Multilevel selection on quantitatively evolvable selfishness gives rise to rock-paper-scissor like dynamics.

Shreya Ray

Manawa Diwekar

Milind Watve \*

Indian Institute of Science Education and Research, Pune

Dr. Homi Bhabha Road

Pashan  
Pune 4110 021

India.

\*Corresponding author email: milind@iiserpune.ac.in

**Whether behavioural traits beneficial for a group but detrimental to an individual will evolve owing to between group selection being more effective than within group selection is an unresolved debate in evolution. Most group selection models treat altruistic and selfish behaviors as qualitatively distinct traits. We treat altruism and selfishness on a continuum such that the level of selfishness along this continuum can freely evolve. This approach reveals that the net or realized fitness arising out of the interaction of within and between group selection as a function of selfishness level is non-monotonic. If the absolute selfishness level decides within and between group fitness, a stable optimum level of selfishness evolves. However if the fitnesses are decided by relative selfishness, a rock-paper-scissor like dynamics arises between low, moderate and high selfishness levels. Removing group selection leads to a monotonic increase in selfishness so that sociality becomes extinct. Therefore even a weak form of group selection which is not sufficient to fix an altruistic allele, has important consequences for the evolutionary dynamics of social behavior.**

Multilevel selection operates when the costs and benefits of a behavior are executed at different levels. For example if the cost goes to the actor and benefit is shared by a group it is called altruistic behaviour and when benefit is enjoyed by the actor and cost is shared by the group it is selfish behavior. The principles behind the evolution and stability of social behavior and particularly those involving altruistic characters are still largely debated1. Group selection is one of the earliest explanations for the evolution and stability of socially beneficial behaviors that exert a cost on individuals. Seeds of the concept existed from the time of Darwin but the concept was stated more clearly by Carr-Saunders2 and developed further by Wynne Edwards3. Facing severe criticism in the 1960s and 70s the original concept underwent many revisions and variations4, variously called ‘group selection’, ‘interdemic selection’, ‘intrademic group selection ’ or ‘multilevel selection’. After more than half a century the debate has not died down but renewed with a new vigor5. Much of the debate is because of semantic confusion6. Unlike the semantic debate, most mathematical models7–13 converge on the inference that group selection “works” i.e. can lead to evolution of group beneficial traits under a certain set of conditions but how realistic are the conditions is debated9,14,15. A number of experiments claim to have demonstrated that between group selection can be a significant force in evolving group beneficial traits in experimental populations 16. Interestingly the debate appears to have got arrested into a narrow vision of whether or not altruism will evolve by between group selection. As a result other interesting aspects and outcomes of the interaction of two or more levels of selection have largely remained unexplored. Using models similar to the traditional models but asking a set of different questions we show here that an interaction of within and between group selection is necessary for social behavior to exist. Sociality is unlikely to evolve and stabilize if selection operates on only a single level.

We consider a haploid asexual population for simplicity of the model7. As will be seen later the results are robust and can be extended beyond the simple set of assumptions. The model consists of two distinct levels of selection namely within group and between group. The population consists of *N* individuals that are divided into random groups of size *n* in which individuals interact. There are individuals displaying two levels of selfishness (*C1* and *C2*) in the total population in the proportion *S1* and *S2* respectively. In the absence of interaction the baseline fitness7 of each individual is assumed to be 1 which is contributed by the advantages of grouping alone with no elements of social behaviour. This is assumed to be greater than the fitness returns of solitary life CS < 1. Within a group the fitness of an individual with a level of selfishness *C1* is *1 +K1C1*. An individual’s contribution to group fitness is *1-K2C1.*The total group fitness of each group is calculated depending upon the proportion of the two selfishness traits that formed the group.The effective reproductive success of each individual in the group is calculated as a product of the within group fitness and the group fitness. This continues for time *t* after which all the groups are pooled and redistributed randomly. The total number is normalized again to *N* and new groups with size *n* are assembled again choosing individuals randomly from their new normalized frequencies.

**Model 1- absolute selfishness decides fitness:**

In model 1, within group fitness of the two traits in the *ith* group is given as

 Eq. 1

 Eq. 2

And the group fitness of *ith* group as

 Eq. 3

The default value of K1 is unity and K2 is varied in the simulations. Individuals within each group grow according to these fitness functions for time *t* after which all groups are pooled and redistributed randomly and the entire cycle repeats. The net or realized fitness of the two traits pooled over the *N/n* groups will be

