



UNIVERSITÄT ZU LÜBECK
INSTITUT FÜR MATHEMATIK

Group formation and evolutionary games in finite populations

Gruppenformierung und evolutionäre Spiele in
endlichen Populationen

Masterarbeit

im Rahmen des Studiengangs

Mathematik in Medizin und Lebenswissenschaften

vorgelegt von

Ricarda Mißfeldt

ausgegeben und betreut von

Prof. Dr. Arne Traulsen

mit Unterstützung von

Dr. Jorge Peña

Die Masterarbeit ist im Rahmen einer Tätigkeit in der Abteilung
Evolutionstheorie des Max-Planck-Instituts für Evolutionsbiologie in Plön
entstanden.

Lübeck, den 18. September 2016

Abstract

In game-theoretic models studying the evolution of cooperation, a common assumption is that groups are of constant size. Many natural systems, however, feature variable group sizes that are influenced by the level of cooperation in the population. Hence, the waiting-for-volunteers dilemma, a variant of the volunteer's dilemma, proposes that individuals sequentially join a group up to the point where the critical number of cooperators required for provision of the collective good is reached. The objective of this master's thesis is to study the effect of a such group formation scheme on the evolutionary dynamics of social dilemmas in finite populations. Of focal interest are conditions for natural selection favoring cooperation and for a cooperator having a higher fixation probability than a defector. A striking result is that larger population sizes impede cooperation by toughening these very conditions, whereas in the standard volunteer's dilemma with constant group size, larger population sizes promote cooperation.

Kurzfassung

In spieltheoretischen Modellen zur Evolution von Kooperation wird häufig angenommen, dass Gruppen von konstanter Größe sind. Allerdings weisen viele natürliche Systeme variable Gruppengrößen auf, die durch den Kooperationsgrad der Population beeinflusst werden. Daher sieht das Warten-auf-Freiwillige-Dilemma, eine Variante des Freiwilligendilemmas, vor, dass Individuen sich nacheinander einer Gruppe anschließen bis die kritische Anzahl an Kooperatoren, die für die Bereitstellung des kollektiven Gutes benötigt wird, erreicht ist. Ziel dieser Masterarbeit ist es, den Effekt eines solchen Formierungsschemas von Gruppen auf die evolutionäre Dynamik von sozialen Dilemmas in endlichen Populationen zu untersuchen. Von besonderem Interesse sind Bedingungen dafür, dass natürliche Selektion Kooperation begünstigt, und dafür, dass die Fixierungswahrscheinlichkeit eines Kooperators höher ist als die eines Defektors. Ein erstaunliches Ergebnis ist, dass größere Populationsgrößen durch Verschärfung ebendieser Bedingungen Kooperation hemmen, wohingegen größere Populationsgrößen im klassischen Freiwilligendilemma Kooperation fördern.

Contents

List of Figures	1
1. Introduction	3
2. Background and methods	5
2.1. Public goods games	5
2.2. The frequency-dependent Moran process	5
2.3. Fixation probability	7
2.4. Stationary distribution	8
3. Volunteer's dilemma	11
3.1. Results for general multiplayer games	12
3.2. Results for a threshold public goods game	12
3.2.1. Comparison to the neutral case	13
3.2.2. Comparison of the two types	16
3.2.3. Stationary distribution	18
4. Waiting-for-volunteers dilemma	21
4.1. Group formation via negative hypergeometric sampling	21
4.2. Results for general multiplayer games	22
4.2.1. Expected payoffs	22
4.2.2. Comparison to the neutral case	24
4.2.3. Comparison of the two types	28
4.3. Results for a public goods game	31
4.3.1. Comparison to the neutral case	31
4.3.2. Comparison of the two types	34
4.3.3. Minimal critical benefit-to-cost ratio	36
4.3.4. Stationary distribution	36
5. Discussion and outlook	39
A. Appendix	43
A.1. Additional calculations	43
A.2. R code	44
A.2.1. Stationary distribution for volunteer's dilemma	44
A.2.2. Stationary distribution for waiting-for-volunteers dilemma	45

List of Figures

3.1. Payoff matrix with payoffs depending on the number of opposing cooperators	11
3.2. VD (i): Critical benefit-to-cost ratio for varying group size	14
3.3. VD (i): Critical benefit-to-cost ratio for varying population size . . .	15
3.4. VD (i): Critical benefit-to-cost ratio for varying threshold	15
3.5. VD (ii): Critical benefit-to-cost ratio for varying group size	17
3.6. VD (ii): Critical benefit-to-cost ratio for varying population size . . .	17
3.7. VD: Stationary distributions	19
4.1. Payoff matrix with payoffs depending on the number of participating defectors	22
4.2. WD (i): Critical benefit-to-cost ratio for varying number of required cooperators	33
4.3. WD (i): Critical benefit-to-cost ratio for varying population size . . .	34
4.4. WD (ii): Critical benefit-to-cost ratio for varying number of required cooperators	35
4.5. WD (ii): Critical benefit-to-cost ratio for varying population size . . .	36
4.6. WD: Minimal critical benefit-to-cost ratio	37
4.7. WD: Stationary distributions	38

1. Introduction

Along with selection and mutation, cooperation represents an essential fuel for evolutionary progress. It enables the transition from simple to higher organizational forms, e.g. from genes to genomes, from cells to multicellular organisms, and from individuals to groups and societies (Nowak, 2006a; Szathmary and Maynard Smith, 1995). However, in the absence of any other assumption, natural selection opposes cooperation. Hence, there have to be certain mechanism at work that allow cooperators to outperform defectors (Nowak, 2006b).

Typically, models designed to explore cooperation-enhancing mechanisms are built on the assumption that individuals interact in groups of constant size, such that groups are formed by sampling individuals from the population until an exogenously designated group size is reached (Isaac and Walker, 1988; Powers and Lehmann, 2016).

This assumption is challenged by Pena et al. (2016) who argue that, in many natural systems, group formation is intertwined with the level of cooperation in the population.

An illustrative example is given by bark beetles attacking trees in order to access the inner bark tissue that serves as their breeding site (Berryman et al. (1985), Byers (1989) and Raffa (2001) in Pena et al. (2016)). Because of the host tree’s defense mechanisms, e.g. resin flow, single beetles fail to pierce through the outer bark. Therefore, they summon other bark beetles by releasing a pheromone. Newly arrived beetles either contribute to the effort or defect. Once a critical number of beetles actively attacks the tree by collective tunneling and inoculating with symbiont fungi, part or all of the tree is killed, enabling the beetles to reach the inner bark and lay their eggs. The moment the public good (i.e., access to the inner bark) is provided, the attraction of further beetles is effectively stopped, since the production of aggregation pheromones requires certain substances from the tree’s resin.

Further examples include the production of adhesive proteins by social microbes (Queller et al., 2003), the preparation and burying of carcasses by burying beetles (Scott, 1998) and the collective hunting by social carnivores (Boza and Szamado, 2010).

Pena et al. (2016) introduce a model called the *waiting-for-volunteers dilemma* that features a group formation scheme in which group members are recruited sequentially until there is a certain number of cooperators in the group, leading to variable group sizes.

The proposed model is deterministic, because it assumes an infinite population

size. When moving to a model with finite population size, stochastic effects arise that shift the concept of interest from evolutionary stability to fixation, extinction and maintenance of strategies (Nowak, 2006a; Gokhale and Traulsen, 2014).

This thesis adapts the waiting-for-volunteers dilemma to finite populations. The main objective is to investigate the effect that the alternative sampling scheme exerts on the evolutionary dynamics of cooperation, when comparing results with the classical volunteer's dilemma that features constant group sizes. Means of investigation are fixation probabilities as well as stationary distributions. In particular, the following two questions pertaining to fixation probability are addressed:

- (i) When is cooperation favored by selection?
- (ii) When is the fixation probability of a cooperator larger than the fixation probability of a defector?

The structure of the thesis is as follows.

Chapter 2 presents the background and the methods that are made use of. Specifically, it outlines public goods games, the frequency-dependent Moran process, and the concept of fixation probabilities as well as of stationary distributions.

Chapter 3 is dedicated to the volunteer's dilemma. Results obtained by Gokhale and Traulsen (2010) are revisited, and a threshold public goods game is applied in order to answer the formulated research questions with conditions for the relation between benefit and cost of the public good. Furthermore, the influence of different parameters on the stationary distribution is explored numerically.

Chapter 4 introduces the waiting-for-volunteers dilemma for finite populations. The questions of interest are addressed for general multiplayer games first and subsequently for a public goods game. Moreover, stationary distributions are analyzed numerically for different parameter sets.

Chapter 5 summarizes and compares the obtained results and gives an outlook on possible future projects involving the proposed group formation process.

2. Background and methods

The mathematical framework of the present thesis is composed of evolutionary game dynamics and evolutionary game theory which have arisen from integrating population dynamical and game theoretical methods in biological contexts (Hofbauer and Sigmund, 1998; Nowak, 2006a). Such framework aims at understanding the dynamical process of following situations: Individuals that are born with fixed strategies engage in games (i.e., interactions) with each other, providing them a payoff subject to their strategy. These payoffs determine the individuals' fitness which in turn affects the spread of the strategies in the population.

The thesis focuses on social dilemmas in finite populations that are well-mixed, i.e., encounters between any two individuals are equally likely. This chapter explains the employed concepts, namely, public goods games, that are used to investigate social dilemmas, the frequency-dependent Moran process, that describes the dynamics of the population, and fixation probabilities as well as stationary distributions, that help to identify evolutionary success of strategies.

2.1. Public goods games

Public goods games are multiplayer games with two strategies. Each player either cooperates, i.e., contributes to a public good at a personal cost, or defects, i.e., makes no contribution. The public good is then shared among all players, allowing the defectors to free ride on the cooperators' efforts.

The consequence captures the essence of a social dilemma (Dawes, 1980): From the view point of an individual player, defecting is the better strategy than cooperating, however, if none or too few of the players cooperate, such that the public good cannot be produced, everyone is left with nothing.

2.2. The frequency-dependent Moran process

The Moran process is a simple stochastic process that was first proposed by Moran (1958) and has been widely applied in theoretical biology to model the dynamics in finite populations. The models in this thesis integrate an extension of this process: the frequency-dependent Moran process (Nowak et al., 2004).

Consider a well-mixed population of $N - 1$ wild type individuals (here: strategy to defect) and one mutant type individual (here: strategy to cooperate) that

is introduced into the population. In each time step, one individual is chosen to beget a clonal offspring and one individual is chosen to die. The latter is then being replaced by the offspring of the former. Notably, both choices can fall on the same individual. Thus, in one time step, the number of mutant type individuals in the population can either increase by one, decrease by one or stay the same, whereas the population size is maintained constant throughout the whole time.

Formally, the *frequency-dependent Moran process* $(X_t)_{t \in \mathbb{N}}$ is a family of random variables with state space $\Omega = \{0, 1, 2, \dots, N\}$, where X_t describes the number of mutant type individuals in the population at a given time point t starting from $X_0 = 1$. The transition probabilities are denoted by

$$T_m^+ = P(X_{t+1} = m + 1 | X_t = m) \quad (2.1)$$

and

$$T_m^- = P(X_{t+1} = m - 1 | X_t = m) \quad (2.2)$$

for $m \in \Omega$.

With this notation, the probability to remain in the same state is given by $P(X_{t+1} = m | X_t = m) = 1 - T_m^+ - T_m^-$.

The individual chosen for reproduction is chosen randomly but proportional to its fitness, whereas the individual chosen for death is chosen randomly. Hence, the transition probabilities are calculated as

$$T_m^+ = \frac{m f_C}{m f_C + (N - m) f_D} \frac{N - m}{N} \quad (2.3)$$

and

$$T_m^- = \frac{(N - m) f_D}{m f_C + (N - m) f_D} \frac{m}{N}, \quad (2.4)$$

where f_C and f_D denote the fitness of the cooperators and the defectors, respectively, and also depend on the state of the process, i.e., on m .

Notably, the Moran process has two absorbing states: all wild type individuals ($m = 0$) and all mutant type individuals ($m = N$). Once the population has reached one of these two states, it will remain in the respective state forever.

The classical approach to modeling fitness is to describe it as a linear combination of a background fitness (which has value 1) and the payoff,

$$f_C(m) = 1 - w + w\pi_C(m) \quad \text{and} \quad f_D(m) = 1 - w + w\pi_D(m) \quad (2.5)$$

(Nowak, 2006a; Traulsen et al., 2008), where parameter w denotes the intensity of selection and π_C as well as π_D describe the expected payoff for cooperators and defectors, respectively, that they obtain from playing the designated game.

Neutral drift is expressed by $w = 0$, meaning that an individual's performance in the game has no influence on its fitness. Weak selection is given by $w \ll 1$ and strong selection corresponds to $w = 1$. Due to the restriction that f_C and f_D have to be non-negative for any state $m \in \{0, 1, \dots, N\}$, the selection intensity w has an upper limit if there are negative payoffs. Therefore, Traulsen et al. (2008) suggest to define fitness as an exponential function of payoff, so that

$$f_C(m) = \exp(+w \pi_C(m)) \quad \text{and} \quad f_D(m) = \exp(+w \pi_D(m)), \quad (2.6)$$

which yield fitness values close to zero for negative payoffs and very large fitness values for positive payoffs. In most cases, the exponential mapping exhibits the same properties as the linear mapping while being more general by allowing greater variation in the selection intensity. Consequently, in this thesis, the fitness of the types is modeled by the exponential functions (2.6).

