Comment

Assortment, Hamilton's rule and multilevel selection

Explaining the evolution of cooperation has been under debate for a long time (reviewed in Frank 1998; Lehmann & Keller 2006). Cooperative traits impose a cost on the individual exhibiting the trait to the benefit of other individuals. Prevailing explanations focus on interactions among genetically related individuals (kin selection; Hamilton 1964) and on selection acting at multiple levels of biological organization (multilevel or group selection; Wilson 1975), and both approaches have been shown to be mathematically equivalent (Queller 1992; Bijma & Wade 2008).

Recently, Fletcher & Doebeli (2009; hereafter FD09) elegantly showed that the fundamental requirement for the evolution of cooperation is the assortment between individuals carrying the cooperative genotype and the helping behaviour of others with which these individuals interact. Assortment was previously discussed by Hamilton (1971) and Eshel & Cavalli-Sforza (1982). FD09 also provide an expression of Hamilton's rule and show that, in the context of Hamilton's rule, 'relatedness' is a measure of assortment, irrespective of the mechanisms creating such assortment. Genetic relatedness is merely one of the possible mechanisms that can create the required assortment, rather than the fundamental requirement for the evolution of cooperation.

Pepper (2000) showed that for social traits a distinction can be made between traits that benefit the whole group, including the actor itself ('whole-group traits'), and traits that benefit only group members other than the actor ('other-only traits'). FD09 considered a whole-group trait. Following the biology of their trait (the production of a public good), they specify whole-group benefits and derive a whole-group expression for relatedness, meaning an expression for relatedness including the focal individual itself.

This expression for relatedness presented by FD09 disagrees with some previous statistical interpretations of relatedness as a regression coefficient (discussed extensively in Frank 1998). In the model of FD09, random association, for example, corresponds to a positive relatedness equal to $1/N$, where N denotes group size, rather than a relatedness of zero. This disagrees with the interpretation of relatedness as a regression coefficient, which would be zero with random association. Similarly, maximum negative assortment corresponds to zero relatedness in FD09, rather than to negative relatedness.

Here, we show that these discrepancies originate from the definition of cost and benefit in FD09,

where an amount b/N of the benefit provided by a cooperator feeds back on the cooperator itself (whole-group definition of benefit; Pepper 2000). Those definitions differ from Hamilton's (1964) original parameterization, which refers to net cost and benefit of cooperative behaviour. Irrespective of the biology of a trait, however, that is, whole-group or other-only, one can parameterize social evolution in terms of either whole-group benefits or other-only benefits. Both parameterizations yield different but mathematically equivalent results (Pepper 2000).

By reparameterizing the model of FD09 into net cost to self and net benefit to others, we obtain a measure of relatedness that agrees with previous definitions. This parameterization also connects association to group selection, and extends naturally to interactions between different species. The result shows that the relevant measure of association is the regression coefficient of the phenotype of the partner (i.e. cooperate or defect) on the gene in the focal individual. Our result is mathematically equivalent to that of FD09, but our parameterization clarifies the relationship of assortment with kin and group selection theory. The biological interpretation of the difference between the definitions of r is the inclusion or exclusion of the benefit provided by the focal individual to itself.

In summary, FD09 consider the public goods game in which there are two possible strategies; cooperate (C), which provides a benefit b/N to each of the N group members (including the cooperator itself) at a cost c to the cooperator, and defect (D) which provides no benefit and has no cost. On average across all interaction groups, e_C is the average number of cooperators among the $N - 1$ interaction partners of a cooperator. Analogously, e_D is the average number of cooperators among the $N - 1$ interaction partners of a defector. Therefore, e_C and e_D are the parameters describing association.

We reparameterize this model into net cost to self, c' , and net benefit to others, b' . Net cost to self equals the cost of the behaviour minus the benefit received from own behaviour, $c' = c - b/N$ (table 2, FD09). Net benefit to others equals total benefit minus benefit feeding back to self, $b' = b - b/N$. Solving those expressions for b and c yields $b = b'N/(N - 1)$ and $c = c' + b'/(N - 1)$. Substituting those results into equation 2.3 of FD09 yields Hamilton's rule expressed in terms of net cost and benefit,

$$\left(\frac{e_C - e_D}{N - 1}\right)b' > c'$$

where $r = (e_C - e_D)/(N - 1)$ plays the role of 'relatedness'. Therefore, r equals the difference in the number of

cooperators among the interaction partners between a cooperator and a defector, $e_C - e_D$, divided by the total number of interaction partners of an individual. It is the difference in the proportion of interaction partners providing help between cooperators and defectors.

This result connects assortment to previous definitions of 'relatedness'. The definition of $r = (e_C - e_D)/(N-1)$ is identical to both the regression coefficient and the correlation coefficient of the gene in the partner on the gene in the focal individual (appendix A), which agrees with previous statistical interpretations of 'relatedness' as a regression coefficient (Frank 1998).

