Theoretical Population Biology 104 (2015) 17–25

Contents lists available at ScienceDirect

Theoretical Population Biology

journal homepage: www.elsevier.com/locate/tpb

The evolution of generalized reciprocity in social interaction networks

Bernhard Voelkl *

Department of Zoology, University of Oxford, South Parks Road OX1 3PS, United Kingdom
Institute for Ecology and Evolution, Ethologische Station Hasli, Wohlenstrasse 50a, CH-3032 Hinterkappelen, United Kingdom

ARTICLE INFO

Article history:
Received 11 September 2014
Available online 14 July 2015

Keywords:
Co-operation
Reciprocation
Evolution on graphs
Social networks

ABSTRACT

Generalized reciprocity has been proposed as a mechanism for enabling continued cooperation between unrelated individuals. It can be described by the simple rule "help somebody if you received help from someone", and as it does not require individual recognition, complex cognition or extended memory capacities, it has the potential to explain cooperation in a large number of organisms. In a panmictic population this mechanism is vulnerable to defection by individuals who readily accept help but do not help themselves. Here, I investigate to what extent the limitation of social interactions to a social neighborhood can lead to conditions that favor generalized reciprocity in the absence of population structuring. It can be shown that cooperation is likely to evolve if one assumes certain sparse interaction graphs, if strategies are discrete, and if spontaneous helping and reciprocating are independently inherited.

1. Introduction

Animal cooperation between unrelated individuals has puzzled biologists for a long time as its existence seems to contravene the basic notion of evolutionary biology that natural selection favors genes that promote only their own well-being. It has been suggested that cooperation between unrelated individuals can be established by direct reciprocity, where individuals take turns in helping each other (Trivers, 1971; Axelrod and Hamilton, 1981). Reciprocation is a reactive strategy where individuals condition their behavior on the previous behavior of their interaction partner. The decision to cooperate is based on the expected outcome of future interactions, which is inferred from past experience (Rutte and Taborsky, 2007). Alexander (1987) proposed that large-scale human cooperation could be sustained by a network of indirect reciprocation, where individual A helps individual B, while B is not reciprocating by helping A but individual C instead, etc. -until, at one point, this chain of reciprocation returns to individual A. Under the headings "up-stream tit-for-tat" this idea was formalized by Boyd and Richerson (1989) who could show that reciprocation can evolve if reciprocators are sufficiently common. Introducing the term "up-stream indirect reciprocity", Nowak and Roch (2007) showed that this kind of indirect reciprocity is unlikely to evolve unless it is coupled with some mechanism that ensures assortment of reciprocating individuals, as it is the case in spatial or network models with local reproduction or reputation-based reciprocity.

However, more recently it was suggested that, even in the absence of phenotype assortment, generalized reciprocity alone can enable cooperation if individuals of a population do not interact randomly but only with a small subset of the population (Pfeiffer et al., 2005; Rankin and Taborsky, 2009; van Doorn and Taborsky, 2012). In a recent study van Doorn and Taborsky (2012) presented a simple model for generalized reciprocity, where individuals occupy vertices on a sparse graph and interact with neighboring individuals. The authors assumed two fixed strategies, which they dubbed 'altruists' and 'defectors'. Altruists spontaneously help other individuals and, upon receiving help, also help someone for exactly one time, while defectors never help others. They could show that in this case, the average payoffs for individuals of both strategy types are frequency dependent: if the proportion of altruists exceeds a certain threshold value, then altruists will receive higher payoffs and gain higher fitness, while below this threshold defectors will gain higher payoffs. The threshold value depends not only on the cost–benefit ratio of helping, but also on the structure of the interaction graph, as structuring can ensure that reciprocators are on average more often receivers of help than defecting non-reciprocators. Yet, this model makes one stringent assumption which limits its scope and applicability substantially. By assuming that only individuals who reciprocate acts of helping are those who can also spontaneously initiate help, this model implicitly assumes perfect genetic linkage

* Correspondence to: Department of Zoology, University of Oxford, South Parks Road OX1 3PS, United Kingdom.
E-mail address: bernhard.voelkl@zoo.ox.ac.uk.

http://dx.doi.org/10.1016/j.tpb.2015.06.005
0040-5809/

for two different underlying behaviors. This assumptions seem unwarranted for behavioral phenotypes of biological systems. In the following I will, therefore, provide a generalizations of this model by presenting a discrete model that does not assume genetic linkage between strategies.

2. Population model with two phenotypes

2.1. Population

I assume a finite panmictic population of individuals who settle into a social structure with well-defined neighbor relations. Neighboring individuals can engage in repeated social interactions which affect their fitness (Nunney, 1985). The social neighborhood structure can be represented as a simple undirected graph, where vertices correspond to individuals and edges link potential interaction partners (Lieberman et al., 2005; Taylor et al., 2007). Individuals do not change their position on the graph during their life-time, though the population is panmictic as newly born individuals are place on the graph randomly, independent of the position of their parents. The social interaction of interest is helping, which is defined broadly as a dyadic interaction where one individual performs a behavior at cost c in terms of lifetime fitness, which brings along some benefit b for the other individual, where the benefit is always larger than the cost.

