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An evolutionary explanation for the propensity to migrate

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the propensity to migrate

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CORE

DISCUSSION PAPER



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CORE DISCUSSION PAPER
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AN EVOLUTIONARY EXPLANATION FOR
THE PROPENSITY TO MIGRATE

Alexei SAVVATEEV¹ and Oded STARK²

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Abstract

We explore the evolutionary dynamics of a population that consists of cooperators and defectors, wherein each member of the many pairs of players of a one-shot prisoner's dilemma game is drawn at random, and the number of descendants positively depends on the payoffs in the game. We demonstrate how an inclination to migrate may be mapped onto the overall evolutionary fitness of the cooperators. The threshold value of the inclination to migrate parameter is obtained. Intensities of migration higher than that value guarantee that in the long run, the population will consist entirely of cooperators. The threshold value is characterized by the payoff parameters lying at the base of the evolutionary dynamics.

Keywords: Haystacks-type model; Prisoner's dilemma game; Inclination to migrate; Evolution of cooperation; Taste for migration.

JEL Classification: A12; A13; D64; R23.

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1. Motivation

Societies, economies, and groups differ both in the extent to which they tend to engage in migration and in the elasticity of their migratory response to conventional explanatory variables of migration such as wage differential. For example, numerous studies suggest that those who migrate to a country are more mobile within the country than those who are native-born, or that, by and large, Americans are geographically more mobile than Europeans. At times, the intensity of migration or the migration response, say to an inter-regional wage differential, is considered to be too low or too high from the point of view of productive efficiency or social welfare.¹ Consequently, tinkering with the conventional explanatory variables is thought of, and sought, as a means of inducing additional migration or of curtailing excessive migration. The purpose of this paper is to deepen our understanding of migration behavior by investigating the possibility that a relatively high proclivity of today's population to engage in migration can be attributed to a past evolutionary process that conferred an advantage on migration. Populations that are hardwired with an inclination to migrate will be quite responsive to even small revisions of standard economic and social variables as a means of triggering migration, or harder to subdue if engaging in excessive migration. Thus, one reason why the propensity to migrate is higher in one population than in another is not that in the former the wage differential across markets is higher or that the pecuniary cost of movement is lower, but rather that members of the former population are genetically predisposed to an inclination to migrate. In the presence of biology, economics may need to bow its head somewhat.

2. Introduction

There is a fascinating literature, developed largely outside the field of economics, that seeks to explain the evolution or extinction of cooperation and altruism in a population by resorting to an environment of "haystacks" (Maynard Smith (1964), Cohen and Eshel (1976), Wilson (1987)). Recently, Bergstrom (2002, 2003) has eloquently drawn the attention of economists to this literature.

The key assumptions of the haystacks model are that individuals in a large population, who are either "cooperators" or "noncooperators," are randomly pooled into small groups (the "haystacks"); they reproduce within their groups; their descendents are dispersed to form a new large population; the individuals who constitute the new large population are again randomly

¹For example, with regional specificity of capital, an efficiency gain will be reaped if workers migrate from the region where the marginal product of labor is low to the region where the marginal product of labor is high. The gain will be maximized when M workers migrate such that the marginal products of labor (wage rates) across the two regions are equalized. Any level of migration that falls short of M will be considered too low from the point of view of productive efficiency.

pooled into small groups; and so on. The reproductive outcome of a group depends on the traits of the individuals who constitute the group. The long-term composition of the population by the “cooperator”- “noncooperator” trait emanates from the interplay between the reproductive outcomes of the groups and the dispersal-cum-pooling process.

The purpose of this paper is to explore the dynamics of a simple haystacks-type model in a setting that incorporates migration between haystacks. We show that when the reproductive outcomes are represented by payoff functions in a prisoner’s dilemma game, a sufficient inclination to migrate will, in the long run, yield a population that consists entirely of “cooperators.”²

3. Random allocations without migration

Let there be an environment that consists of a large number of habitats (“haystacks”). Initially, n of the habitats are populated, each by two adult individuals who are drawn at random from a large population the size of $2n$. A habitat cannot accommodate more than two adult individuals. An individual is either a cooperator or a defector, as defined below. Let the proportion of cooperators in the initial population be $x \in (0, 1)$, and let the proportion of defectors be $1 - x$. Thus, $2nx$ of the individuals are cooperators, and $2n(1 - x)$ are defectors.

