LETTERS

Altruism through beard chromodynamics

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The evolution of altruism, a behaviour that benefits others at one's own fitness expense, poses a darwinian paradox. The paradox is resolved if many interactions are with related individuals so that the benefits of altruism are reaped by copies of the altruistic gene in other individuals[1], a mechanism called kin selection[2]. However, recognition of altruists could provide an alternative route towards the evolution of altruism[1,3–5]. Arguably the simplest recognition system is a conspicuous, heritable tag, such as a green beard[1,3]. Despite the fact that such genes have been reported[6–8], the 'green beard effect'[3] has often been dismissed because it is unlikely that a single gene can code for altruism and a recognizable tag[1,3,9]. Here we model the green beard effect and find that if recognition and altruism are always inherited together, the dynamics are highly unstable, leading to the loss of altruism. In contrast, if the effect is caused by loosely coupled separate genes, altruism is facilitated through beard chromodynamics in which many beard colours co-occur. This allows altruism to persist even in weakly structured populations and implies that the green beard effect, in the form of a fluid association of altruistic traits with a recognition tag, can be much more prevalent than hitherto assumed.

If every individual were to behave altruistically the population as a whole would do well. That altruism nevertheless does not readily evolve is illustrated by evolution of cooperation in the prisoner's dilemma game[10]. In this game a player can either help another player by cooperating (playing C), or not help by defecting (playing D). Because the payoff of cooperation is always less than that of defection, cooperation is costly and is thus an act of altruism. As defectors always do better than cooperators in the same situation, cooperation cannot evolve in large, well-mixed populations in which different players are encountered every round, even though the highest average payoff is realized in a population in which all players cooperate. Cooperation can evolve in sufficiently viscous populations where patterns of relatedness create a population structure that allows kin selection to operate[11], if the benefits of cooperation outweigh the effects of kin competition[12,13].

The evolution of altruism is obviously facilitated by mechanisms that allow discrimination against defectors[1,14]. One such mechanism is the green beard effect in which altruists can recognize each other using a conspicuous tag or signal[1,3]. In Dawkins'[3] formulation of the green beard effect this is achieved through a single gene causing both altruistic behaviour and recognition. This tight coupling has been considered a crucial characteristic for the green beard effect to work[4] because if the genes for tag and altruistic trait were loosely coupled then not only altruists can have coloured beards, but also non-altruists would acquire them. Such individuals would receive the benefits of altruistic behaviour without having to pay the cost: they cheat on the interaction, thus potentially preventing the evolution of altruism. However, because a gene that causes both traits is considered to be too complex to be likely[1,3,9] the green beard effect has often been considered implausible.

A number of observations have suggested that the green beard

effect actually does exist in nature[6–8,15], and results from simulation studies suggest that altruism can be maintained through the co-existence of a small number of beard colours[16,17]. Here, we will investigate theoretically if and when the green beard effect can operate. We will do this first for tightly coupled genes for tag and trait. Then, we will explore the consequences of an idea originally suggested by ref. 18: that there exist separate genes, one for beard colour, which facilitates recognition, and one for being altruistic or not. These genes are loosely coupled in that they can be inherited separately and thus can give rise to new tag–trait combinations.

The model that we use for the dynamics of beard colour polymorphism (beard chromodynamics) is based on the prisoner's dilemma game[12,17,19] in a spatial setting, with one extra twist. As in refs 16 and 17, we assume that all individuals have a recognizable tag in the form of a coloured beard and that altruistic actions are only towards individuals with the same beard colour. Each individual plays all its neighbours and receives a score according to the payoff matrix in Table 1. Players put offspring in empty neighbouring sites with a probability proportional to their score. Apart from rare mutations, new tag–trait combinations arise because reproducing individuals have a certain probability to mate with a neighbouring individual, swapping part of their genomes in the process. We carried out explicit simulations (see Supplementary Information for details) of full interaction networks in which we varied the connectedness and topology of the interaction network. We also performed a more in-depth analysis by considering the set of replicator equations[20] that results when a simplifying assumption is made (see Methods and Supplementary Information).

If only a single beard colour is present, no discrimination occurs and the model describes blind kin selection. This can maintain altruism only if the population is sufficiently viscous and the scales of cooperation and competition are sufficiently different[16,13]. Both simulations and mathematical analysis of our model show that the green beard effect does not enhance the possibilities for altruism if tag and trait are always inherited together, because this leads to highly unstable dynamics. To understand why, consider a cooperator with a rare beard colour in a population dominated by other beard colours.

