

Relatedness and the evolution of cooperative
institutions

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Hamilton's rule has played a central role in the modern understanding of the evolution of social behavior. The core idea is that the evolution of altruistic behavior depends on assortment. If individuals interact at random, Hamilton argued in his seminal 1964 paper, the effect of such behavior on social partners does not change the relative fitness of genes in the population, while the fitness costs always fall on individuals carrying genes that cause the behavior, and thus these genes cannot spread. However, if individuals interact assortatively, then individuals carrying such genes are more likely to benefit from the altruistic behaviors of others, and if such benefits exceed the cost, altruistic behavior can spread. Hamilton further argued that the probability that two individuals carried the same gene by common descent was the right measure of assortment, so that an altruistic gene could spread if $rb - c > 0$ where $-c$ is the incremental fitness effect on the actor, b the incremental fitness effect on the recipient, and r is the probability that the two individuals share the same allele by common descent.

These ideas have generated controversy ever since. During the late 1970's and early 1980's, Hamilton was criticized by a number of population geneticists (e.g. Uyenoyama and Feldman 1980) and it soon became evident that Hamilton's rule precisely predicts evolutionary outcomes only when there is no inbreeding, selection is weak, and the effects of genes on fitness are additive (e.g. Grafen 1985). After a period of quiescence, the last decade has seen renewed controversy about Hamilton's rule (Nowak et al 2010, Abbot et al 2011, van Veelen et al 2017). In their excellent review, Birch and Okasha (2016) conclude that there are three distinct versions of Hamilton's rule. The original version is only accurate in a narrow range of circumstances, an approximate version in which weak selection allows nonadditive fitness effects to be dealt with using Hamilton's rule as an approximation that is frequently useful for predicting phenotypic evolution (e.g. Frank 1998), and a general version in which the incremental fitness effects in Hamilton's rule are replaced by partial regression coefficients that predict how an actor's genotype and the genotype of its social partners affect fitness on average across the population (Queller 1992, Gardner West Wild 2011) and that according to some proponents yields a universal law that predicts evolutionary outcomes even when selection is strong and fitness effects are not additive.

Here we will illustrate these issues in the context of a problem that is important in human evolution, the evolution of cooperative institutions. When groups of individuals interact repeatedly, systems of contingent reward and punishment can stabilize a vast range of social arrangements—cooperative production of public goods, systems of property rights, obligations toward kin—often referred to as institutions (Young 2015). We will show that in this context knowing r may not be sufficient to predict evolutionary outcomes even as an approximation when selection is weak and suggest a computationally practical alternative for such problems (Schonmann & Boyd 2016; also see Schonmann, Vicente & Caticha, Schonmann, Boyd & Vicente 2014, Boyd, Schonmann & Vicente 2014). We will also explain why this result is consistent with Gardner, West, and Wild's (2011) claim that the general form of Hamilton's rule is always correct, but we

will also suggest that the general rule is misleading in this case.

Humans live in groups in which social interactions are repeated many times. Individuals share food, engage in coalitions, construct shared facilities, and defend their group from members of other groups. Repeated interaction allows behavioral strategies in which an individual's behavior is contingent on the previous behavior of other individuals. Of particular interest are contingent strategies that support cooperation. Individuals can reward those who have cooperated in the past, or punish those who don't participate in group defense. If the long run benefits of sustained cooperation exceed the short term benefits of defection, then contingent strategies supporting cooperation can be evolutionarily stable. Such equilibria can explain the persistence of cooperation among unrelated individuals. When they are common, contingent strategies may not be altruistic because rare defectors have lower fitness (Gardner, West & Wild 2007). Contingent cooperation in sizable groups is particularly important in the study of human evolution (e.g Trivers 1971, Hagen & Hammerstein 2006).