Imagine a random populating of the habitats. By randomness we mean as follows: overall, given a group of $2n$ objects, the set of pairs contains $C_{2n}^2 = n(2n - 1)$ elements. If initially and exogenously the group is subdivided into two parts of $2nx$ objects and $2n(1 - x)$ objects, say of *cooperators* and *defectors* respectively, then there are three types of pairs in the set of all pairs: $nx(2nx - 1)$ pairs that consist of two cooperators, $n(1 - x)(2n(1 - x) - 1)$ pairs that consist of two defectors, and the remainder $2nx \cdot 2n(1 - x)$ pairs that are mixed.

We assume that in a randomly composed population, the fraction of the three types of pairs are the same as in the set of all $n(2n - 1)$ pairs. Since only n of these $n(2n - 1)$ pairs are realized, we need to divide the three numbers of pairs by a common factor of $2n - 1$, thereby obtaining the following numbers of pairs in a random allocation:

$$\begin{aligned} \frac{nx(2nx - 1)}{2n - 1} &= nx^2 \frac{1 - \frac{1}{2nx}}{1 - \frac{1}{2n}} \text{ pairs of cooperators;} \\ \frac{n(1 - x)(2n(1 - x) - 1)}{2n - 1} &= n(1 - x)^2 \frac{1 - \frac{1}{2n(1 - x)}}{1 - \frac{1}{2n}} \text{ pairs of defectors;} \\ \frac{2nx \cdot 2n(1 - x)}{2n - 1} &= 2nx(1 - x) \frac{1}{1 - \frac{1}{2n}} \text{ mixed pairs.} \end{aligned} \quad (1)$$

²Bergstrom and Stark (1993), Stark (1999 and 2004) and Stark and Wang (2004) have drawn upon a Prisoner’s dilemma payoff function in their study of the evolution of altruism and cooperation.

The two individuals in each habitat procreate asexually. An individual cannot procreate if he is by himself. The individuals and their descendents live in their habitat 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 habitats as there are individuals are populated, each by two individuals drawn at random from the population at large.

Let the number of descendents of each of the original inhabitants at dispersal time be given by the following payoff function of a one-shot prisoner's dilemma game (where $T > R > P > S > 0$):

		Column	Player
		\tilde{C}	\tilde{D}
Row	\tilde{C}	R, R	S, T
Player	\tilde{D}	T, S	P, P

By definition, an individual is a cooperator if he plays \tilde{C} in the single-shot prisoner's dilemma game. An individual is a defector if he plays \tilde{D} in the single-shot prisoner's dilemma game. There is no strategic choice in our environment: the individuals are predisposed to play \tilde{C} or to play \tilde{D} . Individuals inherit the program that they follow from their parents. The numbers T, R, P, S are assumed to satisfy the following requirement: that the overall population never becomes extinct. Alternatively, it can be assumed that only a proportion of a bundle T, R, P, S 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.

It follows then that at dispersal time, the habitats populated by two cooperators each yield $2R$ descendent cooperators, and the habitats populated by one cooperator and one defector each yield S descendent cooperators. Consequently, the total number of cooperators at dispersal time is

$$C' = nx^2 \frac{1 - \frac{1}{2nx}}{1 - \frac{1}{2n}} \cdot 2R + 2nx(1-x) \frac{1}{1 - \frac{1}{2n}} \cdot S; \quad (2)$$

and, by way of an equivalent reasoning, the total number of defectors at dispersal time is equal to

$$D' = n(1-x)^2 \frac{1 - \frac{1}{2n(1-x)}}{1 - \frac{1}{2n}} \cdot 2P + 2nx(1-x) \frac{1}{1 - \frac{1}{2n}} \cdot T. \quad (3)$$

The initial number of cooperators is $C = 2nx$ and the initial number of detectors is $D = 2n(1-x)$.

