NATURAL SELECTION AND AGE-STRUCTURED POPULATIONS

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ABSTRACT

This paper studies the properties of a new class of demographic parameters for age-structured populations and analyzes the effect of natural selection on these parameters. Two new demographic variables are introduced: the entropy of a population and the reproductive potential. The entropy of a population measures the variability of the contribution of the different age classes to the stationary population. The reproductive potential measures the mean of the contribution of the different age classes to the Malthusian parameter. The Malthusian parameter is precisely the difference between the entropy and the reproductive potential. The effect of these demographic variables on changes in gene frequency is discussed. The concept of entropy of a genotype is introduced and 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 covariance in entropy and reproductive potential. This result is an information theoretic analog of Fisher's fundamental theorem of natural selection.

THE Malthusian parameter concept occupies a central place in evolutionary theory. This parameter describes one aspect of population growth, namely the long-run behavior of a population in a density-independent phase. In density-dependent phases, the theory centers on the carrying capacity of the organism. This factor represents the maximum density at which a population may be maintained in a constant environment. These parameters are not valid guides to the results of competition between species. The work of PARK (1955) on the Tribolium model shows that a species with a high carrying capacity may be suppressed in competition by one with a lower density. The experiments of CLATWORTHY and HARPER (1962) on the Lemma model indicate that neither the intrinsic growth rate nor the carrying capacity predicts the outcome of two species in competition.

Selective forces act on the life-history components of a population, namely the developmental period and spacing between births. It is well known that these factors have different effects on the growth rate and carrying capacity of a population. In the case of invading plants, for example, colonizing success is critically determined by the germination phase (HARPER 1965). The work of EHRENDORFER (1965) on the colonizing ability of annuals and perennials underlines the importance of the effects of life history on evolutionary success. On the

theoretical side, HOLGATE (1967), building on the work of COLE (1954), has shown that biennials have less chance of random extinction than annuals, given that both populations have the same growth rate.

A general principal emerges from these facts: populations with the same Malthusian parameter may have different colonizing success depending on whether they are semelparous or iteroparous. This suggests that any study of the effects of ecological factors on genetic theory should involve a parameter that distinguishes between populations with the same Malthusian parameter but different life histories. This paper introduces the concept of entropy as a method of dealing with age-structured populations.

We derive an expression for the entropy of a population. The entropy measures the variability of the contribution of the different age classes to the stationary population. We also introduce a second demographic parameter, the reproductive potential. This parameter measures the mean of the contribution of the different age classes to the growth rate of the population. The Malthusian parameter or intrinsic rate of increase is precisely the difference between the entropy and the reproductive potential. We use this fact to 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 covariance in entropy and reproductive potential. This result is an analog of the fundamental theorem of natural selection. When the reproductive potential of each genotype is zero, entropy is equal to the Malthusian parameter and our theorem reduces to Fisher's theorem (FISHER 1930).

The relation between age structure and gene-frequency change has recently been given considerable attention (CHARLESWORTH 1970, 1972; POLLAK and KEMPTHORNE 1970, 1971). These authors focus on the Malthusian parameter and their refinements and amendments of Fisher's theorem are in that context. Our aim is to show the limitations of the Malthusian parameter in understanding the relation between demographic variables and evolutionary theory and to propose entropy as a complementary concept.

This paper is an application of some recent ideas in ergodic theory to population models. Our sources are BILLINGSLEY (1965) for ergodic theory, KEYFITZ (1968) for demographic models and CROW and KIMURA (1970) for population genetics. The paper is organized as follows. Section 1 deals with a single population in terms of the Leslie model. The main idea is to represent population models as invertible measure-preserving transformations and to apply the Kolmogorov-Sinai theory of entropy to these models. In this section we derive an expression for the entropy of a population. We also introduce the concept of reproductive potential and we state the relation between entropy, reproductive potential and the Malthusian parameter or growth rate of a population.

Section 2 deals with a random mating population. Using the expression derived for the entropy of a population obtained in Section 1, we define the concept of entropy of a genotype, and we prove the analog of Fisher's theorem.

1. We begin with the Leslie model. Consider a population divided into n age classes. Let m_i denote the number of individuals born in the next unit of time

to each parent of age i. Let b_i be the proportion of individuals of age i surviving to age $i + 1$. The change in age structure between time t and time $t + 1$ is given by the equation

$$\vec{x}(t + 1) = A\vec{x}(t)$$

where $A = (a_{ij}) \geq 0$,

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

and $m_j \geq 0$, $0 < b_j \leq 1$, $m_n > 0$. Let $S = \{1, 2, \ldots, n\}$, and let $X = \prod_{-\infty}^{\infty} S_n$, where $S_n = S$. X is the set of doubly infinite sequences composed with the elements of S. Let

$$\Omega = \left\{ (x_i) \ \varepsilon \ X : a_{x_i, x_{i+1}} > 0 \right\} .$$

We now give an interpretation of the set Ω. We first note that the population matrix A is irreducible; that is, for each a_{ij} there exists an $n(i.j)$ such that $a_{ij}^{(n)} > 0$. Let $G(A)$ be the graph associated with the matrix A. This graph is obtained by joining nodes i to j if $a_{ij} > 0$. The irreducibility of A implies that the graph $G(A)$ is connected; that is, given any two nodes, there is a directed path joining them. The set Ω represents the set of all paths in the graph $G(A)$.

