

# Measures of fitness and demographic stability

(Malthusian parameter/entropy/natural selection)

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**ABSTRACT** The concepts of entropy and reproductive potential of a genotype were introduced in a previous paper [Demetrius, L. (1974) *Proc. Natl. Acad. Sci. USA* 71, 4645-4647] and an analogue of the fundamental theorem of natural selection was derived. This paper relates the entropy of a population with the rate of convergence of the population to the stable age distribution. I show that (i) at maximal entropy, no oscillatory components exist and the birth sequence is unaffected by perturbations in the stable age distribution; and (ii) at zero entropy, oscillatory components occur and increase as rapidly as the real exponential component in the birth sequence.

These results have implications towards (i) the relation between population fitness and adaptedness, (ii) modes of selection and the evolution of reproductive strategies, and (iii) the evolution of senescence.

One measure of the stability of a population is its resistance to environmental perturbations, that is, its rate of return to the equilibrium state when disturbed. This property is of crucial importance in understanding the evolution of reproductive strategies under natural selection.

In an earlier paper (2) I analyzed the adaptive properties of iteroparity in terms of an entropy concept introduced in ref 1. Furthermore, I indicated a relation between the entropy of a population and its resistance to environmental changes.

This paper gives a precise formulation of this idea. I use the rate of convergence to the stable age distribution as a measure of demographic stability and show that (i) at maximal entropy, no oscillatory components exist and the population is maximally stable; and (ii) at zero entropy, oscillatory components occur and the period of oscillation is precisely the generation time.

For a more complete account of the demographic facts I cite in Section I, see books by Coale (3) and Keyfitz (4). The results in Section II are based on some deep connections between ergodic theory, statistical mechanics, and population biology. For the mathematical basis of this connection, see refs. 1, 5, and 6.

I. Let  $u(x,t)$  denote the age distribution of the population at time  $t$ , and let  $\mu(x,t)$  be the age-specific death rate. The dynamics of the population is given by the von Foerster equation

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

with boundary conditions

$$u(0,t) = \int_0^\infty m(x,t)u(x,t)dx$$

$$u(a,0) = u_0(a)$$

$m(x,t)$  represents the age-specific fecundity and  $u_0(a)$  denotes the initial age distribution. Eq. [1.1] can be reduced to the renewal equation

$$B(t) = f(t) + \int_0^t V(x,t)B(t-x)dx$$

where  $B(t) = u(0,t)$  and  $f(t) = \int_0^\infty h(x,t)m(x,t)u_0(x-t)dx$ . Also,

$$V(x,t) = l(x,t)m(x,t)$$

and  $h(x,t) = \exp[-\int_0^t \mu(x-t+y,y)dy]$  and  $l(x,t) = \exp[-\int_0^x \mu(y,t-x+y)dy]$ .

Assuming that  $l(x,t)$  and  $m(x,t)$  are independent of  $t$ , we have that the growth rate  $r$  is the unique positive root of the Lotka integral equation

$$\int_0^\infty e^{-rx}V(x)dx = 1. \quad [1.2]$$

Let  $(r_j)$  denote the roots of [1.2]. If these roots are all distinct, then

$$B(t) = \sum_{j=0}^{\infty} Q_j e^{r_j t}$$

where

$$Q_j = \frac{\int_0^\infty f(t)e^{-r_j t} dt}{\int_0^\infty t e^{-r_j t} V(t) dt}$$

II. We now consider Lotka's equation

$$\int_0^\infty e^{-rx}l(x)m(x)dx = 1. \quad [2.1]$$

The net reproductive rate is  $R_0 = \int_0^\infty l(x)m(x)dx$ . The probability density function for the ages at which offspring will be produced is given by

$$q(x) = \frac{l(x)m(x)}{R_0}$$

The entropy of the population is defined as

$$h = -\frac{\int_0^\infty q(x) \log q(x) dx}{\int_0^\infty x q(x) dx}$$

This expression for the entropy can be derived by using a variational principle argument (1). The expectation of  $q(x)$  is  $T = \int_0^\infty x q(x) dx$ . This is the cohort generation time.

