On the Evolutionary Edge of Migration as an Assortative Mating Device

Oded Stark
Doris A. Behrens
Yong Wang

February 2008

Centre of Migration Research
Faculty of Economic Sciences
Warsaw University
Banacha Street 2B
02–097 Warsaw
Poland
Tel.: +48 22 659 74 11
Fax: +48 22 822 74 05
www.migracje.uw.edu.pl
migration.cmr@uw.edu.pl

Contents

On the Evolutionary Edge of Migration as an Assortative Mating Device

Abstract

In a haystack-type representation of a heterogeneous population that is evolving according to a payoff structure of a prisoner's dilemma game, migration is modeled as a process of "swapping" individuals between heterogeneous groups of constant size after a random allocation fills the haystacks, but prior to mating. Migration is characterized by two parameters: an exogenous participation-in-migration cost (of search, coordination, movement, and arrangement-making) which measures the migration effort, and an exogenous technology - of coordinating and facilitating movement between populated haystacks and the colonization of currently unpopulated haystacks - which measures the migration intensity. Starting from an initially heterogeneous population that consists of both cooperators and defectors a scenario is postulated under which "programmed" migration can act as a mechanism that brings about a long-run survival of cooperation.

O przewadze ewolucyjnej migracji jako mechanizmu selektywnego kojarzenia w pary

Abstrakt

Artykuł modeluje migracje jako proces wymiany jednostek między heterogenicznymi społecznościami stałej wielkości. Migracje następują po losowym przydziale jednostek do grup, a przed łączeniem w pary; ewolucja społeczności następuje zaś zgodnie ze strukturą wypłat gry dylematu więźnia. Migracje charakteryzowane są przez dwa parametry: egzogeniczny koszt uczestniczenia w migracji (koszt poszukiwania, koordynacji, przenosin, zawierania porozumień), który mierzy wysiłek, jaki musi być włożony w migrację; oraz egzogeniczną technologię (koordynowania i ułatwiania przemieszczania się między już istniejącymi grupami, oraz zakładaniem nowych -- kolonizacją), która mierzy intensywność migracji. W artykule podany jest scenariusz, zgodnie z którym w wyjściowej heterogenicznej populacji zawierającej zarówno jednostki kooperujące, jak i zdrajców, przy pomocy mechanizmu programowanej migracji strategia kooperacji może na dłuższą metę przetrwać.

1. Introduction

In human societies, individuals often benefit from altruism, especially when it is others who act altruistically. In a sea of altruists, being the only one who behaves selfishly appears to be blissfully attractive. The gain conferred by deviating from behaving altruistically arises from a unilateral exploitation of the altruistic trait of others. These features of human interaction can be embedded in the (iterated) prisoner's dilemma game, where altruism is modeled as executing a cooperative strategy in a single-shot prisoner's dilemma game (cf. Bergstrom and Stark 1993), and where selfishness, labeled as "defection," is modeled as executing a non-cooperative strategy in a single-shot prisoner's dilemma game. Ever since RAND scientists Melvin Dresher and Merrill Flood formulated (what later became known as) the prisoner's dilemma (Flood 1958), the game has been thoroughly investigated by myriads of scientists. The core problems and the focus of research have been, and continue to be, the existence of a unique Nash-equilibrium that fails to be Pareto-optimal, and the survival of a cooperative strategy when the game is played repeatedly.

A fascinating branch of literature, largely developed outside the field of economics, seeks to explain the evolution or extinction of cooperation (altruism) in a population by resorting to an environment of haystacks (Maynard Smith 1964; Cohen and Eshel 1976; Wilson 1987).[1] Key assumptions of the haystack-type models are that (1) individuals in a large population who either behave altruistically (and are thus labeled "cooperators") or who behave selfishly (and are thus labeled "defectors") are randomly pooled together into small groups (the haystacks); (2) the individuals reproduce within their groups (their haystacks); (3) the individuals' descendents are dispersed to form a new large population; (4) the individuals who constitute the new large population are again randomly pooled into small groups (the haystacks); and so on. The reproductive outcome of a group (a haystack) depends on the traits of the individuals who constitute the group. The long-term composition of the population by the cooperator-defector trait emanates from the interplay between the reproductive outcomes of the groups and the dispersal-cum-pooling process.

---

[1] Bergstrom (2002, 2003a) has eloquently drawn the attention of economists to this strand of literature.

