NATURAL SELECTION AND FITNESS ENTROPY IN A DENSITY-REGULATED POPULATION

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ABSTRACT

The entropy $H(p_0,p^*)$ of a population with the initial allele frequency p_0 given the equilibrium polymorphic frequency p^* has been proposed as a measure of natural selection. In the present paper, we have extended this concept to include a particular aspect of density-dependent selection. We compared size trajectory of a population initially at genetic equilibrium, $\hat{N}(t)$, with the size trajectories of populations not initially at $p^*, N(t)$, but which do eventually converge to a common equilibrium allele frequency and equilibrium density, N^*. The following experimentally testable hypothesis was established. The total area defined by the difference between the trajectories of $\hat{N}(t)$ and $N(t)$ as they converge to N^* is directly proportional to the fitness entropy when population size is transformed using the density-dependent fitness value. Two properties of this relationship were noted. First, it is independent of the magnitude of natural selection and, secondly, it does not depend upon the initial population density as long as the equilibrium and nonequilibrium populations have the same initial numbers. This hypothesis was evaluated with experimental data on the flour beetle *Tribolium castaneum*.

IN the single locus, continuous-time, genetic model of natural selection we have (CROW and KIMURA 1970)

$$dp_i/dt = p_i(W_i - W), \quad i = 1,2,\ldots,k \tag{1a}$$
$$dN/dt = NW \tag{1b}$$

where p_i is the frequency of the ith allele, the allele fitness is $W_i = \sum_{j=1}^{k} W_{ij}p_j$, the average fitness is $W = \sum_{i,j}^{k} W_{ij}p_ip_j$, k is the number of alleles and N is the population size.

GINZBURG (1972, 1974, 1977a) introduced into population genetics the equation for the entropy between the nonequilibrium p and the equilibrium polymorphic p^* allele frequencies as

$$H(p, p^*) = -\sum_{i=1}^{k} p_i^* \log_e(p_i/p_i^*) \ . \tag{2}$$

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$H(p,p^*)$ is U-shaped, that is, H is zero when $p = p^*$, is positive for any $p \neq p^*$ and tends to infinity when p goes to fixation. An interesting property of this function is that it can be associated with the growth characteristics of a population. Taking the time-derivative of (2) we have

$$dH(p(t),p^*)/dt = - \sum_{i=1}^{k} (p_i^*/p_i) (dp_i/dt) \ . \tag{3}$$

Notice that while equation (2) contains only p_i and p_i^*, equation (3) has an expression for the change in allele frequency, dp_i/dt. It is this latter relationship that we shall now use to associate entropy and natural selection.

In the classical model it is assumed that the fitnesses are constant. The derivative (3) can be written using (1) as

$$dH/dt = W - \sum_{i=1}^{k} p_i^* W_i \ . \tag{4}$$

Furthermore, integrating (4) with respect to time from 0 to ∞ we arrive at two equivalent but different forms for entropy. The first is GINZBURG's (1977a) macro-equation of natural selection,

$$H(p_o,p^*) = W^* \tau(p_o.p^*) \tag{5a}$$

where p_o is the initial allele frequency, W^* is the average fitness of the population at equilibrium and $\tau(p_o.p^*)$ is the asymptotic time-delay of the real growth curve in comparison with the equilibrium growth curve $\hat{N}(t) = N(0) \exp (W^*t)$. A second density-independent measure proposed by GINZBURG and COSTANTINO (1979) is

$$H(p_o,p^*) = \int_0^\infty [W^*-W(t)]dt \ . \tag{5b}$$

In this form, the area bounded by the equilibrium value W^* and the curve of the average fitness at time $t, W(t)$, is equal to the entropy.

The fitness entropy equations (5) were experimentally examined by COSTANTINO, GINZBURG and MOFFA (1977) and GINZBURG and COSTANTINO (1979) using data on populations of the flour beetle *Tribolium castaneum* Herbst (MOFFA and COSTANTINO 1977). These equations are restricted to density-independent population dynamics, consequently, the Tribolium data analyses were limited to the exponential phase of the population growth. Our objectives in this paper are to extend the entropy measure to include an aspect of density-dependent natural selection and to evaluate this theoretical outcome with the Tribolium data.

FITNESS ENTROPY

Density-regulated fitness: In the last decade, the expanding population size perspective of the classical genetic model has been modified by writing the

fitness as a function of population size, $W_{ij} = W_{ij}(N)$. An early example was based on the familiar logistic equation of population growth (ANDERSON 1971; ROUGHGARDEN 1971). CHARLESWORTH (1971) extended the logistic description to include functions that are strictly decreasing in population size N. ROUGH-GARDEN (1976) and GINZBURG (1977b) established an analog of FISHER's fundamental theorem of natural selection for density-dependence that asserts that selection results in an equilibrium allele frequency that corresponds to a local maximum equilibrium population size. HASTINGS (1978) using the concept of an evolutionary stable strategy also showed that selection is expected to result in a maximization of population size.

