**Simulation Paper Outline: The Evolution Of Kin Preference**

**Sept 2012 (figures at bottom of document)**

**Abstract**

Using an individual-based and genetically explicit model we explore the evolution of kin preference.....

What causes the evolution of kin preference in social groups........?

**Introduction**

*Paragraph 1:*  Background on the evolution of kin preference in the context of cooperation

* Hamilton’s Rule (1964) BR>C

Since the formulation of Hamilton’s (1964) famous rule there has been much debate about the role of kin selection in evolution of social behaviour (e.g. Hughes et al. 2008). Hamilton’s (1964) rule states that altruism should spread within populations if, C, the cost in fitness to the actor is smaller than r, the genetic relationship between the actor and recipients and b, the fitness gain to the recipient . However a big question remains: how and why did kin-selection evolved in the first place?

*Paragraph 2:*  The aim of our model was investigate the

*Paragraph 3:* Explanation of function used in simulation....

*Paragraph 4:* Perhaps sub paragraphs explaining in more detail the function and real world parallels.

**Methods (need more information from Julian)**

*The model (methods copied from Julian’s documents and adapted from Veelen et al. 2010)*

* Assume that individuals have the possibility to come together in groups in order to perform a task that might be done more efficiently together than alone.
* There are two things that will matter for group productivity, group size and the level of cooperation
* In this model, both of them ultimately depend on individual characteristics which we have modelled as three separate traits, the tendency to join groups, the tendency to cooperate and the strength of kin preference.
* Once in a group, individuals can contribute to the overall success of the group by being cooperative. Cooperation increases total group productivity, but lowers the relative fitness of cooperators within their group.
* The first step at every generation step of the model is group formation. Groups are formed by accretion. Individuals start trying to get into the last non-empty group and continue backwards from there. If they do not find a group they form a new one. The process stops when the last group has been occupied (by one individual). We assume that in the initial population all individuals are related.

*The function*

Let i denote the cooperative tendency of individual *i*, and *gi* denote the kin-interaction preference. These two traits very from 0 to 1. The larger i is the more individual *i* cooperates, and the larger *gi* is the higher the preference of individual *i* to interact with highly related individuals. Let *j* denote the group that *i* is trying to join. The probability that *i* joins group *j* is:

where *h(j)* is one if group *j* is below the optimal group size , zero if the size of j is above the expected stable group size, and linearly decreasing in between. Function *h* ensures that the group size does not explode, and is slightly above the optimal group size, as is often observed in natural populations. Function *k* weights the kinship preferences of the group. We assume that the joiner always wants to join the group. The term considers the kinship preferences of the group, is the average kinship preference inside group *j*, and *rij* is the average relatedness of individual *i* to the members of group *j*.

Function *k* is defined as follows:

For *t* equal to zero relatedness does not play a role, that is, individuals have no preference for kin interactions. For *t* equal to 1 we get the equivalent of sibs- only. For *t* = 0:5 we get a linear function that approximates the kin-preference case, always letting in brothers and letting in cousins with a probability close to 1/4, second cousins with probability 1/16 and so on.

Once the group formation process has taken place, we proceed to determine the number of offspring that each individual will contribute to the pool. Following (Avilés, 1999), (Avilés, 2002), (Avilés et al., 2002), (Avilés et al., 2004) and (van Veelen 2010) we assume that the number of offspring produced by an individual is a function of the size of the group it is in, of the cooperativeness of the other group members within that group and of the cooperativeness of the individual itself using the following function:

Here, *n* is the size of the group the individual is in, therefore it will be assumed to be a positive real value, *n*0. Parameter i is the cooperative tendency of the individual itself. The resulting value of *n*, depends on each individual preference for kin interaction.

**Statistical analysis**

*(Statistical description of method closely based on AmNat 2001 paper)*

We used the ANOVA to test for the effect of the various parameters, their second- and third-order polynomial terms and their interactions. We customized the test for each response variable by dropping all nonsignificant terms (P>0.05) terms and their interactions. The r2 of the reduced models was excellent, with r2 values of ranging from 84.3-94.4% (see table x). Kin preference and average cooperation were arcsin transformed while relatedness and group size were log transformed.

**Results**

*Correlations and counter correlations within runs*

Cooperation is correlated with group size and relatedness is correlated with kin preference. However kin preference and relatedness are counter-correlated with cooperation and group size.

