**The Coevolution of Kinship Preferences and Cooperation**

**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

*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 (Julian will write a detailed appendix of the methods if needed)**

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

In this model we assumed 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. In this simulation, as in Aviles et al (2002) and Aviles et al (2004), individuals come together in one-generation breeding associations. Whether an individual is admitted into a group is determined by each individual’s genetically coded kin preference as well as the average kin preference of the group. Within groups, the extent to which individuals help one another is determined by individually coded “cooperative” tendencies. Cooperation increases total group productivity, but lowers the relative fitness of cooperators within their group depending on the cost of cooperation, β.

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.

*Group formation functions*

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 preference of the joiner, how much does the joiner want to join the group given the kinship preference of the joiner. 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.

*Fitness function*

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)*

The model was run for each combination of parameters (table u) once for 50000 generations. The first 2000 generations were discarded before any analysis was carried out.

|  |  |
| --- | --- |
| Factor | Levels |
| r | 0.10, 0.25, 0.50, 0.75, 1.00, 1.50, 2.0 |
| c | 0.20, 0.06, 0.10 |
| β | 0.0, 0.2, 0.6, 0.8 |

Table y:

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, average cooperation and average cooperation were arcsine transformed while relatedness and was log transformed.

**Results**

*Evolution of Group Size*

The size of groups formed was primarily affected by the group carrying capacity, 1/c, with 63.3% of the variation attributable to C (table x.) However intrinsic rate of growth, R, had an effect. When the group carrying capacity was high, (c=0.02) the larger the intrinsic rate of growth, R, the larger the average group size evolved. The cost of cooperation, β, only had an effect on the group size when C and r was small (C=0.02 and R<1.0), keeping groups below the stable group size (figure 1). Otherwise the average group size remained around the stable group size

*Evolution of cooperation*

The level of cooperation that evolved depended on the cost of cooperation, β, with 29.9% of the variation explained by the cost of cooperation. 36.9% of the variation was explained by interaction terms in the ANOVA model (table x). From figure 1 it can been seen that when the group carrying capacity was small (C =0.1) average cooperation evolved to a high level regardless of the cost of cooperation or intrinsic rate of growth. However when both the group carrying capacity and the cost of cooperation is large (C=0.02 and β 0.6, C=0.06 and β =0.8) lower levels of cooperation evolve.

*Evolution of average relatedness within groups*

90.7% of the variability in average relatedness within groups is due to r, the intrinsic rate of growth (table x, figure 1). The intrinsic rate of growth, r, has a very large effect on the average relatedness within groups, with the average relatedness increasing as the intrinsic rate of growth increases. The group carrying capacity, 1/c, and the cost of cooperation, β, have little effect, with β only explaining 2.31% of the variation (table x, figure 1).

*Evolution of kin preference*

The level of kin preference that evolves is most affected by the intrinsic rate of growth (r2=0.88 table x) with higher levels of kin preference evolving as the R increases, with it apparently leveling off as R approaches 1.5 (figure 1). Cost of cooperation, β, only has an effect on kin preference when both R is small (< 1.0) and the group carrying capacity, 1/c, is large (C=0.02) (figure 1).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| 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:** Percentage variance explained by each of the parameters of the model for the average kin preference, relatedness, group size and cooperation within each groups, for each run of the model after it had reached equilibrium.

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*White noise test and within run correlations*

During each run each output parameter oscillates (figure 2). However significant values of the Fisher's κ statistic carried out on a randomly chosen runs, allow us to reject the null hypothesis that the fluctuations observed in the series are due to white noise (table y).

|  |  |  |
| --- | --- | --- |
| **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 |

**Table y:** The Fisher’s κ value and corresponding p value for a randomly choose run.

During the runs the oscillating values of cooperation is correlated with group size and relatedness is correlated with kin preference. Kin preference and relatedness are counter-correlated with cooperation and group size (figure 2). Leticia: I have potentially found a way to test/measure correlations within time series, using a function I found in R. If you agree I think it might be good to test for the amount of correlation within all runs and get the average result, as the magnitude of correlation seems to differ a bit between runs, but not necessarily the direction. (see table z below for an example of cross-correlation tested for one run)

**D:\RFile\Rplot08.tiffFig 2:** 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 run were removed to ensure that the cycle had reached equilibrium.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Cooperation | Kin Preference | Group size | Relatedness |
| Cooperation | NA |  |  |  |
| Kin Preference | -0.052 # not such a strong correlation | NA |  |  |
| Group size | 0.256 | -0.845 | NA |  |
| Relatedness | -0.185 | 0.646 | -0.862 | NA |

Table z: Cross correlations for sample time series

**Discussion**

*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.

*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.