Table 1 | Payoff matrix for the multi-beard prisoner's dilemma

Payoff	C_i	D_i	C_j	D_j
C_i	R	S	P	P
D_i	T	P	P	P
C_j	P	P	R	S
D_j	P	P	T	P

The payoff of a player using a strategy in the first column against a player using a strategy in the first row with $j \neq i$. The strategies are to cooperate (C) and to defect (D); the subscript indicates beard colour. We assumed $T > R > P > S$ and that $T + S > P + R$. For these parameters, the highest payoff is received if one has an opponent who actually cooperates, irrespective of one's own strategy. Because the payoff of a cooperator never exceeds that of a defector, irrespective of the opponent, cooperation is costly for the perpetrator and therefore is an altruistic strategy.

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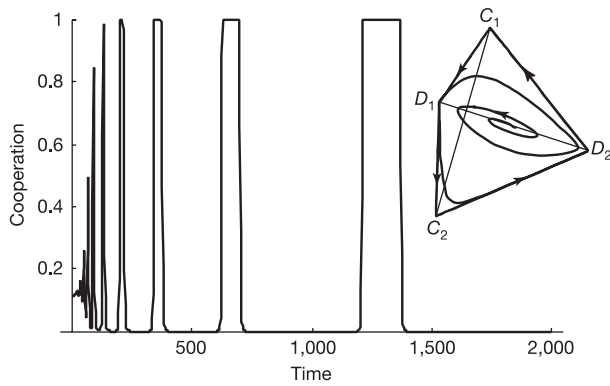
Figure 1 | **The level of cooperation in the population in the approach to the heteroclinic cycle.** The system, specified by equation (1), spends an increasing amount of time in equilibria with a single beard colour. Inset: the dynamics on a three-dimensional simplex. Parameters: $T = 5$, $R = 3$, $P = 1$, $S = 0$, $h = 1$.

Figure 2 | **Evolution of cooperation and beard colour diversity.** The dynamics of the overall level of cooperation (dashed line) and beard colour diversity (solid line) in the simulation model. Beard colour diversity is measured as the exponential of the Shannon index ($\exp[-\sum_i (C_i + D_i)\ln(C_i + D_i)]$), which returns the number of beard colours when they are present in equal densities, and equilibrates well below the maximum value of 6. The simulations were run on a random network of 10,000 sites where every site has eight connections to other sites; all other parameter values are as in Fig. 1 with $h = 1$ (**a**) and $h = 0.9025$ (**b**) (corresponding to $\rho = 0.95$ in the simulation model), and the mutation rate $= 10^{-4}$ per locus. The lattices were seeded with a small proportion of blue-bearded cooperators in a population of random genotypes with a strong bias towards green-bearded defectors. In this simulation cooperation cannot be maintained through blind kin selection alone.

This cooperator will behave as a defector when meeting individuals with different beard colours. It can therefore invade the population if the average cooperation level (and hence the average payoff) is below a threshold level and will eventually come to dominate this population, erasing any beard colour diversity that may have existed up to that point. Once the new colour dominates, defectors carrying beards in this new colour can successfully invade. Hence, the initial fitness advantage of the new beard is lost, with the sole result that the population has changed to a new, single colour. The (re)-invasion of cooperators in rare beard colours, followed by the emergence of defectors in this colour repeats indefinitely. If beard colour and strategy are always inherited together this scenario corresponds to highly unstable dynamics that result in the rapid loss of beard colours. This is confirmed by our analysis (see Supplementary Information), which reveals that if tag and trait are tightly coupled the dynamics are dominated by an attracting heteroclinic cycle on which the population is monochrome for most of the time (Figs 1 and 2).

