). Thus our continuous rule  $\gamma$  arguably makes more versatile provision than the discontinuous rule  $\sigma$  in two respects, namely in being possibly more generous towards low-demanders and in being possibly more generous towards high-demanders.

How does one determine (from the two demand levels  $i$  and  $j$ ) what fraction of the original resource value is available to be divided? This,

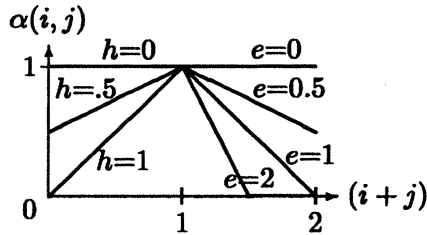
as remarked above, is where the different payoff rules distinguish themselves. The question is answered by the continuous rule  $\gamma(e, h)$  as follows (in effect combining the last two graphs).

Sub-rule providing penalties on high demanding:

$$\alpha(i, j) = \max(0, 1 + e(1 - (i + j))) \text{ when } i + j > 1 \quad (0 \leq e)$$

Sub-rule providing penalties on low demanding:

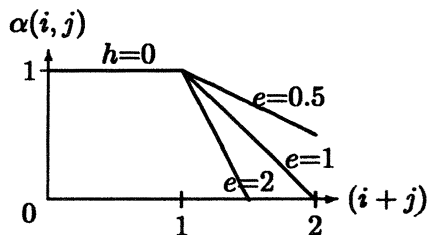
$$\alpha(i, j) = h(i + j - 1) + 1 \text{ when } i + j \leq 1 \quad (0 \leq h \leq 1)$$



Available intact resource value  $\alpha(i, j)$  resulting from varying values of the penalty factor  $e$  on high-demanding and the forfeiture factor  $h$  on low-demanding

The discontinuous rule  $\sigma$  can now be seen to be a special case of the continuous rule:  $\sigma = \gamma(\infty, 1)$ ; or, written another way,  $\sigma = [e = \infty, h = 1]$ . (Thus wherever we have  $[\sigma]$  in the statement of results above, we could instead write  $[e = \infty, h = 1]$ .) The continuous rule simply countenances more of the likely empirical possibilities. The rule we have called  $\gamma$  has the settings  $[e = 1, h = 0]$ .

For the rest of this discussion, we shall set  $h = 0$  when the continuous rule is in effect. Thus we shall be combining the greatest possible degree of generosity towards low demanders ( $h = 0$ ) with varying levels of severity (registered by the penalty factor  $e$ ) towards high-demanders:



Available intact resource value  $\alpha(i, j)$  resulting from varying values of the penalty factor  $e$  on high-demanding and the fixed value 0 for the forfeiture factor  $h$  on low-demanding

Our computations reveal that an ever-so-slight variation of the value of  $e$  can dramatically alter the evolutionary outcome on the purely phenotypic model.

*Example 5.* If we set  $e = 0.8$  then from the initial proportions of our last example,  $1/2$  still spreads to fixity. But if we set  $e = 0.7$  then  $2/3$  repels the invaders. Note moreover that neither of these settings for  $e$  produces any of the zeros of the discontinuous payoff matrix. So what we have here is a phase transition induced by some threshold value of  $e$ , which lies between 0.7546 and 0.7547. (As we lower the value of  $e$ , we reduce the penalty on high-demanders, such as  $2/3$ .)

$$\begin{aligned} (.005, .005, .99) &\text{---}[e = 0.8, h = 0] \text{---}\longrightarrow (0, 1, 0) \\ (.005, .005, .99) &\text{---}[e = 0.7547, h = 0] \text{---}\longrightarrow (0, 1, 0) \\ (.005, .005, .99) &\text{---}[e = 0.7546, h = 0] \text{---}\longrightarrow (0, 0, 1) \\ (.005, .005, .99) &\text{---}[e = 0.7, h = 0] \text{---}\longrightarrow (0, 0, 1) \end{aligned}$$

This is completely new for the purely phenotypic case—quite unlike the two possible outcomes that the purely phenotypic model produces using the discontinuous rule  $\sigma$ , as we saw in Example 4.

Note that the dramatic contrast reported in this section concerns the purely phenotypic model, and comes only from changing the payoff matrix. The purely phenotypic model is so sensitive to initial conditions that it is doubtful whether anything of general predictive or explanatory value can be derived from it. Every evolutionary process governed by the discontinuous payoff rule  $\sigma = [h = \infty, e = 1]$  has as its only stable outcomes either  $(0.5, 0, 0.5)$ , or  $(0, 1, 0)$ . But with the continuous rule  $[h = 0, e < 0.7546]$ , one has the further stable outcome  $(0, 0, 1)$ .