In many settings the ancestral condition is noncooperative. This means that to explain the evolution of cooperation it is necessary to explain how contingent strategies supporting cooperation can increase when rare. In this setting, contingent cooperative strategies *are* typically altruistic. When groups are formed at random, rare cooperators find themselves alone in their group in which other group members are unconditional defectors. The contingent cooperator pays the cost associated with initial cooperation but does not gain any long run benefit, and as a result when cooperators are rare, they are selected against. In a similar way, strategies that punish contingent on others punishing, must punish or make a costly signal of intent to punish in order to determine how many punishers there are in the group (Boyd, Gintis & Bowles 2010).

Contingent strategies supporting cooperation or punishment are often threshold functions. For example, in the iterated public goods game, a plausible strategy is to cooperate during the first period, and then cooperate if θ of the $n - 1$ other individuals in the group cooperated on the previous interaction, otherwise defect (e.g. Joshi 1987, Boyd & Richerson 1988). Plausible punishing strategies also incorporate thresholds (Boyd and Richerson 1992, Boyd, Gintis & Bowles 2010). Such threshold strategies create sharp non-linearities in fitness as a function of the number of cooperators in a group, and as a result, knowing relatedness does not allow the calculation of expected fitness unless population structure is also taken into account.

To see why, consider a simple threshold fitness function. Suppose that individuals interact in groups of size n , and that there are two haploid genotypes, A and N . A focal A type individual in a group in which k of the other $n - 1$ individuals in the group are A types has fitness

$$w_k^A = \begin{cases} w_0 - c & \text{if } k < \theta \\ w_0 + b - c & \text{if } k \geq \theta \end{cases}$$

and an N type has fitness

$$w_k^N = \begin{cases} w_0 & \text{if } k + 1 < \theta \\ w_0 + b & \text{if } k + 1 \geq \theta \end{cases}$$

Thus, A types pay a cost c toward a collective enterprise. If there are $\theta + 1$ A types in the group, the collective enterprise succeeds and produces a benefit b to each individual. If not, it fails and produces no collective benefits.

We want to determine the conditions under which rare A types can invade a population in which N is common. We assume that groups are formed assortatively so that like-types are more likely to be found together in groups than chance alone would dictate and that local density dependent competition is weak enough that its effects on relative fitness can be ignored. Then the expected fitness of the common N types is approximately w_0 because they will rarely be in groups with even a single A type. The expected fitness of rare A types is:

$$w_A = w_0 - c + b\Pr(k \geq \theta|A) \quad (1)$$

where $\Pr(k \geq \theta|A)$ is the conditional probability that there are θ or more A types among other members of the group containing the focal A type. If groups are formed at random, this probability is zero, and cooperators cannot invade. However, if groups are formed assortatively, A types will invade if $c < b\Pr(k \geq \theta|A)$. As you would expect assortment allows the costly, group beneficial behavior to increase. Schonmann & Boyd (2016) show how to extend this result to account for local and global population regulation.

Knowing only the relatedness in groups does not allow you to calculate the probability that there are θ or more cooperators among the other members of the group. Nowadays, relatedness is defined as the regression of genotypic value of an individual's social partners on the individual's genotypic value. Put another way, given the genotypic value of a focal individual, relatedness gives the expected genotypic value of its social partners. This means that given that an individual is a cooperator, relatedness predicts the expected number of cooperators among the other members of the group. However, knowing the expected number of cooperators does not allow you to predict the probability that there are θ or more cooperators among other group members because very different probability distributions can have the same mean. This is not just a mathematical possibility. Variation in group size, mating system, and population structure can yield groups with the same average relatedness, but different probability distributions over numbers of cooperators.