Let T denote the shift transformation

$$T : \Omega \to \Omega$$
$$T : \{x_n\}_{-\infty}^{\infty} \to \{x'_n\}_{-\infty}^{\infty}$$

where $x'_n = x_{n+1}$.

We shall call (Ω, T) the symbolic dynamical system associated with the matrix A.

Since A is irreducible, by the Perron-Frobenius theorem: (1) A has simple positive real dominant eigenvalue λ, (2) there exist unique eigenvectors $\bar{u}$ and $\bar{v}$ with all components positive such that

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

where $\bar{u} = (u_i)$ corresponds to the stationary age distribution, $\bar{v} = (v_i)$ corresponds to the reproductive value, and $\log_e \lambda = $ Malthusian parameter or intrinsic rate of natural increase of the population.

Let

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

Then

$$u_i = l_i / \lambda^i \tag{1.1}$$

$$v_i = k \ \frac{\sum_{j=i}^{n} m_j u_j}{u_i} \tag{1.2}$$

where

$$k = \frac{1}{\sum\limits_{j=1}^{n} j m_j u_j} \, .$$

We transform A into a probability matrix $P = (p_{ij}) \geq 0$. Let

$$p_{ij} = (u_j/\lambda u_i) a_{ij} \, . \tag{1.3}$$

Then clearly

$$\sum_{j=1}^{n} p_{ij} = 1 \, , \qquad 0 \leq p_{ij} \leq 1 \, .$$

The probability matrix P can be written

$$P = \begin{bmatrix} p_1 & p_2 & \cdots & & p_n \\ 1 & 0 & 0 & \cdots & 0 \\ & & & & \\ 0 & 1 & 0 & \cdots & \\ \vdots & & & & \\ 0 & 0 & & \cdots & 1 & 0 \end{bmatrix}$$

where

$$p_j = l_j m_j/\lambda^j \, . \tag{1.4}$$

l_j represents the proportion of individuals surviving to age j. The row vector of stationary states $z = (z_i)$ is given by

$$zP = z \, ,$$
$$z_i = u_i v_i \, .$$

We now use the Markov matrix P to introduce a probability measure μ on the space of sequences Ω. Since $zP = z$, the shift T acting on Ω is measure-preserving and the dynamical system associated with the population matrix A is a Markov shift. For any Markov shift T with transition matrix $P = (p_{ij})$ and stationary distribution $z = (z_i)$, the entropy $H(T)$ is given by

$$H(T) = - \sum_i \sum_j z_i p_{ij} \log p_{ij} \, . \tag{1.5}$$

Using (1.4), we obtain an expression for the entropy of the Markov shift associated with the population model A. From (1.4) and (1.5), the entropy H is given by

$$H = - z_1 \sum_{r=1}^{n} p_r \log p_r$$

where $p_r = l_r m_r/\lambda^r$ and $z_1 = 1/\sum\limits_{r=1}^{n} r \, p_r$. We have

$$H = - \frac{\sum\limits_{r=1}^{n} p_r \log p_r}{\sum\limits_{r=1}^{n} r \, p_r} \, . \tag{1.6}$$

The expression H measures the variability of the contribution of the different age classes to the stationary population.

We note also that the expression $T = \sum_{r=1}^{n} r \, p_r$ is the generation time.

The reproductive potential Φ is defined to be

$$\Phi = - \frac{\sum\limits_{r=1}^{n} p_r \log \lambda^r p_r}{\sum\limits_{r=1}^{n} r\, p_r} \; . \tag{1.7}$$

This expression measures the mean of the contribution of the different age classes to the growth rate of the population.

From (1.6) and (1.7), we have the identity

$$\log_e \lambda = H - \Phi \; . \tag{1.8}$$

It is important to note that the expression for the entropy H and the reproductive potential Φ can be independently derived using certain ideas from ergodic theory and statistical mechanics. This point of view is developed in DEMETRIUS (1974). In the statistical mechanics context, the Malthusian parameter $\log_e \lambda$ is analogous to the Gibbs free energy, the generation time $T = \Sigma_{r=1}^{n} r\, p_r$ is analogous to the inverse of the temperature and the reproductive potential Φ, the mean energy. In effect, Φ can be written in the form

$$\Phi = \int_{\Omega} \Psi \, d\mu$$

where μ is the probability measure induced by the population matrix and Ψ is a real-valued potential function on Ω.