Since in the classical haystack-type model individuals are drawn into haystacks only once in their lifetime, there must be at least one non-vanishing group solely consisting of cooperators to guarantee the survival of altruism.[2] In such a setting, mutation or migration is rather perilous to the survival of cooperation because "genetic or virtual movement" could bring into the group of cooperators a defector whose "non-cooperation" trait could eventually spread over the entire group.[3] Thus, the classical haystack-type model implies that a homogeneous population consisting entirely of cooperators will, in all likelihood, not be immune to an invasion by defectors. This perspective is also addressed, for example, by Cooper and Wallace (2004) who follow the haystack-type model approach described by Sober and Wilson (1998), and who provide conditions under which cooperation and altruism can survive in the haystacks - prisoner's dilemma game. One of these conditions is that groups have to be isolated one from the other for many generations (cutting off inter-group interaction for a long period of time) so as to let cooperation persist within a population. Cooper and Wallace (as others) also find that group size matters. Moreover, positive assortativity (a higher likelihood that cooperators are matched with each other) nourishes the survival of altruism.[4] Bergstrom (2003b) explores an index of positive assortativity in a model of population dynamics under different assumptions about an individual's ability to camouflage his true nature, and studies the resulting long-run composition of the population. In the current paper we develop a framework in which observability of the true nature of individuals is assumed to be perfect while, under some conditions, the initial assortment of individuals into pairs (for playing a pre-programmed, specific two-person game) is assumed to be unstable. Our analysis of a setting in which the "life" of a match is conditioned on how the "programs" of the matched individuals correlate and on the technology and cost of re-matching, and our exploration of the repercussions of the realignment into pairs for the evolution of the composition of the population thus complement recent research.

---

[2] This is a well discussed topic, since "the problem is to explain how a group comes to exist wholly of altruistic individuals in the first place, since in a mixed group altruism will be eliminated by selection" (Maynard Smith 1993, p. 199).

[3] See, for example, Bergstrom and Stark (1993), Stark (1999). Note that it is the intra-group process that drives the results, not the act of an individual.

[4] Note that the absence of (sufficient) assortativity does not only cause the extinction of cooperation in symmetric games such as the prisoner's dilemma game, but also in asymmetric games such as the trust game (Arce 2006).

From the preceding discussion it is apparent that in classical haystack-type models of a heterogeneous population, migration is commonly perceived to be detrimental to the survival of cooperation, because migration is assumed to be "mutation-like." In this paper we look at migration from a different angle. We analyze an evolutionary process that can select for cooperation and altruism in a setting that incorporates a form of migration between haystacks that does not negatively affect homogenous cooperator groups by importing an unwanted pattern of behavior, but rather is responsible for "redeployment" of individuals between heterogeneous groups (without changing though the size of the groups), for forming new homogenous groups, and for eradicating existing heterogeneous haystacks. Given conditions to be specified, we track the consequences of individuals being programmed with a migration trait that, as a mechanism of re-allocating a (sub-) population to haystacks, serves as a structured device for assortative mating. While the idea that positive assortativity can nourish cooperation is not all that new (Wilson and Dugatkin 1997; Bergstrom 2003b; Cooper and Wallace 2004), a systematic analysis of the long-run effect of a "non-mutation-like" migration as the underlying mechanism for the survival of altruism in an initially heterogeneous population is still missing. In particular, the repercussions of the possibility that already-matched individuals migrate in order to change partners, rather than of unmatched individuals migrating in order to find mates, has not been studied closely. Herewith we fill this research gap.

2. Random and systematic allocations in an evolutionary "altruism dilemma[5]"

Let there be an environment that consists of a continuum of haystacks. Initially, a measure n of these haystacks are populated, each by two adult individuals who are drawn at random from a continuum of adult population of measure $2n$. A haystack cannot accommodate more than two adult individuals. Each individual is either programmed to behave cooperatively (associated with executing a strategy "C") or to behave defectively (associated with executing a non-cooperative strategy "D"); no other type of individual exists. The term "strategy" here stands for a predetermined

---

inherited pattern; an individual does not make a choice but follows a program.

Given that at the outset the proportion of cooperators in the heterogeneous population is known to be equal to $x \in (0, 1)$, we infer that initially a measure of $2nx$ of the individuals are cooperators (or of the C-type), and $2n(1-x)$ are defectors (or of the D-type). Then, these individuals of measure $2n$ are pair-wise grouped into a continuum of haystacks of measure n. Drawing on the assumption of a random allocation to the haystacks we know, given a population size of measure $2n$, that the sizes (in measures) of the resulting pairs of type (C,C), type (D,D), and mixed type (C,D) or (D,C), are

$$\frac{2nx}{2n} \cdot \frac{2nx}{2n} \cdot n = x^2 n \quad \text{haystacks of type } (C,C),$$

$$\frac{2n(1-x)}{2n} \cdot \frac{2n(1-x)}{2n} \cdot n = (1-x)^2 n \quad \text{haystacks of type } (D,D), \quad (1)$$

$$2 \cdot \frac{2nx}{2n} \cdot \frac{2n(1-x)}{2n} \cdot n = 2x(1-x)n \quad \text{haystacks of type } (C,D) \text{ or type } (D,C).$$