Our choice for the density-dependent fitness is

$$W_{ij} = W(N, \alpha_{ij}) = \alpha_{ij} f(N) + g(N), \quad i, j = 1, \ldots, k \ . \qquad (6)$$

We will confine our discussion to (6) in which the genetic difference is located in a single parameter, α, that enters the fitness value as a linear coefficient. Also note the symmetry condition $\alpha_{ij} = \alpha_{ji}$. Otherwise the restrictions on these functions satisfy those of GINZBURG (1977b); specifically, $W_{ij}(0) > 0$, $\partial W_{ij}/\partial N < 0$ and $W_{ij}(N) < 0$ for large N. With this formulation, the average allele fitness, W_i, and the average fitness of the population, W, are

$$W_i = W(N, \alpha_i) = \alpha_i f(N) + g(N) \qquad (7a)$$

$$W = W(N, \alpha) = \alpha f(N) + g(N) \qquad (7b)$$

where

$$\alpha_i = \sum_{j=1}^{k} \alpha_{ij} p_j \text{ and } \alpha = \sum_{i=1}^{k} \alpha_i p_i \ .$$

Statement (6) means that population size does indeed affect the rate of approach to genetic equilibrium for

$$dp_i/dt = p_i(\alpha_i - \alpha) f(N), \quad i = 1, \ldots, k \qquad (8)$$

and for the genetic equilibrium to be asymptotically stable, it must be true that $f(N^*) \neq 0$, where N^* is the equilibrium population density. However, while N does alter the magnitude of change in allele frequency, for $k \geqslant 3$ alleles the trajectory of allele frequencies,

$$dp_i/dp_j = p_i(\alpha_i - \alpha)/p_j(\alpha_j - \alpha), \text{ for all } i,j \qquad (9)$$

is independent of N so that the trajectory (9), excluding time, is the same as in the density-independent case with constant fitnesses. (Note that for $k = 2$ alleles the trajectory of frequencies is always independent of N even for more general fitnesses than (6).) Consequently, we shall refer to this special class of density-dependent fitnesses as density-regulated natural selection.

When all of the k-alleles are maintained by natural selection, the time-derivative of the fitness entropy (3) can be written as

$$dH(p(t),p^*)/dt = W[N(t),\alpha(t)] - W[N(t),\alpha^*] \qquad (10)$$

where α^* is the value of the parameter α at genetic equilibrium (see the APPENDIX).

Let us now consider two populations with the same initial population densities. The first population is at genetic equilibrium, $p_o = p^*$, for all time t and has a population size at time t of $\hat{N}(t)$. The second population is not initially at p^* and its population size is given by $N(t)$. Using equation (10), we can establish (see APPENDIX) the following relationship between population size and entropy:

$$H(p_o,p^*) = \lim_{t->\infty} [\log_e(\hat{N}/N)] + \alpha^* \int_0^\infty [f(N) - f(\hat{N})]dt$$
$$+ \int_0^\infty [g(N) - g(\hat{N})]dt . \qquad (11)$$

When population growth is density-regulated, all populations will eventually converge to some finite equilibrium density, N^*. Hence, the limit term in (11) is zero and the fitness entropy can be written as

$$H(p_o,p^*) = \alpha^* \int_0^\infty [f(N) - f(\hat{N})]dt + \int_0^\infty [g(N) - g(\hat{N})]dt . \qquad (12)$$

This equation can be used to evaluate the effects of a nonequilibrium genetic structure on population growth.

We can see from equation (2) that fitness entropy is independent of the magnitude of natural selection. This means that we can calculate H in (11) knowing only the initial frequency p_o and the equilibrium frequency p^*. Furthermore, the right hand side of (11) indicates that we can indirectly observe gene frequency change by comparing functions of N of an evolving population with those of a reference population at equilibrium. To clarify these ideas we will examine fitness entropy for density-independent fitness, logistic fitness, the fixation of a dominant allele and then turn our attention to some experimental observations.

Density-independent fitness: In this situation (GINZBURG 1977a), we have $W_{ij} = \alpha_{ij}, f(N) = 1, g(N) = 0$ and equation (11) becomes

$$H(p_o,p^*) = \lim_{t->\infty} [\log_e(\hat{N}(t)/N(t))] . \qquad (13)$$

For the population that is initially at genetic equilibrium $\hat{N}(t) = \hat{N}(0) \exp(W^*t)$. The population that is not initially in genetic equilibrium will eventually converge to the same maximum growth rate, W^*, but because the selection process takes time, its growth curve, $N(t)$, will lag behind $\hat{N}(t)$. Defining this asymptotic time lag as the "selective delay," $\tau(p_o,p^*)$, we can

write the population density for large values of time as $N(t) = N(0)$ exp $W^*(t-\tau)$. Since $\hat{N}(0) = N(0)$, substitution of $\hat{N}(t)$ and $N(t)$ into (13) gives the fitness entropy and selective delay equation (5a).