Thresholds are not a necessary part of this phenomenon; it will occur anytime fitness is a non-linear function of group composition. The pure threshold function analyzed above maximizes the effect. This function may be an approximation to the fitness effects of several different kinds of social interactions. For example, conflict between groups is often modeled using sigmoidal functions (e.g. Choi and Bowles 2007). If one group has fewer fighters than its opponent it is likely to lose a conflict; if it has more, it is likely to win the conflict. Some productive processes may yield sigmoidal one period payoff functions. For example, it may take θ workers to raise a roof, but adding more than θ doesn't help much. When such interactions are repeated, contingent strategies that cooperate as long as θ or more individuals cooperated during the last interaction will lead to a sharp threshold-like fitness functions. Other kinds of interactions

lead to fitness functions that are intermediate between the pure threshold model and the more typical linear public goods game. For example, the iterated linear public goods game leads to a kinked, nonlinear function (Boyd Schonmann & Vicente 2014). When interactions are repeated many times, the kink is very sharp, and therefore relatedness will not be enough. Instead it is necessary to sum the expected payoffs conditioned on whether there are fewer or more than the threshold number of cooperators.. It is also the case that these fitness functions are not well approximated by a linear fitness function even when selection is weak (Schonmann Boyd & Vicente 2014).

How can this result be squared with Gardner, West and Wild's (2011) claim that the general form of Hamilton's rule is universally true? The answer is that in their regression formulation Hamilton's rule takes the form

$$r\beta_{v,g'|g} + \beta_{v,g|g'} > 0 \quad (2)$$

where $\beta_{v,g|g'}$ and $\beta_{v,g'|g}$ are the slopes in a multiple regression of fitness against the individuals own genotypic value and the genotypic value of its social partners, respectively, taken over the whole population. Relatedness appears to measure assortment as it did in Hamilton's original formulation, but this appearance is deceiving. The form of Hamilton's rule is preserved because (as is shown in the appendix) these regression coefficients are complex expressions that depend on marginal fitness effects *and* information about the distribution of types across groups. For example the effect on social partners is given by

$$\beta_{v,g'|g} = \frac{b \Pr(k \geq \theta) \left(\mathbb{E} \left(\frac{k}{n-1} | k \geq \theta \right) - q \right) - (-c + b \Pr(k \geq \theta)) r}{\left(\frac{1}{n-1} + \left(\frac{n-2}{n-1} \right) r \right) - r^2}$$

where q is the frequency of A types in the population and $\mathbb{E} \left(\frac{k}{n-1} | k \geq \theta \right)$ is the expected fraction of A types given that there are at least θ . The expression for $\beta_{v,g|g'}$ is similar. If these expressions are substituted into (2) they yield the condition given in (1). However, neither regression coefficient can be calculated without knowledge of the complete probability distribution of the number of A types among social partners because they depend on information about patterns of assortment as well as the fitness effects of behavior. Gardner, West and Wild (2011) are well aware of this fact, but argue that the regression approach is the correct formulation because it provides a single unifying law that describes how natural selection shapes behavior. We doubt the usefulness of general universal laws in the study of complex phenomena, and think that, in this case at least, the regression approach conceals more than it reveals. Since the two approaches are mathematically equivalent, the decision about which to use is a matter of taste, but whatever approach is taken, a knowledge of r is not enough to predict the direction of evolution because r is not sufficient to predict the distribution of cooperators across groups.

This is not a happy fact. When two individuals interact repeatedly, relatedness is enough to determine whether contingently cooperative strategies can

invade noncooperative populations, and thus theory can be combined with empirical generalizations about background levels of relatedness to generate useful predictions about whether reciprocating strategies are likely to increase when rare. For example, Axelrod and Hamilton (1981) argued that plausible levels of background relatedness and lengths of interaction made it likely that tit-for-tat and similar strategies in the iterated two person prisoner's dilemma could increase when rare. When individuals interact in larger groups this is not so easy. One of us (R.B.) attempted to circumvent this problem by assuming that rare contingent cooperating strategies were sampled independently into groups with a constant probability r leading to a binomial distribution of the number of cooperators among the other $n - 1$ individuals in a group with a focal cooperator (Boyd and Richerson 1988, Boyd, Gintis & Bowles 2010). However, this approach is inadequate because the processes that generate background relatedness lead to strong statistical interdependencies, and as a result using the binomial underestimates (sometimes badly) the likelihood that cooperative strategies will increase when rare (Schonmann & Boyd 2016). The best approach would be to model the actual processes by which groups are formed, but this may be difficult for both empirical and technical reasons. It would be nice to have a back-of-the-envelope method that would allow a quick estimate of how likely it is that contingent cooperation and punishment could increase.