2.3. Fixation probability

Consider a homogeneous population of individuals of type D (defector). Suppose that during reproduction a rare mutation occurs so that a new type C (cooperator) is introduced into the population. The dynamics of the Moran process will lead either to the extinction of the new type or to its invasion such that, after some time, the population consists of individuals of the mutant type only. The latter case is called the *fixation* of the type C , and the probability for this to happen is called the *fixation probability* which is denoted by ρ_C .

In the absence of selection, meaning that the mutation holds neither a fitness advantage nor a fitness disadvantage, the probability that the mutant becomes fixed in a population of size N is equal to $1/N$ (Nowak, 2006a). This is also referred to as the *neutral case*. However, in case the fitness of the mutant differs from that of the wild type, the fixation probability deviates from $1/N$.

The probability that a mutant of type C becomes fixed in a population of type D individuals is given by

$$\rho_C = \frac{1}{1 + \sum_{l=1}^{N-1} \prod_{m=1}^l \frac{T_m^-}{T_m^+}}. \quad (2.7)$$

For a detailed derivation, see Traulsen and Hauert (2009).

A Taylor approximation of ρ_C (given by equation (2.7)) around $w = 0$ up to the first order term leads to

$$\rho_C \approx \frac{1}{N} + \frac{w}{N} \underbrace{\sum_{l=1}^{N-1} \sum_{m=1}^l (\pi_C - \pi_D)}_{\Gamma}. \quad (2.8)$$

Thus, for weak selection $w \ll 1$, the fixation probability of type C can be approximately calculated by this expression. The first term of the right hand side represents neutral drift, and the second term quantifies the influence of natural selection. For $\Gamma > 0$, the fixation probability is larger than in the neutral case ($w = 0$), meaning that type C is favored by selection.

Another interesting question is the comparison of the fixation probability of a type C individual in a population of D s with the fixation probability of a type D individual in a population of C s. The ratio of the two fixation probabilities can be calculated by the product over the ratios of the transition probabilities T_m^- and T_m^+ (Traulsen and Hauert, 2009):

$$\frac{\rho_D}{\rho_C} = \prod_{m=1}^{N-1} \frac{T_m^-}{T_m^+} = \exp \left[-w \underbrace{\sum_{m=1}^{N-1} (\pi_C - \pi_D)}_{\Phi} \right]. \quad (2.9)$$

It immediately follows that ρ_C is larger than ρ_D if and only if $\Phi > 0$ holds.

2.4. Stationary distribution

The fixation probability of a mutant in a wild type population is investigated under the assumption that mutations are so rare, that the offspring of an individual is always of the same type as its parent. When assuming that during each reproduction a mutation, such that the offspring is of the opposite type, occurs with a certain probability, the process no longer has absorbing states. Instead, the process can keep changing from state to state in the long run. After sufficiently long time, however, the probability for the process to be in a certain state stays the same. These probabilities for all possible states are given by the *stationary distribution* of the process and are calculated as

$$p_m = \frac{\prod_{i=0}^{m-1} \frac{T_i^+}{T_{i+1}^-}}{\sum_{j=1}^N \prod_{i=0}^{j-1} \frac{T_i^+}{T_{i+1}^-} + 1} \quad (2.10)$$

for $m \in \{0, 1, \dots, N\}$ (Claussen and Traulsen, 2005).

When the mutation rate, i.e., the probability that the offspring of an individual is of the opposite type as its parent, is denoted by μ , the transition probabilities read as

$$T_i^+ = \frac{N-i}{N} \left[(1-\mu) \frac{if_C}{if_C + (N-i)f_D} + \mu \frac{(N-i)f_D}{if_C + (N-i)f_D} \right] \quad (2.11)$$

and

$$T_i^- = \frac{i}{N} \left[(1-\mu) \frac{(N-i)f_D}{if_C + (N-i)f_D} + \mu \frac{if_C}{if_C + (N-i)f_D} \right]. \quad (2.12)$$

This is the symmetric case, where the probability that a cooperator creates a defecting offspring and the probability that a defector creates a cooperating offspring are the same, namely μ .

3. Volunteer's dilemma

This chapter presents the volunteer's dilemma for finite populations.

Consider a finite well-mixed population of N individuals whose strategy is either to cooperate or to defect. The composition of the population changes according to the frequency-dependent Moran process. The transition probabilities of this process depend on the respective fitness of the two types which in turn depends on the payoff that the individuals obtain when engaging in an interaction with each other. Not all the individuals of the population at once, but rather a selected group of individuals engages in an interaction that brings potential payoff to the participants.

In the volunteer's dilemma, interactions take place between individuals in a group of constant size g . These groups of players are formed by randomly drawing g individuals from the population. The individuals obtain a payoff according to the payoff matrix displayed in figure 3.1, i.e., when interacting with i cooperators, a focal cooperator receives a payoff c_i and a focal defector receives a payoff d_i .

Number of opposing cooperators	0	1	...	i	...	$g-1$
cooperator	c_0	c_1	...	c_i	...	c_{g-1}
defector	d_0	d_1	...	d_i	...	d_{g-1}

Figure 3.1.: Payoff matrix for an evolutionary game in which the payoff depends on the number of opposing cooperators among the players

The group composition, i.e., the amount of cooperators among the players, can vary each time a group is formed. The probabilities to obtain certain numbers of cooperators in a group of size g are given by the probability mass function of the hypergeometric distribution.

The expected payoffs are then given by the sum of the payoffs weighted by the respective probabilities, yielding

$$\pi_C = \sum_{i=0}^{g-1} \frac{\binom{m-1}{i} \binom{N-m}{g-1-i}}{\binom{N-1}{g-1}} c_i \quad (3.1)$$

and

$$\pi_D = \sum_{i=0}^{g-1} \frac{\binom{m}{i} \binom{N-m-1}{g-1-i}}{\binom{N-1}{g-1}} d_i \quad (3.2)$$

(Gokhale and Traulsen, 2010).

3.1. Results for general multiplayer games

In the case of weak selection $w \ll 1$, cooperators are favored by selection, i.e., $\rho_C > 1/N$, if and only if $\Gamma > 0$ holds in equation (2.8). For multiplayer two-action games with a general payoff matrix of the kind displayed in figure 3.1, Gokhale and Traulsen (2010) derived the following expression for Γ :

$$\Gamma = \frac{1}{g(g+1)} \left[N^2 \left(\sum_{i=0}^{g-1} (g-i)(c_i - d_i) \right) - N \left(\sum_{i=0}^{g-1} (i+1)c_i + \sum_{i=1}^{g-1} (g-i)d_i - g^2 d_0 \right) \right]. \quad (3.3)$$

In order to compare the fixation probabilities of the two types, equation (2.9) is deployed. It implies, that the condition for the fixation probability of cooperators to be greater than the one of defectors is that Φ is positive, i.e.,

The fixation probability of a cooperator exceeds the one of a defector, i.e., $\rho_C > \rho_D$, if and only if $\Phi > 0$ holds in equation (2.9). For Φ , Gokhale and Traulsen (2010) obtained the following result:

$$\Phi = \frac{N}{g} \sum_{i=0}^{g-1} (c_i - d_i) + d_0 - c_{g-1}. \quad (3.4)$$

3.2. Results for a threshold public goods game

In this section, a threshold public goods game is applied to the model. The threshold is denoted by k and represents the number of cooperators needed for the provision of a public good b , that is then shared equally among the g players. The payoff for a cooperator is given by

$$c_i = \begin{cases} \tilde{c} & \text{if } i < k-1, \\ \frac{b}{g} - c & \text{if } i \geq k-1, \end{cases} \quad (3.5)$$

where i is the number of other cooperators in the group, that is, additionally to the focal cooperator. For variable \tilde{c} , a distinction between two cases is made: Either unconditional expression of the cooperative trait holds, i.e., a cooperator pays a cost although the group fails to produce the public good (hence $\tilde{c} = c$), or conditional expression holds, i.e., a cooperator only pays a cost when the public good is effectively produced (hence $\tilde{c} = 0$).

The payoff for a focal defector reads as

$$d_i = \begin{cases} 0 & \text{if } i < k, \\ \frac{b}{g} & \text{if } i \geq k, \end{cases} \quad (3.6)$$

where i is the number of cooperators among the players.

In the following, the conditions for $\rho_C > 1/N$ and $\rho_C > \rho_D$ are reformulated in terms of the benefit-to-cost ratio after applying these payoffs to Γ and Φ .

3.2.1. Comparison to the neutral case

Inserting payoffs (3.5) with $\tilde{c} = -c$ and (3.6) into Γ given by (3.3) and rearranging leads to

$$\Gamma = -c \left[\frac{1}{2} N(N-1) \right] + b \left[\frac{N}{g(g+1)} \left(N \frac{g-k+1}{g} - \frac{2g+2-k}{2} \right) \right]. \quad (3.7)$$

It follows that Γ is always negative for

$$k \geq \frac{2(N-g)(g+1)}{2N-g}. \quad (3.8)$$

If $2N > g^2 - 2g$, inequality (3.8) never holds, because $k \leq g$ holds by design of the game.

Assuming that the threshold k is smaller than the right hand side of inequality (3.8), the condition $\Gamma > 0$ can be reformulated in terms of the benefit-to-cost ratio, i.e., in the case of unconditional expression, cooperation is favored by selection if and only if

$$\frac{b}{c} > \frac{g^2(g+1)(N-1)}{2N(g+1) + k(g-2N) - 2g(g+1)}. \quad (3.9)$$

Replacing payoffs (3.5) with $\tilde{c} = 0$ and (3.6) in Γ given by (3.3) and rearranging yields

$$\begin{aligned} \Gamma = & -c \left[\frac{N}{2g(g+1)} (N(g-k+1)(g-k+2) - g(g+1) + k(k-1)) \right] \\ & + b \left[\frac{N}{2g^2(g+1)} (N(g-k+1) - 2g^2 - 2g + gk) \right]. \end{aligned} \quad (3.10)$$

Under the assumption that

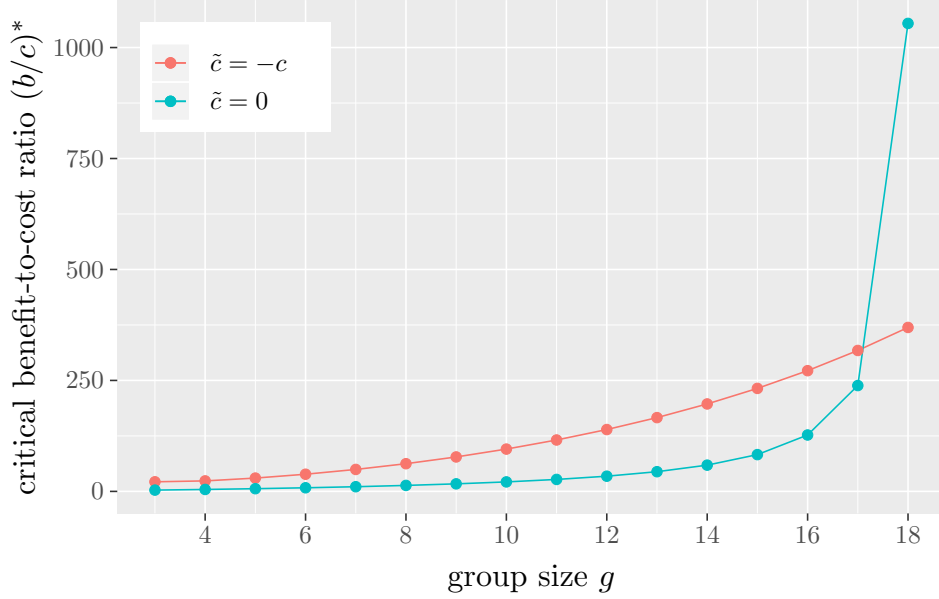


Figure 3.2.: Critical benefit-to-cost ratio for fixed population size $N = 40$ and fixed number of required cooperators $k = 3$

$$k < \frac{(N - 2g)(g + 1)}{N - g} \quad (3.11)$$

holds, which is always fulfilled if $N > g^2 - 2g$, the condition for selection favoring cooperation in the case of conditional expression reads as

$$\frac{b}{c} > \frac{g(N(g - k + 1)(g - k + 2) - g(g + 1) + k(k - 1))}{N(g - k + 1) - 2g(g + 1) + gk}. \quad (3.12)$$

The critical benefit-to-cost ratio $(b/c)^*$ is given by the right hand side of (3.9) and (3.12), respectively. Its dependence on the parameters reflect how the stringency of the conditions depends on the parameters.

Figure 3.2 illustrates the critical benefit-to-cost ratio for varying group size g when population size N and threshold k are fixed and indicates an increase of the critical ratio with increasing slope.

