NATURAL SELECTION AND DENSITY-DEPENDENT POPULATION GROWTH

R. A. DESHARNAIS*,[1] AND R. F. COSTANTINO†

*Department of Biology, Dalhousie University, Halifax, Nova Scotia, B3H 4J1, Canada, and †Department of Zoology, University of Rhode Island, Kingston, Rhode Island 02881

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ABSTRACT

Natural selection was studied in the context of density-dependent population growth using a single locus, continuous time model for the rates of change of population size and allele frequency. The maximization principle of density-dependent selection was applied to a class of fitness expressions with explicit recruitment and mortality terms. Three general results were obtained: First, at low population densities, the genetic basis of selection is the difference between the mean recruitment rate and the mean mortality rate. Second, at densities much higher than the equilibrium population size, selection is expected to act to minimize the mean mortality rate. Third, as the population approaches its equilibrium density, selection is predicted to maximize the ratio of the mean recruitment rate to the mean mortality rate.

IN the genetic model of natural selection in a sexually reproducing diploid population with continuous time, we can describe the change in allele frequency at a single multiallelic autosomal locus and the change in population number, respectively, as (CROW and KIMURA 1970, p.191)

$$dp_i/dt = p_i(W_i - W) \qquad i = 1, \cdots, n \tag{1a}$$

$$dN/dt = WN \tag{1b}$$

where p_i is the frequency of allele i, n is the number of alleles and N is the population size. The W_i represents the marginal fitness of the ith allele, and W is the average population fitness. With the usual assumptions of random mating, weak selection and Hardy-Weinberg genotypic frequencies, W_i and W are calculated using

$$W_i = \sum_{j=1}^{n} W_{ij}p_j \qquad i = 1, \cdots, n \tag{1c}$$

$$W = \sum_{i=1}^{n} W_ip_i = \sum_{i=1}^{n}\sum_{j=1}^{n} W_{ij}p_ip_j. \tag{1d}$$

The genotypic fitness W_{ij} is defined as the contribution of an individual with

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[1] Present address: Department of Populations, Rockefeller University, 1230 York Avenue, New York, New York 10021.

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genotype i,j to the total population growth rate. The average fitness is equal to the Malthusian rate of population growth. One classical result, due to the works of FISHER (1930) and WRIGHT (1935), is that the average fitness of a population will increase monotonically until it reaches a local maximum at genetic equilibrium. If the equilibrium state is polymorphic for all n alleles, then the equilibrium fitness is a global maximum. A refinement of this result which accounts for deviations from Hardy-Weinberg genotypic proportions is given by KIMURA (1958). For an expository discussion of the continuous time model in population genetics see NAGYLAKI (1977, p. 79) and EWENS (1979, p. 48).

In recent years, the expanding population size interpretation of this classical genetic model has been modified by writing the fitnesses of the different genotypes as a function of population size. One early example was based on the Verhulst-Pearl linear logistic equation of population growth (MACARTHUR 1962; ANDERSON 1971; ROUGHGARDEN 1971), and another used the Michaelis-Menten equation in enzyme kinetics (CLARKE 1972, 1973). CHARLESWORTH (1971) extended these descriptions to include fitness values that were strictly decreasing functions of population size. With this latter property, an analog of the Fisher-Wright maximization theorem for density dependence has been established that asserts that selection results in an equilibrium allele frequency that corresponds to a local maximum equilibrium population size (ANDERSON 1971; ROUGHGARDEN 1971, 1976; CHARLESWORTH 1971; GINZBURG 1977a; ASMUSSEN and FELDMAN 1977; HASTINGS 1978; GREGORIUS 1979). Our objective in this paper is to apply this maximization principle to a class of fitness expressions with explicit birth and death terms and thereby identify the relationship between these two important population entities that leads to the local maximization of population number.

Our choice for the genetic fitness expression is

$$W_{ij}(N) = b_{ij}f(N) - d_{ij}g(N), \quad i,j = 1, \cdots, n \tag{2}$$

where b_{ij} and d_{ij} are the per capita density-independent rates of recruitment and mortality, respectively, associated with genotype i,j. The density-dependent recruitment function, $f(N)$, and mortality function, $g(N)$, satisfy the following conditions: (1) $f(N)$ and $g(N)$ are continuous and differentiable, (2) $f(0) = 1$ and $g(0) = 1$, (3) $f(N)$ is nonincreasing ($\partial f/\partial N \leq 0$) and $g(N)$ is nondecreasing ($\partial g/\partial N \geq 0$) and (4) the function $F(N) = f(N)/g(N)$ is strictly montonic decreasing ($\partial F/\partial N < 0$) with $\lim_{N\to\infty} F(N) = 0$. We assume the first condition for convenience. The second condition allows exponential population growth at low densities, and conditions three and four assure density dependence throughout the range of adult numbers. These restrictions on the fitness expression (2) satisfy the conditions of the continuous time model of GINZBURG (1977a).

