

An inclusive fitness analysis of altruism on a cyclical network

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Abstract

A recent model studies the evolution of cooperation on a network, and concludes with a result connecting the benefits and costs of interactions and the number of neighbours. Here, an inclusive fitness analysis is conducted of the only case solved analytically, of a cycle, and the identical result is obtained. This brings the result within a biologically familiar framework. It is notable that the benefits and costs in the inclusive fitness framework need to be derived, and are not the benefits and costs that are the parameters in the original model. The relatedness is a quadratic function of position in a cycle of size N : an individual is related by 1 to itself, by $(N - 5)/(N + 1)$ to an immediate neighbour, and by very close to $-1/2$ to the most distant individuals. The inclusive fitness analysis explains hitherto puzzling features of the results.

Introduction

The evolution of cooperation remains an active topic in biological research, but the power and scope of inclusive fitness theory (Hamilton, 1964, 1970) remain largely unappreciated. Ohtsuki *et al.* (2006) have recently shown how cooperation can evolve on a network. They end by drawing attention to the work of Hamilton (1964):

Finally, we note the beautiful similarity of our finding with Hamilton's rule, which states that kin selection can favour cooperation when $b/c > 1/r$, where r is the coefficient of genetic relatedness between individuals. The similarity makes sense. In our framework, the average degree of a graph is an inverse measure of social relatedness (or social viscosity). The fewer friends I have the more strongly my fate is bound to theirs.

The thrust of the current paper is that the results of Ohtsuki *et al.* (2006) have a much closer connection to Hamilton's work: their results fall into the scope of inclusive fitness theory because the social interactions are additive (at least in the weak selection limit) and so can be derived as a special case of Hamilton's rule itself. Genetic relatedness can be defined for their model. The benefits and costs need to be calculated for use in the inclusive fitness framework, and are not equal to the b and c of their model. The analogy between relatedness

and the inverse of the degree of a graph is called into question.

The present paper integrates the results exactly into inclusive fitness theory for the cycle, the only analytically studied case of Ohtsuki *et al.* (2006). Lehmann *et al.* (2007) integrate the general results of Ohtsuki *et al.* (2006) into inclusive fitness theory using sophisticated population genetic techniques, notably those of Rousset (2004). In one sense, therefore, this paper is a special case of theirs. However, their results do not cover one of the two halves of the analysis here (the Birth–Death process, explained below), and the more simple-minded approach of the current paper reveals some very enlightening details.

Two steps required for inclusive fitness analysis

Natural selection of social behaviour falls within the scope of inclusive fitness theory provided the fitness effects combine additively, as shown explicitly by Grafen (2006). Here, we pursue the special case of the cycle of length N of Ohtsuki *et al.* (2006), and we assume weak selection and so obtain additivity. Once a model falls within inclusive fitness theory, there are two steps that we take in turn. First, to calculate the costs and benefits of the possible actions. Second, to calculate the relatednesses. It is worth noting that although weak selection produces additivity in this case, it does not always do so, for example in the games of Ohtsuki & Nowak (2006).

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The theory of inclusive fitness is a strong theory, in the sense that it dictates how its variables are to be measured. Ohtsuki *et al.* (2006) discuss benefits and costs that, adding together the effects of the cooperative acts towards both of an individual's neighbours, give a benefit of b to each neighbour and $-2c$ to the individual itself. But inclusive fitness theory requires that the benefits and costs be measured in reproduction, namely the effect on the number of descendants (including a surviving self). Thus, we need to see how these 'scores' affect the chance of survival of individuals and the chance of their reproducing, and how these combine to affect the total expected number of descendants, which for the purposes of this paper we will call *fitness*: these all depend strongly on the demographic scheme. Ohtsuki *et al.* (2006) consider a Death–Birth scheme and a Birth–Death scheme which have very different results, and the explanation lies precisely in the process of converting scores into reproduction. It is helpful to agree to call the immediate neighbours '1-neighbours', those two positions away '2-neighbours', and so on.

