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VISCOUS POPULATION EQUILIBRIA

by

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Abstract. Viscosity in a biological population is the tendency of individuals to have a higher rate of interactions with their closer relatives than with similar numbers of more distantly related individuals. This paper presents a simple method of equilibrium analysis to predict the effect of viscosity in biological games. Taking the limit as viscosity goes to zero, a set of fluid population equilibria is defined. The set of fluid population equilibria is nonempty and includes all evolutionary stable strategies.

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## VISCOUS POPULATION EQUILIBRIA

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Biological games differ from economic games in that the choice of strategy is at the genetic level, rather than at the level of individual cognitive choice. That is, a strategy in a biological game is "chosen" through mutation by a kin group or genotype. This distinction is important because members of one kin group can meet and play games against each other.

Even when a genotype is an infinitesimal fraction of the overall species population, individual members of the genotype may meet each other with a positive frequency, because kin groups do not disperse uniformly over the entire range of the species. Parents incur mobility costs, and cannot distribute their offspring at equal density throughout the population. Thus, having a recent common ancestor increases the probability that two individuals have been born near to each other geographically, which in turn increases the probability of their interaction. This tendency of individuals in a biological population to have a higher rate of interactions with their closer relatives (than with similar numbers of more distantly related individuals) has been called viscosity by Hamilton [1964].

This paper presents a simple method of equilibrium analysis to predict the effect of viscosity in biological games. Then, taking the limit as viscosity goes to zero, we define a set of fluid population equilibria which is always nonempty and includes all evolutionary stable strategies.

Suppose that, when two individuals in some given species meet, they play a symmetric game, in which each individual must use a strategy in some nonempty finite set  $C$ . Each individual gets a payoff that depends on its own strategy

$c_1$  and its opponent's strategy  $c_2$  according to some function  $u(c_1, c_2)$ . An individual's payoff represents some contribution to its reproductive fitness, such that each individual's expected number of offspring is maximized by using a strategy that maximizes its expected payoff in this game.

We define a kin group to be a group of individuals who have the same genotype, and therefore use the same strategy in this game, because they share a recent common ancestor. (To simplify the analysis, we assume haploid genetic transmission of characteristics.) We assume that individuals in a kin group cannot discriminate other members of the kin group from the rest of the population before they implement their strategies in this game.

Let us represent the relative frequency of interactions within kin groups by some viscosity parameter  $\delta$ , such that  $0 < \delta < 1$ . That is, we suppose that, whenever an individual plays this game, the probability is  $\delta$  that its opponent is drawn from the same kin group, and otherwise its opponent is drawn at random from the overall population.

Let  $\Delta(C)$  denote the set of all mixed strategies or probability distributions over the set of (pure) strategies  $C$ . That is,  $\sigma \in \Delta(C)$  iff  $\sigma$  is a function from  $C$  into the real numbers  $\mathbb{R}$  such that

$$\sum_{e \in C} \sigma(e) = 1 \quad \text{and} \quad \sigma(c) \geq 0, \quad \forall c \in C.$$

At any point in time, each individual in the species is genetically programmed to implement some strategy in  $C$  whenever it plays the game. The species population can be represented by a distribution  $\sigma$  in  $\Delta(C)$  such that, for each strategy  $c$  in  $C$ ,  $\sigma(c)$  is the fraction of the population that is genetically programmed to use strategy  $c$ .

We may say that  $\sigma$  is a  $\delta$ -viscous population equilibrium iff  $\sigma \in \Delta(C)$  and, for each strategy  $c$  in  $C$ ,

if  $\sigma(c) > 0$  then  $c \in \operatorname{argmax}_{e \in C} (\delta u(e,e) + (1 - \delta) \sum_{d \in C} \sigma(d) u(e,d))$ .

That is, in a  $\delta$ -viscous population equilibrium, the only pure strategies that are used by a positive fraction of the population are those that would be optimal for a kin group if, whenever an individual in the kin group plays this game, the probability is  $\delta$  that its opponent is drawn from the same kin group, and otherwise its opponent is drawn at random from the overall population.