The lowest possible relatedness is obtained with maximum negative assortment, for which $e_C - e_D = -1$ and $r = -1/(N-1)$. As expected, this is a negative value rather than zero, indicating that group members are dissimilar with negative assortment. The value of $r = -1/(N-1)$ can be recognized as the lower bound for an intra-class correlation; a lower value of r would imply that the variance of the mean allele frequencies of groups would be a negative value, which is impossible (Bijma & Wade 2008). When $r = -1/(N-1)$, the variance of mean allele frequency among groups is precisely zero (appendix A), meaning that all groups have exactly the same composition. Thus, maximum negative assortment can be achieved with a single cooperator and $(N-1)$ defectors in each group, as indicated in FD09, but also with, for example, two cooperators and $(N-2)$ defectors in each group, and in fact with any group composition, as long as composition is identical for all groups.

This result connects assortment to multilevel selection. As soon as assortment exceeds its lower bound, $r > -1/(N-1)$, then there is variation in the number of cooperators among groups, and thus variation in mean fitness among groups. Hence, assortment, as measured by $r > -1/(N-1)$, is a fundamental requirement for multilevel selection to occur.

Also in the context of mutualistic cooperation between different species, it makes sense to use net cost to self and net benefit to others instead of gross values; the benefits provided by an individual of one species to an individual of a different species do not usually directly feed back to that same individual. Frank (1994) was the first to propose a measure of 'between-species relatedness' for mutualisms, defined as the regression coefficient of the mutualists' genotypic value on individual host genotypes, which agrees with the result obtained here when using net cost and benefit in the model of FD09 (appendix A). Note that with interactions between members of different species, r can take values in the full range of -1 to $+1$, so that the lower bound for 'relatedness' does not apply.

P. Bijma^{1,*} and D. K. Aanen²

¹Animal Breeding and Genomics Centre,
Wageningen University and Research Centre, PO 338,
6700AH Wageningen, The Netherlands

²Department of Plant Sciences, Laboratory of Genetics,
Wageningen University and Research Centre, 6703BD
Wageningen, The Netherlands

*Author for correspondence (piter.bijma@wur.nl).

APPENDIX A

(a) Assortment as regression or correlation

Let g_1 denote the gene in a focal individual and g_2 the gene in its group member ($g = 1$ for a C individual and $g = 0$ for a D individual), and let p denote the frequency of the cooperative gene in the entire population. Then the correlation between genes in group members equals $\text{Corr}(g_1, g_2) = \text{Cov}(g_1, g_2) / (\sigma_{g_1} \sigma_{g_2}) = \text{Cov}(g_1, g_2) / \sigma_g^2$, where $\sigma_g^2 = p(1-p)$ is the variance of allele frequency among individuals in the entire population. By definition, $\text{Cov}(g_1, g_2) = E(g_1 g_2) - E(g_1)E(g_2)$, where E denotes expectation. The $E(g_1 g_2)$ is obtained as the weighted average over C and D focal individuals, where allele frequency in the focal individual is given by $g_1 = 1$ for a C individual and $g_1 = 0$ for a D individual, and allele frequency in the group member is given by $g_2 = e_C/(N-1)$ for a C focal individual, and $g_2 = e_D/(N-1)$ for a D focal individual. This gives $E(g_1 g_2) = p \cdot 1 \cdot e_C/(N-1) + (1-p) \cdot 0 \cdot e_D/(N-1) = p e_C/(N-1)$. Furthermore, $E(g_1) = E(g_2) = p$. However, $E(g_2)$ can also be written as the weighted mean allele frequency in partners of C and D focal individuals, $E(g_2) = p e_C/(N-1) + (1-p) e_D/(N-1)$. Combining results yields $\text{Cov}(g_1, g_2) = p(1-p)[(e_C - e_D)/(N-1)]$, so that $\text{Corr}(g_1, g_2) = (e_C - e_D)/(N-1)$. Because $\sigma_{g_1} = \sigma_{g_2}$, this is also the regression coefficient of the allele in the partner on the allele in the focal individual (and vice versa). Moreover, $(e_C - e_D)/(N-1)$ also equals the correlation between the gene in the focal individual and the benefit experienced by the focal individual, because replacing the gene in the partner by benefit provided by the partner, that is, replacing $g_2 = 0$ or 1 with $g_2 = 0$ or b , yields the same result. When interactions are between species, the covariance term remains the same, and the variance of allele frequency among focal individuals equals $\text{Var}(g_1) = p(1-p)$, so that $(e_C - e_D)/(N-1) = \text{Cov}(g_1, g_2) / \text{Var}(g_1)$, which is the regression coefficient of the phenotypic type of the partner (i.e. 1 denoting a cooperator or 0 denoting a defector) on the gene in the focal individual.

(b) Variance of mean allele frequency among groups

Mean allele frequency of a group equals $\bar{g}_{\text{group}} = \frac{1}{N} \sum_{i=1}^N g_i$. The variance thereof equals $\text{Var}(\bar{g}_{\text{group}}) = \frac{1}{N^2} [N\sigma_g^2 + N(N-1)\text{Cov}(g_i, g_j)]$. Substituting $\text{Cov}(g_i, g_j) = r\sigma_g^2$ yields $\text{Var}(\bar{g}_{\text{group}}) = \frac{\sigma_g^2}{N} [1 + (N-1)r]$. Hence, $\text{Var}(\bar{g}_{\text{group}})$ is zero when $r = -1/(N-1)$, and $\text{Var}(\bar{g}_{\text{group}})$ increases with increasing r .

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