Computer simulation of group selection models

Working paper by Agner Fog
last updated 2024-01-01

Keywords: group selection, altruism, evolutionary psychology, evolution of warfare, sexual selection, regality theory, leadership.

Abstract

Several models of group selection are simulated with a computer program named Altruist. The models investigated include: selective extinction, selective migration, selective dispersal, outsider exclusion, conformity, altruistic punishment, intrademic group selection, territorial warfare, and leadership according to regality theory. The parameter ranges that lead to egoism, altruism, or polymorphism are mapped. Traditional models of group selection can explain the evolution of altruism only under very limited conditions such as low migration rate, small founder population size, and weak individual selection.

The evolution of reduced virulence in parasites seems to fit under these conditions. Eusociality in insects has likely evolved through a sequence of stages including communal nesting, outsider exclusion, monopolization of reproduction by a queen, and finally extensive collaboration.

The evolution of collective warfare in humans cannot be explained by traditional group selection models, but through common support for a strong leader according to regality theory.

Introduction

Group selection is a controversial topic that has been debated for many years (Leigh, 2010; Hertler et al., 2020). A recent survey among evolutionary informed anthropologists, psychologists, and other scholars found that 38.6% believed that group-level selection has substantially contributed to human evolution. 41.6% did not believe so, while 19.8% answered don't know (Kruger et al., 2023). However, many evolutionary biologists believe that group selection has little or no influence on the evolution of humans and most other social animals (Leigh, 2010).

Group selection theory has often been invoked for explaining phenomena that are difficult to explain by other theories, such as altruism (Bowles, 2006), ageing (Woodberry, 2014; Werfel, et al., 2017), homosexuality (Kirby, 2003), and avoiding overexploitation of resources (Wynne-Edwards, 1986), but these explanations are criticized because invasion by egoists will make the model break down (Leigh, 2010).

Group selection theory is generally proposed for explaining the evolution of behaviors that reduce the reproductive fitness of the individual, but benefits a group that this individual belongs to. This kind of altruism is called parochial altruism. Group selection theory cannot explain altruism towards non-group members.

Much of the debate about group selection has focused on philosophical and semantic questions about how to define units of selection, vehicles, replicators, and interactors (Wilson & Sober, 1994), while quantitative studies are less common. It will be more fruitful to study mathematical models that can tell what will happen if group selection and individual selection are pulling in opposite directions (Leigh, 2010).

Previous mathematical studies and simulations have relied un unrealistic assumptions and approximations. The most common assumptions are that groups live on isolated islands with fixed geographic boundaries and that groups are extinguished completely before the islands are

recolonized. Some studies ignore migration between groups. Some studies are treating gene frequencies as continuous variables, ignoring quantization and genetic drift. Some studies ignore geographic factors and assume that migrants come from a "migrant pool" with the same genetic composition as the metapopulation, while other studies assume that migrants come only from neighbor islands (Boorman & Levitt, 1973; Kimura, 1983; Tanaka, 1996).

The software program named *Altruist* is the result of a longtime work to address the problems in group selection theory with more diverse and more realistic models than previous studies (github.com/AltruistSim). The Altruist program can also be used for analyzing other questions relating to evolution in structured or viscous populations.

The simulated models may involve evolution of a species with a biallelic locus where one allele codes for altruism and the other allele codes for egoism. Possible outcomes of the simulation include fixation of altruism, fixation of egoism, or stable polymorphism.

Unlike some agent-based models, the altruist program is keeping track of the gene pool of each group, but not necessarily of each individual. The program can simulate evolution in a diploid species with discrete non-overlapping generations divided into partially isolated subpopulations or groups.

Almost all events in the simulated models are stochastic. Stochastic events are simulated by calculating the probability distribution of all possible outcomes of an event and generating a random variate with the desired probability distribution to determine the actual outcome. This method is applied to all relevant processes such as mutation, growth, selection, migration, extinction, colonization, etc. Details of how the Altruist program works are described in the altruist manual.

The present document will present several different simulation models and the results of simulating these models. We will vary the parameters of each model in order to find which parameter ranges lead to fixation of one of the alleles.

Island model with selective extinction

The Island model is the traditional model of group selection, inspired by the analogy with individual selection. We will imagine that an animal species is living in an archipelago where each island is inhabited by a group of animals. Geographic barriers make it difficult, but not impossible, for animals to migrate between the islands. The population of an island can go extinct. New groups are formed by members of a nearby group colonizing an empty island. The probability of extinction of a group is a function of a property called *group fitness*. The higher the group fitness, the lower the probability of extinction. The group fitness is a function of the number of phenotypic *altruists* in the group.

Altruists are called so because their behavior is reducing their individual fitness, but increasing the fitness of their group. An example of altruistic behavior is to avoid overexploiting the resources available to the group. Altruists are altruistic only towards their own group. This is called parochial altruism. Individuals without the altruism trait are called *egoists*. The altruism trait in this model is controlled by a biallelic locus with diploid inheritance. The altruism allele can be recessive, dominant, or incomplete dominant, according to Mendel's laws. The simulated evolution goes through discrete nonoverlapping generations. The simulation parameters are described in the Altruist manual.
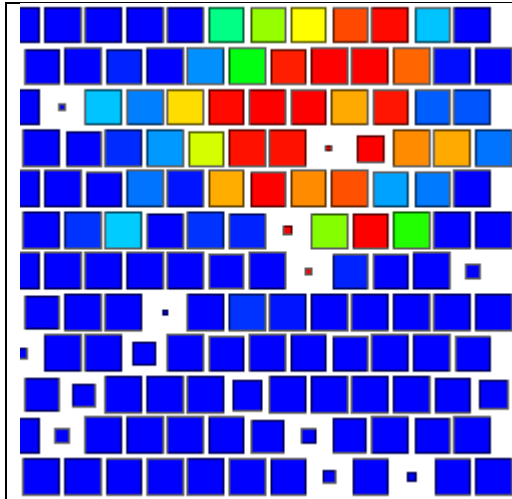
Figure 1.1. Excerpt of habitat showing altruism starting to evolve in a remote corner. Squares represent islands. The size of a square represents the population size. Red islands are inhabited by altruists and blue islands by egoists. Yellow and green islands have mixed populations.
Parameters: Incomplete dominance. Mutation rate = 10^{-5}. Carrying capacity = 50. Colony size = 4. Migration rate = 0.02. Fitness ratio = 0.95. Extinction rate 0.1 for egoism groups, 0.01 for altruism groups.
Parameter file: `island1.altru`

The migration rate is a very critical parameter. Altruist groups can only persist if they are protected from immigrating egoists. Figure 1.2 shows that the altruism allele can be fixated only if the migration rate is low. The group fitness is calculated as $G = f^{\varphi}$, where f is the fraction of phenotypic altruists and φ is called group fitness exponent. A convex group fitness function ($\varphi < 1$) can lead to stable polymorphism, while a concave group fitness function ($\varphi > 1$) is more likely to lead to fixation of either egoism or altruism, depending on the migration rate (Fontanari & Serva, 2014).
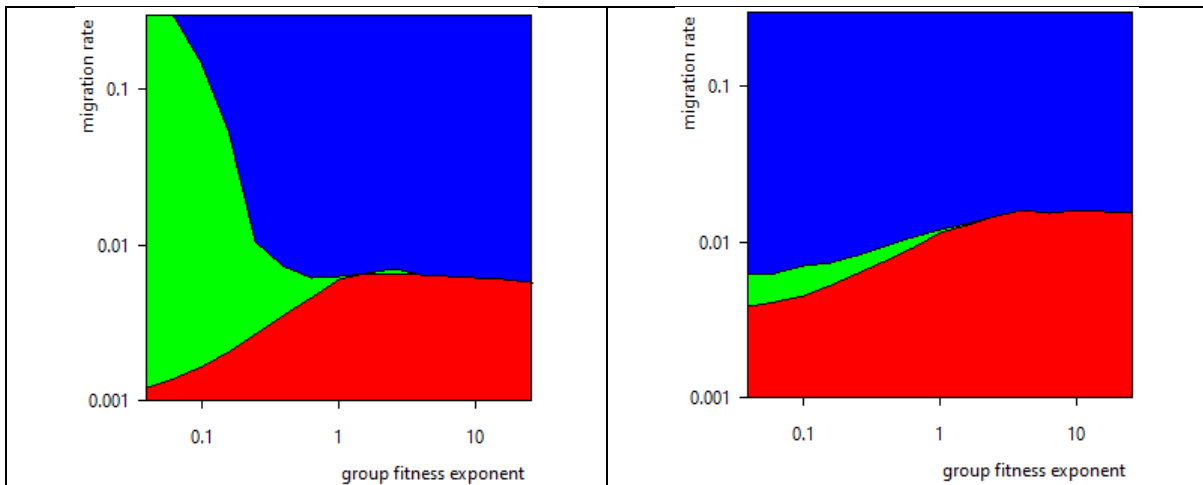

Figure 1.2. Parameter map showing ranges of migration rate and group fitness exponent leading to fixation of altruism (red), egoism (blue), or stable polymorphism (green).
Left: altruism recessive, right: dominant.
Parameters: Partial dominance. Carrying capacity = 100. Colony size = 5. Fitness ratio = 0.875. Extinction rate 0.1 for egoism groups, 0.01 for altruism groups.
Parameter file `island2.altru`

Figure 1.3 shows the effect of individual fitness and migration rate. A low ratio of altruist fitness over egoist fitness leads to fixation of egoism even at very low migration rates. A ratio close to 1.0 leads to fixation of altruism at relatively high migration rates.

Figure 1.3. Parameter map showing ranges of migration rate and individual fitness ratio leading to fixation of altruism (red), egoism (blue), or polymorphism (green).
Parameters: Partial dominance. Carrying capacity = 100. Colony size = 5. Extinction rate 0.1 for egoism groups, 0.01 for altruism groups.
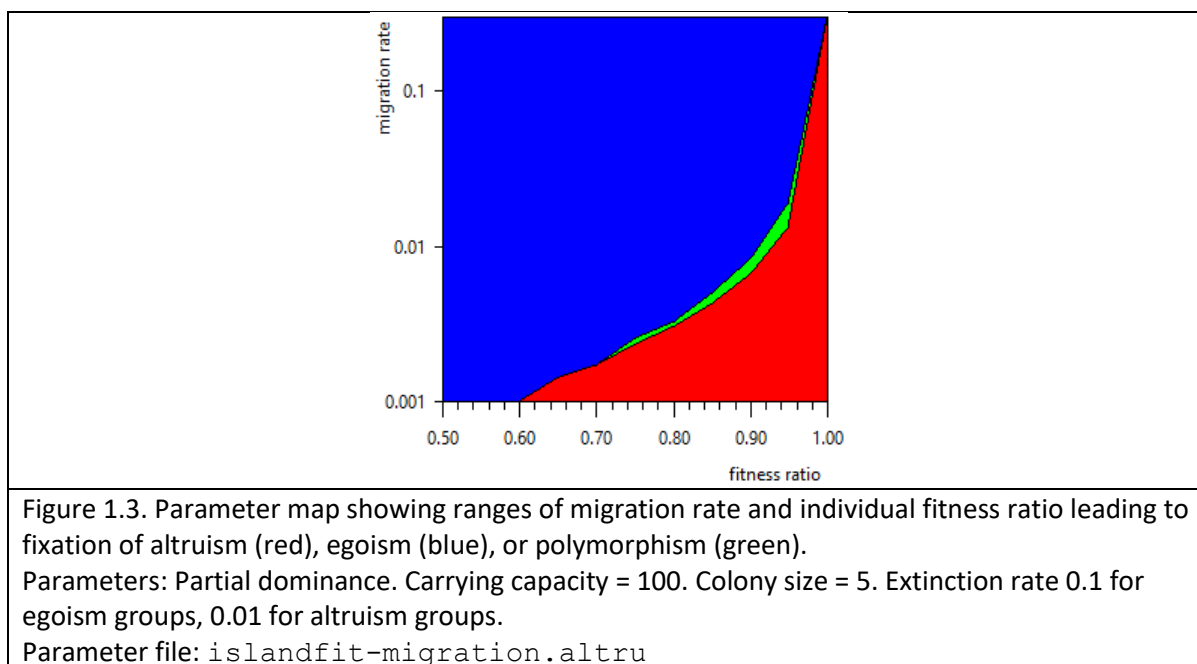Parameter file: `islandfit-migration.altru`

Figure 1.4 shows the effect of the group extinction rate. A high extinction rate for egoist groups is necessary for altruism to spread if the migration rate is more than negligible.

Figure 1.4. Parameter map showing ranges of migration rate and group extinction rate leading to fixation of altruism (red), egoism (blue), or polymorphism (green).
Parameters: Partial dominance. Carrying capacity = 100. Colony size = 5. Fitness ratio = 0.875.
Extinction rate of altruist groups = 0.01. Extinction rate of egoist groups going from 0.00 to 0.25.
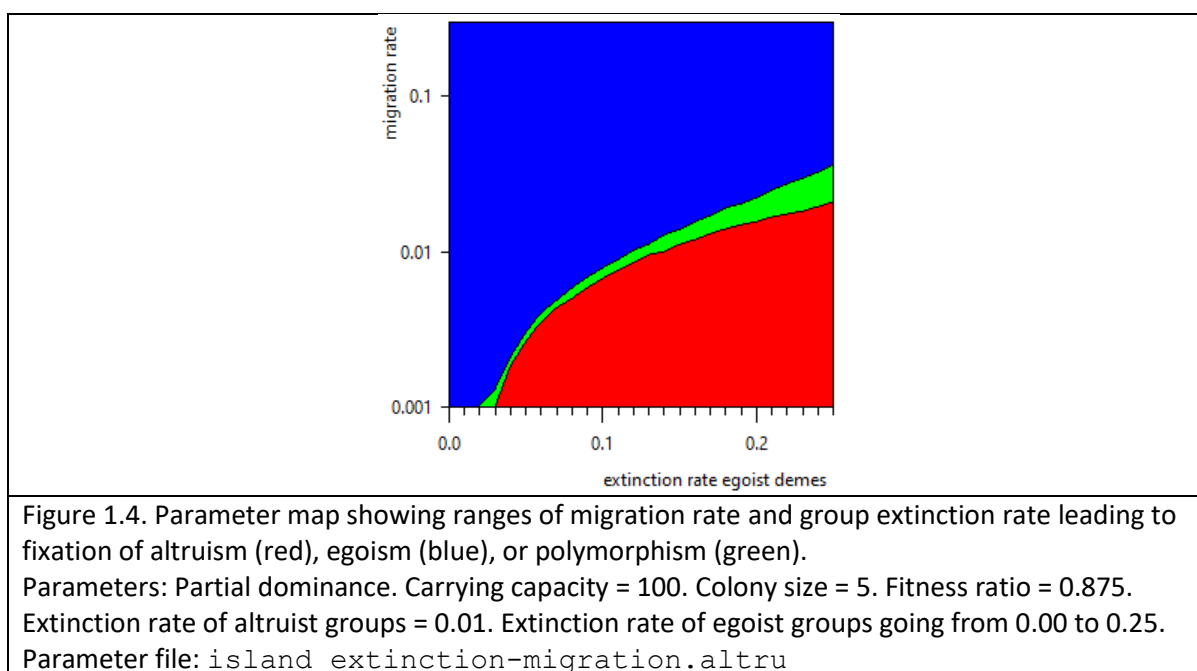Parameter file: `island_extinction-migration.altru`

