GROUP SELECTION REVEALED!

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INTRODUCTION

This program demonstrates the features of group selection. Group selection is particularly interesting when it favors the evolution of altruism.

An altruistic individual is one that benefits its group as a whole at a cost to its own reproduction or survival. In this simulation, altruists make group survival more likely, but they have lower fecundity than do selfish individuals (egotists). As a result, selection between groups favors the spread of altruists but selection within groups tends to eliminate them. This simulation shows how the balance of between-group and within-group selection affects the evolution of altruism.

To begin a simulation -- or to resume after Pause or Restart -- just hit any key. Other features of the program are evident from the menus.

BRIEF EXPLANATION

The screen shows up to 8 populations, each of which can contain up to 64 individuals. These populations could be demes, social groups, or microhabitats.

By default, altruistic individuals are represented by black spots, egotists by red spots. If you prefer other colors (or want to hide one kind of individual), make your choice in the Colors menu.

The Control menu allows you to Restart a new run with new randomly chosen groups. In the initialization process, groups with different numbers of altruists are all equally probable. You can also Pause at any time during a run (for instance to see what has happened or to change settings -- but changing colors restarts the program). You can select Step to pause after each episode of reproduction, migration, or mortality. You can also select Cycle to pause after each complete generation. Current settings are displayed across the bottom.

Each generation consists of episodes of (1) reproduction, (2) migration between populations (only if selected in the Migration menu), and (3) mortality. At the end of each generation, mortality reduces the number of individuals in each population to no more than half the maximal population (in other words, 2, 8, or 32 individuals as determined by Population Size in the Populations menu). Every few generations (determined by Generations/Cycle in the Settings menu), an extinction crisis occurs. In these crises all populations that do not have enough altruists are wiped from the face of the screen!

Cycles of repeated generations between extinction crises continue indefinitely until all populations are extinct or all surviving individuals are altruists.

By selecting the correct parameters, you can make each of these outcomes happen. It is also possible to obtain a mixture of altruists and egotists that will continue for a long time -- perhaps indefinitely!

The default settings make it very unlikely that altruists will prevail. Yet it is not too difficult to find some conditions in which they do sometimes or even frequently prevail -- or to find an apparently steady state with a mixture of altruists and egotists. In the latter case, altruists actually promote the survival of egotists.

Try different values of reproductive rates (Altruist Ro and Egotist Ro in the Demographics menu). Ro = number of offspring/adult altruist or egotist, respectively. Values of 1.4 and 1.6 produce interesting results. Also try different population sizes. Then experiment with Migration. Also try altering the Threshold for the number of altruists required for group survival. The other parameters affecting group survival (Offset and Slope, explained below) are more complicated.

Once you have explored the parameters that affect the evolution of altruism in this simulation, consider the following question. Do any conditions that allow the persistence of altruists seem likely to apply to actual populations?

MORE DETAILED EXPLANATIONS

The following sections explain in more detail how the program works. Recall that one or more cycles of reproduction-migration-mortality occur between episodes of group extinction. Altruists have disadvantages within groups (as a result of lower reproductive rates) but increase the chances of group survival during episodes of extinction. Note how extinctions tend to spread altruists -- after an episode of extinctions, the remaining groups have more altruists than those that disappeared. Extinctions enrich the proportion of altruists in the population as a whole.

Reproduction

Reproduction is clonal -- egotists produce only egotistic offspring, altruists only altruistic offspring. The rates of reproduction (Ro, number of offspring/adult) by egotists and altruists are set in the pull-down menus in the Settings menu. Note that clonal reproduction is like reproduction of alleles (without mutation) or chromosomes (without mutation or crossing-over).

When a population includes fewer than 10 individual egotists or altruists, the relevant Ro sets the probability that each individual produces a single offspring. When a population has more than 10 egotists or altruists, the number of offspring is simply the number of individuals times Ro.

Migration

Migration (dispersal) between populations occurs following reproduction, provided this option is selected in the Migration menu. Migrants are selected randomly from all populations (all individuals have an equal chance of migrating) and are distributed equally to all populations with vacancies (each population has an equal chance to receive a particular migrant). The Migration menu allows choices of the percentage of the total population attempting to migrate and the percentage surviving during migration. When all populations are full no further migration is possible.

Notice that, without migration, a population that becomes entirely altruistic never subsequently acquires any egotistic individuals. Such populations almost never go extinct during an extinction crisis (depending on the threshold number of altruists required to avoid extinction) and thus almost never receive colonists following extinction, as explained below.

Mortality

Mortality affects all individuals equally. Randomly chosen individuals die (wiped from the screen!). A simulation of group selection might include differences between altruists and egotists in mortality as well as, or instead of, differences in reproduction -- but, to keep things simple, this simulation focuses on differences in reproduction.

