**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**

It has long been recognized that high levels of relatedness allow the evolution of costly altruistic behaviours (refs). Therefore, One might expect that, given a choice, social groups will tend to be formed with close relatives. Several factors, however, may prevent groups from being restricted to only close relatives. One scenario, for instance, involves the ecological need to form groups that are larger than the number of available relatives, either because the fecundity of a species is low (e.g., •••) or the size of the groups that need to be formed is large (e.g., •••) (Avilés et al. 2004). It may also be that locating close relatives or building up a group with a sufficiently large number of close relatives is not practical given a limited time to form groups. Additionally it may not be possible for individuals to discriminate close kin from non-relatives. The kin composition of social groups may thus be largely dictated by demographic and ecological factors, a possibility that has hardly been considered (but see Avilés et al. 2004).

Here we investigate the evolution of kin admission rules in a model where cooperative interactions cause group-living individuals to have greater fitness than individuals living solitarily or in very small groups. We consider how the kin composition of social groups evolves in response to demographic and ecological factors such as the intrinsic fecundity of a species and an externally dictated group carrying capacity. Assuming that cooperative interactions range from mutualistic to highly altruistic, we consider how kinship rules of admission evolve, influencing or being influenced by the level of cooperation that evolves within groups.

We base our model on the equation proposed by Avilés (1999) where cooperative interactions have a synergistic effect on fitness. This model has been previously used to study the coevolution between cooperative and grouping tendencies, either among nonrelatives (Avilés et al. 2002) or assuming different kinship structures (Avilés et al. 2004). While in these models group size evolves in response to the coevolution of grouping and cooperation, here we assume that group size is externally fixed by ecological factors and allow instead the evolution of the degree to which individuals discriminate against kin when becoming associated in social groups.

We find that the factor that has by far the largest effect on the kin composition of social groups is the intrinsic fecundity of a species, which explains close to 90% of the variance. Interestingly, the group carrying capacity was only a minor influence, except for a combination of very high group carrying capacity and very low fecundity, in which case groups of low relatedness formed when the relative fitness costs of cooperation were high. We also find that levels of cooperation, group size, and the kin composition of social groups oscillate through time, with cooperation and group size oscillating in parallel and being counter correlated with the degree of relatedness of the groups formed.

**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 rather than alone. In this simulation, as in Aviles et al (2002), Aviles et al (2004) and (van Veelen 2010), individuals come together in one-generation breeding groups. 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. However this simulation departs from previous ones it that the admission to groups is controlled by the strength of an individual’s genetically coded kin preference as well as the average kin preference of the group members. Both an individual’s cooperative tendencies and strength of kin preference is able to evolve.

**Per Capita Group Productivity and Relative Fitness within Groups**

We assume that the number of offspring produce per capita is maximized in groups of intermediate size as this reflects that the benefits to an individual of being a group (e.g. protection from predators, …) is balanced by the costs (e.g. crowding, resource competition)

Following (Avilés, 1999), (Avilés, 2002), (Avilés et al., 2002), (Avilés et al., 2004) and (van Veelen 2010) we therefore 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 function,

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| --- | --- |
| , | (1) |

where n is the size of the group, r is the intrinsic rate of growth parameter, c is the inverse of the group carrying capacity (so the smaller c, the larger the group carrying capacity), β is the cost of cooperation, controlling the extent to which cooperative interactions are mutualistic (β=0) versus altruistic (β>0) and represents cooperative tendencies , ranging between 0 and 1. Therefore i is the cooperative tendencies of the individual and is the average cooperative tendencies within the group.

From equation (1) it can be seen that er is the reproductive output of an individual in the absence of interactions with conspecifics and e-cn represents the negative effects of grouping on an individual’s reproductive output and represents the synergistic effects of grouping due to cooperation. is the relative fitness function, which allows for the possibility that cooperators may suffer a relative fitness cost within their groups.

**Genetic and breeding systems**

Individuals are diploid with cooperative and kinship preference each represented by 15 binary loci with 0 or 1 as possible alleles. These translate additively to phenotypic values between 0.0 and 1.0 , which is the proportions of 1’s in a diploid complement. Haploid gametes are procured through processes mimicking meiosis and recombination. Mutation is at a rate of 10-2 per locus per generation. It is implemented through an inversion/translocation mechanism to avoid bias against the most common allele that occurs by simply mutating randomly chosen sites to the opposite allele.

For simplicity, we model a single sex, with individuals performing the female function but also able to contribute sperm. Because individuals choose mates at random from the global population prior to group formation, selfing is avoided and the system is equivalent to a two-sex system in which males are only able to fertilize eggs. This model therefore replicates species with outbreed breeding systems, such as those where males move between groups or where mating takes place before the group formation phase. (reference) However this model is not appropriate for organisms characterised by inbred social groups such as naked mole rats (Faulkes et al. 1997; Burland et al. 2002) or social spiders (Aviles 1997). To facilitate relatedness calculations, all offspring in a clutch are sired by the same father.

**Group Formation**

Groups are formed by accretion. The group formation phase involves individual leaving the global pool and one at a time at random. Each individual starts by trying to get into the last non-empty group and continues backwards from there. Because newly dispersed relatives occupy the most recently formed groups, this creates a linearly viscous population structure that maximizes encounters between relatives. If an individual is unable to join any groups it establishes a new one. We assume that there are ecological limits on the size of the global population by having only a limited number of available nesting sites. Individuals that do not get admitted to any of the nesting sites are discarded. Note that since individuals are chosen at random to join groups, this procedure does not bias selection.