We suggest the following: Analyses of the evolution of cooperation have often assumed that low levels of relatedness due to viscous population effects allow the invasion of rare reciprocating strategies (e.g Hamilton 1975). Thus, we need an expression for the distribution of types across groups in a viscous population. Schonmann and Boyd (2016) derived such an expression in an island model that allows for arbitrary levels of selection migration and local and global population regulation. While this expression is a bit unwieldy, we have also shown that when groups are large, migration rates are low, and selection is weak, the fraction of groups in which a fraction $k/(n - 1)$ of the other group members are cooperators has a beta distribution with parameters $\alpha = 1$ and $\beta = 2nm \approx \frac{1-r}{r}$. Moreover, as can be seen in figure 1, this beta distribution is an adequate approximation to the exact distribution of cooperators for groups as small as ten and fairly high migration rates. A more formal test of the adequacy of the beta approximation is given in Schonmann and Boyd (2016). Thus, given an estimate of r , the expectation of a nonlinear fitness function can be easily computed using the appropriate beta distribution.

In the spring of 1982, the first author happened to be sitting next to W. D. Hamilton at a conference held at Northwestern University. This was a time when Hamilton's work was being subjected to heavy criticism by a number of population geneticists. The speaker, Robert Abugov, sketched a population genetic model which described the circumstances under which selection maximized inclusive fitness. When Abugov was done, Hamilton leaned over and said that if his rule was only true when selection was weak and fitness effects were additive, he was quite happy. In the next few years, Alan Grafen, David Queller and others showed that Hamilton's rule applies more widely than this, so perhaps Hamilton was unnecessarily modest. However, it is worth keeping

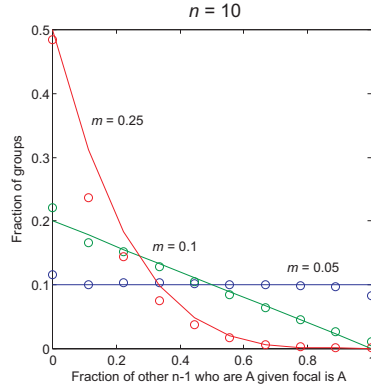


Figure 1:

The beta approximation is useful even when groups are small and migration rates are high. The figure compares the exact probability distribution (solid lines) of the number of cooperators among other group members in an island model to the beta probability density approximation (open circles). The exact distribution assumes that there is no selection, groups have 10 individuals and migration is equal to 0.25, 0.1 and 0.05. The beta distribution has parameters $\alpha = 1$ and $\beta = 2nm$ which means that expected fraction of cooperators among the other other individuals in a group of a focal cooperator is r . Values of the beta density were converted to discrete probabilities by multiplying by $\frac{1}{n-1}$. Taking differences between exact values of the cumulative beta distribution yields qualitatively similar results.

mind that all mathematical models of evolutionary processes are necessarily much simpler than the phenomena that they represent, and, in this light, perhaps Hamilton's pragmatic modesty should serve as a model for contemporary evolutionary theorists.

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Appendix: Computing regression coefficients

The goal is to calculate the regression terms in display (5) in Gardner et al (2011) (= GWW). We have found that the pure threshold strategy can increase when rare if

$$b \Pr(k \geq \theta) - c > 0$$

According to GWW the general rule is

$$\beta_{v,g|g'} + r\beta_{v,g'|g} > 0$$

where the betas are the slopes in of a multiple regression of fitness against an individual’s own genetic value [$g=0,1$] and the genetic value of its social partners, the fraction of A types among other members of its group $g' = \frac{k}{n-1}$. Here we