**Figure 1: representative graph of correlations within one run**

*Test for white noise*

Significant values of the Fisher's κ statistic allow us to reject the null hypothesis that fluctuations in the series are due to white noise. We tested whether the oscillations apparent in figure 1 were simply due to whitenoise or whether there was intrinsic periodicity.

|  |  |  |
| --- | --- | --- |
| **Parameter** | **Fisher’s κ** | **P value** |
| Average cooperation | 672.3 | <<0.001 |
| Average group size | 1380.3 | <<0.001 |
| Relatedness | 730.1 | <<0.001 |
| Kin preference | 1757.4 | <<0.001 |

*Anova tests*

**Figure 2: Graphs of the average of cooperation, group size, relatedness and kin preference**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Parameter | Kin Preference (asin transformed) | Relatedness (asin transformed) | Group size (log transformed) | Ave Coop (log transformed) |
| r (intrinsic rate of growth) | 88.4 | 90.7 | 15.8 | 11.1 |
| C (inverse of gp carrying capacity) | 0.10 | 0.53 | 63.3 | 6.4 |
| β (cost of cooperation) | 2.31 | 0.31 | 4.7 | 29.9 |
| Interactions | 2.49 | 0 | 10.6 | 36.9 |
| Total (r2) | 93.3 | 91.4 | 94.4 | 84.3 |

Table x:

**Discussion**

*Explanations of correlations*

* Relatedness is correlated with kin preference because, as the amount of kin preference exhibited increases so does the levels of relatedness within groups.
* Average group size is correlated with cooperation as in order for larger groups to be maintained, i.e. for the benefits of grouping behaviour to be greater than the cost, high levels of cooperation need to be present.
* Group size is counter-correlated with kin preference and relatedness because as kin preference increases, entry to groups becomes more restrictive and therefore group sizes decreases.

*Explanation of effects of R, Beta and C*

*Effects of R:*

As R increases, more relatives are available in the population to form part of groups, so groups become more restrictive in their admission requirements, thus causing average within group relatedness to increase. With greater within group relatedness, greater levels of cooperation can evolve. With larger R, larger groups can form, but the effect is more marked when larger group carrying capacities (1/c) require the formation of larger groups.

Interestingly kin preference does not go to zero, even for very small R. This may because leaving relatives out has an indirect fitness cost as these individuals will be eliminated from the population

*Effects of 1/c:*

The group carrying capacity parameter affects primarily the size of the groups formed. With larger 1/c, larger groups form (this is obvious). The group carrying capacity parameter, however, also seems to interact with **: when 1/c is large, ** has an effect in all four variables.

If there is a large group carrying capacity (large 1/c) cost of cooperation important. If group carrying capacity is large it is much harder to admit only kin, therefore the effects of high cooperation cost cannot be mitigated as much by the admission of kin only.

When the group carrying capacity (1/c) is small higher levels of cooperation can be maintained even when cooperation is costly because the groups that form are small and therefore can be more restrictive in terms of group entry, only allowing kin to join the group. However when group carrying capacity is large they can no longer be so restrictive therefore levels of cooperation are not able to be maintained at high levels.

Therefore if the group carrying capacity is large and the intrinsic rate of growth is small, groups are no longer able to maintain cooperation if the cost of cooperation (β) is high as they are unable to restrict group entry only to kin as they need to meet ecologically-determined group sizes.

*Effect of β:*

Interestingly, the cost of cooperation parameter has little effect or no effect on all variables when the group carrying capacity is small due to the ability of small groups to restrict entry. When 1/c is large, however, lower levels of cooperation and smaller groups, with somewhat lower relatedness evolve when the costs of cooperation are greater.

**Figures**

**D:\RFile\Rplot08.tiff**

**Fig 1:** Time series showing oscillations for R=0.1, c=0.06, β=0.2. Lines shown are cubic spline fits with flexibility parameter λ= 0.001 on the original data. The first 10000 records of the re run were removed to ensure that the cycle had reached equilibrium.

D:\RFile\RplotFULL.tiff

**Fig 2:** Graphs of the average of cooperation, group size, relatedness and kin preference for each run with the first 10000 generations removed. Curves are cubic spline fits with λ=0.001