SELECTION ON RECRUITMENT

In the first genetic situation, we shall associate the genotype differences only with the density-independent rates of recruitment. The death rates and the density-dependent recruitment and mortality functions are the same for all genotypes so that (2) reads

$$W_{ij}(N) = b_{ij}f(N) - dg(N). \tag{3}$$

Substituting (3) into the description of natural selection (1) yields

$$dp_i/dt = p_i(b_i - \bar{b})f(N) \tag{4a}$$

$$dN/dt = (\bar{b}f(N) - dg(N))N \tag{4b}$$

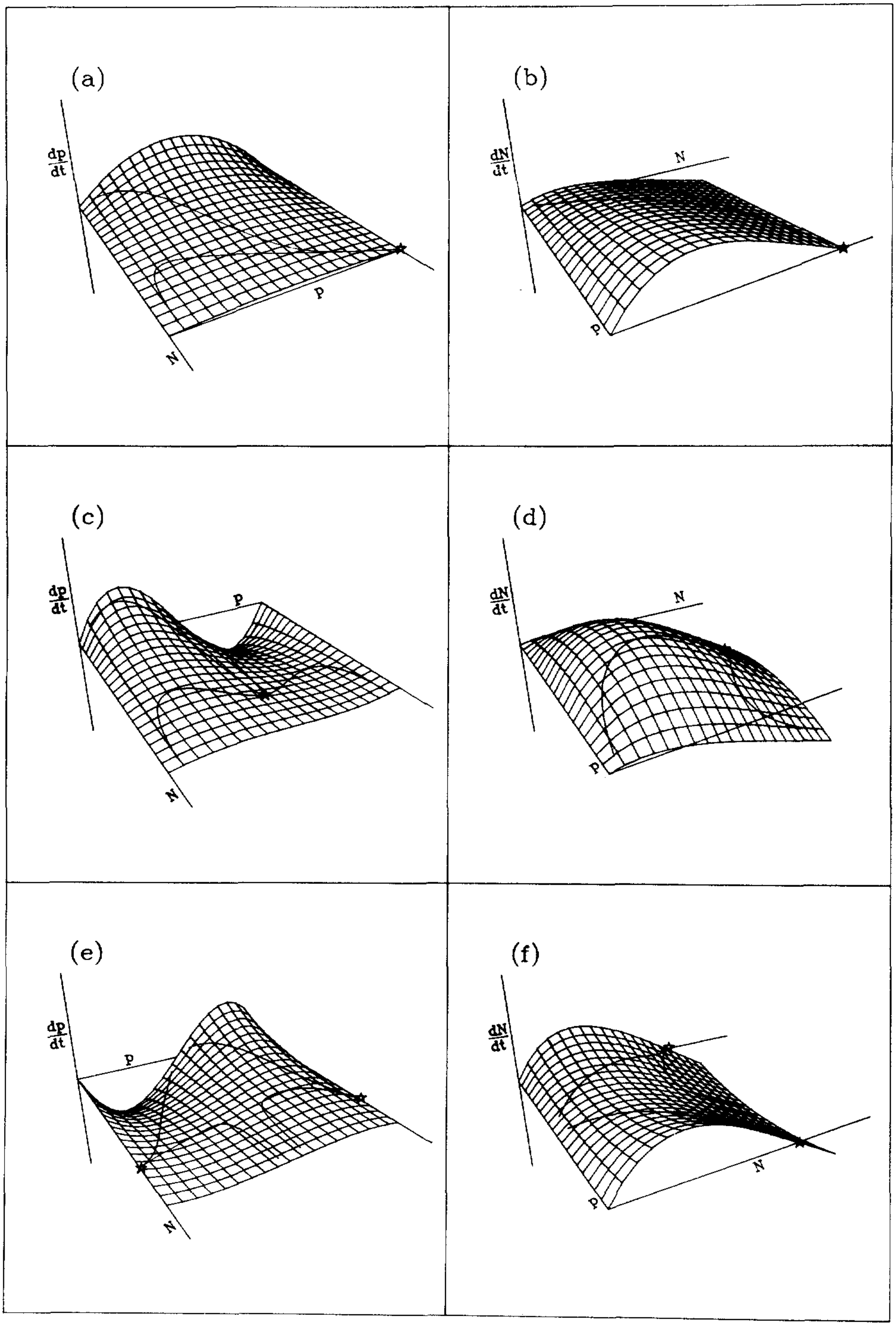
where $b_i = \sum_{j=1}^{n} b_{ij}p_j$ and $\bar{b} = \sum_{i=1}^{n} b_ip_i$.

The equilibrium allele frequencies, p_i^*, are obtained in the usual way by setting equation (4a) equal to zero and solving for p_i. The equilibria and the stability properties of p_i^* are the same as the classical model with constant fitnesses. A single nontrivial equilibrium population size, $N^* > 0$, is found from equation (4b) when $F(N) = d/\bar{b}^*$. The asterisk, *, notation indicates that $\bar{b}$ is evaluated at $p = p^*$. Since the function F is strictly monotonic, the equilibrium is given by $N^* = F^{-1}(d/\bar{b}^*)$, where F^{-1} is the inverse function of F, *i.e.*, $F^{-1}(F(N)) = N$. This equilibrium is locally stable provided $\bar{b} > d$. Natural selection will result in N^* being a local maximum by maximizing $\bar{b}^*$.