 Eq. 4

 Eq. 5

Our model so far is very similar to traditional models of multilevel selection. However we differ in the way we treat selfishness. With the exception of Wilson and Dugatkin17all models consider altruist and selfish as two discrete traits. We consider selfishness on a scale ranging between -1 to +*1/K2*, zero denoting an effect equivalent to symmetric cost benefit distribution. In the negative range the behavior is altruistic i.e. the actor pays the cost and benefit goes to group. A positive selfishness score denotes individual benefit and group cost. This limit is natural since at C = -1, individual fitness goes to zero and at C = *1/K2* , the fitness of a group composed of all selfish individuals goes to zero. Beyond this limit any trait will not be viable in the long run. Most models use similar expressions for within and between group selection but differ in **w**hether the groups are dissolved and individuals mix13,18 or groups split above a certain size19 or individuals migrate across groups13,19. We use the frequently used assumption of groups dissolving periodically and individuals reassembling randomly. However, we use this model to ask a different set of interrelated questions (i) if default *K1* is unity *C1* is zero, what value of *C2* confers maximum fitness (ii) whether the optimum *C2* is dependent or independent of *C1* and (iii) whether there is a global optimum level of selfishness which is not invaded by any other.

Simulations using model 1 showed that the fitness of *C2* with a constant *C1* is a non-monotonic function. It increases upto a unique value of *C2* and then decreases with further increase in *C2* (fig 1). The unique optimum *C2* is independent of *C1* and is not invasible by any other level of selfishness. The position of the optimum is decided by the model parameters mainly *n* and *K*2. Increase in *K*2 strengthens group selection and pushes the optimum to the left, i.e. relatively less selfish or more altruistic. Increase in *n* reduces the strength of group selection and pushes the optimum to the right. Group selection in this model is driven by chance differences in the proportions of traits across the randomized groups. No assortative grouping or drift is assumed.

We observed that a simple intuitive mathematical framework can closely reproduce the simulation results. The simpler equation giving the realized fitness of a trait pooled over all *n* groups is

 Eq. 6

If we start with a population ratio of 1:1, the population ratio S2/S1 after a few generations is given by where m is decided by the net growth rate and time. It was observed that this equation always gave a close fit to the simulation results over the range of parameters used. The value of can be estimated empirically while fitting the above equation to the simulation results (fig 1). This equation explains the non-monotonicity of the fitness curve in a simple way (fig 2).

The parameter g which denotes the strength of group selection is composed of two components one being *K2* and the other a function of between group variance in the proportion of the two traits. If between group differences are zero g becomes zero. Since assortative grouping can boost group selection17 simulation of the other limiting case that is completely assortative grouping were carried out that gave a non-monotonic fitness curve in which *g* always became numerically equal to *K2*. The shape of the curve between these two extreme points of *g=0* and *g= K2*is likely to be affected by *t* 13, *n*, mono or polygenic nature of the character, sexual or asexual reproduction, dominant or recessive character of the altruistic trait and environmental viscosity9,20. Kin selection is claimed to be equivalent to group selection6,15,21 therefore the same equation could be written in the form of kin selection as

 Eq 7

where *r* is the genetic relatedness. Altruism can evolve if *C2 < 0* and. This condition can be shown to be mathematically equivalent to Hamilton’s rule if *K2* is taken as Hamiltonian b and *1/(1+C2)*as Hamiltonian *c*. Eq. 7 has an advantage over Hamilton’s inequality. There can be more than one values of *C2* that satisfy Hamilton’s condition and Hamilton’s rule does not indicate exactly which of them will evolve whereas equation 7 gives the unique optimum level of altruism that is evolutionarily stable.

As g increases, the optimum selfishness is pushed towards left. At g =1 the optimum lies at 0 and at g >1 it is negative i.e. altruism evolves. The condition g >1 is mainly governed by *K2* since at limiting assortativeness g becomes equal to *K2.* The maximum value of *r* also being unity, altruism would be mainly driven by *K2*, a result agreeing with Nowak et al1. Further the distribution of the optimum around zero is highly asymmetric (fig 4). At g <1, it can quickly approach *+1/K2* but the optimum extends to the left very reluctantly and never reaches -1 (extreme altruism) (fig 4). In numerical simulations the optimum C never decreased below -0.5 even with *K2* = 108. This is because with greater negative *C2* individual advantage rapidly approaches zero but group or kin advantage cannot compensate proportionately. This means that eusociality or extreme altruism where individuals completely forgo reproduction cannot evolve genetically by kin or group selection along with ecological advantage of any magnitude. How do we observe eusociality then? If the extreme altruistic behavior is decided stochastically and the altruistic allele has a probabilistic opportunity of being on the actor’s or receptor’s side of the altruistic act, the net gambled success of the gene can be substantially greater than -1 and still one can observe extreme altruism in some individuals in real life. Therefore gambling 22 is a necessary component in the evolution of eusociality. In other words although eusociality stands at -1 on our scale for some of the individuals, for the gene it may stand much above -1 because of gambling benefits. Thus eosociality is not possible without the three components namely kin or group selection, large ecological advantage and gambling work in concert.