Individuals procreate pair-wise within their haystacks where the size of populated haystacks by type is given by (1), and where procreation is asexual. An individual cannot procreate if he is by himself. The number of descendents of each of the initial inhabitants depends on whom they are paired with (that is, on the type of haystack they live in), and is given by the payoff of the following one-shot prisoner's dilemma game (where $0 < S < P < R < T$):

		Column player	
		C	D
Row player	C	R,R	S,T
	D	T,S	P,P

The numbers of descendents, S, P, R, T, are assumed to satisfy the requirement that the

overall population never becomes extinct.[6]

The individuals constituting the initial population and their descendents live in their haystacks for a fixed period of time. At the end of that period, the adult individuals die, and their descendents, all of whom reach adulthood, are dispersed into a single population. Then, again, half as many haystacks as there are individuals are populated, each by two individuals drawn at random from the population at large.

In the wake of a perfectly random mating process in an iterated prisoner's dilemma game ($0<S<P<R<T$), where defectors have a higher payoff (in terms of descendents) than cooperators, it is well-known that defectors will eventually spread over the entire population (consult, for example, Weibull 1995; Henrich 2004). Thus, cooperation (altruism) is doomed. However, if cooperators preferentially (have the possibility to) pair with other cooperators instead of with defectors, then the cooperator trait may survive within a heterogeneous population (Bergstrom 2003b).

Let us consider next the other extreme possibility, namely that the initial allocation of individuals to the haystacks of measure n is perfectly systematic (rather than perfectly random). In such a setting, the haystacks populated by two cooperators have a measure of nx, the haystacks populated by two defectors have a measure of $n(1-x)$, and there are no mixed haystacks at all; the entire population consists of two types of homogenous haystacks.[7] The size of cooperators in the initial population is $2nx$, and the size of defectors is $2n(1-x)$. Each haystack initially populated by two cooperators yields $2R$ cooperators, and each haystack initially populated by two defectors yields $2P$ defectors. The ratio of the size of defectors to the size of cooperators at dispersal time, D'/C', can be obtained as a function of the ratio of the size of defectors to the size of cooperators at the initial time, D/C,

$$\frac{D'}{C'} = \frac{n(1-x)\cdot 2P}{nx\cdot 2R} = \frac{2n(1-x)}{2nx}\cdot\frac{P}{R} = \frac{D}{C}\cdot\frac{P}{R} \ . \tag{2}$$

---

[6] Alternatively, it can be assumed that only a proportion of a bundle, S, P, R, T, matters, and that the overall population is held constant, in which case our inquiry seeks to unravel only the change in the composition of the population.

[7] Note that this scenario corresponds to the haystack model of Maynard Smith (1964), where it is assumed that mixed haystacks are eliminated immediately.

From the ranking of the payoffs ($0 < S < P < R < T$) we know that (P/R) < 1. Hence we can draw the conclusion that in the wake of each cycle of perfectly systematic matching, cohabiting, procreation, generational replacement, and dispersal, the ratio of defectors to cooperators in the overall population will decline. This is in line with, for example, Bergstrom (2003b), and Cooper and Wallace (2004). In contrast to the long-run composition of a repeatedly randomly allocated population, in a repeatedly systematically allocated population cooperators will prevail and defectors will eventually become extinct (having a measure of zero), and this will be so independently of the ratio of defectors to cooperators in the initial population. Thus, as time goes by, a small fraction of cooperators will be sufficient to transform - via a systematic allocation - a population consisting largely of defectors into a homogeneous population of cooperators.

We next present the idea that migration can constitute a "medium" between a perfectly random allocation and a perfectly systematic allocation and thus, that it can support the survival of cooperation.

3. Random allocations with an inclination to migrate

We start with a heterogeneous population of an arbitrary size, such as the population that is described in section 2, consisting of a continuum of individuals of measure $2n$. The proportion of cooperators is known to be equal to $x \in (0, 1)$, and the allocation of individuals to the n initially populated haystacks is perfectly random. We also assume that upon realization of the draw, individuals will either migrate to form new haystacks or stay put in their current haystacks, as delineated later. But who initiates migration, who is "dragged" into migration, where do migrants go to, and under what conditions does it all happen?

Consider the three types of haystacks, the sizes of which are given in (1), resulting from the initial random allocation. A cooperator in a (C,C)-type haystack is not programmed to move in order to be paired with another C-type individual (because then the number of (the pre-migration cost) offspring will remain unchanged at R) or in order to be paired with any of the D-type individuals (because then the number of

(the pre-migration cost) offspring will decline by $(R-S)$).

