Growth Rate, Population Entropy, and Perturbation Theory

LLOYD DEMETRIUS

Max Planck Institut für Biophysikalische Chemie, 3400 Göttingen, West Germany

Received 2 December 1987; revised 11 July 1988

ABSTRACT

This paper is concerned with the connection between two classes of population variables: measures of population growth rate—the Malthusian parameter, the net reproduction rate, the gross reproduction rate, and the mean life expectancy; and measures of demographic heterogeneity—population entropy. It is shown that the entropy functions predict the response of the growth rate parameters to perturbations in the age-specific fecundity and mortality schedule. These results are invoked to introduce the notion of environmental intensity. The intensity function, expressed in terms of the entropy parameters, is applied to give a comparative study of the effect of environmental factors on the dynamics of Swedish and French populations.

INTRODUCTION

The population variables studied in demographic theory as developed by Lotka [16], can be described in terms of two classes: (1) individual variables, namely, age-specific fecundity and mortality; and (2) aggregate variables such as the Malthusian parameter, net reproduction rate, gross reproduction rate, and mean life expectancy. A recurrent issue of both theoretical and practical import in demographic studies concerns the response of the aggregate variables to arbitrary perturbations in the values of the individual parameters. This response clearly depends on the shape of the fecundity-mortality function. Thus in order to assess these effects, one needs quantitative measures of the dispersion of the age-specific fecundity-mortality distribution.

A class of functions characterizing these distributions was introduced in earlier work [5, 6]. The generic term *entropy* was used to describe these functions on account of their connection to certain concepts in thermodynamic theory. In effect, these measures of heterogeneity of the age-specific fecundity-mortality distributions were obtained by showing that the Malthusian parameter satisfies an extremal principle that is formally identical to the

159

minimization of free energy in statistical mechanics. This variational principle was invoked to derive a precise correspondence between the parameters in demographic models and the concepts in thermodynamic theory. A detailed account of this development is given in [7] and [8].

This paper is concerned with certain perturbation properties of the demographic parameters. We show that the entropy functions predict both the magnitude and direction of the response of the classical population variables growth rate, reproduction rate, and mean life expectancy to arbitrary perturbations in the individual age-specific parameters.

The results we obtain for the four population variables considered can be summarized as follows:

The Malthusian parameter r. This parameter represents the asymptotic growth rate of the population. We show that the response of r to arbitrary perturbations in the net fecundity distribution is given by the entropy of the probability distribution of the age of the reproducing individuals in the stable population.

The net reproduction rate R. This parameter describes the increase in population per generation and represents the average number of offspring for individuals who from birth are subject to a given fecundity and mortality schedule. We show that the relative response of R to arbitrary perturbations in the net fecundity distribution is determined by the entropy of the net fecundity distribution.

The gross reproduction rate \overline{m} . This describes the average number of offspring born for individuals who throughout the reproductive period give birth to offspring according to the age-specific fecundity schedule. We show that the relative response of \overline{m} to arbitrary perturbations in age-specific fecundity is determined by the entropy of the age-specific fecundity schedule.

The mean life expectancy e_0 . This variable measures the average expectation of life at birth. We show that the relative response of e_0 to arbitrary perturbations in the life table is determined by the entropy of the life table.

These results, which predict the response of the growth rate parameters to perturbations, are important in the study of human populations in assessing:

- (a) The effect of mortality changes, such as the elimination of heart disease and cancer, on the mean life expectancy
- (b) The influence of fertility changes, such as the introduction of new contraceptive measures, on gross fecundity
- (c) The response of population growth rate due to the influx of new migrants

Indeed, one item in this set of problems has been investigated by Keyfitz [14] in an application of the entropy of the survivorship curve. Keyfitz

showed that the response of the mean life expectancy to uniform changes in the shape of the survivorship curve was determined by the entropy of the survivorship curve and used this fact to give an empirical study of the effect of the elimination of cancer on mean life expectancy.

These perturbation results can be invoked to introduce the notion of environmental intensity. Factors such as epidemics, famines, improved nutrition, and health care induce changes in the age-specific fertility and mortality schedules and consequently changes in the growth rate parameters. The intensity of these environmental factors can be expressed, using the perturbation results, in terms of the entropy functions and the change in the growth rate parameters. This measure of environmental intensity is important in studying the dynamics of evolutionary change in populations subject to different environmental forces. This paper applies this notion of environmental intensity to give a comparative study of the dynamics of Swedish and French populations.

This paper is organized as follows: Section 1 describes the individual variables that appear in demographic theory and the aggregate variables, which are functions of the individual parameters. We distinguish explicitly between the classical population parameters—growth rate and net reproduction rate—which are integral to the Lotka theory and the new class of population parameters called entropy, derived from the demographic models introduced in [5] and [6]. In Section 2, we study the response of the classical population variables to arbitrary perturbations in the age-specific fecundity and mortality schedule and show that this response is completely determined by the entropy functions. In Section 3 we introduce the notion of environmental intensity and use the perturbation results to define this quantity. A comparative study of the environmental effects on evolutionary change in Sweden and France is given in Section 4.