Logistic fitness: With genetic variance in parameter K of the logistic equation of population growth, the fitness expression (6) is

$$W(N,\alpha_{ij}) = r(1-N/K_{ij}) \tag{14}$$

with $\alpha_{ij} = 1/K_{ij}, f(N) = -rN$ and $g(N) = r$. Substituting (14) into (12) we obtain

$$H(p_o,p^*) = (r/K^*) \int_0^\infty [\hat{N}(t) - N(t)]dt \tag{15}$$

where $K^* = 1/\alpha^*$ is the harmonic mean of the K_{ij}'s at genetic equilibrium. The total difference in adult numbers between the equilibrium and nonequilibrium genetic state, the integral in (15), is directly proportional to $H(p_o,p^*)$. This is a testable hypothesis because one can estimate the integral in (15) with the appropriate data.

We have sketched some trajectories of $\hat{N}(t)$ and $N(t)$ for the logistic example (Figure 1) with two alleles and $p_o = 0.01$ and $p^* = 0.5$. Using equation (2), $H = 1.6145$. Notice that whether we begin the experiment below the equilibrium density, N^*, or at N^* or above N^* (Figures 1a, b, c respectively) in each case the entropy is the same. That is to say, H does not depend upon the initial population density as long as the nonequilibrium and equilibrium populations have the same initial numbers, $N(0) = \hat{N}(0)$. Furthermore, in the example used in Figure 1d, the selective differences were increased by a factor of ten, nevertheless, H is unchanged at 1.6145, thus demonstrating that entropy is independent of the magnitude of natural selection. In this numerical example, the coefficient r/K^* of equation (15) is 0.001 so that the total difference between $\hat{N}(t)$ and $N(t)$ equals 1614.5 individual-years of life (or whatever the appropriate time scale) which were not realized due to $p_o \neq p^*$.

Fixation of a dominant allele: Until now, we have only considered cases where all k alleles are maintained by natural selection. In general, the fitness entropy approach cannot be extended to all cases where natural selection results in the elimination of some subset of the alleles segregating at an autosomal locus. However, in the biologically important case where a single dominant allele is selected to fixation ($p_1^* = 1$, $\alpha^* = \alpha_{11}$, and all $\alpha_j^* = \alpha_{1j} = \alpha_{11}$), the entropy expression (5b) now reads

$$H(p_o,p^*) = -\log_e p_o = \int_0^\infty [W(N,\alpha^*) - W(N,\alpha)]dt \tag{16}$$

(see APPENDIX for details). For two alleles with constant genotypic fitness values of $W_{11} = W_{12} > W_{22}$ we have $W^* = W_1 = W_{11}$ and from (1a) $W(t) = W_{11} \cdot p^{-1}$ (dp/dt). Substituting W^* and $W(t)$ into (16) gives

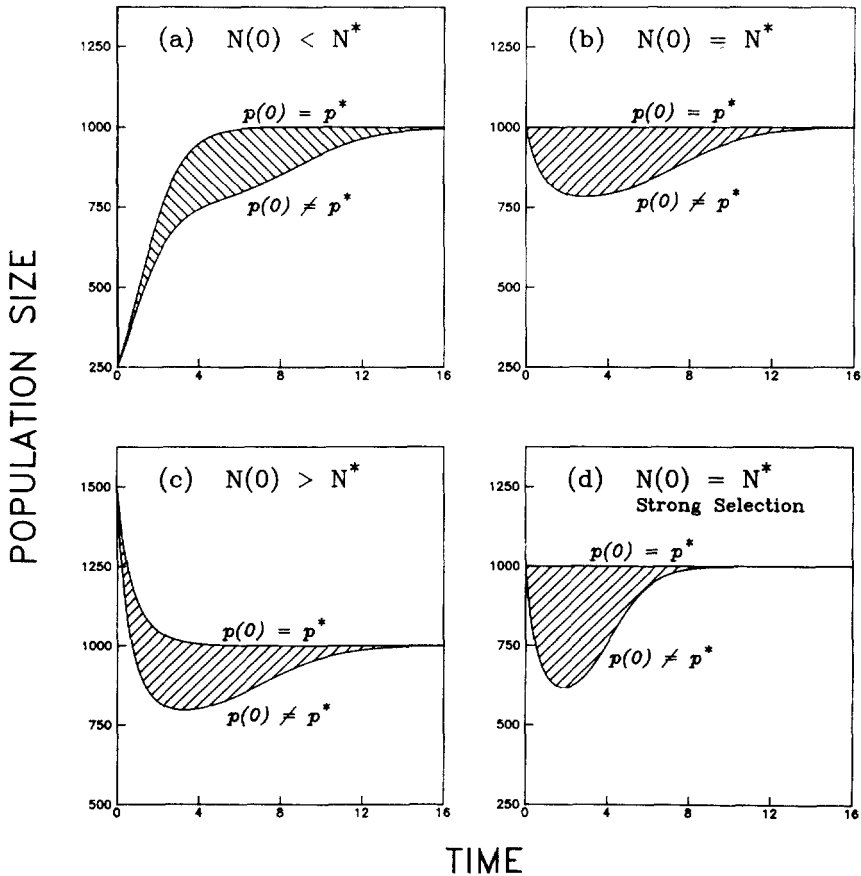$$H(p_o,p^*) = \int_{p_o}^1 p^{-1} dp = -\log_e p_o \ . \tag{17}$$