)

Differentiating,

To obtain the maximum,

Therefore,

In the baseline model, we assume that K1 is equal to unity, therefore when g>1, then C2 is negative, and when g <1, then C2 is positive. And when g is very large then C2 tends to -0.5.

We can segregate the effects of within and between group selection in the model. At *K1=0* the within group fitness difference can be made zero and only between group selection remains. This leads to evolution of extreme altruism where individual fitness ultimately goes to zero and the population becomes extinct. On the other hand at *=0*, only within group selection is operative. If we assume *= 0* but *K2>0* (i.e. selfishness does affect group performance but between group selection is not permitted by the absence of variation between groups) the net fitness increases linearly with selfishness. As a result there will be a directionally increasing selection for higher and higher selfishness to reach a stage where either the entire population will collapse or the net fitness will decrease below *Cs* so that solitary behaviour may invade the social population. Thus when level of selfishness is free to evolve, social behavior is not stable unless two levels of selection interact. Unlike the historical debate as to whether group selection can help survival of altruism, we show that group selection is necessary for survival of selfishness too.

**Model 2- relative selfishness decides fitness:**

It is likely that when two traits with different selfishness levels interact, it is the relative rather than absolute selfishness that decides evolutionary fitness. This conceptual dichotomy is parallel to the hard and soft selection dichotomy 23. This assumption can be incorporated in to the models assuming *C2*>*C1* as,

 Eq. 8

 Eq. 9

And the group fitness as

 Eq. 10

The intuitive simple form that fits this model is

 Eq. 11

 Eq. 12

Using this variation of the model the dynamics of evolution changes dramatically. Even in this model the fitness curve is non-monotonic. However since this curve is relative to *C1*, there is no more a unique optimum absolute selfishness but there is an optimum selfishness difference that gives maximum advantage to the more selfish trait. Any level of selfishness that has a net fitness >1 can invade the prevailing population. However as this traits becomes common the optimum shifts further. This process may appear to lead to maximum selfishness resulting into collapse of the population. However, owing to the non-monotonicity, after some threshold selfishness, *f2n < 1* and the population can be invaded back by a trait with very low selfishness (fig 4). This can happen when < 1, i.e. when *C2-C1*> (1-g)/g. The low selfishness trait itself is unstable since it can be invaded by another slightly more selfish trait. This gives rise to a rock-paper-scissor like dynamics on a continuous scale. Low selfishness can be invaded by intermediate selfishness, which can be invaded further by higher selfishness but very high selfishness can be invaded back by very low selfishness. Since C ranges between -1 to +1/K2 , the maximum value of *C2-C1* is *1 + 1/K2*. Therefore RPS is possible when *g > 1/(2+1/K2)*.

Classical RPS dynamics is known to result into stable or oscillating coexistence of the three traits both theoretically and empirically24. Since in our case there can be many intermediate selfishness players we expect here a stable or oscillating coexistence of three or more levels of selfishness. It can be seen further that the threshold difference in selfishness above which an extreme altruist can invade the selfish population is decide mainly by. Thus any factors that strengthen group selection will reduce the amplitude of oscillation or the variance in selfishness across a population along with a reduction in the mean. This is a novel effect of group selection not appreciated by earlier models.

The RPS like dynamics is not sensitive to any particular form of equation used. The within and between group effects of selfishness can be non-linear. For example the within group benefits of selfishness can be saturating instead of being linear. Incorporating saturating, exponential or sigmoid effects in the within or between group fitness functions still allows an RPS like dynamics (results not shown) over at least some parameter space. A saturating within group fitness or exponential between group fitness spreads the area of RPS effects whereas an exponential within group or saturating between group fitness restricts it. The most important condition necessary for an RPS like dynamics is that the relative rather than absolute selfishness decides the within and between group fitnesses and that the realized fitness is a non-monotonic function of selfishness. Such an RPS like dynamics was predicted for the evolution of copy number in bacterial plasmids 25 which is a well known real life case of multi level selection.

The new insights obtained in this study are a result of considering selfishness as a continuous and evolvable trait which has rarely been considered by earlier models. Wilson and Dugatkin17 treated selfishness on a continuous scale but they assumed that there was an optimum for the within group level and another optimum for between group level. A typical multilevel selection situation is obtained when the benefit of an act is obtained at one level and the cost at another level. If this is true then there is no reason why there should be non-monotonicity within a level. Our model portrays group selection in an entirely new dimension. The thinking needs to move now from ‘group selection versus individual selection’or in general ‘this selection versus that selection’ to the mosaic of effects of the different types of selections interacting in a variety of ways.

1. Nowak, M. A., Tarnita, C. E. & Wilson, E. O. The evolution of eusociality. *Nature* **466,** 1057–1062 (2010).

2. Carr-Saunders, A. M. (Alexander M. *The population problem; a study in human evolution*. (Oxford : Clarendon Press, 1922).

