

Cultural Transmission Can Explain the Evolution of Cooperative Behavior

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Introduction

Cooperative behavior can harm the individual's fitness and increase the fitness of its competitor (Axelrod and Hamilton, 1981). Yet, cooperative behavior occurs in many non-human animals (Dugatkin, 1997), for example rats (Rice and Gainer, 1962) and birds (Krams et al., 2008). Therefore, the evolution of cooperative behavior is an important open question in evolutionary biology.

Cultural evolution is an evolutionary theory of social change. Culture has significant impact on the behavior of humans (Ihara and Feldman, 2004; Jeong et al., 2018) as well as non-human animals (Bonner, 2018). Under the view of cultural evolution, an individual can acquire its behavior from another individual in its social group through learning or other modes of cultural transmission (Richerson and Boyd, 2008). Here we attempt to determine to what extent cultural transmission can explain the evolution of cooperative behavior.

Theories for evolution of cooperation

Three major theories have been proposed to explain the evolution of cooperative behavior.

Kin selection theory suggests that natural selection can favor cooperative behavior between kin. The importance of relatedness to the evolution of cooperation and altruism was shown by Hamilton (1964). According to Hamilton, kin selection causes allele to increase in frequency when the reproductive cost to the actor, c , is less than the benefit to the recipient, b , times the genetic relatedness between the recipient and the actor, r . This is also known as Hamilton's Rule:

$$c < b \cdot r. \quad (1)$$

There is an ongoing debate about to what extent kin selection explains evolution of cooperation and altruism. It has been suggested that kin selection to explain the cooperative behavior of eusocial insects like the honey bee. The most significant argument against kin selection is that cooperation can evolve with zero relatedness (Wilson, 2005). This makes Hamilton's rule incomplete according to Wilson (2005). Foster et al. (2006) reject this claim. They argue that altruism without relatedness can not evolve. They refer us to Hamilton who claimed that relatedness can arise without recent common ancestry. Wilson (2005) also criticizes kin selection on the grounds that environmental or ecological factors probably be more important than relatedness in determining social actions. On the other hand, Foster et al. (2006) argue that kin selection does not ignore ecology. Hamilton's rule shows that environmental factors causing a high benefit-to-cost ratio will favor cooperation.

Reciprocity suggests repeating interactions or individual recognition as key factors for explaining the evolution of cooperation. In *direct reciprocity* there are a repeated encounters between the same two individuals. In every encounter, each player has a choice between cooperation and defection. If I cooperate now, you may cooperate later. Hence, it may pay off to cooperate. This game-theoretic framework is known as the repeated Prisoner's Dilemma. Direct reciprocity can only lead to the evolution of cooperation if the cost is less than the benefit b times the probability for another encounter between the same two individuals, w ,

$$c < b \cdot w. \quad (2)$$

Direct reciprocity assumes that both players are in a position to cooperate. Direct reciprocity can not explain cooperation in asymmetric interactions. In humans, such interactions happen often, for example humans often donate money.

Indirect reciprocity has been suggested to explain this behavior. Nowak (2006) claims that direct reciprocity is like a barter economy based on the immediate exchange of goods, while indirect reciprocity resembles the invention of money. The money that "fuels the engines" of indirect reciprocity is reputation. However, Reciprocity assume repeating interactions and therefore, has difficulty explaining evolution of cooperation if the no repeating interactions occurs.

