

On the dynamics of grouping

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ABSTRACT

We introduce a one-dimensional grid model that describes the evolutionary dynamics of grouping behavior when groups provide some protection against predation. The model allows exploring the effects of predation on the dynamics of group formation under various evolutionary scenarios. It shows the formation of larger groups the more intense natural selection favors cooperation. The frequency distribution of group sizes achieved is similar to that from natural groups in the field for a variety of animals. The model suggests that small selective advantages provided by cooperation between neighbors is enough to stabilize large groups and that the frequency distributions of group sizes can reveal the strength of natural selection favoring grouping. We show the advantages and disadvantages of this model testing the effects of the interaction between cooperators and free riders and cooperators and non-cooperators in the process of group formation.

Key words: social, simulation, interactions, group size, selfish herd, evolution

INTRODUCTION

A very popular example of biological evolution shaping sociality is that of the “selfish herd”, a concept introduced by Hamilton in 1971. It explains why animals are less at risk when the density of co-specifics around them is greater. Here, the geometry of aggregates confers protection against predation to grouping animals (Hamilton 1971). This perspective is congruent with the origin of grouping behavior based solely on selective grounds, without further need of additional assumptions. Since then, a wide range of other benefits are known to favor grouping or are positively correlated with the formation of groups and group size (Bertram 1978, Pulliam et al. 1982, Pulliam 1973, Packer & Abrams 1990, Lima 1990, Dehn 1990, McNamara & Houston 1992, Pöysä 1994, Roberts 1996, Beauchamp 2003).

In a very simple model mimicking a biological setting, interacting organisms subject to predation (i.e., perturbation) are able to form groups just by following

two strategies. Individuals can either (a) cooperate, that is, always helping to reduce the chances of predation of their immediate neighbors (e.g., help fighting against the predator), or (b) not to cooperate, not affecting the predation rates on immediate neighbors. Cooperative individuals, living in groups, also benefit from the protection of their co-specifics, while non-cooperative individuals fight predators by themselves. Given this model and granting the same conditions for both strategies, organisms living in groups (i.e., all immediate neighbors of cooperative individuals) have a lesser chance to be killed by a predator than those living around a non-cooperative individual. Consequences of grouping on the fitness of the individuals are obvious.

But, what happens on the dynamics of grouping when some individuals are allowed to exploit and to take advantage of the cooperative behavior of their neighbors (i.e., in this particular case), without responding equivalently when neighbors are in need. These individuals, always defecting - not without taking advantage of the benefits offered by the strategies of others - are known as ‘free riders’ (i.e., ‘the free rider problem’, Grossman and Hart 1980). The potential effects of free riders in grouping are probably better foreseen when we look at classic models such as the ‘Prisoner’s Dilemma’ game (e.g., Maynard-Smith 1982, Weibull 1995).

Here, we use a one-dimensional grid model to study the emergence of groups and the effects of free riders and non-collaborators in the dynamics of group formation when individuals are subject to predation. We based our model on the phenomenon of reduction in individual predation risk at higher group sizes, known as the “dilution of confusion hypothesis” (Roberts 1996). The hypothesis that supports this model is that a social dynamic system – a system in which groups are dynamically formed and maintained through time – is driven by natural selection. We refer to natural selection as the measurable fitness difference among phenotypes within a single generation (Lande & Arnold 1987). In consequence, selective pressure is represented by predation.

THE MODEL

A time-discrete, one-dimensional, grid model represents our population made of individuals with two phenotypes. Cells may represent three different states: cooperative members (*co*), non-cooperative members (*nco*) or free riders (*fr*), and empty spaces (*e*).

The model has oscillatory boundaries for what every single cell may have direct interactions with both immediate neighbors. In consequence, two and three cooperative individuals make the minimal expected group size S even if groups of larger sizes may result

from the dynamics of the model. A group is defined as an uninterrupted sequence of two or more cells occupied by cooperative individuals.

The state of every cell in the population is sequentially recorded each iteration. The community dynamics evolves following these rules (Figure 1):

1. An empty cell is occupied by a new recruit, *co*, *nco* or *fr*, with probability r_{co} , r_{nco} or r_{fr} , respectively. Members reproduce during lifetime but reproduction is stochastic and at no cost to individuals. This step simulates vertical transmission.
2. Each member is subject to predation according to the state of both its neighbor cells. The probability of predation of a member i is a function of the state of both immediate neighbors: (a) a cooperative member with two cooperative neighbors is predated with probability p_{2n} ; (b) a cooperative member with one cooperative neighbor, with probability p_{1n} ; (c) a cooperative member without cooperative neighbors, with probability p_{0n} ; (d) a non-cooperative member or a free rider (alone), with probabilities p_{nco} and p_{fr} , respectively.
3. Free riders with one and two cooperative neighbors are predated with probabilities p_{1n} and p_{2n} , same as those of cooperators with one and two neighbors, respectively.
4. Each member dies according to a fixed rate of natural mortality, m .