3. Wynne-Edwards, V. *Animal Dispersion in Relation to Social Behaviour*. (Oliver and Boyd, 1962).

4. Damuth, J. & Heisler, I. Alternative formulations of multilevel selection - Springer. *Biol. Philos.* **3,** 407–430 (1988).

5. Wilson, E. O. *The social conquest of Earth*. (Liveright Publishing Corp., 2013).

6. West, S. A., Griffin, A. S. & Gardner, A. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J. Evol. Biol.* **20,** 415–432 (2007).

7. Wilson, D. S. A theory of group selection. *Proc. Natl. Acad. Sci.* **72,** 143–146 (1975).

8. Boorman, S. A. & Levitt, P. R. Group Selection on the Boundary of a Stable Population. *Proc. Natl. Acad. Sci.* **69,** 2711–2713 (1972).

9. Gadgil, M. Evolution of Social Behavior Through Interpopulation Selection. *Proc. Natl. Acad. Sci. U. S. A.* **72,** 1199–1201 (1975).

10. Gilpin, M. *Gilpin, M.E.: Group Selection in Predator-Prey Communities. (MPB-9).* (Princeton University Press, 1975).

11. Levin, B. R. & Kilmer, W. L. Interdemic Selection and the Evolution of Altruism: A Computer Simulation Study. *Evolution* **28,** 527 (1974).

12. Matessi, C. & Jayakar, S. D. Conditions for the evolution of altruism under darwinian selection. *Theor. Popul. Biol.* **9,** 360–387 (1976).

13. Cohen, D. & Eshel, I. On the founder effect and the evolution of altruistic traits. *Theor. Popul. Biol.* **10,** 276–302 (1976).

14. Maynard Smith, J. Group selection. *Q. Rev. Biol.* **51,** 277–283 (1976).

15. Grafen, A. in *J R Krebs N B Davis Ed. Behav. Ecol.* (Blackwell, 1984).

16. Goodnight, C. Multilevel selection: the evolution of cooperation in non-kin groups. *Popul. Ecol.* **47,** 3–12 (2005).

17. Wilson, D. & Dugatkin, L. Group selection and assortative interactions. *Am. Nat.* **149,** 336–351 (1997).

18. Wilson, D. Weak altruism, strong group selection. *Oikos* **59,** 135–140 (1990).

19. Traulsen, A. & Nowak, M. Evolution of cooperation by multilevel selection. *Proc. Natl. Acad. Sci.* **103,** 10952–55 (2006).

20. Crow, J. & Aoki, K. Group selection for a polygenic behavioral trait: a differential proliferation model. *Proc. Natl. Acad. Sci.* **79,** 2628–2631 (1982).

21. Queller, D. Quantitative genetics, inclusive fitness and group selection. *Am. Nat.* **139,** 540–558 (1992).

22. Gadagkar, R. in *Perspect. Entomol. Researach* (Scientific publishers, 1994).

23. Goodnight, C., Schwartz, J. & Stevens, L. Contextual analysis of models of group selection, soft selection, hard selection and the evolution of altruism. *Am. Nat.* **140,** 743–761 (1992).

24. Sinervo, B. & Lively, C. M. The rock-paper-scissors game and the evolution of alternative male strategies. *Nature* **380,** 240–243 (1996).

25. Watve, M. M., Dahanukar, N. & Watve, M. G. Sociobiological Control of Plasmid Copy Number in Bacteria. *PLoS ONE* **5,** e9328 (2010).

Footnotes to figures:

Fig 1: The net or realized fitness as a function of different selfishness levels ranging from -1 (extreme altruism) to +1 (extreme selfishness). Results of simulations of competition between two traits with different levels of selfishness. *C1* is kept 0, the starting population ratio is 1:1 and the relative fitness of *C2* is calculated as ratio of the two populations after running simulations for 10 generations. Note the non-monotonicity of the fitness curve. Markers indicate means of 10 simulation runs each, curve represents equation 6 fitted to it. Other parameters in this curve *n=5* and *t=1*, *K1=K2=1.* Throughout a wide range of parameters used (n = 1 to 50, t = 1 to 50 and *K2 = 0.1 to 4*) equation 6 offered excellent fit to all the simulation results.

Fig 2: The linear within and between group fitness functions result into a non-monotonic net fitness curve (solid line secondary axis). If the slope of the within group selection line (dotted line) is steeper than the between group selection line (dashed line) the optimum is positive, if between group selection is steeper, it is negative.

Fig 3: The effect of g on the optimum selfishness: The fitness curves change with increasing g (ranging from 0 to 2) with the optimum (highest point on the curve) progressively shifting to the left. The decrease in the optimum selfishness (shown with black crosses joined by solid black line) with g is nonlinear (inset). The distribution of the optimum on the positive and negative side is asymmetric. The optimum never decreases below -0.5.