Mortality occurs after migration (if migration is selected). It reduces each population to no more than half the maximal size of the populations (32, 8, or 2 individuals). If the population has fewer individuals, none dies. The maximum for each population at the end of each generation can be thought of as the carrying capacity of each population's habitat.

Group Survival

During an extinction crisis, each group has a probability of survival that depends on how many altruists it contains. Survival is proportional to the number of altruists above a threshold.

Here is the equation that determines group survival:

(probability of group survival) = (offset) + (slope)(number of altruists)

There are two exceptions to this equation: (1) group survival = 0 if number of altruists < threshold; and (2) group survival reaches its maximum at 1.0 and its minimum at 0. To see how intercept, slope, and threshold interact to affect group survival as a function of the number of altruists, try some sketches on graph paper.

The Settings menu provides choices for the slope and the y-intercept (offset) of the equation determining group survival -- and for the threshold number of altruists below which extinction of a group always occurs.

Colonization of Vacancies

Following extinctions, colonization of vacant habitats occurs by dispersal from the remaining populations. First, all remaining populations reproduce, as during a normal generation. Then populatons that exceed half their carrying capacity (in other words, those with > 32, 8, or 2 individuals) contribute the excess individuals, randomly chosen, to a pool of colonists. These colonists are then randomly distributed to the vacant habitats. Neither altruists nor egotists have precedence in colonization, so the proportion of altruists among the colonists is equal (within random error) to the proportion of altruists in the remaining populations before colonization.

Generations per Cycle

The Settings menu also provides choices for the number of generations occurring between extinction crises. This parameter is as important as the difference between altruists' and egotists' fecundities or the effects of altruists on group survival. Like these parameters, the number of generations per cycle affects the balance between altruists' disadvantages within groups and their advantages for group survival. Nevertheless, the effects are not always intuitive.

Density-dependence

A carrying capacity creates density-dependence in mortality. In this simulation, the mortality rate in a population equals 0 until the carrying capacity is exceeded, then it increases in proportion to the number of individuals in the population following reproduction. Density-dependence also affects migration, as migration only occurs when densities exceed carrying capacities. Finally, extinction incorporates some reverse density-dependence, as smaller populations are less likely to meet the conditions for survival. In all of these ways, this simulation presumably resembles the real world. Despite the controversy in past decades over density-dependence in natural and laboratory populations, it is difficult to imagine real populations that lack all density-dependence in demography. It is equally difficult to produce reasonable computer simulations without any density dependence!

OTHER SCENARIOS FOR GROUP SELECTION

This program adopts a particular scenario for group selection. Altruists have lower fecundity than egotists within a group but confer advantages for survival of the group as a whole. Altuists sacrifice some of their own fecundity in the interest of group survival.

Group selection occurs whenever groups of individuals differ in overall survival or reproduction in accordance with differences in the frequencies of alleles among the consituent individuals. Group selection thus applies to traits that produce advantages within groups as well as to those that produce disadvantages. In this case, both within- and between-group selection promote the spread of these traits, so their evolution presents no problems. You can try this possibility in the present simulation simply by setting altruists' Ro higher than egotists'. Group selection becomes interesting when disadvatanges within groups counteract advantages between groups, as in the evolution of altruism.

The disadvantages incurred by altruists could take many forms other than lower fecundity -- higher risks of mortality, for instance. The advantages they create for the group as a whole could also take other forms -- fecundity or survival of egotists might increase with the number of altruists in their group, for instance, so that groups with altuists would produce more colonists for randomly occurring vacancies. This latter scenario is not too different from the one in the program. Note that egotists benefit as a result of colonization of vacancies following extinctions -- so altruists in a group increase the chances for egotists to survive and reproduce. These various manifestations of the relationships between altruists and egotists all share the basic features of this program -- altruists lose in the short term within their groups but benefit all group members in the long term.

The program allows some options for studying the effects of the size of groups. Smaller groups experience more genetic drift, which can favor the spread of altruism in some circumstances.

The program has no provision for altruists to recognize each other and thereby to associate preferentially. Such behavior would increase the chances for altruism to spread by group selection. This "green-beard effect" could also provoke an evolutionary response in egotists: egotists might evolve to look like altruists, in order to get the advantages of associating with them.

The program also has no provision for punishment of egotists and reward of altruists within groups. Punishment might, for instance, lower the reproductive rate of egotists with respect to altruists. Of course, such policing can encourage the spread of altruists. Arrangements to reward altruistic behavior within groups would have similar consequences. Recent publications have argued that group selection has played a large role in human evolution. These arguments rely on some form of punishment or reward that can reduce or reverse the disadvantage of altruists in relation to egotists within groups.

Finally, the program includes no provision for association of genealogically related individuals, another condition that would promote the spread of altruistic behavior.

In conclusion, even without genealogical relatedness, punishment, reward, or recognition, some demographic conditions do allow the fixation or indefinite maintenance of altruistic alleles by means of group selection. Nonetheless, the conditions for such evolution are stringent.

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