FIGURE 1.—Comparison of the population size trajectories of a population at genetic equilibrium, $p^* = 0.5$, with populations initially at $p_o = 0.01$ but which do eventually converge to p^* for the logistic model with genetic differences in parameter K (equation 14). The shaded area is the total difference in population size due to a nonequilibrium initial allele frequency. In (a), (b) and (c) $K_{11} = K_{22} = 750$ and $K_{12} = 1500$ but the initial population sizes are 250, 1000 and 1500, respectively. In (d) the initial population size is 1000, but the magnitude of selection has been increased ten-fold $(K_{11} = K_{22} = 525, K_{12} = 10500)$. In all examples $r = 1$ and $K^* = 1000$. The shaded areas in (a) — (d) are equal.

This is HALDANE's (1957) cost of a gene substitution which is independent of the intensity of selection. For two alleles with logistic genotypic fitnesses (14) and $K_{11} = K_{12} > K_{22}$ we can use (15) to write

$$(K^*/r) \ (-\log_e p_o) = \int_0^\infty [\dot{N}(t) - N(t)]dt \ . \tag{18}$$

Equation (18) is a precise statement of MACARTHUR's (1962) analogue of the cost principle for density-regulated population growth which in the words of MACARTHUR (pg. 1897, 1962) "enables us to estimate the number of animal-hours of life which are lost due to poor genotype."

EXPERIMENTAL OBSERVATIONS

We now want to deal with a fitness expression that appears to be appropriate for species of the genus Tribolium (DESHARNAIS and COSTANTINO 1980, 1982; COSTANTINO and DESHARNAIS 1981). If we let C be the rate at which a single adult inhibits recruitment, then the probability that a potential recruit will survive to adulthood can be written as $\exp(-CN)$, where N is the number of adults. Combining this expression with the density-independent adult recruitment rate, X, and mortality rate, D, we have the following equation for the change in adult number,

$$dN/dt = N\,W(N) = N[X\exp(-CN)-D] \ . \tag{19}$$

With genetic differences in the parameter X (MOFFA and COSTANTINO 1977, DESHARNAIS and COSTANTINO 1980), the fitness expression (6) is

$$W(N,\alpha_{ij}) = X_{ij}\exp(-CN)-D \tag{20}$$

where X_{ij} is the rate at which potential recruits with alleles i and j are produced per adult. Substituting $\alpha_{ij} = X_{ij}$. $f(N) = \exp(-CN)$ and $g(N) = -D$ into (12) we obtain the entropy measure

$$H(p_o,p^*) = X^* \int_0^\infty [\exp(-CN(t)) - \exp(-C\dot{N}(t))]dt \ . \tag{21}$$

Denoting the integral in (21) as $Q(p_o,p^*)$ we have

$$H(p_o,p^*) = X^*Q(p_o,p^*) \ . \tag{22}$$

We expect, therefore, a linear relationship between the fitness entropy H, and the "selective difference area", Q. We shall now describe our test of this hypothesis.

In the study of MOFFA and COSTANTINO (1977), laboratory populations of the flour beetle *Tribolium castaneum* were initiated with ten male and ten female adults and with frequencies of the corn-oil sensitive (*cos*) allele ranging from 0–1 in increments of 0.1. Each culture was censused every two weeks for 68 weeks and the *cos* allele frequencies were estimated at regular intervals. Since the populations segregating at the *cos* locus converged to a polymorphic equilibrium allele frequency ($p^* = 0.25$), these data can be used to test the predictions based upon fitness entropy.

COSTANTINO, GINZBURG and MOFFA (1977) used the adult census data at weeks 2, 4 and 6 to experimentally evaluate the density-independent fitness entropy given in equation (5a). We can now extend that analysis. Specifically, the mean number of adults from weeks 2 to 30 recorded by MOFFA and COSTANTINO (1977, Table 4) were used. The population initiated with the allele frequency of 0.3 was specified as the equilibrium population, $\hat{N}(t)$, and for each

initial nonequilibrium population, $N(t)$, we computed the integral in equation
(21) as below. The rate of adult inhibition of the immatures was set at $C = 0.014$
(DESHARNAIS 1979). To illustrate these computations, the experimental observa-
tions are sketched in Figure 2. The desired entity, $Q(p_o,p^*)$ is simply the shaded
area lying above $\exp(-C\hat{N}(t))$ minus the shaded area lying below this curve.