This definition of a  $\delta$ -viscous population equilibrium assumes that there is a global competitive standard which all successful genotypes must meet. That is, although we allow that the reproductive fitness of an individual may depend on local variations in the population, we assume that the threshold level of average fitness that a kin group needs to reproduce itself is the same throughout the species population. This assumption seems quite reasonable when viscosity is low, because low viscosity implies that kin groups are dispersing and competitively mixing with the general population. When viscosity is high, this assumption may also be justified by supposing that the game that we are studying is played by individuals during a growth phase that precedes a more mobile reproductive phase or sporulation in the life cycle. (See also Wilson [1983, 1987].) For example, interactions between caterpillars might include a high proportion of interactions between siblings, but the fitness that an individual achieves as a caterpillar is then used to support its reproductive activities as a moth in a broader competitive universe. See Pollock [1983, 1989] for models of viscous populations in which different local competitive standards may be applied in regions that are dominated by different genotypes.

Under the assumption that the strategy set  $C$  is finite, the existence of at least one  $\delta$ -viscous population equilibrium (for any  $\delta$  between 0 and 1)

can be proven by a standard fixed-point argument, as in the proof of the Nash [1951] equilibrium existence theorem. A  $\delta$ -viscous population equilibrium corresponds to a symmetric Nash equilibrium of the perturbed game in which a player gets payoff

$$\delta u(c,c) + (1 - \delta)u(c,d)$$

when the player uses strategy  $c$  against an opponent using strategy  $d$ . This perturbed game may be called the  $\delta$ -viscous perturbation of the original game.

To describe species in which kin groups diffuse rapidly and so viscosity is very small, we examine the limit of  $\delta$ -viscous population equilibria as  $\delta$  goes to zero. We say that  $\sigma$  is a fluid population equilibrium iff there exist sequences  $(\delta^k)_{k=1}^{\infty}$  and  $(\sigma^k)_{k=1}^{\infty}$  such that  $0 < \delta^k < 1$  and  $\sigma^k$  is a  $\delta^k$ -viscous population equilibrium, for every  $k$ ,  $\lim_{k \rightarrow \infty} \sigma^k(c) = \sigma(c)$ , for every  $c$  in  $C$ , and  $\lim_{k \rightarrow \infty} \delta^k = 0$ . By compactness of  $\Delta(C)$ , at least one fluid population equilibrium must exist.

If  $\sigma$  is a fluid population equilibrium then  $(\sigma, \sigma)$  is a Nash equilibrium. To prove this fact, suppose that  $\sigma(c) > 0$  and  $e$  is any other strategy in  $C$ . Then, for all sufficiently large  $k$ ,  $\sigma^k(c) > 0$  and so

$$\begin{aligned} & \delta^k u(c,c) + (1 - \delta^k) \sum_{d \in C} \sigma^k(d) u(c,d) \\ & \geq \delta^k u(e,e) + (1 - \delta^k) \sum_{d \in C} \sigma^k(d) u(e,d). \end{aligned}$$

As  $k \rightarrow \infty$ , this inequality converges to

$$\sum_{d \in C} \sigma(d) u(c,d) \geq \sum_{d \in C} \sigma(d) u(e,d).$$

For some games, however, there exist Nash equilibria that do not correspond to fluid population equilibria. For example, consider the game in which  $C = \{\alpha, \beta, \gamma\}$  and each player's payoff depends on its own strategy and its opponent's strategy as follows:

|               |          | Opponent's strategy: |         |          |
|---------------|----------|----------------------|---------|----------|
|               |          | $\alpha$             | $\beta$ | $\gamma$ |
| Own strategy: | $\alpha$ | 1                    | 0       | 3        |
|               | $\beta$  | 1                    | 2       | 0        |
|               | $\gamma$ | 0                    | 2       | 3        |

(This and the following example are taken from Swinkels [1990].) This game has four symmetric Nash equilibria: an equilibrium where each player chooses  $\alpha$  and gets payoff 1; an equilibrium where each player chooses  $\beta$  and gets payoff 2; an equilibrium where each player chooses  $\gamma$  and gets payoff 3; and an equilibrium where each player uses the fully mixed strategy  $(6/11)[\alpha] + (3/11)[\beta] + (2/11)[\gamma]$  and gets expected payoff  $12/11$ . (We use here the notation  $\sigma = \sum_{e \in C} \sigma(e)[e]$ .)