1. THE POPULATION PARAMETERS

1.1. THE INDIVIDUAL PARAMETERS

The age composition of a population that neither gains nor loses by migration and lives in a stable environment is determined by the individual parameters—age-specific fecundity m(x) and age-specific mortality $\mu(x)$. The dynamics of the age distribution u(x,t) are given by

$$\frac{\partial u}{\partial x} + \frac{\partial u}{\partial t} = -\mu(x)u(x,t) \tag{1.1}$$

The boundary conditions are

$$u(0,t) = \int_0^\infty m(x) \, u(x,t) \, dx \tag{1.2}$$

$$u(a,0) = f(a) \tag{1.3}$$

where f(a) denotes the initial age distribution.

The age-specific survivorship l(x) is given by

$$l(x) = \exp\left[-\int_0^x \mu(t) dt\right]$$
 (1.4)

1.2. THE AGGREGATE PARAMETERS

The aggregate parameters are functions of age-specific fecundity and the mortality schedule. We will distinguish between two classes of aggregate parameters. The first class consists of the growth rate and the net reproduction rate, which are derived from the Lotka theory [16], which is based on the dynamics of the age distribution. The second class consists of the entropy functions, which are derived from the dynamics of the distribution of genealogies [5, 8].

Growth and Reproduction Rate Parameters. The models which form the basis of the Malthusian parameters revolve around the notion of a stable age distribution. This notion describes the state of the population when the relative proportion of individuals in each age class is constant.

The Malthusian parameter r is the rate of increase of the population at the stable age distribution. This parameter r can be shown, using the dynamical system described by (1.1), to be the unique real root of the equation

$$\int_{0}^{\infty} \exp(-rx) \, l(x) \, m(x) \, dx = 1 \tag{1.5}$$

The net reproduction rate R, which is the rate of growth of population numbers per generation, is given by the expression

$$R = \int_0^\infty l(x) m(x) dx \tag{1.6}$$

This number is precisely the area under the net maternity function V(x) = l(x)m(x) and represents the number of offspring who from birth are subject to the fecundity schedule m(x) and survivorship schedule l(x).

The expressions for the gross reproduction rate and mean life expectancy can be derived from R.

The gross reproduction rate is the average number of offspring born to individuals who pass through the entire childbearing span giving birth to offspring according to the schedule m(x). This number \overline{m} is given by

$$\overline{m} = \int_0^\infty m(x) \ dx \tag{1.7}$$

The quantity \overline{m} can be considered the rate of increase per generation of a population with fecundity schedule m(x) and a mortality schedule given by l(x) = 1.

The mean life expectancy e_0 is the average expectation of life at birth. This quantity is given by

$$e_0 = \int_0^\infty l(x) \ dx \tag{1.8}$$

The number e_0 can be considered the rate of increase per generation of a population with mortality schedule l(x) and a fecundity schedule m(x) = 1.

The Entropy Parameters. The models that constitute the basis of the entropy parameters revolve around the notion of a genealogy [7, 8]. A genealogy describes the set of descendants and ancestors of a given individual, these ancestors and descendants being indexed by the age at which they produce offspring.

The equilibrium distribution of the genealogies is given by a probability measure whose marginal distribution expressed in terms of the age of reproducing individuals in the stable population is given by

$$p(x) = \exp(-rx)l(x)m(x)$$

Here r is the Malthusian parameter defined by (1.5).

The asymptotic rate of increase per unit time of the number of typical genealogies is given by the quantity

$$H = -\frac{\int_0^\infty p(x) \log[p(x)] dx}{\int_0^\infty x p(x) dx}$$
 (1.9)

This number is the ratio of the entropy of the probability distribution p(x) and the mean age of childbearing in the stable population. This mean age, denoted by T, is called the *generation time*. The quantity H is bounded if T is finite; we have (see the appendix)

$$H \leq (1 + \log T)/T$$

The rate of increase per generation of the number of typical genealogies is the quantity H_R given by

$$H_R = -\int_0^\infty q(x)\log[q(x)] dx \tag{1.10}$$

where

$$q(x) = l(x)m(x)/R$$

Expression (1.10) is the entropy of the net fecundity distribution q(x). The quantity H_R is bounded provided

$$\alpha = \int_0^\infty x q(x) \ dx$$

is finite. We have (see appendix)

$$H_R \leq 1 + \log \alpha$$

The expressions for the entropy of the fecundity distribution and the life table can be derived from H_R .

The entropy of the fecundity distribution H_m is given by

$$H_{m} = -\int_{0}^{\infty} \frac{m(x)}{\overline{m}} \log \frac{m(x)}{\overline{m}} dx$$
 (1.11)

where \overline{m} is given by (1.7). This quantity describes the dispersion of the fecundity distribution and can be considered to measure the entropy of the net fecundity distribution for a population with a fecundity distribution m(x) and a life table l(x) = 1.