We seek to calculate D'/C' as a function of D/C . After dividing throughout by the common

term $\frac{n}{1 - \frac{1}{2n}}$, we have

$$\begin{aligned}
\frac{D'}{C'} &= \frac{(1-x)^2 \cdot \left(1 - \frac{1}{2n(1-x)}\right) \cdot 2P + 2x(1-x)T}{x^2 \cdot \left(1 - \frac{1}{2nx}\right) \cdot 2R + 2x(1-x)S} \\
&= \frac{1-x}{x} \cdot \frac{(1-x) \cdot \left(1 - \frac{1}{2n(1-x)}\right) \cdot P + xT}{x \cdot \left(1 - \frac{1}{2nx}\right) \cdot R + (1-x)S} \\
&= D/C \cdot \frac{(1-x) \cdot \left(1 - \frac{1}{2n(1-x)}\right) \cdot P + xT}{x \cdot \left(1 - \frac{1}{2nx}\right) \cdot R + (1-x)S} \\
&= D/C \cdot \frac{(1-x)P + xT - \frac{P}{2n}}{(1-x)S + xR - \frac{R}{2n}}. \tag{4}
\end{aligned}$$

Hence, we have

$$\begin{aligned}
\frac{D'/C'}{D/C} &= \frac{(1-x)P + xT - \frac{P}{2n}}{(1-x)S + xR - \frac{R}{2n}} \\
&= 1 + \frac{(1-x)(P-S) + x(T-R) + \frac{R-P}{2n}}{(1-x)S + xR - \frac{R}{2n}} \\
&> 1 + \frac{\min\{P-S, T-R\}}{R} = 1 + Const., \tag{5}
\end{aligned}$$

where $Const. > 0$, since for any prisoner's dilemma game, $T > R$ and $P > S$.³

Thus, after k iterations we will have

$$(D'/C')_k = (D/C) \cdot (1 + Const.)^k \rightarrow \infty, \tag{6}$$

that is, the share of cooperators in the population approaches zero exponentially. Thus, the predicament is that in the wake of each cycle of matching, cohabiting, procreation, generational replacement and dispersal, the ratio of defectors to cooperators in the overall population will rise exponentially and the proportion of cooperators will decline exponentially: cooperators will become extinct. (Recall Weibull (1995), and Stark (1999)).

³In the last but one fraction of (4), let us estimate the numerator from below, and the denominator from above. As for the numerator, $(1-x)(P-S) + x(T-R) + \frac{R-P}{2n} > (1-x)(P-S) + x(T-R) \geq (1-x) \min\{P-S, T-R\} + x \min\{P-S, T-R\} = \min\{P-S, T-R\}$. As for the denominator, $(1-x)S + xR - \frac{R}{2n} < (1-x)S + xR < (1-x)R + xR = R$.

4. Systematic allocations without migration

Suppose, alternatively, that the initial allocation to the n habitats is perfectly systematic rather than perfectly random. In such a setting, the number of habitats populated by two cooperators is nx , and the number of habitats populated by two defectors is $(1-x)n$. There are no mixed habitats. The habitats populated by cooperators each yield $2R$ cooperators, and the habitats inhabited by defectors each yield $2P$ defectors. Let us, again, calculate the ratio of the number of defectors to the number of cooperators at dispersal time. We obtain

$$D'/C' = \frac{2Pn(1-x)}{2Rnx} = \frac{1-x}{x} \cdot (P/R) = (D/C) \cdot (P/R). \quad (7)$$

Since $P/R < 1$, we now have the opposite predicament: cooperators will prevail and defectors will exponentially become extinct.

Note that by continuity, in the long run the population will consist of only cooperators even if the allocation to habitats is nearly systematic rather than perfectly systematic.