Although $f(N)$ does not alter the equilibrium allele frequencies nor the time-independent trajectory of frequencies, $dp_i/dp_j = p_i(b_i - \bar{b})/p_j(b_j - \bar{b})$, this density-dependent recruitment function can influence the rate of approach to genetic equilibrium. Specifically, if $\partial f/\partial N < 0$, then the magnitude of change in allele frequency will decrease with increases in population size, N. In other words, given a set of populations with the same fitness values, b_{ij}, and the same initial allele frequencies, $p_i(0)$, the population with the smallest initial density, $N(0)$, is predicted to approach genetic equilibrium at the quickest rate.

We will now illustrate what happens with this type of natural selection by examining some graphical representations of the rates of change of allele frequency and population size under directional selection, balancing selection and disruptive selection (Figure 1). With $f(N) = \exp(-cN)$ and $g(N) = 1$ we obtain a model of population growth that has been widely discussed, for example, in fisheries biology by RICKER (1954, 1975a,b), in general population theoretical studies by MORAN (1950), COOK (1965), MAY (1974, 1976, 1980), SMITH (1968, 1974), HOPPENSTEADT (1975), OSTER (1976), MAY and OSTER (1976), THIEME (1979), HUNT (1980), FISHER, GOH and VINCENT (1979), LEVIN and GOODYEAR (1980), CULL (1981) and in Tribolium research by DESHARNAIS and COSTANTINO (1980, 1982a,b) and COSTANTINO and DESHARNAIS (1981). Although we use this particular model in order to present this analysis, the general findings are not unique to, *e.g.*, $f(N) = \exp(-cN)$, but are appropriate for any $f(N)$ that is a monotonic decreasing function of population size.

In the case of directional selection, the rates of change for allele frequency and population number are plotted in Figure 1, a and b, respectively. The change in allele frequency is uniformly positive, however, it is a decreasing function of N and the change in population size is a maximum at p^*. All population trajectories eventually converge to the globally stable equilibrium


(a)
$\frac{dp}{dt}$
P
N
(b)
$\frac{dN}{dt}$
N
P
(c)
$\frac{dp}{dt}$
P
N
(d)
$\frac{dN}{dt}$
N
P
(e)
$\frac{dp}{dt}$
P
N
(f)
$\frac{dN}{dt}$
N
P

point of $p^* = 1$ and $N^* = \log_e(\bar{b}^*/\mathrm{d})/\mathrm{c}$ is maximized by natural selection maximizing $\bar{b}^*$.

With balancing selection (heterozygote superior) the change in allele frequency (Figure 1c) is positive for $p_o < p^*$ and is negative for $p_o > p^*$. The magnitude of dp/dt, as before, is a decreasing function of population size. The sketch of the change in adult number (Figure 1d) reveals that, for $p = p^*$, dN/dt is a maximum. All trajectories of the population converge to the globally stable equilibrium point given by $0 < p^* < 1$ and N^* is maximum.

The graphs of dp/dt and dN/dt for the heterozygote inferior are presented in Figure 1, e and f, respectively. The patterns of population trajectories are different from the other two genetic situations. For $p_o < p^* = 0.5$, the population moves toward $p^* = 0$, and for $p_o > p^* = 0.5$ the population becomes genetically fixed at $p^* = 1$. For the unstable equilibrium $p^* = 0.5$, dN/dt is always a minimum. At the locally stable genetic equilibria $p^* = 0$ and $p^* = 1$, the corresponding equilibrium population sizes are local maxima.

SELECTION ON MORTALITY

In the second genetic possibility, the genotype differences are visualized in the per capita density-independent death rates, d_{ij}, so that equation (2) is

$$W_{ij}(N) = bf(N) - d_{ij}g(N). \tag{5}$$

The rates of change in allele frequency and population size are given by

$$dp_i/dt = p_i(\bar{d} - d_i)g(N). \tag{6a}$$

$$dN/dt = (bf(N) - \bar{d}g(N))N \tag{6b}$$

where $d_i = \sum_{j=1}^{n} d_{ij}p_j$ and $\bar{d} = \sum_{i=1}^{n} d_ip_i$.

As in the case of selection on recruitment, the equilibrium allele frequencies are independent of population size, and the stability properties are the same as in the classical model. Also, the trajectory of allele frequency, dp_i/dp_j, is again independent of population size, and the effect of gene frequency on the rates of change in adult number is qualitatively the same in both cases, *i.e.*, for a given value of N, dN/dt is always maximum for a stable p^* and a minimum when p^* is unstable.

The most striking comparison between recruitment and mortality selection is that with selection on mortality the magnitude of change in allele frequency

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FIGURE 1.—A series of three-dimensional plots of the change in allele frequency, dp/dt, and the change in adult numbers, dN/dt, as functions of allele frequency, p, and adult numbers, N, for a single locus genetic model with two alleles described by equation (4) with $f(N) = \exp(-cN)$, $g(N) = 1$, $d = 0.25$ and $c = 0.02$: (a)–(b) directional selection $b_{11} = 3$, $b_{12} = 2$, $b_{12} = 1$, (c)–(d) balancing selection $b_{12} = 3$, $b_{11} = b_{22} = 0.5$ (e)–(f) disruptive selection $b_{12} = 0.5$, $b_{11} = b_{22} = 1.75$. The solid curves represent sample trajectories for nonequilibrium populations that were generated using a Runge-Kutta numerical method. The stable equilibria are shown by stars. The effects of selection are dampened by increasing adult numbers. Population size is maximized at the genetic equilibria.

is forecast to *increase* as N approaches N^*, whereas when the genetic differences are associated with the per capita density-independent rates of recruitment, the magnitude of dp_i/dt is predicted to *decrease* as population size approaches its equilibrium. In addition, a high mortality represents a low fitness; consequently, the equilibrium population size $N^* = F^{-1}(\bar{d}^*/b)$ will be a local maximum because natural selection will minimize $\bar{d}$.