Tne entropy of the life table is given by

$$H_{l} = -\int_{0}^{\infty} \frac{l(x)}{e_{0}} \log \frac{l(x)}{e_{0}} dx$$
 (1.12)

where e_0 is given by (1.8). This expression measures the heterogeneity in the age-specific survivorship curve. The quantity H_l can be considered as describing the entropy of the net fecundity distribution for a population with a fecundity distribution m(x) = 1 and a life table l(x).

2. PERTURBATION THEORY

The parameters that emerge from the dynamics of the age distribution determine population numbers. The parameters that emerge from the dynamics of the genealogies determine the rates at which population numbers fluctuate when deviations from the stable age distribution occur [6].

We will show in this section that the entropy functions measure the effect of fluctuations in another sense: The entropy functions determine the response of the population parameters to arbitrary perturbations in the shape of the fecundity and mortality distributions.

2.1. PERTURBATIONS OF THE FECUNDITY-MORTALITY PATTERNS

We will consider continuous perturbations of the net fecundity distribution. We denote by a and b the lower and upper limits, respectively, of the age of reproduction, and we consider a continuous function g(x), where

$$-\varepsilon \leqslant g(x) \leqslant \varepsilon \quad \text{for } a \leqslant x \leqslant b$$

We consider perturbations in V(x) given by the function

$$V^*(x) = V(x)^{1+g(x)}$$
 (2.1)

The change $\delta V(x)$ in the net reproductive function is

$$\delta V(x) = V(x) \left[V(x)^{g(x)} - 1 \right]$$

Hence, we have

$$\delta V(x) = V(x) \left[\exp[g(x)\log V(x)] - 1 \right] \tag{2.2}$$

Expression (2.2) describes the change in the net maternity function due to perturbations given by (2.1). Throughout the analysis in Section 2, we assume that the following condition holds:

Condition A. There exists a k > 0 such that either (i) $V(x) \ge 1 + k$ for $a \le x \le b$ or (ii) $V(x) \le 1 - k$ for $a \le x \le b$.

Condition A implies that $V(x) \neq 1$ and hence that $\log V(x)$ does not change sign in the interval $a \leq x \leq b$. Condition A is fulfilled by most human populations.

Expressions similar to (2.2) exist if the continuous perturbations in V(x) are restricted to the fecundity and mortality distributions, respectively. The changes $\delta m(x)$ and $\delta l(x)$ due to continuous perturbations in the fecundity and mortality distributions, respectively, are given by

$$\delta m(x) = m(x) \{ \exp[g_m(x) \log m(x)] - 1 \}$$
 (2.3)

$$\delta l(x) = l(x) \left\{ \exp\left[g_l(x)\log l(x)\right] - 1 \right\} \tag{2.4}$$

Here $g_m(x)$ and $g_l(x)$ are the analogues of g(x).

We now analyze the effect of perturbations of type (2.2)–(2.4) on the different aggregate parameters. Our analysis exploits the methods of functional differentiation. An excellent introduction to these methods suitable for demographers is developed in Arthur [1]. Arthur was concerned with the response of the Malthusian parameter to changes in the shape of the fecundity-mortality distribution and derived closed-form expressions for

the changes in this growth rate parameter. These results extended the work of earlier researchers [4, 12, 13]. The analysis in this paper applies the method of functional differentiation to obtain analogous closed-form expressions for the growth rate parameters. We then consider perturbations of the form described by (2.2)–(2.4) and, by invoking the mean value theorem for integrals, show that the responses of the growth rate parameters are completely determined by the entropy functions originally derived from the study of the model based on the genealogies.

2.2. THE MALTHUSIAN PARAMETER AND ENTROPY

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

$$\int_{a}^{b} \exp(-rx) V(x) dx = 1$$
 (2.5)

By differentiating (2.5), we obtain

$$\int_{a}^{b} \exp(-rx) \, \delta V(x) \, dx = \delta r \int_{a}^{b} x \exp(-rx) \, V(x) \, dx \tag{2.6}$$

We have from (2.6)

$$\delta r = \frac{\int_a^b \exp(-rx) \, \delta V(x) \, dx}{T} \tag{2.7}$$

where $T = \int_a^b x p(x) dx$ is the mean generation time and

$$p(x) = \exp(-rx)V(x) \tag{2.8}$$

The closed-form expression (2.7) was originally derived in [1].