5. Random allocations with an inclination to migrate

Suppose that allocation is perfectly random, yet upon realization of the draw, individuals can migrate between habitats. Given that $T > R > P > S$, cooperators who are not matched with cooperators will want to be matched with cooperators, as will defectors. The inclination to migrate is premised on the assumption that if a revised matching is expected to yield more offspring than the original matching, the revised matching will be preferred, and hence sought. For a revised matching to occur, the two individuals in a newly-formed habitat need to be aware of, and 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 habitats *and* to admit migrant cooperators from other habitats. Suppose that the prisoner's dilemma payoff function observes $R - S > T - P$ (while still maintaining $T > R > P > S$). This additional inequality implies that the gain to a cooperator who migrates from a mixed habitat to team up with a cooperator is greater than the gain to a defector who migrates from a defector-defector habitat to team up with a cooperator.⁴

In the presence of such a payoff structure, a cooperator in a mixed habitat will either migrate to another mixed habitat to team up with the cooperator there, or accept a migrant cooperator from another mixed habitat as his new cohabitant; and a defector in a mixed habitat will end

⁴We can reinterpret the differences in the parameters as follows: $(P - T)$ is the loss to a defector from cohabiting with a defector rather than with a cooperator, whereas $(S - R)$ is the loss to a cooperator from cohabiting with a defector rather than 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.

up pairing with a defector from another mixed habitat. Individuals in cooperator-cooperator habitats and in defector-defector habitats will stay put. This post-allocation migration pattern is premised on the following considerations. When a cooperator from a mixed habitat migrates to another mixed habitat, motivated to do so by the anticipated net gain in terms of added offspring, the arriving cooperator has a competitive edge over defectors in pairing with the cooperator in the destination mixed habitat because, given the payoff structure ($R > S$ and $R - S > T - P$), the cooperator in the destination habitat will choose to play the one-shot game with the arriving cooperator and the defector's "power" to resist being crowded out is weaker than the cooperator's "power" of crowding himself in. On the other hand, since the cooperator in a mixed habitat will either migrate to another mixed habitat or pair up with a cooperator who migrates in from another mixed habitat, a defector in a mixed habitat will eventually end up seeking pairing with a defector from another mixed habitat because otherwise he will have no partner at his original habitat with whom to play the one-shot prisoner's dilemma game and hence, he will end up with no descendants at all. Obviously, cooperators in cooperator-cooperator habitats have no incentive to move. In spite of their obvious desire to migrate in order to be paired up with cooperators, defectors who in the wake of a random allocation end up in defector-defector habitats or, for that matter, defectors in newly-formed defector-defector habitats, will not be able to so migrate since in this migration cum matching process they have no competitive edge.⁵

Notice that the condition $R - S > T - P$ is tantamount to the assumption that a population that consists of equal numbers of cooperators and defectors will have a survival edge upon cooperators being paired with cooperators and defectors being paired with defectors, as opposed to each cooperator being paired with a defector.

To see the joint result of random allocations and migration, we have to specify the intensity of the migration process. If the intensity is very high, it is natural to expect that almost all the cooperators will be successful in their migratory pursuits, and therefore, the outcome of the process will be nearly systematic, which in turn will result in a long-run prevalence of cooperators. Our natural inclination then is to relax the assumption of a very high intensity of migration, and explore the ensuing outcome.

⁵Because this inability to initiate successful pairing with cooperators, whether or not (any of) defectors have the inclination to migrate is immaterial in the migration cum matching process. Hence, we will focus only on the ramifications of the inclination to migrate, or the lack of it, among cooperators. Note that although defectors cannot initiate migration, they may be forced into (passive) migration between mixed habitats that are either cohabited with migration-inclined cooperators or visited upon by migrant cooperators.

6. The threshold intensity of migration

Let us analyze the long-run composition of a population in which, after each cycle of reproduction, generational replacement and random allocation, cooperators who are matched with a defector are searching for a cooperator to match with, and either become successful in this pursuit or give up and pair with a defector. Clearly, we should expect the outcome to lie somewhere between that of a random allocation and that of a systematic allocation. To measure the intensity of migration (to model the technology of migration) we introduce a parameter $m \in [0, 1]$, such that after each cycle, if previously there were a fraction μ_C of cooperators and a fraction $\mu_D = 1 - \mu_C$ of defectors, we will have a proportion $\mu_C^2 + m\mu_C\mu_D$ of cooperator-cooperator haystacks, a proportion $\mu_D^2 + m\mu_C\mu_D$ of defector-defector haystacks, and a remainder proportion $2(1 - m)\mu_C\mu_D$ of mixed haystacks. Our assumption means approximately that a fraction m of cooperators from mixed haystacks will be successful in finding another mixed haystack with the ensuing formation of a cooperator-cooperator pair and a defector-defector pair.