Group selection theory posits that cooperation is favored because of the advantage to the whole group, if selection acts at the group level in addition to the individual level. A common model for group selection work as is: the population is divided into groups. In each groups there are cooperators, which help to other group members and defectors which do not help. Individuals reproduce proportional to their fitness. Offspring are added to the same group. If a group reaches a certain size it can split to two groups. A group that grow faster will split more often. Groups of cooperators are growing faster than group of defectors. Therefore, cooperation can evolve in this model when the cost c is less than the benefit b times the ratio between the the number of groups m and the sum of m and the maximum group size n ,

$$c < b \cdot \frac{m}{m + n}. \quad (3)$$

Group selection was criticized by biologists advocate gene-centered view of evolution. Group selection has been criticized due to the fact that the trait like cooperation evolves in the total population. According to natural selection, if cooperation took over the population it must have better fitness. However, in group selection the fitness of cooperator in the individual level is lower. The fact that a trait with a lower fitness took over the population is a contradiction. Eldakar and Wilson (2011) reject this argument. They believe that this argument is a tautology and does not qualify as an argument against group selection. The distinction between individual and group selection requires a comparison of fitness differentials within and among groups in a multi group population. When a trait is evolve by group selection, despite the fact that it has lower fitness within the group, it has a better fit, all thing considered.

All the above theories assume that cooperation is genetically determined. This raises the question, is it possible that cooperation is determined by non-genetic factors? Recent work by Lewin-Epstein et al. (2017) sheds some light on this question. Lewin-Epstein et al. (2017) have hypothesised that microbes that manipulate their hosts to act altruistically can be favored by selection, and may play a role in the widespread occurrence of cooperative behavior. Indeed, it has been shown that microbes can mediate behavioral changes in their hosts (Poulin, 2010; Dobson, 1988). Therefore, natural selection on microbes may favor manipulation of the host so that it cooperates with others. Microbes can be transmitted *horizontally* from one host to another during host interactions. Following horizontal transfer, the recipient host may carry microbes that are closely related to the microbes of the donor host, even when the two hosts are (genetically) unrelated (Lewin-Epstein et al., 2017). Microbes can also transfer vertically, from parent to offspring. As a result, a microbe that induces its host to cooperate with another host and thereby increases the other host fitness will increase the vertical transmission of the microbes of the receiving individual. Kin selection among microbes could therefore favor microbes that induce cooperative behavior in their hosts, thereby increasing the transmission of their microbial kin.

Cultural evolution of cooperation

Lewin-Epstein et al. (2017) have demonstrated that *non-vertical transmission* can help to explain the evolution of cooperative behavior. Non-vertical transmission could be either a horizontal or oblique. Horizontal transmission occurs between individuals from the same generation. Oblique transmission occurs from an adult to an offspring. Evolution under either of these transmission models is can be be more rapid than under pure vertical transmission (Ram et al., 2018).

Here we suggest a model in which behavioral changes are mediated by cultural transmission that can occur during social interaction. For example, if an individual interacts with a cooperative individual, it might learn that cooperation is a positive behavior and will cooperate in the future. Surprisingly, some of the analysis made by Lewin-Epstein et al. (2017) can be applied to cultural transmission, because cultural transmission is mathematically akin to transmission of infectious diseases (Cavalli-Sforza and Feldman, 1981).

Here, we hypothesize that non-vertical cultural transmission can explain the evolution of cooperation. We are develop cultural evolution models that include both vertical and non-vertical transmission of cooperation and investigate these models using both mathematical analysis and simulations.

Models and Methods

First, we focus on the evolution of cooperation in a fully mixed population where cooperation is modeled using the prisoner's dilemma.

Consider a very large population whose members are characterized by their phenotype ϕ , which can be of two types, $\phi = A$ for cooperators or $\phi = B$ for defectors, with corresponding fitness values w_A and w_B , which depend on the frequency of the phenotypes (see below). An offspring inherits its phenotype from its parent via vertical transmission with probability v or from a random individual in the parental population via oblique transmission with probability $(1 - v)$. Following Ram et al. (2018), given that the parent phenotype is ϕ and assuming uni-parental inheritance, the conditional probability that the phenotype ϕ' of the offspring is A is

$$P(\phi' = A \mid \phi) = \begin{cases} v + (1 - v)p, & \text{if } \phi = A \\ (1 - v)p, & \text{if } \phi = B \end{cases} \quad (4)$$

where $p = P(\phi = A)$ is the frequency of A among all adults in the parental generation.

