**The evolution of kin preferences and the kin composition of social groups**

**v. 13 Feb 2013, for Avilés lab meeting**

**L. Aviles, J. García, and R. Sharpe**

**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. Therefore one might expect that, given a choice, social groups will tend to be formed with close relatives. However, some studies that measured intergroup relatedness in social groups found lower levels of relatedness than expected (refs from LA 2004), which suggests that in order to understand the evolution of group living it is not sufficient to only consider genetic relatedness. We also need to consider the costs and benefits of group living from an ecological perspective

Ultimately, individuals form groups because their fitness is increased if they are in a group compared to being a lone individual. This can be seen in lions and African wild dogs which are able to defend kills from hyenas for longer when in larger groups (Cooper, 1991; Fanshawe and Fitzgibbon, 1993), flocks of birds where more eyes means a greater chance of spotting a food source e.g. (Drent and Swierstra, 1977; Templeton and Giraldeau, 1995, 1996), colonial nesting bird where group living helps protect nests from predators e.g. (Picman et al., 1988; Robinson, 1985) or the colonization of harsh environment such as social spiders which are able to capture prey far too large for them to capture individually, thus allowing them to colonize habitats that they wouldn’t be able to if solitary (Various references ••••).

However there are also costs to forming groups which include competition between group members for food or space eg (Grant et al., 2002; Sirot, 2000; Stillman et al., 2000), mate competition eg (Dobson, 1982; Keddar et al., 2013; Perrin and Mazalov, 2000) and increased conspicuousness to predators (Cresswell, 1994; Lindström, 1989) with these costs potentially increasing as group size increases this can limit the size of groups that form. In this paper we are assuming therefore, that the function linking individual fitness to group size is a unimodal humped function with individual fitness being maximized at some intermediate group size (eg (Aviles and Tufino, 1998).

However the costs and benefits of group living are not necessarily evenly distributed amongst all group members. For example, if interactions take place between two individuals, each individual can have differing fitness gains or losses. Strongly altruistic behavior has been therefore been defined as a behaviour performed by an individual that reduces that individual’s fitness but increases the fitness of others (Fletcher and Zwick, 2004). For example it is know that vampire bats will regurgitate blood for other individuals who have been unable to feed (Wilkinson, 1984). This is reflected in our model as a cost of cooperation whereby an individual that cooperates has a fitness loss, which can be offset if there are sufficient cooperators within the group.

Therefore an individual could take advantage of the systems by gaining fitness benefits from others, but not contributing in return with non-cooperators would benefit at the expense of cooperators. Groups can avoid this situation by restricting entry to groups only to kin, allowing the evolution of highly altruistic behaviors, as evidenced by eusocial insects (Bourke, 1995; Crozier and Pamilo, 1996; Hughes et al., 2008; Queller and Strassmann, 1998) (Crozier and Pamilo, 1996; Foster et al., 2006; Hughes et al., 2008; Queller and Strassmann, 1998)

However this cannot be the only explanation for the evolution of highly altruistic behaviours as there are many altruistic behaviours that occur between non-kin. There may be extrinsic or intrinsic factors that prevent groups being restricted to only close kin. 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 such as in the Australian cloughs which need a minimum of four individuals to raise one chick per year (Heinsohn, 1992). As the reproductive rate of these birds is low they kidnap and raise birds from other groups to help with brood care (Heinsohn, 1991). or the size of the groups that need to be formed is large so that locating close relatives or building up a group with a sufficiently large number of close relatives is not practical. For example the tree-killing bark beetle needs a large number of individuals to overcomes a tree’s defences to gain resources (Raffa and Berryman, 1987). The kin composition of social groups may thus largely be determined by demographic and ecological factors that cannot be circumvented, a possibility that has hardly been considered (but see Avilés et al. 2004). Here we investigate the evolution of kinship rules of admission using 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 base our model on the equation proposed by Avilés (1999) where cooperative interactions have a synergistic effect on fitness. This model has previously been 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 earlier 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. Additionally we find that cooperation evolves to high levels in the majority of parameter combinations. 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 among members 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 come together in one-generation breeding associations where they perform tasks more efficiently together than alone, as in Aviles et al (2002, 2004) and van Veelen et al (2010). This is appropriate for species that form breeding colonies such as the fieldfare (Wiklund, 1982), redwing blackbirds (Picman et al., 1988) . The size of the groups formed reflects the expected balance between costs and benefits of group living, given an externally-imposed group carrying capacity and the average cooperative tendencies of existing group members. Within groups, the extent to which individuals help one another is determined by individually coded “cooperative” tendencies. Cooperation increases group productivity, but lowers the relative fitness of cooperators within their group depending on the cost of cooperation. In addition to being dependent on a group’s current size, the admission of particular individuals to a given group depends on its degree of relatedness to existing group members, as a function of the individual’s genetically coded kin preference and the average kin preference of existing group members. Both individual cooperative tendencies and the strength of kin preference evolve in the simulations.