Let x be the initial share of cooperators, and let y be the initial share of defectors. Then, we have

$$2n [2R(x^2 + mxy) + 2S(1 - m)xy] \quad (8)$$

new cooperators emerging and, similarly, we have

$$2n [2P(y^2 + mxy) + 2T(1 - m)xy] \quad (9)$$

new defectors emerging.

Following the line of reasoning in the preceding sections, and recalling that old individuals die, we can calculate the ratio of the share of defectors to the share of cooperators in the next round:

$$\begin{aligned} (y'/x') &= \frac{2P(y^2 + mxy) + 2T(1 - m)xy}{2R(x^2 + mxy) + 2S(1 - m)xy} \\ &= (y/x) \frac{P(y + mx) + T(1 - m)x}{R(x + my) + S(1 - m)y}. \end{aligned} \quad (10)$$

We will expect this ratio to decline iff

$$\begin{aligned} P(y + mx) + T(1 - m)x &< R(x + my) + S(1 - m)y \Leftrightarrow \\ x \cdot [T(1 - m) + mP - R] &< y \cdot [S(1 - m) + mR - P] \Leftrightarrow \\ x \cdot A(m) &< y \cdot B(m), \end{aligned} \quad (11)$$

where $A(m) = T(1 - m) + mP - R = (T - R) - (T - P)m$ and $B(m) = S(1 - m) + mR - P - (P - S) + (R - S)m$ are both linear in m . However, $A(m)$ is decreasing in m , whereas $B(m)$ is increasing in m . Both $A(m)$ and $B(m)$ cross zero, and particularly $A(\underline{m}) = 0$ for $\underline{m} = \frac{T - R}{T - P}$ and $B(\bar{m}) = 0$ for $\bar{m} = \frac{P - S}{R - S}$.

It is easy to show that $\underline{m} < \bar{m}$. Indeed, this inequality is equivalent to our assumed inequality $R - S > T - P$.⁶ Hence, the path of the two functions is as per Figure 1. We have three intervals for m : for small values of m , $A(m)$ is positive and $B(m)$ is negative, implying that the inequality in (11) does not hold; for medium values of m , both $A(m)$ and $B(m)$ are negative and the inequality in (11) either holds or not, depending on the value of y/x ; and for values of m that are close to 1, $A(m)$ is negative and $B(m)$ is positive, implying that the inequality in (11) definitely holds.

In the medium interval, as m rises, the last inequality in (11) is more likely to hold. This reflects the fact that the higher the intensity of migratory efforts by cooperators, the more likely they will prevail ultimately in the population.

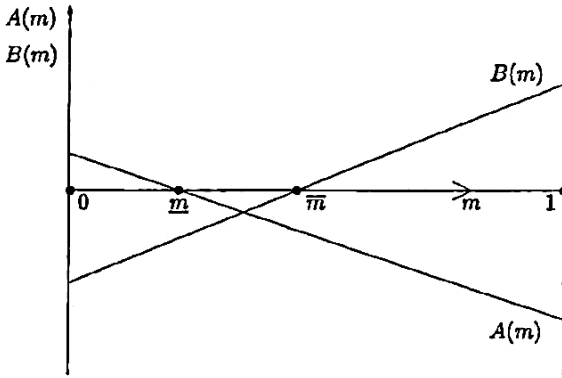


Figure 1. A diagrammatic joint representation of $A(m)$ and $B(m)$.

We designate these three intervals as “cases:”

Case 1. $m < \underline{m}$. Irrespective of the initial ratio y/x , unless it is exactly zero, y/x will rise and ultimately approach exponentially quickly infinity; in the long run the entire population will consist of defectors.

Case 2. $m > \bar{m}$. Irrespective of the initial ratio y/x , unless it is infinity, y/x will approach exponentially quickly zero; defectors will become extinct and the entire population will consist of cooperators.

