A little more than kind and less than kin:
The unwarranted use of kin selection in spatial models of communication

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Abstract. It has become increasingly apparent that spatial and other forms of ecological situatedness can introduce radical differences in the evolutionary outcome of models of conflictive social behavior. Cooperative interactions are often found to have an increased viability in spatially situated models. One possible explanation for this phenomenon makes use of kin-selective arguments according to which high relatedness between neighbors stabilizes cooperation. Unfortunately, in some cases the argument does not go beyond the merely verbal. This paper shows that an explanation in terms of kin selection can easily be tested in a computer simulation and that, in the particular case treated here, the result of such verification is negative thus strengthening previous conclusions regarding the relevance of other factors such as discreteness, stochasticity and ecological organization.

1 Introduction

A possible contribution of Artificial Life to real biology is in the use of relatively novel techniques for addressing already established problems in the biological literature. Such is the case, for instance, of studies that take a problem from evolutionary biology and try to complement what is known about it with extended models mainly in the form of computer simulations (Bullock, 1997; Noble, 1998; Di Paolo 1997 and others).

The type of contribution provided by these models does not differ much from the use of similar techniques by biologists themselves (e.g. Durrett & Levin, 1994; Krakauer & Page, 1995). The difference is perhaps one of style and maturity. Theoretical biologists tend to be conservative and address specific issues. In contrast, many Artificial Life models tend to be more exploratory, addressing different issues at the same time and mixing (sometimes, but not always, in a less than clear manner) points regarding evolutionary stability, ecological and physical constraints, cognitive mechanisms, etc.

This wider exploratory attitude is simultaneously a source of excitement and inventiveness as well as a source of poor scientific methodology. With very few exceptions (e.g. Noble & Cliff, 1996) researchers have failed to turn a critical
eye on their own work and that of others. This article is intended to be viewed as belonging to this rare class. However, instead of critically addressing other specific models it will concentrate on showing how an assumption has been repeatedly used as an explanation for what goes on in such models without any warrants for its applicability and, worse still, without any confirmation that the conditions were met for its use when such confirmation should be relatively easy to obtain.

It has become apparent that spatial situatedness can enhance the evolutionary viability of cooperative social behaviors under circumstances of conflict of interest (e.g., Krakauer & Pagel, 1995; Nakamaru, Matsuda & Iwasa, 1997; van Baalen & Rand, 1998). A common situation is that, for certain interaction games, cooperation is unviable in the mixed medium approach but stable if players are spatially distributed and interact locally. There are different possible explanations for this phenomenon, but one of the most favored, at least intuitively, is the use of kin-selective arguments according to which most games are played between highly related individuals (due to the limited dispersal or 'viscosity' of population) and therefore cooperation is understood as the strategy that maximizes inclusive fitness (Hamilton 1964; see also section 3).

Unfortunately, in some cases this explanation has been merely verbal despite the potential for actually confirming its applicability (e.g., Ackley & Littmann 1994, Oliplant 1996 and others). This careless appeal to kin-selective arguments is dangerous. One is tempted to wrongly infer that spatial situatedness always implies the validity of such arguments\(^1\) and, on the flip-side, one is tempted to ignore other possible factors that may play a significant role. It is also bad science since the means exist for verifying whether the chosen explanation is correct or not and there is no justification for not doing so.

This paper will show in some detail that a verification of the applicability of kin-selective arguments can be achieved fairly simply. The study will be based on an evolutionary model presented elsewhere (Di Paolo, 1997, 1999, submitted) but, due to limitations of space, will not go much into the details of that model. Finally, the paper will support the conclusion that cooperative outcomes in spatial games need not be tied to kin-selective arguments and that other ecological factors such as spatial organization, discreteness and stochasticity can be responsible for the selective stability of cooperative behaviors. The paper will, therefore, be less than exciting and perhaps a little on the boring, but necessary, side of scientific research.