*Per Capita Group Productivity and Relative Fitness within Groups*

We assume that the number of offspring produced per capita is maximized in groups of intermediate size, reflecting a balance between benefits (e.g. protection from predators, greater foraging success) and costs (e.g. crowding, resource competition) of group living.

As in earlier models (Avilés, 1999, 2002, Avilés et al., 2002, 2004; van Veelen 2010), we assume that the number of offspring produced by an individual is a function of the size of its group, the average cooperative tendencies of group members, and the cooperative tendencies of the individual itself, according to the function,

|  |  |
| --- | --- |
| , | (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 group living 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, which would occur 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 (Burland et al., 2002; Faulkes et al., 1997) 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

|  |  |
| --- | --- |
|  | (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 groups form at a size between the optimum and stable group size, as is often observed in natural populations (Giraldeau, 1988).

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

|  |  |
| --- | --- |
|  | (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 associating with kin. 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 of earlier simulations (Avilés et al. 2004), 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 existing group members. *m* corresponds to the genetically-coded kinship preference levels.

*Simulation and analysis* *(Statistical description of method closely based on AmNat 2002 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.

|  |  |
| --- | --- |
| 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 and their second- and third-order polynomials and their interactions. We customized the test for each response variable by dropping all nonsignificant (P>0.05) terms and their interactions. The r2 of the reduced models ranged from 84.3-94.4% (see table 2). Kin preference and average cooperative tendencies were arcsine transformed, while relatedness and group size were log transformed prior to analysis.

Additionally each individual run was tested to see if there were correlations between average group size, relatedness within groups, cooperation and kin preference. This was done by determining the maximum absolute value of the maximum cross-correlation and the time lag at which this maximum occurs for each run using the cross-correlation function in R. The maximum time lag tested set to 5000 generations. The first 10000 generations were removed from each run and the data was transformed to ensure the data was stationary, see (Probst et al., 2012). The mean maximum correlation and mean lag at maximum correlation was calculated with one outlier removed from the mean correlation between group size against relatedness calculation as for every run the lag at maximum absolute correlation was zero except for this one outlier which had a value of 1848 generations.

**Results**

*Kin preference, relatedness, cooperation and group size*

In the simulations, the intrinsic rate of growth, *r*, was the main determinant of the level of kin preference that evolved. As *r* increased so did the genetically-coded level of kin preference, until a value of about 0.9 was reached (figure 2). Along with an increase in the degree of kin preference, the degree of relatedness within groups also increased. Therefore the intrinsic rate of growth largely dictated the kin composition of the groups formed, explaining 88.4% of the variance in kin preference and 90.7% of the degree relatedness within groups. Surprisingly, the cost of cooperation had little effect on the degree of kin preference that evolved (2.31% of the variance), except when the intrinsic rate of growth was small and the group carrying capacity large, in which case high costs of cooperation were correlated with lower cooperative tendencies, smaller groups, and groups that were less restrictive in their degree of kin preference (figure 2).

