Pairwise Competition and the Replicator Equation

JOHN MORGAN

Haas School of Business,
University of California,
Berkeley,
USA

KEN STEIGLITZ[*]

Department of Computer Science,
Princeton University,
35 Olden Street,
08544-2087 Princeton, NJ,
USA

E-mail: ken@cs.princeton.edu

Spite in Hamilton's sense is defined as the willingness to harm oneself in order to harm another more. The standard replicator dynamic predicts that evolutionarily stable strategies are payoff-maximizing equilibria of the underlying game, and hence rules out the evolution of spiteful behavior. We propose a modified replicator dynamic, where selection is based on local outcomes, rather than on the population 'state', as in standard models. We show that under this new model spite can evolve readily. The new dynamic suggests conditions under which spite in animals might be found.

1. INTRODUCTION

Hamilton (1970) asked, '...would we ever expect an animal to be ready to harm itself in order to harm another more?'. Such behavior has become accepted as the informal definition of spite, but the problem of whether spiteful behavior in animals exists, or even *can* exist under evolutionary pressure, has had a controversial history, often involving definitional issues, and is far from resolved (Foster *et al.*, 2001). The most restrictive form of spite, and perhaps the most difficult to explain, is *indiscriminate* spite, where behavior is assumed to be oblivious to relatedness of rivals. After Verner (1977) argued that territoriality provided empirical evidence for such spite in birds, Rothstein (1979), and Knowlton and Parker (1979) concluded from specialized mathematical models that indiscriminate spite can be supported only to a small extent, and only for small populations. In this paper we

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[*]Author to whom correspondence should be addressed.

re-examine the behavioral foundation of spite, propose a revised dynamic model for its evolution, and show how this dynamic can easily give rise to the selection of what would ordinarily be viewed as spiteful behavior. The selection dynamic we study applies to human as well as animal behavior, and to cultural as well as biological evolution.

Gadagkar (1993) points out that, 'Conventional wisdom has it that to be spiteful is the prerogative of humans alone'. He goes on to suggest, however, that, given the ambiguous nature of examples proposed so far, a more detailed examination of the issue may lead to greater understanding of animal evolution in general, even if the ultimate conclusion is that such apparently paradoxical behavior is actually selfish. Our model thus represents one additional step in this research program—offering theoretical underpinnings to suggest where indiscriminate spite might be expected to flourish.

Apart from explaining spite in animals, there is also the problem of explaining apparently spiteful behavior in *Homo sapiens*. We examined this question within the narrow context of equilibrium behavior in auctions elsewhere (Morgan *et al.*, 2003). In the present paper we seek to extend some of these findings to dynamic models.

As we shall see, our conclusion in this paper is that when reproductive success is determined to a significant extent by relative fitness measured on a *one-on-one* basis, spite in Hamilton's sense can evolve, despite the fact that the standard replicator model, which measures relative fitness on the basis of current population state, predicts otherwise. Thus, one should look for indiscriminate spite in situations where pairwise outcomes are influential in determining survival.

2. MODEL

We consider the following general model (Weibull, 1995; Hofbauer and Sigmund, 1998; Gintis, 2000). In an infinite population, pairs of individuals interact, one random pair at a time. Each individual has associated with it one of n pure strategies, which we think of as representing its genotype ('type'). At any time t, there is a distribution of individuals across the n types $\{x_i\}, i = 1, \ldots, n$, where $x_i \geq 0$ and $\sum_i x_i = 1$. Denote the n-dimensional vector with components x_i by $\mathbf{x}$.

Assume that when an individual of type i engages in a contest with an individual of type j, the result has expected payoff $\pi_{ij}(\mathbf{x})$ to the individual of type i. Notice that, in general, this payoff can depend on both i and j, as well as the state of the population, $\mathbf{x}$.