The entropy,  $h$ , measures the variability of the contribution of the different age classes to  $R_0$ . In ref. 1 I used a measure of entropy based on  $p(x) = e^{-rx}l(x)m(x)$ , the probability density function for the age of reproducing individuals. See ref. 7 for a discussion concerning the relation between these two measures of entropy. From [2.1] we have

$$\frac{1}{R_0} = \int_0^\infty e^{-rx} q(x) dx.$$

Now, let  $\psi(-r)$  denote the cumulant generating function of  $q(x)$ . Then  $\psi(-r) = -\log_e R_0 + 2n\pi i$  ( $n = 0, \pm 1, \pm 2, \dots$ ).

And

$$\log_e R_0 - 2n\pi i = r\mu_1 - \frac{1}{2!}r^2\mu_2 + \frac{1}{3!}r^3\mu_3 - \dots \quad [2.2]$$

where  $\mu_n$  is the  $n$ th cumulant of the distribution.

The positive real root of [2.1] is given when  $n = 0$ . In this case, we have

$$\log_e R_0 = r\mu_1 - \frac{1}{2!}r^2\mu_2 + \frac{1}{3!}r^3\mu_3 - \dots \quad [2.3]$$

where  $\mu_n = \mu_n(T)$ . We call [2.3] the *equation of state* of a population. This equation was known to Lotka (8).

We recall that the demographic parameters considered in this paper all have analogues in statistical physics. In particular, the generation time corresponds to the reciprocal of the temperature. We use the term "equation of state" to describe [2.3] since this equation is analogous to the classic equation of state for gases. In this case, the cumulants  $\mu_n$  are functions of temperature and are known as the virial coefficients. Particular expressions for the virial coefficients will yield the van der Waals equation.

We now examine the stability of a population under two conditions.

**Maximal entropy.** There is a unique distribution that maximizes  $h$  for a given generation time  $T$ . We have

$$q(x) = e^{-x/T}/T, \quad x \geq 0.$$

The characteristic function for this distribution is given by

$$\phi(t) = 1/(1 - itT).$$

The cumulants of all orders exist and

$$\begin{aligned} \mu_n &= \text{coefficient of } (it)^n/(n!) \text{ in } -\log(1 - itT) \\ &= (n-1)! T^n. \end{aligned}$$

The roots of the Lotka integral equations are given by

$$\log_e R_0 + 2n\pi i = rT - \frac{1}{2}r^2T^2 + \frac{1}{3}r^3T^3 - \dots$$

It is easy to show that this equation has no complex roots. The unique real root  $r_0$  is given by  $r_0 = (R_0 - 1)/T$ . The birth sequence is

$$B(t) = Q_0 e^{r_0 t}.$$

Clearly the birth sequence is immediately stabilized when the stable age distribution is perturbed.

**Zero entropy.** At zero entropy, reproduction occurs at a single age, say  $x = \alpha$  and  $q(x) = \delta(x - \alpha)$ , where  $\delta(x)$  is the Dirac-delta function.

Consider the Gaussian distribution  $q^*(x)$  with mean  $T$  and variance  $\sigma^2$ .

$$q^*(x) = \frac{1}{\sigma\sqrt{2\pi}} \exp[-(x - T)^2/2\sigma^2].$$

Let  $\mu_n^*$  denote the  $n$ th cumulant of the distribution. Then  $\mu_1^* = T$ ,  $\mu_2^* = \sigma^2$  and  $\mu_n^* = 0$ ,  $n > 2$ . Now  $\delta(x - T) = \lim_{\sigma \rightarrow 0} 1/\sigma\sqrt{2\pi} \exp[-(x - T)^2/2\sigma^2]$ . Hence, in the case of the Dirac-delta function, the roots  $r_n$  of [2.2] are given by

$$\log_e R_0 = r_n T + 2n\pi i$$

and

$$r_n = (\log_e R_0/T) - (2n\pi i/T).$$

The birth sequence is

$$B(t) = R_0^{t/T} \sum_{n=0}^{\infty} Q_n e^{2n\pi i t/T}.$$

The behavior is a purely oscillatory component and a constant multiplied by the same real exponential factor. The period of oscillation is precisely the generation time,  $T$ .

I should point out that Coale (3) and Keyfitz (9) have studied some aspects of the effects of the maternity function  $V(x)$  on the rate of convergence to the stable age distinction. These authors, however, were unaware of the unifying force of the entropy concept as a measure of population resonance.

