The Demographic Evolution of Human Populations: The Role of Selection and Environmental Factors

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Selection (genetic and cultural) and environmental variation are the principal mechanisms determining patterns of demographic change in human populations. Conditions exist under which the nature and intensity of these forces can be inferred from temporal trends in the demographic variables. These conditions, which can be expressed in terms of relations between the Malthusian parameter and population entropy, provide a means for evaluating the effect of selective and nonselective factors on demographic trends in human populations. The distinction between the roles of selection and environmental factors is illustrated by a study of the demographic transition in Sweden (1778–1965). This study shows that demographic changes during the pre- and posttransitional phases are determined mainly by environmental factors, whereas the changes during the transitional phase are mainly due to cultural selection. This analysis provides, for all three phases of the demographic transition, quantitative measures of the intensity of the forces (selective and nonselective) acting on both mortality and fecundity distributions.

One of the outstanding biological facts of our time is the rapid multiplication of the human species. The growth rate has undergone immense variation throughout human history. Aged skeletal series from hunting and gathering cultures suggest an annual rate of increase of 0.015 per 1,000 during this period. The census data in modern times show an annual rate of increase of 17.1 per 1,000. Whereas the modern period represents only about 0.02 percent of man's history, 80 percent of that increase occurred during this period. The question this article addresses is: To what degree can we determine the nature and intensity of the forces underlying these trends in the birth and death rates?

Evolutionary theory distinguishes between two principal mechanisms determining changes in the demographic parameters in human populations. (1) The force of *selection*: This arises from the differential reproduction and mortality of the types constituting the population. The magnitude of this force depends on the amount of variability among the types and the nature of the transmission mechanisms, which may be cultural or genetic. (2) The force of *environmental action*: This is a generic term used to describe the changes in the birth and death rates due to environmental factors. These factors include wars, epidemics, and famines, which have a direct effect on mortality, or general cultural changes and behavior patterns, which have an indirect effect on fecundity and mortality. The problem to be addressed can now be made more precise. To what extent can we assess, from trends in the birth and death rates, the relative effect of selective and nonselective forces? Given that the changes are due to selection, what fraction of these changes can be ascribed to cultural transmission and what fraction to genetic transmission? What proportion of the change is associated with mortality differences and what fraction to fertility differences? Given that the changes are due to environmental action, what fraction of the change is due to,

say, improved nutrition (which may increase fertility), and what fraction is due to, say, the elimination of diseases (which may reduce mortality)?

This group of problems has been a major preoccupation in evolutionary studies of human populations (Cavalli-Sforza and Bodmer, 1971; Ward and Weiss, 1976). Previous attempts to resolve these issues have been based on a theory of the evolution of demographic parameters that goes back to Fisher (1930). This theory, the mathematical basis of which was developed extensively in Charlesworth (1980), revolves around the Malthusian parameter as the unique index determining evolutionary change. The theory analyzes the changes of this parameter under selection due to genetic transmission and implicitly neglects the effect of environmental forces. The distinction between genetic and cultural transmission and between selective and nonselective forces is not resolved in the applications of the Fisher theory. The problem confronted by the Fisherian approach derives not only from the neglect of cultural variation and environmental action but also from the lack of a suitable measure of the heterogeneity in the life cycle. This heterogeneity in age-specific fecundity and mortality conditions the response of populations to both selective and nonselective forces; hence a quantification of this notion is central to any theory of the evolution of demographic parameters.

The concept of demographic heterogeneity, as measured by the parameter population entropy, is the cornerstone of the theory introduced in Demetrius (1974; 1975). This theory (the mathematical basis of which is reviewed in Demetrius, 1983) assumes that evolutionary change can be described in terms of two parameters: the Malthusian parameter, which determines the rate of increase of population numbers, and population entropy, which determines the stability of population numbers. The difference between these two parameters is called the reproductive potential. This parameter measures the response of the Malthusian parameter to fluctuations in the age-specific fecundity and mortality distributions. This article investigates the changes of the variables, the Malthusian parameter, and entropy under the forces of natural selection and environmental action.

Selection refers to the changes in the population parameters from generation to generation that are due to differential fertility and mortality of the types constituting the population. The dynamics of selection under genetic modes of transmission have been intensively investigated for models in which age-specific fecundity and mortality rates remain constant in time. For these models, approximate equations for the change in gene frequency under weak selection have been derived (Charlesworth, 1980:ch. 4). These equations form the basis for the study of the changes in the growth rate and entropy under *weak* selection: The rate of change of the mean growth rate is determined by the additive genetic variance in the growth rate (Charlesworth, 1980: Fisher, 1930; Lande, 1982). The rate of change of the mean entropy is determined by the covariance in entropy and the population growth rate (Demetrius, 1974; Emlen, 1985:ch. 12). The validity of these results for selection under defined modes of cultural transmission is discussed in Demetrius and Demongeot (in press). Environmental action refers to the change in population parameters due to the action of environmental factors such as wars, famines, epidemics, and improved health care. Environmental action may induce an increase or a decrease in the population variables, Malthusian parameter, and entropy; the magnitude and direction of the changes are determined by the intensity of the environmental factor and the reproductive potential (Demetrius, 1989).

This group of results enables us to predict the local changes in the Malthusian parameter and entropy given the intensity of selection and of the environmental force. This article is concerned with the converse problem: Given the local changes in the Malthusian parameter and entropy, to what extent can we distinguish between the different underlying forces causing these changes?

The problem is not a statistical one that can be resolved by more reliable data on the age-specific fecundity and mortality schedule. Indeed, demographic data in human populations are the most reliable that exist. The problem is a theoretical one that arises from the demographic, genetic, and cultural heterogeneity in human populations. Because of this heterogeneity, the demographic equilibrium of these populations need not be attained. Departures from the equilibrium state of the different types can induce fluctuations in the age-specific fecundity and mortality of the total population and, consequently, variations in the Malthusian parameter and entropy. The inability to distinguish between the fluctuations due to demographic disequilibrium and those due to the forces of selection and environmental action imposes certain intrinsic limits on our ability to distinguish the actions of selective and nonselective forces from trends in the demographic data. These constraints can be formally described in terms of certain relations between the Malthusian parameter and entropy (Demetrius and Demongeot, in press). This article exploits these relations to investigate the role of selective and nonselective forces on the demographic history of human populations.