Suppose, in addition, that the "migration gain" of a C-type individual who comes from a mixed haystack (a heterogeneous group) to team up with a cooperator is greater than the migration gain of a D-type individual who comes from a (D,D) haystack (a homogenous group) to team up with a cooperator.[8] In terms of the prisoner's dilemma payoffs $(S<P<R<T)$ this additional requirement translates into

$$R-S>T-P. \tag{3}$$

In the presence of a payoff structure as given by condition (3), C-type individuals who are not matched with C-type individuals will seek to be matched with C-type individuals (they are programmed to seek to escape from the "relationship" they are "trapped" in after the random allocation process and prior to the mating process). D-type individuals also seek matches with C-type individuals so as to exploit the cooperative trait of their partners. In spite of their inclination to migrate in order to be paired with cooperators, defectors who, in the wake of a random allocation, end up in (D,D)-type haystacks do not migrate.[9]

Imagine now that a cooperator from a mixed haystack migrates to another mixed haystack. Then, the arriving cooperator has a competitive edge over the incumbent defector in pairing with the cooperator there because, given the payoff structure $(R>S$ and condition (3)), the cooperator in the destination haystack is programmed to play the one-shot game with the arriving cooperator as "tailored" by biological proclivity: the defector's "power" to resist being crowded out is weaker than the cooperator's "power" to crowd in. On the other hand, since a cooperator in a mixed haystack will

---

[8] We can reinterpret the differences in the parameters as follows: $(P-T)$ is the loss to a defector from cohabiting with a defector instead of with a cooperator, whereas $(S-R)$ is the loss to a cooperator from cohabiting with a defector instead of with a cooperator. Since $(P-T)$ and $(S-R)$ are losses, what we have assumed is that $-(S-R)>-(P-T)$; the loss to a cooperator from cohabiting with a defector is higher than the loss to a defector from cohabiting with a defector.

[9] Because the inability to initiate successful pairing with cooperators, whether or not any of the defectors has an inclination to migrate is immaterial in the migration cum matching process. Hence, we will focus only on the ramifications of an inclination to migrate, or of the absence of an inclination to migrate, among cooperators. Note that although defectors cannot initiate migration, they may be forced into migration between mixed haystacks that are either cohabited with migration-inclined cooperators or are absorbing migrant cooperators.

either migrate to another mixed haystack or pair up with a cooperator who migrates in from another mixed haystack, a defector in a mixed haystack affected by the migration behavior of its initial cooperator co-inhabitant is programmed to seek pairing with a defector from another mixed haystack because, if left on his own, he will have no partner at his original haystack with whom to play the one-shot prisoner's dilemma game and hence, he will end up with no descendents at all.

As elaborated above, the cooperator's programmed inclination to migrate is motivated by the fact that if a revised matching can be expected to yield a higher payoff (and, thus, more descendents) than the original random matching, the revised matching will be "preferred," and hence "sought." For a revised matching to occur (and to hold), the two individuals in a newly-formed ("revised") haystack are programmed to duly respond to the mutual gains conferred by a revised matching. The inclination to migrate is thus manifested in a "willingness" to resort to migration to other haystacks, and to admit migrant cooperators from other haystacks by cooperators who were initially allocated to mixed haystacks. To reiterate, the inclination to migrate is not modeled as the result of an individual's choice; rather it is a programmed trait complementing the programmed cooperator/defector trait.[10]

Thus, within the framework of the model presented in section 2, migration is defined as a structured process of forming new groups and of liquidating existing groups, based on the mutual fit of individual programs, and it depends on two parameters:

- A cost of migration, which is assumed to be exogenously given. The participation-in-migration cost - the search, coordination, movement, and arranging (that is, waiting and "preparing a haystack") cost - is represented by a parameter $\varepsilon \geq 0$ that measures the migration effort. Specifically, a cooperator who is initially paired with a defector and who acts upon his programmed inclination to separate from the defector and to pair with another cooperator from a mixed haystack has to incur a participation-in-migration cost of ε, measured in terms of descendents. Put

---

[10] The programmed migration trait of cooperators - seeking out and/or admitting other cooperators upon finding themselves in mixed haystacks - is consistent, however, with behavior patterns premised on rational economic considerations. As such, the migration trait can be thought of as being acquired over a typical Darwinian evolutionary process of "survival of the fittest."

differently, all the participating-in-migration *C*-type individuals are confronted by the same search and coordination cost, and are programmed to behave indifferently with respect to moving to another haystack or waiting and preparing (arranging) their haystack for the arrival of the cooperator with whom they are about to pair; migration is costly not only for the *C*-type individuals who initiate the migration process. Moreover, migration is equally costly for the "leftover" *D*-type individuals who are "dragged" into follow-up migration because (say after the *C*-type partner walks away) they are programmed to search for a defector to pair with (as they cannot find another *C*-type individual to pair with for obvious reasons), recalling that they cannot procreate merely by themselves.