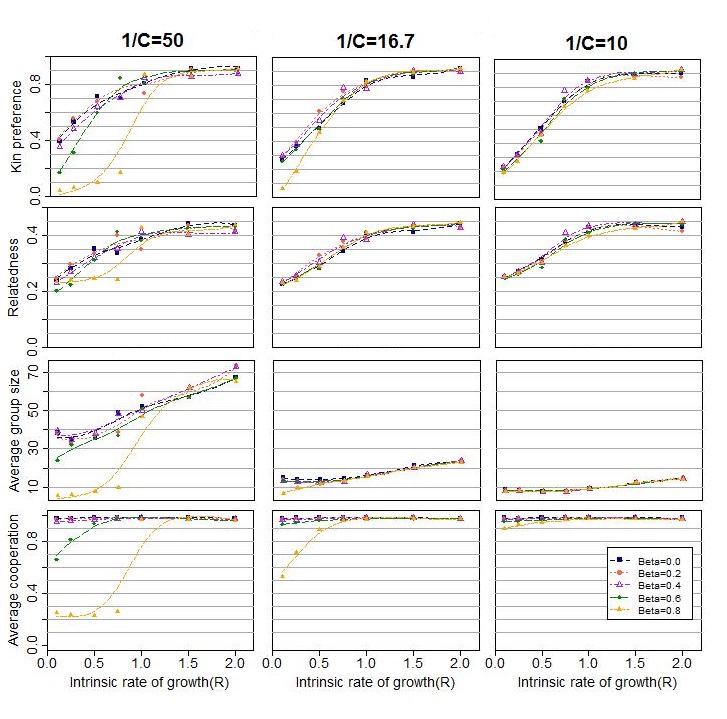
The size of the groups that formed depended mainly on the group carrying capacity (63.3% of the variance) and the intrinsic rate of growth (15.8%), with larger group carrying capacities and rates of growth producing larger groups (figure 2). Again group size was affected little by the cost of cooperation with only 4.7% of the variance in group size explained by this parameter (table 2), except when the group carrying capacity was high and the intrinsic rate of growth low, in which case the groups formed were small (figure 2).

It must be noted that the size of groups that formed was not under direct selection, but rather reflected how the value of the parameters in the group admission function (equation 2) changed as the system evolved. The group admission function depends on optimum and stable group sizes, which are both a function of the group carrying capacity (a non-evolving parameter of the model) and the evolving cooperative tendencies of group members (Avilés 1999; Avilés et al. 2004; van Veelen et al. 2010), with the stable group size being also a function of the intrinsic rate of growth (Avilés 1999). Larger groups also formed as the levels of kin preference and relatedness within groups increased. From figure 3 (bottom panel), it can be seen that the average size of the groups oscillates just below or around the optimum group size. It never gets near the stable group size with the average group size around 6 times smaller than the stable group size. From equation (1), the optimum group size can be calculated as (Avilés et al., 2004; van Veelen et al., 2010).

The level of cooperation that evolved was relatively invariant, evolving close to 1 under the majority of parameter combinations (table 2). Counter-intuitively, this included cases where cost of cooperation was high, except when both the intrinsic rate of growth was small (< 1.0) and the group carrying capacity, 1/c, was large (C=0.02) (figure 1). In the latter case, increasing the cost of cooperation lowered the average level of cooperation that evolved and also the size of groups formed. This could be reflected in the relatively large contribution interaction effects make towards the level of cooperation that evolved (36.9% of the variance). Only 29.9% of the variance in cooperative tendencies was attributable to the costs of cooperation. Interestingly relatedness does not drop below 0.2 even if kin preference is close to zero.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Parameter | Kin Preference | Relatedness | Group size | Cooperative tendencies |
| r (intrinsic rate of growth) | 85.27 | 90.48 | 17.30 | 10.66 |
| C (inverse of group carrying capacity) | 0.04 | 0.49 | 62.30 | 7.36 |
| β (cost of cooperation) | 3.64 | 0.44 | 4.16 | 28.70 |
| Interactions | 4.33 | 0.00 | 10.61 | 38.13 |
| Total (r2) | 93.29 | 91.38 | 94.38 | 84.85 |

**Table 2:** Percentage variance explained by each of the parameters of the model for the average kin preference, relatedness, group size, and level of cooperation that evolved in the simulations once equilibrium had been reached.