A least-squares linear regression of the computed Q-values on H indicated a
significant linear relationship and the hypothesis that the intercept was zero
was accepted. Both of these tests were performed at the 0.05 level of probability.
With this result, we recomputed the least-squares estimate of the slope, with the
intercept zero, to be 1.7015 ± 0.2760 (Figure 3). The coefficient of determination,
R^2, was 0.8445. Since $H = X^*Q$, the inverse of the slope provided an estimate of
$X^* = 0.5877 \pm 0.0953$. The standard error of X^* was computed using the method
described by KENDALL and STUART (1969 pg. 231).

The experimentally-computed density-independent fitness measure, $W^*\tau(p_o,$
$p^*)$, and its density-regulated counterpart, $X^*Q(p_o,p^*)$, together with the theo-
retical $H(p_o,p^*)$ are sketched as a function of the initial allele frequency in
Figure 4.

<center>DISCUSSION</center>

In this paper we have extended the original entropy measure to include an
aspect of density-dependent natural selection (see equation 12). This measure,
written here for Tribolium, is $H(p_o,p^*) = X^*Q(p_o,p^*)$. The "selective difference
area" Q is the difference between the population size trajectories of the equili-
brium and nonequilibrium populations as they converge to the equilibrium
density. The function $Q(p_o,p^*)$ is analogous to the concept of selective delay,
$\tau(p_o,p^*)$, which is the asymptotic time-delay of the growth curve of the non-
equilibrium population in comparison with the equilibrium growth curve $\hat{N}(t) =$
$N(0) \exp(\hat{W}^*t)$. It is the experimentally measurable entities $Q(p_o,p^*)$ and
$\tau(p_o,p^*)$ that allows one to indirectly infer gene frequency change by comparing
functions of population size of an evolving population with those of a population
at genetic equilibrium.

In these Tribolium data (Figure 4), the estimates of $W^*\tau(p_o,p^*)$ were uni-
formly positive. That is to say, during the exponential phase of population growth
$\hat{N}(t)$ was greater than $N(t)$ for all the initial allele frequencies. On the other
hand, the estimates of $X^*Q(p_o,p^*)$ for $p_o = 0.2$ and $p_o = 0.4$ were negative. For
these two frequencies, both in the neighborhood of $p^* = 0.3$, $N(t)$ was greater
than $\hat{N}(t)$ (Figure 2). The closer p_o is to p^* the closer the trajectories of the
equilibrium and non-equilibrium populations are expected to be and the more
difficult it is to experimentally identify these differences. This procedure is more
effective if the initial population genetic structure p_o is far from the equilibrium
p^*.

Our estimates of $X^*Q(p_o,p^*)$ were based on the recorded adult numbers from
week 2 to week 30, however, data were available to week 68. In the deterministic
theory, eventually, $p_o -> p^*$ and $N(t) -> N^*$. While this is a reasonable ap-
proximation, we are confronted with stochastic effects. The trajectories of $\hat{N}(t)$