- A technology **-** available to coordinate and facilitate migration between haystacks **-** which is assumed to be given exogenously. This technology is represented by a parameter $m \in [0,1]$, which can be interpreted to imply that the technology allows a fraction of the cooperators from mixed haystacks to initiate the aforementioned migration and succeed in finding another mixed haystack with the ensuing formation of a cooperator-cooperator pair (and, consequently, of a defector-defector pair). The non-availability of a migration technology corresponds to a parameter value $m = 0$, and the best possible migration technology available is represented by a parameter value $m = 1$. Thus, as long as the participation-in-migration cost is smaller than the "migration gain," $m = 1$ will yield a perfectly systematic allocation.

Consequently, migration can be defined by a cost-technology pair, (ε, m), such that an *m* fraction of *C*-type individuals who are being allocated to mixed haystacks is programmed either to migrate to another mixed haystack to team up with the cooperator there, or to accept a migrant cooperator from another mixed haystack as a new cohabitant, after incurring a participation-in-migration cost of ε by each *C*-type migrant. For the remainder of the discussion, we assume the following "migration conditions:"

$$\varepsilon < R - S. \tag{4}$$

Condition (4) ensures that the gain from migration (given by the number of added

9

offspring) outweighs the cost (in terms of the number of lost offspring) of undertaking migration. The condition gives credence to the programmed migration by C-type individuals who initially were allocated to mixed haystacks.

As already intimated, migration is costly not only for those who are programmed to initiate it, but also for those who are programmed to be "dragged" into it. The D-type individuals who are left in the formerly mixed haystacks are programmed to team up with each other, *if* the number of expected offspring from this matching exceeds the participation-in-migration cost, that is, if for each of these individuals,

$$P > \varepsilon .^{11} \tag{5}$$

We can generalize and state that, given that condition (4) is satisfied, the size of the added (C,C)-type haystacks due to the programmed migration is equal to $mx(1-x)n$. The same addition applies to the (D,D)-type haystacks, given that condition (5) is satisfied. Consequently, the size of the mixed haystacks declines by $2mx(1-x)n$ due to migration. Thus, it follows from (1) that the population composition that emerges from the joint application of random allocation and programmed migration is

$$
\begin{aligned}
x^2n + mx(1-x)n & \quad \text{haystacks of type } (C,C), \\
(1-x)^2n + mx(1-x)n & \quad \text{haystacks of type } (D,D), \\
2(1-m)x(1-x)n & \quad \text{haystacks of type } (C,D) \text{ or type } (D,C).
\end{aligned}
\tag{1'}
$$

If the intensity m is very high (measured absolutely, as well as in comparison to ε), almost all the cooperators will pursue migration and the outcome will be a nearly systematic allocation, which in turn will result in a long-run prevalence of cooperators and thereby of altruism (as already noted in section 2).

Let us therefore analyze the long-run composition of the population. Recall that the initial share of cooperators is represented by $x \in [0,1]$, and let $(1-x) \in [0,1]$ denote the initial share of defectors. According to condition (4) we know that m percent of the C-type individuals from mixed haystacks follow their migration program at a cost of 2ε

---

[11] Clearly, if $P < \varepsilon < R - S$, D-type individuals in mixed haystacks are doomed; left on their own and not programmed to migrate, they end up with no descendents at all.

(lost descendents) per successful pairing. Moreover, we know that whether an individual initiates migration or is "dragged" into migration, a participation-in-migration cost of 2ε is associated with migration cum pairing. But since our interest is in the long-run prevalence of cooperation (which, to recall, becomes extinct in the absence of migration), we can abstract from the participation-in-migration cost incurred by defectors and assume that only C-type individuals have to bear the burden of participation-in-migration cost. Noting that in this extreme scenario cooperation can survive in the long run, we can maintain that the result also holds in general because assuming a zero-migration cost for the defectors is, of course, superior to them than any scenario in which a positive migration cost is assumed.

We then have from (1') that

$$n[(x^2 + mx(1-x))2R + 2(1-m)x(1-x)S - mx(1-x)2\varepsilon] \tag{6}$$

new cooperators emerge and, similarly, that

$$n[((1-x)^2 + mx(1-x))2P + 2(1-m)x(1-x)T] \tag{7}$$

new defectors emerge.[12]

Recalling that the old individuals die before dispersal time, we can calculate the ratio of the share of defectors to the share of cooperators in the next round (denoted by $(1-x)'/x'$) as a function of the ratio of the share of defectors to the share of cooperators in the preceding round (denoted by $(1-x)/x$):

$$\frac{(1-x)'}{x'} = \frac{n[((1-x)^2 + mx(1-x))2P + 2(1-m)x(1-x)T]}{n[(x^2 + mx(1-x))2R + 2(1-m)x(1-x)S - mx(1-x)2\varepsilon]}$$

$$= \frac{1-x}{x} \cdot \frac{((1-x)+mx)P + (1-m)xT}{(x+m(1-x))R + (1-m)(1-x)S - m(1-x)\varepsilon}. \tag{8}$$

We will expect this ratio to decline iff

---

[12] If $m = 1$ and $\varepsilon = 0$, the numbers of cooperators and defectors at dispersal time are as in Eq. (2).

