SOME GENERAL RELATIONSHIPS IN POPULATION DYNAMICS

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September 1983

WP-83-89

INTERNATIONAL INSTITUTE FOR APPLIED SYSTEMS ANALYSIS
2361 Laxenburg, Austria

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Important recent research by Samuel Preston and Ansley Coale (1982) extends the Lotka system of stable population equations (Lotka 1939) to *any* population. Here we present an alternative general system and describe its duality with the Preston-Coale system. We derive these results by considering the calculus of change on the surface of population density defined over age and time. We show that analysis of this Lexis surface leads to all the known fundamental relationships of the dynamics of single-region human populations, as well as some interesting new relationships.

The Lexis Surface

A useful concept in population dynamics is the notion of a population surface that represents the size-density of a population at various ages and times (Lotka 1926, 1931, and 1940; Preston and Coale 1982). Let $N^o(a,t)$ be the number of live individuals in some population in a unit age and time interval, at age a and time t. Over the age and time plane, $N^o(a,t)$ will form a surface, with discontinuities at the boundaries of each small age-time interval. If the population is large, we can approximate this $N^o(a,t)$ surface with a continuously differentiable surface $N(a,t)$ which we may interpret as representing the density of the population at instantaneous age a and time t. Generalizing the notion of a Lexis diagram, we will call the surface defined by $N(a,t)$ a Lexis surface.

The Fundamental Local Identity

Assume, for the time being, that the population is closed to migration. In exploring the dynamics of change in population size, it is useful to focus on rates of change in three directions--as age increases, as time increases, and as age and time increase in tandem. It is convenient to work with relative or proportional rates of change known as intensities, rather than with absolute rates. Consequently, define:

$$r(a,t) = (\partial N(a,t)/\partial t)/N(a,t), \tag{1}$$

$$\nu(a,t) = -(\partial N(a,t)/\partial a)/N(a,t), \tag{2}$$

$$\mu(a,t) = -(\partial N(a+x,t+x)/\partial x)/N(a,t), \quad at\ x = 0. \tag{3}$$

The importance of the age-specific growth rate r was brought to the attention of demographers by Preston and Coale (1982). The age intensity ν, which gives the relative rate of change in the density of the population with age, is also a useful quantity to consider, as we will show. The value μ gives the relative rate of change in the density of the population in the cohort direction where age and time increase together. In a population closed to migration, μ is equivalent to the well-known force of mortality[1].

The values of r, ν and μ are related by what we might call the fundamental local identity of the Lexis surface. In any population at any age a and time t:

$$\mu(a,t) = \nu(a,t) - r(a,t). \tag{4}$$

Preston and Coale prove this result in the appendix to their 1982 paper. (See also Horiuchi 1983.) Here we give an alternative derivation that may be of some pedagogical value. As shown in Figure 1, one can imagine r, μ, and ν as vectors pointing in three directions in a Lexis surface. In one unit of time, the height of the surface, N, changes at an intensity r. Similarly, over one unit of age, N changes at an intensity $-\nu$. Over the diagonal, N falls off at an intensity μ--but this diagonal is $\sqrt{2}$ long, so the change over one unit of distance is $-\mu/\sqrt{2}$. Projecting r and ν in this 45° direction must also give this magnitude[2]:

$$r\cos(45) + (-\nu)\cos(45) = -\mu/\sqrt{2}\,. \tag{5}$$

Substituting $1/\sqrt{2}$ for cos(45) and multiplying by $-\sqrt{2}$ yields (4), the fundamental local identity.

The fundamental local identity in (4) turns out to be equivalent to one of the main representations of population dynamics. Substituting (1) and (2) in (4) and multiplying by $-N(a,t)$ yields the von Förster (1959) equation:

1 The minus sign in the definition of ν and μ and its absence in the definition of r is a mathematical nuisance. This convention, however, is consistent with demographic usage and has the advantage that in a population closed to migration μ will always be positive and in many populations r and ν will be positive at most ages.
2 Technically, r and ν are the components of the (normalized) gradient of $N(a,t)$. Projecting this gradient into the cohort direction must yield $-\mu/\sqrt{2}$.