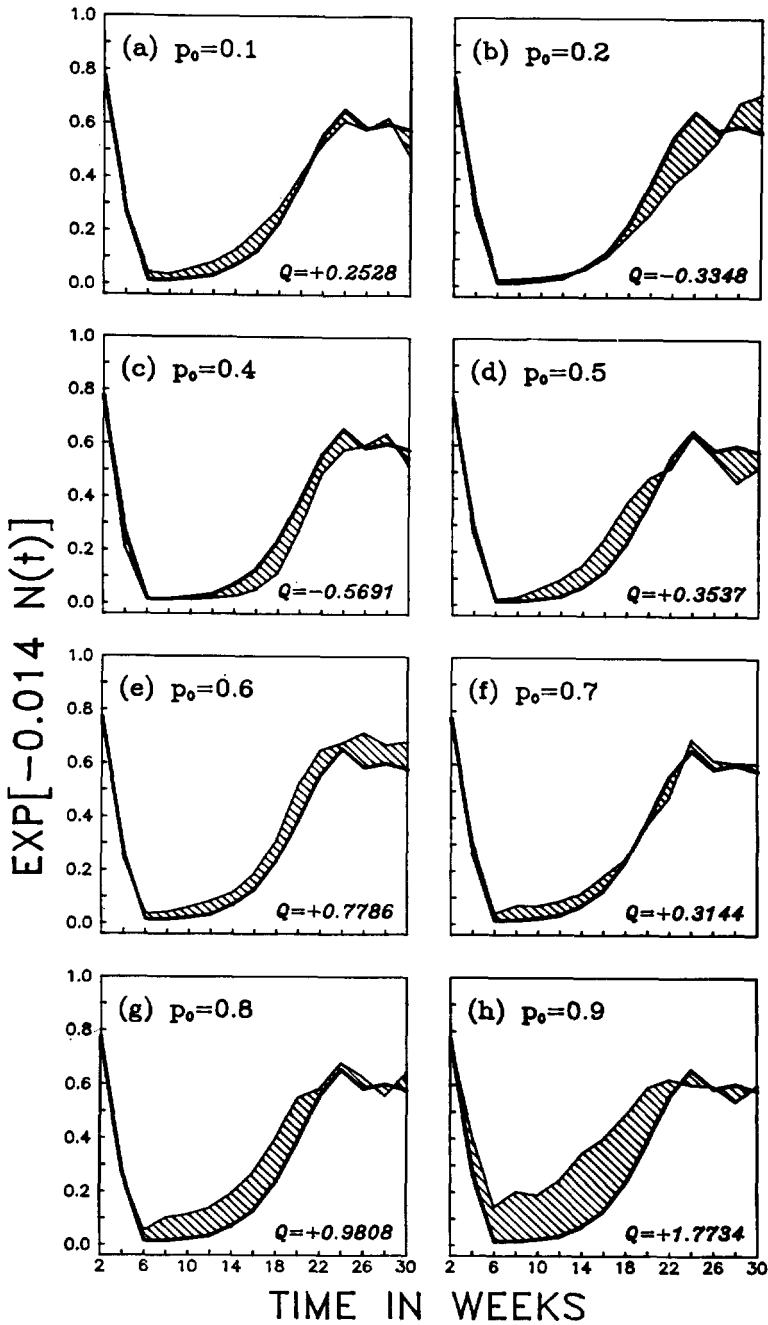FIGURE 2.—Calculation of the selective difference area, $Q(p_0,p^*)$, represented by the integral in equation (21) using the Tribolium adult census data, $N(t)$, for weeks 2 to 30 with $C = 0.014$. In (a) — (h) the heavy line represents the population which was initially at genetic equilibrium $(p_0=p^*=0.3)$ and each narrow line represents the populations with different non-equilibrium initial allele frequencies $(p_0 \neq p^*)$. In each case, $Q(p_0,p^*)$ equals the shaded area lying above the heavy line minus the shaded area lying below it.
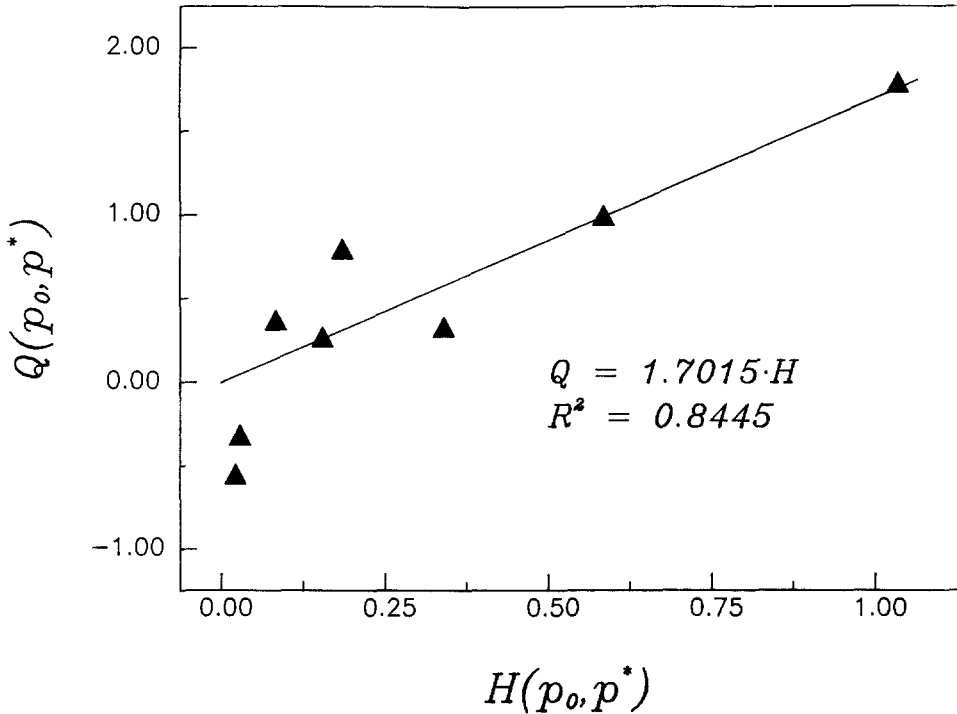
FIGURE 3.—Graph of the experimentally obtained $Q(p_o,p^*)$ and the theoretical $H(p_o,p^*)$ with the least squares line $Q = 1.7015\,H$ inserted. R^2 is the coefficient of determination.

and $N(t)$ do converge (Figure 2) but then fluctuate in the region of their steady-state. Indeed, COSTANTINO and DESHARNAIS (1981) incoporated stochasticity into the deterministic model (19) and characterized the steady-state probability distribution of adult numbers as a gamma distribution. Consequently, we limited our analysis to week 30. Perhaps the inclusion of stochastic effects into an entropy measure will allow an even more complete analysis of these data.