The connection between the Malthusian parameter and entropy is derived by analyzing (2.7) using the continuous perturbations given by (2.2). We note from (2.2) and (2.7) that

$$\delta r = \frac{1}{T} \int_{a}^{b} \exp(-rx) V(x) \{ \exp[g(x) \log V(x)] - 1 \} dx$$
 (2.9)

By condition A, $\log V(x) \neq 0$, and hence expression (2.9) becomes

$$\delta r = \int_{a}^{b} \frac{p(x) \log V(x)}{T} \left[\frac{\exp[g(x) \log V(x)] - 1}{\log V(x)} \right] dx \qquad (2.10)$$

Thus

$$\delta r = \int_{a}^{b} \frac{p(x) \log V(x)}{T} F(x) dx \tag{2.11}$$

where

$$F(x) = \frac{\exp[g(x)\log V(x)] - 1}{\log V(x)}$$
 (2.12)

Since $p(x) \ge 0$, we conclude from condition A that $p(x)\log V(x)$ does not change sign in the interval $a \le x \le b$. We can now apply the mean value theorem to the right-hand side of (2.11). We conclude that there exists a number η , $a \le \eta \le b$, such that

$$\delta r = F(\eta) \int_{a}^{b} \frac{p(x) \log V(x)}{T} dx \tag{2.13}$$

where

$$F(\eta) = \frac{\exp[g(\eta)\log V(\eta)] - 1}{\log V(\eta)}$$
 (2.14)

Write

$$g(\eta) = \delta$$

Now consider the expression for δr given by (2.13) and let r^* denote the perturbed Malthusian parameter and $\Delta r = r^* - r$. Using (2.13) and (2.14) and expanding $F(\eta)$ in terms of δ , we obtain

$$\lim_{\delta \to 0} \frac{\Delta r}{\delta} = \int_{a}^{b} \frac{p(x)\log V(x) dx}{T}$$
 (2.15)

Write

$$\Phi = -\int_{a}^{b} \frac{p(x)\log V(x) dx}{T}$$

This expression is called the *reproductive potential*. We have from (1.9) that the following identity holds;

$$r = H - \Phi \tag{2.16}$$

Hence from (2.15) and (2.16)

$$\left. \frac{dr}{d\delta} \right|_{\delta = 0} = -\Phi = r - H \tag{2.17}$$

Equation (2.17) asserts that the changes in the Malthusian parameter due to small age-specific perturbations in the life cycle are determined by the entropy of the fecundity-mortality distribution.

For δ small, (2.17) becomes

$$\Delta r \simeq -\Phi \delta = (r - H)\delta \tag{2.18}$$

2.3. THE NET REPRODUCTION RATE AND ENTROPY

The net reproduction rate R is given by

$$R = \int_{a}^{b} V(x) dx \tag{2.19}$$

To assess the effect of continuous perturbations in V(x) on R, we use (2.2) and obtain

$$\delta R = \int_{a}^{b} V(x) \left[\exp\{ (gx) \log V(x) \} - 1 \right] dx$$
 (2.20)

Thus

$$\delta R = \int_{a}^{b} V(x) \log V(x) \left[\frac{\exp[g(x) \log V(x)] - 1}{\log V(x)} \right] dx \qquad (2.21)$$

By applying the mean value theorem as in (2.13), we observe that there exists an η , $a \le \eta \le b$, such that

$$\delta R = F(\eta) \int_a^b V(x) \log V(x) \ dx \tag{2.22}$$

where F(x) is given by (2.12).

Write $g(\eta) = \delta$ and let $\Delta R = R^* - R$, where R^* denotes the new value of R that results from the perturbation. By a repeat of the argument given in Section 2.2 we have

$$\lim_{\delta \to 0} \frac{1}{\delta} \left(\frac{\Delta R}{R} \right) = \frac{\int_a^b V(x) \log V(x) \, dx}{\int_a^b V(x) \, dx} \tag{2.23}$$

Write

$$\Phi_R = -\frac{\int_a^b V(x) \log V(x) dx}{\int_a^b V(x) dx}$$

We have, from the expression for H_R given by (1.10), the following identity:

$$\log R = H_R - \Phi_R \tag{2.24}$$

From (2.23), we obtain, using (2.24),

$$\left. \frac{d(\log R)}{d\delta} \right|_{\delta = 0} = -\Phi_R = \log R - H_R \tag{2.25}$$

Expression (2.25) asserts that the relative change in the net reproduction rate due to arbitrary perturbations in the net maternity function is determined by the entropy of the net maternity distribution.

Expression (2.25) can be written

$$\frac{\Delta R}{R} \simeq -\Phi_R \delta = (\log R - H_R) \delta \tag{2.26}$$

These expressions are analogous to expression (2.18), which is valid for the Malthusian parameter.

2.4. GROSS REPRODUCTION RATE AND ENTROPY

The gross reproduction rate \overline{m} given by (1.7) satisfies the identity

$$\log \overline{m} = H_m - \Phi_m \tag{2.27}$$

where H_m is the entropy give by (1.11) and Φ_m is the expression

$$\Phi_m = -\frac{\int_a^b m(x) \log m(x) dx}{\int_a^b m(x) dx}$$

The argument given in Section 2.3 can be repeated with the new perturbed function given by (2.3). We obtain a result analogous to (2.25), namely,

$$\left. \frac{d(\log \overline{m})}{d\delta} \right|_{\delta = 0} = -\Phi_m = \log \overline{m} - H_m \tag{2.28}$$

This result asserts that the relative change in the gross reproduction rate due to arbitrary perturbations in the net fecundity distribution is determined by the entropy of the fecundity distribution.

