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"Population Dynamics in Variable Environments: The Demography and Evolution of Iteroparity"

Shripad TULJAPURKAR
Stanford University
Department of Biological Sciences
Stanford, CA 94305
U.S.A.

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POPULATION DYNAMICS IN VARIABLE ENVIRONMENTS. VII. THE DEMOGRAPHY AND EVOLUTION OF ITEROPARITY

STEVEN HECHT ORZACK AND SHRIPAD TULJAPURKAR

Department of Ecology and Evolution, University of Chicago, 1103 East 57th Street, Chicago, Illinois 60637; Department of Biological Sciences, Stanford University, Stanford, California 94305

Most work on the evolution of life-history traits stems from Cole's 1954 paper on the evolutionary advantage of reproducing once or many times during life. His conclusion that semelparity (reproducing once) is evolutionarily superior to iteroparity (reproducing many times) forms the basis of Cole's paradox and represents the beginning of modern investigations into the evolutionary basis of differences in life-history traits within and between species. Despite the large amount of work devoted to this general problem, there is as yet no single model of life-history evolution that incorporates (1) age structure, (2) random environmental variability, (3) life histories of arbitrary length, (4) age-specific variation and covariation of components of the life history, and (5) genotypic differences in life history.

We describe here an analytic framework with these features and use it to determine the evolutionary consequences of spreading reproduction in different ways over a lifetime. The life histories included in this analysis encompass those traditionally regarded as semelparous and iteroparous. However, we regard this dichotomy as too simple and potentially misleading. Instead, we assume the temporal clumping and positioning of reproduction during life to be a continuous character. From this continuum, we have chosen various character states in order to compare a reasonable set of life histories. One biological motivation for this approach is that many species described as semelparous contain individuals that reproduce more than once on some time scale (e.g., an "annual" plant species in which individuals have multiple times of seed set or in which there is a significant seed bank; see Fritz et al. 1982; Kirkendall and Stenseth 1985).

GENETIC AND DEMOGRAPHIC BACKGROUND

We assume a discrete-time model of population growth in a temporally variable environment such that

$$N_{t+1} = X_{t+1} N_t = X_{t+1} X_t \cdot \ldots \cdot X_1 N_0,$$

1

where N_t denotes the age-structure vector at time t and X_t denotes a Leslie matrix appearing at time t (for a general discussion, see Leslie 1945; Keyfitz 1968). On the top row of such a matrix are fertilities at age i, say, m_{it}; each has an average, m_i, and a variance, which are evaluated with respect to all environmental states. On the subdiagonal are age-specific survival probabilities (p_{it}), each with an average, p_i, and a variance. All other entries are zeros. For analytic and numerical simplicity, we often refer to a transformed version of this equation in which "net" fertility values at age i and time t are specified as $\phi_{it} \ (= p_{1t}p_{2t} \cdots \cdot p_{i-1,t}m_{it} = l_{it}m_{it})$. These have time averages, ϕ_i, and a variance. We use l_i to denote the average value of l_{it}. The dynamics of the process are unchanged by the transformation.

We assume here that the matrices representing vital rates in different environments are chosen according to a stationary Markovian stochastic process. The resulting population dynamics have been studied extensively (Cohen 1977, 1979a,b; Tuljapurkar and Orzack 1980; Tuljapurkar 1982a,b; Orzack 1985). Several results are important to note here. First, a population whose dynamics are governed by such a process has an asymptotic (nonrandom) growth rate:

$$a = \frac{1}{t} \, E\left[\ln \frac{M_t}{M_0}\right], \qquad (1)$$

where $t \to \infty$ and M_0 and M_t represent the population sizes at times 0 and t (Cohen 1979a). E( ) denotes an arithmetic expectation. Henceforth, we refer to a as the stochastic growth rate. Second, a biologically important feature of the dynamics is that the long-run distribution of population size is lognormal (Tuljapurkar and Orzack 1980). Hence, the expected growth rate of an ensemble of populations is in general unrepresentative of the typical behavior, as is also true with scalar growth processes (Lewontin and Cohen 1969). Third, the stochastic growth rate, a, is the key to studying life-history evolution. This is a consequence of a simple genetic analysis. In particular, assume that there are two alleles, B and b, at one locus. The relative ordering of the growth rates for the three genotypes determines the fate of rare alleles (Tuljapurkar 1982b). For example,

$$a_{BB} < a_{Bb} > a_{bb} \qquad (2)$$

is a sufficient condition for a polymorphism to be maintained. In this equation, a_{Bb} represents the stochastic growth rate (eq. 1) of a monomorphic population possessing the vital rates of Bb. Analogous inequalities for the geometric means of the underlying vital rates do not necessarily predict the outcome of natural selection even in a temporally uncorrelated environment (Orzack 1985). Inequality (2) and the obvious related inequalities (e.g., $a_{BB} > a_{Bb} > a_{bb}$) represent the stochastic analogues of the conditions derived for polymorphism and selection in constant environments by Charlesworth (1980). Although these inequalities strictly determine only allelic invasion, they often predict dynamic behavior away from the boundary (i.e., fixation; Orzack 1985).