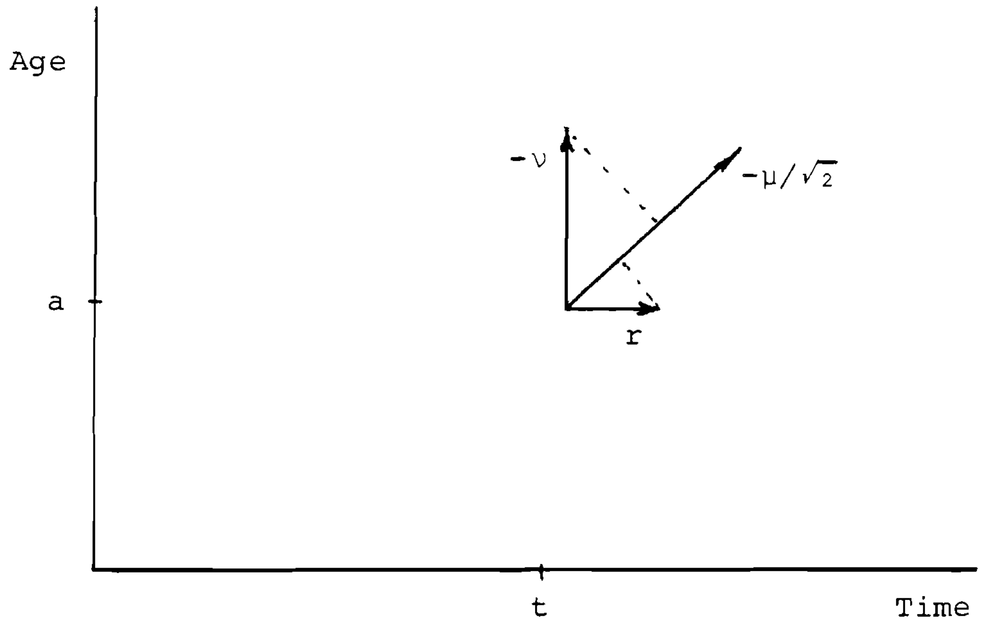

Figure 1. Vector proof of the fundamental local identity.

$$\partial N(a,t)/\partial a + \partial N(a,t)/\partial t = -\mu(a,t)\, N(a,t)\,. \tag{6}$$

Through Time and Age on a Lexis Surface

The fundamental local identity and its von Förster equivalent describe local relationships at a point on the Lexis surface. We now introduce a calculus of line integrals that permits comparisons of population densities at distant points on the surface in terms of the local intensities defined above. To begin, recall that the standard differential equation

$$dy\,/\,dx = k(x)\, y(x) \tag{7}$$

has the solution (see Coddington and Levinson 1955):

$$y(x_2) = y(x_1)\, e^{\int_{x_1}^{x_2} k(s)\, ds}\,. \tag{8}$$

Using this equation, population densities at different ages and times can be related by integrating intensities of change over appropriate directions. For example, to arrive at:

(i) the population density at some age a_2 knowing that of a younger age a_1, at the same point in time t, we use (2)

$$\partial N(x,t)/\partial x = -\nu(x,t)\, N(x,t)$$

so that

$$N(a_2,t) = N(a_1,t)\, e^{-\int_{a_1}^{a_2} \nu(x,t)dx} \quad ; \tag{9}$$

(ii) the population density at a given age a at some time t_2 knowing that at an earlier time t_1, we use (1)

$$\partial N(a,y) / \partial y = r(a,y) N(a,y)$$

so that

$$N(a,t_2) = N(a,t_1)\, e^{\int_{t_1}^{t_2} r(a,y)dy} \quad ; \tag{10}$$

(iii) the population density for a cohort at some age a_2 knowing that at an earlier age and time a_1,t_1, we use (3) in an equivalent form

$$\partial N(a_1+x,t_1+x) / \partial x = -\mu(a_1+x,t_1+x) N(a_1+x,t_1+x)$$

so that

$$N(a_2,t_1+a_2-a_1) = N(a_1,t_1)\, e^{-\int_0^{a_2-a_1} \mu(a_1+x,t_1+x)dx} \tag{11}$$