In these data. we knew from previous work that parameter X was under selection pressure (MOFFA and COSTANTINO 1977; DESHARNAIS and COSTANTINO 1980). If D were the parameter of interest,

$$W(N,\alpha_{ij}) = X \exp(-CN) - D_{ij}$$

and substituting $\alpha_{ij} = D_{ij}, f(N) = 1$ and $g(N) = X\exp(-CN)$ into (12) we find

$$H(p_o,p^*) = X \int_0^x [\exp(-CN(t)) - \exp(-C\hat{N}(t))]dt \ .$$

This expression with $X = X^*$, is the same as when we considered genetic differences in parameter X (equation 21). Clearly, the observation of a linear relationship between the fitness entropy H and the selective difference area, Q,
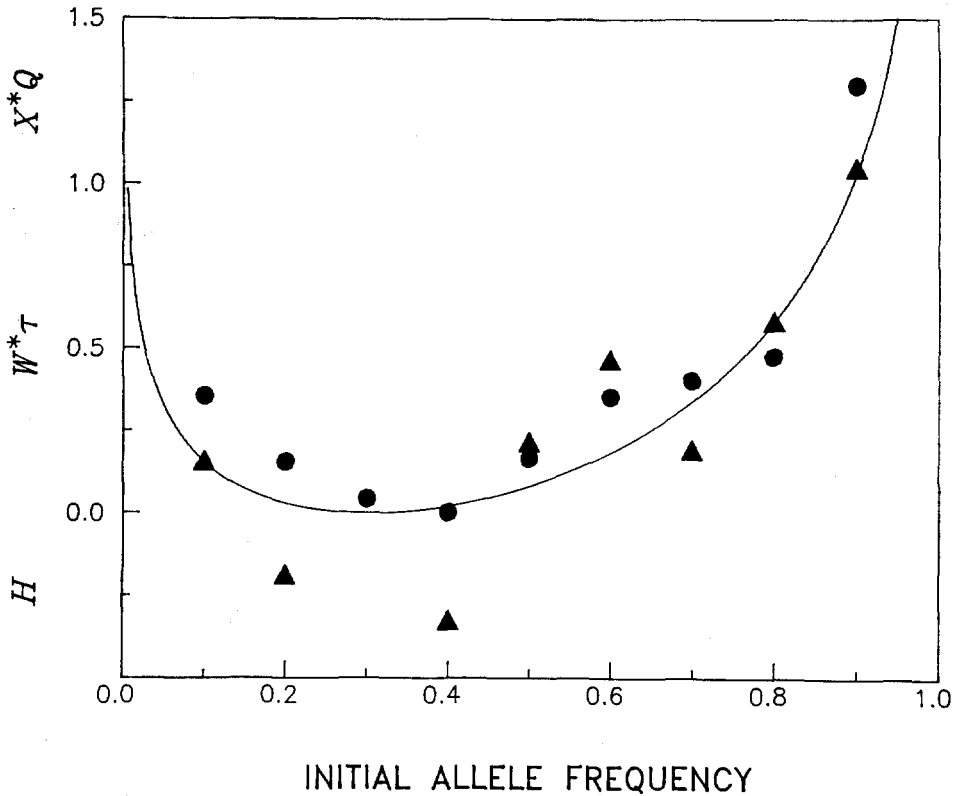
INITIAL ALLELE FREQUENCY

FIGURE 4.—An experimental check of $H(p_o, p^*=0.3)$, solid line with $W^*\tau(p_o, p^*)$, circles and $X^*Q(p_o, p^*)$, triangles.

does not allow us to distinguish between natural selection on X or D; in either case, the theoretical expectation is the same.

With each of the three fitness entropy measures suggested, the data of MOFFA and COSTANTINO (1977) on Tribolium has been used as an experimental check of the theory. Clearly, more data on different organisms are needed. In that regard, the proposed density-regulated measure (12) does allow a somewhat larger class of data sets to be considered.

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APPENDIX

Derivation of equation (10): Computing the time-derivative of the fitness entropy (3) taking into account equations (1) with the density-regulated definitions of W_i and W given in equations (7), we have

$$dH(p(t),p^*)/dt = W(N,\alpha) - g(N) - f(N) \sum_{i=1}^{k} \sum_{j=1}^{k} p_i^* p_j \alpha_{ij} \ . \tag{A1}$$

We now want to show that the double summation term in (A1) is α^*, *i.e.*, the value of the parameter α at genetic equilibrium.