Table 1 shows the benefits and costs as the effects on scores, and the effects on fitness under both demographic schemes. We now proceed to explain the biological significance of the benefits and costs. Consider the Death–Birth scheme first, in which each individual has an equal chance of being the one individual to die, and then one of the immediate neighbours of the vacated slot place an offspring in that slot, with probabilities proportional to their scores. An individual's own score is reduced by $-2c$, but the details of the pairwise competition mean that a given fitness effect has only a quarter of its effect in reproduction in a given competition (this calculation is in Appendix A). Thus, the $-2c$ gives an expected advantage of $-c/2$ for the case where the right-hand neighbour dies, and a further expected advantage of $-c/2$ when the left-hand neighbour dies.

There is always exactly one dead individual to replace, so the fitness effect on self of $-c/2$ to one side must be exactly counter-balanced by the effect on the fitness of the rival in that competition to fill the 1-neighbour slot. The fitness effect on the 2-neighbour on that side is therefore $+c/2$. The b given directly to the score of a 1-neighbour has a fitness effect of $b/4$ to each side, by the same 'quartering principle'. And the zero-sum property

shows that the 3-neighbour must therefore lose out, with a fitness effect of $-b/4$. However, if j herself dies, both the competing neighbours have gained b for their score, and so the chances of them winning are unaltered by the altruism. These are all the fitness effects for the Death–Birth scheme, shown in Table 1, and the arguments just given show that they make perfect biological sense.

One of the unexplained aspects of the results of Ohtsuki *et al.* (2006) is the difference between the demographic schemes, so consider now the Birth–Death scheme, in which one individual is chosen at random to reproduce, with probabilities proportional to scores, and then the reproducing individual's offspring is placed in the slot of a neighbour chosen at random with equal probabilities. The impact of score in this case is very different. In contrast to the 'quartering' of the Death–Birth scheme, here an individual suffers the full $-2c$ loss in fitness from her own score reduction, as it directly reduces her chance of being selected as the individual to reproduce. Further, she also suffers a $-b/2$ loss from each neighbour, for the simple reason that increasing your neighbour's score by b increases the chance she is selected to reproduce by b , and then with half a chance it is you who are selected to be replaced. The $-b/2$ for each neighbour gives the total effect on the individual's fitness as $-b - 2c$. Just as in the previous scheme, these effects have their equal and opposite reactions in the zero sum game in reproduction, leading to gains of $b + c$ for each immediate neighbour, and losses of $-b/2$ for 2-neighbours.

The more biological approach of inclusive fitness theory therefore readily provides an explanation of the difference caused by the demographic scheme. To complete the analysis, the relatednesses to neighbours at varying distances are required. Using a method closely modelled on those of Taylor *et al.* (2007b) and Rousset (2004), it is shown in Appendix B that the relatedness on a cycle of size N to a neighbour at distance k is

$$r_{N,k} = 1 - \frac{6k(N-k)}{N^2-1} \quad (1)$$

Table 1 shows these relatednesses, and the costs and benefits, itemized by neighbour. By multiplying and summing, we can calculate the inclusive fitness effect of a

Table 1 Effects of actor on neighbours.

Individual	$j-3$	$j-2$	$j-1$	j	$j+1$	$j+2$	$j+3$
Relatedness	$\frac{N^2-18N+53}{N^2-1}$	$\frac{N^2-12N+23}{N^2-1}$	$\frac{N-5}{N+1}$	1	$\frac{N-5}{N+1}$	$\frac{N^2-12N+23}{N^2-1}$	$\frac{N^2-18N+53}{N^2-1}$
Score	0	0	b	$-2c$	b	0	0
Fitness (Death–Birth)	$-b/4$	$c/2$	$b/4$	$-c$	$b/4$	$c/2$	$-b/4$
Fitness (Birth–Death)	0	$-b/2$	$b+c$	$-b-2c$	$b+c$	$-b/2$	0

The effect of j being a cooperator on neighbouring individuals. The effect on score is the immediate consequence of the interaction. The effects on fitness (the expected number of descendants, including the surviving individual as a descendant) are different, however, in the Death–Birth and Birth–Death demographic schemes. The values are calculated in Appendix A.