****

**Figure 3: Global** 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.

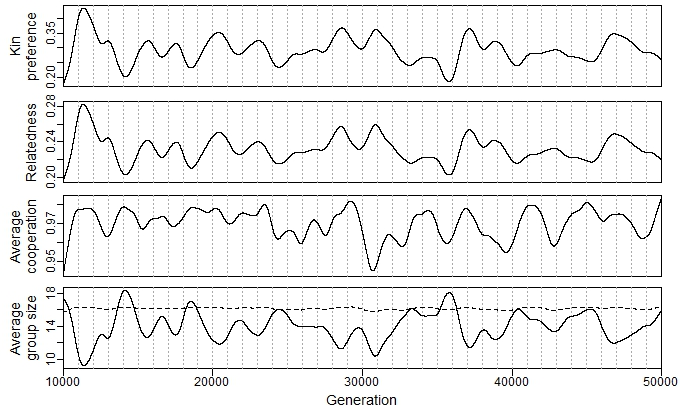
*White noise test and within run correlations*

During every run each output parameter oscillated (see figure 3 for representative run). Significant values of the Fisher's κ statistic carried out on 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 are 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).

|  |  |  |
| --- | --- | --- |
| **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.

Group size is highly counter-correlated with relatedness at a lag of zero, meaning that as group size increases relatedness decreases at the same time (table 4, figure 4). Group size is slightly, but significantly, correlated with cooperation at a time lag in 55 runs but with a time lag of zero in 60 runs. Cooperation and relatedness are correlated with a time lag, whereas kin preference and group size are counter-correlated with a time lag (table 4)

|  |  |  |
| --- | --- | --- |
|  | Mean maximum correlation | Mean absolute Lag |
| Group size vs relatedness | -0.79 | 0.0 |
| Average group size vs cooperation | 0.13 | 371 |
| Cooperation vs relatedness | 0.12 | 924 |
| Kin preference vs group size | -0.58 | 72 |

Table 4: Mean correlation and the absolute lag between various outputs. The correlations and lags were calculated independently for each run and the mean was calculated from each of these. If the mean correlation is negative then the outputs are counter-correlated. All correlations are significant.

**Discussion**

It has been demonstrated many times that the evolution of costly altruistic behaviours can be facilitated when groups consist of close relatives eg (Crozier and Pamilo, 1996; Eberhard, 1975; Foster et al., 2006; Hughes et al., 2008). However, it has not often been considered that there are ecological and demographic factors that may prevent groups from restricting themselves to close kin (but, see Avilés et al. 2004). Understanding the conditions that influence the evolution of kinship rules of admission will thus give us insight into why and how the composition of social groups varies among species and environments (Beckerman et al., 2011; Clutton-Brock, 2002; Pamilo et al., 1997; Ross, 2001).

Our model shows how the demographic characteristics of a species play a fundamental role in determining the kin composition of its social groups. 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. Intriguingly, the group carrying capacity and the cost of cooperation only had a small influence on the composition of the social groups, except in cases where the intrinsic rate of growth was very low and costs of cooperation high (Fig. 3).

*Explanation of effects of r, Beta and c*

Other studies have suggested that there should be a trade-off when forming social groups between group size and kin restrictiveness (Altmann, 1979; Avilés et al., 2004; Chesser, 1998; Lukas et al., 2005). Our evolutionary simulations demonstrate that if groups must reach a certain size for the full advantage of group living to be realized, the fecundity of a species is the most powerful determinant of the level of kin preference that evolves and thus the kin composition of the groups that form. As the fecundity of a species increases, more relatives are available to form groups. This, in turn, allows groups to be more restrictive in their admission requirements, thus the level of kin preference exhibited can increase. This is a very important point as it is rarely considered that the ecology of a species could have a large effect on the degree and nature of group living that evolves. This has been demonstrated empirically in chimpanzees where the level of relatedness within groups was related to the size of the groups, with smaller groups consisting of closer kin than larger groups. However it should be noted that in this model we represented semelparous species with new groups reforming every generation. If one considers species that reproduce multiple times, given enough time, groups of close kin could be formed by internal recruitment (Avilés et al., 2004), in which case the fecundity of the species may not be as important.

It is also interesting to note that average relatedness does not drop below 0.20 even if kin preference is close to zero (figure 3). This could be because when the growth rate is low the global population is small. If there is a small global population then the relatedness within the global pool will be greater than zero so relatedness within groups to also be above zero purely by chance. If this is the case there is no need for kin preference to evolve until the global population increases. This situation might arise in species that have a low fecundity that is coupled with short dispersal distances.

Counter-intuitively, under the majority of parameter combinations, cooperation evolves to a high level, even if relatedness within groups remains low. 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 a further increase in an individual’s cooperative tendency would decrease its absolute 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, what is considered ‘large’ also increases. From van Veelen (2010,figure 1) it is demonstrated 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 predicted, 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) 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.