Perhaps the most familiar example of population growth with density-regulated mortality is the Verhulst-Pearl equation. As formulated by MACARTHUR (1962), ANDERSON (1971), ROUGHGARDEN (1971) and CHARLESWORTH (1971), the genotypic fitness is $W_{ij}(N) = r_{ij}(K_{ij} - N)/K_{ij}$. If we let $r_{ij} = b - d_{ij}$ and define K_{ij} as the equilibrium density of an imaginary population composed entirely of i,j genotypes, then we have an example of density-regulated mortality with $f(N) = 1$, $g(N) = N + 1$ and $K_{ij} = F^{-1}(d_{ij}/b) = r_{ij}/d_{ij}$. In this case, the equilibrium population size $N^* = F^{-1}(d^*/b) = (b/\bar{d}^*) - 1$ corresponds to a "harmonic mean of the K_{ij} weighted by the r_{ij}" (CHARLESWORTH 1971, p. 470). It is clear that N^* is maximized when natural selection minimizes the arithmetic mean mortality $\bar{d}$.

A series of three-dimensional graphs of the change in allele frequency and population number as functions of p and N are sketched in Figure 2 for logistic model with selection on mortality. We can see that the magnitude of change in allele frequency is increased with population size; this is completely opposite to the model with genotypic differences in the rate of recruitment (Figure 1).

SELECTION ON BOTH RECRUITMENT AND MORTALITY

We now imagine that the genetic locus effects both the rate of recruitment and the rate of mortality. The rates of change in allele frequency and population size are

$$dp_i/dt = p_i[(b_i - \bar{b})f(N) + (\bar{d} - d_i)g(N)], \quad i = 1,2, \cdots, n \tag{7a}$$

$$dN/dt = N[\bar{b}f(N) - \bar{d}g(N)] \tag{7b}$$

where $b_i = \sum_{j=1}^{n} b_{ij}p_j$, $\bar{b} = \sum_{i=1}^{n} b_ip_i$, $d_i = \sum_{j=1}^{n} d_{ij}p_j$, and $\bar{d} = \sum_{i=1}^{n} d_ip_i$.

The equilibria are found by setting the system (7) equal to zero. The equilibrium population size is

$$N^* = F^{-1}(\bar{d}^*/\bar{b}^*) \tag{8}$$

where $F(N) = f(N)/g(N)$. Setting equations (7a) to zero we have

$$(b_i^* - \bar{b}^*)F(N^*) - (d_i^* - \bar{d}^*) = 0, \quad i = 1, \cdots, n \tag{9}$$

From (8) we know that $F(N)^* = \bar{d}^*/\bar{b}^*$, and substituting this into (9) we obtain

$$\bar{b}^* - (b_i^*/d_i^*)\bar{d}^* = 0 \quad i = 1, \cdots, n \tag{10}$$

where the asterisk notation indicates that these averages are evaluated at $p = p^*$. In particular, note from equation (10) that the ratios $b_i^*/d_i^* = \bar{b}^*/\bar{d}^*$ at the genetic equilibria. The local maxima of the ratio $\bar{b}/\bar{d}$ coincide exactly with the

