**The evolution of kin preference, Aviles et al.**

**Abstract**

Using an individual-based, genetically explicit model we explore the co-evolution of cooperation and kin preference, and hence kin composition of social groups. We find that the parameter that has the largest effect on the kin composition of social groups is the species fecundity, which explains almost 90% of the variance in kin preference, and therefore group relatedness observed. The group carrying capacity only had a minor influence on the level of kin preference that evolves except if the fecundity is low, the carrying capacity very high and the cost of cooperation high. In this case high levels of cooperation did not evolve and kin preference remained low.

**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 an individual based, genetically explicit 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 optimum 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**

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

In this model we assume 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 et al (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 as 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 tendency 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 the benefits to an individual of being a group (e.g. protection from predators, greater foraging success) 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 which range between 0 and 1. Therefore is the cooperative tendency 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, 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 proportion of 1’s in a diploid complement. Haploid gametes are procured through processes mimicking meiosis and recombination. Mutation occurs 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. 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 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 of the 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 able to rise 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. Relatedness is computed by keeping track of pedigree relationships for every individual up to the great grandmother generation, a task that is facilitated by the fact that all offspring within one clutch have the same father.

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 1).



**Figure 1**: Kinship weighting function which describes the probability of admittance to a group depending on an individual’s average relatedness to the group members. m is the different values of genetically coded kinship preference levels.

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

The model was run for each combination of parameters values (table 1) once for 50000 generations. The first 2000 generations were discarded before any analysis was carried out to ensure that the simulations had reached equilibrium.

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| 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 1:** The values of each parameter used in the simulations in a fully factorial design

We used an 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 2). Kin preference, average cooperation and average cooperation were arcsine transformed while relatedness and was log transformed prior to analysis.

**Results**

*Kin preference, relatedness, cooperation and group size*

The intrinsic rate of growth, r, is the main parameter that determines the level of kin preference that evolves. As r increases so does the individually genetic coded level of kin preference until a threshold of about 0.9 is reached (figure 2). As the individual levels of kin preference increases so does the degree of relatedness within groups. Therefore the intrinsic rate of growth largely dictates both the kin preference and the kin composition of groups, explaining 88.4% of the variation of kin preference and 90.7% of the degree relatedness within groups. Surprisingly, the cost of cooperation has little effect on kin preference (r2=2.31) unless the intrinsic rate of growth is small, in which case a high cost of cooperation reduces the level of kin preference that evolves (figure 2).

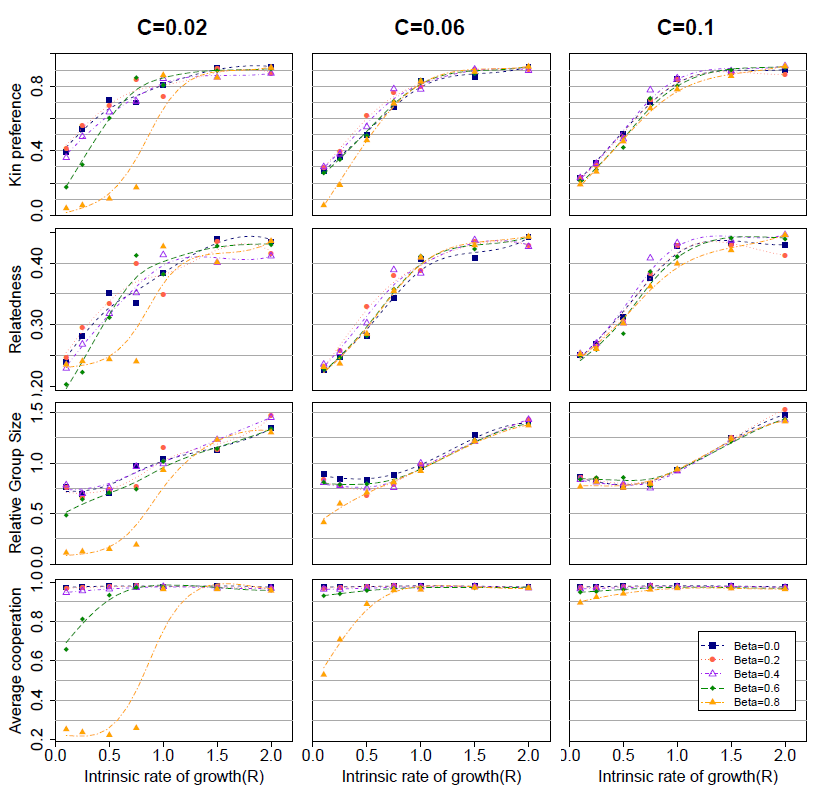
The size of the groups that form depend mainly on the group carrying capacity (r2=63.3) and the intrinsic rate of growth (r2= 15.8), with larger group carrying capacities and rates of growth producing larger groups (figure 2). Again group size is affected little by the cost of cooperation with only 4.7% of the variation in group size being explained by cost of cooperation (table 2), unless the group carrying capacity is high and the intrinsic rate of growth is low in which case groups remain small (figure 2).