This article is organized as follows: In the next section I briefly describe the dynamical changes in the Malthusian parameter and population entropy under the action of natural selection and environmental action. In the subsequent section I describe how the nature and magnitude of these two forces may be inferred from local changes in the two parameters. The rules described in this section are illustrated by an analysis of the demographic transition in Sweden. I exploit these rules to infer the nature and magnitude of the forces underlying the changes in birth and death rates in Sweden over the past 200 years.

Predicting the Future

The theory of the evolution of demographic parameters proposed in Demetrius (1974) asserts that the evolutionary change in populations can be characterized in terms of the dynamical changes in two parameters: the Malthusian parameter r, which determines the rate of increase of population numbers, and population entropy H, which determines the stability of population numbers. These two parameters can be explicitly expressed in terms of the age-specific survivorship $l(x)$ and the age-specific fecundity $m(x)$.

The Malthusian parameter r is the unique real root of the equation

$$1 = \int_0^\infty \exp(-rx)V(x)\, dx \tag{1}$$

where $V(x) = l(x)m(x)$ is the net fecundity distribution. The parameter r is the rate of increase of the population at demographic equilibrium, that is, when the stable age distribution is attained.

The entropy H is given by

$$H = -\frac{\int_0^\infty p(x)\log p(x)\, dx}{\int_0^\infty x p(x)\, dx} \tag{2}$$

Here $p(x) = \exp(-rx)V(x)$ represents the probability distribution of the age of reproducing individuals in the population. The parameter H measures the spread of the fecundity—mortality distribution and can be considered a measure of iteroparity. Semelparous populations—such as annual plants, in which reproduction is concentrated at a single period in the individual's lifetime and at which all individuals die at the same age—have an entropy

of zero. Iteroparous populations—that is, populations that spread their reproductive activity over several age classes—have positive entropy.

The denominator in equation (2) is the mean generation time T. The parameter H measures the stability of population numbers in the sense that it determines the rate at which a population perturbed from its stable age structure returns to the stable state (Demetrius, 1977; Tuljapurkar, 1982). The maximum value that H may assume, for a given generation time T, is given by $H = (1 + \log T)/T$. A population characterized by this value of entropy is maximally stable; the population will return to the stable state at the maximal rate when perturbations in the stable age distribution occur.

There are two main mechanisms by which the parameters r and H undergo change: selection and environmental action.

The Effect of Selection: Genetic and Cultural

Selection occurs if there are differences in the age-specific fecundity and mortality of the types in the population. The differences, when transmitted from generation to generation, will induce changes in the relative frequencies of the types constituting the population.

Genes may influence vital rates. Certain genotypes that confer susceptibility to diseases may have an effect on individual health and vigor and thus may indirectly influence fecundity and mortality. The genes, when transmitted from one generation to the next, will ultimately cause changes in such demographic parameters as the growth rate and entropy.

Culture may also influence vital rates. Individuals in certain social classes are known to exhibit behavior patterns that are related to public health, age at marriage, and desired family size. These patterns of behavior, which can be transmitted by cultural mechanisms from one individual to the next, can also influence fecundity and mortality. Transmission may be between different social classes (oblique transmission) or between individuals in the same social class. In the latter case, one speaks of vertical transmission (adult to child) or horizontal transmission (adult to adult).

Genetic transmission, when the linkage between genes is weak, obeys Mendelian rules. For these Mendelian models, explicit dynamics describing the changes in the relative frequencies of the genetic variants under weak selection can be derived. The rules describing cultural transmission have not yet been elucidated. Accordingly, to understand the effect of cultural selection on demographic parameters, assumptions are made that are considered to reflect the main biological processes occurring. In this article, I assume that vertical transmission of behavior patterns is the dominant mode of cultural selection. When this condition holds, the changes in the frequencies of types for both genetic and cultural models can be shown to be formally identical (Demetrius and Demongeot, in press).

Thus when genetic selection is due to Mendelian transmission with weak linkage between genes, and when cultural selection is primarily due to vertical transmission, the dynamics describing changes in the *mean r* and the *mean H* have similar expressions.

Under weak selection, the change in the mean Malthusian parameter is given by

$$d\bar{r}/dt = V_r \,. \tag{3}$$

Here V_r denotes the additive variance in r. This dynamic predicts that under weak selection, small increases in the Malthusian parameter will occur until the variance in the growth rate parameter is exhausted.

Under weak selection, the change in the mean entropy $\bar{H}$ is given by

$$d\bar{H}/dt = C_{H,r} \,. \tag{4}$$

Here $C_{H,r}$ denotes the covariance in entropy and the Malthusian parameter. The quantity $C_{H,r}$ can be expressed in the form

$$C_{H,r} = V_H - C_{H,\Phi} , \tag{5}$$

where Φ, a demographic parameter called the reproductive potential, is given by

$$\Phi = - \frac{\int_0^\infty p(x)\log V(x)\, dx}{\int_0^\infty xp(x)\, dx} . \tag{6}$$

Equation (4) asserts that under weak selection, the mean entropy may increase or decrease. The direction of change is determined by the correlation between entropy and the growth rate r.

The weak selection condition, furthermore, implies that the differences in the reproductive potential of the types constituting the population are small. When this condition holds, $C_{H,\Phi}$ is approximately zero and the growth rate and population entropy are positively correlated. Numerical studies have shown that this positive correlation holds for a large class of natural populations (Emlen, 1985:ch. 12, p. 353).

The changes in *absolute* values for the growth rate and entropy are analogous to equations (3) and (4). This follows from the approximations described in Charlesworth (1980:ch. 4). We have

$$\Delta r = V_r \Delta t \tag{7}$$

and

$$\Delta H = C_{H,r} \Delta t. \tag{8}$$

For genetic models, V_r and $C_{H,r}$ refer to the amount of genetic variation for fecundity and mortality. For models of cultural evolution, the expressions describe the amount of cultural variation for the demographic variables.

The fact that genetic and cultural transmission can lead to the same general demographic trends imposes, as will be discussed later, difficulties in distinguishing between genetic and cultural mechanisms simply from the trends in the aggregate parameters.

The Effect of Environmental Factors

Environmental action is the generic term used to describe the changes in fecundity and mortality from generation to generation that are due to environmental factors. Environmental agents such as famines, wars, and epidemics influence primarily the survivorship of individuals in the population. The force due to an environmental agent such as an epidemic caused by an infectious disease is determined by such parameters as the number of susceptible individuals, the number of infective individuals, and the contact rate between the two classes. This environmental force can be measured by the change in the shape of the survivorship curve induced by the disease. Figure 1 illustrates the change in the survivorship curve due to some external environmental factor. The intensity of the environmental factor is measured by the quantity δ, which characterizes the change.