Figure 3.3 presents the critical benefit-to-cost ratio depending on N for fixed g and k . The critical ratio decreases monotonically and approaches its lower bounds, that are given by

$$(b/c)_\infty^* = \lim_{N \rightarrow \infty} (b/c)^* = \frac{g^2(g + 1)}{2(g + 1) - 2k} \quad (3.13)$$

for $\tilde{c} = -c$, and

$$(b/c)_\infty^* = \lim_{N \rightarrow \infty} (b/c)^* = g(g - k + 2) \quad (3.14)$$

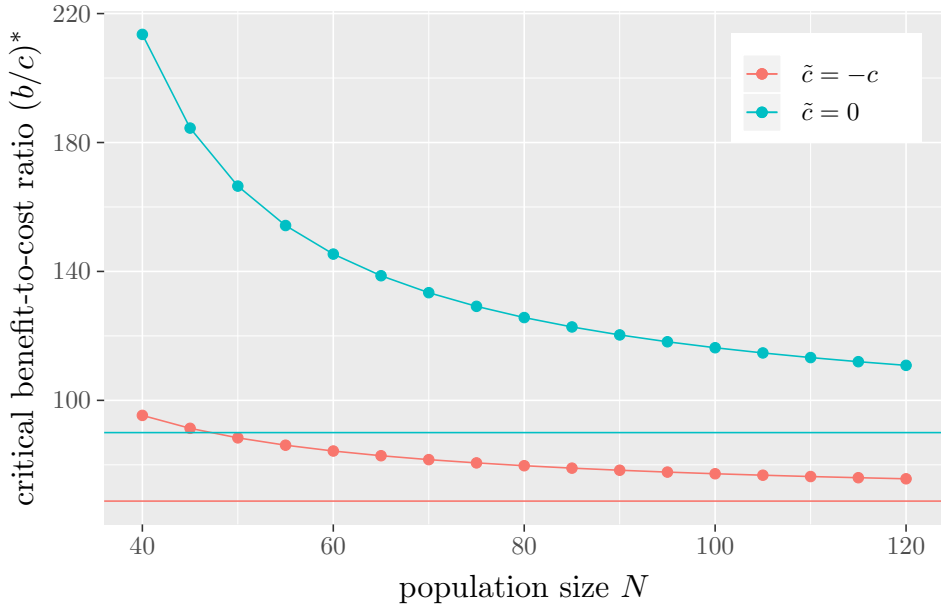


Figure 3.3.: Critical benefit-to-cost ratio for fixed group size $g = 10$ and fixed number of required cooperators $k = 3$ with limits for $N \rightarrow \infty$

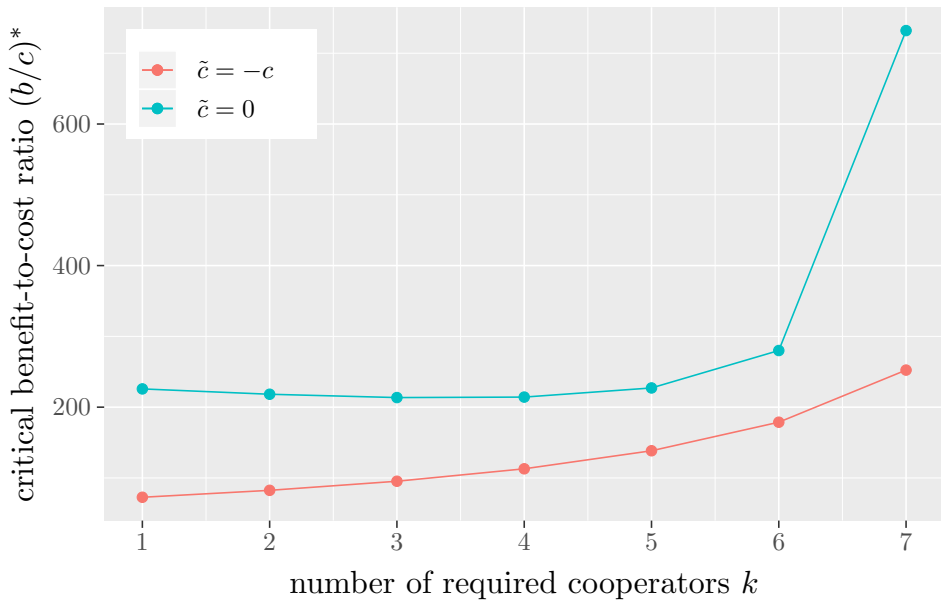


Figure 3.4.: Critical benefit-to-cost ratio for fixed population size $N = 40$ and fixed group size $g = 10$

for $\tilde{c} = 0$.

Figure 3.4 shows the critical benefit-to-cost ratio for varying threshold k and indicates that for $\tilde{c} = -c$, the critical ratio increases monotonically in k , and for $\tilde{c} = 0$, it is a non-monotonic function of k .

3.2.2. Comparison of the two types

Applying payoffs (3.5) with $\tilde{c} = -c$ and (3.6) to Φ given by (3.4) and rearranging leads to

$$\Phi = -c(N-1) + b\frac{N-g}{g^2}. \quad (3.15)$$

For $g = N$, this expression is always negative, meaning that a cooperator's fixation probability is always smaller than a defector's fixation probability. For $g = k, \dots, N-1$, the condition $\rho_C > \rho_D$ reformulated in terms of the benefit-to-cost ratio reads as

$$\frac{b}{c} > g^2 \frac{1-1/N}{1-g/N}. \quad (3.16)$$

Using $\tilde{c} = 0$ when applying payoffs (3.5) and (3.6) to Φ , yields

$$\Phi = -c\frac{N(g-k+1)-g}{g} + b\frac{N-g}{g^2}. \quad (3.17)$$

For $g = N$, this expression is never positive, implying that a cooperator's fixation probability is never larger than the fixation probability of a defector. For $g = k, \dots, N-1$, the condition $\rho_C > \rho_D$ is equivalent to

$$\frac{b}{c} > g + \frac{g(g-k)}{1-g/N}. \quad (3.18)$$

In both cases ($\tilde{c} = -c$ and $\tilde{c} = 0$), the respective critical benefit-to-cost ratio, given by the right hand side of inequality (3.16) and (3.18), respectively, is monotonically increasing in d and monotonically decreasing in N . In the limit $N \rightarrow \infty$, the critical benefit-to-cost ratio approaches its lower bound

$$(b/c)_\infty^* = \lim_{N \rightarrow \infty} (b/c)^* = g^2 \quad (3.19)$$

for $\tilde{c} = -c$, and

$$(b/c)_\infty^* = \lim_{N \rightarrow \infty} (b/c)^* = g(g-k+1) \quad (3.20)$$

for $\tilde{c} = 0$.

Interestingly, the critical ratio does not depend on the threshold k when $\tilde{c} = -c$, and decreases linearly in k when $\tilde{c} = 0$.

Figure 3.5 illustrates the critical benefit-to-cost ratio for a fixed population size N and increasing group size g . It indicates monotonic increase with increasing slope.

Figure 3.6 shows the critical benefit-to-cost ratio decreasing for an increased population size and approaching its lower bound g^2 and $g(g-k+1)$, respectively.

3.2. Results for a threshold public goods game

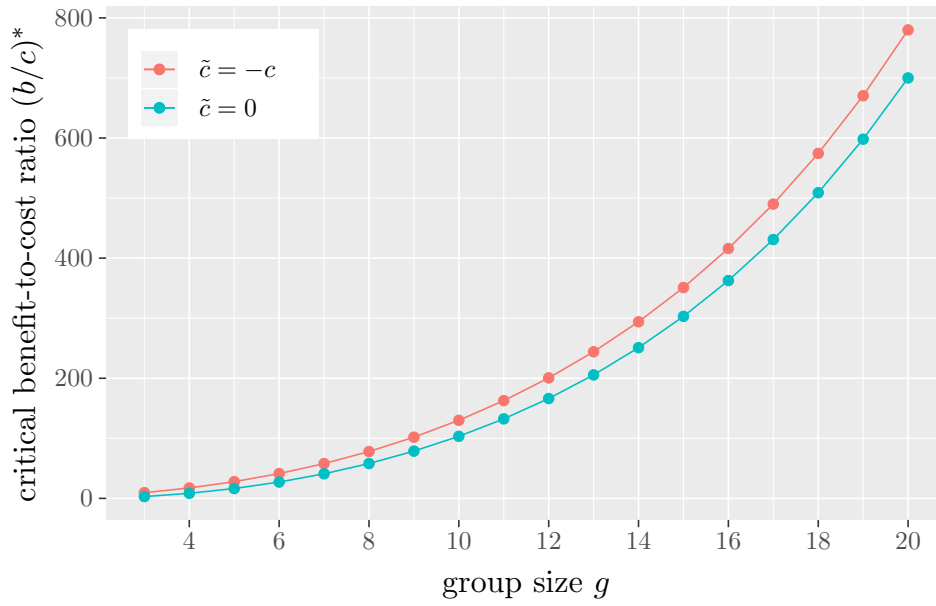


Figure 3.5.: Critical benefit-to-cost ratio for fixed population size $N = 40$ and fixed number of required cooperators $k = 3$

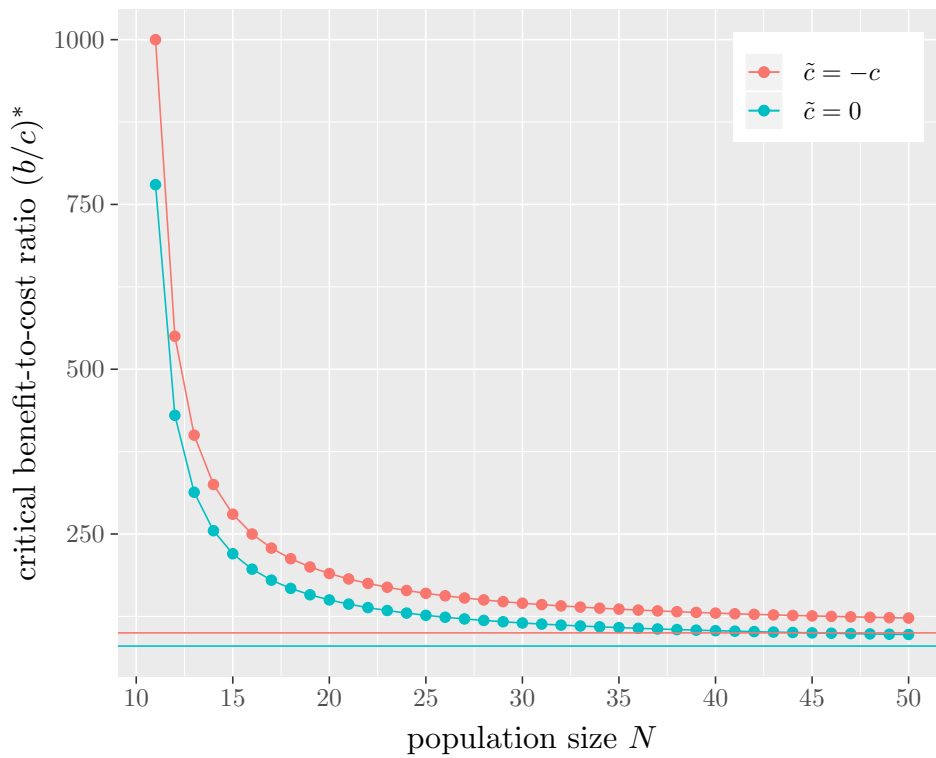


Figure 3.6.: Critical benefit-to-cost ratio for fixed group size $g = 10$ and fixed number of required cooperators $k = 3$ with limits for $N \rightarrow \infty$

3.2.3. Stationary distribution

The stationary distributions were calculated as (2.10) using R (R Core Team, 2016).

Figure 3.7 illustrates the stationary distribution for varying group sizes g as well as varying population sizes N and for a fixed benefit-to-cost ratio b/c as well as fixed threshold k .

Smaller group sizes promote higher abundance of cooperators, whereby larger population sizes seem to reinforce this effect.