With these three expressions in hand, it is possible to navigate at will around a Lexis surface. For instance as shown in Figure 2, to construct the population density at a position (a_2,t_2), knowing it at a reference position (a_1,t_1) (where $a_2 > a_1$ and $t_2 > t_1$) one illustrative (if not very useful) route would be to travel down the cohort line from a_1 and t_1 to some point a_3 and $t_1+a_3-a_1$, then to move along the time line to t_2, and finally to move up the age line to a_2. The formula for the entire voyage would be

$$N(a_2,t_2) = N(a_1,t_1)\, e^{\int_0^{a_1-a_3} \mu(a_1-x,t_1-x)dx + \int_{t_1-a_1+a_3}^{t_2} r(a_3,y)dy - \int_{a_3}^{a_2} \nu(x,t_2)dx} \tag{12}$$

A New Generalized System

This "navigational" calculus can be used to derive a new generalized system of demographic relations as well as the Preston-Coale system. The relationship at time t between the population density at age a compared with the population density at birth could be expressed via an infinite number of different routes on a Lexis surface. One particularly simple route is to travel back from t along the birth axis and then follow the appropriate cohort up the diagonal to age a. For convenience in notation let $g(y,t)$ equal $r(0,t-y)$, so that $g(y,t)$ gives the growth rate of births y years before time t:

$$g(y,t) = -(\partial N(0,t-y) / \partial y) / N(t-y) . \tag{13}$$

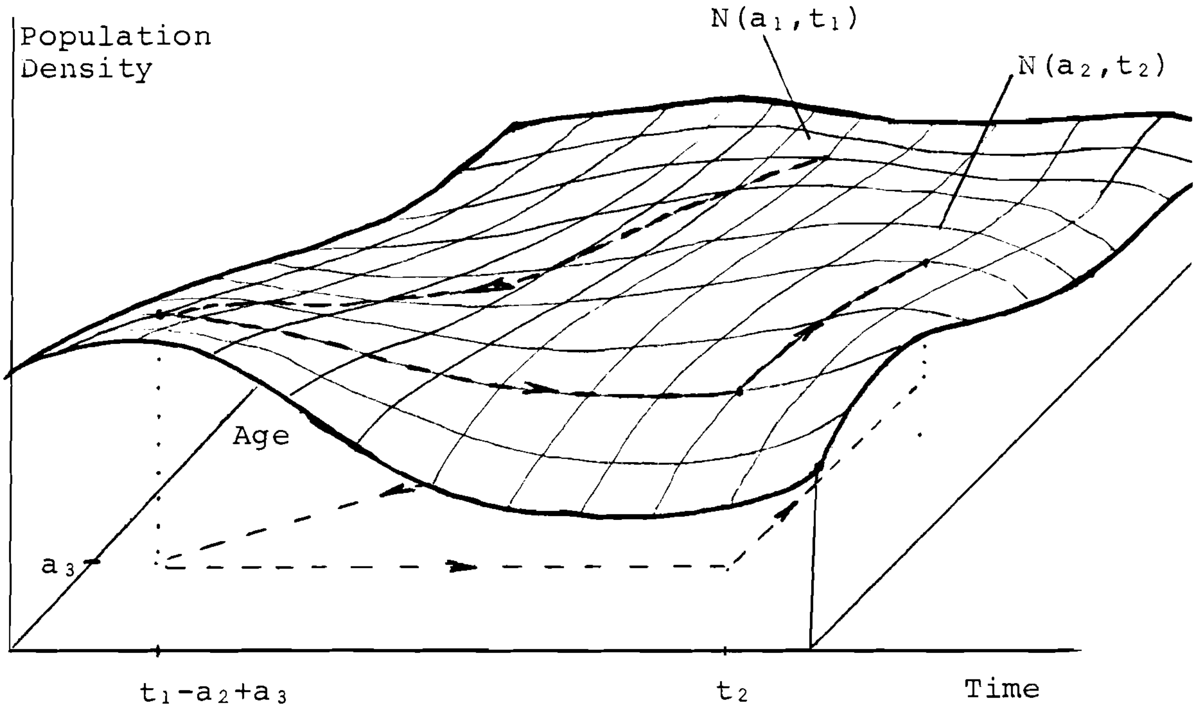

Figure 2. A voyage on a Lexis surface.