cooperator in the Death–Birth and Birth–Death schemes, respectively, as

$$\frac{6}{N^2 - 1}((b - 2c)N + 4(c - b)), \quad \frac{6}{N^2 - 1}(-cN + (c - b)) \quad (2)$$

The benefits and costs do not depend on N , but the formula for the relatednesses shows that relatedness to close neighbours approaches one as N increases. For large N , eqn (2) gives the same answers as Ohtsuki *et al.* (2006), that cooperation spreads when $b/2 - c > 0$ in the Death–Birth scheme, and when $c < 0$ in the Birth–Death scheme. Ohtsuki & Nowak (2006) give exact results for the more general case of games on the cycle, whereas here we consider only cooperation so the effects of different individual's actions add up. But their exact results for N , under weak selection, are given in their equation (2.4), and they agree exactly with the results just given when additivity is indeed assumed. Thus, the analytic result of Grafen (2006) that the inclusive fitness approach gives exact results is confirmed here, and in addition it provides a biologically meaningful explanation of selection of cooperation on a cycle.

The biological interpretation can now be pressed further, to explain why the effect of the benefit is halved, compared with the cost, in the Death–Birth scheme – that is, why is the condition for the spread of altruism $b/2 - c > 0$? We will assume large N , so that according to eqn (1) the relatednesses of the focal individual j to her neighbours can be taken to be decreasing linearly from one in both directions. Whatever is given in fitness to j herself has an equal and opposite reaction on the 2-neighbours, and the net effect is the product of the effect on self with the two steps' worth of relatedness difference. Whatever is given to a 1-neighbour, say $j - 1$, has to be considered in two halves. On half of the occasions when it matters, the dead individual is j herself, and the loser is $j + 1$. But $j - 1$ and $j + 1$ are equally related to j , and so the net effect on her inclusive fitness is zero. On the other half of occasions, it is $j - 2$ who dies, and $j - 3$ who suffers the balancing loss. The difference in relatedness to j between $j - 1$ and $j - 3$ is equal to the difference in relatedness to j between j and her 2-neighbours, owing to the linearity of relatedness. Thus, the only difference in the impact on the inclusive fitness of j between helping herself and helping her 1-neighbour is the fact that with the 1-neighbour, half of the occasions have a zero effect. This is the precise source of the factor of two by which b must be discounted in evaluating the inclusive fitness effect of j 's action.

Moving on to interpret the Birth–Death process, the disadvantage to j herself results in advantages of equal summed magnitude to her 1-neighbours. Thus, the net effect on inclusive fitness is the disadvantage to herself multiplied by one step's worth of relatedness difference. Next, we consider the effect of giving b to a 1-neighbour,

say $j - 1$. This has an equal and opposite effect shared equally between $j - 2$ and j herself. But the linearity of relatedness means that the net effect of the disadvantages to $j - 2$ and j therefore exactly equals in magnitude the net effect of the advantage to $j - 1$, so far as j 's inclusive fitness is concerned, leaving a net effect of zero. This is the precise source of the irrelevance of b to the effect of natural selection.

These explanations for the extent to which the value of b affects the spread of altruism show that it does not derive from genetic or other kind of similarity or extent of dependence between the actor and her neighbour. The inclusive fitness analysis, therefore, does not support the quotation from Ohtsuki *et al.* (2006) earlier in this paper, which analogizes their result to Hamilton's rule. It is also worth noting that despite its very general rhetorical appeal, the quotation focusses on the Death–Birth demographic scheme and ignores the Birth–Death case.

It is worth remarking that the total inclusive fitness effects in eqn (2) are of order $1/N$ because only one individual of the N dies each generation, and this dependency is therefore an artefact of the schemes. There would be merit in presenting the results as the cumulative effect over N periods, to make one 'generation'.