2.2. Strategies

I envisage two discrete and fixed actions for helping: an individual can either spontaneously help another individual in its direct neighborhood (phenotype A), or it cannot (phenotype D). Upon receiving help, an individual of type A will reciprocate by helping one randomly selected individual from its neighborhood for exactly one time. Individuals of type D never reciprocate upon receiving help. A single individual adheres to the same actions for spontaneous and conditional helping over its whole lifetime. Note that strategies A and D are equivalent to the strategies "altruist" and "defector" in the model presented by van Doorn and Taborsky (2012). For better comparability I keep the same notation (A and D), though I do not refer to the strategy A as "altruist", because the strategy does not comply with the original meaning of the term. It is assumed that spontaneous initiation of helping is a rare event. Once, it happens that an A type individual spontaneously helps a randomly chosen individual of its neighborhood, this can lead to a "chain reaction" of conditional reciprocation, which terminates as soon as help is directed towards a non-reciprocating D-type individual (Fig. 1). The time from spontaneous initiation to the termination of the chain of reciprocation is called one round. As initiation is considered to be rare, no further initiation events can occur within one round. At the end of the round, payoffs arising from all helping interactions are evaluated and added to the individuals' payoff-values.

2.3. Results for the cycle

The cycle is a simple, symmetric graph where each vertex has exactly two neighbors. In a population of size N where the two strategy phenotypes A and D occur at frequencies a/N and d/N respectively, we can evaluate the expected payoff for a single individual of each strategy type. Assuming that all individuals make their decisions independently, the likelihood that within a given time period an individual will spontaneously help is dependent on the proportion of A individuals in the population. Once, an A individual has spontaneously helped someone and, thereby, initiated a random walk of reciprocal help, the random walk will stop no sooner as it hits a D-type individual. Hence, the expected length of such a random walk will depend on the proportion of D individuals in the population. Each time help is given to a D-type individual, this individual receives a benefit of b at no cost. As all D-individuals are equally likely to be on the receiving end of help, the expected payoff for any D-type individual is, therefore, indirect proportional to the number of D-individuals in the population and dependent on the proportion of spontaneous initiators (A-type individuals):

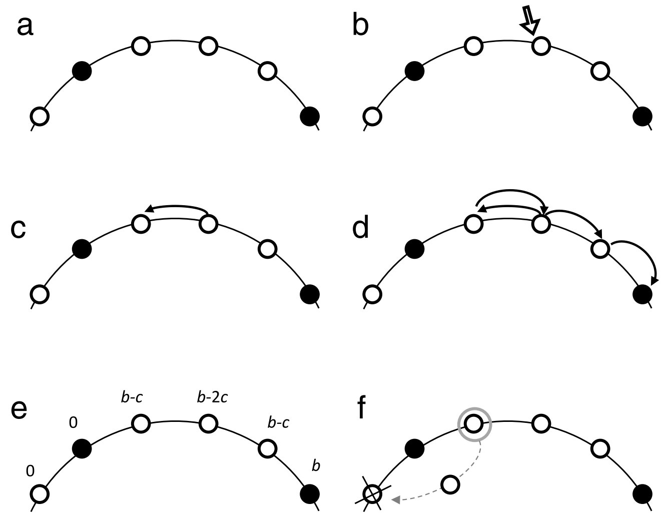

Fig. 1. Scheme of one round of the game. Reciprocating individuals (open circles) and non-reciprocating individuals (filled circles) are randomly placed on a cycle graph (a). One individual is randomly chosen as initiator (b). The initiator randomly chooses one neighbor and helps it for one time (c). If the recipient of help is a reciprocator, it will itself randomly chose one of its neighbors and help this neighbor for one time. This process is repeated until help is directed towards a non-reciprocator (d). Payoffs of all individuals are evaluated and added to their fitness value (e). One individual is randomly selected for reproduction, proportional to its fitness, and the offspring replaces a randomly chosen individual in the population (f).

$$\Pi_D = \frac{a}{N}\frac{1}{d}b = \frac{1}{N}\frac{ab}{d}. \tag{1}$$

Spontaneous helping by an A-type individual is associated with a cost of $-c$ for A. Thereafter, every time an A-type receives help it will reciprocate, earning a net benefit of $b - c$. Consequently, evaluating the expected payoff for an A-type individual requires considering the expected length of the chain of conditional reciprocation. For the cycle the chain of reciprocal helping can be modeled as a symmetric random walk in one dimension on a segment of the cycle consisting only of A-type individuals and enclosed on both sides by D-type individuals. For a symmetric random walk in one dimension with boundaries 0 and $j+1$ starting at u the expected length of the walk is given by $u(j+1-u)$, where j is the length of the segment (i.e. the number of A-type individuals aligned next to each other). It can be shown that for a segment on the circle consisting of j A-type individuals the expected length of the random walk started by a randomly chosen A individual is given by

$$\frac{(j+1)(j+2)}{6} - 1. \tag{2}$$

If we denote with φ_j the probability of hitting a segment of j A-type individuals by randomly selecting an A-type individual, we get the expected payoff for an A-type individual as

$$\Pi_A = \frac{1}{a}\frac{a}{N}\left(-c + \sum_{j=1}^{a}\left(\frac{(j+1)(j+2)}{6} - 1\right)\varphi_j(b-c)\right). \tag{3}$$