Then,

$$N(0,t-a) = N(0,t)\, e^{-\int_0^a g(y,t)dy} \qquad (14)$$

and from (11)

$$N(a,t) = N(0,t-a)\, e^{-\int_0^a \mu(x,t-a+x)dx} \,. \qquad (15)$$

The exponential in (15) simply the cohort survival function $p_c(a,t)$. Combining (14) and (15) thus yields the relationship we seek

$$N(a,t) = N(0,t)\, e^{-\int_0^a g(y,t)dy}\, p_c(a,t) \,. \qquad (16)$$

This identity will form the basis of the new generalized system.

Let the crude birth rate at time t be defined by

$$b(t) = N(0,t) / \int_0^\omega N(a,t)da \;, \qquad (17)$$

where ω is some advanced age beyond which no one survives. Let the proportional age distribution of the population be given by

$$c(a,t) = N(a,t) / \int_0^\omega N(a,t)da \;.$$

so that from (17)

$$c(a,t) = b(t)\ N(a,t) / N(0,t) \tag{18}$$

And let $m(a,t)$ be the maternity function such that

$$N(0,t) = \int_0^\omega N(a,t)\ m(a,t)\ da\ . \tag{19}$$

Using (16) to substitute for $N(a,t)$ in (17), (18) and (19), and canceling $N(0,t)$ where possible, we obtain,

$$b(t) = 1 / \int_0^\omega e^{-\int_0^a g(y,t)dy}\ p_c(a,t)\ da\ . \tag{20}$$

$$c(a,t) = b(t)\ e^{-\int_0^a g(y,t)dy}\ p_c(a,t)\ . \tag{21}$$

$$1 = \int_0^\omega e^{-\int_0^a g(y,t)dy}\ p_c(a,t) m(a,t)\ da\ . \tag{22}$$

The new generalized system is given by (20), (21) and (22). As with the Preston-Coale system, this system is valid over age and time for *any* closed population and is readily extended, as noted below, to any population open to migration.

When the population is stable, p_c, m, and the growth rate in births, g, are constant over time, so that the system reduces to the standard Lotka set of equations:

$$b = 1 / \int_0^\omega e^{-ga}\ p_c(a)\ da\ , \tag{23}$$

$$c(a) = b\ e^{-ga}\ p_c(a)\ , \tag{24}$$

$$1 = \int_0^\omega e^{-ga}\ p_c(a)\ m(a)\ da\ . \tag{25}$$

It turns out that just as the fundamental local identity is the von Förster equation in a different guise, the new general system is closely related to the Lotka-Volterra integral equation, the most standard representation of population dynamics (see Keyfitz 1968). Let $B(t)$, instead of $N(0,t)$ denote the number of births at time t. The identity in (14) implies

$$e^{-\int_0^a g(y,t)dy} = B(t-a) / B(t)\ . \tag{26}$$

Making the substitution in the characteristic equation (22) and multiplying through by $B(t)$ yields

$$B(t) = \int_0^\omega B(t-a)\ p_c(a,t)\ m(a,t)\ da\ , \tag{27}$$

which is the familiar homogeneous form of the Lotka-Volterra integral equation.

The Preston-Coale System

The Preston-Coale system can also be readily derived using the calculus of the Lexis surface. Taking the direct route from age zero to age a at time t yields

$$N(a,t) = N(0,t)\, e^{-\int_0^a \nu(x,t)dx} . \tag{28}$$

Using the fundamental local identity in (4), the exponential term in (28) may be rewritten as:

$$e^{-\int_0^a r(x,t)dx}\; e^{-\int_0^a \mu(x,t)dx} .$$

The second term in this expression is simply the period survival function $p_p(a,t)$. Thus,

$$N(a,t) = N(0,t)\, e^{-\int_0^a r(x,t)dx}\; p_p(a,t) , \tag{29}$$

which is the identity that forms the basis of the Preston-Coale system. As illustrated in Figure 3, this identity can be thought of as describing a route from age 0 to age a at time t that consists of a series of tacks, up the cohort direction, then back along the time direction, and so on. The new generalized system is based, on the other hand, on a voyage back in time along the birth axis and then up the cohort diagonal[3].