Environmental agents such as new contraceptive practices influence primarily the age-specific fertility distribution. The force due to this environmental agent will depend on such factors as the effectiveness of the device. This force can be measured by the change induced in the shape of the fertility distribution. Figure 2 describes the response of the fertility distribution to an environmental force whose intensity is measured by δ.
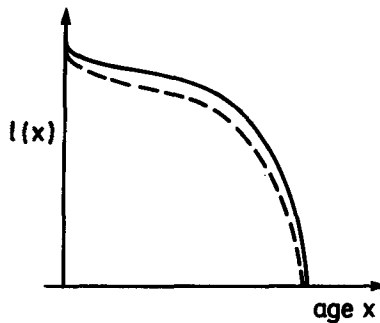
Figure 1. The change in the shape of the survivorship curve due to an
environmental factor whose intensity is given by δ. —, Original
survivorship curve; – –, perturbed survivorship curve.

The cumulative effect of environmental factors on the net-fertility distribution is de-
scribed in Figure 3. The response of r and H to environmental factors can be determined
by expressing the changes in both r and H in terms of the environmental intensity. This
change can be formalized as follows.

We describe the change in the shape of the net-fertility function due to an environmental
factor by a function $g(x)$. The net-fertility distribution, $V^*(x)$, that results from a perturbation
of $V(x)$ by the function $g(x)$ is given by $V^*(x) = V(x)^{1+g(x)}$. The incremental changes, Δr
and ΔH, due to the environmental force described by the perturbation $g(x)$ can be expressed
in terms of the population parameters and a number, δ, that represents the mean value of
the function $g(x)$ (Demetrius, 1989; Demetrius and Demongeot, in press).

The change Δr in the Malthusian parameter is given by

$$\Delta r = -\Phi\delta, \tag{9}$$

where Φ, the reproductive potential, is given by equation (6). The reproductive potential
can assume both positive and negative values, depending on the values of $V(x)$.

The result in equation (9) asserts that under the action of an external force, the change
in the growth rate is a product of the reproductive potential and the force. Hence when the
reproductive potential of the population is zero, external forces will induce no changes in
the growth rate. Populations with different reproductive potentials, when subject to the same
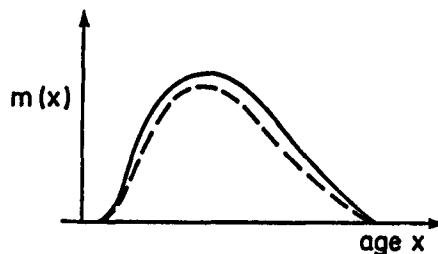force δ, will have different increases in growth rate.

Figure 2. The change in the shape of the fertility distribution due to an
environmental force with intensity δ. —, Original fertility distribution;
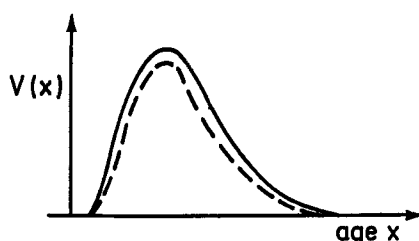– –, perturbed fertility distribution.

Figure 3. The change in the shape of the net-fertility distribution due to an environmental force with intensity δ. —, Original net-fertility distribution; – –, perturbed net-fertility distribution.

The incremental change ΔH in population entropy is given by

$$\Delta H = -P(\Phi)\delta, \qquad (10)$$

where

$$P(\Phi) = \frac{\displaystyle\int_0^\infty [x\Phi + \log V(x)]^2 p(x)\, dx}{\displaystyle\int_0^\infty xp(x)\, dx}. \qquad (11)$$

The function $P(\Phi)$, which can assume only nonnegative values, is called the reproductive energy. The result in equation (10) predicts that the response of the stability parameter H to an external force is a product of the reproductive energy and the force. Populations with different reproductive energies, when subject to the same force δ, will have different increases in entropy.

Table 1 summarizes the relations between the principal parameters discussed and the local changes of the Malthusian parameter and population entropy under the forces of natural selection and environmental action. The response due to selection is determined by the variance V_r and the covariance $C_{H,r}$; the response due to environmental action is determined by the environmental intensity δ.

Reconstructing the Past

Selection or Environmental Action?

The dynamical equations described by equations (3) and (4) show the changes in the growth rate and stability parameters as a consequence of selection. These equations enable

Table 1. The response of growth rate and population entropy to the forces of selection and environmental action

Force	Response	
	Growth rate	Population entropy
Natural selection	$\Delta r = V_r \Delta t$	$\Delta H = C_{H,r} \Delta t$
Environmental action	$\Delta r = -\Phi \delta$	$\Delta H = -P(\Phi)\delta$

us to predict the changes in r and H given the inherent variability in the population. The variance V_r is always nonnegative. When H is positively correlated with r, a condition that holds under weak selection, the covariance $C_{H,r}$ is nonnegative. Hence under weak selection, we have

$$\Delta r \geq 0, \quad \Delta H \geq 0. \tag{12}$$

Environmental action can induce increases and decreases in both r and H. We have from equations (9) and (10) that

$$\Delta r \Delta H = \Phi P(\Phi)\delta^2. \tag{13}$$

The expression $P(\Phi)$ is always nonnegative. The function Φ may be positive, zero, or negative. When Φ is positive, a condition that holds for most human populations, the function $P(\Phi)$ is also positive; and from equation (13), under environmental action,

$$\Delta r \Delta H > 0. \tag{14}$$

The problem of reconstructing the past involves invoking the local trends in r and H to distinguish between the action of natural selection and environmental action. The main difficulty in reconstructing the dynamics from the local changes arises because the changes in the aggregate parameters may result from the cumulative action of both environmental action and selection. To obviate this difficulty, I assume that at any instant the changes in demographic variables are due mainly to natural selection or mainly to environmental action. In other words, I claim that the demographic history of the human population can be described by periods of slow change under selective forces interrupted by episodes of abrupt demographic change due to environmental action (wars, epidemics, famine). Data on modern populations give some support to this claim. The data adapted from Turpeinen (1982) (see Fig. 4) describe the demographic history of Finland from 1751 to 1975.

The data show that both mortality and fertility have undergone a slow downward trend except for certain periods of abrupt changes of limited duration. The slow downward trend in mortality and fertility corresponds to changes in the frequency of the different types within the population due to the differential growth rate of the types. The episodic changes in mortality correspond to the incidence of wars, epidemics, and famines, which have a "point effect." Abrupt changes in fertility, such as the baby boom (1945–1950), are the result of changes in customs that also exert a point effect on childbearing practices. These patterns are characteristic of most modern populations.