The probability r that a recruit with a particular social role occupies an empty space at time t is a function of the fraction of members of that social role in the population at time $t - 1$.

To test the effects of natural selection on the formation of groups, we run the grid model, determined the group size, S , distribution for each scenario, setting all predation probabilities to 0, and compared it with the distribution of S obtained from combinations of these probabilities giving groups in each simulation, an increasing degree of selective advantage.

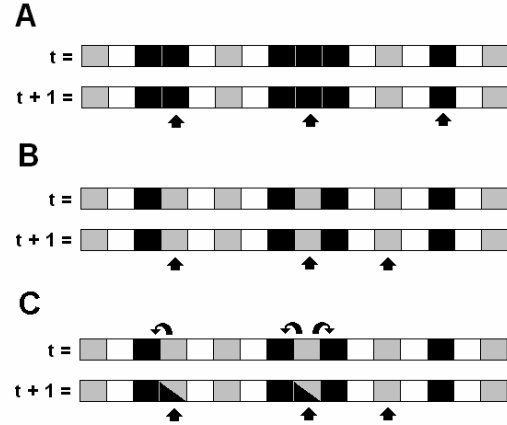


Figure 1. Diagram of strategies followed by members in the model. Black cells: cooperative; gray cells: non-cooperative or free riders; and white cells: empty spaces. A. If one or both neighbors of a cooperative member are cooperative, all respond to predation as a group; B. Non-cooperative members, alone or with cooperative members, always respond to predation in the same way; C. If free riders are alone, they respond to predation as if they were non-collaborators, but if they are close to one or two collaborators, they respond as collaborators as well (gray + black squares). Arrows point to individuals to be subject to predation; t are relative iterations.

In order to test our model, we compared the theoretical distributions of S with those of groups of living organisms: (a) a 7-year aggregated data set from three pooled species of tuna fish, *Thunnus albacares*, *T. obesus*, and *Katsuwonus pelamis*, collected between 1976 and 1982 on the Tropical Atlantic Ocean (Bonabeau et al. 1999), and (b) an 18-year aggregated data set from two pooled species of sardines, *Sardinella maderensis* and *S. aurita*, collected between 1970 and 1987 on the West South African coast (Bonabeau et al. 1999); (c) a data set of herd sizes of African buffaloes, *Syncerus caffer* (Bonabeau et al. 1999); (d) a data set of relative frequencies of alpine marmot, *Marmota marmota*, collected in the Bavarian Alps between 1982 and 2003 (Grimm, et al. 2003); and (e) a data set of the bottlenose dolphin, *Tursiops truncatus*, from shore watches made at the Shannon Estuary, Ireland, between 1994 and 1999 (Rogan et al. 2000).

We implemented the grid model using MS Visual Basic®, ver 5.0. We run 10^5 iterations in each simulation on populations with 10^4 cells. The initial spatial distributions of cooperative and non-cooperative members, as well as that of cooperative members and free riders, were random uniform and all members were equally represented. In this study $r_{co} = co / (nco + co + fr)$. The same applies to r_{nco} and r_{fr} .

To understand the effects of free riders in the formation of groups, we modeled one-dimensional populations in two different competing scenarios: (a) cooperators vs. non-cooperators, and (b) cooperators vs. free riders. We tested three predation conditions in which the selective pressure always favored groups. (i) Very strong selection (VS) ($p_{2n} = 0.1$; $p_{1n} = 0.1$; $p_{0n} = 0.9$; $p_{nco} = 0.9$); (ii) Strong selection (SS) ($p_{2n} = 0.1$; $p_{1n} = 0.1$; $p_{0n} = 0.5$; $p_{nco} = 0.5$); (iii) Low selection (LS) ($p_{2n} = 0.1$; $p_{1n} = 0.1$; $p_{0n} = 0.2$; $p_{nco} = 0.2$); and (iv) a Control (C) ($p_{2n} = 0$; $p_{1n} = 0$; $p_{0n} = 0$; $p_{nco} = 0$).

RESULTS AND DISCUSSION

Group size distributions

The effect on the frequency distribution of group sizes is presented in Figure 2. The distribution of group size resulting from the dynamics of the model may be adjusted to an exponential, of the form

$$N(S) = k \cdot \theta^{S^\gamma}$$

where $N(S)$ is the frequency of groups size S , k is a constant, θ is the base constant, and γ is the power. It is important to notice that locating individuals at random on the grid model also produces an exponential distribution of group sizes ($|\gamma| = 0.3$). Cross symbols in Figure 2, represent the random distributions of group sizes just before starting the simulations, at time $t = 0$. In those plots with log-transformed frequencies, differences between the distributions of group sizes forming at random or as the product of model dynamics are appreciated by comparing the absolute value of the slopes of the regression lines, $|\gamma|$. In a biological simulation (Figure 2A), the absolute values of slopes from populations subject to predation are lower than those obtained from random grouping. This means that distributions formed with predation have fewer small groups and more large groups than distributions formed at random.