Let the probability that an individual of type i interacts with another individual in a small time interval dt be proportional to dt and the fraction of type i individuals in the population. If the relative fitness $\pi_{ij}(\mathbf{x}) - \pi_{ji}(\mathbf{x}) < 0$, the individual of type i switches to type j with some probability, and vice versa. We adopt the usual assumption that this probability is proportional to the difference in fitness

between i and j. Writing the change in the state $\mathbf{x}$ from t to $t + dt$, taking the limit in the usual way, and normalizing time, yields the differential equations

$$\dot{x}_i = x_i \sum_j x_j (\pi_{ij}(\mathbf{x}) - \pi_{ji}(\mathbf{x})). \tag{1}$$

In the standard treatment of replicator dynamics, the expected payoff function for i depends on i's relative fitness compared to an average individual, and does not depend on j's identity. That is, we define

$$\pi_{ij}(\mathbf{x}) = \pi_i(\mathbf{x}) = \sum_k x_k a_{ik}, \tag{2}$$

where the matrix $A = [a_{ik}]$ is the payoff matrix of some game that ultimately defines the pairwise interaction of individuals. Equation (1) then becomes

$$\dot{x}_i = x_i \sum_j x_j \pi_i(\mathbf{x}) - x_i \sum_j x_j \pi_j(\mathbf{x}) = x_i (\pi_i(\mathbf{x}) - \bar{\pi}(\mathbf{x})), \tag{3}$$

where $\bar{\pi}(\mathbf{x}) = \sum_j x_j \pi_j(\mathbf{x})$ is the average payoff of the population as a whole. Informally, the rate of change of the density of an evolutionary strategy is proportional to the difference between its fitness and the average fitness of the entire population. This is referred to by Hofbauer and Sigmund (1998) as the 'basic tenet of Darwinism'.

Consider as an alternative the model where the switching probability depends, not on the average fitness of the individuals in the particular state of the population at time t, but rather on the *relative* strengths of the individuals as determined by the game's payoff matrix A. Survival in this situation is determined only by the payoffs to the two particular individuals, and, as shown below, can lead to selection of behaviors that would be termed spiteful in the sense of Hamilton. Thus, we call this the *spiteful* replicator dynamic, to distinguish it from the standard case. The expected payoff function in equation (1) is $\pi_{ij}(\mathbf{x}) = a_{ij}$, not a function of the population state $\mathbf{x}$, and the spiteful replicator dynamic, corresponding to equation (3), becomes

$$\dot{x}_i = x_i \sum_j x_j (a_{ij} - a_{ji}). \tag{4}$$

Rewriting the standard replicator dynamic, equation (3), as

$$\dot{x}_i = x_i \left(\sum_j x_j a_{ij} - \bar{\pi}(\mathbf{x}) \right), \tag{5}$$

the critical difference between the two models becomes apparent. The game payoff matrix $[a_{ij}]$ is replaced by the matrix $[a_{ij} - a_{ji}]$, and the average fitness term is zero.

To characterize situations intermediate between the standard and the spiteful replicator dynamic, we introduce the parameter $0 \leq \alpha \leq 1$ and define the expected payoff in a pairwise encounter as the convex combination

$$\pi_{ij}(\mathbf{x}) = (1 - \alpha)\pi_i(\mathbf{x}) + \alpha a_{ij}. \tag{6}$$

Using this in equation (1), the dynamic becomes

$$\dot{x}_i = x_i \left[\sum_j x_j (a_{ij} - \alpha a_{ji}) - (1 - \alpha)\bar{\pi}(\mathbf{x}) \right]. \tag{7}$$

We can interpret this as follows. The convex combination of standard and spiteful dynamics has exactly the same form as the standard replicator dynamic, equation (5), with only this difference: the original game matrix $[a_{ij}]$ is replaced by $[a_{ij} - \alpha a_{ji}]$. It is this modified matrix that determines equilibrium behavior in the spiteful dynamic. We expand the definition of the spiteful replicator dynamic to include this model whenever $\alpha > 0$.

Because the spiteful replicator dynamic can be put in the form of the standard replicator dynamic—with an appropriately modified game matrix—stability results for standard replicator dynamics [see, for example, Björnerstedt and Weibull (1996)] carry over without change. In particular, if a population distribution in the spiteful replicator dynamic of equation (7) is Lyapunov stable, then it is a Nash equilibrium of the corresponding game. Furthermore, every strict Nash equilibrium is asymptotically stable.