When the processes of selection and environmental action act independently of each other, there exists a set of conditions under which the nature of the forces can be inferred from the local changes in the population variables. These conditions, which are derived in Demetrius and Demongeot (in press), are immediate consequences of the dynamical equations (12) and (14). These conditions, which are valid for populations whose reproductive potential Φ is positive, are expressed in terms of the relations between Δr and ΔH.

Natural selection acts when the following relations hold:

$$\Delta r = 0, \quad \Delta H > 0 \tag{15}$$

and

$$\Delta r > 0, \quad \Delta H = 0. \tag{16}$$

Condition (15) asserts that when the growth rate is stationary, local increases in population entropy imply the action of selection. Condition (16) asserts that when population entropy remains constant, local increases in the growth rate imply the action of selection.
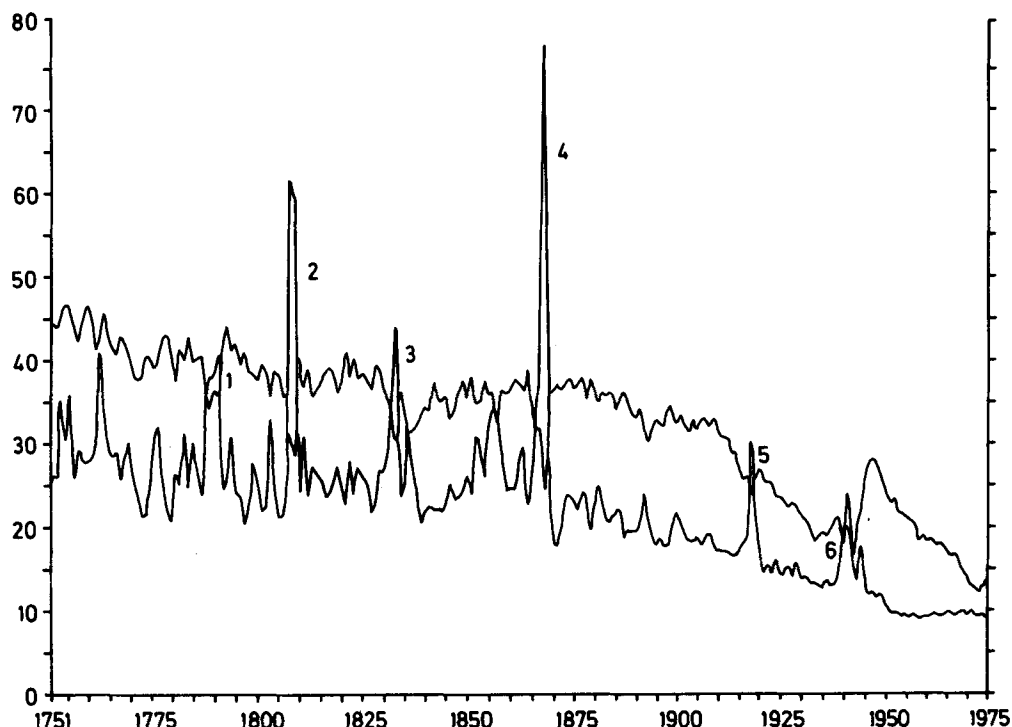
Figure 4. The variation in the crude birth and death rates for Finland (1751–1975). (1) 1778–1791—
epidemic following war with Russia; (2) 1807–1808—epidemics following war with Russia;
(3) 1832–1833—famine and epidemics; (4) 1867–1868—famines and epidemics;
(5) 1908—civil war; (6) 1939–1941 and 1941–1944—wars with the
Soviet Union. *Source:* Turpeinen (1982).

Environmental factors act when the following relation holds:

$$\Delta r < 0, \quad \Delta H < 0. \tag{17}$$

This condition states that simultaneous decreases in r and H imply environmental action.

The Intensity of Selection

Selection is an *internal* force the magnitude of which at each instant depends on the variance in demographic parameters within the population. The variance in age-specific fertility and mortality at any instant will result in both a variance in the Malthusian parameter and a variance in population entropy. As the dynamical equations describing selection indicate, the variance in the Malthusian parameter will induce a change in the growth rate, whereas the variance in population entropy will induce a change in the population stability. Hence the force of selection has two components: a component I_r, which represents the force due to the variance in growth rate, and a component I_H, which represents the force due to the variance in entropy. These two intensities can be measured by the changes Δr and ΔH in growth rate and population entropy, respectively.

These two measures of selective intensity can be separated into mortality and fertility components. In the case of the intensity I_r, the mortality component is measured by the change Δe_o in the mean life expectancy, e_o. This parameter is defined by $e_o = \int_0^\infty l(x)\,dx$. The fertility component is described by the change $\Delta \overline{m}$ in gross fertility $\overline{m}$, where $\overline{m} =$

$\int_0^\infty m(x)\, dx$. Similarly, the measure of the selective intensity I_H has a mortality component ΔH_l, where H_l is given by

$$H_l = -\int_0^\infty \frac{l(x)}{e_o} \log \frac{l(x)}{e_o}\, dx. \qquad (18)$$

The function H_l measures the variability in age-specific survivorship. When $\int_0^\infty x l(x)\, dx = \mu$ is finite, the quantity H_l is bounded. We have

$$H_l \leq 1 + \log(\mu/e_o). \qquad (19)$$

The fertility component of the selective intensity I_H is measured by ΔH_m, where

$$H_m = -\int_0^\infty m(x)/\overline{m} \, \log[m(x)/\overline{m}]\, dx. \qquad (20)$$

This expression measures the variability in the age-specific fertility distribution. When $\int_0^\infty x m(x)\, dx = \gamma$ is finite, the quantity H_m is also bounded. We have

$$H_m \leq 1 + \log(\gamma/\overline{m}). \qquad (21)$$

The proofs of the relations (19) and (21) are given in Demetrius (1989).

The Intensity of Environmental Action

Environmental action is a force the magnitude and direction of which is determined by the environmental factors that impinge on the population. This force, in contrast to the force of selection, is *external* and its action persists over a short period of time. The intensity of this force, in the case of epidemics, can be described in terms of the parameters characterizing the epidemic, such as the number of infective individuals and the contact rate. The effect of the force is measured by its action on the age-specific fecundity and mortality schedules and, consequently, by the change in the population growth rate and stability.