Figure 1.5 shows the effect of group size. We can see that the effect of group selection is very weak for large groups.
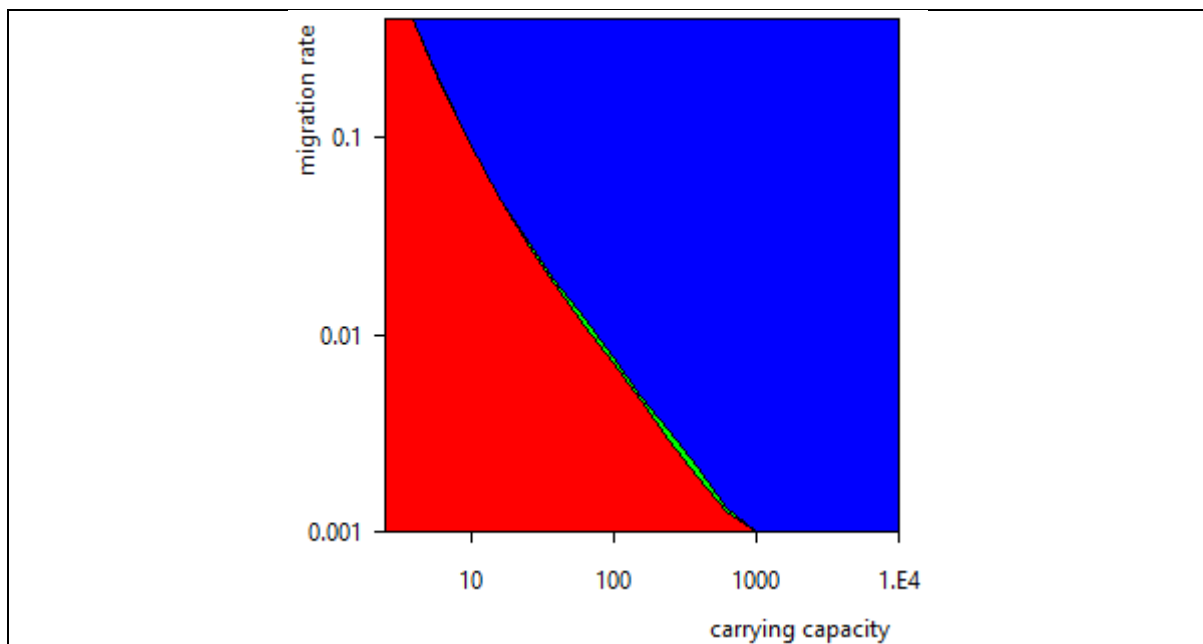
Figure 1.5. Parameter map showing ranges of migration rate and group size leading to fixation of altruism (red), egoism (blue), or polymorphism (green).
Parameters: Partial dominance. Colony size = 4. Fitness ratio = 0.875. Extinction rate 0.1 for egoism groups, 0.01 for altruism groups. Max group size going from 1 to 10000.
Parameter file: `island_capacity-migration.altru`

Figure 1.6 shows that group selection is inefficient if a few individuals survive group selection.
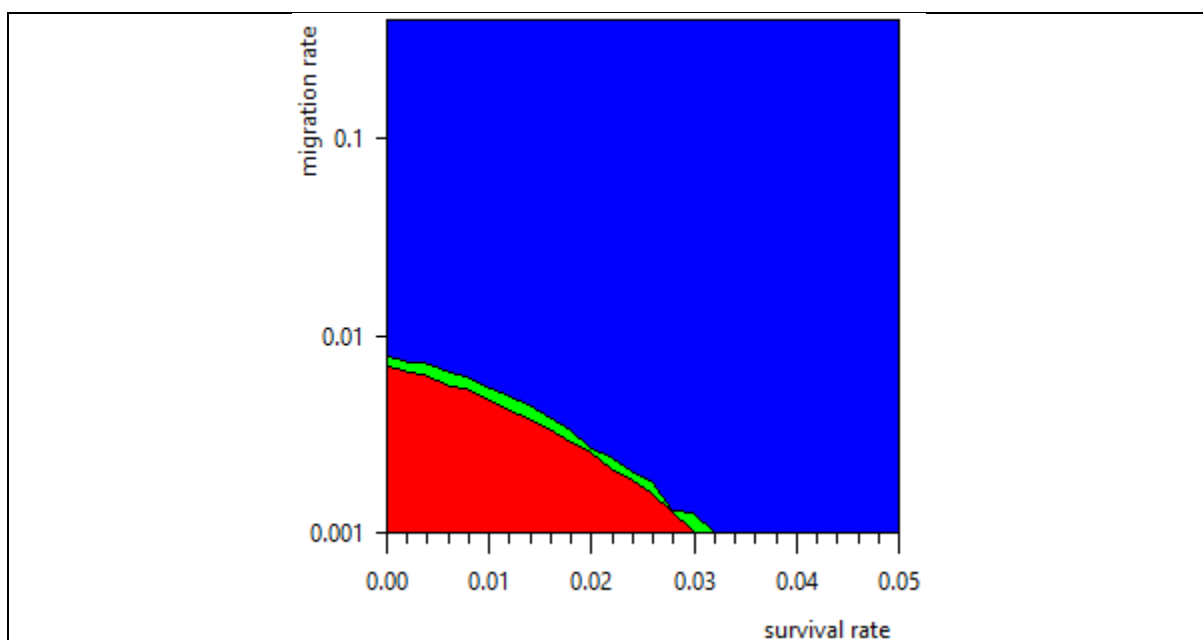

Figure 1.6. Parameter map showing ranges of migration rate and survival rate leading to fixation of altruism (red), egoism (blue), or polymorphism (green).
Parameters: Partial dominance. Carrying capacity = 100. Colony size = 5. Fitness ratio = 0.875. Extinction rate 0.1 for egoism groups, 0.01 for altruism groups.
Parameter file: `island_survival-migration.altru`

Figure 1.7 shows the effect of the size of founder populations or new colonies and different colonization patterns. The results show that group selection is stronger if all members of a new colony come from the same island than if they have mixed origin. Altruism is increased if colonizers come from the strongest group rather than from a random group because this adds a new extra mechanism of group selection.
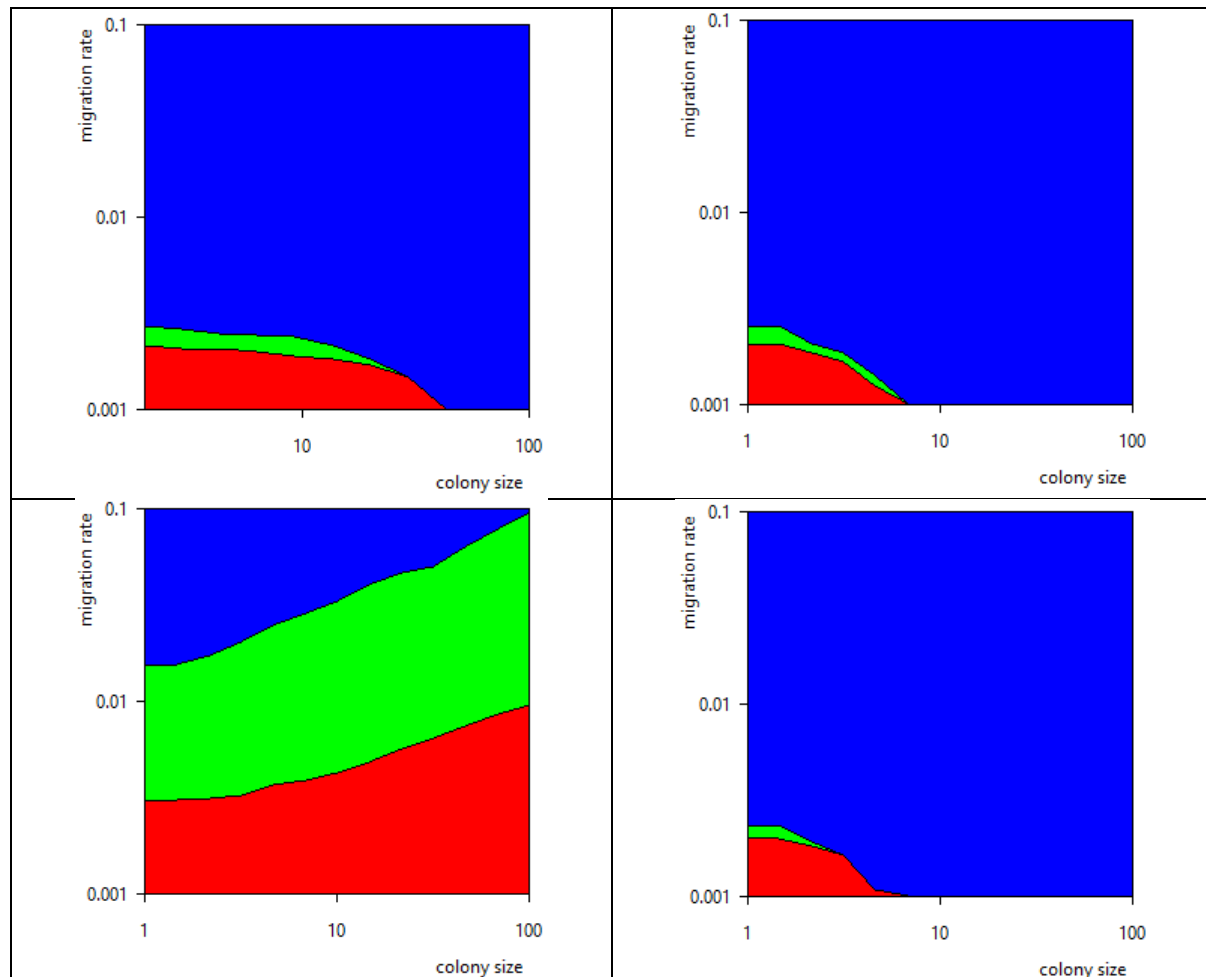

Figure 1.7. Parameter map showing ranges of migration rate and colony size leading to fixation of altruism (red), egoism (blue), or polymorphism (green).
Parameters: Partial dominance. Carrying capacity = 1000. Fitness ratio = 0.95. Extinction rate 0.1 for egoism groups, 0.01 for altruism groups. Survival rate = 0.
Top left: colonizers come from a random neighbor group.
Top right: colonizers are mixed from six neighbor groups.
Bottom left: colonizers come from the strongest neighbor group.
Bottom right: colonizers are mixed from the entire metapopulation.
Parameter file: `island_colony-migration.altru`

We can conclude that group selection according to the island model can lead to fixation of an allele for altruism only under quite restrictive conditions. The most important conditions that favor the evolution of altruism are: division of the population into distinct groups, low rate of migration between groups, weak individual selection for egoism, strong group selection for altruism, small group size, small size of founder groups, a linear or concave group fitness function, few or no survivors after group extinction, high relatedness within founder groups, and limitation of the geographic distance that migrants and founder groups can travel. These conditions are rarely met in

nature. Most group-living species (including humans) have rates of migration between groups that far exceed the limits that would make group selection effective.

The best example of selective extinction is pathogen-host interaction. Parasites and viruses are often undergoing group selection for decreased virulence because high virulence may kill their host. The effectiveness of group selection here depends on small founder populations and low rates of re-infection (Frank, 1996).

Selective migration model

This model is not based on group extinction but on selective migration between groups. This model assumes that groups with many altruists have a higher fertility for both egoist and altruist members. Such groups are able to send out more emigrants than groups dominated by egoists (Rogers, 1990). In the simulations below, each group receives immigrants in each generation from one neighbor group chosen with probability proportional to the production in excess of the carrying capacity of each neighbor group.

Figure 2.1 shows that some migration is necessary for the model to work, while higher migration rates do not increase altruism because of the reduced variance between groups. The altruism gene can be maintained only if the individual selection against altruism is weak.
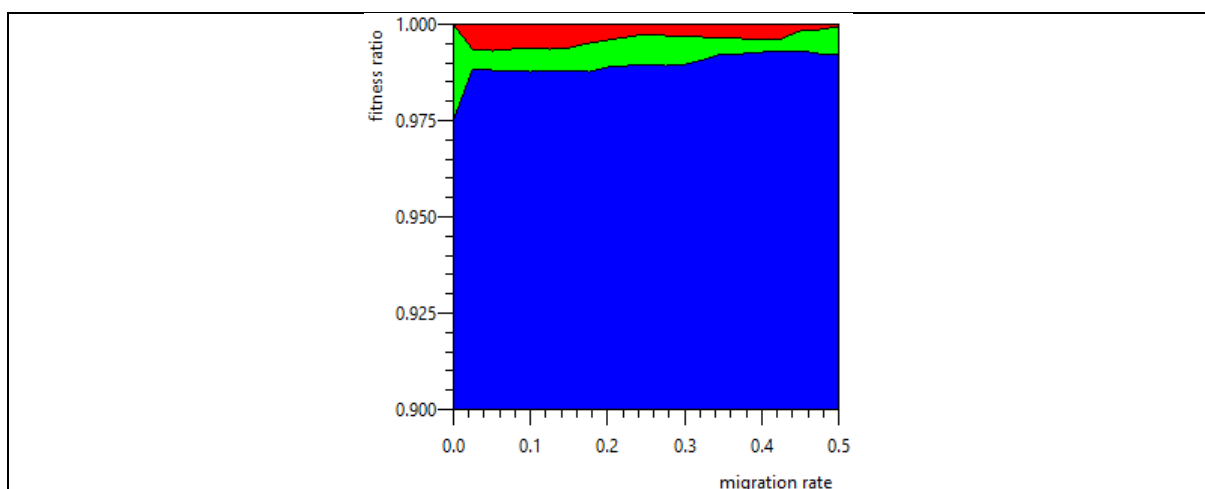

Figure 2.1. Parameter map showing ranges of migration rate and individual fitness ratio leading to fixation of altruism (red), egoism (blue), or polymorphism (green).
Parameters: Partial dominance. Carrying capacity = 100. Colony size = 10. Reproductive fitness of egoists in egoist groups = 2.0, in altruist groups = 3. Extinction rate = 0.
Parameter file: `selective_migr_fit-migration.altru`

Figure 2.2 shows that a higher ratio of growth in altruist groups relative to egoist groups will increase the level of individual selection that this mechanism can withstand, but still at a very low level.

emigration = excess. without extinction

Figure 2.2. Parameter map showing ranges of group fitness ratio and individual fitness ratio leading to fixation of altruism (red), egoism (blue), or polymorphism (green).
Parameters: Partial dominance. Carrying capacity = 100. Colony size = 10. Migration rate = 0.1. Extinction rate = 0.
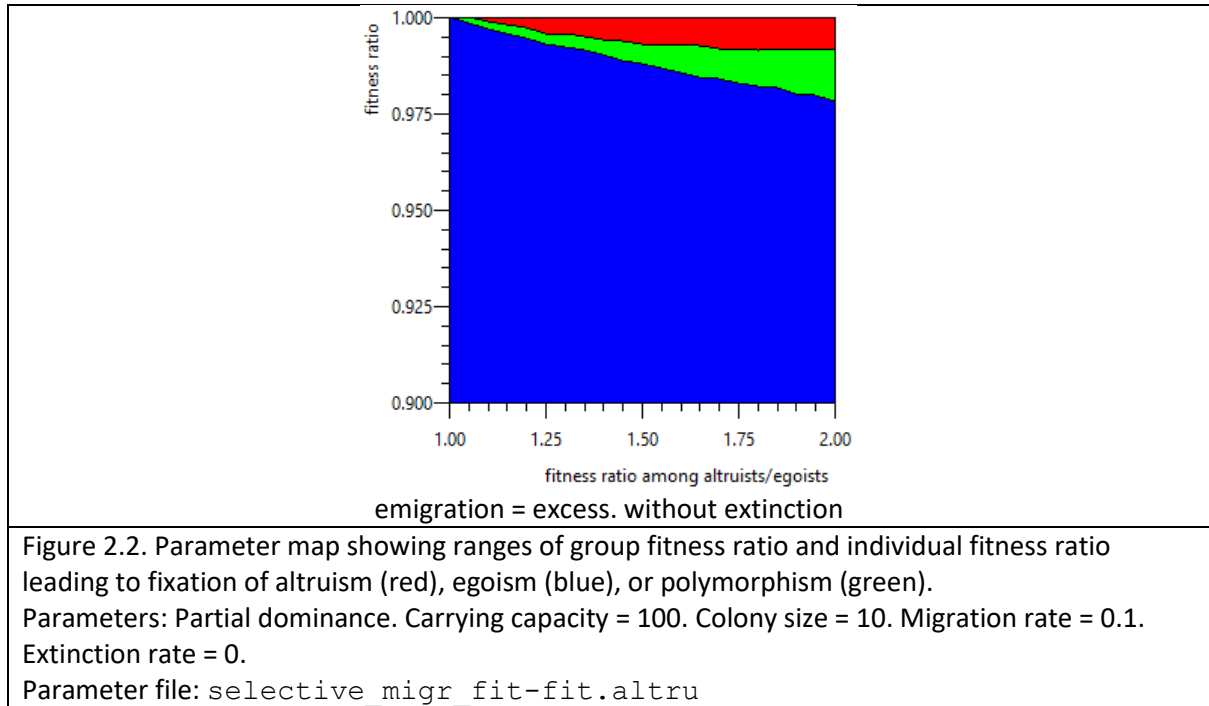Parameter file: `selective_migr_fit-fit.altru`

Figure 2.3 shows that the selective migration effect is strongest when the carrying capacity of each island is low. The effect is decreasing strongly when the population of each island is higher than 10.

