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Formal Relationship 15

# Age-specific growth, reproductive values, and intrinsic **r**

## **Robert Schoen**

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## Age-specific growth, reproductive values, and intrinsic r

#### Robert Schoen<sup>1</sup>

## Abstract

The age-specific growth function of an observed population and the reproductive value function based on the population's current vital rates determine the intrinsic rate of growth implied by those vital rates through the simple relationship given in equation (1). That equation establishes the analytical significance of age-specific growth, and leads to relationships that quantify a population's approach to stability and that specify the extraordinarily close connection between reproductive values and population momentum.

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#### 1. Introduction

A simple and elegant relationship links the intrinsic rate of natural increase (Lotka's r) with age-specific growth and age-specific reproductive value functions. Specifically

(1) 
$$r = \int r(x,t)q(x,t)dx$$

where the integral ranges over all ages x; the age-specific growth function, r(x,t) is defined as

(2) 
$$r(x,t) = \frac{\left[\frac{\partial N(x,t)}{\partial t}\right]}{N(x,t)}$$

where  $\partial$  indicates partial differentiation and N(x, t) is the population age x at time t; and reproductive fraction q(x, t) is given by

(3) 
$$q(x,t) = \frac{N(x,t)v(x)}{Q(t)}$$

As defined below, Q(t) is the stable equivalent number of births at time t. The reproductive function v(x) represents the contribution from age x to the number of births in the stable population that is specified by the given vital rates underlying v(x). Mathematically

(4) 
$$v(x) = \frac{\int\limits_{x}^{\infty} e^{-ra} p(a) f(a) \mathrm{d}a}{\left[A^* e^{-rx} p(x)\right]}$$

where p(a) is the probability of surviving from birth to age  $\underline{a}$  under the given mortality rates, f(a) is the fertility rate at age  $\underline{a}$ , and  $A^*$  is the mean age at childbearing in the stable population (cf. Schoen 2006, 30). The product  $v(x) \cdot A^*$  is a reproductive value that can be interpreted as the "present value" of future children born to a person age x, i.e. the future number of children that a person age x will have discounted back to age x at an interest rate equal to intrinsic r. Division by the stable mean age at childbearing,  $A^*$ , expresses that reproductive value on an annual basis.

The stable equivalent number of births at time t, Q(t), can be thought of as the number of births in the time t stable population that, growing exponentially at rate r, becomes identical in size and composition to the stable population that ultimately arises from the observed time t population, i.e. the N(x, t), as it grows under the given vital rates. That stable equivalent number of births can be written as

(5) 
$$Q(t) = \int N(x,t)v(x)dx$$

where the integral spans all ages x. The function q(x, t) can thus be interpreted as the fraction of the time t stable equivalent number of births that is contributed by persons age x.

Equation (1) indicates that if vital rates are constant for even an instant at time t, then the intrinsic growth rate (r) implied by those vital rates is a weighted average of the observed population's age-specific growth rates, where the weights are each age's fractional contribution to the time t stable equivalent number of births. Although both the r(x, t) and the q(x, t) are mixtures of vital rates and the number of persons in the observed time t population, their accumulated product, r, is completely independent of the N(x, t).

#### 2. Proof

The proof of equation (1) follows from considering how the stable equivalent number of births, Q(t), grows over time. Since the vital rates are assumed to be constant, we must have

(6) 
$$\frac{\mathrm{d}\,Q(t)}{\mathrm{d}t} = r\,Q(t)$$

because, at all ages, the stable equivalent grows exponentially at the intrinsic rate implied by the constant vital rates. At the same time, equation (5) indicates that

(7) 
$$\frac{\mathrm{d}\,Q(t)}{\mathrm{d}t} = \frac{\mathrm{d}\left[\int N(x,t)\,v(x)\mathrm{d}x\right]}{\mathrm{d}t} \\ = \int r(x,t)\,N(x,t)\,v(x)\mathrm{d}x$$

where the second equality follows from equation (2). Equating equations (6) and (7) and dividing by Q(t) yields

(8) 
$$r = \int r(x,t) \frac{N(x,t)v(x)}{Q(t)} dx$$

which, by equation (3), is the desired result.