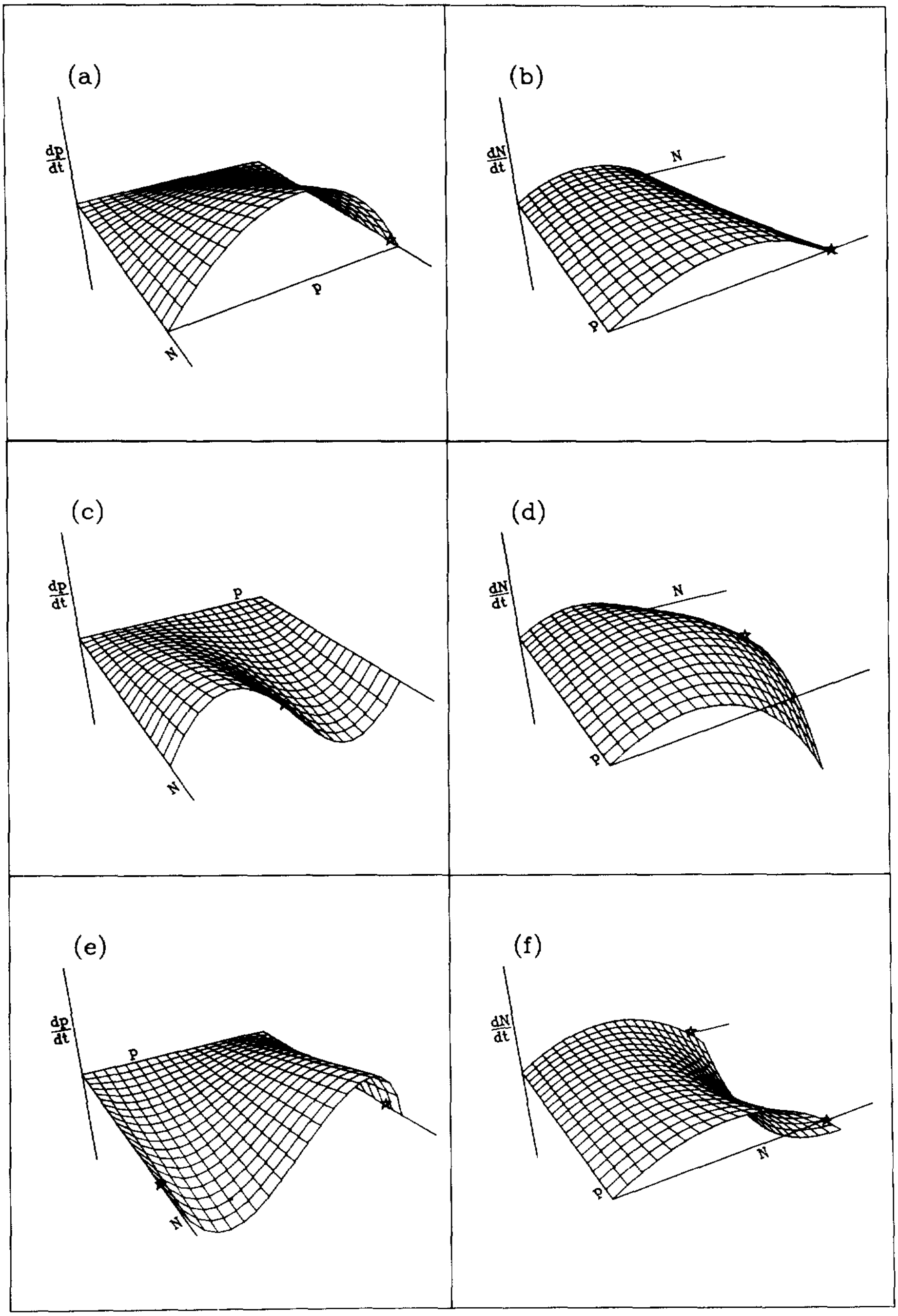

FIGURE 2.—A series of three-dimensional graphs of the change in allele frequency, dp/dt, and the change in adult numbers, dN/dt, as functions of allele frequency, p, and adult numbers, N, for a single locus genetic model with two alleles described by equations (6) with $f(N) = 1$, $g(N) = N + 1$ and $b = 2$: (a)–(b) directional selection $d_{11} = 0.0167$, $d_{12} = 0.0202$, $d_{22} = 0.0231$, (c)–(d) balancing selection $d_{12} = 0.0086$, $d_{11} = d_{22} = 0.0266$, (e)–(f) disruptive selection $d_{12} = 0.0290$, $d_{11} = d_{22} = 0.0176$. The stable equilibria are shown by stars. The effects of selection are enhanced by increasing adult numbers. Population size is maximized at the genetic equilibria.

stable equilibria p^*. This suggests that with selection on both recruitment and mortality natural selection will maximize N^* by maximizing the *ratio* of the density-independent rates of recruitment to mortality, $\bar{b}/\bar{d}$.

This conjecture can be demonstrated by using GINZBURG's (1977a) result which states that $N^* = F^{-1}\ (\bar{d}^*/\bar{b}^*)$ is maximized at a stable p^* and by recalling that F^{-1} is a continuous monotonic decreasing function. Alternatively, one can use equation (10) to show that the characteristic values, λ, of the pencil of the form $\bar{b} - \lambda\bar{d}$ are $\lambda = \max\ (b/d)$ and that these maxima are assumed for the characteristic vectors, p^*, of the pencil (GANTMACHER 1959, pp. 317–323).

An important property of the rates of change in allele frequency for selection imposed on either recruitment or mortality is that the trajectory of allele frequency, dp_i/dp_j, is independent of N. With selection on both recruitment and mortality this time-independent trajectory is indeed now a function of population size. For example, when N is small (*i.e.*, $N \ll N^*$ such that $F(N) = f(n)/g(N) \doteq 1$) the genetic differences in fitness (equation 2) are determined by $b_{ij} - d_{ij}$, and selection will change allele frequencies so as to maximize the exponential rate of population growth $\bar{b} - \bar{d}$. Alternatively, when N is large (*i.e.*, $N \gg N^*$ such that $F(N) = f(N)/g(N) \doteq 0$) differences among the d_{ij}'s dominate, and selection will alter allele frequencies so as to minimize the mean mortality rate $\bar{b}$. But, as we have already shown, selection will ultimately maximize the ratio $\bar{b}/\bar{d}$ when population density has reached its equilibrium. Since the allele frequencies corresponding to a maximum of $\bar{b} - \bar{d}$, a minimum of $\bar{d}$ and a maximum of $\bar{b}/\bar{d}$ may be quite different, qualitative changes in the direction of selection can occur.