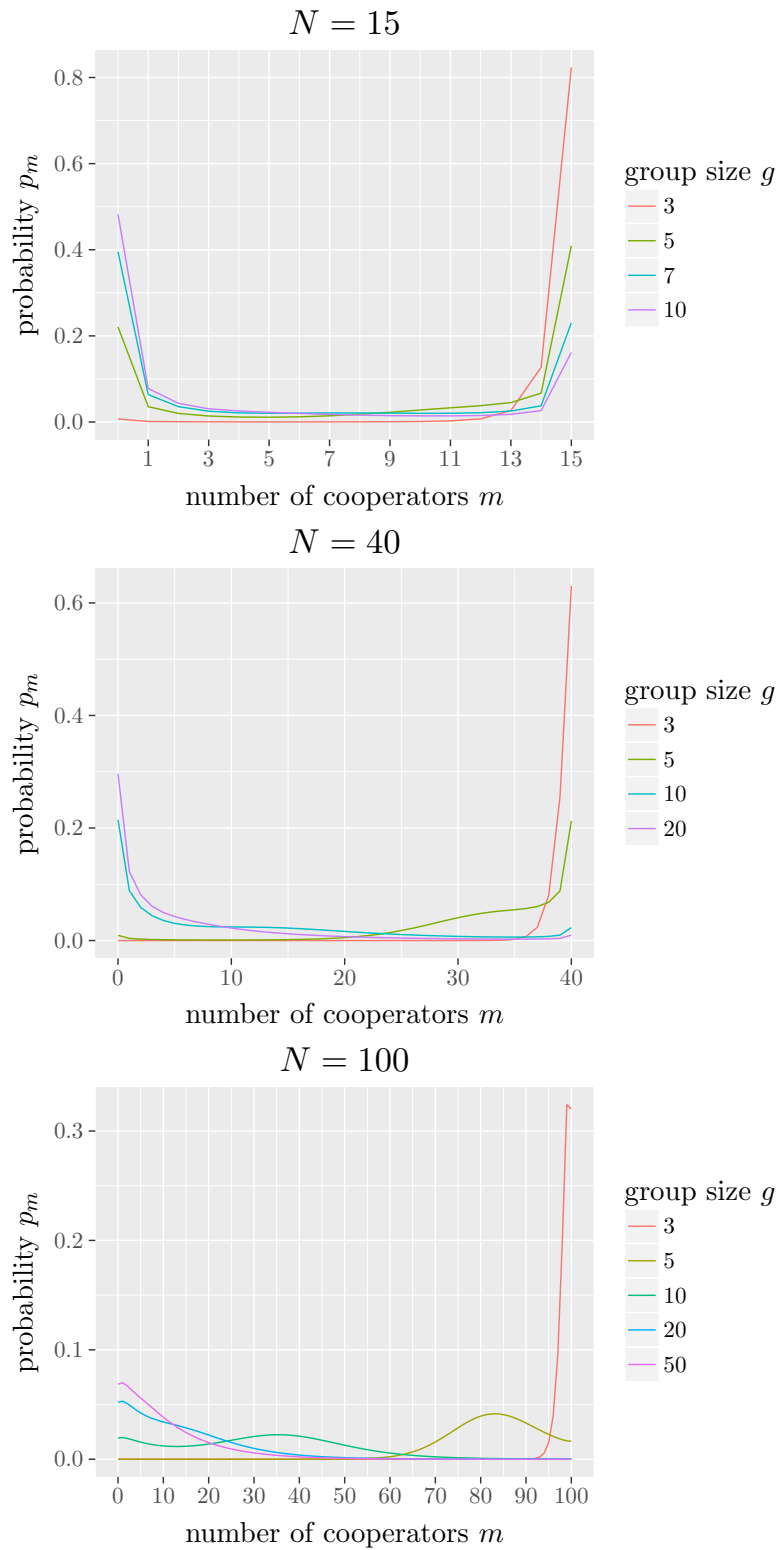


Figure 3.7.: Stationary distributions of the Moran process for parameters $w = 0.1$, $\mu = 0.01$, $b/c = 50$ and $k = 3$

4. Waiting-for-volunteers dilemma

This chapter adapts the waiting-for-volunteers dilemma (introduced for infinite populations by Peña et al. (2016)) to finite populations.

Same as for the volunteer's dilemma described in chapter 3, the model considers a finite well-mixed population of size N consisting of cooperators and defectors. The dynamics of the population is governed by the frequency-dependent Moran process. Within selected groups, individuals play games that determine the fitness of the types which in turn influences the transition probabilities of the Moran process.

The waiting-for-volunteers dilemma differs from the volunteer's dilemma in the way how groups of players are formed. Recall that in the volunteer's dilemma, group size is assumed to be constant and groups are hence formed via hypergeometric sampling.

4.1. Group formation via negative hypergeometric sampling

The waiting-for-volunteers dilemma assumes that a successful interaction requires a certain number of individuals that cooperate. Therefore, groups of players are formed by sequentially drawing random individuals from the population until a certain number k of cooperators is reached.

Depending on the current state of the process, one of the following two situations can occur: Either the process is in a state where less than k cooperators live in the population ($m < k \leq N$), or the process is in a state where the population hosts at least k cooperators ($k \leq m \leq N$).

In the first case, all the individuals are sampled from the population, because the stop criterion, to have k cooperators in the group, is never fulfilled.

In the second case, individuals are sampled until there are k cooperators among them. Then, sampling is stopped and the selected group engages in a game. Each time such a group of players is formed, there can be a different number of defectors involved.

Let $Y^{(m)}$ denote a random variable with corresponding state space $\Omega^{(m)} = \{0, \dots, N - m\}$ that describes the number of defectors in the group. Its distribution is a negative hypergeometric, meaning that the probability to have j defectors participating in the game is given by

Number of participating defectors	0	1	...	j	...	$N - k$
cooperator	c_0	c_1	...	c_j	...	c_{N-k}
defector	d_0	d_1	...	d_j	...	d_{N-k}

Figure 4.1.: Payoff matrix for an evolutionary game in which the payoff depends on the number of defectors among the players

$$P(Y^{(m)} = j) = \frac{\binom{j+k-1}{k-1} \binom{N-k-j}{m-k}}{\binom{N}{m}}. \quad (4.1)$$

This probability mass function is explained as follows.

Imagine that m cooperators and $N - m$ defectors are first lined up in a sequence and then numerated. There are $\binom{N}{m}$ different possible orders for the sequence. The probability to have j defectors in the group is the same as the probability to sample the k^{th} cooperator in the $(j + k)^{\text{th}}$ draw, or, in other words, the probability that the k^{th} cooperator is at place number $j + k$ in the sequence. The therefor suitable arrangements have $k - 1$ cooperators in the first $j + k - 1$ places, for which there are $\binom{j+k-1}{k-1}$ possibilities, and $m - k$ cooperators in the last $N - j - k$ places, for which there are $\binom{N-k-j}{m-k}$ possibilities. Combining these two requirements ensures that the $(j + k)^{\text{th}}$ place is occupied by the k^{th} cooperator. Hence, the number of suitable arrangements is given by the product of the two binomial coefficients, and the probability by the frequency of suitable orders.

4.2. Results for general multiplayer games

Once the group formation process is completed, group members engage in an interaction with each other where individuals of the same type receive the same payoff, i.e., the game is symmetric.

In the case $m < k \leq N$, every cooperator of the population obtains a payoff \tilde{c} and every defector a payoff \tilde{d} .

In the case $k \leq m \leq N$, the number of defectors in a focal group varies. The assumption that payoffs depend on the number of participating defectors, yields a payoff matrix presented in figure 4.1.

Individuals that do not participate in the game obtain a payoff of zero.

4.2.1. Expected payoffs

The fitness of each type is determined by the expected payoff that an individual of the type receives from the game. Therefore, the expected payoffs for

cooperators and defectors are derived in the following.

In the case $m < k \leq N$, all the individuals are sampled for playing, hence, the expected payoff is equal to \tilde{c} and \tilde{d} , respectively:

$$\pi_C = \tilde{c} \quad \text{and} \quad \pi_D = \tilde{d}. \quad (4.2)$$

On the other hand, if $k \leq m \leq N$, an individual obtains a payoff only if it is sampled for playing, otherwise it gets a payoff of zero.

A cooperator receives the payoff c_j when it is chosen to play the game and when there are j defectors chosen to play as well. This case occurs with probability $P(A \cap \{Y^{(m)} = j\})$, where A denotes the event that the focal cooperator is sampled as a player. The expected payoff for a cooperator is the sum over all possible payoffs weighted by the probability to obtain the respective payoff:

$$\pi_C = \sum_{j=0}^{N-m} P(A \cap \{Y^{(m)} = j\}) c_j. \quad (4.3)$$

Applying Bayes' rule for conditional probabilities yields

$$P(A \cap \{Y^{(m)} = j\}) = P(A|Y^{(m)} = j)P(Y^{(m)} = j). \quad (4.4)$$

The probability that the focal cooperator is among the sampled players is independent of the number of defectors sampled, i.e., $P(A|Y^{(m)} = j) = P(A)$, because during each group formation process, k out of the m cooperators are randomly selected with the same probability, hence $P(A) = k/m$.

It follows that the expected payoff for a cooperator is given by

$$\pi_C = \frac{k}{m} \sum_{j=0}^{N-m} P(Y^{(m)} = j) c_j. \quad (4.5)$$

Similarly, a defector obtains the payoff d_j , if it is selected for playing and if there are j defectors (including itself) sampled as players. The probability of this event is $P(B \cap \{Y^{(m)} = j\})$, where B denotes the event that the focal defector is among the players. The expected payoff for a defector is obtained by summing all possible payoffs weighted by the probability to receive the respective payoff:

$$\begin{aligned} \pi_D &= \sum_{j=1}^{N-m} P(B \cap \{Y^{(m)} = j\}) d_j \\ &= \sum_{j=1}^{N-m} P(B|Y^{(m)} = j)P(Y^{(m)} = j) d_j, \end{aligned} \quad (4.6)$$

whereby Bayes' rule is used again. The conditional probability, that a defector is chosen to play, when j out of $N - m$ defectors are chosen to play, is simply $P(B|Y^{(m)} = j) = j/(N - m)$, so that the expected payoff of a defector is given by

$$\pi_D = \frac{1}{N - m} \sum_{j=0}^{N-m} j P(Y^{(m)} = j) d_j. \quad (4.7)$$

4.2.2. Comparison to the neutral case

In the case of weak selection $w \ll 1$, cooperators are favored by selection, i.e. $\rho_C > 1/N$, if and only if $\Gamma > 0$ holds in equation (2.8). Hence, an expression of Γ for multiplayer games with a general payoff matrix of the kind displayed in figure 4.1 is derived in the following.

First, Γ is decomposed into two parts with respect to the cases $m \geq k$ and $m < k$:

$$\begin{aligned} \Gamma &= \sum_{l=1}^{k-1} \sum_{m=1}^l (\pi_C - \pi_D) + \sum_{l=k}^{N-1} \sum_{m=1}^l (\pi_C - \pi_D) \\ &= \underbrace{\sum_{l=1}^{k-1} \sum_{m=1}^l (\pi_C - \pi_D) + \sum_{l=k}^{N-1} \sum_{m=1}^{k-1} (\pi_C - \pi_D)}_{\Gamma_1} + \underbrace{\sum_{l=k}^{N-1} \sum_{m=k}^l (\pi_C - \pi_D)}_{\Gamma_2} \end{aligned} \quad (4.8)$$

In the first term, the difference of the expected payoffs simply reads as $\pi_C - \pi_D = \tilde{c} - \tilde{d}$, so that Γ_1 can be written as

$$\begin{aligned} \Gamma_1 &= \sum_{l=1}^{k-1} \sum_{m=1}^l (\tilde{c} - \tilde{d}) + \sum_{l=k}^{N-1} \sum_{m=1}^{k-1} (\tilde{c} - \tilde{d}) \\ &= (\tilde{c} - \tilde{d})(k-1) \left(N - \frac{k}{2} \right). \end{aligned} \quad (4.9)$$

For the second term, Γ_2 , the expected payoffs are given by (4.5) and (4.7), yielding

$$\Gamma_2 = \sum_{l=k}^{N-1} \sum_{m=k}^l \sum_{j=0}^{N-m} P(Y^{(m)} = j) \left[\frac{k}{m} c_j - \frac{j}{N-m} d_j \right]. \quad (4.10)$$

Deploying the notation

$$f(j, m) := P(Y^{(m)} = j) \left[\frac{k}{m} c_j - \frac{j}{N-m} d_j \right], \quad (4.11)$$

the three nested sums in equation (4.10) can be reduced to two nested sums in the following way:

$$\begin{aligned} \sum_{l=k}^{N-1} \sum_{m=k}^l \sum_{j=0}^{N-m} f(j, m) &= \sum_{m=k}^{N-1} (N-m) \sum_{j=0}^{N-m} f(j, m) \\ &= \sum_{m=k}^{N-1} \sum_{j=m}^N (N-m) f(N-j, m). \end{aligned} \quad (4.12)$$

Inserting (4.11) yields

$$\begin{aligned} \Gamma_2 &= \sum_{m=k}^{N-1} \sum_{j=m}^N P(Y^{(m)} = N-j) \left[\frac{N}{m} k c_{N-j} - k c_{N-j} - (N-j) d_{N-j} \right] \\ &= \sum_{m=k}^N \sum_{j=m}^N P(Y^{(m)} = N-j) \left[\frac{N}{m} k c_{N-j} - k c_{N-j} - (N-j) d_{N-j} \right], \end{aligned} \quad (4.13)$$

where the last step follows because the expression in square brackets is zero for $m = N$ and $j = N$.