$$((1-x)+mx)P+(1-m)xT \ < \ (x+m(1-x))R+(1-m)(1-x)S-m(1-x)\varepsilon \ \Leftrightarrow$$

$$x\cdot[(1-m)T+mP-R] \ < \ (1-x)\cdot[(1-m)S+(R-\varepsilon)m-P] \ \Leftrightarrow$$

$$x\cdot A(m)<(1-x)\cdot B(m,\varepsilon), \tag{9}$$

where $A(m)=(T-R)-(T-P)m$ and $B(m,\varepsilon)=-(P-S)+(R-S-\varepsilon)m$ are both linear in m. However, $A(m)$ is decreasing in m, whereas $B(m,\varepsilon)$ is increasing in m, but decreasing in ε. Both $A(m)$ and $B(m,\varepsilon)$ cross zero and, in particular, $A(\underline{m})=0$ for $\underline{m}=(T-R)/(T-P)$, and $B(\overline{m},\varepsilon)=0$ for $\overline{m}=(P-S)/(R-S-\varepsilon)$.

From the assumption regarding the payoffs of the prisoner's dilemma game and the "migration condition" $R-S>\varepsilon$ (cf. Eq. (4)), it follows that $\underline{m}$ is positive. Furthermore, it is easy to show that $\underline{m}<\overline{m}$. Indeed, for $\varepsilon=0$ the inequality $\underline{m}<\overline{m}$ is equivalent to the assumption that $R-S>T-P$ (cf. Eq. (3)).[13] Since $\overline{m}$ increases for a non-zero participation-in-migration cost, $0<\underline{m}<\overline{m}$ always holds. Hence, the paths of $A(m)$ and $B(m,\varepsilon)$, as a function of the migration technology m, are as depicted in Fig. 1. Their intersections with the abscissa yield three intervals for the measure of the migration technology m: (i) for small values of m $A(m)$ is non-negative and $B(m,\varepsilon)$ is negative, implying that (9) does not hold; (ii) for high values of m $A(m)$ is negative and $B(m,\varepsilon)$ is non-negative, implying that (9) definitely holds; and (iii) for medium values of m both $A(m)$ and $B(m,\varepsilon)$ are negative and (9) may hold, depending on the initial value of $(1-x)/x$.

---

[13] $R-S > T-P \Leftrightarrow R+P > T+S \Leftrightarrow (R+P)(R-P) > (T+S)(R-P) \Leftrightarrow R^2-P^2 > TR+SR-TP-$
$SP \Leftrightarrow TP+PS-P^2 > TR+SR-R^2 \Leftrightarrow TP+PS-P^2-TS > TR+SR-R^2-TS \Leftrightarrow (T-P)(P-$
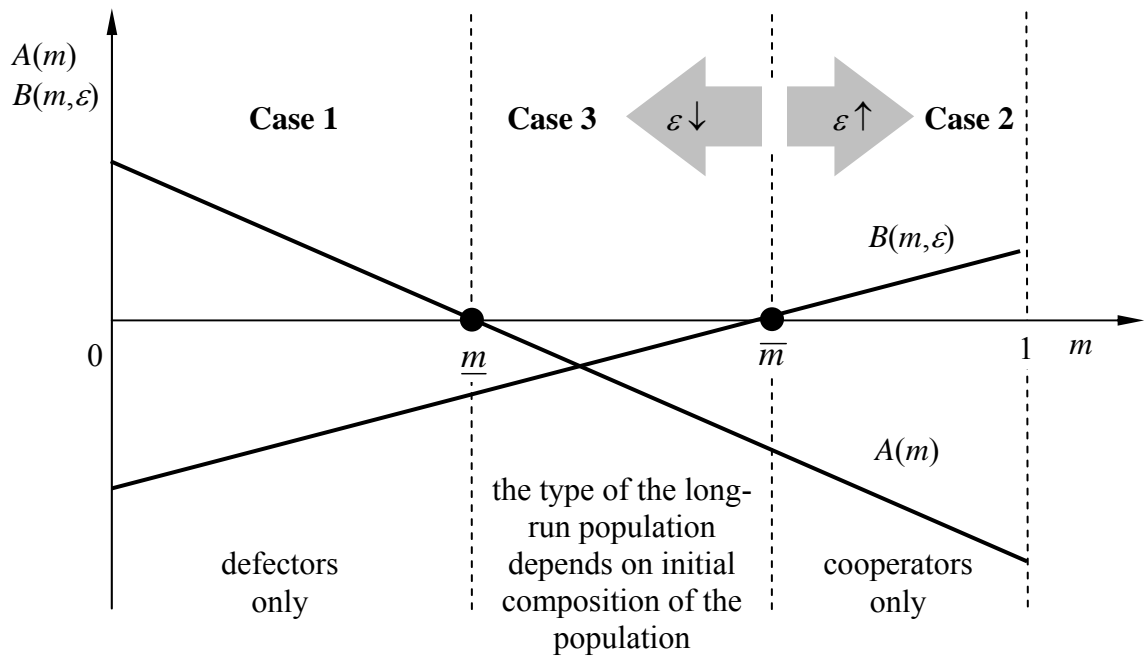$S) > (T-R)(R-S) \Leftrightarrow \dfrac{P-S}{R-S} > \dfrac{T-R}{T-P}.$

Figure 1. A diagrammatic representation of $A(m)$ and $B(m,\varepsilon)$, and of the long-run composition of the population

We designate these three intervals as "cases."

