

Demographic Parameters and Natural Selection

(Malthusian parameter/entropy/reproductive potential/fundamental theorem)

LLOYD DEMETRIUS*

Division of Applied Mathematics, Brown University, Providence, R.I.

Communicated by S. Smale, September 13, 1974

ABSTRACT This paper introduces two new demographic parameters, the entropy and the reproductive potential of a population. The entropy of a population measures the variability of the contribution of the different age classes to the stationary age distribution. The reproductive potential measures the mean of the contribution of the different age classes to the growth rate. Using a relation between these measures and the Malthusian parameter, it is shown that in a random mating population in Hardy-Weinberg equilibrium, and under slow selection, the rate of change of entropy is equal to the genetic variance in entropy minus the genetic covariance of entropy and reproductive potential. This result is an analogue of Fisher's fundamental theorem of natural selection.

INTRODUCTION: The Malthusian parameter reflects an important aspect of population growth, namely, the long-run behavior of the population. This parameter does not completely determine the adaptive properties of a population, distinct populations may achieve identical growth rates with different life-history patterns. This paper introduces two new demographic concepts, entropy and reproductive potential. The entropy measures the variability in the contribution of different age classes to the stationary age distribution and the reproductive potential measures the mean of the contribution of the different age classes to the Malthusian parameter. We show that in a random mating population in Hardy-Weinberg equilibrium and under slow selection, the rate of change of entropy is equal to the genetic variance in entropy minus the genetic covariance of entropy and reproductive potential. When the reproductive potential of each genotype is zero, entropy is equal to the Malthusian parameter and, as a corollary, we obtain Fisher's fundamental theorem of natural selection which states that in a random mating population in Hardy-Weinberg equilibrium and under slow selection, the rate of change of fitness is equal to the genetic variance in fitness. Fitness in this case is measured by the Malthusian parameter.

This paper is an application of some recent ideas in ergodic theory to population dynamics. Our sources are Billingsley (1) and Spitzer (2) for ergodic theory, Keyfitz (3) for demographic models, and Crow and Kimura (4) for population genetics. An emphasis on the biological aspects of ideas treated in this paper will appear in ref. (5).

1. Consider a population divided into n age groups. Let m_j denote the number of offspring an individual in age group j at

time t contributes to the first age group at time $(t + 1)$. Let b_j denote the proportion of individuals of age j at time t surviving to age $j + 1$ at time $t + 1$. The population model can be represented by the $n \times n$ matrix $A = (a_{ij}) \geq 0$, where

$$a_{ij} = \begin{cases} m_j & \text{for } i = 1 \\ b_j & \text{for } i = j + 1 \\ 0 & \text{otherwise} \end{cases} \quad [1.1]$$

and $m_j \geq 0, 0 < b_j \leq 1, m_n > 0$.

Since the matrix A is irreducible, we conclude from the Perron-Frobenius theorem that

(i) A has a simple positive real dominant eigenvalue λ .

(ii) There exist eigenvectors \bar{u}, \bar{v} with all components positive such that

$$A\bar{u} = \lambda\bar{u}$$

$$\bar{v}A = \lambda\bar{v}$$

$$(\bar{u}, \bar{v}) = 1.$$

$\bar{u} = (u_i)$ corresponds to the stationary age distribution; $\bar{v} = (v_i)$ is a measure of the relative contribution made to the stationary population in the future by the individual age groups; $\log_e \lambda$ is the intrinsic rate of natural increase or the Malthusian parameter.

Let

$$l_j = \begin{cases} 1 & \text{for } j = 1 \\ \prod_{r=1}^{j-1} b_r & \text{for } j \geq 2 \end{cases} \quad [1.2]$$

and

$$k = \frac{1}{\sum_{j=1}^n j m_j u_j}.$$

Then

$$u_i = l_i / \lambda^i \quad [1.3]$$

and

$$v_i = \frac{k \sum_{j=i}^n m_j u_j}{u_i}.$$

2. We shall now consider the population as a system composed of a number n of interacting age classes. The ideas we now describe revolve around the studies of Ruelle (6) on the

* Present Address: Dept. of Mathematics, Rutgers University, New Brunswick, N.J. 08903

statistical mechanics of one-dimensional lattice systems. Let $S = \{1, 2, \dots, n\}$, Z the integers and let $X = S^Z$. Give S the discrete topology and X the product topology. X is a compact Hausdorff space. Let

$$\Sigma = \{(x_k) \in X : a_{x_k, x_{k+1}} > 0 \text{ for all } k \in Z\}.$$

The set Σ is a closed subset of X and is compact. Consider the shift $T: \Sigma \rightarrow \Sigma$ defined by

$$T\{x_k\}_{-\infty}^{+\infty} = \{x'_k\}_{-\infty}^{+\infty} \quad \text{where } x'_k = x_{k+1}.$$