Finally, the biological significance of these models may be considered in the context of the explanation of their results. As presented by Ohtsuki *et al.* (2006), the factor of b in the Death–Birth scheme condition $b/2 - c > 0$ is presented as analogous to relatedness, but we have rejected this interpretation here. Further, the value of two is seen as a rather particular consequence of the details of the model, and it is clear that if j interacted so far as scores were concerned with her 2-neighbours in the Birth–Death scheme, b would again be irrelevant to selection. Thus, it is a fair conclusion that the model is too special and particular to be taken as having great biological significance in itself, but this is not to detract from the value of the model in assisting exploration of the complex subject of cooperation in geographically structured populations.

Conclusions

Network models have a great potential for exploring the evolution of social behaviour. Applying systematically the inclusive fitness methodology of Hamilton (1964, 1970) will lead to the most productive use of that resource. Indeed, after submission of the current paper, a breakthrough by Taylor *et al.* (2007a) has provided very general results about selection in viscous populations, which are further developed by Grafen & Archetti (unpublished work).

In the case considered here, the biological understanding of Ohtsuki *et al.*'s (2006) model is greatly enhanced by calculating the fitness effects on neighbours at varying distances, and the relatedness of neighbours at varying

distances, and putting these together to calculate the inclusive fitness effect. The difference between the two demographic schemes is then easily understood.

The cycle is the only analytically considered case of Ohtsuki *et al.* (2006), who deal with the general case with approximate methods. The link of inclusive fitness to that general case, and to other results in social graph theory, is established in great generality by Lehmann *et al.* (2007). The present paper emphasizes the interpretative advantages and rigour of an inclusive fitness analysis in a special and simple case. By contrast, Lehmann *et al.* (2007) establish much more general results, through the use of inclusive fitness methodology, and show that all of the results of social theory on graphs can be derived that way. They therefore express their main results using the notation and concepts of graph theory.

One interesting aspect of the current analyses is how in viscous populations the effects of relatedness and competition can combine in many ways (Grafen, 1984; Taylor, 1992; Wilson *et al.*, 1992). Overlapping generations seem to play a significant role (Taylor & Irwin, 2000; Irwin & Taylor, 2001; Lehmann *et al.*, 2007). There is a need for a fuller biological explanation of these results.

Another interesting aspect is that an individual has, approximately, positive relatednesses to the closest 43% of the population, and negative relatednesses to the most distant 57%. The most positive relatedness is of course one to itself, and the most negative is very close to $-1/2$, for all population sizes. The structure of the population thus allows some individuals to have a considerable negative relatedness. On other hand, the premiss of the current model is that those individuals do not interact, so here there is no scope for spiteful behaviour.

The most important conclusion is that inclusive fitness theory is a very general and powerful theory, with great explanatory force. Models of social evolution should either be presented in terms of inclusive fitness or, if there are reasons for adopting an alternative approach, reconciled to it explicitly. Mathematical frameworks for easing this process are increasingly available (Taylor *et al.*, 2000; Rousset, 2004; Grafen, 2006; Lehmann & Keller, 2006), and are currently being used to establish retrospectively the consistency of published work with inclusive fitness theory (e.g. Grafen, 2007; Lehmann *et al.*, 2007).

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Appendix A: Calculating the fitness effects

The method of calculating fitness effects is straightforward once it is clear that we need to take the demographic scheme (called the ‘updating scheme’ by Ohtsuki *et al.* (2006), but this term does not reflect the full

biological significance of the aspects covered) as well as the score into account to calculate the expected number of descendants, and in essence we follow Taylor & Frank (1996). Let x_j denote the genotype of individual j , and equal 1 for a cooperator and 0 for a noncooperator. Following the notation of Ohtsuki *et al.* (2006), we also prepare for the assumption of weak selection by supposing $b = \delta B$ and $c = \delta C$, where δ is a parameter we will tune towards zero. The score s_j is given by

$$s_j = 1 - 2cx_j + b(x_{j-1} + x_{j+1}) = 1 + \delta(-2Cx_j + B(x_{j-1} + x_{j+1}))$$

where the subscripts are understood to be modulo N , the number of individuals in the ring.