2 The game

The model presented in (Di Paolo, 1997; submitted) describes a simple action-response (two-role) game with tuneable degree of conflict of interest, two out-

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\(^1\) Quite on the contrary, some models have shown that under certain circumstances the positive effect of higher relatedness between neighbors is actually cancelled by the negative effect of increased local competition (Taylor, 1992a; 1992b; Wilson, Pollock & Dugatkin, 1992). See also (Kelly, 1992; van Baalen & Rand, 1998).
comes (cooperative coordination and non-coordination) and four different strategies. The game is played by a population of individuals distributed in space who interact locally within a fixed neighborhood of their positions. Players subsist on the energy gained by playing the game and reproduce with a rate which is proportional to their capacity for accumulating extra energy. This capacity depends obviously on the strategy they play, on the local pool of strategies of the other players and also on ecological factors such as the density of local players and the density of local resources.

Each time the game is played the energy contained in a local food source is at stake. If the players cooperate they share this energy equally; if they do not, then the first player gets a proportion c which is greater than one half and the second player gets nothing. The parameter c is a measure of the degree of conflict between the first player and the second (low conflict for c near 0.5 and high conflict for c near 1). The outcome of the game depends on the strategies played which remain fixed during each individual’s lifetime. Certain combinations of initiating actions (first player) and responses (second player) are cooperative and others are non-cooperative. Players do not choose directly whether to cooperate or not, they just “choose” (in evolutionary terms) which actions and responses to play.

With a basic repertoire of two possible actions and two possible responses the number of different strategies is four. Of these, two may be called “self-cooperative” in the sense that two players playing one such strategy will always cooperate independently of the rules they play. The other two are called “non-self-cooperative” (“non-cooperative” for short). Both simple and extended game-theoretic analyses have been performed for the mixed-medium approach and all of them resulted either in oscillations in the composition of the population or in a combination of non-cooperative strategies as the evolutionarily stable outcome. In both cases the overall proportion of games resulting in cooperation was equal to the baseline level that is expected to occur by chance (50%). Never was a single self-cooperative strategy a non-invadable solution.

Similar results were also observed using a partial differential equations approach in which players are spatially distributed and interactions occur within a finite local range (Di Paolo, 1999, submitted). However, in a spatially extended, individual-based model of the same game the outcome was different. In this model players are not treated as continuous densities of strategies but are rather implemented as discrete individuals and all interactions are subject to different kinds of noise. Strategies are encoded for each individual in a binary haploid genotype and an evolutionary algorithm is run ². It is observed, in contradistinction with the game-theoretic results, that for values of c slightly higher than

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² Other details: 2-D toroidal arena (100 × 100), square local neighborhood of size 10 × 10, variable population size, overlapping generations, sexual reproduction, local selection of reproductive mates and local allocation of offspring. Offspring’s genotype is built by uniformly recombining the parental genotypes and adding point mutations (probability of no modification after a mutation event: 0.94), see (Di Paolo, 1999; submitted).
0.5 the population tends to be constituted by a single self-cooperative strategy and a small density of a competing non-cooperative one and, as $c$ is increased, the global level of cooperation decreases in a more or less linear fashion until $c \approx 0.65$ where the baseline level is obtained (see Fig. 1).

![Coordination diagram](image)

**Fig. 1.** Average value for the level of cooperative coordination for different values of $c$. Each point is the average of 5 simulation runs. For each run the level of coordination is averaged in time over the steady state. The line represents a linear regression, (correlation coefficient: -0.982, slope: -3.32, null hypothesis no variation with $c$, $P < 0.005$). Error bars indicate standard deviation.

In (Di Paolo, 1997), and later in more detail in (Di Paolo, 1999; submitted), an explanation is offered of this and other observations in terms of the effects introduced by the spatial organization of the population into discrete, separate and relatively stable clusters of players. The ecological forces that account for the stability of these clusters are also responsible for breaking many of the inbuilt symmetries between the roles in the game. Thus individuals at the center of a cluster play the second role more often than those at the periphery because of the better opportunities for being selected by other players as partners in the game. Moreover, other geometrical factors enter into play. For instance, the length of genealogies surviving without interruption tends to be longer if they start near the center of the cluster than if they start near the border so that all players tend to reflect the strategy played at the center.