To illustrate what happens with genetic differences in both recruitment and mortality we let $f(N) = \exp(-cN)$ and $g(N) = \exp\ (mN)$. At low populations densities the change in allele frequency (Figure 3a) is uniformly positive, and natural selection will maximize the difference between the mean recruitment and the mean mortality rates. At these low densities, allele frequency will move toward unity. However, as the population continues to grow natural selection will no longer maximize the difference $\bar{b} - \bar{d}$ but will maximize the ratio $\bar{b}/\bar{d}$. The direction of dp/dt will become negative and the population will then move toward the equilibrium allele frequency of 0.29. The equilibrium population density is $N^* = \log_e(\bar{b}^*/\bar{d}^*)/(c + m) = 75.8$. The graphical representation of the change in population size (Figure 3b) reveals that, for a given N, dN/dt is not always maximum at p^*.

At this point, it is worth reiterating the fact that we have been examining the effects of natural selection on the density-independent recruitment and mortality rates, that is, the entities $\bar{b}$ and $\bar{d}$. However, at demographic equilibrium, the expression $dN/dt = 0$ means that the overall rates of recruitment and mortality are equal or, in terms of our model, $\bar{b}f(N^*) = \bar{d}g(N^*)$. This constraint defines N^* as an implicit function of the allele frequencies. As selection maximizes the ratio $\bar{b}/\bar{d}$, N^* increases to a value that minimizes the ratio $f(N^*)/g(N^*)$, thus preserving the identity $(\bar{b}/\bar{d})[f(N^*)/g(N^*)] = 1$. In other words, at demographic equilibrium genetically based changes in the density-independent components of recruitment and mortality are balanced by ecologically based changes in the density-dependent components of recruitment and

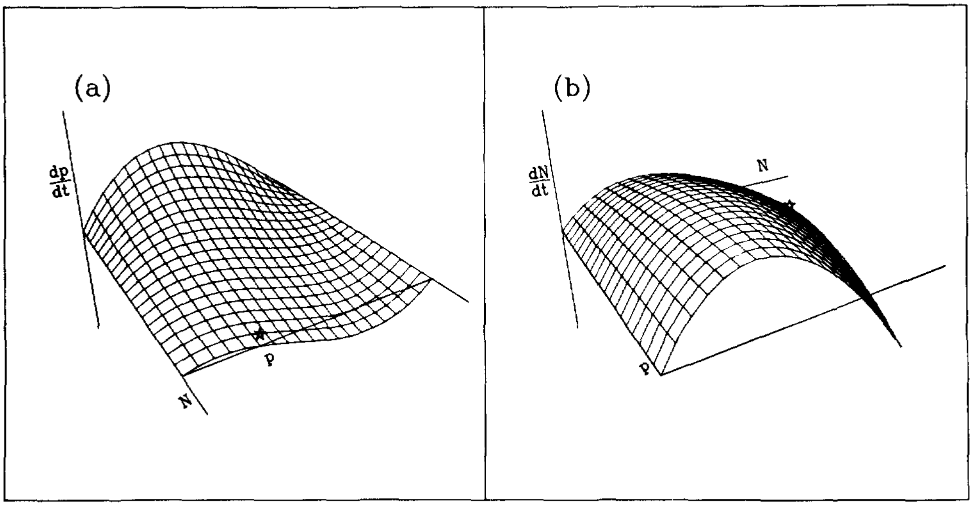

FIGURE 3.—Selection on both recruitment and mortality. (a), The change in allele frequency, dp/dt, and (b) the change in population size, dN/dt, as functions of allele frequency, p, and density, N, for a single locus genetic model with two alleles described by equations (7) with $f(N) = \exp(-cN)$, $g(N) = (mN)$, $c = 0.02$, $m = 0.003$, recruitment rates $b_{11} = 2$, $b_{12} = 1.5$, $b_{22} = 1$ and mortality rates $d_{11} = 0.5$, $d_{12} = d_{22} = 0.2$. The stable equilibria are shown by stars.

mortality with the net result being the maximization of the implicit function N^*.

Finally, a discrete time version of the continuous time model can be obtained by integrating equations (7) over consecutive finite time intervals of size Δt. Since $b_{ij}f(N)$ and $d_{ij}g(N)$ are rates we can let $R_{ij}(t) = \exp[\int_t^{t+\Delta t} f(N(\tau))d\tau]$ be the number of new recruits per individual for genotype ij and $S_{ij}(t) = \exp[-\int_t^{t+\Delta t} d_{ij}g(N(\tau))d\tau]$ be the genotypic survivorship over the time interval t to $t+\Delta t$. The discrete time analogs of equations (7) are

$$p_i(t + \Delta t) = p_i(t)[R_i(t)S_i(t)]/[\bar{R}(t)\bar{S}(t)], \quad i = 1, \cdots, n \tag{11a}$$

$$N(t + \Delta t) = N(t)\bar{R}(t)\bar{S}(t) \tag{11b}$$

where $R_i(t) = \exp[\int_t^{t+\Delta t} b_i(\tau)f(N(\tau))d\tau]$, $\bar{R}(t) = \exp[\int_t^{t+\Delta t} \bar{b}f(N(\tau))d\tau]$, $S_i(t) = \exp[-\int_t^{t+\Delta t} d_i(\tau)g(N(\tau))d\tau]$, and $\bar{S}$ (t) $= \exp[-\int_t^{t+\Delta t} \bar{d}(\tau)g(N(\tau))d\tau]$. Equations (11) show the relationship between the rates of recruitment and mortality in our continuous time model and the product of recruit numbers and survivorship common to discrete time formulations (CROW and KIMURA 1970, p. 191).