Changing the order of summation using

$$\sum_{m=k}^N \sum_{j=m}^N = \sum_{j=k}^N \sum_{m=k}^j, \quad (4.14)$$

Γ_2 can be rewritten as

$$\begin{aligned} \Gamma_2 &= \sum_{j=k}^N \sum_{m=k}^j \frac{\binom{N-j+k-1}{k-1} \binom{j-k}{m-k}}{\binom{N}{m}} \left[\frac{N}{m} k c_{N-j} - k c_{N-j} - (N-j) d_{N-j} \right] \\ &= \underbrace{\sum_{j=k}^N k c_{N-j} \binom{N-j+k-1}{k-1} \sum_{m=k}^j \frac{N}{m} \frac{\binom{j-k}{m-k}}{\binom{N}{m}}}_{U_1} \\ &\quad - \underbrace{\sum_{j=k}^N k c_{N-j} \binom{N-j+k-1}{k-1} \sum_{m=k}^j \frac{\binom{j-k}{m-k}}{\binom{N}{m}}}_{U_2} \\ &\quad - \underbrace{\sum_{j=k}^N (N-j) d_{N-j} \binom{N-j+k-1}{k-1} \sum_{m=k}^j \frac{\binom{j-k}{m-k}}{\binom{N}{m}}}_{U_3}. \end{aligned} \quad (4.15)$$

In each component (i.e. U_1, U_2 and U_3), the term summing over m can be rewritten as a term without a sum. First, this is shown for the term $\sum_{m=k}^j \frac{\binom{j-k}{m-k}}{\binom{N}{m}}$

which occurs in U_2 as well as in U_3 . By drawing out common factors of the summands and rearranging, the quotient of binomial coefficients can be expressed as a product of binomial coefficients:

$$\sum_{m=k}^j \frac{\binom{j-k}{m-k}}{\binom{N}{m}} = \frac{(j-k)!}{N!} k!(N-j)! \sum_{m=k}^j \binom{m}{k} \binom{N-m}{N-j}. \quad (4.16)$$

Next, an index shift yields

$$\begin{aligned} \sum_{m=k}^j \binom{m}{k} \binom{N-m}{N-j} &= \sum_{m=0}^{j-k} \binom{N-k-m}{N-j} \binom{k+m}{k} \\ &= \sum_{m=0}^{N-k} \binom{N-k-m}{N-j} \binom{k+m}{k}, \end{aligned} \quad (4.17)$$

where the last step follows because $j-k \leq N-k$ holds, and for $m > j-k$ it implies $N-k-m < N-j$; thus by the definition of the binomial coefficient $\binom{N-k-m}{N-j} = 0$ holds for $m > j-k$.

A variant of Vandermonde's convolution, i.e.,

$$\sum_{i=0}^l \binom{l-i}{m} \binom{q+i}{n} = \binom{l+q+1}{m+n+1} \quad (4.18)$$

(Graham et al., 1994), can be applied to (4.17), yielding

$$\sum_{m=0}^{N-k} \binom{N-k-m}{N-j} \binom{k+m}{k} = \binom{N+1}{N-j+k+1}. \quad (4.19)$$

In conclusion, the term with the sum over m occurring in U_2 and U_3 can be rewritten as

$$\sum_{m=k}^j \frac{\binom{j-k}{m-k}}{\binom{N}{m}} = \frac{(j-k)!}{N!} k!(N-j)! \binom{N+1}{N-j+k+1}. \quad (4.20)$$

Analogously, the term $\sum_{m=k}^j \frac{N}{m} \frac{\binom{j-k}{m-k}}{\binom{N}{m}}$, appearing in U_1 (equation (4.15)), can be rewritten as

$$\sum_{m=k}^j \frac{N}{m} \frac{\binom{j-k}{m-k}}{\binom{N}{m}} = \frac{(j-k)!}{(N-1)!} (k-1)!(N-j)! \binom{N}{N-j+k}. \quad (4.21)$$

Replacing equations (4.20) and (4.21) into U_1 , U_2 and U_3 of (4.15) leads to

$$\begin{aligned} U_1 &= \sum_{j=k}^N k c_{N-j} \binom{N-j+k-1}{k-1} \frac{(j-k)!}{(N-1)!} (k-1)! (N-j)! \binom{N}{N-j+k} \\ &= \sum_{j=k}^N c_{N-j} \frac{kN}{N-j+k}, \end{aligned} \quad (4.22)$$

$$\begin{aligned} U_2 &= \sum_{j=k}^N k c_{N-j} \binom{N-j+k-1}{k-1} \frac{(j-k)!}{N!} k! (N-j)! \binom{N+1}{N-j+k+1} \\ &= \sum_{j=k}^N c_{N-j} \frac{k^2(N+1)}{(N-j+k+1)(N-j+k)} \end{aligned} \quad (4.23)$$

and

$$\begin{aligned} U_3 &= \sum_{j=k}^N (N-j) d_{N-j} \binom{N-j+k-1}{k-1} \frac{(j-k)!}{N!} k! (N-j)! \binom{N+1}{N-j+k+1} \\ &= \sum_{j=k}^N d_{N-j} \frac{k(N+1)(N-j)}{(N-j+k+1)(N-j+k)}. \end{aligned} \quad (4.24)$$

Thus, equation (4.15) reduces to

$$\begin{aligned} \Gamma_2 &= U_1 - U_2 - U_3 \\ &= \sum_{j=k}^N \left[\frac{kN}{N-j+k} - \frac{k^2(N+1)}{(N-j+k+1)(N-j+k)} \right] c_{N-j} \\ &\quad - \frac{k(N+1)(N-j)}{(N-j+k+1)(N-j+k)} d_{N-j} \\ &= \sum_{j=0}^{N-k} \frac{k}{j+k} \left[\left(N - \frac{k(N+1)}{j+k+1} \right) c_j - \frac{(N+1)j}{j+k+1} d_j \right], \end{aligned} \quad (4.25)$$

so that the following expression for Γ in (2.8) is obtained:

$$\begin{aligned} \Gamma &= (\tilde{c} - \tilde{d})(k-1) \left(N - \frac{k}{2} \right) \\ &\quad + \sum_{j=0}^{N-k} \frac{k}{j+k} \left[\left(N - \frac{k(N+1)}{j+k+1} \right) c_j - \frac{(N+1)j}{j+k+1} d_j \right]. \end{aligned} \quad (4.26)$$

Cooperation is favored by selection if and only if $\Gamma > 0$.

4.2.3. Comparison of the two types

In order to compare the fixation probabilities of the two types, equation (2.9) is deployed. It implies, that the condition for the fixation probability of cooperators to be greater than the one of defectors is that Φ is positive, i.e.,

$$\rho_C > \rho_D \Leftrightarrow \Phi > 0. \quad (4.27)$$

In the following, an expression of Φ for multiplayer games with a general payoff matrix of the kind displayed in figure 4.1 is derived.

First, Φ is split up with respect to the cases $m < k$ and $m \geq k$, yielding

$$\Phi = \underbrace{\sum_{m=1}^{k-1} (\pi_C - \pi_D)}_{\Phi_1} + \underbrace{\sum_{m=k}^{N-1} (\pi_C - \pi_D)}_{\Phi_2}. \quad (4.28)$$

For the first part, Φ_1 , the difference of expected payoffs has the form $\tilde{c} - \tilde{d}$, so that

$$\Phi_1 = \sum_{m=1}^{k-1} (\tilde{c} - \tilde{d}) = (\tilde{c} - \tilde{d})(k-1). \quad (4.29)$$

For the second part, Φ_2 , where $m \geq k$, the expected payoffs are given by (4.5) and (4.7), yielding

$$\begin{aligned} \Phi_2 &= \sum_{m=k}^{N-1} \sum_{j=0}^{N-m} \frac{\binom{j+k-1}{k-1} \binom{N-k-j}{m-k}}{\binom{N}{m}} \left[\frac{k}{m} c_j - \frac{j}{N-m} d_j \right] \\ &= \sum_{m=k}^{N-1} \sum_{j=m}^N \frac{\binom{N-j+k-1}{k-1} \binom{j-k}{m-k}}{\binom{N}{m}} \left[\frac{k}{m} c_{N-j} - \frac{N-j}{N-m} d_{N-j} \right] \\ &= \sum_{m=k}^{N-1} \left(\sum_{j=m}^{N-1} \frac{\binom{N-j+k-1}{k-1} \binom{j-k}{m-k}}{\binom{N}{m}} \left[\frac{k}{m} c_{N-j} - \frac{N-j}{N-m} d_{N-j} \right] + \frac{\binom{N-k}{m-k}}{\binom{N}{m}} \frac{k}{m} c_0 \right) \\ &= \underbrace{\sum_{m=k}^{N-1} \sum_{j=m}^{N-1} \frac{\binom{N-j+k-1}{k-1} \binom{j-k}{m-k}}{\binom{N}{m}} \left[\frac{k}{m} c_{N-j} - \frac{N-j}{N-m} d_{N-j} \right]}_{V_1} \\ &\quad + \underbrace{\sum_{m=k}^{N-1} \frac{\binom{N-k}{m-k}}{\binom{N}{m}} \frac{k}{m} c_0}_{V_2}. \end{aligned} \quad (4.30)$$

Now the term V_1 can be manipulated in a way analogous to the calculations in section 4.2.2. After changing the order of summation (see (4.14)), the term is

again split into two components, W_1 and W_2 :

$$\begin{aligned}
 V_1 &= \sum_{j=k}^{N-1} \sum_{m=k}^j \frac{\binom{N-j+k-1}{k-1} \binom{j-k}{m-k}}{\binom{N}{m}} \left[\frac{k}{m} c_{N-j} - \frac{N-j}{N-m} d_{N-j} \right] \\
 &= \underbrace{\sum_{j=k}^{N-1} k c_{N-j} \binom{N-j+k-1}{k-1} \sum_{m=k}^j \frac{1}{m} \frac{\binom{j-k}{m-k}}{\binom{N}{m}}}_{W_1} \\
 &\quad - \underbrace{\sum_{j=k}^{N-1} (N-j) d_{N-j} \binom{N-j+k-1}{k-1} \sum_{m=k}^j \frac{1}{N-m} \frac{\binom{j-k}{m-k}}{\binom{N}{m}}}_{W_2} \quad (4.31)
 \end{aligned}$$

Calculations similar to the ones in (4.16)-(4.20) lead to

$$\sum_{m=k}^j \frac{1}{m} \frac{\binom{j-k}{m-k}}{\binom{N}{m}} = \frac{(j-k)!}{N!} (k-1)! (N-j)! \binom{N}{N-j+k} \quad (4.32)$$

as well as

$$\sum_{m=k}^j \frac{1}{N-m} \frac{\binom{j-k}{m-k}}{\binom{N}{m}} = \frac{(j-k)!}{N!} k! (N-j-1)! \binom{N}{N-j+k}. \quad (4.33)$$

Therefore, W_1 and W_2 of equation (4.31) can be rewritten as

$$\begin{aligned}
 W_1 &= \sum_{j=k}^{N-1} k c_{N-j} \binom{N-j+k-1}{k-1} \frac{(j-k)!}{N!} (k-1)! (N-j)! \binom{N}{N-j+k} \\
 &= \sum_{j=k}^{N-1} \frac{k}{N-j+k} c_{N-j} \quad (4.34)
 \end{aligned}$$

and

$$\begin{aligned}
 W_2 &= \sum_{j=k}^{N-1} (N-j) d_{N-j} \binom{N-j+k-1}{k-1} \frac{(j-k)!}{N!} k! (N-j-1)! \binom{N}{N-j+k} \\
 &= \sum_{j=k}^{N-1} \frac{k}{N-j+k} d_{N-j}. \quad (4.35)
 \end{aligned}$$

Replacing these two expressions into equation (4.31) yields

$$\begin{aligned}
 V_1 &= W_1 - W_2 = \sum_{j=k}^{N-1} \frac{k}{N-j+k} c_{N-j} - \sum_{j=k}^{N-1} \frac{k}{N-j+k} d_{N-j} \\
 &= \sum_{j=1}^{N-k} \frac{k}{j+k} (c_j - d_j). \quad (4.36)
 \end{aligned}$$

The term V_2 of equation (4.30) can be manipulated analogously, yielding

$$V_2 = \sum_{m=k}^{N-1} \frac{\binom{N-k}}{\binom{m-k}} \frac{k}{m} c_0 = c_0 \frac{N-k}{N} \quad (4.37)$$

Inserting the expressions for V_1 and V_2 found in (4.36) and (4.37) back into equation (4.30) results in

$$\Phi_2 = V_1 + V_2 = \sum_{j=1}^{N-k} \frac{k}{j+k} (c_j - d_j) + c_0 \frac{N-k}{N}, \quad (4.38)$$

so that, in conclusion, Φ reduces to

$$\Phi = (\tilde{c} - \tilde{d})(k-1) + \sum_{j=1}^{N-k} \frac{k}{j+k} (c_j - d_j) + c_0 \frac{N-k}{N} \quad (4.39)$$

The fixation probability of a cooperator is greater than the fixation probability of a defector if and only if $\Phi > 0$.

4.3. Results for a public goods game

In this section, a public goods game is applied to the model.

A number k of cooperators are required to produce a public good, at a personal cost c . The public good provides a benefit of value b , which is shared equally among all players in the group, although defectors do not contribute anything.