We now give a continuous-time version of (1.6). The Malthusian parameter r is defined to be the real root of the equation

$$\int_0^{\infty} e^{-rx}\, l(x)\, m(x)\, dx = 1 \; .$$

Let

$$p(x) = \frac{l(x)\, m(x)}{e^{rx}} \; .$$

The entropy H is defined to be

$$H = - \frac{\int_0^{\infty} p(x) \log p(x)\, dx}{\int_0^{\infty} x\, p(x)\, dx} \; . \tag{1.9}$$

The reproductive potential Φ is defined to be

$$\Phi = - \frac{\int_0^{\infty} p(x) \log \left[l(x) m(x) \right] dx}{\int_0^{\infty} x\, p(x)\, dx} \; . \tag{1.10}$$

Clearly $r = H - \Phi$.

We now give some interpretations of (1.6).

A. Let $U_r = l_r m_r$. The function U_r characterizes the reproductive schedule of the population. In terms of U_r,

$$\Phi = - \frac{\sum\limits_{r=1}^{n} (U_r/\lambda^r) \log U_r}{\sum\limits_{r=1}^{n} (rU_r/\lambda^r)} \ .$$

Hence, if U_r assumes only values of 0 and 1, $\Phi = 0$ and the entropy is equal to the intrinsic rate of increase.

B. Consider

$$H = - \frac{\sum\limits_{r=1}^{n} p_r \log p_r}{\sum\limits_{r=1}^{n} r\, p_r} \ .$$

Clearly

$$H \geq 0 \ .$$

$H = 0$ if and only if $p_n = 1$ and $p_r = 0$ for $r < n$. In this case, $m_n = \lambda^n/l_n$. This means that semelparous strategies correspond to zero entropy and iteroparous organisms have positive entropy. Semelparity and iteroparity are life-history properties of a population and depend on the age structure and reproductive schedule.

It is well known (COLE 1954; LEWONTIN 1965; DEMETRIUS 1969) that different life-history features may have different adaptive values. However, the Malthusian parameter does not distinguish between semelparity and iteroparity, whereas entropy does. Since entropy reflects both the Malthusian parameter and the reproductive schedule of a population, it seems a more appropriate measure of the fitness of an age-structured population. This point is argued in DEMETRIUS (1975), where the precise reproductive schedule that corresponds to maximum entropy is given.

1. In this section we derive an information-theoretic analog of the fundamental theorem of natural selection. We shall consider a random mating population and we shall assume an arbitrary number m of alleles at a single locus. Let $l_{ij}(x)$ be the probability of survival of an A_iA_j individual from birth to age x, and $m_{ij}(x)$ be the rate at which a member of the genotype A_iA_j, aged x, produces offspring. Let r_{ij} denote the real root of the equation

$$\int\limits_{0}^{\infty} \exp(-r_{ij}x)\, l_{ij}(x)\, m_{ij}(x)\, dx = 1 \ .$$

We define r_{ij} to be the Malthusian parameter of the genotype A_iA_j.

The offspring produced by A_iA_j individuals are not necessarily of the type A_iA_j; hence, as pointed out by MORAN (1962, p. 66), the Malthusian parameter of a genotype is not necessarily the intrinsic rate of increase of the genotype.

The entropy H_{ij} of the genotype is defined as in (1.9) by

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

where

$$p_{ij}(x) = \frac{l_{ij}(x) \, m_{ij}(x)}{e^{r_{ij}x}} \ .$$

These definitions are meaningful only for populations in a density-independent phase and growing in a constant environment. The reproductive potential Φ_{ij} is given by

$$\Phi_{ij} = - \frac{\int_0^\infty p_{ij}(x) \log [l_{ij}(x) \, m_{ij}(x)] \, dx}{\int_0^\infty x \, p_{ij}(x) \, dx}$$

$$H_{ij} = r_{ij} + \Phi_{ij} \ . \qquad (2.2)$$

Let r denote the mean Malthusian parameter:

$$r(t) = \sum_i \sum_j r_{ij} x_{ij}(t) \ .$$

where $x_{ij}(t)$ is the frequency of the genotype $A_i A_j$.
Let x_i denote the frequency of the allele A_i and define

$$r_i = \frac{\sum_j r_{ij} x_{ij}}{x_i}$$

$$\Phi_i = \frac{\sum_j \phi_{ij} x_{ij}}{x_i}$$

$$H_i = \frac{\sum_j H_{ij} x_{ij}}{x_i} \ .$$

Under slow selection, the rate of change of gene frequency is given by KIMURA (1958)

$$dx_i/dt = x_i(r_i - r) \ . \qquad (2.2)$$

Let H denote the mean entropy and Φ the mean reproductive potential. If the population is in Hardy-Weinberg equilibrium, then $x_{ij}(t) = x_i(t)x_j(t)$, and

$$dH/dt = \sum_i \sum_j H_{ij} x_i \frac{dx_i}{dt} + \sum_i \sum_j H_{ij} x_j \frac{dx_i}{dt}$$