On the other hand, it can be shown that this game has no evolutionary stable strategies. A mixed strategy  $\sigma$  is an evolutionary stable strategy (or ESS) iff  $(\sigma, \sigma)$  is a symmetric Nash equilibrium of the game and, for any mixed strategy  $\tau$  such that  $\tau \neq \sigma$  and  $\tau$  is a best response to  $\sigma$ , playing  $\sigma$  would be better than playing  $\tau$  against an opponent who plays  $\tau$ . (See, for example, Maynard Smith [1982].) For this game, the equilibrium at  $\alpha$  would be overturned by the  $\beta$  strategy, because  $\beta$  is as good as  $\alpha$  against  $\alpha$  but  $\beta$  is better than  $\alpha$  against  $\beta$ . Similarly, the equilibrium at  $\beta$  would be overturned by the  $\gamma$  strategy, the equilibrium at  $\gamma$  would be overturned by the  $\alpha$  strategy, and the fully mixed equilibrium would be overturned by any pure strategy.

When  $\delta > .3$ , the unique  $\delta$ -viscous population equilibrium is  $\gamma$ , which yields the Pareto efficient outcome in which each player gets payoff 3.

When  $\delta < .3$ , there are three  $\delta$ -viscous population equilibria:

$\gamma$ ,  $(2\delta/(1-\delta))[\alpha] + ((1-3\delta)/(1-\delta))[\gamma]$ , and

$((6+2\delta)/(11-11\delta))[\alpha] + ((3-10\delta)/(11-11\delta))[\beta] + ((2-3\delta)/(11-11\delta))[\gamma]$ .

The first two of these  $\delta$ -viscous population equilibria converge to  $\gamma$  as  $\delta$  goes to zero. The third  $\delta$ -viscous population equilibrium converges to  $(6/11)[\alpha] + (3/11)[\beta] + (2/11)[\gamma]$  as  $\delta$  goes to zero. Thus, there are two fluid population equilibria:

$\gamma$  and  $(6/11)[\alpha] + (3/11)[\beta] + (2/11)[\gamma]$ .

The Nash equilibria  $(\alpha, \alpha)$  and  $(\beta, \beta)$  do not correspond to fluid population equilibria.

For this example, each of the pure strategy equilibria (as a singleton set) is also unstable in the sense of Kohlberg and Mertens [1986]. In particular,  $(\gamma, \gamma)$  would not be an equilibrium if we changed the payoff  $u(\alpha, \gamma)$  to be any number greater than 3. Nevertheless, the Pareto-efficient strategy  $\gamma$  is a fluid population equilibrium.

For any game, if a pure-strategy equilibrium is Pareto efficient then it must be a fluid population equilibrium. More generally, if  $(e, e)$  is an equilibrium in pure strategies and  $u(e, e) \geq u(d, d)$  for every pure strategy  $d$  such that  $d \in \operatorname{argmax}_{c \in C} u(c, e)$ , then  $e$  must be a fluid population equilibrium. That is, if the pure strategy  $e$  is a best response to itself, and the symmetric payoff for  $e$  is not less than the symmetric payoff for any other best response to  $e$ , then  $e$  is a fluid population equilibrium. To prove this proposition, notice that these conditions imply that  $e$  is also a best response to itself in the  $\delta$ -viscous perturbation game, for any  $\delta$  between 0 and 1.

The set of evolutionary stable strategies is always a subset of the set of fluid population equilibria. To prove this inclusion, suppose that  $\sigma$  is



any evolutionary stable strategy. Consider the truncated game that is derived from the original game by eliminating all pure strategies that are not best responses to  $\sigma$ . The conditions for an ESS imply that  $(\sigma, \sigma)$  is the unique symmetric Nash equilibrium in this truncated game. Now, consider sequences  $(\sigma^k)_{k=1}^\infty$  and  $(\delta^k)_{k=1}^\infty$  such that  $\lim_{k \rightarrow \infty} \delta^k = 0$  and, for each  $k$ ,  $(\sigma^k, \sigma^k)$  is a symmetric Nash equilibrium of the  $\delta^k$ -viscous perturbation of this truncated game. (Any symmetric game has a symmetric Nash equilibrium.) The sequence of mixed strategies  $(\sigma^k)_{k=1}^\infty$  must converge to  $\sigma$  as  $k \rightarrow \infty$ , because the Nash correspondence is upper-hemicontinuous in the payoffs of the game. For all sufficiently large  $k$ , the set of best responses to  $\sigma^k$  in the  $\delta$ -viscous perturbation of the original game cannot include any of the strategies that were excluded in the truncated game, because the best-response correspondence is upper-hemicontinuous in both payoffs and mixed strategies. Thus, for all sufficiently large  $k$ ,  $(\sigma^k, \sigma^k)$  is a Nash equilibrium of the  $\delta$ -viscous perturbation of the original game. So  $\sigma$  is a fluid population equilibrium.