The shift T is a homeomorphism of Σ . Let M denote the set of all T -invariant probability measures on Σ . We shall interpret the space Σ as the configuration or phase space of the system. An element $\mu \in M$, is a state. For any state $\mu \in M$, we consider the dynamical system (Σ, μ, T) . We now define the Kolmogorov entropy of the action T . We refer to (1) for details.

Let $\mathcal{G} = (A_1, A_2, \dots, A_n)$ be a finite partition of Σ into measurable sets. The entropy of the partition \mathcal{G} is defined by

$$h(\mathcal{G}) = - \sum_{i=1}^n \mu(A_i) \log \mu(A_i).$$

Let

$$\mathcal{G}_{(n)} = \bigcup_{r=0}^{n-1} T^{-r}(\mathcal{G}).$$

The entropy of \mathcal{G} relative to T is

$$h(\mathcal{G}, T) = \lim_{n \rightarrow \infty} \frac{1}{n} h(\mathcal{G}_{(n)})$$

and the entropy of T is

$$H(T) = \sup h(\mathcal{G}, T)$$

where the supremum is taken over all partitions \mathcal{G} .

Now let ψ be any real valued function defined on the space Σ . The expression $\int_{\Sigma} \psi d\mu$ is the mean energy in the state μ . The free energy E_{μ} is defined by

$$E_{\mu} = H_{\mu} + \int_{\Sigma} \psi d\mu;$$

A state μ is called an equilibrium state if

$$E_{\mu} = \sup_{\mu \in M} \left(H_{\mu} + \int_{\Sigma} \psi d\mu \right).$$

Hence an equilibrium state is a state that maximizes the entropy for a fixed mean energy.

We now consider a potential ψ defined by

$$\psi(x) = -\log a_{x_0=t, x_1=j}$$

where a_{ij} is given by 1.1. The value of this function ψ at the point $x = (x_k) \in \Sigma$ thus depends only on two coordinates (x_0, x_1) . This potential ψ represents the interaction between the age classes i and j . The biological reasons for the choice of this potential are discussed in ref. 5.

Using a theorem due to Ruelle (6) we conclude that

- (a) the system (Σ, μ, ψ, T) has a unique equilibrium state μ
- (b) μ is a Markov measure.

This Markov measure μ is derived from the stochastic matrix

$$P = (p_{ij}) \geq 0$$

where $p_{ij} = u_j a_{ij} / \lambda u_i$. From 1.3, we have

$$p_{ij} = \begin{cases} p_j & \text{for } i = 1 \\ 1 & \text{for } i = j + 1 \\ 0 & \text{otherwise} \end{cases} \quad [2.1]$$

where

$$p_j = \frac{l_j m_j}{\lambda^j}.$$

The expression p_j is the probability distribution for the age of reproducing individuals in a stationary population. Let us denote $\int_{\Sigma} \psi d\mu$ by Φ_{μ} . The free energy E_{μ} , the entropy H_{μ} , and the mean energy Φ_{μ} in the equilibrium state μ can be computed using 2.1. Details will appear elsewhere. We have

$$\begin{aligned} E_{\mu} &= \log_e \lambda, \\ H_{\mu} &= - \sum_{j=1}^n p_j \log p_j / \sum_{j=1}^n j p_j, \\ \Phi_{\mu} &= - \frac{\sum_{j=1}^n p_j \log \lambda^j p_j}{\sum_{j=1}^n j p_j}. \end{aligned}$$

We shall call H_{μ} the entropy H of the population and Φ_{μ} the reproductive potential Φ . We note that the free energy in the equilibrium state is precisely the Malthusian parameter or the intrinsic rate of increase of the population. The entropy H is a measure of the variability of the contribution of the different age classes to the stationary age distribution and the reproductive potential Φ is a measure of the mean of the contribution of the different age classes to the growth rate of the population. We have the identity

$$\log_e \lambda = H - \Phi.$$

The expression $\sum_{j=1}^n j p_j$ is the generation time of the population.

The entropy H and reproductive potential Φ have continuous time analogues.