As expected, the absolute value of slopes also changes when the effects of predation are removed from the model. Very large groups of cooperative individuals are formed in the absence of predation ($|\gamma| \gg 10$). In some cases, without the effects of selection the population evolves to a single group of cooperative members, with 10^4 individuals.

The overall shapes of real-world group size distributions of bottlenose dolphins and marmots (Figure 2B), African buffaloes (Figure 2C), and sardines and tuna fish (Figure 2D) fit well those produced by our model. According to Bonabeau et al. (1999), in nature, group size distributes as a truncated power law distribution, even though the distribution of some groups may also be a mixture of a power law,

and a tail that is better described by an exponential (i.e., such as the case of buffaloes).

Sardines and tuna fish data sets have values not well described by the exponential distribution: they have a larger proportion of smaller groups than those predicted by our model. These values are shown by triangles in Figure 2D and were not used to fit the regression lines.

The one-dimensional structure of our model also constrains the interaction between members and hence, constrains the dynamics of group formation. According to Bonabeau et al. (1999), the space in which animals move does not have to have an integer dimension (i.e., can be fractal) and the resulting dynamics of groups formation is affected by the dimension in which animals move. Even so, this simple grid model represents a population of individuals following particular strategies and forming groups under a simple evolutionary setting of cooperation, driven by predation. Indeed, the space-explicit model is the simplest biological abstraction possible in which groups and cooperation can be modeled. Processes that affect group size are reflected in the distribution of this parameter. Then, in our model, $|\gamma|$ is related to the strength or intensity of natural selection. Caution is advised when interpreting $|\gamma|$ values from natural populations given that processes shaping the distribution of group sizes are diverse. The parameter $|\gamma|$ should be best interpreted as the result of the overall effects of all mechanisms capable of forming groups.

Distributions of group sizes produced by our model approximate well enough some of those found in natural systems and those produced by other multidimensional models as to ask general questions about its dynamics.

Effects of free riders and non-cooperators

The free-rider problem has been widely studied in the economics and social literature related to game theory (e.g., Grossman and Hart 1980, Fletcher and Zwick 2000, Leininger 2002). Most of this interest rests on the fact that the pure free rider strategy (i.e., defector) is capable of invading many different cooperative strategies, but only benefiting individuals. This section of the paper does not intend to be an exhaustive study and literature review on the free rider problem, but rather an example on the advantages and limitations of the group forming model that we are work in. Effects of free riders in the formation of groups under the VS condition resulted in $|\gamma|$ values that oscillated between 0.06 and 0.3, with an average group size of 7.9. Distribution of groups formed by non-cooperators also showed values of $|\gamma|$ oscillating between those mentioned above and average group size of 8.1. Even