Case 1. $m \in [0, \underline{m}]$. Irrespective of the initial ratio of the share of defectors to the share of cooperators, $(1-x)/x$, unless it is exactly zero, will rise and ultimately approach exponentially quickly infinity. Thus, the available technology of migration is too poor (m is too low) to accomplish the long-run survival of cooperation and altruism; eventually the entire population will consist of defectors.

Case 2. $m \in [\overline{m}, 1]$. Irrespective of the initial ratio of the share of defectors to the share of cooperators, $(1-x)/x$, unless it is infinity, will approach exponentially quickly zero. Thus, the available technology of migration is sufficient to accomplish the long-run survival of altruism; defectors will eventually become extinct and the entire population will consist of cooperators. Moreover, a higher cost of migration can only be outweighed by an even more advanced migration technology (an increased m) without affecting the long-run composition of the population. In terms of Fig. 1, this means that an increase in the cost (ε going up) shifts $B(m, \varepsilon)$ downwards and thereby it shifts $\overline{m}$ to the right, indicating that the "cooperators only" range, irrespective of the

initial ratio $(1-x)/x$ (as a function of the migration technology level m), shrinks. A poorer migration technology (a smaller m) can be compensated by a lower migration cost without affecting the long-run outcomes. Note that the "cooperators only" interval exists as long as the cost of migration is sufficiently small, that is, as long as $\varepsilon < R - P$. In particular, this condition is equivalent to $R - \varepsilon > P$. In this case, even net of the cost of migration (C, C)-type haystacks reproduce "faster" than (D, D)-type haystacks.

Case 3. $m \in (\underline{m}, \overline{m})$. We now have dependence on the initial ratio of the share of defectors to the share of cooperators $(1-x)/x$. We introduce

$$\kappa = \frac{A(m)}{B(m, \varepsilon)} = \frac{(T-R)-(T-P)m}{-(P-S)+(R-S-\varepsilon)m} > 0 \quad \text{for} \quad m \in (\underline{m}, \overline{m}). \qquad (10)$$

We then have the following explicit **Case 3** rule:

- If initially $(1-x)/x < \kappa$, then in the long run, the population will consist entirely of cooperators.

- If initially $(1-x)/x > \kappa$, then in the long run, the population will consist entirely of defectors.[14]

Thus, an all-cooperator population is able to hold up for the intermediate range of the migration technology $m \in (\underline{m}, \overline{m})$, as long as the initial defector-to-cooperator ratio, $(1-x)/x$, is below the threshold level, κ, which is given in (10) and depends (among other parameters) on the cost of migration, ε. When migration becomes less costly, the threshold ratio increases as ε falls ($\partial\kappa/\partial\varepsilon < 0$), rendering the survival of cooperators more likely. Alternatively, in an all-cooperator population, if an invasion by a very small fraction of defectors occurs then only a fraction $m > \underline{m}$ of cooperators needs to migrate to ensure that the all-cooperator population survives. In this case,

---

[14] If it so happens that initially $(1-x)/x = \kappa$, then this is an unstable equilibrium point; this exact value of the ratio will remain constant, but once it is perturbed by some external shock, it will approach exponentially quickly either zero or infinity, depending on the sign of the shock. Note, however, that $(1-x)/x = \kappa$ is not a special case of (9).

what the cooperators who are programmed to migrate (by the presence of the invading defectors) will lose in terms of their descendants, will be well compensated for by their migration-ensuing gains of descendants so that, on the whole, cooperators will reproduce at a faster rate than the invading defectors and hence the overall "fitness" of a population that consists only of cooperators is assured. Put differently, under a migration technology of $m > \underline{m}$, an all-cooperator population is stable.

4. Concluding comments

A mutation that, say, instills a taste or a proclivity for migration in cooperating individuals (or even in both types of individuals under the condition $R - S > T - P$) is likely to be sustained if, as a consequence of carrying the mutation, the carrier's likelihood of dynastic survival is enhanced (Falk and Stark 2001). In the long run then, the (initially heterogeneous) population will consist only of cooperators who are hard-wired with a taste for migration. A proclivity to engage in migration that was critical to the cooperator's ability to fend off extinction and that conferred an evolutionary advantage over the millennia that constitute the long run, is unlikely to dissipate swiftly.