The probability that a new member is accepted into a group is

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| --- | --- |
|  | (2) |

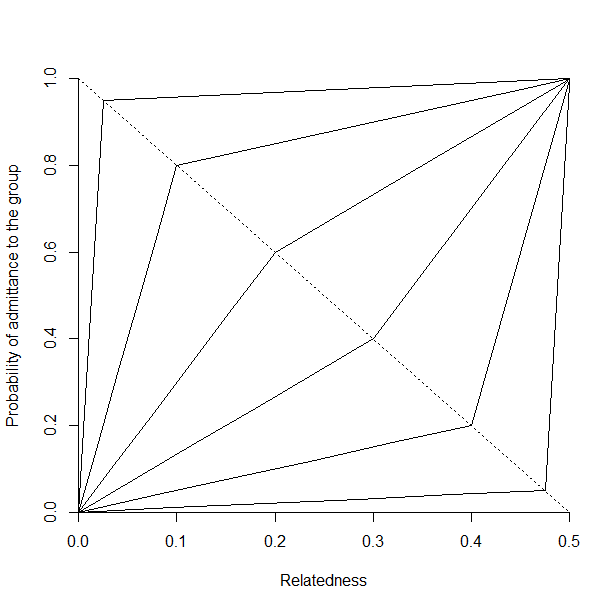
Function h(j) is a group size dependent admission probability which equals 1 if the group *j* is below the optimal group size , zero if the size of j is above the expected stable group size, and linearly decreasing in between. This ensures that the group size does not explode, and is slightly above the optimal group size, as is often observed in natural populations (ref see Giraldeau 1988).

Function k weights the kinship preferences of the joiner and existing group members,

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| --- | --- |
|  | (3) |

where Rij is the relatedness of individual i to j, m is the kinship preference with being the average kinship preference within group j and being the kinship preference of individual i.

For *m* =0 relatedness does not play a role, that is, individuals have no preference for kin interactions. For *m* equal to 1 only full sibs are admitted. For *m* = 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 (figure w).



m=0.05

m=0.20

m=0.4

m=0.6

m=0.8

m=0.95

Figure w: Kinship weighting function with different values of kinship preference, m

We assess relatedness by keeping track of pedigree relationships up to the great grandmother generation, a task that is facilitated by the fact that all offspring within one clutch have the same father.

As generations of group formation proceeds, cooperative tendencies and degree of kin preference evolves.

**The simulations and Analyses**

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

The model was run for each combination of parameters values (table y) 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 prior to analysis.

**Results**

Summary paragraph describing how the intrinsic rate of growth is the main parameter determining the evolution of kin preference, which in turn would dictate the kin composition of social groups.

The intrinsic rate of growth, r, is the main parameter that the determines the level of kin preference that evolves in the system. As the intrinsic rate of growth increases the level of kin preference increases until a threshold of about 0.9 is reached (figure graphs). This, therefore, dictates the composition of groups, the higher the level of kin preference that has evolved the higher the average level of relatedness within groups.

Then talk about how the size of the groups formed depends on the group carrying capacity and on the average cooperative tendencies of groups, which in turn are influenced by the relative fitness costs of cooperation (see Van Veelen et al. 2010 to understand how cooperation and group size attain a mutually dependent equilibrium). Note that in the simulations the size of the groups formed depends on a group admission function, which, in addition to relatedness, depends on the optimum and stable group sizes, which can be calculated directly from the group carrying capacity parameter and the average cooperative tendencies of the groups—see equations (3) in Avilés (1999) and eq (4) and (5) in the Appendix of Avilés et al. 2004).

*Evolution of kin preference*

Make this and the next section one, as these things are directly related to each other. 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).

*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 Group Size*

Discuss group size formation third, noting that grouping tendencies, per se, are not evolving, but rather that the size of the groups formed depends on the group carrying capacity parameter and the evolving levels of cooperative tendencies, given the equation that determines group admission probabilities as a function of the optimum and stable group sizes. 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 the 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 size of the groups that formed. 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*

Discuss the evolution of cooperation last, since it will depend partly on values attained by degree of relatedness and group size, in addition to the costs 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.

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| --- | --- | --- | --- | --- |
| Parameter | Kin Preference (arcsin transformed) | Relatedness (arcsin 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).

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

Ruth: The discussion should relate the results to other papers, such as the Avilés et al. 2004 and the Van Veelen et al. 2010 and others from the literature, for you to find. There should also be some examples of actual organisms to which these various things may apply. Start with the examples from the Avilés et al. 2004, but look for more recent references that may be relevant.

*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 be because leaving relatives out of a group 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) the cost of cooperation parameter becomes 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 groups can no longer be so restrictive, thus causing levels of cooperation to drop.

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 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.
* 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.
* The close correlation between group size and level of cooperation reflects the fact that optimum and stable group sizes are directly proportional to the averagecooperative tendencies in the groups, as seen in eq (3) in Avilés (1999); eqs (4 & 5) in Appendix of Avilés et al. (2004), and Table 1 of Van Veelen et al. (2010).

The counter-correlation between the cooperation/group size and kin preference/relatedness time series may reflect the following series of events: as kin preference, and thus degree of relatedness within groups, increases, greater levels of cooperation evolve, albeit with a certain time lag (in the graphs, we see cooperation raising following a peak of relatedness). Greater levels of cooperation, however, favor the formation of larger groups (since the optimum group size is directly dependent of average cooperative tendencies, gamma/c). The formation of larger groups may require less restrictive admission requirements, thus causing the kin preference rules to bounce back to lower levels. This will in turn lower the degree of relatedness within groups. which would then allow the accumulation of less cooperative cheaters within groups. This may then lead to lower group productivity and thus favour again groups that are more restrictive in their kinship admission rules.

The above is merely speculative. It would be nice to figure out ways to test these suggestions in the simulations themselves.