Equations (9) and (10) describe the change in the Malthusian parameter and population entropy, respectively, due to the action of an external force on the mortality–fecundity distribution.

In terms of the effect on growth rate, the intensity δ is given, using equation (9), by

$$\delta = -(1/\Phi)\Delta r. \qquad (22)$$

The quantity $-(1/\Phi)$ can be considered as characterizing a kind of growth inertia of the population. Thus expression (22) indicates that the intensity can be empirically assessed given the reproductive potential of the population and the increase in growth rate. In terms of its effect on population entropy, the intensity δ is given, using equation (9), by

$$\delta = -[1/P(\Phi)]\Delta H. \qquad (23)$$

The quantity $-[1/P(\Phi)]$ can be considered as a kind of stability inertia of the population. Expression (23) indicates that to compute the intensity, we need to know the reproductive energy and the increase in entropy.

The overall changes in r and H can be induced either by changes in nutrition, which will affect fertility, or changes in health care, which will affect mortality. The force δ can be broken down into components associated with mortality and fertility effects, respectively. The force on the mortality distribution is given by

$$\delta_l = -(\Delta e_o/e_o)(1/\Phi_l), \qquad (24)$$

where

$$\Phi_l = -\frac{\displaystyle\int_0^\infty l(x)\log l(x)\, dx}{\displaystyle\int_0^\infty l(x)\, dx}. \tag{25}$$

The expression Φ_l measures the convexity of the mortality distribution and is related to H_l by

$$\Phi_l = H_l - \log e_o. \tag{26}$$

Moreover, from equation (19), we have

$$\Phi_l \leq 1 + \log(\mu/e_o^2). \tag{27}$$

In effect, when $\mu/e_o \leq e_o$, a condition satisfied by most human populations, we have $\Phi_l \leq 1$.

The magnitude of the force δ_l indicates its mode of action. Larger values for δ_l indicate that the force affects predominantly juveniles; smaller values indicate that the mortality of older individuals has been mainly affected.

The force on the fecundity distribution is given by

$$\delta_m = -(\Delta m/\overline{m})(1/\Phi_m), \tag{28}$$

where

$$\Phi_m = -\frac{\displaystyle\int_0^\infty m(x)\log m(x)\, dx}{\displaystyle\int_0^\infty m(x)\, dx}. \tag{29}$$

This expression is related to H_m by

$$\Phi_m = H_m - \log \overline{m}. \tag{30}$$

Bounds for Φ_m analogous to those in equation (27) exist. Using equation (21),

$$\Phi_m \leq 1 + \log(\gamma/\overline{m}^2). \tag{31}$$

The mathematical basis for the expressions for the force given by equations (24) and (28) derives from the fact that the responses of the mean life expectancy e_o to changes in $l(x)$ and the mean fecundity $\overline{m}$ to changes in $m(x)$ satisfy relations analogous to that in equation (9) (Demetrius, 1989).

Expression (25), which describes the convexity of the life table, has been studied by several demographers in other contexts. The reader may refer to Vaupel (1986) and Vaupel and Yashin (1987) for studies concerning the impact of heterogeneity on mortality and Goldman and Lord (1986) and Mitra (1979) for studies relating equation (25) to other demographic parameters.

Table 2 summarizes the expression for determining the intensity of selection and environmental action in terms of changes in the demographic variables r and H.

An Indeterminacy Relation

The derivation of the conditions described by equations (15)–(17) is based on an important assumption: at any instant, either selection or environmental action predominates,

Table 2.   The intensity of selection and environmental action

Force	Total population	Mortality component	Fertility component
Selection			
Due to variance in H	ΔH	ΔH_l	ΔH_m
Due to variance in r	Δr	Δe_o	$\Delta \bar{m}$
Environmental action	$-\dfrac{\Delta r}{\Phi}$	$-\dfrac{\Delta e_o}{e_o}\dfrac{1}{\Phi_l}$	$-\dfrac{\Delta \bar{m}}{\bar{m}}\dfrac{1}{\Phi_m}$

so the demographic trends observed can be ascribed mainly to a single cause. Even when these conditions hold, however, there are intrinsic limitations to inferring the nature of the cause from the trends in the Malthusian parameter and entropy (Demetrius and Demongeot, in press). Fluctuations in the age distribution of the different types due to demographic disequilibrium may induce variations in the age-specific fecundity and mortality distributions of the total population and consequently fluctuations in the Malthusian parameter and population entropy. The inability to distinguish between these fluctuations and the variations in the Malthusian parameter and entropy due to selection and environmental action is the basis for these constraints. A formal characterization of these limits can be derived from equations (12) and (14) and is given by the condition

$$\Delta r > 0, \quad \Delta H > 0. \tag{32}$$

This condition asserts that a simultaneous increase in both r and H could be due to either selection or environmental action. When this condition holds, no inferences can be made concerning the selective or nonselective basis for the changes in demographic variables. Condition (32) makes explicit the limitations inherent in inferring the nature of the forces from the dynamical behavior of the demographic variables.

The Demographic Transition

During the last 200 years, the demographic experience common to most developed countries has been characterized by a major reduction in both fertility and mortality, the decline in mortality preceding that in fertility (Coale, 1974). In the 18th century, mean life expectancy was 35 years and the mean number of births per woman was 6.5. The present mean life expectancy is 70 years or more and the mean fertility has dropped to about 2 births per woman. This trend in birth and death rates, called the *demographic transition*, has been observed to accompany a nation's progression from a largely rural, agrarian, and at least partly illiterate society to a primarily urban, industrial society.

The transition is characterized by three phases:

1. The initial phase with high levels of mortality and with large fluctuations in the rates.

2. The transitional phase, characterized by a steady decline in mortality followed by a corresponding fertility decline.

3. Low mortality and fertility levels with small variations from year to year.

The causes of the events that determine these trends have been a source of debate among social historians and demographers (see Bengtsson, 1986; Coale, 1984; Teitelbaum, 1975).

The high mortality rate in phase 1 is considered a consequence of the absence of modern forms of sanitation, agriculture, and medicine. The decline in mortality in phase 2 is attributed to improved diet and a reduced incidence of epidemics. The further decline

in phase 3 is considered to be the result of better health care and the reduced incidence of diseases.

The high fertility rate in phase 1 is due to pronatalist norms developed to compensate for the high mortality rates. The decline in fertility is considered to be the result of changes in the perceived benefits of having children.