Figure 2.3. Parameter map showing ranges of island carrying capacity and individual fitness ratio leading to fixation of altruism (red), egoism (blue), or polymorphism (green).
Parameters: Partial dominance. Colony size = 10. Migration rate = 0.1. Reproductive fitness of egoists in egoist groups = 2.0, in altruist groups = 3. Extinction rate = 0.
Parameter file: `selective_migr_fit-capacity.altru`
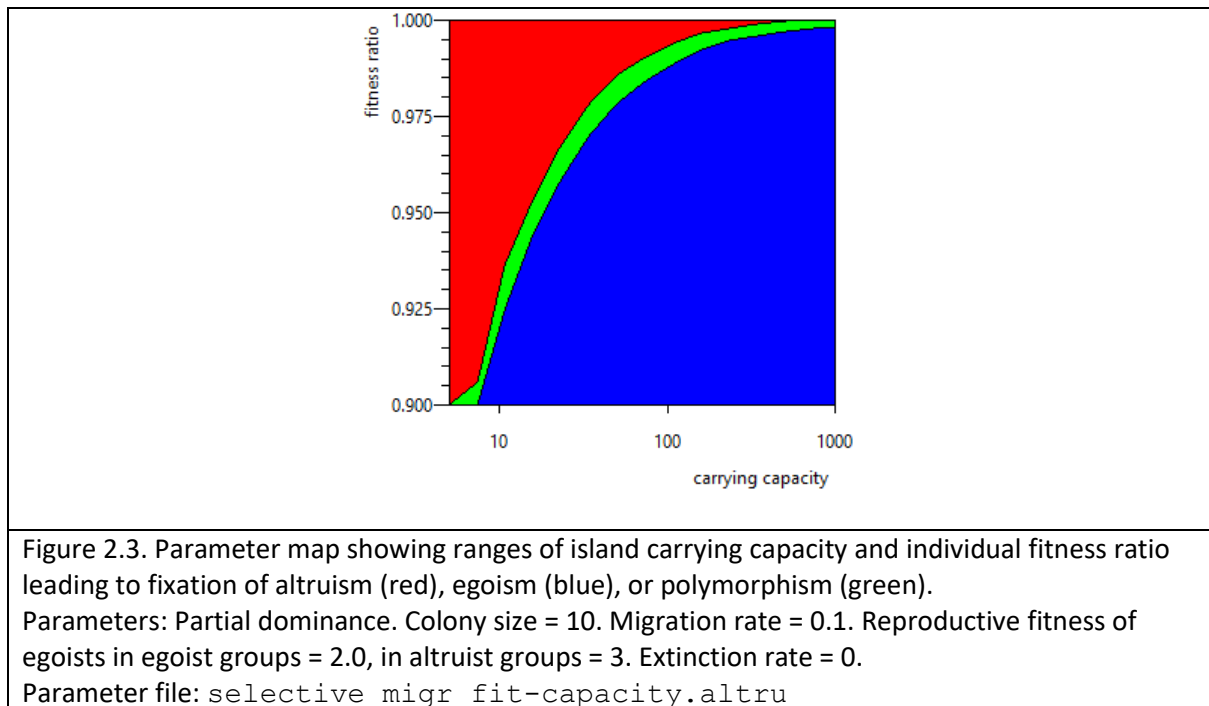
The conclusion is that selective migration can lead to fixation of an altruism gene only when groups are small, individual selection against the altruism gene is weak, and altruism increases the growth rate of a group very strongly.

Selective dispersal model

This model is based on selective forming of daughter groups (Mitteldorf & Wilson, 2000; Kawata, 1999). In the simulations described here, groups go extinct with a constant probability that is independent of group properties. Empty islands are colonized by founder populations from a neighbor group. The probability that the founder population comes from a particular neighbor group is proportional to the production of that neighbor group in excess of the carrying capacity.

Figure 3.1 shows that the selective dispersal model is very sensitive to migration between established groups. It works best when the migration rate is low or zero.
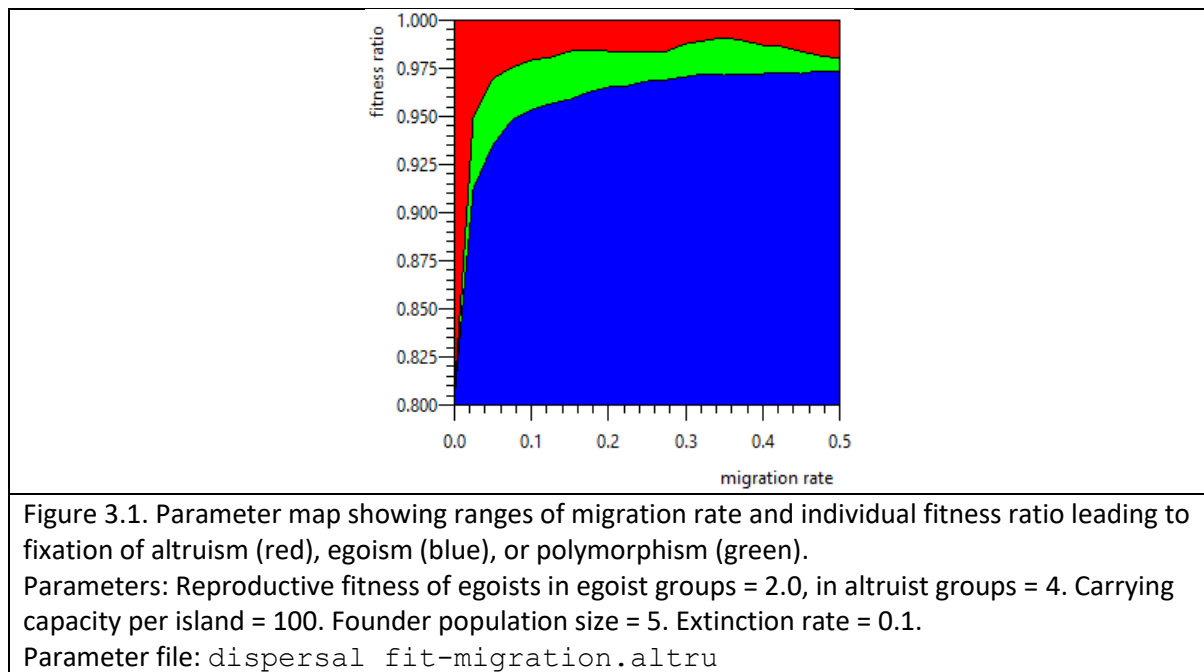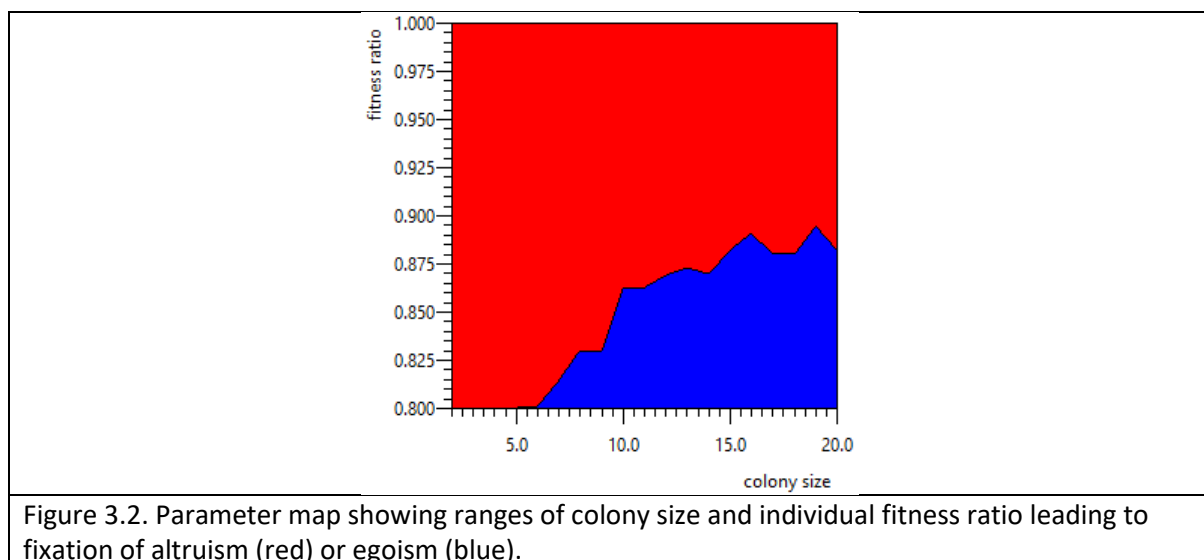

Figure 3.1. Parameter map showing ranges of migration rate and individual fitness ratio leading to fixation of altruism (red), egoism (blue), or polymorphism (green).
Parameters: Reproductive fitness of egoists in egoist groups = 2.0, in altruist groups = 4. Carrying capacity per island = 100. Founder population size = 5. Extinction rate = 0.1.
Parameter file: `dispersal_fit-migration.altru`

Figure 3.2 shows that the dispersal model is most effective when founder populations are small.

Figure 3.2. Parameter map showing ranges of colony size and individual fitness ratio leading to fixation of altruism (red) or egoism (blue).

Parameters: Reproductive fitness of egoists in egoist groups = 2.0, in altruist groups = 4. Carrying capacity per island = 100. Extinction rate = 0.1. Migration rate = 0.
Parameter file: `dispersal_fit-colony.altru`

Figure 3.3 shows the relationship between individual selection and group selection. A high level of group selection is necessary for counterbalancing a high level of individual selection.

Figure 3.3. Parameter map showing ranges of group fitness ratio and individual fitness ratio leading to fixation of altruism (red) or egoism (blue).
Parameters: Carrying capacity per island = 100. Colony size = 5. Extinction rate = 0.1. Migration rate = 0. (The curve becomes less jagged if all neighbors contribute proportionally to founder populations)
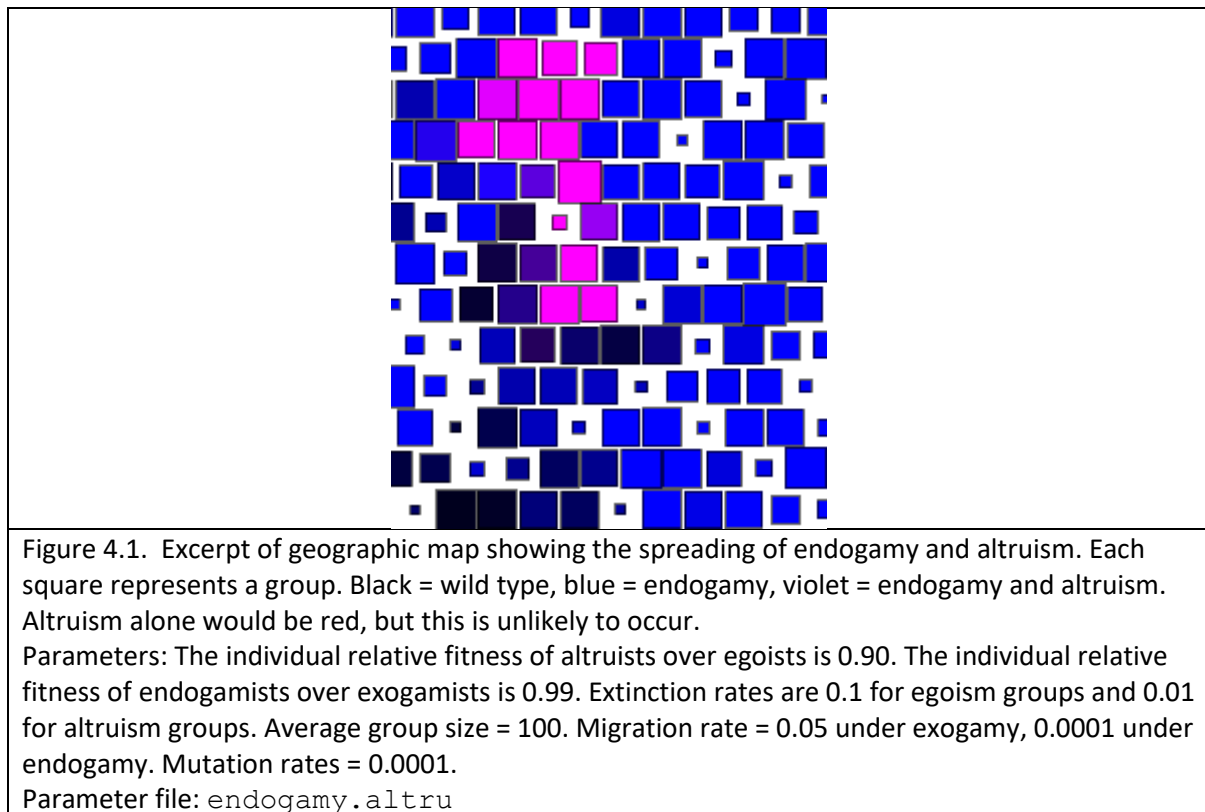Parameter file: `dispersal_fit-fit.altru`
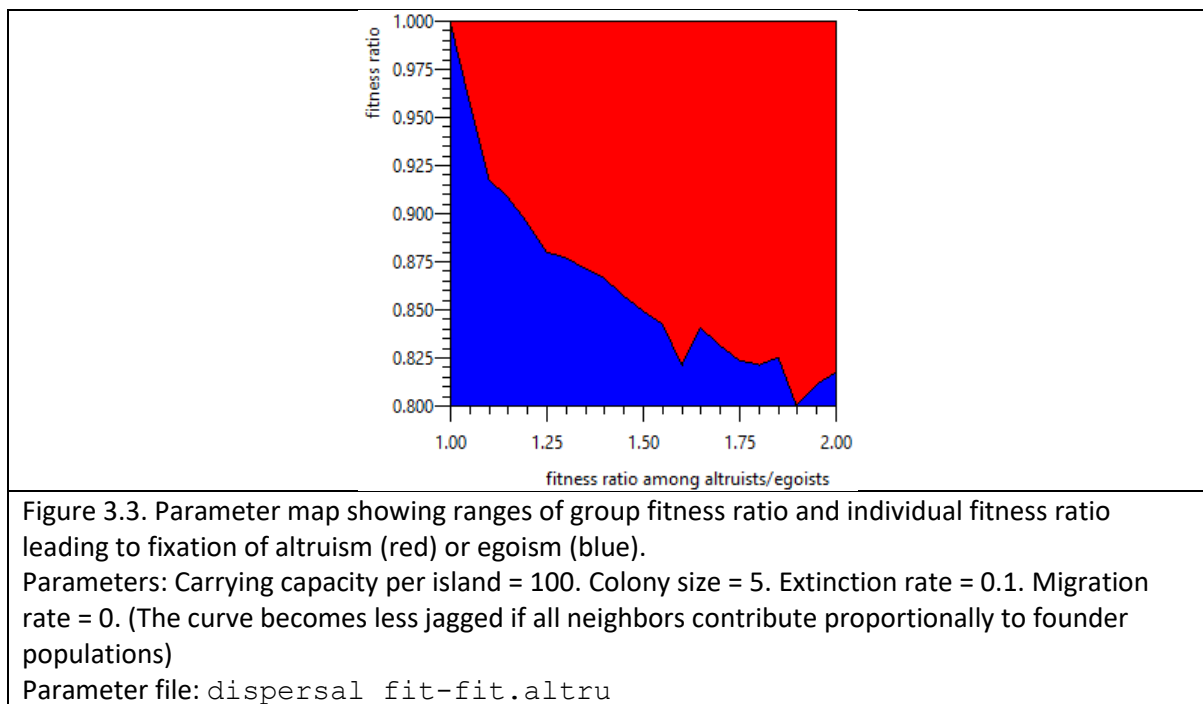
The conclusion is that selective dispersal can lead to fixation of altruism if the rate of migration between groups is very low and founder groups are small and group selection is strong relative to individual selection. This model is relevant for eusocial insects and for certain other animals with communal nesting.