We study first the Death–Birth process, in which an individual is chosen at random, and is replaced by the asexual offspring of an immediate neighbour, with probabilities proportional to their scores. The fitness is the expected number of descendants in the next generation, counting the surviving adult as one descendant. Survival of an individual occurs with probability $(N - 1)/N$. If a neighbour dies (with probability $1/N$), j reproduces in competition with the individual on the far side of that neighbour. Thus

$$w_j = \frac{N - 1}{N} + \frac{1}{N} \frac{s_j}{s_j + s_{j-2}} + \frac{1}{N} \frac{s_j}{s_j + s_{j+2}}$$

The fitness effect b_{ijt} is given on the assumption of weak selection by

$$b_{ijt} = \begin{cases} \delta x_i \left(\frac{\partial}{\partial x_i} \frac{\partial w_j}{\partial \delta} \Big|_{\delta=0, x_i=0} \right) & t = |i - j| \\ 0 & \text{otherwise} \end{cases} \quad (3)$$

The role t has been allotted one of four values: 0, for the effect on self, and 1, 2 and 3 for the effect on neighbours that number of positions away. This choice will make the calculations of relatedness cleaner. Use of eqn (3) provides

$$Nb_{ijt} = \begin{cases} -c, & t = 0, j = i \\ b/4 & t = 1, j = i \pm 1 \\ c/2 & t = 2, j = i \pm 2 \\ -b/4 & t = 3, j = i \pm 3 \\ 0 & \text{otherwise} \end{cases} \quad \text{when } x_i = 1$$

$$Nb_{ijt} = 0 \quad \text{when } x_i = 0$$

and these are the values in Table 1.

The scores are the same for the Birth–Death process, but the link to fitness is different. A random individual is chosen to reproduce, with the probability of being chosen proportional to their score s_j . Then a random 1-neighbour of the reproducer is killed to make a space for the offspring. In this case, we need to consider the cases in which a distant individual reproduces, a neighbour reproduces and j herself reproduces, to write w_j as

$$w_j = \sum_{i:|i-j| \geq 2} \frac{s_i}{S} (1) + \sum_{i:|i-j|=1} \frac{s_i}{S} \left(\frac{1}{2} \right) + \frac{s_j}{S} (2)$$

where $S = \sum_i s_i$. Applying eqn (3) provides

$$Nb_{ijt} = \begin{cases} -b - 2c & t = 0, j = i \\ b + c & t = 1, j = i \pm 1 \\ -b/2 & t = 2, j = i \pm 2 \\ 0 & \text{otherwise} \end{cases} \quad \text{when } x_i = 1$$

$$Nb_{ijt} = 0 \quad \text{when } x_i = 0$$

This completes the derivation of the values shown in Table 1.

Appendix B: Relatednesses

It remains to calculate the relatedness to the different kinds of neighbour. A calculation of relatedness based on common ancestry can be derived following the principles of Rousset (2004) and Taylor *et al.* (2007b), as follows, providing a long-run average appropriate to the case of weak selection.

We first establish a recursion for the probability q_k^t that individuals k slots apart are identical-by-descent in period t , in the absence of selection, and the result is the same in both the Death–Birth and Birth–Death processes. A mutation rate of u per reproductive event is assumed. With probability $(N - 2)/N$ neither individual is killed, and each is killed with probability $1/N$. In that eventuality, there is half a chance the new individuals have the same identity-by-descent probability as a pair $k - 1$ individuals apart in period t , and half a chance the same as a pair $k + 1$ apart. Hence $q_0^t = q_N^t = 1$ and for $1 \leq k \leq N - 1$,

$$q_k^{t+1} = \frac{N - 2}{N} q_k^t + \frac{2}{N} \left(\frac{1 - u}{2} q_{k-1}^t + \frac{1 - u}{2} q_{k+1}^t \right) \quad (4)$$

and the solution to this recursion can be found by matrix inversion and is easily confirmed to be