This explanation has generated considerable controversy, as the changes in fertility and mortality rates described are compatible with quite different mechanisms. Changes in fertility can arise either from the perceived benefits of having children and the cultural transmission of the idea of an ideal family size (cultural selection) or from the changes in laws and customs regulating marriage (environmental action). Changes in mortality can arise either from the adoption and spread of new sanitary measures (cultural selection) or from the introduction of vaccines to protect against diseases (environmental action).

To distinguish between these different mechanisms, one needs (a) criteria that distinguish between the effects of selection and those of environmental forces and (b) a quantitative description of the intensity of these two forces. The theory described in this article provides such criteria and gives analytic expressions for the intensity of the selective and nonselective forces. I will exploit this theory to characterize the different forces underlying the evolution of the demographic variables.

My analysis is based on the Swedish population, since the detailed demographic data for this population go back to the early 18th century. Data for the Swedish population are given in Demetrius and Ziehe (1984), based on the age-specific mortality and fertility schedule given in Keyfitz and Flieger (1968).

Table 3 gives the values for the parameters r, H, Φ, e_o, $\overline{m}$, H_l, H_m, Φ_l, and Φ_m. These values are based on the fertility and mortality schedules of the female population. Thus the quantity e_o represents the mean life expectancy of the female population and $\overline{m}$ describes the mean number of female offspring produced by a female during her lifetime.

Demographic Trends: Description

Prior to an analysis of the trends given in Table 1, several points must be made concerning the properties of the parameters and the range of values they assume. These remarks discuss the relation between parameters with similar properties and also compare the responses of the parameters to environmental changes.

Population Entropy: Intrinsic and Cohort.   The theory described in this article revolves around the parameters r, H, and Φ, which are related as follows: $r = H - \Phi$. An equivalent theory can be shown to hold for the parameters R, H^*, and Φ^* with the relation $\log R = H^* - \Phi^*$. The parameters R, H^*, and Φ^*, which are discussed in Demetrius (1979), are defined as follows:

$$R = \int_0^\infty l(x)m(x)\,dx$$

$$H^* = -\frac{\int_0^\infty q(x)\log q(x)\,dx}{\int_0^\infty xq(x)\,dx}$$

$$\Phi^* = -\frac{\int_0^\infty q(x)\log l(x)m(x)\,dx}{\int_0^\infty xq(x)\,dx},$$

where

$$q(x) = \frac{l(x)m(x)}{R}$$

The expression H given by equation (2) may be called the intrinsic entropy because it is defined in terms of the function $p(x)$, which depends on the stable age distribution. The expression H^* may be called the cohort entropy because it is defined in terms of the function $q(x)$, which depends on the net reproductive rate.

Numerical studies using the Swedish data have shown that H and H^* show the same trends. Therefore, analyses based on intrinsic and cohort entropy should yield similar results concerning the incidence of selective and nonselective factors.

Changes in r and H. Expressions (9) and (10) describe the changes in r and H due to environmental action. Numerical studies using equations (9) and (10) have shown that the changes in r are in general greater than the changes in H. Hence under environmental

Table 3.   Values of the demographic parameters, Sweden

Year	e_o	m_o	Φ_l	Φ_m	H_l	H_m	r	H	Φ
1778	41.38	2.21	0.626	0.915	4.348	1.708	0.0062	0.0493	0.0431
1783	39.46	2.00	0.658	1.008	4.333	1.701	0.0020	0.0491	0.0471
1788	40.25	2.19	0.634	0.952	4.329	1.735	0.0048	0.0491	0.0443
1793	43.10	2.19	0.585	0.907	4.348	1.690	0.0077	0.0489	0.0413
1798	41.83	2.03	0.602	0.987	4.318	1.695	0.0047	0.0488	0.0442
1803	43.49	2.08	0.567	0.965	4.374	1.697	0.0067	0.0490	0.0423
1808	35.74	2.10	0.695	0.942	4.271	1.683	0.0017	0.0486	0.0470
1813	43.64	2.13	0.569	0.922	4.345	1.678	0.0074	0.0485	0.0411
1818	43.77	2.20	0.565	0.893	4.344	1.681	0.0084	0.0485	0.0400
1823	49.19	2.30	0.474	0.847	4.369	1.679	0.0131	0.0487	0.0356
1828	44.14	2.21	0.544	0.878	4.333	1.671	0.0093	0.0481	0.0388
1833	47.48	2.28	0.497	0.838	4.357	1.662	0.0120	0.0479	0.0359
1838	47.02	2.16	0.504	0.878	4.355	1.648	0.0099	0.0471	0.0372
1843	47.99	2.13	0.491	0.883	4.362	1.639	0.0099	0.0467	0.0368
1848	49.04	2.10	0.475	0.900	4.367	1.642	0.0100	0.0466	0.0366
1853	45.37	2.09	0.538	0.911	4.352	1.648	0.0075	0.0465	0.0390
1858	49.24	2.23	0.487	0.853	4.384	1.655	0.0111	0.0469	0.0357
1863	49.90	2.20	0.475	0.871	4.385	1.659	0.0112	0.0472	0.0360
1868	49.62	2.01	0.478	0.957	4.382	1.655	0.0085	0.0470	0.0384
1873	49.93	2.20	0.483	0.882	4.393	1.670	0.0111	0.0480	0.0369
1878	52.14	2.10	0.453	0.938	4.406	1.679	0.0107	0.0485	0.0377
1883	53.72	2.09	0.428	0.950	4.411	1.687	0.0115	0.0488	0.0373
1888	55.02	2.00	0.404	0.997	4.411	1.690	0.0111	0.0490	0.0380
1893	56.61	1.96	0.385	1.013	4.421	1.685	0.0112	0.0493	0.0381
1898	56.79	1.94	0.381	1.030	4.420	1.693	0.0111	0.0499	0.0388
1903	59.24	1.84	0.314	1.082	4.390	1.692	0.0109	0.0502	0.0393
1908	61.35	1.73	0.314	1.149	4.430	1.697	0.0103	0.0509	0.0406
1913	61.99	1.50	0.304	1.299	4.431	1.704	0.0062	0.0510	0.0448
1918	61.08	1.38	0.315	1.375	4.427	1.697	0.0036	0.0513	0.0477
1923	66.07	1.12	0.248	1.593	4.438	1.706	−0.0008	0.0514	0.0522
1928	66.44	0.93	0.241	1.774	4.437	1.701	−0.0060	0.0520	0.0580
1933	68.45	0.83	0.214	1.877	4.440	1.690	−0.0090	0.0520	0.0610
1938	70.73	0.93	0.186	1.629	4.445	1.556	−0.0046	0.0521	0.0566
1943	72.40	1.22	0.167	1.444	4.449	1.643	0.0046	0.0525	0.0479
1948	74.92	1.12	0.138	1.529	4.454	1.642	0.0026	0.0536	0.0510
1953	76.28	1.09	0.125	1.518	4.459	1.604	0.0019	0.0531	0.0512
1958	77.22	1.08	0.117	1.492	4.464	1.568	0.0017	0.0524	0.0506
1965	77.93	1.18	0.112	1.400	4.467	1.565	0.0048	0.0528	0.0480

action, r should show greater variability than H. This is evident from the data. The differences in variation between r and H are most pronounced during the periods 1778–1858 and 1928–1963. The changes during these two periods, as the analysis will indicate, are determined primarily by environmental action.