If, however, tag and trait are coded by separate, loosely linked genes a different pattern emerges. Loose coupling results in dynamics that are less unstable and in which cooperation arises through the dynamic coexistence of different beard colours (Fig. 2). The reason for this difference is that loose coupling prevents a single beard colour from dominating the dynamics. Whereas tightly coupled genes create dynamics that go through cycles with ever deeper troughs in which eventually fixation occurs, loose coupling continuously generates new tag–trait combinations that prevent fixation and stabilizes the dynamics. In our spatial simulations this boom–bust scenario can be observed through clusters of cooperators with same-coloured beards in an environment otherwise dominated by defectors. These clusters increase in size over time until a defector with the same beard colour appears in the vicinity of the cluster. Once this happens the cluster is taken over by defectors, until a cooperator in a novel beard colour appears. This results in a shifting mosaic of beard colours (Fig. 3). The tighter the coupling, the smaller the chance of a new type appearing and hence the larger the size of these clusters and the more unstable the dynamics are. The crucial mechanism that stabilizes the dynamics is the regular local appearance of novel tag–trait combinations. In our model such new combinations are created through recombination, which we consider the most likely mechanism to operate in natural populations. However, other mechanisms that can introduce new heritable tag–trait combinations in local clusters, such as high levels of mutation, infrequent long distance dispersal or gene flow, can accomplish the same stabilizing effect[16,17].

Under recombination, successive invasions of new beard colours tend to increase beard-colour diversity up to a point where no new
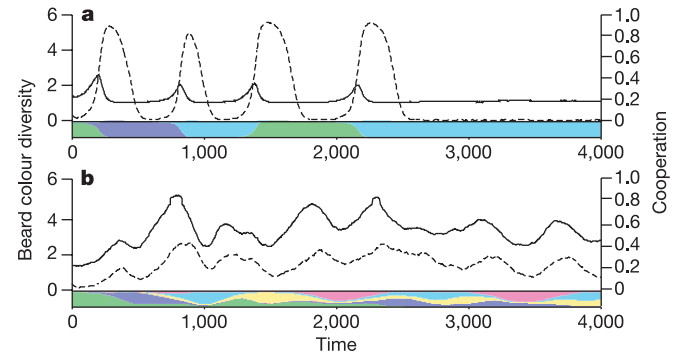
beard colours can invade and diversity saturates (Fig. 2). Our analysis reveals how this diversity is regulated: cooperators will, on the whole, encounter fewer defectors with a similar beard colour and thus be exploited less if the diversity in beard colours is high. Therefore, the average payoff increases with the number of beard colours that are established in the population. Because all mutant beard colours have a constant fitness when rare (independent, in particular, of beard colour diversity), it becomes increasingly difficult for new colours to establish themselves in the population when the beard colour diversity increases (see Methods and Supplementary Information). Beard colour diversity is thus regulated at a definite level (Figs 2 and 4). Our analysis confirms that loose coupling is necessary for the evolution of tag-based cooperation. Nevertheless, the coupling should not be too loose. Coupling that is too loose causes the correlation between tag and trait to be too weak for the tag to serve as a proxy for the trait, whereas a coupling that is too tight means not only that clusters of cooperators will be homogeneous for beard colour, but also that the consequences will be dramatic when neighbouring cheats eventually acquire the same beard colour.

The final beard colour diversity depends on viscosity. An increase in connectedness leads to a decrease in the average cooperation level and the average payoff, if the number of beard colours is kept constant. However, a lower average payoff allows new beard colours to become established, resulting in an increase in beard colour diversity, which, in turn, counteracts the decrease in the level of cooperation (Fig. 4). This mechanism causes the number of beard colours to be negatively correlated with viscosity: the less the population is structured, the higher the beard colour diversity. Importantly, this mechanism maintains altruism in populations in which blind kin selection alone cannot.