Why will a population consisting only of cooperators have a survival edge over a population consisting only of defectors? In a related paper (Stark 1998) it was shown how, in a setting in which nature is an additional player, the presence of a defector in a community, combined with a bad state of nature, leads to extinction, whereas an all-cooperator community is not so doomed. In the present setting too, an all-cooperator population has a survival edge over an all-defector population. When nature plays a role, a bad state of nature can wipe out a large number of individuals. In such a circumstance, by the mere fact that $R > P$, more individuals will always survive in an all-cooperator population than in an all-defector population.

The possibility of migration in a haystack-type model has been explicitly acknowledged before. In a study of the evolution of altruism in the haystack-type model (Wilson 1987, p. 1070) the author writes: "Groups usually are initiated by more than one individual, and migration between groups takes place prior to global

dispersal." Equally noteworthy is the conclusion that follows: "These events decrease the conditions for the evolution of altruism." Interpreting altruism as playing "cooperate" in a single-shot prisoner's dilemma game (cf. Bergstrom and Stark 1993), the present paper predicts an outcome that is the opposite of the outcome predicted by Wilson. Similarly, upon reviewing several versions of the haystack-type model Bergstrom (2002, p. 77) concludes: "For some parameter values, a population of cooperators will be sustained in equilibrium. This is more likely if the migration rate [between haystacks] is relatively small." We have shown that migration can be sensibly modeled, such that the opposite may hold.

Moreover, we hint at the idea that if the evolutionary edge of programmed migration, as modeled in this paper, can translate into a genetic disposition, that is, into an inclination to migrate as a trait, then the role and prominence of economic variables in explaining and accounting for migration behavior could be reduced somewhat (as if in the presence of biology, economics may need to bow its head somewhat). In this case, the wellbeing of human populations can be attributed to a variation in the incidence of migration-induced cooperation. We conjecture that the variation in the proclivities of populations to engage in migration might be attributed to a past evolutionary process that conferred upon some populations an advantage emanating from engagement in migration while less so, or not at all, upon other populations. A study of the role of variables other than the wage differential and pecuniary costs - such as the historical legacy of migration - in explaining present-day migration is at the frontiers of research on migration and economic well-being, and an intriguing topic for further research.

References

Arce, Daniel G. (2006) "Taking corporate culture seriously: group effects in the trust game," *Southern Economic Journal* 73, pp. 27-36.

Bergstrom, Theodore C. (2002) "Evolution of social behavior: individual and group selection," *Journal of Economic Perspectives* 16, pp. 67-88.

Bergstrom, Theodore C. (2003a) "Group selection and randomness: reply," *Journal of Economic Perspectives* 17, pp. 211-212.

Bergstrom, Theodore C. (2003b) "The algebra of assortative encounters and the evolution of cooperation," *International Game Theory Review* 5(3), pp. 211-228.

Bergstrom, Theodore C., and Stark, Oded (1993) "How altruism can prevail in an evolutionary environment," *American Economic Review* 83, pp. 149-155.

Cohen, D., and Eshel, I. (1976) "On the founder effect and the evolution of altruistic traits," *Theoretical Population Biology* 10, pp. 276-302.

Cooper, Ben, and Wallace, Chris (2004) "Group selection and the evolution of altruism," *Oxford Economic Papers* 56, pp. 307-330.

Falk, Ita, and Stark, Oded (2001) "Dynasties and destiny: the roles of altruism and impatience in the evolution of consumption and bequests," *Economica* 68, pp. 505-518.

Flood, Merrill M. (1958) "Some experimental games," *Management Science* 5, pp. 5-26.

Henrich, Joseph (2004) "Cultural group selection, coevolutionary processes and large-scale cooperation," *Journal of Economic Behavior and Organization* 53, pp. 3-35.

Maynard Smith, John (1964) "Group selection and kin selection," *Nature* 201, pp. 1145-1147.

Maynard Smith, John (1993) *The theory of evolution,* Cambridge: Cambridge University Press.

Sober, Elliott, and Wilson, David S. (1998) *Unto others: the evolution and psychology of unselfish behavior*, Cambridge, MA: Harvard University Press.

Stark, Oded (1998) "On the economics of vanishing," *Economics Letters* 61, pp. 261-266.

Stark, Oded (1999) "Siblings, strangers, and the surge of altruism," *Economics Letters* 65, pp. 135-142.

Weibull, Jörgen (1995) *Evolutionary game theory*, Cambridge, MA: MIT Press.

Wilson, David S. (1987) ''Altruism in Mendelian populations derived from sibling groups: the haystack model revisited,'' *Evolution* 41, pp. 1059-1070.

Wilson, David S., and Dugatkin, Lee A. (1997) ''Group selection and assortative interactions,'' *The American Naturalist* 149, pp. 336-351.