Due to the symmetry $\alpha_{ij} = \alpha_{ji}$, we can write this double sum as

$$\sum_{j=1}^{k} p_j \left[\sum_{i=1}^{k} p_i^* \alpha_{ji} \right] = \sum_{j=1}^{k} p_j \alpha_j^* \ . \tag{A2}$$

The k-equations of the change in allele frequency are

$$dp_j/dt = p_j(\alpha_j - \alpha)f(N) \quad j = 1, \ldots, k \ .$$

At equilibrium $dp_j/dt = 0$, $\alpha_j = \alpha_j^*$ and $\alpha = \alpha^*$. We require that $f(N^*) \neq 0$ and $p_j^* \neq 0$; therefore $\alpha_j^* = \alpha^*$ for $j = 1, \ldots, k$. Consequently, the summation in (A2) is simply α^* and we arrive at the derivative of the fitness entropy stated in equation (10) in the text.

Derivation of equation (11): To obtain the relationship between population size and entropy expressed in equation (11), we note that the difference in the average fitness of the non-equilibrium, $W(N,\alpha)$, and the equilibrium, $W(\hat{N},\alpha^*)$ populations is

$$W(N,\alpha) - W(\hat{N},\alpha^*) = d \log N(t)/dt - d \log \hat{N}(t)/dt . \tag{A3}$$

Since

$$W(N,\alpha^*) = W(\hat{N},\alpha^*) + \alpha^* [f(N)-f(\hat{N})] + [g(N)-g(\hat{N})] \tag{A4}$$

we can substitute (A3) and (A4) into equation (10) to obtain

$$dH/dt = d \log (N/\hat{N})/dt + \alpha^* [f(\hat{N})-f(N)] + [g(\hat{N})-g(N)] . \tag{A5}$$

Integrating (A5) from zero to time t gives

$$H(p(t),p^*) - H(p_0,p^*) = \log [N(t)/\hat{N}(t)] - \log [N(0)/\hat{N}(0)] +$$

$$\alpha^* \int_0^t [f(\hat{N})-f(N)] \, dt + \int_0^t [g(N)-g(N)] \, dt .$$

As $t - > \infty, p(t) - > p^*$ so that $H(p(t),p^*) = H(p^*,p^*) = 0$. Since $N(0) = \hat{N}(0)$ the term $\log [N(0)/\hat{N}(0)] = 0$ and we obtain (11).

The time derivative of entropy when alleles are lost: Here we consider the more general case where natural selection results in the elimination of one or more alleles. Without loss of generality we can let $p_i(t)$ $(i=1,\ldots,k)$ represent the frequency of alleles maintained in the population by selection $(p_i^* > 0)$ and $p_i(t)$ $(i=k+1,\ldots,n)$ represent the frequency of alleles eliminated during the selection process $(p_i^*=0)$. The time derivative of fitness entropy (2) is

$$dH(p(t),p^*)/dt = W(N,\alpha) - g(N) - f(N) \sum_{i=1}^{k} \sum_{j=1}^{n} p_i^* p_j \alpha_{ij} \tag{A6}$$

which is analogous to (A1). In the first section of this appendix we show that

$$\sum_{i=1}^{k} p_i^* \alpha_{ij} = \sum_{i=1}^{k} p_i^* \alpha_{ji} = \alpha_j^* = \alpha^* \quad \text{for } j=1,\ldots,k .$$

Hence, the double summation term in (A6) can be written as

$$\sum_{j=1}^{n} p_j \left[\sum_{i=1}^{k} p_i^* \alpha_{ij} \right] = \alpha^* \sum_{j=1}^{k} p_j + \sum_{j=k+1}^{n} p_j \alpha_j^*$$

$$= \alpha^* \left[1 - \sum_{j=k+1}^{n} p_j \right] + \sum_{j=k+1}^{n} p_j \alpha_j^* = \alpha^* + \sum_{j=k+1}^{n} (\alpha_j^* - \alpha^*) p_j . \tag{A7}$$

Substituting (A7) into (A6) and using the definitions given in equation (7) we have

$$dH(p(t),p^*)/dt = W(N,\alpha) - W(N,\alpha^*) + f(N) \sum_{j=k+1}^{n} (\alpha^* - \alpha_j^*) p . \tag{A8}$$

which is analogous to equation (10). If no alleles are eliminated during the selection process $(n=k)$ then the last term of (A8) equals zero and we obtain the main result derived in the second section of this appendix. However, if natural selection results in the elimination of some of the alleles initially present when the selection process begins $(n > k)$, then the last term of (A8) will equal zero for all $t \geqslant 0$ only when $\alpha_j^* = \alpha^*$ for $j = k+1,\ldots,n$. This latter condition describes some additional genetic situations to which one can apply the fitness entropy approach. One biologically important case (fixation of a dominant allele) is discussed in the main text.