Hence for δ small, we have

$$\frac{\Delta \overline{m}}{\overline{m}} \simeq -\Phi_m \delta = (\log \overline{m} - H_m) \delta \tag{2.29}$$

2.5. MEAN LIFE EXPECTANCY AND ENTROPY

The mean life expectancy e_0 , given by (1.8), satisfies the identity

$$\log e_0 = H_I - \Phi_I \tag{2.30}$$

where H_i is the entropy given by (1.12) and Φ_i is the expression

$$\Phi_l = -\frac{\int_0^\infty l(x) \log l(x) dx}{\int_0^\infty l(x) dx}$$

The perturbation of the survivorship distribution is given by (2.4). An argument similar to that in Section 2.3 yields

$$\left. \frac{d(\log e_0)}{d\delta} \right|_{\delta=0} = -\Phi_l = \log e_0 - H_l \tag{2.31}$$

Hence for δ small we have

$$\frac{\Delta e_0}{e_0} \simeq -\Phi_l \delta = \log e_0 - H_l \tag{2.32}$$

Relation (2.32) was shown by Keyfitz [14] to hold for age-independent perturbations [the case $g(x) = \delta$]. See also [11], [17], and [18] for discussions and applications of this case.

Relation (2.32) states that the relative change in the mean life expectancy due to arbitrary perturbations in the survivorship curve is determined by the entropy of the survivorship curve.

3. THE FORCES OF EVOLUTIONARY CHANGE

The evolutionary changes in the demographic parameters in large human populations are due to two main forces: natural selection and environmental action. Natural selection occurs if there are differences in the age-specific fecundity and mortality of the types constituting the populations. The changes in growth rates due to selective forces are determined by the amount of genetic variation for fertility and mortality that exists within the populations. The dynamics of these changes in age-structured populations have been extensively studied; see Charlesworth [2].

The term *environmental action* refers to the changes in growth rate due to environmental factors such as famines, epidemics, wars, improved health care, and nutrition. The changes in growth rate due to environmental action are conditioned by the demographic heterogeneity within the population. The perturbation results we have derived describe the effect of these forces on the different growth rate parameters.

3.1. THE INTENSITY OF SELECTION AND ENVIRONMENTAL ACTION

Crow [3] introduced a notion called the "intensity of selection" to characterize the force that determines evolutionary change under natural selection in populations with nonoverlapping generations. This intensity measure can be separated into mortality and fertility components and thus provides a means of relating the effect of genetic differences in mortality and fertility in determining the evolutionary change in growth rate for demographically homogeneous populations.

We propose an analogue of the notion of selective intensity for heterogeneous populations whose dynamics are determined by the action of environmental factors. The dynamics of the change in the growth rate parameters due to environmental action are given by (2.18), (2.26), (2.29), and (2.32). These equations predict the changes in the growth rate parameters that result from an environmental perturbation whose mean effect is given by δ .

We therefore define the environmental intensity δ by the equation

$$\delta = -(1/\Phi) \, \Delta r \tag{3.1}$$

The intensity δ can be separated into mortality and fertility components. The intensity of the environmental factor as measured by the mortality component is given by

$$\delta_l = -\frac{\Delta e_0}{e_0} \left(\frac{1}{\bar{\Phi}_l} \right) \tag{3.2}$$

Here e_0 is the mean life expectancy. The function Φ_l , we recall, is related to the entropy H_l of the survivorship curve by the identity

$$\Phi_l = H_l - \log e_0$$

The intensity of the environmental factor as measured by the fertility component is given by

$$\delta_m = -\frac{\Delta \overline{m}}{\overline{m}} \left(\frac{1}{\Phi_m} \right) \tag{3.3}$$

where \overline{m} is the gross reproduction rate. The function Φ_m is related to the

entropy H_m of the fertility distribution by

$$\Phi_m = H_m - \log \overline{m}$$

We will use these measures of environmental intensity to make a comparative study of Swedish and French populations during the period 1928-1965.

We should note that a set of criteria based on the demographic parameters r and H have been derived to determine, from local trends in the demographic variables, the nature of the evolutionary force, selection or environmental action, acting on the population [10]. These criteria suggest that the dominant factors determining evolutionary change in France and Sweden during the period 1928–1965 is environmental action. We will not discuss these criteria in this article. Other considerations, such as the large variations in demographic variables, suggest an environmental cause. We will therefore simply assume for illustrative purposes that the dominant mechanism during this episode is due to environmental forces and use (3.1)–(3.3) to evaluate the intensity of these forces and compare the evolutionary trends in the two populations.

4. DEMOGRAPHIC TRENDS IN FRENCH AND SWEDISH POPULATIONS

The data for the Swedish and French populations are based on the age-specific fecundity and mortality schedule given in Keyfitz and Flieger [15]. Tables 1 and 2 give the values for the parameters $r, H, \Phi, e_0, \overline{m}, H_l, H_m, \Phi_l, \Phi_m$ for the period 1928–1968 based on these data. These tables are adapted from [9].