## 7. Qualitative Results from Combining the Two Innovations.

*7.1. Over-Dominance.* We saw in Example 1 how in the case of over-dominance with the discontinuous rule  $\sigma$  in effect, a new allele  $b$  for higher demanding can invade the gene pool and establish a polymorphism. Changing the payoff rule dramatically changes the end-result:

*Example 6.* When the continuous rule is used—with penalty factor  $e = 1$ —instead of the discontinuous rule, and allele  $b$  is the invader, it spreads to fixity, making up over 99.99% of the gene pool by generation 600.

$$\begin{pmatrix} aa & bb & ab \\ 1 - 10^{-7} & 0 & 10^{-7} \end{pmatrix} \text{---}\begin{bmatrix} e & h \\ 1 & 0 \end{bmatrix} \xrightarrow{600} \begin{pmatrix} aa & bb & ab \\ 0 & 1 & 0 \end{pmatrix}$$

The result is also very sensitive to the magnitude of the penalty factor  $e$ :

*Example 7.* If the penalty factor in the continuous rule is decreased to around 0.3, one suddenly obtains a phase transition, to a stable equilibrium by around generation 250:

$$\begin{pmatrix} aa & bb & ab \\ 1 - 10^{-7} & 0 & 10^{-7} \end{pmatrix} - \begin{bmatrix} e & h \\ .3 & 0 \end{bmatrix} \xrightarrow{250} \begin{pmatrix} aa & bb & ab \\ .0614 & .3728 & .5659 \end{pmatrix}$$

It is easy to understand why we obtain the last result: in the case of over-dominance, it is the heterozygote that is the highest demander. Reducing the penalty on high demanding therefore boosts heterozygote fitness. Once boosted above a certain level, heterozygote fitness ensures that the new allele  $b$  does not spread to fixity and drive out allele  $a$ , but will instead be held in check in a stable polymorphic equilibrium with allele  $a$ .

*7.2. Intermediate Inheritance.* We saw in Example 3 how in the case of intermediate inheritance with the discontinuous rule  $\sigma$  in effect, invasions by alleles for either low- or high-demanding resulted in the same equilibrium  $\begin{pmatrix} aa & ab & bb \\ .3967 & .4663 & .1370 \end{pmatrix}$ . Changing from the discontinuous rule to the continuous rule has a marked effect on the nature of the equilibrium attained:

*Example 8.* With the continuous rule for payoffs, with penalty factor  $e = 1$ , and with the allele  $a$  for low demanding being the mutant trying to get a look-in,

$$\begin{pmatrix} aa & ab & bb \\ 0 & 10^{-7} & 1 - 10^{-7} \end{pmatrix} - \begin{bmatrix} e & h \\ 1 & 0 \end{bmatrix} \xrightarrow{600} \begin{pmatrix} aa & ab & bb \\ .0601 & .3701 & .5698 \end{pmatrix}$$

When allele  $b$  for high demanding is the mutant trying to get a look-in, the same equilibrium is achieved, but more quickly:

$$\begin{pmatrix} aa & ab & bb \\ 1 - 10^{-7} & 10^{-7} & 0 \end{pmatrix} - \begin{bmatrix} e & h \\ 1 & 0 \end{bmatrix} \xrightarrow{436} \begin{pmatrix} aa & ab & bb \\ .0601 & .3701 & .5698 \end{pmatrix}$$

Again, we see the effect of changing the penalty factor  $e$ :

*Example 9.* With the continuous rule for payoffs, but with the higher penalty factor  $e = 2$ , the equilibrium achieved in each of the two invasion scenarios is more nicely representative:

$$\begin{pmatrix} aa & ab & bb \\ 0 & 10^{-7} & 1 - 10^{-7} \end{pmatrix} - \begin{bmatrix} e & h \\ 2 & 0 \end{bmatrix} \xrightarrow{100} \begin{pmatrix} aa & ab & bb \\ .2660 & .4995 & .2345 \end{pmatrix}$$

When allele  $b$  is the mutant trying to get a look-in, the same equilibrium is achieved, but more slowly:

$$\begin{pmatrix} aa & ab & bb \\ 1 - 10^{-7} & 10^{-7} & 0 \end{pmatrix} \xrightarrow{\begin{bmatrix} e & h \\ 2 & 0 \end{bmatrix}^{276}} \begin{pmatrix} aa & ab & bb \\ .2660 & .4995 & .2345 \end{pmatrix}$$

The contrast between the rates of invasion by allele  $a$  or by allele  $b$  in the last two examples is explained by the penalty factor  $e$  on the allele  $b$  for high-demanding. High-demanders suffer from this penalty more when they are in the majority—hence invasion by the allele  $a$  for low-demanding is made easier and swifter as  $e$  takes higher values.