Case 3. $m \in [\underline{m}, \bar{m}]$. Then, we have dependence on the initial ratio of the share of defectors to the share of cooperators. Namely, introduce

$$\kappa = \frac{A(m)}{B(m)} = \frac{T(1-m) + mP - R}{S(1-m) + mR - P}. \quad (12)$$

⁶ $R - S > T - P \Leftrightarrow R + P > T + S \Leftrightarrow (R+P)(R-P) > (T+S)(R-P) \Leftrightarrow R^2 - P^2 > TR + SR - TP - SP \Leftrightarrow TP + PS - P^2 > TR + RS - R^2 \Leftrightarrow TP + PS - P^2 - TS > TR + RS - R^2 - TS \Leftrightarrow (T-P)(P-S) > (T-R)(R-S) \Leftrightarrow \frac{P-S}{R-S} > \frac{T-R}{T-P}$.

We then have the following explicit Case 3 rule:

- If initially $y/x < \kappa$, then in the long run, the population will consist entirely of cooperators.
- If initially $y/x > \kappa$, then in the long run, the population will consist entirely of defectors.

And, if it so happens that initially $y/x = \kappa$, 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 this shock.

7. Introducing costly migration

It is interesting and instructive to assume now that migration entails a cost of ϵ . That is, a cooperator who is initially paired with a defector and who wants to separate from the defector in order to pair with a cooperator from a mixed pair, loses ϵ in terms of descendents.

We now get that the ratio y/x falls iff

$$P(y + mx) + T(1 - m)x < R(x + my) + S(1 - m)y - my\epsilon \Leftrightarrow$$

$$x \cdot [T(1 - m) + mP - R] < y[S(1 - m) + m(R - \epsilon) - P]. \quad (13)$$

Replicating the calculations of the preceding section, we get that the threshold levels are now $\frac{T-R}{T-P}$ and $\frac{P-S}{R-S-\epsilon}$, and we have three new intervals for m :

Case 1'. $m < \frac{T-R}{T-P}$. Irrespective of the initial ratio y/x , unless it is exactly zero, y/x will rise and ultimately approach exponentially quickly infinity; in the long run the entire population will consist of defectors.

Case 2'. $m > \frac{P-S}{R-S-\epsilon}$. Irrespective of the initial ratio y/x , unless it is infinity, y/x will approach exponentially quickly zero; defectors will become extinct and in the long run the entire population will consist of cooperators.

Case 3'. $m \in \left[\frac{T-R}{T-P}, \frac{P-S}{R-S-\epsilon} \right]$. Then, again, we have dependence on the initial ratio of the share of defectors to the share of cooperators, with a new κ' :

$$\kappa' = \frac{A(m)}{B(m)} = \frac{T(1 - m) + mP - R}{S(1 - m) + m(R - \epsilon) - P}. \quad (14)$$

What is extremely interesting is that the main conclusion, namely, that an all-cooperator population will not change its composition under $m > \frac{T-R}{T-P}$ holds irrespective of ϵ ! Indeed, all that changes is the threshold initial *ratio* of cooperators to defectors: it increases, rendering cooperators prevailing only less likely. Once we know that the initial ratio is equal to 1, we infer that it surely exceeds the threshold, whatever the threshold may be.

To aid intuition at this point, consider a population that consists of cooperators only. Then, only infinitesimal migration is needed to fend off a small invasion of defectors. That is, the only cooperators who would be induced to migrate are those who are paired with defectors, and

what these cooperators will lose in terms of their descendents will be largely compensated for the arrival of the descendents of the “lucky” cooperators. The overall “fitness” of a population that consist only of cooperators is assured.

8. Concluding comments

A mutation that, say, instills a taste for migration in cooperating individuals (or even in both types of individuals under $R - S > T - P$) 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 population will consist of cooperators who are hard-wired with a taste for migration. The 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 the realization of 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 circumstances, 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 haystacks model has been acknowledged before. In a study of the evolution of altruism in the haystacks 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 exactly the opposite of the outcome predicted by Wilson. Similarly, upon reviewing several versions of the haystacks model (Bergstrom 2002, p.77) the author 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 the opposite may hold.

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