DISCUSSION

Fitness in the continuous model with overlapping generations is measured in terms of the Malthusian parameter, m (FISHER 1930). For the genotype A_iA_j, CROW and KIMURA (1970, p. 190) let $m_{ij} = b_{ij} - d_{ij}$. In this paper we have modestly extended this viewpoint by writing the fitness $W_{ij}(N)$ explicitly in terms of genotypically determined birth and death rates coupled with the density-dependent factors $f(N)$ and $g(N)$ (see equation 2). We can accommodate the classical interpretation by setting $f(N) = g(N) = 1$. In this situation, population growth does not effect either the magnitude nor the direction of change in allele frequency, and selection results in the maximization of the population's exponential rate of growth. On the other hand, in the presence of density-dependent factors our findings indicate that (1) when population size N is small selection will maximize $\bar{b} - \bar{d}$, (2) when N is much larger than its equilibrium density N^* selection will act to minimize $\bar{d}$ and (3) when population density has reached N^* selection will maximize the ratio $\bar{b}/\bar{d}$.

HAIRSTON, TINKLE and WILBUR (1970) actually suggested the terms "b selection" and "d selection." This viewpoint was not embraced by PIANKA (1972) who favored the MACARTHUR (1962) and MACARTHUR and WILSON (1967) concept of r and K selection. CASWELL (1982) argued that r-K theory is based on the Verhulst-Pearl equation and cannot serve as a basis for demographic predictions. In our formulation if one defines K as N^*, then the concepts of r and K selection can be related directly to the parameters $\bar{b}$ and $\bar{d}$. Using the concept of fitness entropy (GINZBURG 1972, 1977b; COSTANTINO, GINZBURG and MOFFA 1977; GINZBURG and COSTANTINO 1979) DESHARNAIS and COSTANTINO (1980) showed that MACARTHUR's (1962) analogue of Haldane's cost of a gene substitution for density-dependent population growth can be interpreted using the birth-death definition of fitness. But, more importantly, by writing the fitness as $W_{ij}(N) = b_{ij}(N) - d_{ij}g(N)$ the ecological-genetical arguments and conclusions are not based on a particular growth model (*e.g.*, VERHULST or RICKER) but are appropriate to many forms of density-dependent population growth. Indeed, so many animal population growth models are written in terms of birth and death that a compatible definition of Darwinian fitness may allow for a smoother transition between ecology and population genetics. Moreover, the experimentalist interested in the analysis of density sensitivity (as a recent example see MARKS 1982) may find the characterization proposed here (equation 2) of value in the design of experiment by focusing attention on the birth rate b or the death rate d, or density-dependent recruitment $f(N)$ or density-dependent mortality $g(N)$, or some combination of these.

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LITERATURE CITED

ANDERSON, W., 1971 Genetic equilibrium and population growth under density regulated selection. Am. Nat. **105:** 489–498.

ASMUSSEN, M. A. and M. W. FELDMAN, 1977 Density dependent selection. 1. A stable feasible equilibrium may not be attainable. J. Theor. Biol. **64:** 603–618.

CASWELL, H., 1982 Life history theory and the equilibrium status of populations. Am. Nat. **120:** 317–339.

CHARLESWORTH, B., 1971 Selection in density-regulated populations. Ecology **52:** 469–474.

CLARKE, B., 1972 Density-dependent selection. Am. Nat. **106:** 1–13.

CLARKE, B., 1973 Mutation and population size. Heredity **31:** 367–379.

COOKE, L. M., 1965 Oscillation in the simple logistic growth model. Nature **207:** 316.

COSTANTINO, R. F. and R. A. DESHARNAIS, 1981 Gamma distributions of adult numbers for *Tribolium* populations in the region of their steady states. J. Anim. Ecol. **50:** 667–681.

COSTANTINO, R. F., L. R. GINZBURG and A. M. MOFFA, 1977 An experimental check of fitness entropy vs. selective delay. J. Theor. Biol. **68:** 317–320.

CROW, J. F. and M. KIMURA, 1970 *An Introduction to Population Genetics Theory.* Harper and Row, New York.

CULL, P., 1981 Global stability of population models. Bull. Math. Biol. **43:** 47–58.

DESHARNAIS, R. A. and R. F. COSTANTINO, 1980 Genetic analysis of a population of *Tribolium.* VI. Stability: response to genetic and demographic perturbations. Can. J. Genet. Cytol. **22:** 577–589.

DESHARNAIS, R. A. and R. F. COSTANTINO, 1982a The approach to equilibrium and the steady-state probability distribution of adult numbers in *Tribolium brevicornis.* Am. Nat. **119:** 102–111.