Not all adults become parents due to natural selection, and we denote the frequency of phenotype A among parents with \tilde{p} . Therefore, the frequency \hat{p} of phenotype A among juveniles (after selection and vertical and oblique transmission) is

$$\begin{aligned} \hat{p} &= \tilde{p}[v + (1 - v)p] + (1 - \tilde{p})[(1 - v)p] \\ &= v\tilde{p} + (1 - v)p. \end{aligned} \quad (5)$$

Individuals interact in a social interaction modeled as a prisoner's dilemma. Specifically, individuals interact in pairs, cooperators pay a fitness cost $0 < c < 1$, and their partner gains a fitness benefit b , where we assume $b > c$. The following payoff matrix shows the fitness of an individual with phenotype ϕ_1 when interacting with a partner with phenotype ϕ_2 ($b > c > 0$):

Social interactions occur randomly. So, two individuals with phenotype A interact with probability \hat{p}^2 , two individuals with phenotype B interact with probability $(1 - \hat{p})^2$, and two individuals with different phenotypes interact with probability $2\hat{p}(1 - \hat{p})$.

$$\begin{array}{ccc}
& \phi_2 = A & \phi_2 = B \\
\phi_1 = A & b - c & -c \\
\phi_1 = B & b & 0
\end{array}$$

Horizontal cultural transmission occurs between peers. It may occur between social partners with probability α , or between a random pair with probability $1 - \alpha$ (see **Figure 1**). Horizontal transmission is not always successful, as one peer may reject the other's phenotype. The probability for successful transmission of phenotypes A and B are T_A and T_B , respectively.

Table 1 contains the probability of first interactor to be A following interaction by interaction type. Therefore, the frequency p' of phenotype A among adults in the next generation, after horizontal transmission, is

$$\begin{aligned}
p' = & \hat{p}^2[\alpha + (1 - \alpha)(\hat{p} + (1 - \hat{p})(1 - T_B))] \\
& + \hat{p}(1 - \hat{p})[\alpha(1 - T_B) + (1 - \alpha)(\hat{p} + (1 - \hat{p})(1 - T_B))] \\
& + (1 - \hat{p})\hat{p}[\alpha T_A + (1 - \alpha)\hat{p}T_A] \\
& + (1 - \hat{p})^2[(1 - \alpha)\hat{p}T_A],
\end{aligned} \tag{6}$$

which can be simplified into

$$p' = \hat{p}^2(T_B - T_A) + \hat{p}(1 + T_A - T_B). \tag{7}$$

The frequency of A among parents follows a similar dynamic, but also includes the effect of natural selection, and is therefore

$$\begin{aligned}
\bar{w}p' = & \hat{p}^2(1 + b - c)[\alpha + (1 - \alpha)(\hat{p} + (1 - \hat{p})(1 - T_B))] \\
& + \hat{p}(1 - \hat{p})(1 - c)[\alpha(1 - T_B) + (1 - \alpha)(\hat{p} + (1 - \hat{p})(1 - T_B))] \\
& + (1 - \hat{p})\hat{p}(1 + b)[\alpha T_A + (1 - \alpha)\hat{p}T_A] \\
& + (1 - \hat{p})^2[(1 - \alpha)\hat{p}T_A],
\end{aligned} \tag{8}$$

where fitness values are taken from Table 1, and

$$\bar{w} = \hat{p}w_A + (1 - \hat{p})w_B = 1 + \hat{p}(b - c) \tag{9}$$

is the population mean fitness. Eq 8 can be simplified to

$$\begin{aligned}
\bar{w}p' = & \hat{p}^2(1 + b - c)(1 - (1 - \hat{p})(1 - \alpha)T_B) \\
& + \hat{p}(1 - \hat{p})(1 - c)(\hat{p}(1 - \alpha)T_B + 1 - T_B) \\
& + (1 - \hat{p})\hat{p}(1 + b)(\hat{p}(1 - \alpha) + \alpha)T_A \\
& + (1 - \hat{p})^2\hat{p}(1 - \alpha)T_A.
\end{aligned} \tag{10}$$