#### 3. A brief history

The concept of the reproductive value goes back to the great statistician R.A. Fisher. In the 1930s, Fisher interpreted demography's stable population characteristic equation as describing how individuals repaid the "loan" of a life at birth by their reproduction over the life course. The age x reproductive value was simply the amount still owed at age x (cf. Schoen 2006, 30). The later development of the discrete stable model by Leslie (1945) and others showed that reproductive value functions were the elements of the dominant left eigenvector of a population projection (Leslie) matrix. Along with Lotka's r (the dominant eigenvalue of a Leslie matrix), and the stable population age composition (the dominant right eigenvector of a Leslie matrix), the reproductive value emerged as a fundamental demographic quantity.

The concept of age-dependent growth emerged in work by Bennett and Horiuchi (1981), which was generalized by Preston and Coale (1982). The motivation was to develop new demographic relationships that could be used to estimate a broad range of population measures. Kim (1986) extended the "variable-r" approach to discrete relationships, but pointed out that the variable-r relationships were essentially tautologies. If data were available to calculate the age-dependent growth rates, those data could be used directly, without introducing r(x, t) values. In some applications, however, the variable-r approach has been shown to be analytically useful (cf. Preston, Heuveline, and Guillot 2001, 184-189).

Preston (1986) pointed out that in any observed population there was an age at which the sum of the age-specific growth rates up to that age equaled the intrinsic growth rate implied by the population's current vital rates. Preston (1986) approximated that age by Lotka's generation length, T, though Wachter (1988) later showed that T was not a reliable estimate. Schoen and Kim (1991) sought analytical linkages between the r(x,t)function and conventional demographic variables. That work derived equation (1) and explored the relationships discussed in the next section.

#### 4. Related results

Three noteworthy analytical relationships follow from equation (1). First, the change in the q(x,t) function over time depends directly on the difference between r(x,t) and r, as

(9) 
$$\frac{\mathrm{d}\,q(x,t)}{\mathrm{d}t} = q(x,t)[r(x,t)-r].$$

Equation (9) is reminiscent of the central relationship in Guillot (2009), a previous contribution to the Formal Relationships Special Collection.

Second, equation (1) leads to a "Fundamental Principle" of population dynamics that sees every observed population as always moving toward the stable population implied by its *current* vital rates. Let us define the stable equivalent population at age x and time

t, S(x, t), by

(10) 
$$S(x,t) = Q(t)e^{-rx}p(x)$$

and age-specific momentum at time t,  $\Omega(x, t)$ , as

(11) 
$$\Omega(x,t) = \frac{S(x,t)}{N(x,t)}$$

Here, the term "momentum" is used to indicate the growth associated with any transition to stability, not just with the transition to a zero-growth population. The extent to which an observed population moves toward stability is then given by the q-weighted covariance between the r(x, t) and the natural logarithm of the  $\Omega(x, t)$  (cf. Schoen 2006, 71).

Third, the discrete form of equations (1) and (2) leads to an intimate relationship between reproductive contributions and population momentum (Schoen and Kim 1992). Let  $N_{ijt}$  be the number of persons in component *i* and age group *j* of the population at time *t*, where component 1 is the dominant component of the spectral decomposition of the Leslie matrix. The symbol  $N_{jt}$  represents the observed number of persons, in all components, in age group *j* at time *t*. Age-component-specific momentum,  $\Omega_{ijt}$ , is then

(12) 
$$\Omega_{ijt} = \frac{N_{ijt}}{N_{jt}}$$

Analogously, the age-component-specific reproductive contribution function,  $q_{ijt}$ , can be written

(13) 
$$q_{ijt} = \frac{N_{jt} v_{ij}}{Q_{it}}$$

If matrix  $\Omega_t$  has  $\Omega_{ijt}$  as its element in row *i* and column *j*, and matrix  $q_t$  has  $q_{ijt}$  as its (i, j)th element, then

(14) 
$$\Omega_{\mathbf{t}} = \mathbf{q}_{\mathbf{t}}^{-1}$$

or the inverse of the age-component-specific reproductive contribution matrix gives the age-component-specific population momentum matrix.

#### 5. Acknowledgements

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