The payoffs of the game are hence given by:

$$\begin{aligned} c_j &= \frac{b}{j+k} - c & \tilde{c} &= -c \quad \text{or} \quad \tilde{c} = 0 \\ d_j &= \frac{b}{j+k} & \tilde{d} &= 0 \end{aligned} \tag{4.40}$$

Depending on whether unconditional or conditional expression of the cooperator's contribution is assumed, variable \tilde{c} takes on the values c or 0 , respectively.

4.3.1. Comparison to the neutral case

After replacing (4.40) into equation (4.26), the condition for $\rho_C > 1/N$ can be reformulated in terms of the benefit-to-cost ratio b/c .

First, unconditional expression of the cooperative trait, i.e., $\tilde{c} = -c$, is assumed. Replacing the payoffs introduced in (4.40) into equation (4.26) and rearranging yields

$$\begin{aligned} \Gamma &= -c(k-1) \left(N - \frac{k}{2} \right) \\ &+ \sum_{j=0}^{N-k} \frac{k}{j+k} \left[\left(N - \frac{k(N+1)}{j+k+1} \right) \left(\frac{b}{j+k} - c \right) - \frac{(N+1)j}{j+k+1} \cdot \frac{b}{j+k} \right] \\ &= c \underbrace{\left((1-k) \left(N - \frac{k}{2} \right) + \sum_{j=0}^{N-k} \frac{k}{j+k} \left[\frac{k(N+1)}{j+k+1} - N \right] \right)}_{\alpha} \\ &+ b \underbrace{\left(\sum_{j=0}^{N-k} \frac{k}{(j+k)^2} \left[N - \frac{k(N+1)}{j+k+1} - \frac{(N+1)j}{j+k+1} \right] \right)}_{\beta}. \end{aligned} \tag{4.41}$$

The expressions for α and β can be simplified to

$$\alpha = N + \frac{k}{2}(1-k) - Nk \sum_{j=k}^N \frac{1}{j} \tag{4.42}$$

and

$$\beta = Nk \sum_{j=k}^N \frac{1}{j^2} - N + k - 1, \quad (4.43)$$

so that the condition for the fixation probability of a single cooperator being greater than $1/N$ is given by

$$c \left(\frac{k}{2}(1-k) + N - Nk \sum_{j=k}^N \frac{1}{j} \right) + b \left(k - 1 - N + Nk \sum_{j=k}^N \frac{1}{j^2} \right) > 0. \quad (4.44)$$

For the special case $k = N$, the left hand side of (4.44) reduces to $(c/2)N(1-N)$, a non-positive term for all $N \geq 1$, which implies that the cooperators' strategy is never favored by selection.

However, for all $1 \leq k < N$ it holds that $\beta > 0$ (see A.1). Thus, the condition for $\rho_C > 1/N$ can be expressed via benefit-to-cost ratio in the following manner:

$$\frac{b}{c} > \frac{\frac{k}{2N}(k-1) - 1 + k \sum_{j=k}^N \frac{1}{j}}{\frac{k-1}{N} - 1 + k \sum_{j=k}^N \frac{1}{j^2}}. \quad (4.45)$$

Now consider the case where $\tilde{c} = 0$. The expression Γ then reads as

$$\begin{aligned} \Gamma &= \sum_{j=0}^{N-k} \frac{k}{j+k} \left[\left(N - \frac{k(N+1)}{j+k+1} \right) \left(\frac{b}{j+k} - c \right) - \frac{(N+1)j}{j+k+1} \frac{b}{j+k} \right] \\ &= c \underbrace{\left(\sum_{j=0}^{N-k} \frac{k}{j+k} \left[\frac{k(N+1)}{j+k+1} - N \right] \right)}_{\alpha} \\ &\quad + b \underbrace{\left(\sum_{j=0}^{N-k} \frac{k}{(j+k)^2} \left[N - \frac{k(N+1)}{j+k+1} - \frac{(N+1)j}{j+k+1} \right] \right)}_{\beta}. \end{aligned} \quad (4.46)$$

While the β stays unchanged in comparison to equation (4.41), α is altered to

$$\alpha = k(1-k) + kN - kN \sum_{j=k}^N \frac{1}{j}. \quad (4.47)$$

For $k = N$, it follows that $\Gamma = 0$, yielding fixation probabilities equal to the neutral case. For $1 \leq k < N$, the condition for the fixation probability of a single cooperator to be greater than $1/N$ can be rewritten as

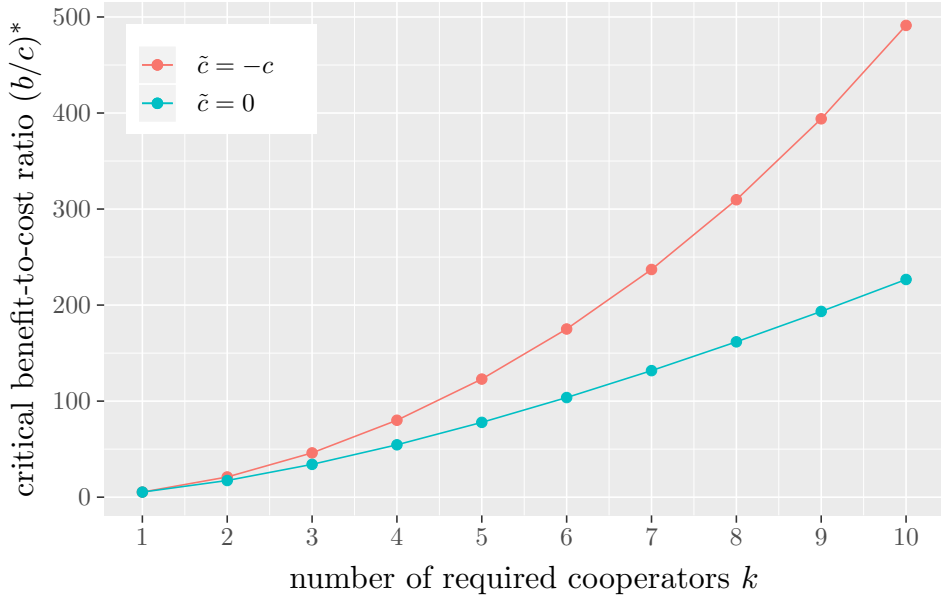


Figure 4.2.: Critical benefit-to-cost ratio for fixed population size $N = 40$

$$\frac{b}{c} > \frac{\frac{k}{N}(k-1) + k \left(\sum_{j=k}^N \frac{1}{j} - 1 \right)}{\frac{k-1}{N} - 1 + k \sum_{j=k}^N \frac{1}{j^2}}. \quad (4.48)$$

Figure 4.2 illustrates the dependence of the critical benefit-to-cost ratio on the number of required cooperators k when the population size N is fixed. For the two cases considered, $\tilde{c} = -c$ and $\tilde{c} = 0$, an increase of the critical ratio with increasing slope can be observed when k is increased.

Figure 4.3 shows the critical benefit-to-cost ratio for varying population size N and fixed number of required cooperators k . For the case $\tilde{c} = 0$, a monotonic increase with decreasing slope in the critical ratio can be observed. For $\tilde{c} = -c$, however, the ratio first decreases until it reaches a minimum, and then increases with decreasing slope. In both cases, the critical ratio goes to infinity in the limit $N \rightarrow \infty$, making the condition impossible to fulfill.

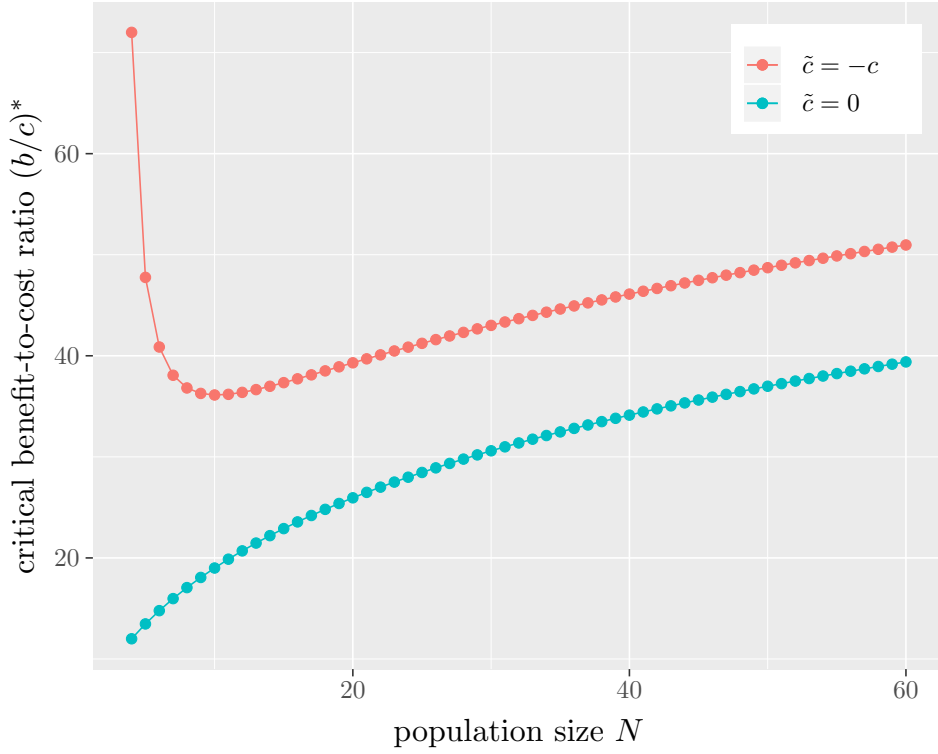


Figure 4.3.: Critical benefit-to-cost ratio for fixed number of required cooperators $k = 3$

4.3.2. Comparison of the two types

Replacing the payoffs (4.40) with $\tilde{c} = -c$ into the expression (4.39) of Φ and rearranging yields

$$\Phi = -c \underbrace{\left(k - 1 + \sum_{j=1}^{N-k} \frac{k}{j+k} + \frac{N-k}{N} \right)}_{\alpha} + b \underbrace{\frac{N-k}{kN}}_{\beta}. \quad (4.49)$$

For $k = N$ follows $\Phi = -c(N-1) < 0$ and hence $\rho_C < \rho_D$ for all $N > 1$. It holds that $\beta > 0$ for all $1 \leq k < N$. Thus the condition for $\rho_C > \rho_D$ can be formulated in terms of the benefit-to-cost ratio in the following way:

$$\frac{b}{c} > \frac{k^2 \left(1 - \frac{1}{N} + \sum_{j=k+1}^N \frac{1}{j} \right)}{1 - \frac{k}{N}}. \quad (4.50)$$

Under the assumption of conditional expression ($\tilde{c} = 0$), the expression for Φ becomes

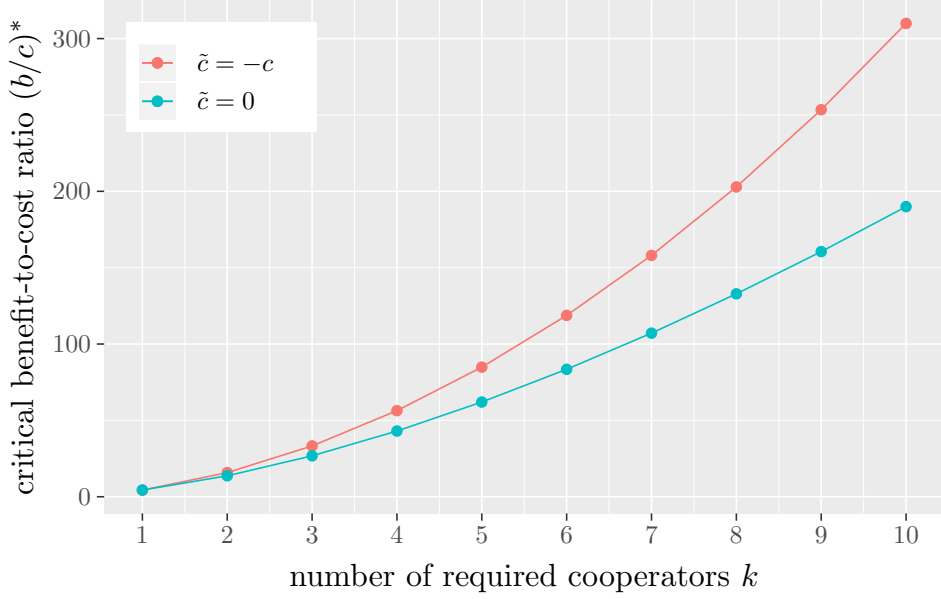


Figure 4.4.: Critical benefit-to-cost ratio for fixed population size $N = 40$

$$\Phi = -c \left(\sum_{j=1}^{N-k} \frac{k}{j+k} + \frac{N-k}{N} \right) + b \frac{N-k}{kN}. \quad (4.51)$$

Thus, the condition for $\rho_C > \rho_D$ reads

$$\frac{b}{c} > \frac{k \left(1 - \frac{k}{N} + k \sum_{j=k+1}^N \frac{1}{j} \right)}{1 - \frac{k}{N}}. \quad (4.52)$$

Figure 4.4 illustrates the behavior of the critical benefit-to-cost ratio under the influence of the number of required cooperators when the population size is fixed. Qualitatively, the same behavior as in section 4.3.1 can be observed: In both cases, $\tilde{c} = -c$ and $\tilde{c} = 0$, the critical ratio increases monotonically with increasing slope in k .