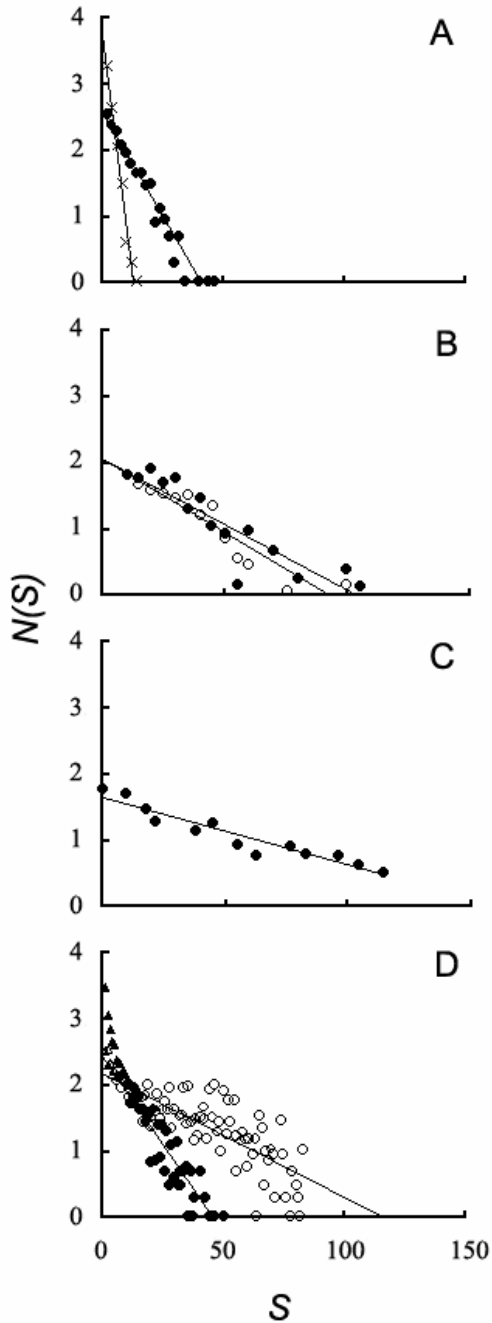


Figure 2. Frequency distributions of S . All frequencies, $N(S)$, are log-transformed (i.e., $\theta = 10$ in the exponential equation). Black circles: frequencies after simulating populations with 10^4 cells during 10^5 time iterations with groups having selective advantage ($p_{2n} = 0.1$; $p_{1n} = 0.1$; $p_{0n} = 0.5$; $p_{nc0} = 0.5$) ($|\gamma| = 0.06$). Crosses: initial random distribution of data ($|\gamma| = 0.4$). B. Black circles: bottleneck dolphins ($|\gamma| = 0.10$) (Rogan et al. 2000). White circles: marmots ($|\gamma| = 0.11$) (Grimm et al. 2003). Each 5 units of S represent 1 marmot or dolphin. C. African buffaloes ($|\gamma| = 0.001$) (Bonabeau et al. 1999). Each unit of S represents 100

buffaloes. D. White circles and triangles: 3 species of tuna fish from the Atlantic Ocean ($|\gamma| = 0.06$). Black circles and triangles: two species of sardines from South Africa ($|\gamma| = 0.02$) (Bonabeau et al. 1999). Triangles were not used to fit regression lines.

if both contests produce longer tails in the group size distribution, differences are not existent. Eventually, in these simulations, free riders or non-cooperators vanished from the populations and cooperators dominated.

Under the HS condition, the distribution of groups sizes in the population with free riders and that with non cooperative members produced the same value of $|\gamma| = 0.06$. As in the VS condition, free riders and non-cooperators could not outcompete cooperators, which stabilized at approximately 0.85% of the maximum population capacity, that is, 10000 cells. Other spaces were empty.

In populations resulting from the LS condition both slopes also were similar, $|\gamma| = 0.30$ for free riders and $|\gamma| = 0.31$ for non-cooperators. As above, in both simulations cooperative members dominated the final population.

The slope of the control groups size distribution, generated using a uniform random distribution of members, was $|\gamma| = 0.40$. Non-cooperators dominate on of the final populations, and cooperators and free riders oscillate along all the 10^5 iterations, alternating their relative frequency. All the values discussed above are different from these obtained in our control simulations.

A one-dimensional model limits the topology of the interactions of the individuals in the system. The interactions are forced to be one-to one, and no more than two links are present in each individual. The model is simple because it delegates the responsibility of building groups to the geometric restriction: groups are formed because individuals appear and end up one besides the other. There is no actual movement of individuals. Group splitting is also a consequence of the geometrical constraint. In this model, large groups split when a predator kills one cooperative member belonging to a relative large group and a non-cooperator or a free rider takes its cell position. The chance to eliminate the free rider from that location is as low as to eliminate another cooperative member. That is not true for non-cooperators, whose predation probability always runs under that of cooperators (when selection favors grouping). This constraint explains why in some simulations, when contests of cooperators vs. non-cooperators resulted in distributions of group sizes with larger tails, that is, with more frequent groups of larger size, the resulting average group size was still large: the maximum

number of cells is fixed and more groups (i.e., more free-riders that survive) mean smaller sizes.

CONCLUSIONS

We present here a very simple one-dimensional model that simulates group formation, by populating cells with members following different pure strategies. In this study we used members following to pure strategies: (a) cooperators and non-cooperators, and (b) cooperators and free riders.

The resulting distributions produced by the model are very similar to those existing in nature, or at least, fit the exponential tail of real group size distributions. Hence, the model is intuitive and may be used to study group dynamics and evolution.

We used this model to analyze, as an example, the effects of free riders and non-cooperators in grouping under a biological setting. The contest cooperators vs. free riders and cooperators vs. non-cooperators produced distributions oscillating between an overlapping range of shapes. The range of overlapping was related to the selective pressure acting on grouping and non-grouping members.

This one-dimensional model possesses some geometric constraints affecting group formation and splitting. They work in the model only by changes in the occupancy of cells, either by recruitment or death, but not by displacement. Moreover, the one-dimensional topology limits the interaction of members to only two at a time. On the other hand, the given that the interaction occurs with a small number of neighbors, the model suggests that small selective advantages provided by cooperation between neighbors is enough to stabilize large groups and that the frequency distributions of group sizes can be a proxy to the strength of natural selection favoring grouping.

We are currently working on an improved version of the model that will consider the interaction among all of its members.

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