Interaction Type	Frequency	Fitness	Probability of first interactor to be A following interaction	
			Horizontal transmission from partner, probability α	Horizontal transmission from population, probability $1 - \alpha$
AxA	\hat{p}^2	$1 + b - c$	1	$\hat{p} + (1 - \hat{p})(1 - T_B)$
AxB	$\hat{p}(1 - \hat{p})$	$1 - c$	$1 - T_B$	$\hat{p} + (1 - \hat{p})(1 - T_B)$
BxA	$\hat{p}(1 - \hat{p})$	$1 + b$	T_A	$\hat{p}T_A$
BxB	$(1 - \hat{p})^2$	1	0	$\hat{p}T_A$

Table 1: Fitness and probability of first interactor to be A following interaction by interaction type

Results

We start by inspecting specific cases, for which we can derive general results. Afterwards, we use numerical simulation to analyze more complex cases.

Without Oblique Transmission

With only vertical and horizontal transmission, i.e. $\nu = 1$, eq. 5 becomes $\hat{p} = \tilde{p}$, and eq. 10 for the change in frequency p' of phenotype A among parents can be written as

$$\begin{aligned}\bar{w}\tilde{p}' &= \tilde{p}^2(1+b-c)[1-(1-\tilde{p})(1-\alpha)T_B] \\ &\quad + \tilde{p}(1-\tilde{p})(1-c)[\tilde{p}(1-\alpha)T_B + 1 - T_B] \\ &\quad + \tilde{p}(1-\tilde{p})(1+b)[\tilde{p}(1-\alpha) + \alpha]T_A \\ &\quad + (1-\tilde{p})^2\tilde{p}(1-\alpha)T_A\end{aligned}\tag{11}$$

We find the following result and corollaries.

Result 1: Vertical and horizontal transmission of cooperation. If

$$c \cdot (1 - T_B) < b \cdot \alpha T_A + (T_A - T_B)[1 + b\tilde{p}(1 - \alpha)],\tag{12}$$

then $\tilde{p}' > \tilde{p}$, and the frequency of the cooperator phenotype A among parents increases every generation.

Corollary 1.1: Symmetric horizontal transmission. If $T = T_A = T_B$, then

$$c < b \cdot \frac{\alpha T}{1 - T},\tag{13}$$

which can be seen as a cultural version of *Hamilton's rule* (eq. 1), where $r_H = \alpha T / (1 - T)$ can be thought of as *horizontal relatedness*. Therefore, if the cost c is less than the benefit b times the horizontal relatedness r_H , then cooperation will take over of the population (see **Figure 2a**).

Corollary 1.2: Complete correlation between transmission and cooperation.

In this case $\alpha = 1$, and horizontal transmission can only occur as a result of cooperative interactions. Therefore, eq. 12, which determines the conditions for evolution of cooperation, becomes

$$c \cdot (1 - T_B) < b \cdot T_A + (T_A - T_B).\tag{14}$$

This is equivalent to a result by Lewin-Epstein et al. (2017, eq. 1).

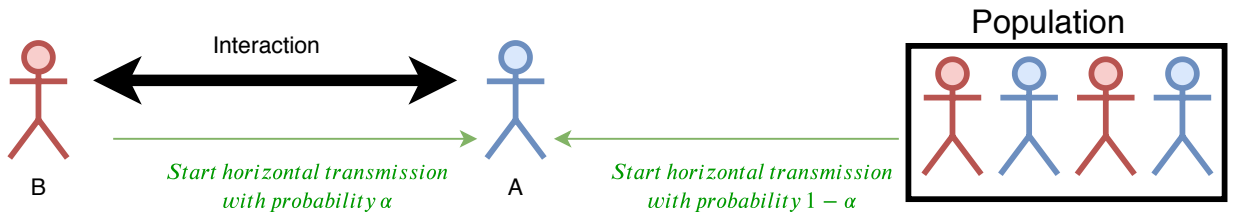


Figure 1: **Cultural horizontal transmission.** Transmission occurs between interaction partners with probability α (left) or between two random peers with probability $1 - \alpha$.