Analysis of the viscous population equilibria that converge to a fluid population equilibrium can generate predictions about behavior in subgames that have zero probability in the fluid population equilibrium. Such analysis is methodologically similar to the use of trembling-hand perturbations in the theory of perfect and sequential equilibria (see Selten [1975] and Kreps and Wilson [1982]), but it generates substantively different predictions about subgame behavior. To illustrate such analysis, consider a second example, in which each player's payoff depends on its strategy and its opponent's strategy as follows:

|               |          | Opponent's strategy: |         |          |
|---------------|----------|----------------------|---------|----------|
|               |          | $\alpha$             | $\beta$ | $\gamma$ |
| Own strategy: | $\alpha$ | 3                    | 3       | 3        |
|               | $\beta$  | 3                    | 5       | 0        |
|               | $\gamma$ | 3                    | 6       | 1        |

This game is the normal representation of an extensive-form game in which the players first decide whether to play the Prisoners' Dilemma game. The  $\alpha$  strategy represents refusing to play the Prisoners' Dilemma, and the players will avoid the Prisoners' Dilemma subgame if either player chooses  $\alpha$ . When neither player uses strategy  $\alpha$ , the strategy  $\beta$  specifies the generous move in the Prisoners' Dilemma subgame, and the strategy  $\gamma$  specifies the selfish move in the Prisoners' Dilemma subgame. Each player would prefer to avoid the Prisoners' Dilemma if its opponent would use the selfish move, but would prefer to play the Prisoners' Dilemma subgame if its opponent would use the generous move. Playing the Prisoners' Dilemma subgame has probability zero in all Nash equilibria of this game, and the only symmetric Nash equilibrium is  $(\alpha, \alpha)$ .

However,  $\alpha$  is not an evolutionary stable strategy, because it is overturned by  $\beta$ . That is, if everyone would use strategy  $\alpha$ , then a mutant kin group could do better by choosing  $\beta$ , so that two members of the group would increase their payoff to 5 whenever they meet each other. Of course,  $\beta$  is not an evolutionary stable strategy either, because a mutant kin group could gain by playing  $\gamma$  when everyone else plays  $\beta$  (if viscosity is low).

When  $\delta > 1/5$  for this example, the unique  $\delta$ -viscous population equilibrium is  $\beta$ , so that everyone gets payoff 5. When  $\delta < 1/5$ , the unique  $\delta$ -viscous population equilibrium is

$$((1-5\delta)/(1-\delta))[\alpha] + (2\delta/(1-\delta))[\beta] + (2\delta/(1-\delta))[\gamma],$$

which converges to the fluid population equilibrium  $\alpha$ , as  $\delta$  goes to zero. These  $\delta$ -viscous population equilibria convey information about behavior in the Prisoners' Dilemma subgame that we would miss, however, if we only looked at the limiting fluid population equilibrium. In the  $\delta$ -viscous population equilibria, for any  $\delta$  less than  $1/5$ , the number of generous-players ( $\beta$ ) is equal to the number of selfish-players ( $\gamma$ ) in the population. Thus, conditionally on a randomly-sampled individual agreeing to play the Prisoners' Dilemma subgame, the probability of this individual being generous is  $1/2$ . Because of viscosity, however, the players' moves in the Prisoners' Dilemma subgame are not stochastically independent. When a  $\beta$ -programmed individual plays the Prisoners' Dilemma subgame, the probability of its opponent using the generous move is

$$(\delta + (1-\delta)2\delta/(1-\delta))/(\delta + (1-\delta)2\delta/(1-\delta) + (1-\delta)2\delta/(1-\delta)) = 3/5.$$

On the other hand, when a  $\gamma$ -programmed individual plays the Prisoners' Dilemma subgame, the probability of its opponent using the generous move is

$$((1-\delta)2\delta/(1-\delta))/(\delta + (1-\delta)2\delta/(1-\delta) + (1-\delta)2\delta/(1-\delta)) = 2/5.$$

So a  $\beta$ -programmed or  $\gamma$ -programmed individual gets an expected payoff of 3 when it plays the Prisoners' Dilemma subgame, because  $5 \times 3/5 + 0 \times 2/5 = 3 = 6 \times 2/5 + 1 \times 3/5$ . Thus,  $\beta$ -programmed individuals and  $\gamma$ -programmed individuals get the same expected payoff as  $\alpha$ -programmed individuals, who always get a payoff of 3.

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