DESHARNAIS, R. A. and R. F. COSTANTINO, 1982b Natural selection and fitness entropy in a density regulated population. Genetics **101:** 317–329.

EWENS, W. J., 1979 *Mathematical Population Genetics.* Springer-Verlag, New York.

FISHER, M. E., B. S. GOH and T. L. VINCENT, 1979 Some stability conditions for discrete time single species models. Bull. Math. Biol. **41:** 861–875.

FISHER, R. A., 1930 *The Genetical Theory of Natural Selection.* Claredon Press, Oxford.

GANTMACHER, F. R., 1959 *The Theory of Matrices,* Vol. 1. Chelsea Publishing Company, New York.

GINZBURG, L. R., 1972 Diversity of fitness and generalized fitness. J. Gen. Biol. **33:** 77–81 (in Russian).

GINZBURG, L. R., 1977a The equilibrium and stability for n-alleles under the density-dependent selection. J. Theor. Biol. **68:** 545–550.

GINZBURG, L. R., 1977b A macro-equation of natural selection. J. Theor. Biol. **67:** 677–686.

GINZBURG, L. R. and R. F. COSTANTINO, 1979 On the rate of genetic adaptation under natural selection. J. Theor. Biol. **77:** 307–316.

GREGORIUS, H. R., 1979 Deterministic single-locus density-dependent selection. J. Math. Biol. **8:** 375–391.

HAIRSTON, N. G., D. W. TINKLE and H. M. WILBUR, 1970 Natural selection and the parameters of population growth. J. Wildl. Manage. **34:** 681–690.

HASTINGS, A., 1978 An evolutionary optimization principle. J. Theor. Biol. **75:** 519–525.

HOPPENSTEADT, F., 1975 *Mathematical Theories of Populations: Demographics, Genetics and Epidemics,* Conference Board of the Mathematical Sciences, Vol. 20. Society for Industrial and Applied Mathematics Publication, Philadelphia.

HUNT, F., 1980 On the persistence of spatially homogeneous solutions of a population genetics model with slow selection. Math. Biosci. **52:** 185–206.

KIMURA, M., 1958 On the change of population fitness by natural selection. Heredity **12:** 145–167.

LEVIN, S. A. and C. P. GOODYEAR, 1980 Analysis of an age-structured fishery model. J. Math. Biol. **9:** 245–274.

MACARTHUR, R. H., 1962 Some generalized theorems of natural selection. Proc. Natl. Acad. Sci. USA **38:** 1893–1897.

MACARTHUR, R. H. and E. O. WILSON, 1967 *The Theory of Island Biogeography.* Princeton University Press, Princeton, New Jersey.

MARKS, R. W., 1982 Genetic variability for density sensitivity of three components of fitness in *Drosophilia melanogaster.* Genetics **101:** 301–316.

MAY, R. M., 1974 Ecosystem patterns in randomly fluctuating environments. pp. 1–50, In: *Progress in Theoretical Biology*, Edited by R. ROSEN and F. SNELL. Academic Press, New York.

MAY, R. M., 1976 Simple mathematical models with very complicated dynamics. Nature **261:** 459–467.

MAY, R. M., 1980 Mathematical models in whaling and fisheries management. pp. 1–64. In: *Some Mathematical Questions in Biology*, Vol. 13, Edited by G. F. OSTER. American Mathematical Society, Providence, Rhode Island.

MAY, R. M. and G. F. OSTER, 1976 Bifurcations and dynamic complexity in simple ecological models. Am. Nat. **110:** 573–599.

MORAN, P. A. P., 1950 Some remarks on animal population dynamics. Biometrics **6:** 250–258.

NAGYLAKI, T., 1977 *Selection in One- and Two Locus Systems.* Springer-Verlag, New York.

OSTER, G. F., 1976 Internal variables in population dynamics. pp. 37–68. In: *Some Mathematical Questions in Biology*, Vol. 7, Edited by S. A. LEVIN. American Mathematical Society, Providence, Rhode Island.

PIANKA, E. R., 1972 r and K selection or b and d selection? Am. Nat. **106:** 581–588.

RICKER, W. E., 1954 Stock and recruitment. J. Fish. Res. Board Can. **11:** 559–623.

RICKER, W. E., 1975a Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191.

RICKER, W. E., 1975b The historical development. pp. 1–26. In: *Fish Population Dynamics*, Edited by L. A. GULLAND. Wiley, London.

ROUGHGARDEN, J., 1971 Density-dependent natural selection. Ecology **106:** 683–718.

ROUGHGARDEN, J., 1976 Resource partitioning among competing species: a coevolutionary approach. Theor. Pop. Biol. **9:** 388–424.

SMITH, J. M., 1968 *Mathematical Ideas in Biology.* Cambridge University Press, Cambridge.

SMITH, J. M., 1974 Models in Ecology. Cambridge University Press, Cambridge.

THIEME, H. R., 1979 Density-dependent regulation of spatially distributed populations and their asymptotic speed of spread. J. Math. Biol. **8:** 173–187.

WRIGHT, S., 1935 Evolution in populations in approximate equilibrium. J. Genet. **30:** 257–266.

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