It must be noted, however, that the size of groups that form is not due to direct evolution or selection on the size of groups, but rather it is due to the group admission function (equation 2) and how the value of the parameters in the admission function change as the system evolves. The group admission function depends on optimum and stable group size, as well as the levels of kin preference and relatedness within groups. From figure 3 bottom panel, it can be seen that the average group size oscillates around the optimum group size. It never gets near the stable group size with the average group size around 6 orders of magnitude smaller than the stable group size. Using equation (1) van Veelen et al (2010) calculated the equilibrium values for group size as .

The level of cooperation that evolves is relatively invariant, in the majority of parameter combinations, evolving close to 1 (table 2). Counter-intuitively this includes the level of cooperation that evolves evolves, with only 29.9% of the variance in attributable to cost of cooperation, except when both the intrinsic rate of growth is small (< 1.0) and the group carrying capacity, 1/c, is large (C=0.02) (figure 1). In this case increasing the cost of cooperation lowers the average level of cooperation that evolves and therefore also lowers the size of groups that emerge. This could be reflected in the relatively large contribution interaction effects make towards the level of cooperation that evolves (r2= 36.9).

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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 2:** 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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**Figure 3:** Average kin preference, relatedness, relative group size and cooperation against intrinsic rate of growth, Beta (cost of cooperation) and C (inverse of group carrying capacity). Relative group size is calculated by multiplying the average group size by C.

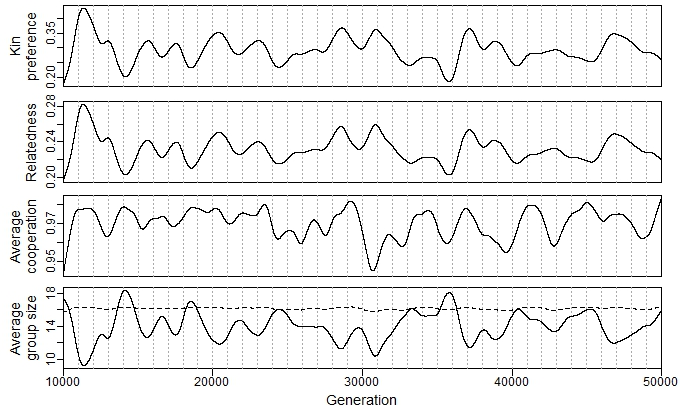
*White noise test and within run correlations*

During every run each output parameter oscillates (see figure 3 for representative run). 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 3).

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).

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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 3:** The Fisher’s κ value and corresponding p value for a randomly choose run (R=0.1, C=0.06, β=0.2) . As all p values were below 0.05 we can conclude that the oscillations we not due to white noise.



**Fig 4:** 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. The dotted line in the bottom panel is the optimum group size.

**Discussion**

It has been demonstrated many times that the evolution of costly altruistic behaviours can be facilitated if social groups restrict themselves to close relatives (refs •••) However, it has not often been considered that there are ecological and demographic factors that can prevent groups form being formed of close relatives and this in turn can affect the evolution of social groups (refs•••). Understanding under what conditions kin preference traits can evolve will give us insight into why and how the evolution and therefore composition of social groups varies between species and environments (Pamilo et al. 1997; Ross 2001; Clutton-Brock 2002; Beckerman et al. 2011).

Our model demonstrates that the ecology and demographic characteristics of a species does have the potential influence the type and composition of social groups that can evolve. Our main finding is that, if the size of the groups is externally determined, the fecundity of the species has the largest effect on the kin composition of groups that were formed. Intriguingly, group carrying capacity and the cost of cooperation to the individual only had a small influence on the evolution of groups, except cases where the intrinsic rate of growth was very low and cost of cooperation high.