Observe that the equilibrium corresponding to the modified matrix is not generally an equilibrium in the actual game. The point is that the modified game matrix rewards behavior reducing an individual i's own payoff, if, by doing so, this has the effect of harming a rival j even more (weighted by α), since survival is determined by $a_{ij} - \alpha a_{ji}$. This is consistent with the notion of indiscriminate spite.

3. EXAMPLE: THE HAWK–DOVE GAME

To illustrate how spiteful replicator dynamics can lead to spiteful behavior in equilibrium, consider the Hawk–Dove game, a simple and familiar example, but one that illustrates all we need. Following Maynard Smith (1982), the matrix form of the Hawk–Dove game is

	H	D
H	$(V - C)/2$	V
D	0	$V/2.$

(8)

That is, in fights over a resource of value V, Dove–Dove contests split the resource equally, but Hawk–Hawk contests incur a cost C.
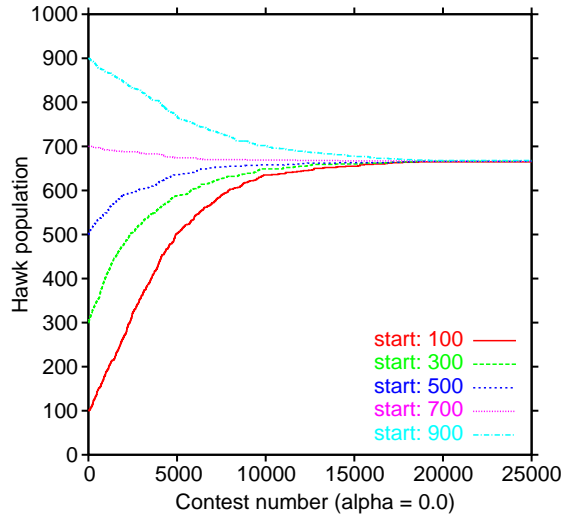
Figure 1. Discrete simulation, $\alpha = 0.0$, for different starting populations of Hawks.

With the spiteful replicator dynamic, our analysis above shows that the evolution of the population is determined by the matrix $[a_{ij} - \alpha a_{ji}]$. Thus, we consider the matrix where the diagonal payoff terms are multiplied by $1 - \alpha$, and the off-diagonal terms are incremented by $-\alpha$ times the reflected entry:

$$
\begin{array}{c|cc}
 & H & D \\
\hline
H & (1 - \alpha)(V - C)/2 & V \\
D & -\alpha V & (1 - \alpha)V/2.
\end{array}
\tag{9}
$$

When $V \geq C$, Hawk is a dominant strategy, regardless of α. When $V < C$, the analysis is more interesting. For $\alpha < (C - V)/(C + V)$, there is a mixed equilibrium where the fraction of Hawk play is $(V/C) \cdot [(1 + \alpha)/(1 - \alpha)]$. Notice that this fraction is increasing in α; that is, increasing the marginal benefit of harming an opponent leads to more Hawkish play. When $\alpha \geq (C - V)/(C + V)$, the gains from reducing a rival's payoff are such that Hawk is again a dominant strategy.