Eq. 14 can be written as

$$1 - (1 - T_B)(1 - c) < T_A \cdot (1 + b), \quad (15)$$

which provides an interesting interpretation for the success of cooperation. Consider an interaction between two individuals: a cooperator and a defector. $(1 - T_B)(1 - c)$ is the probability that the cooperator remains cooperative and also reproduces. Therefore, $1 - (1 - T_B)(1 - c)$ is the probability that either the cooperator becomes a defector, *or* that it fails to reproduce. This is the effective cost for cooperation from this interaction. $T_A \cdot (1 + b)$ is the probability that the defector becomes cooperative and reproduces. This is the effective benefit for cooperation from this interaction. So, eq. 15 means that cooperation can evolve if effective cost is less than the effective benefit.

Corollary 1.3: No correlation between transmission and cooperation.

In this case $\alpha = 0$, and horizontal transmission is entirely independent from cooperative interactions. Then, eq. 12 becomes

$$c \cdot (1 - T_B) < b \cdot \tilde{p} (T_A - T_B) + (T_A - T_B). \quad (16)$$

Therefore, because all the parameters are all positive, cooperation cannot take over the population (and furthermore will become extinct) if cooperators doesn't have a horizontal transmission bias, i.e. if $T_A \leq T_B$. When such a bias does exist, $T_A > T_B$, then cooperation will evolve if $\tilde{p} > \tilde{p}^*$, where (see also **Figure 2b**)

$$\tilde{p}^* = \frac{c}{b} \cdot \frac{1 - T_B}{T_A - T_B} - \frac{1}{b}. \quad (17)$$

A sufficient condition for evolution of cooperation is that $\tilde{p}^* < 0$, which occurs if

$$c < \frac{T_A - T_B}{1 - T_B}. \quad (18)$$

Without Vertical Transmission

With only oblique and horizontal transmission, i.e. $v = 0$, eq. 5 becomes $\hat{p} = p$ and eq. 7 becomes

$$p' = p^2(T_B - T_A) + p(1 + T_A - T_B). \quad (19)$$

We find the following results.

Result 2: Oblique and horizontal transmission of cooperation. If there is a horizontal transmission bias in favor of cooperation,

$$T_A > T_B, \quad (20)$$

then $p' > p$, and the frequency of the cooperator phenotype among adults increases every generation. Therefore, cooperation will evolve if the cooperator phenotype has a horizontal transmission bias (see **Figure 2c**).

With Vertical and Oblique Transmission

In this case $0 < v < 1$, and the equation system is more complex. Therefore, we focus on local, rather than global, stability.

To proceed, we note that eq. 5 can give \hat{p}' as a function of both p' and \tilde{p}' , eq. 7 gives p' as a function of \hat{p} , and eq. 10 gives \tilde{p}' as a function of \hat{p} . Combining these equations, we find an equation for \hat{p}' as

a function of \hat{p} . We then determine the equilibria of this equation, that is, solutions for $\hat{p}' = \hat{p}$, and their stability.