Outsider exclusion model

The outsider exclusion model is an extension of the island model and the selective dispersal model. A gene named endogamy at a biallelic locus with the same name controls a trait that reduces immigration into groups where this trait is frequent. A theoretical study has found that a gene that makes group members exclude outsiders or mate only with members of the same group can spread simply because it is reducing competition from other alleles (Peck, 1990). Simulation of the endogamy model confirms this theoretical prediction.

We have seen that group selection of altruism is very vulnerable to invasion by egoism. Outsider exclusion can pave the way for the evolution of altruism by reducing the rate of immigration into a group. In other words, the evolution of outsider exclusion can be a preadaptation for the evolution of altruism according to the selective extinction model or the selective dispersal model. Figure 4.1 shows that endogamy evolves first, and altruism starts to spread only after endogamy has become widespread in the population.

Figure 4.1. Excerpt of geographic map showing the spreading of endogamy and altruism. Each square represents a group. Black = wild type, blue = endogamy, violet = endogamy and altruism. Altruism alone would be red, but this is unlikely to occur.
Parameters: The individual relative fitness of altruists over egoists is 0.90. The individual relative fitness of endogamists over exogamists is 0.99. Extinction rates are 0.1 for egoism groups and 0.01 for altruism groups. Average group size = 100. Migration rate = 0.05 under exogamy, 0.0001 under endogamy. Mutation rates = 0.0001.
Parameter file: `endogamy.altru`

This model is useful for explaining the evolution of eusociality in insects and other animals with communal nesting, such as naked mole rats (Sherman, et al., 1991) and sponge-dwelling shrimps (Duffy, et al., 2000). The theory is that communal nesting evolves first, perhaps because it provides protection against predators or reduces energy consumption (Mainwaring, et al., 2023). Exclusion of outsiders evolves next (Peck, 1990). Monopolization of reproduction by a queen has likely evolved by a combination of kin selection, cooperative breeding, and active policing (Ratnieks & Wenseleers, 2008; Boomsma, et al., 2011). Cooperation and self-sacrificial behavior can then evolve more easily by selective dispersal when workers are already prevented from reproducing.

A problem with the outsider exclusion model is that a high degree of endogamy can cause inbreeding depression.
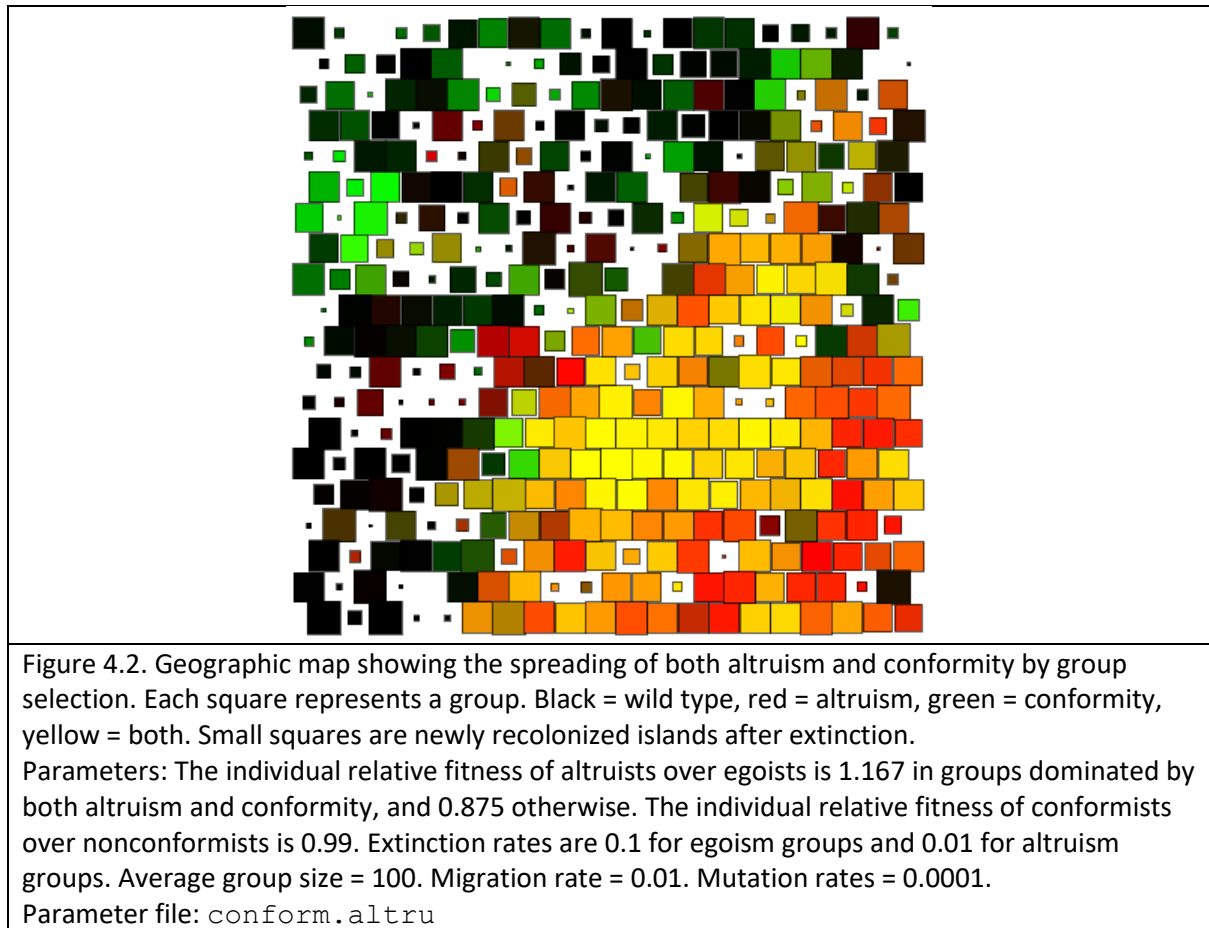
Conformity model

The conformity model is an extension of the island model. A gene named conformity at a biallelic locus with the same name controls a trait that reduces the fitness of egoists in groups dominated by altruists. In other words, the fitness of egoists is lower than the fitness of altruists in groups dominated by both altruism and conformity. In all other cases, egoists have higher individual fitness than altruists.

Simulation shows that conformity can enhance the evolution of altruism, but the conformity allele is only spreading under a narrow range of conditions. The conformity allele is not selected for by individual selection, but only by group selection, and only when the altruism and egoism alleles are both present. This mechanism is fragile because it depends twice on group selection. The altruism allele is likely to spread in groups where the conformity allele is frequent. This can lead to elimination of the egoism allele in a subpopulation dominated by conformity. But without the egoism allele, there is no group selection for the conformity allele. A weak individual selection against the conformity allele will make the frequency of conformity go down again. The conformity allele can only be maintained if there is a continuous supply of the egoism allele due to migration or back mutation.

Figure 4.2 shows an example where the altruism allele and the conformity allele are spreading together from the lower right corner of the figure. Far from the progressing front, the conformity allele starts to regress due to lack of egoism alleles, followed by a return of the egoism allele. The result is random oscillations.

Note that the parameters for figure 4.2 have been carefully adjusted to enable the spreading of conformity. The conditions under which the conformity allele will spread are quite limited.

Figure 4.2. Geographic map showing the spreading of both altruism and conformity by group selection. Each square represents a group. Black = wild type, red = altruism, green = conformity, yellow = both. Small squares are newly recolonized islands after extinction.
Parameters: The individual relative fitness of altruists over egoists is 1.167 in groups dominated by both altruism and conformity, and 0.875 otherwise. The individual relative fitness of conformists over nonconformists is 0.99. Extinction rates are 0.1 for egoism groups and 0.01 for altruism groups. Average group size = 100. Migration rate = 0.01. Mutation rates = 0.0001.
Parameter file: `conform.altru`

Simulation experiments show that combined evolution of a conformity allele and an altruism allele by group selection is possible only under certain conditions. These conditions are close to the conditions that would make altruism spread even in the absence of conformity. Furthermore, the conformity allele can only be maintained if there is a continuous supply of the egoism allele from migration or back mutation.

The result of the simulations is that this model likely leads to oscillations rather than to fixation of the conformity allele. We must conclude that a genetically determined conformity trait is unlikely to evolve if the only effect of this trait is to reduce the fitness of egoists among altruists. If a general pressure towards conformity is established by other mechanisms, then it may facilitate the evolution of altruism as a side effect. It has been suggested that conformity can arise by cultural evolution rather than biological evolution (Henrich & Boyd, 2001).

Altruistic punishment

Many scientists have proposed that altruistic punishment can explain the evolution of altruism. The theory of altruistic punishment suggests that humans may voluntarily punish

wrongdoing by others in matters that they are not personally involved in. It is assumed that punishment can suppress egoistic behavior and free riding. The act of punishing is an altruistic act if it incurs a cost on the punisher that exceeds his or her share of the group-level benefit resulting from the act, assuming that this benefit is shared equally among all members of the group. The theory of altruistic punishment relies on the assumption that the fitness cost of punishing is low while the cost of being punished is high. This will facilitate the evolution of altruism by replacing the high fitness cost of altruistic behavior by the lower cost of punishing egoists (Bowles & Gintis, 2011; Boyd et al., 2003; Strobel, 2016).

A further expansion of this theory assumes that higher orders of altruistic punishment is possible. The hypothetical scenario is that a person number 3 can punish a person number 2 for failing to punish a person number 1 for egoistic behavior. This can be expanded to an n-person game. It is assumed that the cost of punishing is decreasing with the order n (Henrich & Boyd, 2001). The theory of higher order altruistic punishment is ignoring what economists call transaction costs. It is costly to gather information about everybody's behavior, evaluating evidence, resolving disagreements about guilt, and making regulations about who should punish what. In fact, anthropologists have found no evidence of second and higher order altruistic punishment in traditional human societies (Bowles & Gintis, 2011).

Altruistic punishment may also involve the costs of disagreement, unfriendship, retaliation, and escalation of conflict. Altruistic punishment rarely takes the form of physical violence because of the risks of retaliation and escalation. More common forms of altruistic punishment include giving the culprit a bad reputation, refusing help, or withholding resources (Neumann, 2020). Ostracism is seen in more severe cases (Bowles & Gintis, 2004).

The simplest way to model altruistic punishment is to replace the fitness costs of altruistic behavior in the island model with the lower fitness costs of altruistic punishment. In this model, there is no gene for first-hand altruism, but instead a gene for altruistic punishment. Figure 1.3 shows that the evolution of altruism is more likely the lower the individual fitness costs of the inherited trait.

However, there is a complication to this model. If the act of altruistic punishment has low costs, then we can assume that a single person can afford to do many such acts. The consequence of this is that one or a few altruistic punishers in a group is enough to effectively suppress egoism in the group (Krasnow, et al., 2015). Adding more than a few altruistic punishers will have little or no additional effect. This means that we have a highly convex group fitness function. The group fitness as a function of the fraction of altruistic punishers in the group has a steep increase in the beginning. After this, it levels off as the fraction of altruistic punishers goes towards its maximum. Figure 1.2 shows that a highly convex group fitness function, with a group fitness exponent near zero, leads to stable polymorphism rather than to fixation of the allele that codes for altruistic punishment. The hypothetical allele for altruistic punishment will remain at a low frequency in the population.

Another possible model is to assume that there are two separate loci. The first locus has an allele that codes for altruism. A second locus has an allele that codes for altruistic punishment. The presence of altruistic punishers in a group will reduce the fitness of egoists and thereby facilitate the spreading of the altruism gene. This model is equivalent to the conformity model described above. The group-level effect of conformity will be a convex function of the fraction of conformists or altruistic punishers. This has the consequence that the frequency of the allele for conformity or altruistic punishment will remain low. We saw above that the conformity model only has a weak effect. This effect is further weakened when we apply it to altruistic punishment because of the convex group conformity function.

Both models show that altruistic punishment is unlikely to evolve as a separate genetically determined trait. Nevertheless, there is plenty of evidence that altruistic punishment takes place in human societies (Boccadoro, et al., 2021). This can only be explained if we assume that altruistic punishment is part of a more general system of sociality, rather than an independent genetic trait (Gintis, 2003; Fowler, 2005). This system of sociality may include a more complex social organization,

possibly including repeated interactions, enforcement of cultural norms, and some kind of advantage to the altruistic punisher (Sigmund, 2007).

Haystack model

This model is a thought experiment proposed by John Maynard Smith (Smith, 1964). Imagine that groups of mice live in haystacks. Each haystack is colonized by a small founder population early in the season. Their descendants stay in the same haystack until the end of the season when the haystacks are removed. In a second period where there are no haystacks, the mice live elsewhere and the entire metapopulation is mixed until next season when new haystacks are colonized. There are two different phenotypes: altruists who limit their consumption of resources, and egoists who eat more than necessary. Haystacks with altruist mice leave more mice to the metapopulation at the end of the haystack season than haystacks with egoist mice. This mechanism is also called intrademic group selection. The parameter file `haystack.altru` contains an example of this model.