In the same way that the new system can be derived from (16), the Preston-Coale system follows from (29):

$$b(t) = 1 / \int_0^\omega e^{-\int_0^a r(x,t)dx}\; p_p(a,t)da , \tag{30}$$

$$c(a,t) = b(t)\, e^{-\int_0^a r(x,t)dx}\; p_p(a,t) , \tag{31}$$

$$1 = \int_0^\omega e^{-\int_0^a r(x,t)dx}\; p_p(a,t)\, m(a,t)da . \tag{32}$$

As Preston and Coale remark, when population is stable this system also reduces to the familiar Lotka system.

3 Other routes on the Lexis surface lead to other systems. Such routes run from some arbitrary point $N(a,t)$ to some reference point $N(a_0,t)$, where a_0 does not have to be zero but could be five, say, or fifty. The simplest route, straight up the age line from age zero, is described by (28). The corresponding system is:

$$b(t) = 1 / \int_0^\omega e^{-\int_0^a \nu(x,t)dx}\, da ,$$

$$c(a,t) = b(t)\, e^{-\int_0^a \nu(x,t)dx} ,$$

$$1 = \int_0^\omega e^{-\int_0^a \nu(x,t)dx}\, m(a,t)\, da .$$

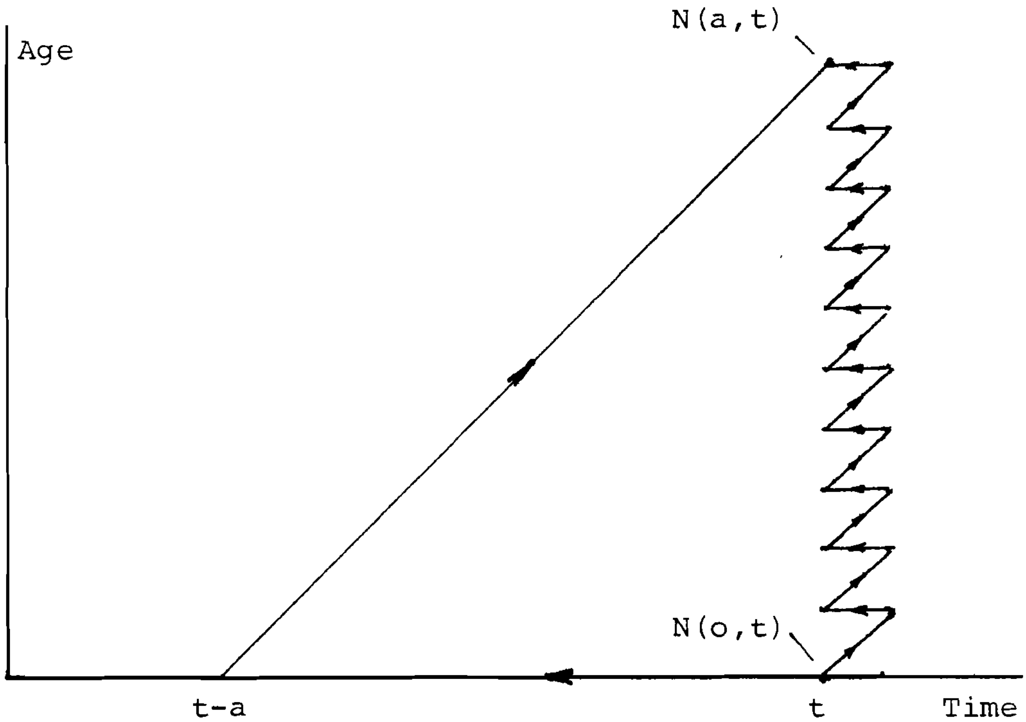

Figure 3. Two routes between $N(0,t)$ and $N(a,t)$ on a Lexis surface (viewed from above).

The Duality Between the Two Systems

The equational form of the new general system is the same as that of the Preston-Coale system although the meaning of the symbols is quite different: the two systems are essentially complementary or dual to each other. Where Preston and Coale use r along the age axis, the new system uses it (as g) along the time axis. Where Preston and Coale use the period lifetable, the new system uses the cohort one. Preston and Coale require information on age-specific rates of population change, the new system requires information on rates of change of births over time.