The data in Keyfitz and Flieger are given in five-year intervals. The population parameters have been interpolated to refer to one-year intervals. The data refer only to the female populations. Thus, e_0 is the mean life

TABLE 1
Demographic Data, Sweden, 1928–1965

	e_0	\overline{m}	Φ_{l}	Φ_m	H_l	H_m	r	H	Φ
1928-32	66.44	0.93	0.241	1.774	4.437	1.701	-0.0060	0.0520	0.0580
1933-37	68.45	0.83	0.214	1.877	4.440	1.690	-0.0090	0.0520	0.0610
1938-42	70.73	0.93	0.186	1.629	4.445	1.556	0.0046	0.0521	0.0566
1943-47	72.40	1.22	0.167	1.444	4.449	1.643	0.0046	0.0525	0.0479
1948-52	74.92	1.12	0.138	1.529	4.454	1.642	0.0026	0.0536	0.0510
1953-57	76.28	1.09	0.125	1.518	4.459	1.604	0.0019	0.0531	0.0512
1958-62	77.22	1.08	0.117	1.492	4.464	1.568	0.0017	0.0524	0.0506
1963-68	77.93	1.18	0.112	1.400	4.467	1.565	0.0048	0.0528	0.0480

	e_0	\overline{m}	Φ_{l}	Φ_m	H_{l}	H_m	r	H	Φ
1929-33	62.20	1.09	0.287	1.539	3.843	1.625	-0.0025	0.0528	0.0554
1934-38	64.62	1.02	0.258	1.591	3.910	1.611	-0.0037	0.0526	0.0564
1938-45a	_	_		_	_		_	_	
1945-47	66.13	1.35	0.253	1.290	3.938	1.590	0.0049	0.0504	0.0456
1949-53	71.89	1.38	0.176	1.242	4.099	1.571	0.0086	0.0506	0.0421
1954-58	74.55	1.32	0.148	1.284	4.163	1.561	0.0074	0.0504	0.0429
1959-63	76.22	1.37	0.131	1.232	4.202	1.547	0.0092	0.0504	0.0412
1964-68	77.21	1.37	0.123	1.221	4.223	1.536	0.0096	0.0506	0.0410

TABLE 2

Demographic Data, France, 1928–1968

expectancy of females and \overline{m} is the mean number of female offspring produced by each mother during her lifetime.

4.1. TRENDS IN THE ENTROPY PARAMETERS

Several general observations can be made concerning the data in Tables 1 and 2. The appendix gives bounds on the parameters. These bounds indicate the range of values these parameters may assume.

(1)

$$\Phi_l = -\frac{\int_0^\infty l(x) \log l(x) dx}{\int_0^\infty l(x) dx}$$

The parameter Φ_l measures the proportional rate at which the mean life expectancy e_0 changes as a result of the environmental factor. The data for both France and Sweden show a strong correlation between e_0 and Φ_l . The parameter e_0 increases continuously whereas Φ_l decreases. The decrease in Φ_l expresses the fact that the survivorship curve tends toward a more rectangular form. The rectangular form corresponds to the case where the mean life expectancy and the maximum life expectancy coincide. In this instance Φ_l assumes the value zero.

Related expressions for Φ_l and an analysis of the range of values that Φ_l may assume are discussed in Goldman and Lord [11] and Mitra [17].

(2)

$$\Phi_m = -\frac{\int_0^\infty m(x) \log m(x) dx}{\int_0^\infty m(x) dx}$$

The parameter Φ_m measures the proportional rate at which the gross fertility \overline{m} changes as a result of the environmental factors. The irregular temporal

^a No data were given in Keyfitz and Flieger for France during the period 1938-1945.

trends in \overline{m} and Φ_m , in contrast to the monotonic changes in e_0 and Φ_l , indicate that the environmental forces that condition fertility vary irregularly with time. Changes in fertility are dependent primarily on social custom and norms, which vary considerably over time. Mortality changes, on the other hand, are determined primarily by medical care and nutrition. The monotonic trends in e_0 and Φ_l indicate that these environmental agents exert a constant and uniform effect on the age-specific mortality.

(3)

$$H_{l} = -\int_{0}^{\infty} \frac{l(x)}{e_{0}} \log \frac{l(x)}{e_{0}} dx$$

The parameter H_l is a measure of the variance of the mortality distribution. The irregular trend in H_l in both countries indicates that the external factors such as better health care and nutrition, which cause the increase in mean life expectancy, do not act uniformly over all age classes. The changes in mean life expectancy arise quite probably from the elimination of infectious diseases that affect younger people and also from a reduction in cardiovascular diseases, which normally affect older cohorts.

(4)

$$H_m = -\int_0^\infty \frac{m(x)}{\overline{m}} \log \frac{m(x)}{\overline{m}} dx$$

The parameter H_m is a measure of the variance of the fertility distribution. The steady monotonic decrease in H_m in both populations corresponds to the increased concentration of childbearing into a short period of years. Childbearing that is concentrated at a single age will correspond to an entropy value of zero.