This model depends on variation in gene frequencies between founder groups, where this variation comes from genetic drift only. This drift is high when founder groups are small, and low when founder groups are large. Figure 5.1 shows that group selection can compete with weak individual selection, but only if founder populations are small.
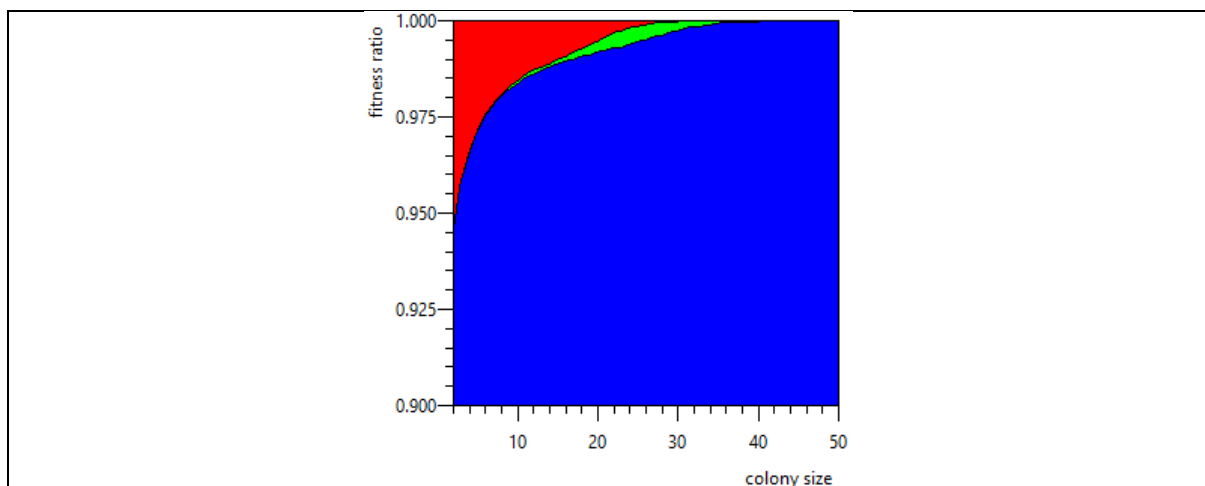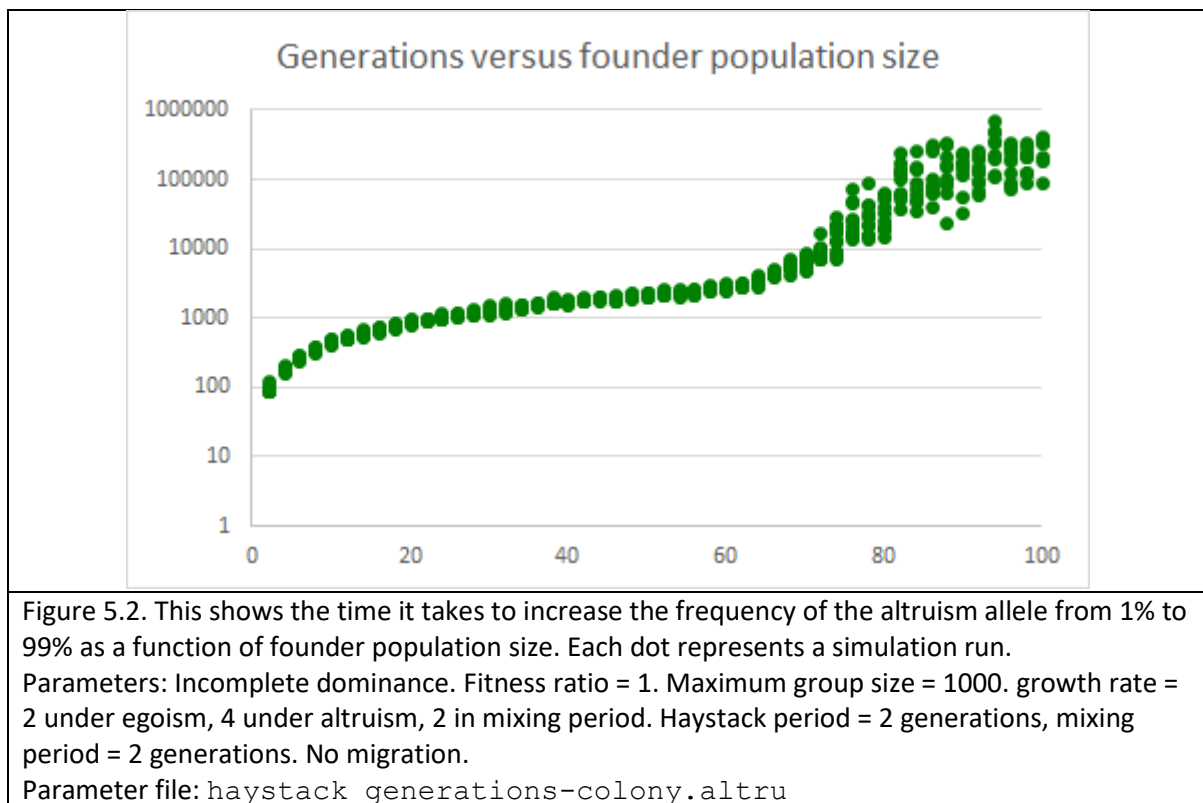

Figure 5.1. Parameter map showing ranges of founder population size and individual fitness ratio leading to fixation of altruism (red) or egoism (blue). The green area indicates that neither gene has reached a frequency of 0.95 after 100,000 generations, starting at a frequency of 0.50. Parameters: Incomplete dominance, reproductive fitness of egoists = 2.0 under egoism, 2.2 under altruism. Individual fitness of altruists relative to egoists ranging from 0.90 to 1.00. Maximum group size = 1000. Haystack period = 5 generations, mixing period = 2 generations. No migration. Parameter file: `haystack_fit-colony.altru`

Group selection in the haystack model is not only weak when founder populations are bigger than a few individuals, it is also extremely slow. Figure 5.2 shows the time it takes to evolve altruism as a function of founder population size without individual selection.

Figure 5.2. This shows the time it takes to increase the frequency of the altruism allele from 1% to 99% as a function of founder population size. Each dot represents a simulation run.
Parameters: Incomplete dominance. Fitness ratio = 1. Maximum group size = 1000. growth rate = 2 under egoism, 4 under altruism, 2 in mixing period. Haystack period = 2 generations, mixing period = 2 generations. No migration.
Parameter file: `haystack_generations-colony.altru`

The haystack model is less sensitive to migration than the island model. Figure 5.3 shows that altruism can be fixated even for high migration rates if the haystack period is short and the fitness loss of altruists is small.

Figure 5.3. Parameter map showing ranges of migration rate and fitness ratio leading to fixation of altruism (red) or egoism (blue).
Parameters: Incomplete dominance. Reproductive fitness of egoists = 2.0 under egoism, 2.2 under altruism. Individual fitness of altruists relative to egoists ranging from 0.90 to 1.00. Maximum group size = 100. Founder population size = 5. Haystack period = 4 generations, mixing period = 2 generations, no migration.
Parameter file: `haystack_fit-migration.altru`

Figure 5.4 shows the balance between individual selection and group selection. An increase of fitness in altruist groups over egoist groups of around 10% can balance out an individual selection

of about 3% here. A higher fitness of altruist groups also means higher growth rate so that the carrying capacity of the "haystacks" is reached. This makes it difficult to reach fixation of either gene.
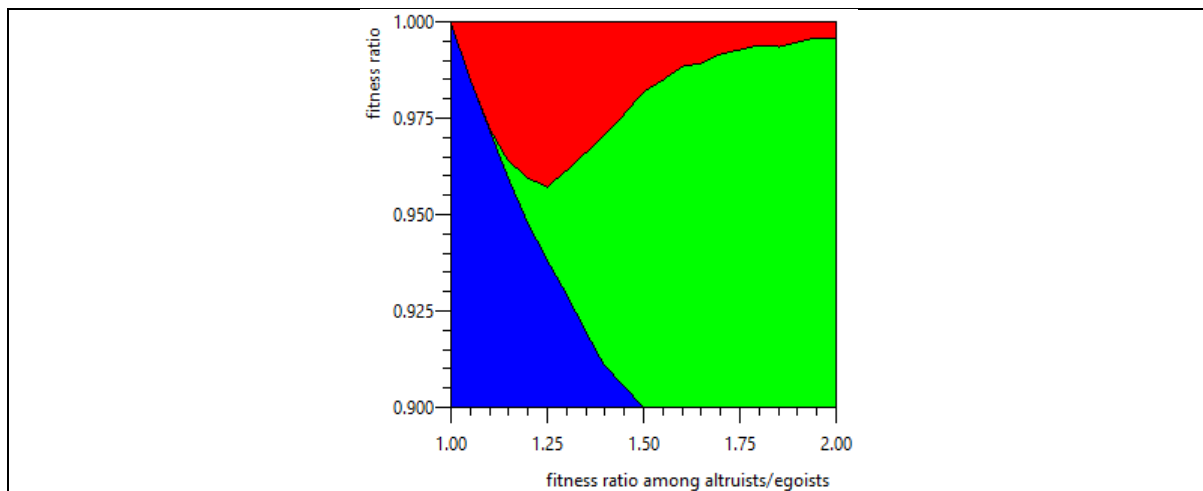

Figure 5.4. Parameter map showing ranges of group fitness ratio and individual fitness ratio leading to fixation of altruism (red) or egoism (blue). The green area indicates that neither gene has reached a frequency of 0.95 after 100,000 generations, starting at a frequency of 0.50. Parameters: Incomplete dominance, reproductive fitness of egoists in egoist groups = 2.0. Individual fitness of altruists relative to egoists ranging from 0.90 to 1.00. Fitness in altruist groups relative to egoist groups ranging from 1.00 to 2.00. Maximum group size = 100. Founder population size = 4. Haystack period = 4 generations, mixing period = 2 generations, no migration. Parameter file: `haystack_fit-fit.altru`

Figure 5.5 shows how the carrying capacity of the "haystacks" can limit the group selection. A sufficiently large carrying capacity will allow the differential growth of groups to proceed throughout the haystack period.
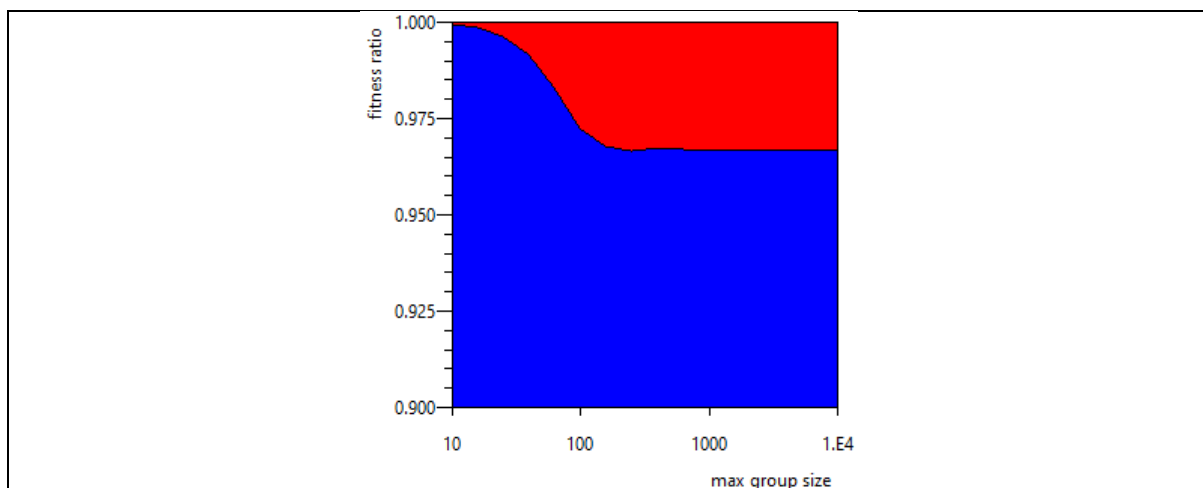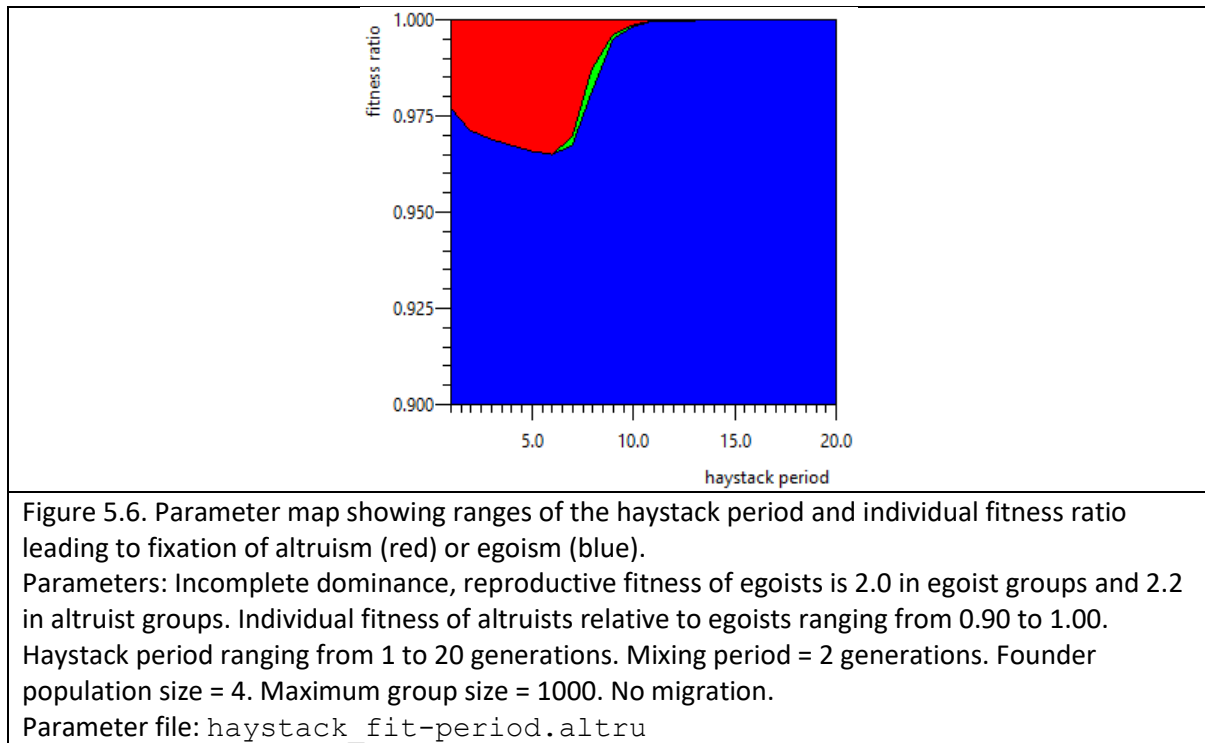

Figure 5.5. Parameter map showing ranges of carrying capacity and individual fitness ratio leading to fixation of altruism (red) or egoism (blue).
Parameters: Incomplete dominance, reproductive fitness of egoists is 2.0 in egoist groups and 2.2 in altruist groups. Individual fitness of altruists relative to egoists ranging from 0.90 to 1.00. Maximum group size ranging from 10 to 10000. Founder population size = 4. Haystack period = 4 generations, mixing period = 2 generations, no migration. Parameter file: `haystack_fit-groupsize.altru`

However, if the mice stay in the haystacks for many generations, they will eventually reach the carrying capacity of the haystacks where the population number is no longer determined by differential growth rates. Figure 5.6 shows that the effect of group selection disappears for longer haystack periods.

Figure 5.6. Parameter map showing ranges of the haystack period and individual fitness ratio leading to fixation of altruism (red) or egoism (blue).
Parameters: Incomplete dominance, reproductive fitness of egoists is 2.0 in egoist groups and 2.2 in altruist groups. Individual fitness of altruists relative to egoists ranging from 0.90 to 1.00. Haystack period ranging from 1 to 20 generations. Mixing period = 2 generations. Founder population size = 4. Maximum group size = 1000. No migration.
Parameter file: `haystack_fit-period.altru`

We can conclude from these simulations that group selection according to the haystack model is theoretically possible, but the mechanism is weak and often very slow. Altruism can be fixated in this model if individual selection is weak, the size of founder groups is small, and the carrying capacity of the "haystacks" is high.

It is difficult to find real world examples where the haystack mechanism is actually working. Parasite-host interaction is a possibility, but in many cases, we may prefer other models. The island model may be more appropriate if the main contribution to the evolution of altruism is that hosts die when parasites are too virulent. If parasites do not reproduce outside of the hosts, then we may prefer the selective propagation model, described above.