Let

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

and

$$\Phi = - \frac{\int_0^{\infty} p(x) \log [l(x) m(x)] dx}{\int_0^{\infty} x p(x) dx}$$

where $p(x) = e^{-rx} l(x) m(x)$. The function $l(x)$ is the probability that an individual survives to age x and $m(x)$ is the number of offspring born per individual at age x . The Malthusian parameter r , is the unique real root of the equation $\int_0^{\infty} e^{-rx} l(x) m(x) dx = 1$. Clearly, we also have the identity

$$r = H - \Phi. \quad [2.2]$$

3. We shall now consider a random mating population and assume an arbitrary number m of alleles at a single locus. Let $l_{ij}(x)$ be the probability of survival of an $A_i A_j$ individual from birth to age x , and let $m_{ij}(x)$ be the rate at which a member aged x , of the genotype $A_i A_j$, produce offspring.

The Malthusian parameter of the genotype $A_i A_j$ is defined to be the unique real root of the equation

$$\int_0^\infty e^{-r_{ij}x} l_{ij}(x) m_{ij}(x) dx = 1.$$

The entropy H_{ij} of the genotype is defined by

$$H_{ij} = - \frac{\int_0^\infty p_{ij}(x) \log p_{ij}(x) dx}{\int_0^\infty x p_{ij}(x) dx}$$

where

$$p_{ij}(x) = e^{-r_{ij}x} l_{ij}(x) m_{ij}(x).$$

Let Φ_{ij} denote the reproductive potential of the genotype $A_i A_j$. Then as in 2.2,

$$r_{ij} = H_{ij} - \Phi_{ij}. \tag{3.1}$$

Let x_i denote the frequency of the i th allele A_i , and x_{ij} the frequency of the genotype $A_i A_j$.

Let

$$\Phi_i = \frac{\sum_j \Phi_{ij} x_{ij}}{x_i}.$$

r_i and Φ_i are defined analogously.

The expressions Φ , r , and H will denote the mean reproductive potential, mean Malthusian parameter, and mean entropy, respectively.

Under slow selection the rate of change of gene frequency is given by

$$\frac{dx_i}{dt} = x_i(r_i - r). \tag{3.2}$$

If the population is in Hardy-Weinberg equilibrium, then $x_{ij} = x_i x_j$ and the mean entropy

$$H = \sum_{i,j} H_{ij} x_i x_j.$$

Hence

$$\frac{dH}{dt} = \sum_i H_i \frac{dx_i}{dt} + \sum_j H_j \frac{dx_j}{dt}.$$

Using 3.1 and 3.2, we have

$$\begin{aligned} \frac{dH}{dt} &= 2 \sum_i x_i H_i (H_i - H) - 2 \sum_i x_i H_i (\Phi_i - \Phi) \\ &= 2 \sum_i x_i (H_i - H)^2 - 2 \sum_i x_i (H_i - H) (\Phi_i - \Phi) \\ &= V_H - C_{H,\Phi} \end{aligned}$$

where V_H is the genetic variance in entropy and $C_{H,\Phi}$ is the genetic covariance of entropy and reproductive potential.

We now have an analogue of Fisher's fundamental theorem.

I. In a random mating population in Hardy-Weinberg equilibrium, the rate of increase of entropy is equal to the genetic variance in entropy minus the covariance of entropy and reproductive potential.

If the reproductive potential of each genotype is zero, then the entropy is equal to the Malthusian parameter and as a corollary to I we have Fisher's theorem. In the following statement of Fisher's theorem, fitness is measured in terms of the Malthusian parameter.

II. In a random mating population in Hardy-Weinberg equilibrium, the rate of increase of fitness is equal to the genetic variance in fitness.

REMARK: Under strong selection, Equation 3.2 is no longer valid, and departures from Hardy-Weinberg equilibrium occur (7). Refinements of II to accommodate these changes are known. It has been shown by Kimura (see ref. 4 for a discussion and reference to the original papers) that

$$\frac{dr}{dt} = V + \sum_{i,j} x_{ij} \frac{dr_{ij}}{dt} + \sum_{i,j} x_{ij} d_{ij} \frac{d\theta_{ij}}{dt}$$

where V is the additive genetic variance in Malthusian parameter, d_{ij} the dominance deviation from linearity, and $\theta_{ij} = x_{ij}/x_i x_j$ the departure from Hardy-Weinberg proportions.

The entropy analogues are of the same form as above. Details will appear elsewhere.

The author is indebted to James Crow and Richard Lewontin for criticism of preliminary drafts of the manuscript. This research was supported by the National Science Foundation under Grant GP 15132.

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