This situation combines with the fact that players are discrete entities and therefore for invasion of a mutant strategy to occur a minimal threshold density must be achieved so that the average extra gain of the invader rises above fluctuations and the new strain is able to assert itself (see for instance de la Torre & Holland, 1990; Tsimring, Levine & Kessler, 1996; Abramson & Zanette, 1998; Goodnight, 1992). The asymmetries introduced by the ecological organization makes the achievement of threshold density easier for self-cooperative strategies.
if $c$ is near 0.5 and the equilibrium density of non-cooperative strategies increases more or less linearly with $c$ until their capability for invasion is regained. This is how the behavior shown in Fig. 1 is explained. Of course, it is possible to ask whether this complicated picture in which selective arguments are mixed with ecological dynamics is indeed necessary for explaining the results. Perhaps a simpler explanation in the form of a kin-selective argument would be enough and more economical. This is something that has to be tested.

3 Kin Selection

As mentioned above, it has often been found that cooperative interactions under circumstances of conflict can be stable if a spatial dimension is added to the evolutionary scenario even when simpler selective arguments predict the contrary. This has been demonstrated both by mathematical considerations and computer models in the case of the Prisoner's Dilemma (Axelrod, 1984; Nakamaru et al., 1997) and communication games (Ackley & Littman, 1994; Krakauer & Page, 1993; Oliphant, 1996). Depending on the particular features of the model there may be more than one possible explanation for this phenomenon. For instance, Axelrod argues that spatial clustering favors reciprocity in the case of the TIT-FOR-TAT strategy (Axelrod, 1984, p. 65 - 69). A different explanation is preferred by Ackley & Littman (1994) and by Oliphant (1996) for their respective models. Such explanation involves the concept of kin selection (Hamilton, 1964). It is argued that, since the spatial regions where mating partners are chosen from and offspring allocated into tend to coincide with areas where game co-participants are selected from, this ensures that players will be highly related so that a cooperative player will tend to increase, on average, the frequency of genes identical to its own in other players, i.e. its inclusive fitness.

If fitness is related to the degree to which an organism can pass copies of its own genes to the next generation, inclusive fitness is a generalization of this concept so that it can also account for the presence of traits that help the transmission of copies of identical genes that happen to be located in other individuals. As the well known example goes, a behavior that is detrimental for an individual but which produces benefits of a same magnitude for two or more siblings will tend, under certain circumstances, to increase the inclusive fitness associated with that behavior and therefore it will be favored by selection. This is so because the probability of finding the same given gene in a sibling is, in haploid and diploid genetic systems, equal to 1/2. Thus, the general condition, known as Hamilton's rule, for a trait or behavior in individual $i$ to be selected is not that it has an individual positive fitness effect $W_{ind}^i$ but that it has a positive inclusive fitness effect $W_{inc}^i$:

$$W_{inc}^i = W_{ind}^i + \sum_j r_{ij} W_{ind}^j > 0$$  \hspace{1cm} (1)

where $r_{ij}$ is the degree of relatedness between $i$ and another individual $j$ (defined carefully below) whose own individual fitness is affected by a quantity $W_{ind}^j$ by
the actions of \( i \). The sum is extended over all the other individuals who may be affected by the trait or behavior in question. Even in cases where \( W_{i,j}^{\text{ind}} < 0 \), inclusive fitness can still be positive as long as the remaining terms in the sum are large enough.

Here it is clear why the restricted dispersal induced by space can play a relevant role. If interaction and reproduction are local processes, i.e. if co-participants as well as reproductive mates are selected from an individual's vicinity and offspring are allocated into the same vicinity, then the average value for the \( r_{ij} \)'s could be expected to be higher than in a mixed population. Therefore, cooperative behaviors at the expense of one individual but which benefit others in the local vicinity could at the same time tend to be beneficial to individuals that are highly related\(^3\); a situation which may result in \( W_{i,ac} > 0 \).