show two conditions relate. We start with the definition from GWW

$$\begin{aligned}\beta_{v,g|g'} &= \frac{\frac{\text{cov}(v,g)}{\text{var}(g)} - \frac{\text{cov}(v,g')}{\text{var}(g')} \frac{\text{cov}(g',g)}{\text{var}(g)}}{1 - \frac{(\text{cov}(g',g))^2}{\text{var}(g')\text{var}(g)}} \\ &= \frac{\text{cov}(v,g) \text{var}(g') - \text{cov}(v,g')\text{cov}(g',g)}{\text{var}(g') \text{var}(g) - \text{cov}(g',g)^2}\end{aligned}$$

where for an A type

$$v_{A,k} = \begin{cases} -c & \text{if } k < \theta \\ -c + b & \text{if } k \geq \theta \end{cases}$$

and for an N type

$$v_{N,k} = \begin{cases} 0 & \text{if } k < \theta + 1 \\ b & \text{if } k \geq \theta + 1 \end{cases}$$

Similarly

$$\begin{aligned}\beta_{v,g'|g} &= \frac{\frac{\text{cov}(v,g')}{\text{var}(g')} - \frac{\text{cov}(v,g)}{\text{var}(g)} \frac{\text{cov}(g',g)}{\text{var}(g)}}{1 - \frac{(\text{cov}(g',g))^2}{\text{var}(g')\text{var}(g)}} \\ &= \frac{\text{cov}(v,g') \text{var}(g) - \text{cov}(v,g)\text{cov}(g',g)}{\text{var}(g') \text{var}(g) - \text{cov}(g',g)^2}\end{aligned}$$

Assume that q is the frequency of A types in the population. Assume q is very small. First compute the variances,

$$\text{var}(g) = q(1 - q) \approx q$$

and

$$\text{var}(g') = \left(\frac{1}{n-1} + \left(\frac{n-2}{n-1} \right) r \right) \text{var}(g) \approx q \left(\frac{1}{n-1} + \left(\frac{n-2}{n-1} \right) r \right)$$

Next the covariances.

$$\begin{aligned}\text{cov}(g, g') &= \sum_{k=0}^{n-1} \left((\text{Pr}(k|g=1) q) \left(\frac{k}{n-1} \right) \cdot 1 + (\text{Pr}(k|g=0) (1-q)) \left(\frac{k}{n-1} \right) \cdot 0 \right) \\ &\quad - \text{E}(g)\text{E}(g')\end{aligned}$$

The second term in the sum is zero because $g = 0$. The expectations of g and g' are equal to q . Let p_k be the conditional probability that k of the other individuals are A types given that the focal is an A type.

$$\begin{aligned}\text{cov}(g, g') &= q \sum_{k=0}^{n-1} \left(\frac{k}{n-1} \right) p_k - q^2 \\ &= q(r + (1-r)q) - q^2 \\ &= rq - rq^2 \\ &= rq(1-q) \\ &\approx rq\end{aligned}$$

Then individual covariance is

$$\begin{aligned} \text{cov}(v, g) &= \sum_{k=0}^{n-1} ((\Pr(k|g=1)q) \cdot 1 \cdot v_{A,k} + (\Pr(k|g=0)(1-q)) \cdot 0 \cdot v_{N,k}) \\ &\quad - q \sum_{k=0}^{n-1} (\Pr(k|g=1)q v_{A,k} + \Pr(k|g=0)(1-q)v_{N,k}) \end{aligned}$$

Since $\Pr(k|g=0)$ is zero for $k > 0$ and $v_{N,0} = 0$ the second term in both sums are zero. Then

$$\begin{aligned} \text{cov}(v, g) &= q \sum_{k=0}^{n-1} (\Pr(k|g=1) v_{A,k}) - q^2 \sum_{k=0}^{n-1} (\Pr(k|g=1) v_{A,k}) \\ &= q(1-q) \sum_{k=0}^{n-1} p_k v_{A,k} \\ &= q(1-q) \left(-c + b \sum_{k=\theta}^{n-1} p_k \right) \\ &\approx q(-c + b \Pr(k \geq \theta)) \end{aligned}$$