## DISCUSSION

**Fitness and Adaptedness.** Adaptedness of a population describes the ability of a population to live and reproduce in a wide variety of environments. The fitness of a genotype refers to the average contribution that carriers of that genotype make to the gene pool of successive generations. These are two of the most fundamental concepts in population biology, and several attempts have been made to give these notions a quantitative basis. The pioneering work of Fisher (10) has revolved around the Malthusian parameter as a measure of fitness. Attempts to explain the evolution of reproductive strategies, as in the work of MacArthur and Wilson (11) on  $r$  and  $K$  selection and of Medawar (12), Williams (13), and Hamilton (14) on the evolution of senescence, have essentially been based on Fisher's ideas.

Recently, however, theoretical and experimental studies (15, 16) on populations in random and fluctuating environments have shown the imperfect correlation between the Malthusian parameter and population adaptedness.

These results have stimulated the search for measures of fitness that predict population stability and persistence under varying environmental regimes. The work of Lerner has been influential in this regard. In ref. 17, the term genetic homeostasis was used to describe the condition of population equilibrium in which phenotypic composition was insensitive to environmental changes. This stability is achieved by the superior adaptedness of heterozygous genotypes. Genetic homeostasis has a demographic correlate. We use the term "demographic homeostasis" to describe the ability of the birth sequence to maintain its stable trajectory when subject to environmental disturbances. This condition is characterized by the variability of the contribution of the different age classes to the stable age distribution. This is measured by the entropy parameter. The mathematical relation between entropy and stability suggests that the demographic parameters, growth rate, entropy, and generation time, give a complete description of the adaptive properties of a population.

**Modes of Selection.** The theory of  $r$  and  $K$  selection proposed by MacArthur and Wilson (11) claims that in variable and fluctuating environments, genotypes with high  $r$  will be constantly favored.  $K$  selection is described as selection favoring competitive ability, which is considered crucial in stable environments where populations are at their carrying capacity, which is given by  $K$ . This theory, which ignores the complexity of the life cycle of the population, implicitly assumes that the parameters  $r$  and  $K$  completely describe the evolutionary dynamics of a population.

However, in a variable environment, a population can avoid certain extinction if its mean growth rate  $r$  is larger than  $\omega^2/2$ , where  $\omega^2$  denotes the environmental variance (18). For populations without age structure, there will be an intense selection for a high  $r$ , as there exist no internal mechanism to reduce the

effects of environmental variance. For populations with complex life cycles, the effects of environmental variance can be reduced by selection favoring genes that confer a resistance to environmental fluctuations. These genotypes have high entropy. This mode of selection, whereby population stability is increased through its effect on the homeostatic ability of genotypes, is termed *h* selection (2).

**Senescence.** The term senescence describes an organism's increasing likelihood of death with increasing age. This condition, which appears to be the antithesis of adaptation, has been studied from an evolutionary point of view by several workers (12–14). These authors claim that senescence is due to the action of pleiotropic genes, which have positive effects on adaptedness at early ages and adverse effects at later stages in the life history. These arguments all point to aging as evolving under the effect of indirect selective pressures.

However, senescence can be considered as one of a large class of life-history patterns that have evolved to maximize entropy, with constraints on the generation time and the variance in generation time. For a given generation time, *T*, the maximum entropy is given by a maternity function which is negative exponential. The following inferences may be drawn concerning the life history of a population at maximum entropy.

(a) If the age-specific death rate is bounded by the reciprocal of the generation time, then fecundity decreases with age.

(b) If the age-specific death rate is equal to the reciprocal of the generation time, then fecundity is independent of age.

(c) If the age-specific death rate is greater than the reciprocal of the generation time, then fecundity increases with age.

When the age-specific death rate is a constant, then its reciprocal is precisely the prospective life time of an individual. Hence (b) can be described as follows: (b)' if the prospective life-time is equal to the mean generation time, then fecundity is independent of age.

By imposing further constraints on the demographic parameters, we restrict the set of life-history patterns that are compatible with the maximization of entropy. If we fix the variance in generation time, then the net maternity function that maximizes entropy is a Gaussian distribution. This yields life-history patterns similar to (a) and (c).

Possibilities (a) and (c) are both compatible with an age-specific death rate that increase with age. However, for (c) we have senescence associated with a fecundity that increase with

age, whereas for (a) senescence is always associated with a fecundity that decreases with age; (b) corresponds to nonsenescent populations.

This point of view not only explains the nonuniversal nature of senescence, but specifies the kind of demographic constraints that may operate when senescence prevails.

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