*Explanation of effects of R, Beta and C*

Other studies have suggested that there is a trade-off when forming social groups between group size and kin restrictiveness (Avilés et al. 2004; Altmann 1979; Chesser 1998; Lukas et al. 2005) (I need to double check these references). Within this model, however, groups have to reach ecologically determined group size for it to be advantageous to be in a group. Therefore, instead of the size of the group determining how restrictive group entry can be, the number of kin available to form groups, intrinsic rate of growth, limits the kin preference levels that can evolve. As the fecundity of a species increases, more relatives are available to form groups. This, in turn, allows groups the ability to be more restrictive in their admission requirements, thus the level of kin preference exhibited can increase. It should be noted that in this model we represented semelparous species with new groups reforming every generation. If you consider species that breed multiple times close kin groups could be formed by internal recruitment (Avilés et al. 2004) so the fecundity of the species may not be so important.

However, the average group size does change a bit relative to the group carrying capacity. As the intrinsic rate of growth increases so the average group size increases (figure 2). Even though the level of cooperation remains close to one, if groups are too large, cheaters can invade more easily. Allowing only kin group admittance prevents this from occurring. There could therefore be a trade-off between group size and average relatedness within groups, where being unable to restrict your group to kin reduces the size of groups (refs •••) . For example, Lukas et al. (2005) demonstrated that in chimpanzees social groups, demonstrated that the level of relatedness within individual groups was related to the size of the groups.

Counter-intuitively, cooperation nearly always evolves to very high levels. van Veelen et al. (2010) demonstrated analytically using the fitness function we use here (equation 1) , that it pays for an individual to cooperate if it finds itself in a small group that already has a certain average level of cooperation. However it becomes unfavourable to cooperate if an individual finds itself in a large group. ‘Large’ is defined as the point where an increase an individual’s cooperative tendency decreases its overall fitness. What ‘large’ is depends on the ecological constraints of a species and population, such as the cost of cooperation, the group carrying capacity and the average cooperation level within the group an individual finds itself in. As the cost of cooperation and the group carrying capacity increases, so what is considered ‘large’ also increases. From figure 1 van Veelen (2010) they showed that if groups were not ‘large’ then the direction of selection is towards a maximum cooperative tendency and an intermediate group size. However, even though deterministically maximum cooperative tendency is predicated, within the simulation mutation keeps this figure slightly lower.

Within our simulation groups are only ‘large’ when a high cost of cooperation is coupled with a high group carrying capacity. Within nature, this can be considered as the situation when the cost of cooperating is too high or the tasks needed to be performed by a group require so many members, that having only a few individuals cooperating does not increase an individual’s fitness and could even decrease it (eg bark beetles refs •••). However, the reduction in an individual’s direct fitness is mitigated if groups admit only kin. Even with high costs of cooperation and large group carrying capacity, if there are enough kin around high levels of cooperation and altruism can evolve. An example of organisms where restrictive kin admission rules allows the formation of very large social groups is the eusocial insects eg (••••)

Interestingly we show that kin preference does not go to zero, even for very small rates of growth. This may be because leaving relatives out of a group has an indirect fitness cost as these individuals will be eliminated from the population. So this implies that groups forming in nature will not purposefully exclude from social groups (unless there is direct competition between kin)

*Explanations of correlations within runs*

Another interesting result is the periodic cycles that emerge within individual runs, with cooperation correlated with group size, both of which are counter-correlated with relatedness and kin preference. It is obvious that relatedness should be correlated with kin preference. 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 within the runs, entry to groups becomes more restrictive and therefore group sizes decreases. It should be noted that this is contrary to the overall averages (figure 2), where an increased kin preference is correlated with an increase in group size. Within runs there is likely to be a direct causal effect of kin preference to group size, but other factors affect kin preference and group size when comparing between runs with different parameter values.

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). As the average level of cooperation increases, so the optimum group size increases which causes group size to increase and vice versa.

The cycling observed and the counter-correlation between the cooperation/group size and kin preference/relatedness time series is interesting. It is plausible that as kin preference, and thus degree of relatedness within groups, increases, greater levels of cooperation evolve, albeit with a certain time lag. Greater levels of cooperation, however, favour the formation of larger groups due to the increase in the optimum group size. 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.

Modelling the evolution of cooperation and kin preference as a two trait optimization process has demonstrated that how restrictive a group can be admitting only kin depends on the demographic and ecological characteristics of a species or population. However it is also of note that being unable to restrict your group to kin does not affect the level of cooperation that evolves, except when the cost to the individual of cooperation is very high and the ecologically determined optimum group size is hard to attain.