Figures 1–4 show the results of finite-population, discrete-time simulations of the spiteful replicator model. At each generation, the population is updated as follows. An individual i is selected at random from the population, and that individual engages in a contest with a randomly selected individual j. The relative fitness $\Delta = \pi_{ij} - \pi_{ji}$ is computed according to the hybrid payoff in equation (6). If $\Delta < 0$, the type of i is switched to the type of j with probability $-\Delta$; if $\Delta > 0$, the type of j is switched to the type of i with probability Δ. We choose the proportionality constant so that the effective 'probabilities' are less than one. The time scale is measured in *contests*, but is somewhat arbitrary, both because of the proportionality constant that determines the switching, and the fact that in a real situation, many contests can take place simultaneously.
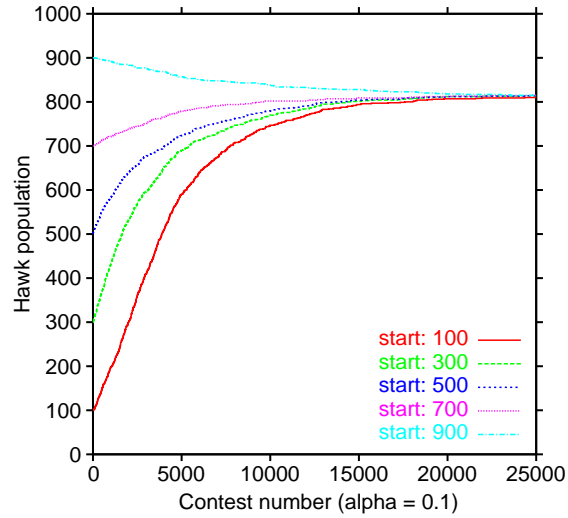
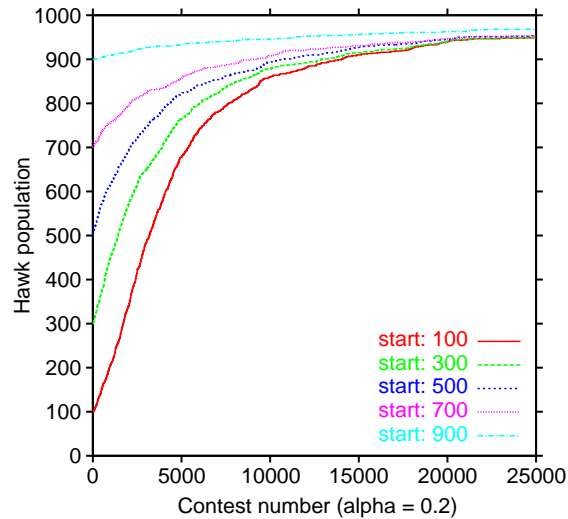Figure 2. Discrete simulation, $\alpha = 0.1$, for different starting populations of Hawks.

Figure 3. Discrete simulation, $\alpha = 0.2$, for different starting populations of Hawks.

The simulations show results for the cases $\alpha = 0.0$, 0.1, 0.2 and 0.4, and various initial Hawk populations. The game is defined by $V = 0.4$ and $C = 0.6$, and the population is fixed at 1000. We observe convergence to Hawk populations of 667, 815, 1000 and 1000, respectively, as predicted. The higher the value of the spite parameter α, the more aggressive—spiteful—the predicted behavior.
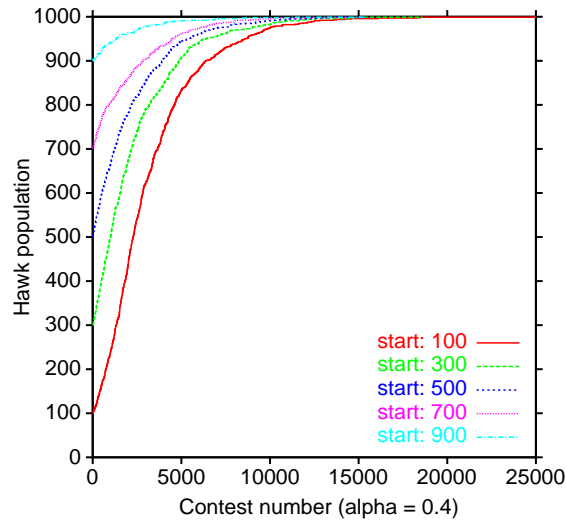
Figure 4. Discrete simulation, $\alpha = 0.4$, for different starting populations of Hawks.

As can be observed from the figures, convergence to the final value is slowest when $\alpha = 0.2$, and faster when it is either smaller or larger than 0.2. This can be explained by the appearance of a double root on the right-hand side of the replicator equation for the fraction of Doves in the population. Explicitly, this differential equation is, from equation (3),

$$\dot{x}_2 = (1 - \alpha)\frac{C}{2}x_1 x_2 \left(x_1 - \frac{V}{C}\frac{1 + \alpha}{1 - \alpha}\right), \tag{10}$$

where x_1 and x_2 are the fractional populations of Hawks and Doves, respectively. When $\alpha > 0.2$, the right-hand side has a single root at $x_2 = 0$, and near convergence to the point $x_2 = 0$ (extinction of Doves), the differential equation for x_2 becomes $\dot{x}_2 \approx cx_2$, where c is a constant. This implies that at convergence, $x_2 = O(e^{-ct})$. However, when $\alpha = 0.2$, the differential equation becomes $\dot{x}_2 \approx cx_2^2$ near convergence to extinction of Doves, and $x_2 = O(1/t)$. When $\alpha < 0.2$, the right-hand side has a single root at $x_1 = (V/C) \cdot [(1+\alpha)/(1-\alpha)] < 1$, and convergence is once again exponential. This explains the much slower convergence observed at (and near) the case $\alpha = 0.2$.