We start with the simpler case of symmetric horizontal transmission, $T = T_A = T_B$. We apply eqs. 5, 7, and 10 to define $f(\hat{p})$ as

$$f(\hat{p}) = \bar{w}(\hat{p}' - \hat{p}) = \hat{p}(1 - \hat{p})[\alpha bvT - cv(1 - T)]. \quad (21)$$

The equilibria \hat{p}^* are solutions to $f(\hat{p}^*) = 0$, or $\hat{p}^{*'} = \hat{p}^*$. It is easy to verify that fixation of either phenotype is an equilibrium, that is,

$$\hat{p}_0^* = 0, \hat{p}_1^* = 1. \quad (22)$$

An equilibrium \hat{p}^* is locally stable when the derivative of $f(\hat{p})$ at \hat{p}^* is negative, $f'(\hat{p}^*) < 0$. Since the derivative is

$$f'(\hat{p}) = (1 - 2\hat{p})[\alpha bvT - cv(1 - T)], \quad (23)$$

then the condition for local stability of \hat{p}_1^* is

$$f'(1) = -\alpha bvT + cv(1 - T) < 0, \quad (24)$$

which gives us the following result.

Result 3: Oblique and vertical transmission with symmetric horizontal transmission. If horizontal transmission is symmetric, $T = T_A = T_B$, and if

$$c < b \cdot \frac{\alpha T}{1 - T}, \quad (25)$$

then fixation of the cooperator phenotype A is locally stable. This is the same condition we found in Corollary 1.1, Eq. 13.

We now turn to the general case where $T_A \neq T_B$. We have

$$f(\hat{p}) = \bar{w}(\hat{p}' - \hat{p}) = \beta_1 \hat{p}^3 + \beta_2 \hat{p}^2 + \beta_3 \hat{p}, \quad (26)$$

where

$$\begin{aligned} \beta_1 &= [c(1 - v) - b(1 - \alpha v)](T_A - T_B) \\ \beta_2 &= -\beta_1 - \beta_3 \\ \beta_3 &= \alpha bvT_A - cv(1 - T_B) + (T_A - T_B). \end{aligned} \quad (27)$$

Since $f(\hat{p})$ is a cubic polynomial, three equilibria exist. We already know that $\hat{p}_0^* = 0$ and $\hat{p}_1^* = 1$ are equilibria. By solving $f(\hat{p})/[\hat{p}(1 - \hat{p})] = \beta_3 - \beta_1 \hat{p} = 0$ we can find the third equilibrium,

$$\hat{p}_2^* = \frac{\beta_3}{\beta_1}. \quad (28)$$

Note that the sign of the cubic $f(\hat{p})$ at positive (negative) infinity is equal (inverse) to the sign of β_1 . If $T_A > T_B$, then

$$\beta_1 < [c(1 - \alpha v) - b(1 - \alpha v)](T_A - T_B) = (1 - \alpha v)(c - b)(T_A - T_B) < 0, \quad (29)$$

since $c < b$, and $1 > \alpha v$. So the sign of the cubic at positive and negative infinity is negative and positive, respectively. First, if $\beta_3 < \beta_1$ then $0 < \hat{p}_2^* < 1$ and therefore $f'(0) < 0$ and $f'(1) < 0$, that is, both fixations are locally stable and \hat{p}_2^* separates the domains of attraction. Second, if $\beta_1 < \beta_3 < 0$ then $1 < \hat{p}_2^*$ and therefore $f'(0) < 0$ and $f'(1) > 0$, that is, fixation of the defector phenotype B is the

only locally stable legitimate (i.e. between 0 and 1) equilibrium. Third, if $0 < \beta_3$ then $\hat{p}_2^* < 0$ and therefore $f'(0) > 0$ and $f'(1) < 0$, that is, fixation of the cooperator phenotype A is the only locally stable legitimate equilibrium.

Similarly, if $T_B > T_A$, then

$$\beta_1 > [c(1 - \alpha v) - b(1 - \alpha v)](T_A - T_B) = (1 - \alpha v)(c - b)(T_A - T_B) > 0, \quad (30)$$

since $c < b$, and $1 > \alpha v$. So the sign of the cubic at positive and negative infinity is positive and negative, respectively. First, if $\beta_3 < 0$ then $\hat{p}_2^* < 0$ and therefore $f'(0) < 0$ and $f'(1) > 0$, that is, fixation of the defector phenotype $A = B$ is the only locally stable legitimate equilibrium. Second, if $0 < \beta_3 < \beta_1$ then $0 < \hat{p}_2^* < 1$ and therefore $f'(0) > 0$ and $f'(1) > 0$, that is, both fixations are locally unstable and \hat{p}_2^* is a stable polymorphic equilibrium. Third, if $\beta_1 < \beta_3$ then $\hat{p}_2^* > 1$ and therefore $f'(0) > 0$ and $f'(1) < 0$, that is, fixation of the cooperator phenotype A is the only locally stable legitimate equilibrium.