Next the covariance of fitness with the genetic value of partners

$$\begin{aligned} \text{cov}(v, g') &= \sum_{k=0}^{n-1} \left((\Pr(k|g=1)q) \left(\frac{k}{n-1} \right) v_{A,k} + (\Pr(k|g=0)(1-q)) \left(\frac{k}{n-1} \right) v_{N,k} \right) \\ &\quad - q \sum_{k=0}^{n-1} (\Pr(k|g=1)q v_{A,k} + \Pr(k|g=0)(1-q)v_{N,k}) \end{aligned}$$

Again the second terms in both sums are zero. Thus

$$\begin{aligned} \text{cov}(v, g') &= \sum_{k=0}^{n-1} \left((\Pr(k|g=1)q) \left(\frac{k}{n-1} \right) v_{A,k} \right) - q \sum_{k=0}^{n-1} (\Pr(k|g=1)q v_{A,k}) \\ &= \sum_{k=0}^{n-1} p_k \left(q \left(\frac{k}{n-1} \right) - q^2 \right) v_{A,k} \\ &= -c \sum_{k=0}^{n-1} p_k \left(q \left(\frac{k}{n-1} \right) - q^2 \right) + b \sum_{k=\theta}^{n-1} p_k \left(q \left(\frac{k}{n-1} \right) - q^2 \right) \\ &= b \sum_{k=\theta}^{n-1} p_k \left(q \left(\frac{k}{n-1} \right) - q^2 \right) \\ &= qb \Pr(k \geq \theta) \left(E \left(\frac{k}{n-1} | k \geq \theta \right) - q \right) \end{aligned}$$

We can now calculate the regressions

$$\begin{aligned}\beta_{v,g|g'} &= \frac{q(-c + b\Pr(k \geq \theta))q\left(\frac{1}{n-1} + \left(\frac{n-2}{n-1}\right)r\right) - qb\Pr(k \geq \theta)\left(\mathbb{E}\left(\frac{k}{n-1}|k \geq \theta\right) - q\right)rq}{q\left(\frac{1}{n-1} + \left(\frac{n-2}{n-1}\right)r\right)q - r^2q^2} \\ &= \frac{(-c + b\Pr(k \geq \theta))\left(\frac{1}{n-1} + \left(\frac{n-2}{n-1}\right)r\right) - rb\Pr(k \geq \theta)\left(\mathbb{E}\left(\frac{k}{n-1}|k \geq \theta\right) - q\right)}{\left(\frac{1}{n-1} + \left(\frac{n-2}{n-1}\right)r\right) - r^2}\end{aligned}$$

Similarly

$$\begin{aligned}\beta_{v,g'|g} &= \frac{qb\Pr(k \geq \theta)\left(\mathbb{E}\left(\frac{k}{n-1}|k \geq \theta\right) - q\right)q - q(-c + b\Pr(k \geq \theta))rq}{q\left(\frac{1}{n-1} + \left(\frac{n-2}{n-1}\right)r\right)q - r^2q^2} \\ &= \frac{b\Pr(k \geq \theta)\left(\mathbb{E}\left(\frac{k}{n-1}|k \geq \theta\right) - q\right) - (-c + b\Pr(k \geq \theta))r}{\left(\frac{1}{n-1} + \left(\frac{n-2}{n-1}\right)r\right) - r^2}\end{aligned}$$

Thus

$$\begin{aligned}\beta_{v,g|g'} + r\beta_{v,g'|g} &= \frac{(-c + b\Pr(k \geq \theta))\left(\left(\frac{1}{n-1} + \left(\frac{n-2}{n-1}\right)r\right) - r^2\right)}{\left(\frac{1}{n-1} + \left(\frac{n-2}{n-1}\right)r\right) - r^2} \\ &= -c + b\Pr(k \geq \theta)\end{aligned}$$

and thus conditions (1) and (2) in the text are equivalent. Notice that r is relevant because it will tend to be positively correlated with $\Pr(k \geq \theta)$.