In a biological context, it seems likely that the effect of the spiteful measure (where fitness is based on the pairwise contest) will be mediated by the standard measure (where fitness is based on the entire population). Thus, in real situations, α is likely to be small. In this case, the equilibrium fraction of Hawk play is $(V/C) \cdot [(1 + \alpha)/(1 - \alpha)] \approx (V/C)(1 + 2\alpha)$, showing that the marginal effect of spiteful behavior on equilibrium behavior is linear in α for small α.

4. EXAMPLE CONTINUED: INVASION OF SPITEFUL MUTANTS

The crux of the matter is whether we have satisfied the definition of spite. Continuing with the Hawk–Dove example, consider the Hawk–Dove game with $V = 1$ and $C = 2$, in the pure spite case, $\alpha = 1$. The actual game matrix is

$$
\begin{array}{c|cc}
 & H & D \\
\hline
H & -1/2 & 1 \\
D & 0 & 1/2.
\end{array}
\tag{11}
$$

Using the standard replicator dynamic, behavior is predicted to converge to an evolutionarily stable 50/50 mixture of Hawks and Doves. To see this directly, consider a large population with a fraction ρ of Hawks (H's) and $(1 - \rho)$ of Doves (D's). The average payoff to an H is $\rho(-1/2) + (1 - \rho)(1)$, and to a D, $\rho(0) + (1 - \rho)(1/2)$. Thus, the standard model predicts that a deviation from D to H is profitable if and only if the payoff in the first case is greater than in the second, or when $\rho < 1/2$. Any invasion of H's will be halted exactly when the 50/50 equilibrium is attained, and beyond that point, invasion of an H is an unprofitable deviation.

Consider, in contrast, the predictions of the spiteful replicator dynamic. When an H plays an H, nothing happens, but when an H plays a D, it can replace it, because $a_{ij} - a_{ji} = 1$. Thus, the H's will eventually drive out all the D's.

Notice that beyond the 50% point the invading mutant H's harm themselves using average payoff as the criterion in the given population state (we saw above that beyond that point their invasion is an unprofitable deviation), but their total invasion is made possible because they harm incumbent D's more than themselves in individual contests. H types do *not* have the highest absolute fitness, yet they come to dominate the population.

5. DISCUSSION

It may seem paradoxical that a rare, spiteful mutant can invade a very large population of individuals that are fitter in an absolute sense. After all, a mutant can cause harm to only an infinitesimal fraction of the population. The point is that the mutant can be successful if pairwise conflicts are sufficiently important in determining reproductive success. Our spiteful replicator dynamic captures this by including competition between individuals on the basis of one-on-one fitness. The extent of this effect defines our spectrum from standard to spiteful replicator equations.

We should also point out that Maynard Smith's (1982) 'playing the field', is not at all what we are discussing. He is dealing with the situation when the payoffs are possibly nonlinear functions of the population state. More recent work certainly

uses pairwise models (in fact our starting point), but always (to our knowledge) winds up using expected payoff against the population state in the replicator equations, with the result that the actual equilibria are unchanged from the original evolutionarily stable equilibria. Thus, it is the fact that, in our model, replacement is determined by the payoffs from the pairwise interactions, independent of the population state, that results in the key differences in the predictions of our model relative to the extant literature.

The general form of our spiteful replicator dynamic is not at all new or complicated; it falls under the rubric of 'imitation dynamics' [see, for example, Hofbauer and Sigmund (1998)], and is used to model learning by example. The crucial difference is our retention, in the relative fitness terms, of the dependence on the identity of the opponent.

To summarize, we have shown that spite, precisely in the sense proposed by Hamilton, can evolve under our model of specific pairwise conflict. We hope that this will at the least suggest where spite is most likely to be found in animals, if it exists, and provide an improved basis for understanding spiteful human behavior in game settings.

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