The following result summarizes these findings.

Result 4: Oblique and vertical transmission of cooperation with asymmetric horizontal transmission. The cultural evolution of a cooperator phenotype will follow on of the following scenarios, depending on the signs of the horizontal transmission bias $T_A - T_B$, the coefficient β_3 , and ratio β_3/β_1 :

1. *Fixation of the cooperative phenotype A*, if $T_A > T_B$ and $0 < \beta_3$, or $T_A < T_B$ and $\beta_1 < \beta_3$.
2. *Fixation of the defector phenotype B*, if $T_A > T_B$ and $\beta_1 < \beta_3 < 0$, or $T_A < T_B$ and $\beta_3 < 0$.
3. *Protected polymorphism, or co-existence of both phenotypes*, if $T_A < T_B$ and $0 < \beta_3 < \beta_1$.
4. *Fixation of either phenotype depending on initial frequency*, if $T_A > T_B$ and $\beta_3 < \beta_1$.

Discussion

We hypothesized that non-vertical transmission can explain the evolution of cooperation. We used a model with non-vertical transmissions and have found that if eq. 12 is satisfied cooperation will take over the population in fully mixed population with prisoner's dilemma payoff. In addition, we found that when horizontal transmission cannot occur after interaction ($\alpha = 0$) cooperation will always become extinct. Our results improve our understating of cultural evolution of cooperation. Our model shows that cooperation can evolve even in a fully mixed population, where the population is non-structured, there are no repeating interactions and nor individual recognition.

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Appendix A

In the section, we start with eq. 11 and we want to investigate when $\tilde{p} < \tilde{p}'$.

$$\begin{aligned}\bar{w}\tilde{p} &< \tilde{p}^2(1+b-c)(1-(1-\tilde{p})(1-\alpha)T_B) \\ &+ \tilde{p}(1-\tilde{p})(1-c)(\tilde{p}(1-\alpha)T_B + 1 - T_B) \\ &+ \tilde{p}(1-\tilde{p})(1+b)(\tilde{p}(1-\alpha) + \alpha)T_A \\ &+ (1-\tilde{p})^2\tilde{p}(1-\alpha)T_A\end{aligned}\tag{31}$$

First divide by \tilde{p} , thus eq. 31 becomes

$$\begin{aligned}\bar{w} &< \tilde{p}(1+b-c)(1-(1-\tilde{p})(1-\alpha)T_B) \\ &+ (1-\tilde{p})(1-c)(\tilde{p}(1-\alpha)T_B + 1 - T_B) \\ &+ (1-\tilde{p})(1+b)(\tilde{p}(1-\alpha) + \alpha)T_A \\ &+ (1-\tilde{p})^2(1-\alpha)T_A\end{aligned}\tag{32}$$

We know that the mean fitness $\bar{w} = 1 + \tilde{p}(b-c)$, thus eq. 32 becomes

$$\begin{aligned}1 + \tilde{p}(b-c) &< \tilde{p}(1+b-c)(1-(1-\tilde{p})(1-\alpha)T_B) \\ &+ (1-\tilde{p})(1-c)(\tilde{p}(1-\alpha)T_B + 1 - T_B) \\ &+ (1-\tilde{p})(1+b)(\tilde{p}(1-\alpha) + \alpha)T_A \\ &+ (1-\tilde{p})^2(1-\alpha)T_A\end{aligned}\tag{33}$$

Eq. 33 can be simplified into eq. 12.