The Preston-Coale system has been applied usefully to estimate various demographic statistics when two censuses are available (Preston and Coale 1982; and Preston 1983). In more advanced countries reliable birth series and cohort survival functions can be obtained, so that the new system might in principle also be used for estimation. The new system has the disadvantage that it asks for data from the past; but it has a certain convenience in that (26) provides a simple way of calculating the exponential involving g.

The basic identities underlying the two systems are (16) and (29). Equating these identities gives a duality or correspondence between the period and cohort lifetables:

$$e^{-\int_0^a r(x,t)dx}\, p_p(a,t) = e^{-\int_0^a g(y,t)dy}\, p_c(a,t) . \qquad (33)$$

This complementarity condition expresses a simple and general relationship between period and cohort lifetables that holds for any closed population (and that is readily generalized, as noted below, to any population). Where three of the functions r, g, p_p or p_c are available, the fourth can be deduced. Where all are available, (33) provides a consistency check on the data.

We can use (33) to express the period lifetable explicitly in terms of the cohort lifetable. Let $\varphi(a,t)$ denote the intensity of change over time in the cohort survival function p_c:

$$\varphi(a,t) = [\partial p_c(a,t)/\partial t]/p_c(a,t) . \tag{34}$$

By substituting p_c in (15) and the resulting expression in (1) and then using the product rule of differentiation, it can be shown that

$$r(a,t) = g(a,t) + \varphi(a,t) . \tag{35}$$

Note that this identity implies that r will change over time if either the number of births changes or if mortality rates change. Multiplying (33) through by its first term, and substituting φ for $r-g$ yields:

$$p_p(a,t) = p_c(a,t)\, e^{\int_0^a \varphi(x,t)dx} . \tag{36}$$

Horiuchi (see footnote 2 in Preston and Coale's 1982 paper) presents a similar result. In general studies, either (33) or (36) could be used to evaluate the error in using period instead of cohort lifetables.

Three Time-Specific Averages

The fundamental local identity

$$\mu(a,t) = \nu(a,t) - r(a,t)$$

looks similar in form to the basic time-specific identity

$$d(t) = b(t) - r(t) , \tag{37}$$

where $d(t)$ is the crude death rate at time t, $b(t)$ is the crude birth rate and $r(t)$ is the crude growth rate. The calculus of the Lexis surface permits a deeper correspondence to be drawn: the identity in (37) can be seen to follow from the fundamental identity (4) via three remarkable equivalences:

$$d(t) = \int_0^\omega c(a,t)\, \mu(a,t)\, da , \tag{38}$$

$$b(t) = \int_0^\omega c(a,t)\, \nu(a,t)\, da , \tag{39}$$

$$r(t) = \int_0^\omega c(a,t)\, r(a,t)\, da . \tag{40}$$

Knowing that

$$\int_0^\omega c(a,t)\, da = 1 , \tag{41}$$

$d(t)$, $b(t)$, and $r(t)$ can be interpreted as population-weighted averages or population mean values of $\mu(a,t)$, $\nu(a,t)$, and $r(a,t)$. Collectively, the three relationships might be called the basic time-specific averages of demographic accounting.

Proof of (38), (39), and (40) and derivation of (37) from the fundamental local identity is as follows:

(i) To prove (38) note that, by definition, $d(t)$ gives the proportional decrease, in the cohort direction where time and age increase in tandem, in the total size of a population. Formally,

$$d(t) = -(\partial\{\int_{-x}^{\omega-x} N(a+x,t+x)da\}/\partial x / \int_0^\omega N(a,t)da \ , \qquad at\ x = 0 \tag{42}$$

Reversing the order of differentiation and integration in the numerator (permissible here), and substituting (3) yields

$$d(t) = (\int_0^\omega N(a,t)\mu(a,t)\ da)/\int_0^\omega N(a,t)\ da \tag{43}$$

which reduces via (18) to (38).

(ii) To prove (39), use the fact that $N(\omega,t)$ is zero, so that

$$\int_0^\omega (\partial N(a,t)/\partial a)da = N(\omega,t) - N(0,t) = -N(0,t)$$

whence from (2)

$$b(t) = N(0,t)/\int_0^\omega N(a,t)da = \int_0^\omega \nu(a,t)N(a,t)da / \int_0^\omega N(a,t)da \tag{44}$$

which is (39).