Group territoriality model

The group territoriality model is a new model introduced with the Altruist software program. This model defines a species of social animals living in groups. Each group has its own territory. A group can conquer territory from a neighbor group, possibly through violent conflict. The winning group will gain more territory, while the territory of the losing group gets smaller. The carrying capacity of a group territory is proportional to its area.

There are two phenotypes: altruists who are willing to fight for their group in territorial conflicts, and egoists who are not. Altruism is controlled by a biallelic locus. Altruists have lower individual fitness than egoists because they may suffer injury or death in violent conflicts. Groups with many altruists have higher group fitness, which means higher ability to win territory from weaker neighbor groups. Larger territories can feed more group members and allow the groups to grow bigger. The population of a losing group will be reduced because the smaller territory can sustain fewer individuals.

When a group gets too small, it will be unable to defend its territory and lose it all to an attacking neighbor group. When a group gets too big, it will split into two groups that each gets half of the territory.

This model involves two opposing evolutionary forces. Group selection will favor the allele for altruism because groups with many altruists can grow larger by conquering new territory. Individual selection favors the opposite allele, egoism, that increases the survival rate or reproduction rate of the individual. The purpose of the simulation is to test whether group fitness can win over individual fitness so that the altruistic trait is spreading, and to find the conditions under which this is possible.

The strength of a group is defined as the group fitness multiplied by the number of individuals in the group. The higher the difference in strength between two groups, the more territory can the stronger group win from the weaker group. The mean amount of territory that a group can conquer from a neighbor group is proportional to the war intensity multiplied by the difference in group strength.

Figure 6.1 shows a habitat during evolution. Altruist groups (red) can conquer territory from egoist groups (blue). This makes altruist groups grow in size and eventually split into two groups, while egoist groups perish when they have lost all of their territory. The irregular shapes of especially the altruist groups is a result of the frequent moving of borders.
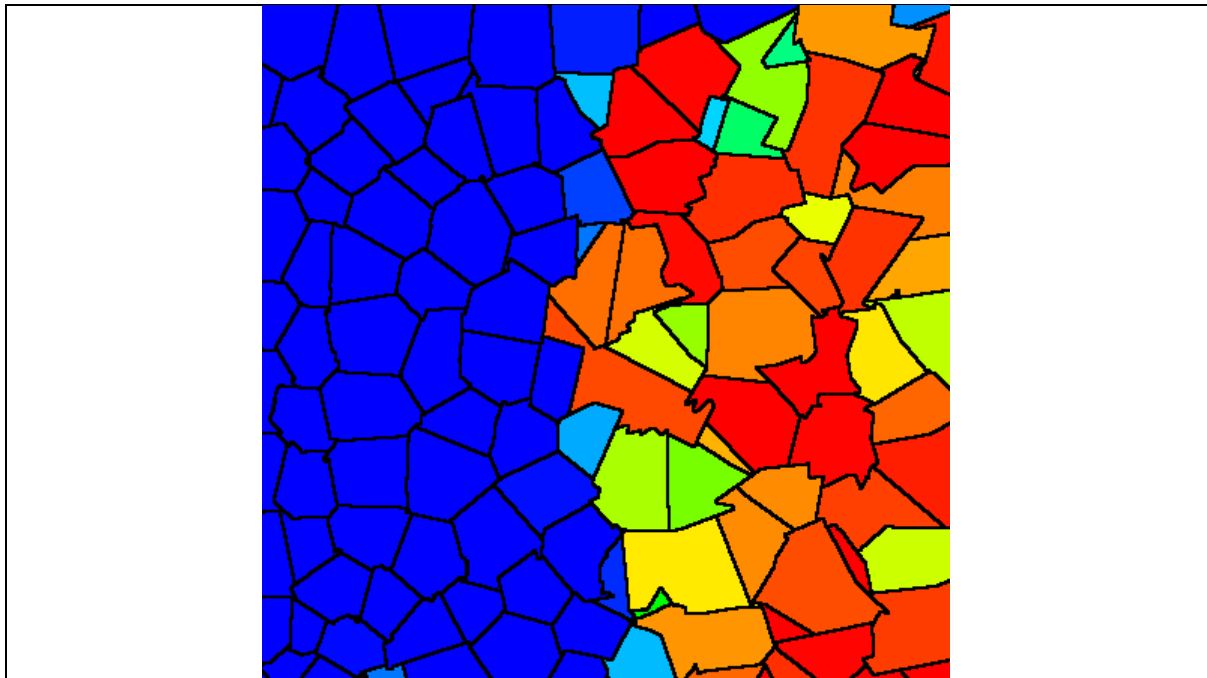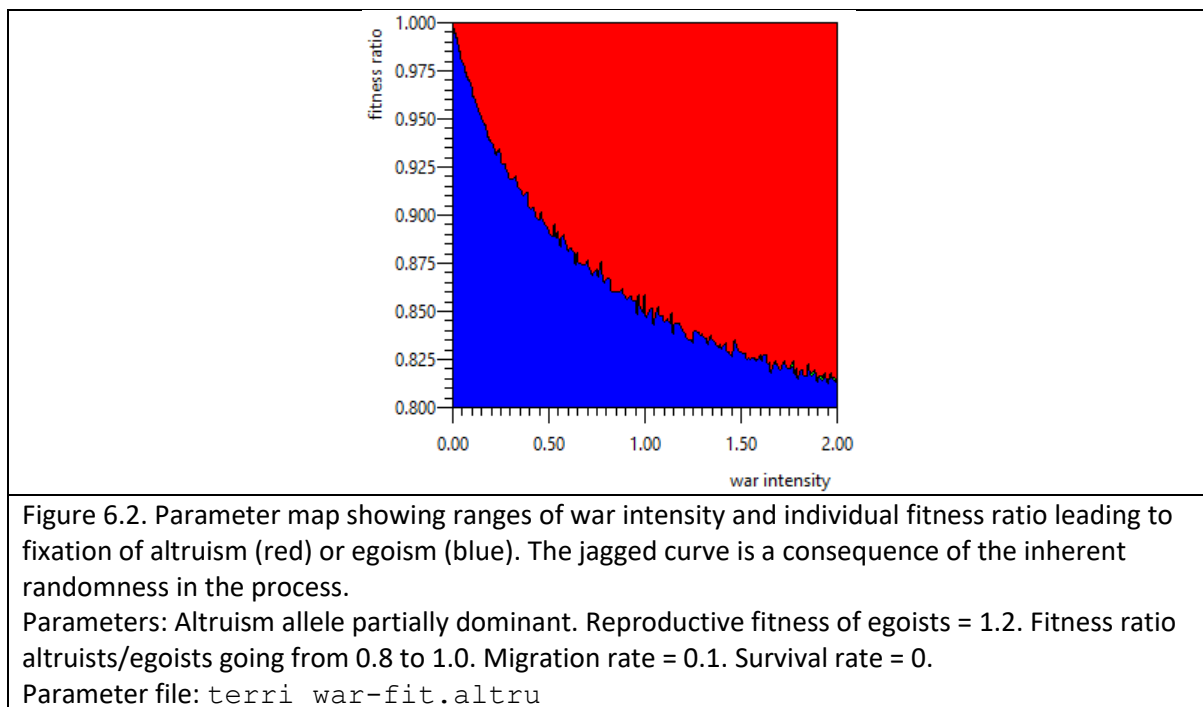

Figure 6.1. Excerpt of habitat during evolution. Blue territories are inhabited by egoists, and red by altruists. Intermediate colors (cyan, green, yellow, orange) indicate mixed populations with increasing proportions of altruists.
Parameters: fitness of altruists relative to egoists = 0.99. War intensity = 0.1. Incomplete dominance. Group fitness function is linear. Migration rate = 0.01. Carrying capacity per area unit = 0.05. Max. territory area = 4000.
Parameter file: `terri.altru`

Figure 6.2 shows the balance between individual selection and group selection. A stronger war intensity can counterbalance a stronger individual selection for egoism.

Figure 6.2. Parameter map showing ranges of war intensity and individual fitness ratio leading to fixation of altruism (red) or egoism (blue). The jagged curve is a consequence of the inherent randomness in the process.
Parameters: Altruism allele partially dominant. Reproductive fitness of egoists = 1.2. Fitness ratio altruists/egoists going from 0.8 to 1.0. Migration rate = 0.1. Survival rate = 0.
Parameter file: `terri_war-fit.altru`

This model is very sensitive to migration. A high war intensity is required for altruism to evolve if the migration rate is high. Figure 6.3 shows the relationship between migration rate and war intensity for different migration patterns. The first pane (top left) shows the situation where immigrants come from all neighbor groups. Altruism can evolve under a higher migration rate if immigrants in one generation all come from the same group, even if this migration is not limited by geographic distance (top right). Altruism is least likely to evolve if immigrants are mixed from all groups (bottom left). Selective migration allows altruism to evolve under high migration rates (bottom right).
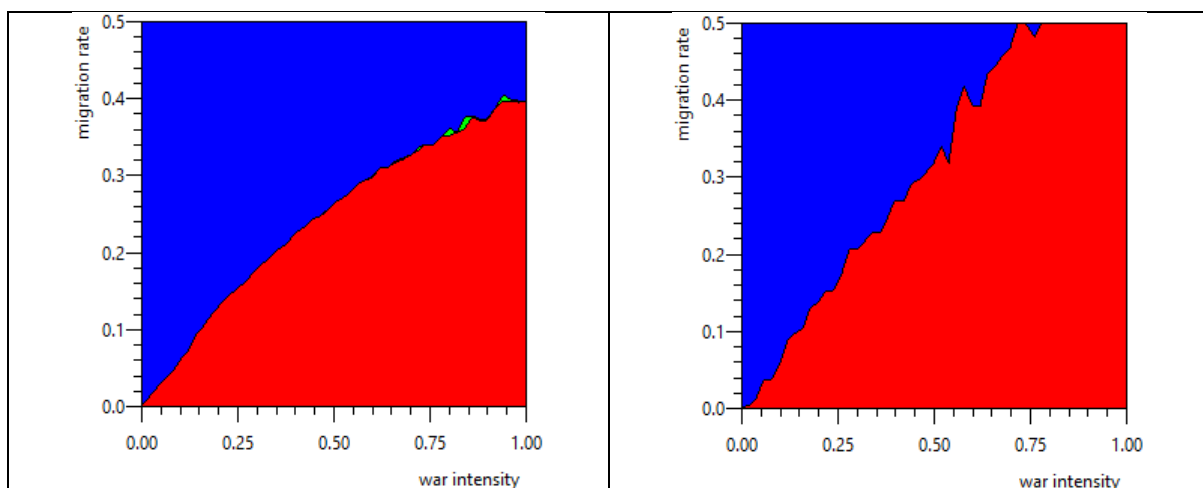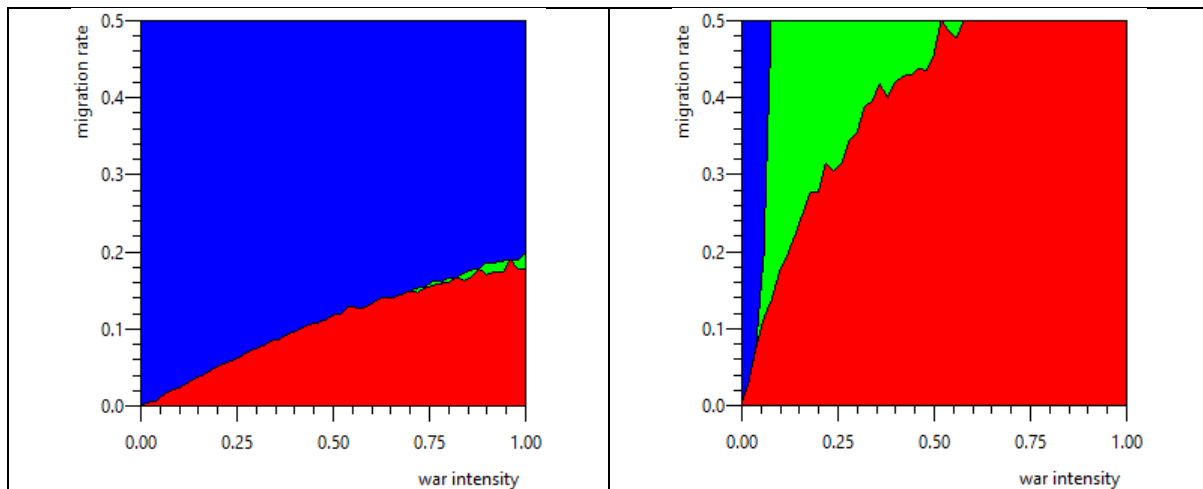
Figure 6.3. Parameter map showing ranges of migration rate and war intensity leading to fixation of altruism (red) or egoism (blue). Green areas still have polymorphism after 100,000 generations. Parameters: Maximum group size = 100. Fitness ratio of altruists over egoists = 0.95. Survival rate = 0.
Top left: immigrants come from all neighbor groups.
Top right: all immigrants in one generation come from the same group, selected randomly regardless of geographic distance.
Bottom left: immigrants are mixed from the entire metapopulation.
Bottom right: immigrants come from all neighbor groups with probability proportional to the fitness of each neighbor group.
Parameter file: `terri_war-migration.altru`

Figure 6.4 shows the situation where some of the inhabitants of conquered territory may survive and enter the winning group after a conflict. The simulations show that such survival has an effect similar to migration.
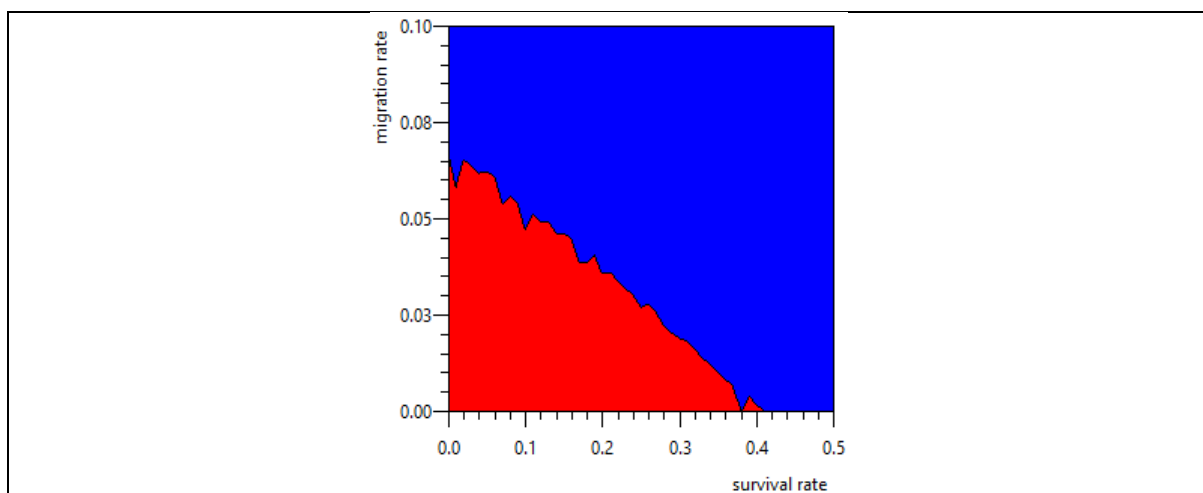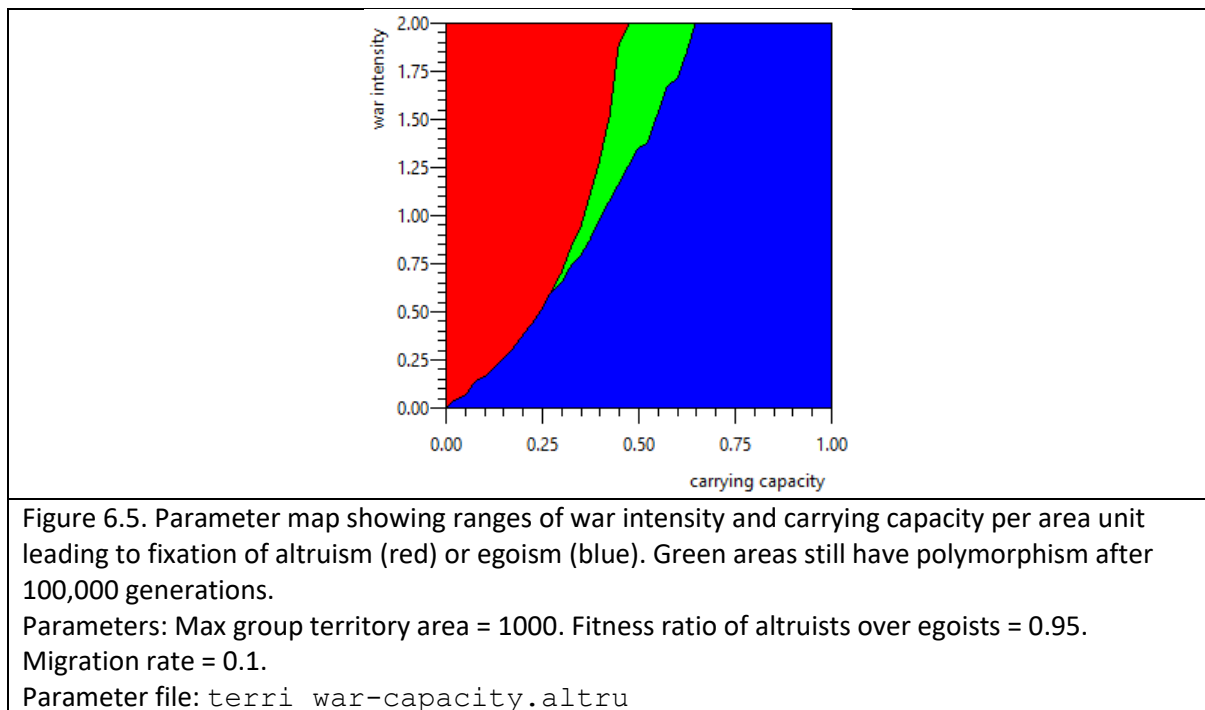