The Parameters Φ_l *and* Φ_m. The observed values of the parameter Φ_l satisfy the condition $0 \leq \Phi_l \leq 1$. The value $\Phi_l = 0$ corresponds to a rectangular survivorship and $\Phi_l = 1$ an exponential curve. The trends in Φ_l show that there has been a continuous change in the shape of the survivorship with a tendency toward the rectangular form. The changes in Φ_m, by contrast, are highly irregular. These differences suggest a basic asymmetry in the dynamic describing the mortality and fertility schedule.

Demographic Trends: Analysis

The trends described by the birth and death rates fall into three main patterns, reflecting the three phases of the demographic transition. The three phases can be roughly described by the periods 1778–1858, 1858–1928, and 1933–1965. An examination of the data will show that it is instructive to decompose the first phase into two periods, 1778–1828 and 1828–1858.

1778–1828. This period is characterized by high levels of mortality and fertility with large variations from year to year. The trends in mortality are described by the low mean life expectancy and large variations in Φ_l. The variations in fertility, as described by $\bar{m}$ and Φ_l, are less pronounced. This period shows strong fluctuations in r and a constant decrease in H. The trends in r and H imply that the dominant force acting is environmental action. In other words, the forces determining evolutionary change are external factors. A more detailed understanding of the nature of these forces can be obtained by partitioning the force δ as described by equation (22) into the mortality and fertility components given by equations (24) and (28).

The changes are described in Table 4. A comparison of the values of δ_l and δ_m indicates that in the early phase in this period, changes were induced primarily by the effect on fertility, which decreased. Subsequently, environmental changes were expressed through the effect on survivorship, with periods in which a very strong reduction in survivorship occurred. In particular, the periods 1803–1808 ($\delta_l = 0.314$) and 1823–1828 ($\delta_l = 0.216$) suggest a very high infant mortality, indicating epidemics as a possible principal cause of death. These observations are consistent with historical data. The very high mortality figures during 1803–1808 coincided with the Finnish War (1806–1809). The period 1823–1828 coincided with

Table 4. The intensity of environmental action on fertility and mortality components, Sweden (1778–1828)

Period	Δe_o	δ_l	$\Delta \bar{m}$	δ_m
1778–1783	−1.92	0.074	−0.21	0.104
1783–1788	0.79	−0.030	−0.19	0.094
1788–1793	2.85	−0.112	0	0
1793–1798	−1.27	0.050	−0.16	−0.080
1798–1803	1.66	−0.066	0.05	−0.024
1803–1808	−7.75	0.314	0.02	−0.009
1808–1813	7.9	−0.318	0.03	−0.015
1813–1818	0.13	−0.005	0.07	−0.035
1818–1823	6.02	−0.246	0.10	−0.051
1823–1828	−5.05	0.216	−0.09	0.046

the incidence of famine. The epidemics that spread during these two periods are known to have had their strongest effects on infant mortality (Hofsten and Lundstrom, 1976).

1828–1858. The fluctuations in mortality and fertility during this period are less severe than that observed in the preceding period. The parameter r undergoes very little change and remains relatively constant over the period 1838–1858. The parameter H shows a continuous decrease. These trends in r and H imply that environmental action is the dominant mechanism. Partitioning these forces into a mortality and a fertility component yields Table 5.

This period is characterized by a general but regular increase in mean life expectancy and a general decrease in mean fecundity. A comparison of δ_l and δ_m shows that the environmental forces acted primarily through the effect on survivorship. The anomalous period (1848–1853) points to a strong environmental component, possibly epidemics, resulting in a change in mean life expectancy. This period coincided with several epidemics of cholera (Hofsten and Lundstrom, 1976). According to the Swedish data, cholera had a major influence on adult mortality and a minor effect on mortality in adolescence. The value of the mortality force for this period ($\delta_l = 0.157$) is consistent with this historical fact. This value should be contrasted with the mortality force ($\delta_l = 0.316$) during 1803–1808, when the epidemic affected primarily juveniles.

1858–1928. This period is characterized by reduced mortality (a constant increase in e_o and a constant decrease in Φ_l) and declining fertility (a constant decrease in $\overline{m}$). The parameter r shows very small fluctuations, whereas H shows a continuous increase. The trends in r and H indicate that natural selection is the dominant mechanism. The indices H_l and H_m also show a constant increase over this period except for the intervals 1898–1903 and 1918–1923. These two periods show a large increase in mean life expectancy. The magnitude of this increase during these two periods suggests an environmental factor such as the elimination of diseases.

The selective force acting on the whole population and the selective forces associated with the mortality and fertility distributions are given in Table 6. These forces are computed by considering the differences ΔH_l and ΔH_m at each period. The data indicate that there is no great difference between selection due to the mortality differences and selection due to fertility differences. I should point out here that the arguments in this article do not in general enable one to distinguish between selection due to genetics and that due to cultural mechanisms. This is simply because, as pointed out earlier, the dynamical equations from which the expressions for Δr and ΔH are derived are valid for models of both genetic and cultural transmission. By examining the range of variation assumed by the parameters ΔH_m and ΔH_l, however, some inference may be drawn from the data concerning the incidence of cultural and genetic transmission.