Alternatively this high level of relatedness could simply be caused by the average relatedness always being above 0.2. As can be seen from (Avilés et al., 2004), if the cost of cooperation is below 0.6 or 0.4, high levels of cooperation can evolve if the social groups contain at least cousins, with cousins having a relatedness coefficient of 0.12.

*Explanations of correlations within runs*

Another interesting result is the periodic cycles that emerge within individual runs. A possible explanation of the cycles and the correlations observed is that as kin preference, and thus degree of relatedness within groups, increases, greater levels of cooperation are able to 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 Group size is positively correlated with cooperation which could reflect 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).This could explain the observed positive correlation between group size and cooperation. The formation of larger groups may then require less restrictive admission requirements, causing the kin preference rules to bounce back to lower levels which could explain the counter-correlation at a lag between kin preference and group size. 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.

It also must be noted that examining the correlation within runs gives us a different perspective on the evolution of the various grouping traits by allow us to get an idea of how the traits could influence each other directly rather than on average as we got from our previous analysis. Within runs there is likely to be a direct causal effect between the parameters, but other factors could affect the patterns observed when comparing between runs.

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 ones 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 difficult to attain.

Literature Cited

Altmann, J. (1979). Age Cohorts as Paternal Sibships. Behav. Ecol. Sociobiol. *6*, 161–164.

Aviles, L. (1997). Causes and consequences of cooperation and permanent-sociality in spiders. In The Evolution of Social Behaviour in Insects and Arachnids, (Cambridge University Press), pp. 476–498.

Aviles, L., and Tufino, P. (1998). Colony size and individual fitness in the social spider Anelosimus eximius. Am. Nat. *152*, 403–418.

Avilés, L., Fletcher, J.A., and Cutter, A.D. (2004). The kin composition of social groups: trading group size for degree of altruism. Am. Nat. *164*, 132–144.

Beckerman, A.P., Sharp, S.P., and Hatchwell, B.J. (2011). Predation and kin-structured populations: an empirical perspective on the evolution of cooperation. Behavioral Ecology *22*, 1294–1303.

Bourke, A.F.G. (1995). Social evolution in ants (Princeton University Press).

Burland, T.M., Bennett, N.C., Jarvis, J.U.M., and Faulkes, C.G. (2002). Eusociality in African mole-rats: new insights from patterns of genetic relatedness in the Damaraland mole-rat (Cryptomys damarensis). Proc. R. Soc. Lond. B *269*, 1025–1030.

Chesser, R.K. (1998). Relativity of behavioral interactions in socially structured populations. J. Mammal. *79*, 713–724.

Clutton-Brock, T. (2002). Behavioral ecology - Breeding together: Kin selection and mutualism in cooperative vertebrates. Science *296*, 69–72.

Cooper, S. m. (1991). Optimal hunting group size: the need for lions to defend their kills against loss to spotted hyaenas. African Journal of Ecology *29*, 130–136.

Cresswell, W. (1994). Flocking is an effective anti-predation strategy in redshanks, Tringa totanus. Animal Behaviour *47*, 433–442.

Crozier, R.H., and Pamilo, P. (1996). Evolution of social insect colonies: sex allocation and kin selection (Oxford University Press).

Dobson, F. (1982). Competition for Mates and Predominant Juvenile Male Dispersal in Mammals. Anim. Behav. *30*, 1183–1192.

Drent, R., and Swierstra, P. (1977). Goose flocks and food finding: field experiments with barnacle geese in winter. Wildfowl *28*, 15–20.

Eberhard, M.J.W. (1975). The Evolution of Social Behavior by Kin Selection. The Quarterly Review of Biology *50*, 1–33.

Fanshawe, J.H., and Fitzgibbon, C.D. (1993). Factors influencing the hunting success of an African wild dog pack. Animal Behaviour *45*, 479–490.

Faulkes, C.G., Abbott, D.H., O’Brien, H.P., Lau, L., Roy, M.R., Wayne, R.K., and Bruford, M.W. (1997). Micro- and macrogeographical genetic structure of colonies of naked mole-rats Heterocephalus glaber. Molecular Ecology *6*, 615–628.

Fletcher, J.A., and Zwick, M. (2004). Strong altruism can evolve in randomly formed groups. J. Theor. Biol. *228*, 303–313.