Figure 6.4. Parameter map showing ranges of survival rate and migration rate leading to fixation of altruism (red) or egoism (blue).
Parameters: Maximum group size = 100. Fitness ratio of altruists over egoists = 0.95. War intensity = 0.1
Parameter file: `terri_survival-migration.altru`

Figure 6.5 shows the effect of group size. A higher carrying capacity per area unit means a higher population per group. Larger groups have more genetic diversity and less drift. More war is required to eliminate all egoism genes from large groups.

Figure 6.5. Parameter map showing ranges of war intensity and carrying capacity per area unit leading to fixation of altruism (red) or egoism (blue). Green areas still have polymorphism after 100,000 generations.
Parameters: Max group territory area = 1000. Fitness ratio of altruists over egoists = 0.95.
Migration rate = 0.1.
Parameter file: `terri_war-capacity.altru`

Regality model

The regality model is similar to the group territoriality model, but based on leadership rather than altruism. Fighting for one's group involves a collective action problem when the cost of fighting is borne by the individual fighter while the benefit resulting from the actions of this individual is divided between all group members. Group selection can explain such altruistic behavior only when the rate of migration between groups is very low, as we have seen in the previous models. Enforcement or policing is central to the evolution of cooperation (Ågren, et al., 2019), and active leadership is necessary if altruistic punishment is insufficient for enforcing cooperation.

A theory called regality theory explains how cooperation can be achieved through strong leadership (www.regality.info). Regality theory is a theory that explains human behavior in war. Humans have evolved a psychological response pattern that makes us support a strong leader in case of war or perceived collective danger, according to regality theory. The leader can compensate individuals for the cost of fighting by rewarding brave warriors and punishing cowards and defectors. The simulation model will test whether collective fighting can be explained by individuals supporting a strong leader.

There is a high fitness advantage in being a powerful leader. In particular, a male leader may use his power to get multiple female partners. This explains why, historically, most wartime leaders have been men (Garfield, et al., 2019).

The fitness advantage of the leader compensates for the cost of leading. The leader has a strong incentive to strengthen the group because of the fitness advantage of being the leader of a large group.

The model works as follows: An allele that we will call regality at a locus with the same name makes individuals support a leader who can organize collective fighting in intergroup conflict. The power of the leader is proportional to the fraction of group members who support him. This gives

the leader more power and fitness at the cost of all other group members who will have less fitness. It is important to note that the loss of fitness applies equally to all non-leaders, regardless of their genes. The regality allele does not involve an increased willingness to fight, but instead a willingness to a support a leader who can make everybody fight, including those who do not have this allele.

The parameter file `regality.altru` gives an example of this model.

The strength of a group is calculated as the size of the group multiplied by the power of the leader. In other words, a large group with many regality members will have more strength to conquer territory from weaker neighbor groups.

The fitness consequences of conquering new territory from a weaker neighbor group or losing territory to a stronger neighbor group are obvious. The consequences of selection within the group, however, are more complicated and difficult to understand.

To explain this, we will first analyze the situation without war. We are assuming that the selection of a leader is unbiased so that individuals with different genotypes have the same probability of becoming a leader. This means that there is no direct selection acting on individuals. The only selection is an indirect selection by the consequences for each individual of its own contribution to group-level phenomena.

Assume that the relative fitness of the leader is $1 + f\Lambda$, where f is the frequency of the regality allele in the group, and Λ is a factor called leader advantage. We are assuming a haploid species here in order to simplify the argument, even though the simulation code involves a diploid species.

When an individual with the regality phenotype supports the leader, the behavior of this individual makes an incremental contribution to the fitness of the leader of the size Λ/N where N is the number of individuals in the group. The fitness of all non-leaders is decreased by the same amount, shared between the N-1 non-leaders. Thus, the individual with the regality allele suffers a fitness loss of $\frac{\Lambda}{N(N-1)}$ as a consequence of its own support for the leader. The mean number of non-leaders with regality is $f(N-1)$ which makes the expected total loss of regality genes equal to $f\Lambda/N$.

The consequence of the behavior of one individual non-leader with regality phenotype to other non-leaders is irrelevant because this individual does not know the genotypes of anybody else. Transferring fitness from other individuals with unknown genotypes to a leader with unknown genotype has no net effect as long as the leader has the same probability (f) of having the regality allele as the other group members.

Here, we have assumed that the fitness gain of the leader is proportional to the number of group members with the regality allele, including the leader himself. In other words, the leader is increasing his own fitness by Λ/N if he has the regality allele. The probability that the leader has regality is f, so that the mean increase in regality due to the leader supporting himself is $f\Lambda/N$. This results in a positive selection for the regality allele by an amount that is exactly equal to the total negative selection for all the non-leaders. The net result is no selection for or against the regality allele at the group level in the absence of war. This result applies also for diploid inheritance as long as the competition for fitness is a zero-sum game and the chance of becoming a leader is independent of the regality allele.

This result is counterintuitive. We would expect negative selection against an allele that makes individual group members transfer some of their fitness to a despotic leader. This apparent flaw in the model comes from the assumption that the leader supports himself only if he has the regality allele. We can remove this effect by assuming that the leader will support himself out of self-interest regardless of whether he has the regality allele or not. This will remove the dependence of the leader's power on his own genes and thereby remove the positive selection for the regality allele, while the negative selection remains. In the following, we will assume that the power of the leader depends on the phenotype of all group members except himself.

Figure 7.1 shows the effect of the leader advantage (Λ) on the selection of the regality allele as a function of the maximum group size. The curve shows simulation results for a leader advantage of 4, which means that the leader will get 5 times as many offspring as everybody else in the group. We can see that even such a strong leader advantage has only a negligible effect on selection of the regality gene for group sizes higher than 100.
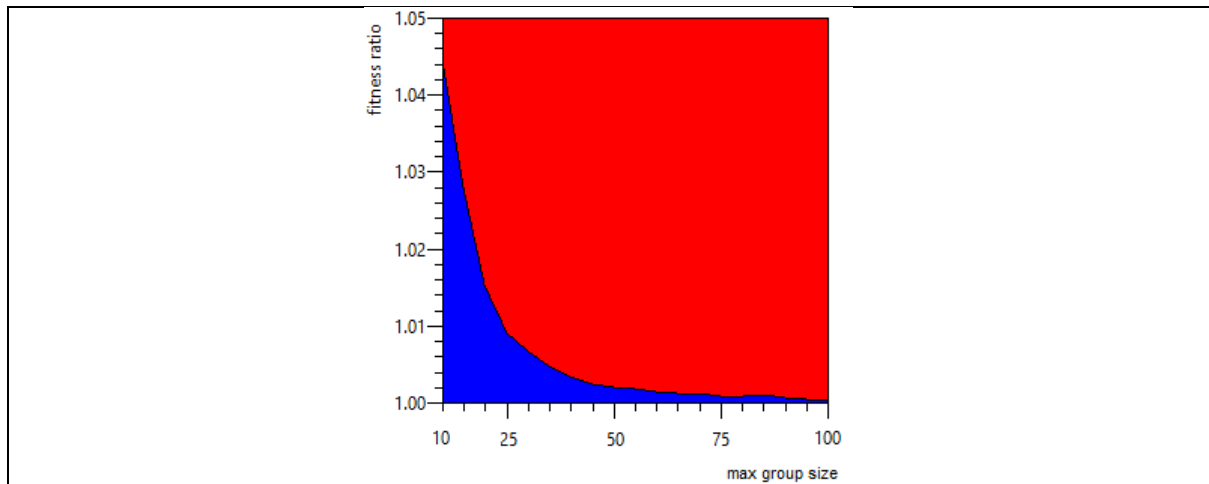

Figure 7.1. This parameter map shows the fitness ratio of regality over non-regality that can offset the effect of a strong leader advantage, depending on the maximum group size.
Parameters: Leader advantage = 4. Migration rate = 0.1. No war. Partial dominance.
Parameter file: `regality_capacity-fit.altru`

Figure 7.2 shows the effect of migration. We can see that fixation of the regality allele is possible even under high migration rates, high survival rates, high leader advantage, and low war intensity.
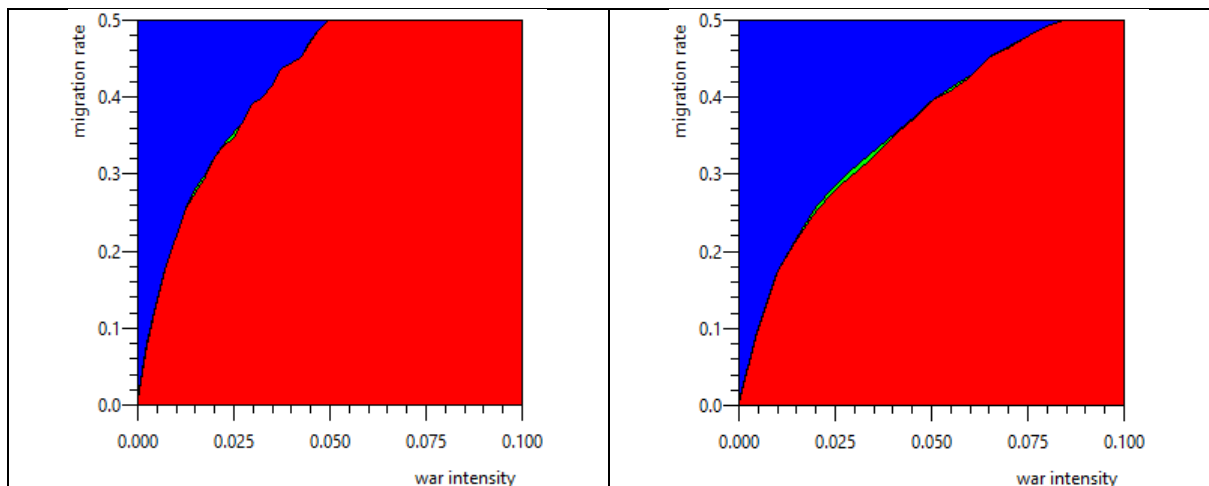

Figure 7.2. Parameter map showing ranges of war intensity and migration rate leading to fixation of regality (red) or non-regality (blue).
Left: Survival rate = 0.0. Right: Survival rate = 0.5.
Parameters: Maximum group size = 100. Leader advantage = 4. Partial dominance.
Parameter file: `regality_war-migration.altru`

The group-level selective effect of a leader advantage is so weak that it is easily overshadowed by other effects. Let us discuss some possible effects that can influence the evolution of regality. Selective migration can enhance the evolution of regality so much that it is likely to evolve even under very low war intensities.

Biased leader selection can make regality evolve even without war. Individuals with the regality phenotype are more likely than others to argue that strong leadership is necessary. We can imagine that individuals who argue for strong leadership might also be more likely than others to be selected as leader. This mechanism may result in a quite strong selection in favor or the regality allele.

Another mechanism is possible if the leader rewards those who support him and punishes those who do not. This will favor the regality allele if only individuals with regality support the leader. However, the leader can only observe behaviors, not genotypes. Behaviors can be faked. We may reject this mechanism as a "green beard" scenario. On the other hand, we may argue that there is no difference between faked behavior and natural behavior in this case because the effects are identical. Hence there can be no selection pressure distinguishing between natural support and faked support for the leader. If there is even a weak correlation between genes and observable behavior in this case then we would expect a significant selection in favor of the regality allele due to reward from the leader.

We also have to consider whether there are any direct fitness costs for supporting a leader. Does support for the leader take the form of costly displays of allegiance? Does it require physical defense in excess of what the leader can compensate by rewards? If there are any significant individual fitness costs associated with the regality phenotype, then the regality model will be more similar to the group territoriality model described above.

The sum of the effects of leader advantage, leader selection, selective migration, rewards for supporting the leader, and costs of showing regality may be positive or negative for the evolution of regality. If there is a net selection against the regality allele, then it may be reversed by even a low intensity of territorial war.

Success in war is probably not the only consequence of having a strong leader. Leadership may have several other consequences that can influence the evolution of regality. Possible consequences of good leadership include improved collaboration, division of labor, food sharing, and suppression of group-internal conflicts. These consequences are group-level effects that are likely to benefit all group members regardless of their genes. Any evolutionary effects of these benefits will work at the group level rather than the individual level. We may speculate that groups with strong leadership and good collaboration are more likely to survive occasional hard times. It is also possible that well-organized groups have a higher emigration rate due to better health and fertility so that regality can spread through selective migration.

Discussion of results

Several theoretical models have been proposed for explaining the evolution of behaviors that decrease the fitness of individuals for the benefit of their groups. We have tested these models by detailed simulations in order to determine whether they work as expected and under what conditions.

Island model with selective extinction. This was the first model that was proposed by evolutionary theorists. This model requires that a species lives in groups isolated by physical boundaries. The island model can lead to the evolution of altruistic behavior only under the following rather restrictive conditions: Extinction of groups is a frequent occurrence. The probability of extinction is strongly reduced by altruistic behavior. Few or no individuals survive an extinction event. Individual selection against altruism is weak. The rate of migration between groups is very low. Groups are small. Founder populations are small.

Few species live under conditions that satisfy all of these conditions. Even a moderate rate of migration between groups can prevent the evolution of altruism.

Some theorists argue that the model of selective extinction is applicable to human evolution (Bowles, 2006), while others argue that immigration by egoists would prevent the evolution of egoism by this mechanism (Pinker, 2015).