4.2. TRENDS IN ENVIRONMENTAL INTENSITY

Tables 3 and 4 give the changes in r, e_0 , and \overline{m} together with the measure of environmental intensity δ , δ_l , δ_m for Sweden and France.

The following features of the data need emphasis.

(1)

$$\delta = -\Delta r/\Phi$$

The intensity δ is a measure of the force of the environmental factors in terms of their effect on demographic change in r. The data indicates an irregular change in this intensity for both Sweden and France. The intensity in Sweden at each period exceeds that in France. This implies that the environmental agents such as improved health care and nutrition exert a stronger effect in Sweden than in France.

TABLE 3

Measures of Environmental Intensity
Sweden

Period	Δr	δ	Δe_0	δ_l	$\Delta \overline{m}$	δ_m
1928-33	0030	.0517	2.01	126	10	.060
1933-38	.0044	072	2.28	156	.10	064
1938-43	.0092	162	1.67	127	.29	191
1943-48	0020	.041	2.52	208	10	.056
1948-53	007	.137	1.36	131	03	.017
1953-58	002	.039	0.94	098	01	.006
1958-63	.003	061	.071	078	.10	062

TABLE 4

Measures of Environmental Intensity
France

Period	Δr	δ	Δe_0	δ_l	$\Delta \overline{m}$	δ_m
1928-34	0012	.0216	2.42	135	07	.042
1934-45	.0086	152	1.51	091	.33	203
1945-49	.0037	081	5.76	344	.03	017
1949-54	0012	.028	2.66	210	06	.035
1954-59	.0018	042	1.67	151	.05	029
1959–65	.0004	009	.099	099	.01	005

It is of interest to note that the intensity for Sweden assumes its maximum value in (1938–1943) and for France in (1934–1945). These periods correspond to the war years, which would evidently exert a strong effect on both mortality and fertility.

(2)

$$\delta_m = -\frac{\Delta \overline{m}}{\overline{m}} \left(\frac{1}{\Phi_m} \right)$$
$$\delta_l = -\frac{\Delta e_0}{e_0} \left(\frac{1}{\Phi_l} \right)$$

Mortality δ_l contributes a greater fraction to the total intensity than fertility δ_m . This is true in both countries except for the year 1943 in Sweden and 1945 in France. The large postwar increase in fertility in France corresponds possibly to the increased desire to have children to compensate for the large mortality incurred during the war.

The generally large contribution of mortality to the total intensity suggests that factors such as health care and nutrition, which control mortality, exert a stronger effect on the population than factors such as birth control

that determine fertility. The monotonic changes in e_0 and Φ_l for both countries support the idea of the preponderance of the mortality component in determining evolutionary change.

CONCLUSION

A class of entropy functions was introduced in demographic theory by considering demographic models in which we focused on the set of genealogies generated by the individuals in the population. It has been shown that these entropy functions characterize the response of the classical demographic parameters—growth rate, net reproduction rate, mean life expectancy, and gross reproduction rate—to fluctuations in the age-specific fecundity and mortality distributions. These relations have been applied to provide quantitative measures of the intensity of environmental factors in terms of the changes in the demographic variables. These intensity measures provide a means of assessing the impact of environmental factors on evolutionary change.

APPENDIX. BOUNDS ON ENTROPY

We prove the following two results:

(A) Let
$$p(x) = \exp(-rx)l(x)m(x)$$
 write

$$T = \int_0^\infty x p(x) \ dx$$

where T is the mean age of childbearing in the stable population. Let

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

If T is finite, then H is bounded and

$$H \leqslant \frac{1 + \log T}{T} \tag{A.1}$$

(B) Let
$$q(x) = l(x)m(x)/R$$
 write

$$\alpha = \int_0^\infty xq(x) dx$$
 and $H_R = -\int_0^\infty q(x)\log q(x) dx$

If α is finite, then H_R is bounded and

$$H_R \leqslant 1 + \log \alpha \tag{A.2}$$

The proofs of (A.1) and (A.2) follow from the following well-known proposition.

PROPOSITION 1

Let f(x) and g(x) be probability distributions and suppose that

$$-\int_0^\infty f(x)\log g(x)\ dx$$

exists and is finite. Then

$$-\int_0^\infty f(x)\log f(x)\ dx$$

exists, and

$$-\int_0^\infty f(x)\log f(x)\ dx \le -\int_0^\infty f(x)\log g(x)\ dx$$

Proof. Define g(x)/f(x) = 0 when f(x) = g(x) = 0. Since $\log b \le b - 1$, we have

$$f(x)\log\frac{g(x)}{f(x)} \le g(x) - f(x)$$

Hence

$$\int_0^\infty f(x)\log g(x) < \int_0^\infty g(x) \, dx - \int_0^\infty f(x) \, dx = 0$$