Foster, K.R., Wenseleers, T., and Ratnieks, F.L.W. (2006). Kin selection is the key to altruism. Trends Ecol. Evol. *21*, 57–60.

Giraldeau, L.-A. (1988). The stable group and the determinants of foraging group size. (Academic Press Inc., San Diego, New York etc.).

Grant, J.W., Girard, I.L., Breau, C., and Weir, L.K. (2002). Influence of food abundance on competitive aggression in juvenile convict cichlids. Animal Behaviour *63*, 323–330.

Heinsohn, R.G. (1991). Kidnapping and reciprocity in cooperatively breeding white-winged choughs. Animal Behaviour *41*, 1097–1100.

Heinsohn, R.G. (1992). Cooperative enhancement of reproductive success in white-winged choughs. Evolutionary Ecology *6*, 97–114.

Hughes, W.O.H., Oldroyd, B.P., Beekman, M., and Ratnieks, F.L.W. (2008). Ancestral monogamy shows kin selection is key to the evolution of eusociality. Science *320*, 1213–1216.

Keddar, I., Andris, M., Bonadonna, F., and Dobson, F.S. (2013). Male-Biased Mate Competition in King Penguin Trio Parades. Ethology *119*, 389–396.

Lindström, \AAke (1989). Finch flock size and risk of hawk predation at a migratory stopover site. The Auk 225–232.

Lukas, D., Reynolds, V., Boesch, C., and Vigilant, L. (2005). To what extent does living in a group mean living with kin? Molecular Ecology *14*, 2181–2196.

Pamilo, P., Gertsch, P., Thoren, P., and Seppa, P. (1997). Molecular Population Genetics of Social Insects. Annual Review of Ecology and Systematics *28*, 1–25.

Perrin, N., and Mazalov, V. (2000). Local Competition, Inbreeding, and the Evolution of Sex‐Biased Dispersal. The American Naturalist *155*, 116–127.

Picman, J., Leonard, M., and Horn, A. (1988). Antipredation role of clumped nesting by marsh-nesting red-winged blackbirds. Behav Ecol Sociobiol *22*, 9–15.

Probst, W.N., Stelzenmüller, V., and Fock, H.O. (2012). Using cross-correlations to assess the relationship between time-lagged pressure and state indicators: an exemplary analysis of North Sea fish population indicators. ICES Journal of Marine Science: Journal Du Conseil *69*, 670–681.

Queller, D.C., and Strassmann, J.E. (1998). Kin selection and social insects. Bioscience *48*, 165–175.

Raffa, K.F., and Berryman, A.A. (1987). Interacting Selective Pressures in Conifer-Bark Beetle Systems: A Basis for Reciprocal Adaptations? The American Naturalist *129*, 234–262.

Robinson, S.K. (1985). Coloniality in the Yellow-rumped Cacique as a defense against nest predators. The Auk 506–519.

Ross, K.G. (2001). Molecular ecology of social behaviour: analyses of breeding systems and genetic structure. Mol. Ecol. *10*, 265–284.

Sirot, E. (2000). An evolutionarily stable strategy for aggressiveness in feeding groups. Behavioral Ecology *11*, 351–356.

Stillman, R.A., Goss-Custard, J.D., and Alexander, M.J. (2000). Predator search pattern and the strength of interference through prey depression. Behavioral Ecology *11*, 597–605.

Templeton, J.J., and Giraldeau, L.-A. (1995). Public information cues affect the scrounging decisions of starlings. Animal Behaviour *49*, 1617–1626.

Templeton, J.J., and Giraldeau, L.-A. (1996). Vicarious sampling: the use of personal and public information by starlings foraging in a simple patchy environment. Behavioral Ecology and Sociobiology *38*, 105–114.

Van Veelen, M., García, J., and Avilés, L. (2010). It takes grouping and cooperation to get sociality. Journal of Theoretical Biology *264*, 1240–1253.

Wiklund, C.G. (1982). Fieldfare (Turdus pilaris) Breeding Success in Relation to Colony Size, Nest Position and Association with Merlins (Falco columbarius). Behavioral Ecology and Sociobiology *11*, 165–172.

Wilkinson, G.S. (1984). Reciprocal food sharing in the vampire bat. Nature *308*, 181–184.