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

$$= 2 \sum_i x_i H_i (H_i - H) - 2 \sum_i x_i H_i (\Phi_i - \Phi)$$

$$= 2 \sum_i x_i (H_i - H)^2 - 2 \sum_i x_i (H_i - H)(\Phi_i - \Phi)$$

$$= V_H - C_{H,\Phi} \ ,$$

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 analog of Fisher's fundamental theorem.

Theorem I: In a random mating population in Hardy-Weinberg equilibrium under slow selection 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 entropy is equal to the Malthusian parameter. Fisher's theorem is now a special case of Theorem I.

Theorem II (Fisher): In a random mating population in Hardy-Weinberg equilibrium, under slow selection, the rate of increase of fitness is equal to the genetic variance in fitness.

Fitness in Fisher's theorem is measured in terms of the Malthusian parameter.

Remark: In Theorem I it is assumed that the entropy H_{ij} is time-independent. In Fisher's theorem it is assumed that the Malthusian parameter r_{ij} is time-independent. CHARLESWORTH [1970] has observed that constant Mathusian parameters and Hardy-Weinberg proportions are biologically stringent conditions. These conditions hold only when selection is weak. Under strong selection, Theorem II must be refined to include terms representing the variation in Malthusian parameter with time and departures from Hardy-Weinberg proportions. The appropriate form of Theorem II to include these factors is due to KIMURA [1958] and is given by the expression

$$ dr\ dt = V + \sum_i \sum_j x_{ij} \frac{dr_{ij}}{dt} + \sum_i \sum_j x_{ij} d_{ij} \frac{d\Theta_{ij}}{dt} \ , \qquad (2.5) $$

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

Entropy analogs of (2.5) can be obtained in the same way as we derived Theorem I.

DISCUSSION

1. Information theory has previously been applied in various areas of biology, notably neurobiology (GRIFFITH 1970) and ecology (PIELOU 1969). GRIFFITH's approach is motivated by certain analogies between the firing of nerve cells and the transmission of information through a communication channel. PIELOU's work is based on a formal similarity between the expression for the diversity of an ecological community and Shannon's measure of information.

The entropy concept we have applied is of a different character. A model of a population is obtained by splitting the population into an arbitrary number of age groups. Consider two models A_1 and A_2 of the same population. A_1 is, say, an $n \times n$ array of birth and death schedules and A_2 an $m \times m$ array. Since these models are derived from the same population, they must be similar or "isomorphic" in some sense. We seek a measure which reflects the intrinsic structure of the model; that is, a measure which is invariant under isomorphism of the models. Entropy, as defined in the Kolmogorov-Sinai theory, achieves this. In

this theory, if two invertible measure-preserving transformations are isomorphic then they have the same entropy. Markov shifts are a special class of invertible measure-preserving transformations. A recent result of FRIEDMAN and ORNSTEIN (1970) asserts that if two mixing Markov shifts have the same entropy, then they are isomorphic. By representing population models as Markov shifts we observe that entropy is an isomorphism invariant for population models. One interpretation of this fact is that entropy gives another description of the life-history features of a population. The Malthusian parameter incompletely specifies the life history, and describes only the long-run behavior of the population.

2. The concept of fitness is central in evolutionary theory and has been given several interpretations. THODAY [1953] defines fitness as the probability of random extinction. SLOBODKIN [1967] suggests that adaptedness should be measured as the "probability of occurrence of particular environmental states and the probability of a population surviving each such state."

Any useful definition of fitness should involve a parameter that is measurable in terms of the life-history components and predicts states such as persistence, a property we would expect well-adapted populations to possess. The Malthusian parameter r and the carrying capacity K are good candidates. However, density does not necessarily confer a competitive advantage, and rarity does not imply extinction. Moreover, as the work of Holgate shows, in the case of populations with the same intrinsic growth rate, random extinction is determined by the spacing between births. These facts limit the relevance of the r and K selection theory proposed by MACARTHUR and WILSON (1967):

The entropy measure complements the Malthusian parameter. Semelparity and iteroparity represent two different life histories of a population with different adaptive values. The Malthusian parameter does not always distinguish between these two strategies. We have shown, however, that semelparous organisms have zero entropy and iteroparous organisms have positive entropy. Thus entropy should reflect the chance of random extinction or persistence of a population, and should be a suitable measure of colonizing success.

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