(iii) To prove (40) note that, by definition, $r(t)$ gives the proportional change over time in total population size:

$$r(t) = [\partial\{\int_0^\omega N(a,t)da\}/\partial t]/\int_0^\omega N(a,t)da \ . \tag{45}$$

Reversing the order of differentiation and integration, and substituting (1) and (18) in the resulting expression, we obtain (40).

(iv) Finally, (37) follows easily from the fundamental local identity (4), simply by multiplying it through by $c(a,t)$ and integrating over age.

Time-Specific Averages for Age Segments

In addition to the relationship between $\mu(a,t)$, $\nu(a,t)$, and $r(a,t)$ at any age and time and the parallel relationship between $d(t)$, $b(t)$, and $r(t)$ across all ages at any time, an analogous relationship exists for any age segment of the population at any time. For a population at time t between the ages of α and β, let the size of the population in the age segment be given by

$$N_{\alpha\beta}(t) = \int_\alpha^\beta N(a,t)da \ , \tag{46}$$

let the age distribution of this age segment be described by

$$c_{\alpha\beta}(a,t) = N(a,t) / N_{\alpha\beta}(t) , \qquad \alpha \le a \le \beta , \tag{47}$$

and let the crude growth rate be denoted by

$$r_{\alpha\beta}(t) = (\partial N_{\alpha\beta}(t) / \partial t) / N_{\alpha\beta}(t) . \tag{48}$$

Define a generalized "birth" rate $b_{\alpha\beta}(t)$ that represents the rate of net inflow into the population segment, i.e., the rate of inflow minus outflow:

$$b_{\alpha\beta}(t) = (N(\alpha,t) - N(\beta,t)) / N_{\alpha\beta}(t) . \tag{49}$$

Then, analogously to (4) and (37), the crude death rate in the population segment is given by:

$$d_{\alpha\beta}(t) = b_{\alpha\beta}(t) - r_{\alpha\beta}(t) . \tag{50}$$

Furthermore, the proofs given above can also be readily extended to show:

$$d_{\alpha\beta}(t) = \int_{\alpha}^{\beta} c_{\alpha\beta}(a,t)\, \mu(a,t)\, da , \tag{51}$$

$$b_{\alpha\beta}(t) = \int_{\alpha}^{\beta} c_{\alpha\beta}(a,t)\, \nu(a,t)\, da , \tag{52}$$

$$r_{\alpha\beta}(t) = \int_{\alpha}^{\beta} c_{\alpha\beta}(a,t)\, r(a,t)\, da . \tag{53}$$

These time-specific averages may be useful in estimating age composition and mortality rates of population segments for which data are sparse or unreliable, for example, the population above age 85. In addition, the relationships may be useful in interpolating the values of c and μ within narrower age segments, such as various five-year segments.

Migration

Consider now a population open to migration. Define the net migration intensity, $\gamma(a,t)$, as the difference between in-migration $I(a,t)$ and out-migration $E(a,t)$ at age a and time t, normalized by population density:

$$\gamma(a,t) = ((I(a,t) - E(a,t)) / N(a,t) \tag{54}$$

The value of μ, defined by (3), can no longer be interpreted as the force of mortality; in a population open to migration μ equals the difference between the force of mortality, μ', and the net-migration intensity γ:

$$\mu(a,t) = \mu'(a,t) - \gamma(a,t) \tag{55}$$

Consequently, the fundamental local identity becomes

$$\mu'(a,t) = \nu(a,t) - r(a,t) + \gamma(a,t) . \tag{56}$$

To separate the effects of migration from the effects of mortality, (55) can be substituted for μ in all the relationships given above that involve μ.

In particular, note that in a population open to migration

$$e^{-\int_0^a \mu(x,t-a+x)dx} = p_c(a,t)\, e^{\int_0^a \gamma(x,t-a+x)dx} \tag{57}$$

and

$$e^{-\int_0^a \mu(x,t)dx} = p_p(a,t)\, e^{\int_0^a \gamma(x,t)dx}\,, \tag{58}$$

where p_c and p_p are the cohort and period survival functions. Hence, in each of the three equations of the new system and of the Preston-Coale system the survival function should be multiplied by the appropriate exponential term involving γ.