With the continuous rule (with  $e = 2$ ), high-demanders are still punished when the combined demand level exceeds 1, but not as severely as they are in the discontinuous case. This change in the interests of realism puts the two alleles almost on a par, in what resembles a Hardy-Weinberg equilibrium for their equal representation. (But of course we have balancing selection here, rather than no selection pressure at all.) With the continuous rule, we clearly have a case of superior heterozygote fitness ensuring that allele  $a$  is never driven to extinction. If, however, we ease the penalty factor  $e$  down below 0.7, a phase transition occurs, and allele  $a$  is then driven to extinction:

$$\begin{pmatrix} aa & ab & bb \\ 1 - 10^{-7} & 10^{-7} & 0 \end{pmatrix} \xrightarrow{\begin{bmatrix} e & h \\ <0.7 & 0 \end{bmatrix}} \begin{pmatrix} aa & ab & bb \\ 0 & 0 & 1 \end{pmatrix}$$

**8. Concluding Remarks.** By omitting genetic considerations, purely phenotypic modeling makes each behavioral type as independent as possible from the others. Their evolutionary fortunes are then determined solely by their interactions, and not by any patterns of allele-sharing.

BDG criticize Skyrms's model for not being realistic enough; but they do not themselves remedy what is perhaps its most unrealistic aspect—namely, the lack of any genetic constraints on degrees of phenotypic freedom. BDG complain that Skyrms “has given us no reason to think that we have genetic proclivities for strategies.” Given the vast amount of evidence about heritability of variable traits in behavioral genetics, however, it would be more appropriate to demand reason to think that we (and other social species) do *not* have such genetic proclivities.

Although Skyrms assumed such genetic proclivities, he omitted to enter any genetic considerations. This omission was not altogether inadvertent. Skyrms wrote

We start by building an evolutionary model. Individuals, paired at random from a large population, play our bargaining game. The cake represents a quantity of Darwinian fitness—expected number of offspring—that can be divided and transferred. Individuals re-

produce, on average, according to their fitness and *pass along their strategies to their offspring*. In this simple model, individuals have strategies *programmed in*, and the strategies replicate themselves in accord with the evolutionary fitness that they receive in the bargaining interactions. . . .

[D]emand 50% is a stable equilibrium. In a population in which everyone demands half of the cake, any mutant who demanded anything different would get less than the population average. Demanding half of the cake is an *evolutionarily stable strategy* . . . and an attracting dynamical equilibrium of the evolutionary replicator dynamics. [fn]

Fair division is thus the unique evolutionarily stable equilibrium strategy of the symmetric bargaining game. . . . For this reason, the Darwinian story can be transposed into the context of *cultural evolution*, in which imitation and learning may play an important role in the dynamics. (1996, 9–11; first two emphases are mine)

The first two emphasized phrases call for a genetic reading, and indeed one on which the phenotypic traits are not only heritable, but also innate; or, at the very least, these phrases call for the *admissibility* of such a reading. This quote shows that Skyrms can be held to take his model as applying, *inter alia*, to the case of three wholly innate phenotypes whose (genetic) heritability could well be 100%. So we would do well to examine the possible genetic bases involved. This is what we have done here; and indeed we have examined the simplest possible such bases.

We discovered considerable differentiation in the broad nature of the qualitative results obtained in the purely phenotypic modeling, once we took into account the possibilities of intermediate inheritance and of over-dominance. That is, the qualitative results emerging from the purely phenotypic model did not prove to be robust under the genetic innovations that we undertook.

The point about how phenotypic equilibria might not be so freely attainable is perfectly general across traits. There is nothing special about behavioral strategies, or indeed the sharing strategies among them, that makes it important to pay attention to the genetic base that might be involved. Any fitness-affecting trait is subject to the same caveat. The purely phenotypic model involved a discrete-valued behavioral trait with three values. But any trait, with however many discrete values, is in principle subject to the same considerations as those we have advanced above, provided only that phenotypic interactions affect fitness in the ways registered in the payoff rule. To the extent, then, that there is a theoretical shortcoming in the purely phe-



notypic modeling of phenotypic interactions, it is a shortcoming deriving from perfectly general considerations about the relation between phenotype and genotype, and from nothing having to do with the complications involved in modeling specifically behavioral traits, or indeed phenotypic interactions in general.

What we have demonstrated in this paper is that the details of a purely phenotypic account are not realizable through at least one of the simplest and most plausible genetic mechanisms that one could imagine underlying the phenotypic trait in the sexual case. We have considered the case where only two alleles are involved for a trait admitting three selectable values, and we have arrived at very different results from those of the purely phenotypic model concerning the existence and stability of evolutionary equilibria in the frequency-dependent selection process. The difference is enough to give one pause before drawing any optimistic philosophical conclusions, about the evolution of fair-dealing, from the purely phenotypic model. Recall our guiding question above: *Can the selection process reliably vouchsafe that fair-dealing will always be an evolutionarily stable strategy?* Skyrms's answer was positive, based on results concerning a purely phenotypic model. At this stage of investigation, however, after paying some attention to genetics, it seems that the answer could well be negative—or at best, undecided.

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