Our model assumes that the green beard effect works through alleles that cause both the tag and recognition of that same tag. The assumption of a single recognition allele is justified if the allele functionally combines the tag and recognition functions, as is conceivable for homophilic cell surface adhesion proteins[6,8,15] or if recognition is self-referent and works through comparing another individual's tag to one's own. Then, a single mutation can change both one's tag and recognition of the tag. Alternatively, recognition could be based on two different alleles, one for the tag and one for
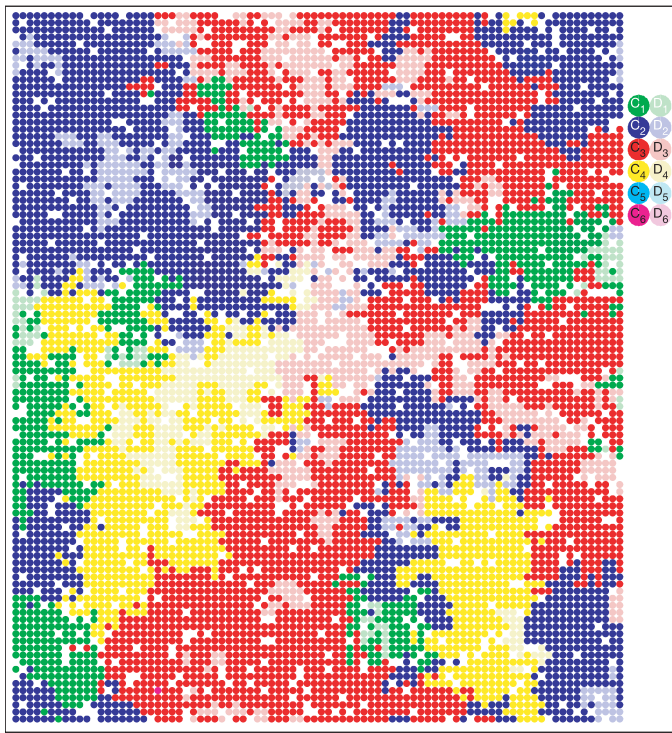
Figure 3 | **An example of a snapshot of spatial beard chromodynamics.** Snapshot taken at $t = 4,000$ on a square lattice (with four neighbours per site). Altruistic individuals are indicated by dark colours; defectors by light colours. Parameters match those of Fig. 2 but with $h = 0.81$ (corresponding to $\rho = 0.90$ in the simulation model).

recognition. Even though this case is not strictly covered by our model, our qualitative results should carry over. Because a mismatch between tag and recognition function is neutral in defectors (relative to the fitness of other defectors with a similar tag), diversity in these alleles can build up in the defector population, providing the potential for the generation, through subsequent mutation on the second allele, of new matching sets of tag and recognition alleles. Even if this process is potentially slow, once it has created a set of matching alleles these will be maintained through selection, as described in our model. Moreover, because selection acts against mismatches in cooperators, one could conjecture that a tight coupling between tag and recognition alleles, as assumed in our model and found in nature[7], naturally arises.

Our results imply that the scope for green beard genes is much wider than often assumed. This is for a number of reasons. First, altruism can be maintained without all the functions for tag, recognition and altruism having to reside in a single locus: loose coupling between a recognition allele and altruistic trait suffices. Second, our results suggest that rather than there being a single green beard gene in a population, one can expect to find a diversity of such genes, especially if the population is weakly structured. A possible reason that so few coloured beards have been reported is the concentration of research on highly structured populations in which the diversity of beard colours is predicted to be low. Our analysis leads to the testable hypothesis that diversity in recognition tags inversely correlates with average relatedness. This suggests that relatively easily observed tag diversity can serve as an indicator for the nature of the underlying social interactions. Third, to detect the green beard effect one should look for cases where tag and trait can dynamically associate[8,16]. A tag that functions as a green beard in one instance need not be associated with altruism in another population or at another instance in time, which obviously has consequences for our capacity to detect green beards.
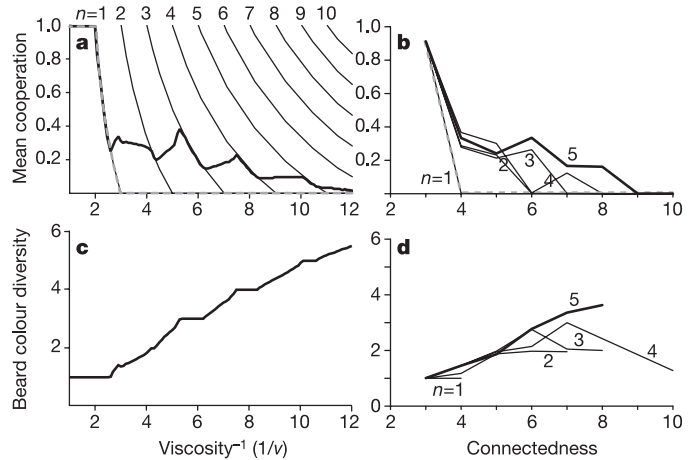

Figure 4 | **Cooperation and diversity versus viscosity. a**, The mean cooperation in the model (equation (1)) is found by letting the beard colour diversity saturate (thick line). The thin lines give the mean cooperation on the symmetrical equilibria for different numbers of beard colours; the grey dashed line is the result for a single beard colour, corresponding to blind kin selection. **b**, As for **a** but for the simulation model. The different curves show mean values over $t \in [3,000, 4,000]$ in simulations on random networks with different average connectivity. The curves differ in the maximum number of beard colours used in the simulation. **c**, The beard colour diversity corresponding to **a**. **d**, The beard colour diversity corresponding to **b**. Parameters are as in Fig. 3.