Table 5.   The intensity of environmental action on fertility and mortality components, Sweden (1828–1863)

Period	Δe_o	δ_l	$\Delta \overline{m}$	δ_m
1828–1833	3.34	−0.139	0.07	−0.036
1833–1838	0.46	−0.019	−0.12	0.063
1838–1843	0.97	−0.041	−0.03	0.015
1843–1848	1.05	−0.044	−0.03	0.016
1848–1853	−3.67	0.157	−0.01	0.005
1853–1858	4.53	−0.185	0.14	0.073
1858–1863	0.66	−0.027	−0.03	0.016

Table 6.   The intensity of selection on fertility and
mortality components, Sweden (1858–1928)

Year	ΔH_l	ΔH_m	ΔH
1858	0.032	−0.007	0.0004
1863	0.001	−0.004	0.0003
1868	−0.003	−0.004	−0.0002
1873	0.001	0.015	0.0010
1878	0.013	0.009	0.0005
1883	0.005	0.008	0.0003
1888	0.000	0.003	0.0002
1893	0.010	−0.005	0.0003
1898	−0.001	0.008	0.0005
1903	−0.030	−0.001	0.0003
1908	0.040	0.005	0.0007
1913	0.001	0.007	0.0001
1918	−0.004	−0.007	0.0003
1923	0.011	0.009	0.0001
1928	−0.001	−0.005	0.0006

Cultural selection and environmental action are strong forces. Although the mechanisms of action of these two forces are distinct, they can exert comparable effects on the life table and fertility schedules. Hence the changes in ΔH_l and ΔH_m due to cultural selection and environmental action will be of the same order of magnitude. Genetic selection, by contrast, is a weak force; hence its effect on the mortality and fertility schedules will be comparatively small. The changes in ΔH_l and ΔH_m due to genetic selection will therefore be of a lower order of magnitude in comparison with changes due to cultural selection or environmental action.

These analyses have shown that the change in the first period (1778–1858) is due to environmental action, whereas that in the second period (1858–1928) is due to selection, which may be cultural or genetic. A comparison of the changes in both ΔH_l and ΔH_m in these periods shows that the variations in these two quantities are of the same order of magnitude in both periods. These observations indicate that the dominant mechanism inducing changes in the second period is cultural selection.

1933–1965.   This period is described by oscillations in birth and death rates. This is indicated by the variations in the parameters e_o and Φ_l, characterizing the mortality rates, and the variations in m_o and Φ_m, characterizing the fertility rates. The parameters r and H also fluctuate. These fluctuations show a tendency toward a decrease in both r and H, implying that environmental action is now the dominant mechanism. The force on mortality and fecundity can also be compared by evaluating δ_l and δ_m.

Table 7 shows the changes in δ_l and δ_m. These changes show that mortality effects make up a large fraction of the intensity of the environmental forces, which is also consistent with historical fact. Most of the demographic change during this period arose from improved health care and improved nutrition, these factors having a strong effect on survivorship.

Summary

The finding that the pretransitional phase (1778–1858) is dominated by environmental effects is consistent with sociological and historical analysis of the period as described in Hofsten and Lundstrom (1976). The analysis given here, however, quantifies the intensity of these environmental effects. The high intensity of environmental action on survivorship

Table 7. The intensity of environmental action on fertility and
mortality components, Sweden (1933–1965)

Period	Δe_o	δ_l	$\Delta \bar{m}$	δ_m
1933–1938	2.01	−0.126	−0.10	0.060
1938–1943	2.28	−0.156	0.10	−0.064
1943–1948	1.67	−0.127	0.29	−0.191
1948–1953	2.52	−0.208	−0.10	0.056
1953–1958	1.36	−0.131	−0.03	0.017
1958–1963	0.94	−0.098	−0.01	0.006
1963–1965	0.71	−0.078	0.10	−0.062

in this period is in accord with historical fact: epidemics exerted a great effect on mortality up to 1820, when compulsory vaccination for all children was instituted.

The observation that the changes in the second period (1858–1928) are due to cultural selection resolves the controversy concerning selection and environmental action as mechanisms of change for this transitional period. A mechanism consistent with my model for cultural selection involves different social groups with small variations between the groups in terms of growth rate, but large variations in terms of both fertility and mortality rates. If one assumes that a high educational level of the individuals in each group is correlated with a low mortality rate (as it improves access to better health care) and a low fertility rate (because of the cost of education), then the spread of education by vertical, oblique, and horizontal transmission will rapidly generate a population with low fertility and low mortality rates.

The finding that in the third period (1933–1965), environmental action dominates is consistent with sociological studies of the period. This analysis provides a sharper understanding by quantifying the intensity of the effects. The large value of the mortality intensity in the first period compared with the third period is consistent with the fact that the increased mortality in the first period (due to famines and epidemics) affected mainly younger individuals, whereas the reduced mortality in the third period (due to nutrition and better health care) affected primarily adults.

Conclusion

The analysis in this article shows that when selective and nonselective factors are relatively independent, then for a large class of populations, criteria exist that specify the nature of the forces determining demographic change. The analysis, when applied to a study of the demographic transition in Sweden, shows that during the transitional period, cultural selection is the dominant mechanism. The problem addressed here has been considered by a large number of demographers, using mainly qualitative arguments. These arguments have the advantage that they can incorporate all of the diverse forces—sociological, economic, and biological—that influence demographic patterns. These arguments lack a sharp quantitative basis, however, and for this reason, mechanisms are sometimes confounded. The controversy concerning the demographic transition attests to the ambiguity that these arguments sometimes generate.

This article has adopted a mathematical approach based on a theory of demographic change that sharply distinguishes between the effects of selective and nonselective factors as well as between genetic and cultural modes of transmission. The approach has the advantage of leading to precise predictions that can be quantitatively assessed. It has the disadvantage that unlike the qualitative models, certain simplifying assumptions must be invoked. Two central assumptions underlie the application of the theory to the Swedish data.

The first assumption concerns weak selection. This mode of selection refers to small differences in the age-specific mortality and fecundity of the types constituting the population. When demographic changes are induced by genetic transmission, this is a valid asssumption because different genotypes in human populations do exhibit very small differences in their reproduction and mortality schedule. When demographic changes are generated by cultural transmission, however, the assumption is no longer valid. In this case the weak selection condition can be relaxed if one now imposes the hypothesis that the demographic changes are induced primarily by vertical transmission. Under this mode of cultural transmission, the different types in the population will evolve independently and the dynamical equations describing the changes in demographic parameters will hold even though the differences in fecundity and mortality of the competing types are large.

The second main assumption concerns the independence of selective and nonselective forces. This condition can be relaxed without invoking further hypotheses. My argument indeed shows that my analysis requires simply that at any instant, the effect of one of the forces be dominant. This condition is fulfilled by most human populations when changes are viewed on a sufficiently long time scale. This is evident from a study of the demographic changes in Finland and Sweden over the 200-year period discussed in this article. On smaller time scales, the notion of a dominant force may be meaningless due to the interaction between the two forces. Hence although there may be episodes of nonselective action during the transitional phase (1850–1930), the model is unable to detect them.

Acknowledgment

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