Equation (55) can also be used to generalize the fundamental time-specific identity and to derive a fourth time-specific average. Let $\gamma(t)$ denote the crude net-migration rate at time t. Then, using the approach sketched above, it can be readily shown that

$$d(t) = b(t) - r(t) + \gamma(t)\,, \tag{59}$$

where

$$\gamma(t) = \int_0^\omega c(a,t)\,\gamma(a,t)da. \tag{60}$$

Discussion

Until recently, much of demographic analysis and demographic estimation has been built upon *stable* population theory, and for a compelling reason. When a population is stable, the Lotka system gives a unique and explicit correspondence between individual life-cycle behavior (as represented by the standard fertility and morality functions) and the proportions at various ages in the aggregate population (as represented by the age distribution). Where demographic behavior is changing over time, this convenient correspondence fails, and the analyst is forced to choose uncomfortably between numerical simulation, and the *assumption* that the population somehow approximates stability--a particularly faulty assumption where transitional behavior is concerned.

In a general time-varying population, the aggregate age distribution at a certain time depends not only on life-cycle behavior at that time, but also on life-cycle behavior in the past. Theoretically then no corr'espondence between the age distribution at one time and life-cycle behavior at that time can exist, but a correspondence could be restored, providing information summarizing past demographic behavior were added. Remarkably, the Preston-Coale system shows that not only is the addition of information on present cohort-growth sufficient to restore the analytical correspondence between life-cycle behavior and the aggregate age distribution but the resulting expressions change only minimally the Lotka three-equation system. With the Preston-Coale system in hand, we might surmise that other information summarizing past behavior--perhaps the past birth sequence--may be sufficient to restore the correspondence between life-cycle behavior and the aggregate age distribution. The new generalized system shows that indeed this is the case;

and once again the additional information necessary can be incorporated with only minor changes to the standard Lotka system.

Where repeated censuses are available, the Preston-Coale system is useful in demographic estimation. Where the past birth sequence is available or can be indirectly reconstructed, the new generalized system may also be useful for estimation. Other identity systems in this paper--the period-cohort duality and the time specific averages for example--may have similar use. Indeed, increasingly it becomes possible to "triangulate" upon unknown qualities from several directions, using different data sources and different identities[4].

It may well be that the new generalized system will find its main application in theoretical investigations. For instance, Arthur (1982) used a discrete form of the characteristic equation (22) to prove the weak and strong ergodic theorems of demography. Where population patterns are changing in some regular fashion--as with the fertility or mortality transition say, or with the "Chinese" constant-birth policy case--the new system may be especially useful in demonstrating the time-varying implications.

Finally, notice that all the relationships presented in this paper are either definitions or accounting identities. They could be applied to any population where entry and exit depend on age (or duration) and time, including, for example, populations of married men, small business, machine tools, or vintage wine[5].

Conclusion

The concept of a Lexis surface is useful in unifying the major ideas of the theory of population dynamics. Local changes are described by the intensities r, μ, and ν. Changes from one point to some distant point are readily calculated by "navigating" on the Lexis surface using the calculus of line integrals. All the major relationships of single-region human population dynamics can be derived within the framework, including the fundamental local identity, the von Förster equation, the Lotka stable population system, the Preston-Coale system, the new generalized system, the Lotka-Volterra integral equation, the duality between period and cohort lifetables, the basic time-specific identity, and the basic time-specific averages for the entire population and for any age segment within it.

Acknowledgments

The authors have benefited from correspondence and conversations with Ansley Coale, Griffith Feeney, Shiro Horiuchi, and Samuel Preston.

4 For example, we can take different sightings on $b(t)$ and cross-check estimates using expressions given in (17), (20), (30) and (39). (See Preston 1983.)

5 Several caveats are in order here. For certain animal populations, the relationships may not capture critical factors such as seasonality or a predator-prey interaction. For other populations, the variables that are used in the relationships may not be the essential ones: the maternity function $m(a,t)$, for example, may not be helpful in characterizing a population where "births" are controlled by a decision maker. Also the continuously differentiable Lexis surface may not appropriately represent the dynamics of a small population, especially in a turbulent environment.

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