A qualitative similarity with the results for the condition $\rho_C > 1/N$ also shows when the number of required cooperators is fixed and the dependence on the population size is analyzed. This is presented in figure 4.5: For $\tilde{c} = -c$, there is an initial decrease to a global minimum followed by increase with decreasing slope, whereas for $\tilde{c} = 0$, the critical ratio increases monotonically with decreasing slope.

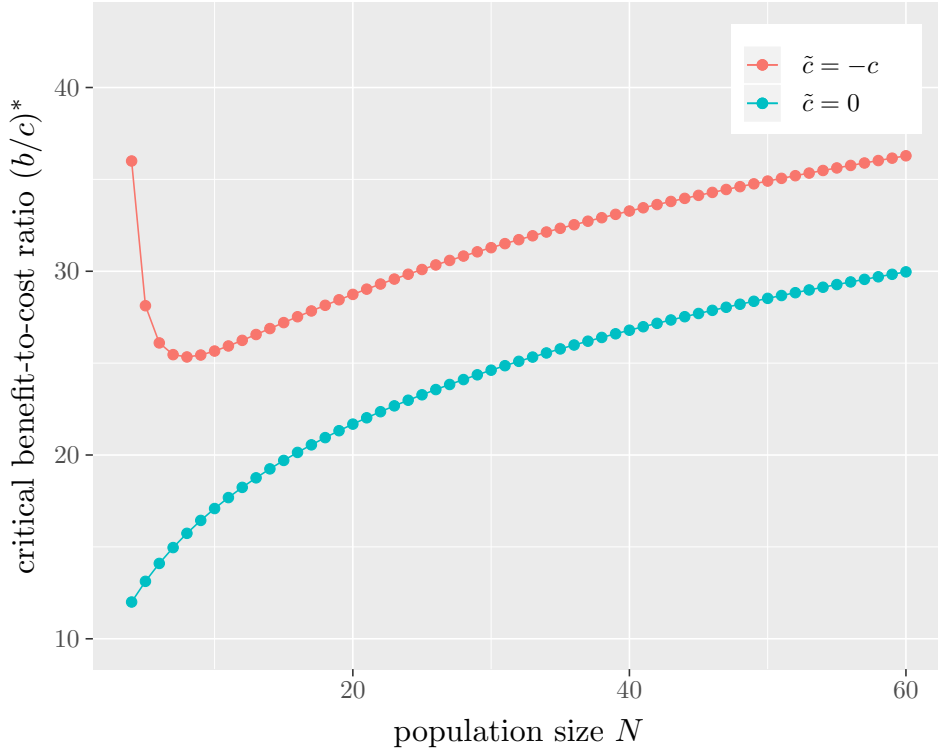


Figure 4.5.: Critical benefit-to-cost ratio for fixed number of required cooperators $k = 3$

4.3.3. Minimal critical benefit-to-cost ratio

For both conditions considered, it was observed that, for a fixed k , there is an $N \neq k + 1$ such that the critical benefit-to-cost ratio is minimal. On the left hand side of figure 4.6 this critical population size N^* is plotted as a function of k , and on the right hand side the corresponding minimal benefit-to-cost ratio is plotted as a function of k .

For both conditions, the left figure shows an almost linear connection between k and the minimizing population size N^* . For increasing k , the minimal critical benefit-to-cost ratio increases with increasing slope.

4.3.4. Stationary distribution

The stationary distributions again were calculated as (2.10) using R (R Core Team, 2016).

Figure 4.7 presents the resulting probabilities for varying number of required cooperators k as well as varying population size N and fixed benefit-to-cost ratio b/c .

The larger the number of required cooperators, the less likely are high abun-

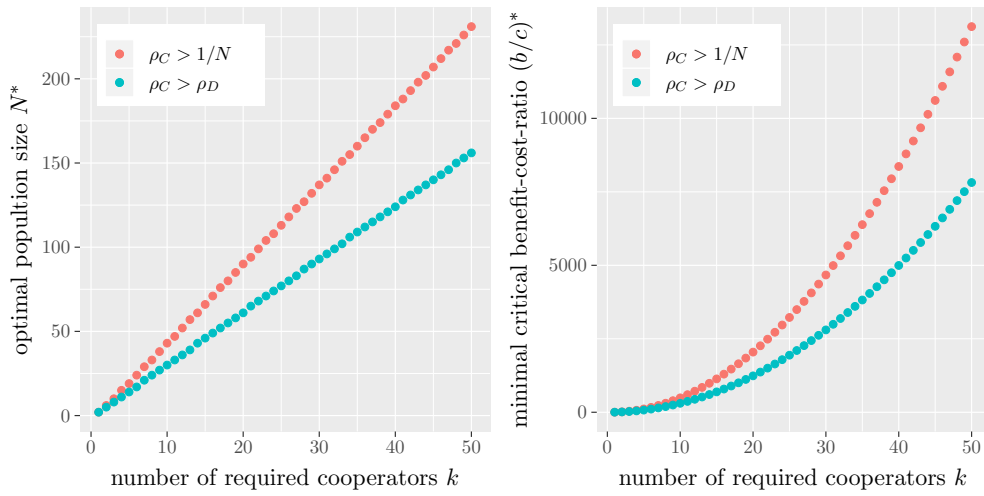


Figure 4.6.: Optimal population size and corresponding minimal critical benefit-to-cost ratio

dances of cooperators and the more likely are low abundances of cooperators. Larger population sizes seem to flatten the distributions shifting more probability mass to intermediate states.

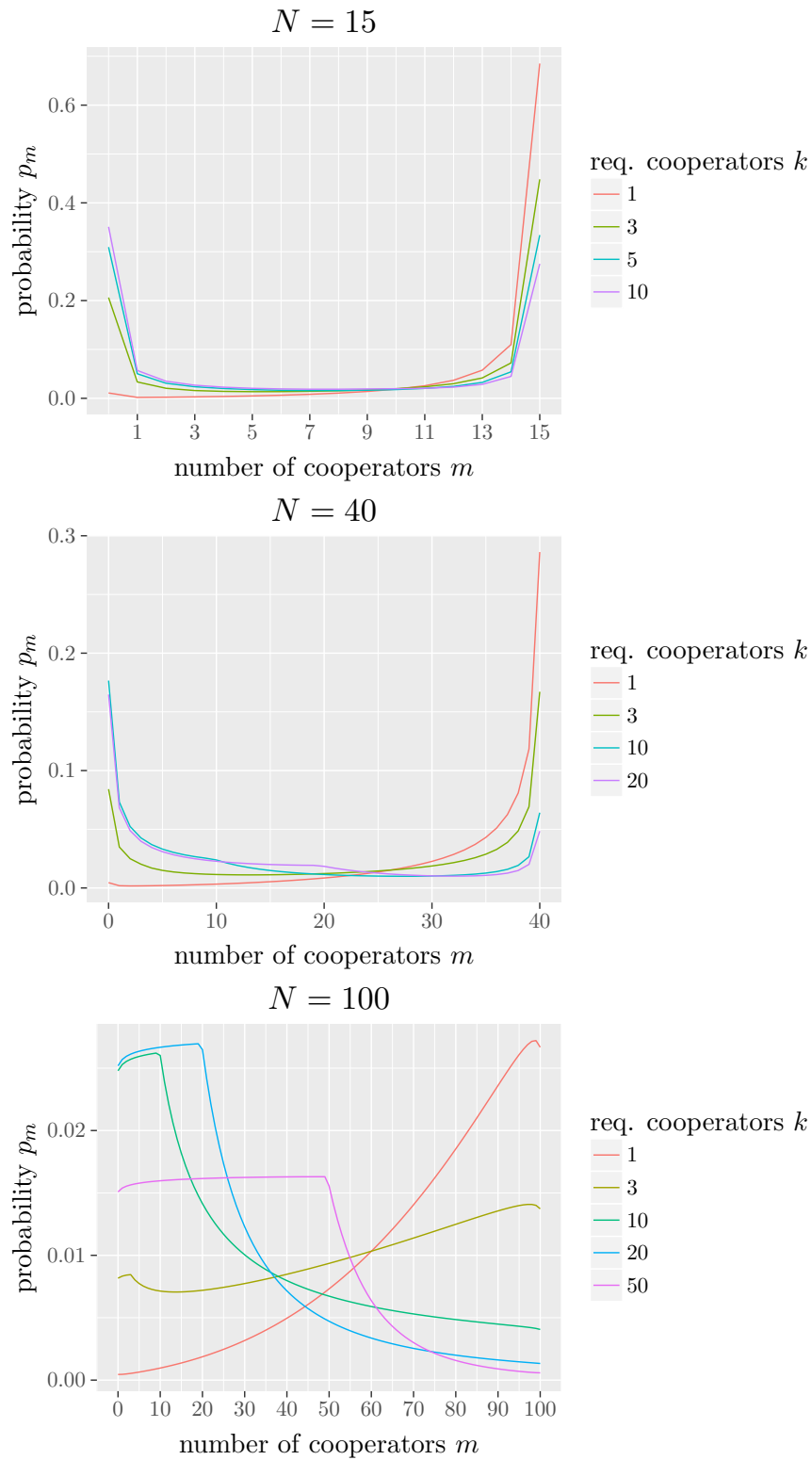


Figure 4.7.: Stationary distributions of the Moran process for parameters $w = 0.1$, $\mu = 0.01$ and $b/c = 50$

5. Discussion and outlook

This thesis introduces a model for studying the evolution of cooperation among unrelated individuals in finite well-mixed populations.

It is aimed at describing natural systems in which a good is created and shared by a group of individuals, whereby the group is formed by sequential recruitment of individuals until the number of cooperators required to produce the good is reached. Then, the good is collectively privatized, hindering further individuals outside the group from receiving a share. As a consequence, only defectors that join the group early enough succeed to free ride on the cooperators' effort, whereby this number of successful defectors varies each time a group is formed.

The results from analyzing the evolutionary consequences of this mechanism are discussed below. To finalize, an outline of possible future projects is presented.

Summary of results

In order to determine the potential of cooperators to invade a population of defectors, the following two questions are addressed:

- (i) When does natural selection favor cooperation?
- (ii) When is the fixation of a cooperator in a population of defectors more likely than the fixation of a defector in a population of cooperators?

Both questions are answered by deriving conditions that depend on general payoffs determined by the number of defectors participating in the so far unspecified game.

In a next step, a public goods game is applied, allowing for rewriting the conditions in terms of the benefit-to-cost ratio of the game. This yields critical values of the ratio that need to be exceeded in order to have cooperators being favored by selection or in order to have a cooperator's fixation probability being larger than the one of a defector. These critical values depend on the population size and on the number of cooperators required for the provision of the collective good.

Critical benefit-to-cost ratios are also derived for the volunteer's dilemma of finite populations by using the conditions derived by Gokhale and Traulsen (2010) and applying a threshold public goods game. In this model, the critical ratios depend on the population size, the group size and, mostly, as well on the threshold, i.e., the number of cooperators needed to produce the public good.

Increasing the number of required cooperators in the waiting-for-volunteers dilemma leads to more stringent conditions for the success of cooperators by raising the critical benefit-to-cost ratios. The same holds for increasing the group size in the volunteer's dilemma, and for increasing its threshold when the first question is addressed. When, however, the second question is addressed, a higher threshold decreases the critical ratio and therefore supports cooperators in case of conditional expression of the cooperative trait. In case of unconditional expression, the threshold exerts no effect on the critical value. Notably, when addressing the first question, the threshold in the volunteer's dilemma is subject to additional restrictions, which makes the conditions harder to fulfill.

A striking qualitative difference between the two models is observed when investigating the influence of the population size on the critical ratios. In the waiting-for-volunteers dilemma, a larger population size impedes the prevailing of cooperators, whereas in the volunteer's dilemma, a larger population size promotes their invasion by reducing the critical benefit-to-cost ratios down to certain lower bounds in the limit of an infinitely large population.

Interestingly, the waiting-for-volunteers dilemma exhibits an optimal population size in the sense that, for a given number of required cooperators, it minimizes the critical benefit-to-cost ratio. Albeit, this is observed in case of unconditional expression only.

The findings are in accord with observations concerning the stationary distributions: an increasing number of required cooperators in the waiting-for-volunteers dilemma and an increasing group size in the volunteer's dilemma reduce the likelihood of states with high abundances of cooperators. Furthermore, in the waiting-for-volunteers dilemma, an increasing population size flattens the distribution making intermediate states more probable, whereas in the volunteer's dilemma, an increasing population size promotes high abundance of cooperators for small group sizes.

Comparing the waiting-for-volunteers dilemma of finite populations to the one of infinite populations (Peña et al., 2016), the following similarity shows. In the waiting-for-volunteers dilemma of infinite populations, the conditions for cooperation to be favored become more stringent as the number of cooperators needed to provide the collective good increases. This finding is qualitatively in accord with the results from the waiting-for-volunteers dilemma of finite populations, as described above.