$$q_k = C^{-1} (z^{k-(N/2)} + z^{(N/2)-k})$$

where

$$z = \frac{1 + \sqrt{2u - u^2}}{1 - u}$$

$$C = z^{N/2} + z^{-N/2}$$

The relatedness to an individual at distance k in an N -cycle is

$$r_{N,k}^t = \frac{q_k^t - \bar{q}^t}{1 - \bar{q}^t}$$

where \bar{q}^t is the average identity by descent to all individuals in the population (including self). The values of interest are the asymptotic values of $r_{N,k}^t$. These are functions of the mutation rate u , and our aim is to find

the limiting values of relatedness, say $r_{N,k}$, as $u \rightarrow 0$. The calculation is complicated by the fact that $q_k \rightarrow 1$, and so $\bar{q} \rightarrow 1$, as $u \rightarrow 0$. We proceed by defining $Q_k = z^{k - (N/2)} + z^{(N/2) - k}$ and \bar{Q} as the average of Q_k , to obtain

$$r_{N,k}(u > 0) = \frac{Q_k - \bar{Q}}{C - \bar{Q}}$$

The numerator and denominator equal zero in the limit. We apply L'Hôpital's rule twice. Using primes to denote derivatives with respect to u , it is useful to define $\tilde{Q}_k = z^{k - N/2} - z^{N/2 - k}$ and $\tilde{C} = z^{-N/2} - z^{N/2}$, and to record the following results

$$\begin{aligned} Q'_k &= \left(k - \frac{N}{2}\right) \left(\frac{z'}{z}\right) \tilde{Q}_k & \tilde{Q}'_k &= \left(k - \frac{N}{2}\right) \left(\frac{z'}{z}\right) Q_k \\ C' &= \left(\frac{N}{2}\right) \left(\frac{z'}{z}\right) \tilde{C} & \tilde{C}' &= \left(\frac{N}{2}\right) \left(\frac{z'}{z}\right) C \\ \bar{Q}' &= \frac{1}{N} \left(\frac{z'}{z}\right) \sum_{k=0}^{N-1} \left(k - \frac{N}{2}\right) \tilde{Q}_k & \bar{\tilde{Q}}' &= \frac{1}{N} \left(\frac{z'}{z}\right) \sum_{k=0}^{N-1} \left(k - \frac{N}{2}\right)^2 Q_k \end{aligned}$$

The successive applications of L'Hôpital's rule each involve cancelling z'/z after the differentiation, as follows:

$$\begin{aligned} \lim_{u \rightarrow 0} \frac{Q_k - \bar{Q}}{C - \bar{Q}} &= \lim_{u \rightarrow 0} \frac{\left(k - \frac{N}{2}\right) \tilde{Q}_k - \frac{1}{N} \sum_{k=0}^{N-1} \left(k - \frac{N}{2}\right) \tilde{Q}_k}{\left(\frac{N}{2}\right) \tilde{C} - \frac{1}{N} \sum_{k=0}^{N-1} \left(k - \frac{N}{2}\right) \tilde{Q}_k} \\ &= \lim_{u \rightarrow 0} \frac{\left(k - \frac{N}{2}\right)^2 Q_k - \frac{1}{N} \sum_{k=0}^{N-1} \left(k - \frac{N}{2}\right)^2 Q_k}{\left(\frac{N}{2}\right)^2 C - \frac{1}{N} \sum_{k=0}^{N-1} \left(k - \frac{N}{2}\right)^2 Q_k} \end{aligned}$$

which using the limits $Q_k \rightarrow 2$, $C \rightarrow 2$ yields

$$r_{N,k} = \frac{\left(k - \frac{N}{2}\right)^2 - \frac{N^2+2}{12}}{\frac{N^2}{4} - \frac{N^2+2}{12}} = 1 - \frac{6k(N-k)}{N^2-1}$$

and this formula conveniently holds also for $k = 0$ and N . Thus relatedness is a quadratic function of k , which takes value 1 at $k = 0$ and N , and reaches, approximately for even N and exactly for odd N , a minimum value of $-1/2$ at the furthest point(s) of the cycle. As n grows large, the relatedness between individuals separated by a fraction x of the cycle is given by $1 - 6y + 6y^2$.