Such is indeed the kind of argument advanced by Ackley & Littman (1994); Oliphant (1996) and others. Unfortunately, none of these authors actually shows that this is the case in their models. They just content themselves with finding a good candidate explanation without verifying if condition (1) is fulfilled, despite the fact that such a verification should be easy enough to perform in the computer models involved.

In the model discussed in the previous section, kin selection arguments are not straightforward in the sense that the actions and responses of the players cannot be said to be intrinsically cooperative or non-cooperative; they depend on the context of the strategies used by the rest of the players. However, under the assumption of weak selection pressure it is possible to postulate a situation of quasi-equilibrium in which the context is fixed and then actions and responses could be seen as cooperative in themselves. This is by no means the general situation in this model but this assumption will be maintained in order to see that even if this situation were true, kin selection would not be enough to explain the obtained results.

In order to test the plausibility of kin selection as a valid explanation for the evolution of cooperative coordination, a calculation is performed of the degree of relatedness between individuals and their average partners in the game. Genetic similarity can be caused by descent but also by other factors such as convergence, founder effects, etc. However, relatedness does not intend to measure just genetic similarity, otherwise all sorts of intra-specific conflicts and competition would be inexplicable. To take into account this subtlety relatedness is defined following (Grafen, 1991) as the degree of genetic similarity between two individuals over and above the average similarity within the population in which the individuals interact. In this way, if the difference in genetic constitution between two individuals is zero then their relatedness is equal to one, which means that from the point of view of gene frequencies for an individual to help the other is the same as to help itself. If the difference between the genetic constitution between the players is the same as the difference between one of them and the average genetic constitution in the population, then for that individual related-

\(^3\) However, this need not be the case; see footnote 1.
ness is zero, since in cooperating with the other player, it is not contributing to
an increase in the frequency of genes similar to its own.

An estimation of relatedness in the current model is straightforward by taking
the perspective of the individual player and keeping track of the average
relatedness with the partners it encounters throughout its lifetime. For each
game that is played the Hamming distance \( d_{ij} \) between the binary genotypes of
the participants is calculated as well as the distance between each genotype
and the population average genetic constitution \( d_{ij}^{\text{avg}} \) and \( d_{j}^{\text{avg}} \). The relatedness of
individual \( i \) to individual \( j \) is

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    r_{ij} = 1 - \frac{d_{ij}}{d_{i}^{\text{avg}}},
\]

(2)

Notice that while \( d_{ij} = d_{ji} \), in general \( r_{ij} \neq r_{ji} \) since for each individual re-
relatedness is defined with respect to its own distance to the population average
constitution. This quantity is averaged for each individual during its lifetime in
order to reflect its mean relatedness to its local partners.

In the present model, if the average genetic constitution is calculated using
the whole population instead of just the population which is bound to be affected
by the actions of a given individual, relatedness will be overestimated. It must
be remembered that clusters have a fairly independent evolutionary history. The
degree of extra similarity that relatedness intends to measure should be in terms
of the mean population with which the player and its offspring have a chance to
interact. Whereas the average constitution used for the first measure involves the
whole population, in a more accurate estimation the average genetic constitution
used for the calculation of relatedness is taken as the one 'seen' by each player
during its lifetime within its economic neighborhood (Queller, 1994). For each
individual, the genetic constitution of all its partners in the game is averaged.
The first estimation or upper bound (averaging over the whole population) is
kept only for the purpose of comparison since it is assumed that the measure of
interest lies much closer to the second estimation.