Outlook

This thesis explores the waiting-for-volunteers dilemma in finite populations by analyzing the fixation probabilities and the stationary distributions. Other quantities suitable to characterize the evolutionary dynamics, are *fixation times*, i.e., the average times it takes to reach fixation starting from certain states of the process (Traulsen and Hauert, 2009). Calculating the fixation times and

exploring how they depend on the population size and the number of required cooperators would be of interest. Furthermore, comparing the results to the ones obtained when investigating fixation times in the volunteer's dilemma, might uncover further qualitative differences between the two models.

In addition, future work could establish a model that combines the group formation processes of the volunteer's dilemma and the waiting-for-volunteers dilemma in the sense that sampling of group members is stopped once a predefined number of cooperators or a predefined maximal group size is reached, whichever occurs first.

Another possibility for future work addresses the integration of the waiting-for-volunteers dilemma of finite populations into infinite populations in the following way. Considering an infinite population, groups of finite size are formed according to binomial sampling. Each group represents a finite population to which one round of the waiting-for-volunteers dilemma is applied. The corresponding expected payoff serves as the payoff obtained by the group in the infinite population. The dynamics in the infinite population can then be modeled by the replicator dynamics.

A. Appendix

A.1. Additional calculations

Statement:

$$k - 1 - N + Nk \sum_{j=k}^N \frac{1}{j^2} > 0 \quad \text{for all } k, N \in \mathbb{N} \text{ with } 1 \leq k < N$$

Proof: It holds

$$k - 1 - N + Nk \sum_{j=k}^N \frac{1}{j^2} > 0 \quad \Leftrightarrow \quad \sum_{j=k}^N \frac{1}{j^2} - \frac{N - k + 1}{Nk} > 0$$

Let $N \in \mathbb{N}$ be fixed. Let $(a_k)_{1 \leq k < N}$ be a finite sequence defined by

$$a_k := \sum_{j=k}^N \frac{1}{j^2} - \frac{N - k + 1}{Nk}.$$

The first and the last elements of the sequence have the following values:

$$\begin{aligned} a_1 &= \sum_{j=1}^N \frac{1}{j^2} - 1 = \sum_{j=2}^N \frac{1}{j^2} > 0 \\ a_{N-1} &= \frac{1}{(N-1)^2} + \frac{1}{N^2} - \frac{2}{N(N-1)} = \frac{1}{N^2(N-1)^2} > 0 \end{aligned}$$

Calculating the difference of two consecutive elements yields

$$\begin{aligned} a_{k+1} - a_k &= \sum_{j=k+1}^N \frac{1}{j^2} - \frac{N - k - 1 + 1}{N(k+1)} - \sum_{j=k}^N \frac{1}{j^2} + \frac{N - k + 1}{Nk} \\ &= -\frac{1}{k^2} - \frac{N - k}{N(k+1)} + \frac{N - k + 1}{Nk} \\ &= -\frac{N(k+1)}{k^2 N(k+1)} - \frac{(N-k)k^2}{N(k+1)k^2} + \frac{(N-k+1)k(k+1)}{Nk^2(k+1)} \\ &= \frac{-Nk - N - k^2 N + k^3 + k^2 N - k^3 + k^2 + Nk - k^2 + k}{k^2 N(k+1)} \\ &= \frac{k - N}{k^2 N(k+1)} < 0 \quad \text{for } 1 \leq k < N. \end{aligned}$$

Thus, since $(a_k)_{1 \leq k < N}$ is a monotonically decreasing sequence with a positive last element, it holds that $a_k > 0$ for all $1 \leq k < N$. \square

A.2. R code

A.2.1. Stationary distribution for volunteer's dilemma

```

1 f_statDistr <- function(N,g,k,w,mu,benefit , cost ){
2   # input parameters:
3   # N = population size
4   # g = group size
5   # k = number of cooperators required for provision of public good
6   # w = intensity of selection
7   # mu = mutation rate
8   # benefit = value of public good
9   # cost = personal cost for production of public good
10
11
12   # densities of number of opposing cooperators
13   # focal cooperator
14   P_H_c <- function(i,m) { if(m==0){return(0)}
15                           else {return(dhyper(i,m-1,N-m,g-1))}}
16   # focal defector
17   P_H_d <- function(i,m) { if(m==N){return(0)}
18                           else {return(dhyper(i,m,N-m-1,g-1))}}
19
20   # payoffs
21   c_pay <- c(rep(-cost,k-2+1),rep(benefit/g-cost,g-(k-2+1)))
22   d_pay <- c(rep(0,k-1+1),rep(benefit/g,g-(k-1+1)))
23
24   # expected payoffs
25   expPayC <- function(m){sum(unlist(
26                               sapply(seq(0,g-1),P_H_c,m=m))*c_pay)}
27   expPayD <- function(m){sum(unlist(
28                               sapply(seq(0,g-1),P_H_d,m=m))*d_pay)}
29
30   # ratio of the exponential fitness functions
31   fitRatio <- function(m) {exp(w*expPayD(m))/exp(w*expPayC(m))}
32
33   # transition probabilities
34   probAsc <- function(m) {
35     (N-m)/N* ((1-mu)*m/(m+(N-m)*fitRatio(m)) +
36              mu*(N-m)*fitRatio(m)/(m+(N-m)*fitRatio(m)))
37   }
38   probDesc <- function(m) {
39     m/N* ((1-mu)*(N-m)*fitRatio(m)/(m+(N-m)*fitRatio(m)) +
40           mu*m/(m+(N-m)*fitRatio(m)))
41   }
42
43   # ratio of  $P(X_{t+1}=m+1|X_t=m)$  and  $P(X_{t+1}=m|X_t=m+1)$ :
44   pAsc <- unlist(sapply(seq(0,N-1),probAsc))
45   pDesc <- unlist(sapply(seq(1,N),probDesc))
46   transRatio <- pAsc/pDesc
47

```

```

48 # calculate sum S
49 S <- sum(cumprod(transRatio))
50
51 # calculate the stationary distribution
52 statDis <- cumprod(transRatio)/(S+1)
53 statDis <- c(1/(S+1),statDis)
54
55 return(statDis)
56 }

```

A.2.2. Stationary distribution for waiting-for-volunteers dilemma

```

1 f_statDistr <- function(N,k,w,mu,benefit , cost){
2 # input parameters:
3 # N = population size
4 # k = number of cooperators required for provision of public good
5 # w = intensity of selection
6 # mu = mutation rate
7 # benefit = value of public good
8 # cost = personal cost for production of public good
9
10
11 # densities of number of defectors playing
12 P_NH <- function(m) {dnhyper(seq(0,N-m)+k,m,N,k)}
13 # payoffs for case m >= k
14 c_pay <- function(m) {benefit/(seq(0,N-m)+k)-cost}
15 d_pay <- function(m) {c(0,benefit/(seq(1,N-m)+k))}
16
17 # expected payoffs
18 expPayC <- function(m){
19   if(m >= k) {k/m*sum(P_NH(m)*c_pay(m))}
20   else(0)
21 }
22 expPayD <- function(m){
23   if (m >= k && m < N) {1/(N-m)*sum(seq(0,N-m)*P_NH(m)*d_pay(m))}
24   else {0}
25 }
26
27 # ratio of the exponential fitness functions
28 fitRatio <- function(m) {exp(w*expPayD(m))/exp(w*expPayC(m))}
29
30 # transition probabilities
31 probAsc <- function(m) {
32   (N-m)/N* ((1-mu)*m/(m+(N-m)*fitRatio(m)) +
33     mu*(N-m)*fitRatio(m)/(m+(N-m)*fitRatio(m)) )
34 }
35 probDesc <- function(m) {
36   m/N* ((1-mu)*(N-m)*fitRatio(m)/(m+(N-m)*fitRatio(m)) +
37     mu*m/(m+(N-m)*fitRatio(m)) )
38 }
39
40 # ratio of P(X_{t+1}=m+1|X_t=m) and P(X_{t+1}=m|X_t=m+1):
41 pAsc <- unlist(apply(seq(0,N-1),probAsc))
42 pDesc <- unlist(apply(seq(1,N),probDesc))

```

```
43  transRatio <- pAsc/pDesc
44
45  # calculate sum S
46  S <- sum(cumprod(transRatio))
47
48  # calculate the stationary distribution
49  statDis <- cumprod(transRatio)/(S+1)
50  statDis <- c(1/(S+1),statDis)
51
52  return(statDis)
53 }
```

Bibliography

- Berryman, A. A., B. Dennis, K. F. Raffa, and N. C. Stenseth (1985). “Evolution of optimal group attack, with particular reference to bark beetles (coleoptera: Scolytidae)”. In: *Ecology* 66.3, pp. 898–903.
- Boza, G. and S. Számadó (2010). “Beneficial laggards: multilevel selection, cooperative polymorphism and division of labour in threshold public good games”. In: *BMC Evolutionary Biology* 10.1, pp. 1–12.
- Byers, J. (1989). “Chemical ecology of bark beetles”. In: *Experientia* 45.3, pp. 271–283.
- Claussen, J. C. and A. Traulsen (2005). “Non-Gaussian fluctuations arising from finite populations: Exact results for the evolutionary Moran process”. In: *Physical Review E* 71. 025101(R).
- Dawes, R. M. (1980). “Social Dilemmas”. In: *Annual Review of Psychology* 31, pp. 169–193.
- Gokhale, C. S. and A. Traulsen (2010). “Evolutionary games in the multiverse”. In: *PNAS* 107.
- Gokhale, C. S. and A. Traulsen (2014). “Evolutionary Multiplayer Games”. In: *Dynamic Games and Application* 4, pp. 468–488.
- Graham, R. L., D. E. Knuth, and O. Patashnik (1994). *Concrete Mathematics - A foundation for computer science*. Addison-Wesley Publishing Company, Inc.
- Hofbauer, J. and K. Sigmund (1998). *Evolutionary Games and Population Dynamics*. Cambridge, UK: Cambridge University Press.
- Isaac, R. M. and J. M. Walker (1988). “Group size effects in public goods provision: The voluntary contributions mechanism”. In: *The Quarterly Journal of Economics* 103.1, pp. 179–199.
- Moran, P. A. P. (1958). “Random processes in genetics”. In: *Mathematical Proceedings of the Cambridge Philosophical Society* 54.1, pp. 60–71.

- Nowak, M. A. (2006a). *Evolutionary dynamics: exploring the equations of life*. Cambridge MA: The Belknap Press of Harvard University Press.
- Nowak, M. A. (2006b). “Five rules for the evolution of cooperation”. In: *Science* 314, pp. 1560–1563.
- Nowak, M. A., A. Sasaki, C. Taylor, and D. Fudenberg (2004). “Emergence of cooperation and evolutionary stability in finite populations”. In: *Nature* 428, pp. 646–650.
- Peña, J., G. Nöldeke, and A. Traulsen (2016). *Waiting for contributors in a volunteer’s dilemma*. (in preparation).
- Powers, S. T. and L. Lehmann (2016). “When is bigger better? The effects of group size on the evolution of helping behaviours”. In: *Biological Reviews*.
- Queller, D. C., E. Ponte, S. Bozzaro, and J. E. Strassmann (2003). “Single-gene greenbeard effects in the social amoeba *Dictyostelium discoideum*”. In: *Science* 299, pp. 105–106.
- R Core Team (2016). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>.
- Raffa, K. F. (2001). “Mixed messages across multiple trophic levels: the ecology of bark beetle chemical communication systems”. In: *Chemoecology* 11.2, pp. 49–65.
- Scott, M. P. (1998). “The ecology and behavior of burying beetles”. In: *Annual Review of Entomology* 43.1, pp. 595–618.
- Szathmáry, E. and J. Maynard Smith (1995). “The major evolutionary transitions”. In: *Nature* 374, pp. 227–232.
- Traulsen, A. and C. Hauert (2009). “Stochastic evolutionary game dynamics”. In: *Reviews of Nonlinear Dynamics and Complexity, Vol II*. Wiley-VCH.
- Traulsen, A., N. Shresh, and M. A. Nowak (2008). “Analytical results for individual and group selection of any intensity”. In: *Bulletin of Mathematical Biology* 70, pp. 1410–1424.

Eidesstattliche Erklärung

Hiermit versichere ich an Eides statt, die vorliegende Arbeit selbstständig und nur unter Benutzung der angegebenen Hilfsmittel angefertigt zu haben.

Lübeck, den 18. September 2016

Danksagung

Ich bedanke mich herzlich bei Herrn Prof. Dr. Arne Traulsen für die Überlassung des Themas, die freundliche Aufnahme am Max-Planck-Institut für Evolutionsbiologie in Plön und die gute Betreuung.

Herrn Prof. Dr. Karsten Keller danke ich für die Bereitschaft, das Zweitgutachten zu übernehmen.

Außerdem danke ich Herrn Dr. Jorge Peña für die tatkräftige Unterstützung bei der Umsetzung des Projektes.

Weiterhin möchte ich mich bei allen Mitgliedern der Abteilung Evolutionstheorie des MPI Plön für die freundliche Atmosphäre und die interessanten Einblicke in das Arbeitsleben von Wissenschaftlern bedanken.