Methods

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

*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 and average cooperation were arcsin transformed while relatedness and group size were log transformed.