The best example of group selection through selective extinction is parasites and viruses that evolve reduced virulence so that they avoid killing their hosts (Frank, 1996).

Selective migration. Altruistic behavior may in principle evolve by selective emigration from altruist groups. However, this effect is quite weak and works only if individual selection against altruism is very weak and groups are small.

This mechanism is too weak to be a likely explanation for observed cases of altruistic behavior, but it may be important when combined with other mechanisms. Most of the other mechanisms discussed here are very sensitive to migration. This sensitivity can be reduced or eliminated if the rate of migration out of groups dominated by altruism is higher than for egoist groups.

Selective dispersal. The simulations show that selective formation of daughter groups can lead to fixation of altruism only if the rate of migration between groups is very low and founder groups are small and group selection is strong relative to individual selection.

This model is relevant for explaining the evolution of eusociality in insects and certain other animals with similar organization.

Outsider exclusion. The simulations confirm that a gene that makes group members actively keep outsiders out of their group can evolve under relevant conditions.

This is an important preadaptation for the evolution of altruism by other mechanisms. Eusocial behavior in bees, ants, termites, and a few other species with communal nesting has probably evolved through the following steps: (1) communal nesting, (2) outsider exclusion, (3) monopolization of reproduction by a queen, and (4) extensive collaboration.

Conformity model. The simulation shows that a hypothetical conformity gene that reduces the fitness of egoists in groups dominated by altruists has only a weak effect on the evolution of altruism, and that the evolution of conformity by this mechanism is prone to oscillations.

While enforcement of conformity is often observed in human societies, it is unlikely to be explained by genetic evolution if its only effect is to reduce the fitness of egoists among altruists. But if conformity has evolved by genetic or cultural evolution for some other reason, then it may contribute to the stabilization of altruism as a side effect.

Altruistic punishment. Many theorists have proposed that the evolution of altruistic behavior can be explained by altruistic punishment. The rationale is that the act of punishing egoistic behavior is less costly than the altruistic behavior it seeks to promote. But the act of punishing egoists is in itself an altruistic act because it is not costless.

It is shown here that a hypothetical gene for this kind of second-order altruism is unlikely to become fixated in the population, but it can be maintained at a low frequency.

It has been argued that altruistic punishment can only lead to a mediocre performance (Fog, 2017). For example, warriors who are induced to fight for their group by threats of punishment, will deliver only the minimum performance necessary to avoid punishment. They may even avoid fighting if they can convincingly fake illness. Rewards, rather than punishments, are needed for making warriors fight to the best of their abilities, and rewards are generally more costly to deliver than punishments.

Haystack model. Simulation shows that this mechanism is inefficient and slow. Altruism can evolve by this mechanism only under very restricted conditions.

Group territoriality model. The simulations show that altruism can evolve by territorial conflicts between groups under the following conditions: Individual selection against altruism is weak. The rate of migration between groups is low. The rate of survivors entering a winning group is small. Groups are small. And the intensity of war is high.

It is questionable whether these conditions have been met in human prehistory or in the evolutionary process of other social species. Several studies indicate that warfare has been common in early hunter-gatherer societies, at least under some circumstances (Allen & Jones, 2014; Keeley, 1996). It has been estimated that the death rate due to warfare in human hunter gatherer societies is between 16 and 19%. 64% of the groups had warfare every 2 years or more frequently. The rate of migration between groups varies between 0.1 and 0.4 (Bowles, et al., 2003; Rogers, 1990). Figures for the rate of survivors from conquered groups that enter the winning group are not found in the literature, but we can assume that it is quite high, especially for women and children.

These figures are probably outside the range that allows the evolution of altruism by the group territoriality model, but it cannot be completely ruled out that this model combined with other mechanisms can promote collective fighting in territorial wars. Possible mechanisms that can promote collective fighting include: selective migration, cultural institutions of reward and punishment, and sexual selection when women are attracted to brave warriors (Rusch, et al., 2015).

Anthropologists have observed that male warriors in hunter-gatherer tribes often capture women from enemy groups in war (Van der Dennen, 1995; Hertler, et al., 2020; McDonald, et al., 2012). This is likely to increase the fitness of the warriors, but it does not promote group selection because the captured women will figure in the model as migrants or survivors.

Regality model. This is the most powerful of the models for explaining collective fighting. The simulations show that support for a strong leader in war can evolve under a wide range of parameters, including a high leader advantage, high migration rates, high survival rates, low war intensity, and both small and large groups. The leader has enough resources for inducing group members to fight in territorial wars by means of both rewards and punishments. Furthermore, the leader has a strong incentive to do so because of the fitness advantage of being the leader of a strong group.

Statistical studies in connection with regality theory have confirmed that humans are likely to support a strong leader in times of war or perceived collective danger. This is confirmed for both traditional societies and modern societies (Fog, 2017, 2023). We can therefore conclude that the regality model is the most likely explanation for the evolution of collective fighting in humans. Whether leadership can also explain collective fighting in other social animals remains to be studied.

Conclusion

We should be careful when formulating a conclusion to these simulation studies. It would be an oversimplification to conclude that regality theory provides a model that can explain human altruistic behavior through group selection. Such a statement could make scholars who do not understand the details revive the group selection controversy and claim that all kinds of social and self-sacrificial behaviors can be explained by group selection, including such diverse phenomena as charity work, concern for animal welfare, celibacy, ageing, and homosexuality.

None of these behaviors can be explained by regality theory. Regality theory can explain pro-social behavior only under conditions of war or perceived collective danger, not under conditions of peace and collective security.

Social behaviors that have been observed to be correlated with war and collective danger include support for a strong leader, strengthening of group identity or nationalistic spirit, authoritarianism, militarism, harsh discipline, strong morality, punishment of deviants, xenophobia, and strict religiosity (Fog, 2017). These are all behaviors that can serve to strengthen a social group in conflict with an enemy group. These behaviors are positively correlated with perceived collective danger, but not with individual danger (Fog, 2023).

Regality theory can explain how the collective action problem in inter-group fighting can be overcome by strong leadership and support for strict discipline. It cannot explain altruistic behavior in other situations unrelated to inter-group conflicts.

I think it would be unwise to associate regality theory with the term group selection because of the history of the group selection controversy and the many phenomena that have traditionally been associated with group selection. Regality theory differs from traditional group selection theories in several aspects. First, there is little or no opposition between individual selection and group-level selection in the regality model. Second, regality theory can explain why certain behaviors depend on the level of perceived collective danger, but it cannot explain altruistic behavior under conditions of peace and collective security. And third, many of the behaviors that various theorists have tried to explain by group selection theory are not explained by regality theory.

I would prefer to reserve the term group selection to the other models, some of which are very useful for explaining social and self-sacrificing behavior in eusocial insects and in parasites, as we have seen.

References

Ågren, J. A., Davies, N. G., & Foster, K. R. (2019). Enforcement is central to the evolution of cooperation. *Nature Ecology & Evolution,* 3(7), 1018–1029. https://doi.org/10.1038/s41559-019-0907-1

Allen, M. W., & Jones, T. L. (2014). *Violence and warfare among hunter-gatherers.* Left Coast Press.

Boomsma, J. J., Beekman, M., Cornwallis, C. K., Griffin, A. S., Holman, L., Hughes, W. O., Keller, L., Oldroyd, B. P., & Ratnieks, F. L. (2011). Only full-sibling families evolved eusociality. Nature, 471(7339), E4–E5. https://doi.org/10.1038/nature09832

Boorman, S., & Levitt, P. R. (1973). *The Genetics Of Altruism.* Elsevier.

Bowles, S. (2006). Group Competition, Reproductive Leveling, and the Evolution of Human Altruism. *Science,* 314(5805), 1569–1572. https://doi.org/10.1126/science.1134829

Bowles, S., Choi, J.-K., & Hopfensitz, A. (2003). The co-evolution of individual behaviors and social institutions. *Journal of Theoretical Biology,* 223(2), 135–147. https://doi.org/10.1016/S0022-5193(03)00060-2

Bowles, S., & Gintis, H. (2004). The evolution of strong reciprocity: Cooperation in heterogeneous populations. *Theoretical Population Biology,* 65(1), 17–28. https://doi.org/10.1016/j.tpb.2003.07.001

Bowles, S., & Gintis, H. (2011). A cooperative species: Human reciprocity and its evolution. Princeton University Press. https://doi.org/10.1515/9781400838837

Boyd, R., Gintis, H., Bowles, S., & Richerson, P. J. (2003). The evolution of altruistic punishment. *Proceedings of the National Academy of Sciences,* 100(6), 3531–3535. https://doi.org/10.1073/pnas.0630443100

Duffy, J. E., Morrison, C. L., & Ríos, R. (2000). Multiple origins of eusociality among sponge-dwelling shrimps (Synalpheus). *Evolution,* 54(2), 503 – 516. https://doi.org/10.1111/j.0014-3820.2000.tb00053.x

Fog, A. (2017). *Warlike and Peaceful Societies: The Interaction of Genes and Culture.* Open Book Publishers. https://doi.org/10.11647/obp.0128

Fog, A. (2023). Psychological and cultural effects of different kinds of danger. An exploration based on survey data from 79 countries. *Culture and Evolution.* https://doi.org/10.1556/2055.2023.00029

Fontanari, J. F., & Serva, M. (2014). Nonlinear group survival in Kimura's model for the evolution of altruism. *Mathematical Biosciences,* 249, 18–26. https://doi.org/10.1016/j.mbs.2014.01.003

Fowler, J. H. (2005). Altruistic punishment and the origin of cooperation. *Proceedings of the National Academy of Sciences,* 102(19), 7047–7049. https://doi.org/10.1073/pnas.0500938102

Frank, S. A. (1996). Models of Parasite Virulence. *The Quarterly Review of Biology,* 71(1), 37–78. https://doi.org/10.1086/419267

Garfield, Z. H., Hubbard, R. L., & Hagen, E. H. (2019). Evolutionary Models of Leadership. *Human Nature,* 30(1), 23–58. https://doi.org/10.1007/s12110-019-09338-4

Gintis, H. (2003). The hitchhiker's guide to altruism: Gene-culture coevolution, and the internalization of norms. *Journal of Theoretical Biology,* 220(4), 407–418. https://doi.org/10.1006/jtbi.2003.3104

Henrich, J., & Boyd, R. (2001). Why people punish defectors: Weak conformist transmission can stabilize costly enforcement of norms in cooperative dilemmas. *Journal of Theoretical Biology,* 208(1), 79–89. https://doi.org/10.1006/jtbi.2000.2202

Hertler, S. C., Figueredo, A. J., & Peñaherrera-Aguirre, M. (2020). *Multilevel selection: Theoretical foundations, historical examples, and empirical evidence.* Springer.

Kawata, M. (1999). The effects of dispersal behaviour in group selection. *Evolutionary Ecology Research,* 1(6), 663–680.

Keeley, L. H. (1996). *War Before Civilization.* Oxford University Press, USA.

Kimura, M. (1983). Diffusion model of intergroup selection, with special reference to evolution of an altruistic character. *Proceedings of the National Academy of Sciences,* 80(20), 6317–6321. https://doi.org/10.1073/pnas.80.20.6317

Kirby, J. (2003). A new group-selection model for the evolution of homosexuality. *Biology and Philosophy,* 18(5), 683–694. https://doi.org/10.1023/A:1026321628276

Krasnow, M. M., Delton, A. W., Cosmides, L., & Tooby, J. (2015). Group Cooperation without Group Selection: Modest Punishment Can Recruit Much Cooperation. *PLoS ONE,* 10(4), e0124561. https://doi.org/10.1371/journal.pone.0124561

Kruger, D. J., Fisher, M. L., & Salmon, C. (2023). What do evolutionary researchers believe about human psychology and behavior? *Evolution and Human Behavior.* https://doi.org/10.1016/j.evolhumbehav.2022.11.002

Leigh Jr, E. G. (2010). The group selection controversy. *Journal of Evolutionary Biology,* 23(1), 6–19. https://doi.org/10.1111/j.1420-9101.2009.01876.x

Mainwaring, M. C., Stoddard, M. C., Barber, I., Deeming, D. C., & Hauber, M. E. (2023). The evolutionary ecology of nests: A cross-taxon approach. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 378(1884), 20220136. https://doi.org/10.1098/rstb.2022.0136

McDonald, M. M., Navarrete, C. D., & Van Vugt, M. (2012). Evolution and the psychology of intergroup conflict: The male warrior hypothesis. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 367(1589), 670–679. https://doi.org/10.1098/rstb.2011.0301

Mitteldorf, J., & Wilson, D. S. (2000). Population Viscosity and the Evolution of Altruism. *Journal of Theoretical Biology,* 204(4), 481–496. https://doi.org/10.1006/jtbi.2000.2007

Neumann, M. (2020). Indirect reciprocity with contagious reputation in large-scale small-world networks. *Journal of Artificial Societies and Social Simulation*, 23(4). https://doi.org/10.18564/jasss.4392

Peck, J. R. (1990). The evolution of outsider exclusion. *Journal of Theoretical Biology,* 142(4), 565–571. https://doi.org/10.1016/S0022-5193(05)80109-2

Pinker, S. (2015). The False Allure of Group Selection. In D. M. Buss, *The Handbook of Evolutionary Psychology,* Volume 2: Integrations, pp. 867–880. Wiley.

Ratnieks, F. L., & Wenseleers, T. (2008). Altruism in insect societies and beyond: Voluntary or enforced? *Trends in Ecology & Evolution,* 23(1), 45–52. https://doi.org/10.1016/j.tree.2007.09.013

Rogers, A. R. (1990). Group Selection by Selective Emigration: The Effects of Migration and Kin Structure. *The American Naturalist,* 135(3), 398–413. https://doi.org/10.1086/285053

Rusch, H., Leunissen, J. M., & van Vugt, M. (2015). Historical and experimental evidence of sexual selection for war heroism. *Evolution and Human Behavior,* 36(5), 367–373. https://doi.org/10.1016/j.evolhumbehav.2015.02.005

Sherman, P. W., Jarvis, J. U., & Alexander, R. D. (1991). *The biology of the naked mole-rat* (Vol. 54). Princeton University Press.

Smith, J. M. (1964). Group selection and kin selection. *Nature,* 201(4924), 1145–1147. https://doi.org/10.1038/2011145a0

Sigmund, K. (2007). Punish or perish? Retaliation and collaboration among humans. *Trends in Ecology & Evolution,* 22(11), 593–600. https://doi.org/10.1016/j.tree.2007.06.012

Strobel, A. (2016). Altruistic Punishment. In M. Reuter & C. Montag (Eds.), *Neuroeconomics* (pp. 211–227). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-35923-1_12

Tanaka, Y. (1996). A quantitative genetic model of group selection. *The American Naturalist,* 148(4), 660–683. https://doi.org/10.1086/285946

Van der Dennen, J. M. G. (1995). The origin of war: The evolution of a male-coalitional reproductive strategy, Vols. 1 & 2. Origin Press. http://psycnet.apa.org/psycinfo/1995-98953-000

Werfel, J., Ingber, D. E., & Bar-Yam, Y. (2017). Theory and associated phenomenology for intrinsic mortality arising from natural selection. *PloS One,* 12(3), e0173677. https://doi.org/10.1371/journal.pone.0173677

Wilson, D. S., & Sober, E. (1994). Reintroducing group selection to the human behavioral sciences. *Behavioral and Brain Sciences,* 17(4), 585–654. https://doi.org/10.1017/S0140525X00036104

Woodberry, O. G. (2014). *Evolutionary biology in silico: Explorations of adaptation in artificial populations.* Thesis, Monash University.

Wynne-Edwards, V. C. (1986). *Evolution through group selection.* Blackwell Scientific Oxford.