Figure 2 shows the variations in the two estimations of relatedness for dif-
ferent values of \( c \), each point obtained by averaging the temporal mean after
transients of 5 simulation runs with identical parameters. It is observed that

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4 The average genetic constitution is simply a string calculated as the sum of all the
genotypes in the chosen sub-population and divided by the number of players. Since
there are only two possible alleles per locus which are represented by 0’s and 1’s, the
result of this calculation is that every component in the average string gives an indi-
cation of the proportion of each allele in that particular locus. In order to calculate
the distance from an individual genotype to this real-valued string, a measure is used
which reduces to the Hamming distance when applied between two binary strings.
This measure involves summing, for each component of the string, the absolute
distance between the individual allele and the corresponding population average. For
instance, the distance between the string (1,0,1,0) and the string (0.7,0.3,0.9,0.2) is
\( d = 0.3 + 0.3 + 0.1 + 0.9 = 1.6 \).

5 This estimation coincides with the one proposed in (Queller & Goodnight, 1989)
using each allele as a neutral genetic marker.
Fig. 2. Average estimations of relatedness vs. $c$. Lines depict linear regressions. Averages over 5 runs and over the steady state. Error bars indicate standard deviation.

neither of the measures varies much with $c$. This behavior can be understood considering that relatedness is given mainly by the spatial relations between players of different generations which should not be affected too much by $c^i$.

By calculating the corresponding inclusive fitness per game per unit of energy it is found that for a first player ($i$) the payoff for no cooperation is $W_{inc}^{NC,i} = c$, and the payoff for cooperation is $W_{inc}^{C,i} = (1 + r_{ij})/2$. Using condition (1) and taking the best estimation of relatedness ($r \approx 0.11$) it can be concluded that cooperation should be the favored outcome only if $c < 0.55$, which is not enough to explain the results.

However, if the estimation of relatedness were as high as the upper bound ($r \approx 0.45$) then cooperation would be stable for $c < 0.72$. So it seems that if a generous estimation of relatedness could be justified, then kin selection would suffice for explaining the evolution of cooperative coordination in the present model. However, the expected result, if such were the case, would be a constant high level of cooperation for any value of $c$ between 0.5 and 0.72, and a step-wise change to no cooperation for $c > 0.72$ which is not what is observed. As seen in Fig. 1, the level of cooperative coordination is a linearly decreasing function of $c$, even in ranges where relatedness does not vary. The condition for the stability of cooperation is given by establishing the sign of the inequality between the inclusive fitness for cooperation and for no cooperation. There are two parameters in this condition: relatedness and $c$. A linear variation of the degree of cooperation with $c$ could only be explained by some spatial variation in relatedness resulting in high values.

\footnote{The high value of relatedness for the upper bound reflects the fact that intra-cluster similarity is much greater than inter-cluster similarity.}
in a linear decrease of the proportion of players for whom cooperation implies the best increase in inclusive fitness. Not only is this variation not observed, but it would also have to be manifested as a decrease in the global average of relatedness. This observation suggests that, whatever the mechanism responsible for the stabilization of cooperation, it must not work equally well for all values of $c$ below 0.72 as kin selection would if relatedness were to be estimated by its upper bound.

Consequently, even after many concessions, the conditions for explaining the results in terms of kin selection are not met.

4 Conclusions

While kin selection remains an important concept for studying the evolution of social behavior, its use is far from being universal or automatic. The theory provides very simple rules for verifying its conditions of applicability and those rules should be used. This paper demonstrates how to do this for an individual-based model instantiated in a computer simulation. Additionally, it shows that the conditions for kin selection fail to be met in this model thus strengthening an alternative explanation in terms of ecological and selective factors.

Independently of this last result, the main point of the paper should be taken as a methodological one. The behavior of computer simulations can be quite hard to understand in itself. There is no reason why anything should be obvious in view of the complexity of contemporary models. Fortunately, the strength of simulations is that any hypothesis regarding what is going on in them can be put to the test with relative ease. To fail to do this is to fail to take advantage of one of the crucial aspects of simulations. In science, a hypothesis or an explanation should be tested against all the available evidence and there is no reason to expect a lesser standard from Artificial Life.

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