Now

$$-f(x)\log f(x) = f(x)\log \frac{g(x)}{f(x)} - f(x)\log g(x)$$

We conclude that

$$-\int_0^\infty f(x)\log f(x)\ dx \le -\int_0^\infty f(x)\log g(x)\ dx$$

Proof of (A.1). To infer (A.1) from Proposition 1, we consider the distribution

$$g(x) = \frac{1}{T} \exp\left(-\frac{x}{T}\right)$$

For any probability distribution p(x), we are given that T is finite, and

$$-\int_0^\infty p(x)\log g(x)\ dx = (1+\log T) < \infty$$

Hence

$$-\int_0^\infty p(x)\log p(x)\ dx \le 1 + \log T$$

and we conclude that

$$H \leqslant \frac{1 + \log T}{T}$$

Proof of (A.2). To infer (A.2), we consider the distribution

$$g(x) = \frac{1}{\alpha} \exp\left(-\frac{x}{\alpha}\right)$$

where α is assumed to be finite. We have that

$$-\int_0^\infty q(x)\log g(x)\ dx = 1 + \log \alpha$$

Hence, using Proposition 1,

$$H_R = -\int_0^\infty q(x)\log q(x) \ dx \le 1 + \log \alpha$$

and the proof is complete.

Analogous bounds for H_l and H_m exist. These are immediate consequences of (A.2). We observe the following:

(C) If
$$\int_0^\infty x l(x) dx = \beta$$
 is finite, then

$$H_l = -\int_0^\infty \frac{l(x)}{e_0} \log \frac{l(x)}{e_0} dx$$
 is bounded

and

$$H_l \leqslant 1 + \log(\beta/e_0) \tag{A.3}$$

(D) If $\int_0^\infty x m(x) dx = \gamma$ is finite, then

$$H_m = -\int_0^\infty \frac{m(x)}{\overline{m}} \log \frac{m(x)}{\overline{m}} dx$$
 is bounded

and

$$H_m < 1 + \log(\gamma/\overline{m}) \tag{A.4}$$

Similar bounds for Φ_l and Φ_m follow from the application of (A.3) and (A.4) to the identities (2.30) and (2.27).

We have

$$\Phi_{I} \leqslant 1 + \log(\beta/e_0^2) \tag{A.5}$$

and

$$\Phi_m \leqslant 1 + \log(\gamma/\overline{m}^2) \tag{A.6}$$

I am very grateful to Jacques Demongeot for many productive discussions as this work progressed. I also wish to thank Paul Einer Hansen for his careful reading of the manuscript and two anonymous referees for helpful comments and criticism. Very special thanks to Ingeborg Lechten for preparing the manuscript.

REFERENCES

- W. B. Arthur, The analysis of linkages in demographic theory, *Demography* 21:109–128 (1984).
- B. Charlesworth, Evolution in Age-Structured Populations, Cambridge Univ. Press, Cambridge, 1980.
- 3 J. Crow, Some possibilities for measuring selection intensity in man, *Human Biol*. 30:1-13 (1959).
- 4 L. Demetrius, The sensitivity of population growth rate to perturbations in the life-cycle components. *Math. Biosci.* 4:129-136 (1969).
- 5 L. Demetrius, Demographic parameters and natural selection, *Proc. Natl. Acad. Sci. USA* 71:4645-4647 (1974).
- 6 L. Demetrius, Measures of fitness and demographic stability, Proc. Natl. Acad. Sci. USA 74:384–386 (1977).
- L. Demetrius, Statistical mechanics and population biology, J. Stat. Phys. 30:709-753 (1983).
- L. Demetrius, Relations between demographic parameters, *Demography* 16:329–338 (1979).

9 L. Demetrius and M. Ziehe, The measurement of Darwinian fitness in human populations, *Proc. Roy. Soc. Lond. B* 222:33-50 (1984).

- 10 L. Demetrius and J. Demongeot, Les facteurs endogenes et exogenes dans l'evolution demographique de la France (1850-1965). *Population* (in press) (1988).
- 11 N. Goldman and G. Lord, A new look at entropy and the life table, *Demography* 23:275-282 (1986).
- 12 L. Goodman, On the sensitivity of the intrinsic growth rate to changes in the age-specific birth and death rates, *Theor. Pop. Biol.* 2:339-354 (1971).
- 13 N. Keyfitz, Linkages of intrinsic age-specific rates, J. Am. Stat. Assoc. 66:275-281 (1971).
- 14 N. Keyfitz, Applied Mathematical Demography, Wiley, New York, 1977.
- 15 N. Keyfitz and R. Flieger, Populations: Facts and Methods of Demography, W. H. Freeman, San Francisco, 1971.
- 16 A. Lotka, Théorie Analytique des Associations Biologiques, Hermann, Paris, 1939.
- 17 S. Mitra, The effect of extra chances to live on life table functions, *Theor. Pop. Biol.* 16:315-322 (1979).
- 18 J. W. Vaupel and A. Yashin, Repeated resuscitation: how lifesaving alters life-tables. Demography, 24:123-136 (1987).