METHODS

The mathematical model that we use is based on the simulation model (see Supplementary Information) and is inspired by the replicator equation[20]. To capture the effects of viscosity we assumed that an individual encounters with a probability v an individual identical at both loci, and with a probability $1 - v$ a random individual from the population. This probability is approximately inversely proportional to the number of neighbours[11]. This results in the following payoffs ϕ_x for phenotype x:

$$\phi_{C_i} = vR + (1 - v)(RC_i + SD_i + (1 - C_i - D_i)P)$$

$$\phi_{D_i} = vP + (1 - v)(TC_i + (1 - C_i)P)$$

The parameters R, P, T and S specify the payoff as defined in Table 1, and C_i (or D_i) is the fraction of the population that has phenotype C_i (or D_i). We also assumed that with a probability, ρ, a gene is inherited from a neighbouring individual. For reasons of simplicity we ignored in the mathematical model the small probability that an individual recombines both tag and trait, and therefore the probability of having the same genotype as the parent is $h = 1 - 2\rho$. Because a neighbouring individual has the same genotype with probability v the effective rate of recombination is $\rho' = (1 - v)\rho$ and players give rise to an exact copy of themselves with probability $h' = h + v(1 - h)$. By changing the parameter h, and thus ρ, we can change the level of linkage between beard colour and altruistic trait. This leads to the system of replicator equations:

$$\dot{C}_i = (h'\phi_{C_i} - \Phi)C_i + \rho'\Phi_i\sum_{j=1}^{n} C_j + \rho'\Phi_C(C_i + D_i)$$

$$\dot{D}_i = (h'\phi_{D_i} - \Phi)D_i + \rho'\Phi_i\sum_{j=1}^{n} D_j + \rho'\Phi_D(C_i + D_i)$$

(1)

where $\Phi = \sum_{j=1}^{n} \phi_{C_j}C_j + \phi_{D_j}D_j$ represents the average fitness in the population, $\Phi_i = \phi_{C_i}C_i + \phi_{D_i}D_i$ represents the average fitness of individuals with beard colour i, $\Phi_C = \sum_{i=1}^{n} \phi_{C_i}C_i$ represents the average fitness of cooperators, and $\Phi_D = \sum_{j=1}^{n} \phi_{D_j}D_j$ represents the average fitness of defectors. This formalism assumes that the death rate is equal to the average fitness so that the total population size remains constant. We implemented mutation by infrequently and randomly changing tag or traits. If the total density of a certain beard colour dropped below 0.0005 we removed this beard colour and normalized the densities.

Because of symmetry between beard colours there exist equilibria in which all beard colours have equal densities. By putting the left-hand sides of equation (1)

to zero, by denoting the equilibrium densities and payoffs by bars and $\bar{C}_i = \bar{C}(n)$, $\bar{D}_i = \bar{D}(n)$ we find by elimination that $\bar{\phi}_{C_i} = \bar{\phi}_{D_i} = \bar{\Phi}$; that is, at equilibrium the average payoff of a cooperator and a defector is equal. Using this and $\bar{C}(n) + \bar{D}(n) = 1$ we find that

$$\bar{C}(n) = \frac{v(R - P) - \frac{1-v}{n}(P - S)}{(1 - v)(T + S - R - P)}.$$

Therefore, because $R > P$, $P > S$ and $T + S > R + P$, the equilibrium density of cooperators with a specific beard colour increases with the number of beard colours, as does the total amount of cooperation, $n\bar{C}(n)$. The average payoff at equilibrium, $\bar{\Phi} = P + (1 - v)(T - P)\bar{C}(n)$, increases with the number of beard colours because $T > P$.

The simulation model differs from the replicator model (equation (1)) in that, for the replicator model the density-dependent regulation acts globally, whereas in the simulation all density dependence is local. Especially if the effective scale on which local regulation operates is of a similar order as the scale over which the altruistic interactions take place, then local regulation can reduce the possibility of altruism[13]. The fact that altruism can be maintained in our simulation model through blind kin selection—provided the viscosity is sufficiently high—demonstrates that this is not an overriding effect. The fact that the different models give qualitatively similar results illustrates that the maintenance of altruism through beard chromodynamics does not critically depend on this aspect.

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