Given this biological framework, it is appropriate to ask how life history and environment interact to determine a. The calculation of an approximation to a for particular life histories is relatively simple using an analytic framework developed

TABLE 1

FLAT LIFE-HISTORY SET USED FOR ANALYTIC AND NUMERICAL RESULTS

Life History	ϕ_i	α	ω	$\ln \lambda_0$	T_0	D
1	0.525	1	2	0.0326	1.492	0.5001
2	0.2625	1	4	0.0196	2.475	0.2501
3	0.175	1	6	0.0140	3.459	0.1668
4	0.13125	1	8	0.0109	4.443	0.1251
5	0.105	1	10	0.0089	5.426	0.1001
6	0.13125	3	10	0.0075	6.460	0.1250
7	0.175	5	10	0.0065	7.481	0.1667
8	0.2625	7	10	0.0057	8.493	0.2500
9	0.525	9	10	0.0051	9.499	0.5000

NOTE.—The analytic and numerical results are presented in figures 1–3 and 5–9. ϕ_i denotes the average value of net fertility for all ages from the first (α) to the last (ω) age at reproduction. λ_0 is the dominant eigenvalue of the average Leslie matrix. T_0 is the mean generation length of the average Leslie matrix. D is a measure of the diversity of the life history. (See the text for further details.)

earlier (Tuljapurkar 1982b). This approach is strongly supported by the results of numerical simulations, as this paper demonstrates. It is important to note that this approximation is composed of a constant term, which represents the contribution of the average vital rates to growth, and two variance terms. The first variance term represents the nonpositive contribution to stochastic growth rate of one-period fluctuations in vital rates. The second represents the contribution of two-period temporal correlations between vital rates and may be positive or negative depending on the sign of the environmental autocorrelation, on which portion of the life history is varying, and on the covariances between vital rates. This term can have an appreciable effect on the stochastic growth rate and may affect the outcome of selection among genotypes (Orzack 1985). However, we ignore the effects of autocorrelated environments because of their analytic and numerical complexity, restricting ourselves here to the still-substantial task of studying serially independent fluctuations in the vital rates.

BIOLOGICAL AND MATHEMATICAL ASSUMPTIONS

Given the demographic and genetic structure outlined above, analysis of the evolutionary consequences of differing reproductive patterns depends on four additional assumptions.

1. *Construction of the set of average life histories.*—We constrained life histories to have identical average amounts of lifetime weighted reproduction ($= R_0 = \Sigma \phi_i$), as did Murphy (1968). The sum is taken over all ages i, and as noted above, the ϕ_i's are stationary averages over all environmental states. Other constraints may be chosen, but we regard this one as biologically plausible and reasonably general. Presumably, a different constraint might lead to qualitatively different results.

Within a life-history set, two general classes of life histories may be distinguished (see tables 1, 2): those with an identical age at first reproduction (α) but

TABLE 2

The Average Values of "Net" Fertility at Each Age

Life History	Age										$\ln\lambda_0$	T_0	D
	1	2	3	4	5	6	7	8	9	10			
Declining													
1	0.5355	0.5145	0.2520	0.2310	0.1435	0.1225	0.0787	0.0578			0.0328	1.482	0.5007
2	0.2940	0.2730	0.1855	0.1645	0.1208	0.0997	0.0735	0.0525	0.0315	0.0105	0.0204	2.375	0.2531
3	0.2275	0.2065	0.1628	0.1417	0.1155	0.0945	0.1208	0.0997	0.0787	0.0578	0.0156	3.107	0.1755
4	0.2048	0.1838	0.1575	0.1365	0.1628	0.1417	0.1855	0.1645	0.1435	0.1225	0.0134	3.599	0.1443
5	0.1995	0.1785	0.2048	0.1838	0.2275	0.2065	0.2940	0.2730	0.2520	0.2310	0.0128	3.780	0.1359
6	0.0	0.0	0.0	0.0	0.0350				0.3355	0.5145	0.0087	5.621	0.1434
7	0.0	0.0	0.0	0.0	0.0						0.0068	7.131	0.1745
8	0.0	0.0	0.0	0.0	0.0						0.0058	8.393	0.2523
9	0.0	0.0	0.0	0.0	0.0						0.0051	9.489	0.5003
Peaked													
1	0.0525	0.6125	0.3325	0.0525		0.0350	0.0742	0.0262	0.0477	0.0210	0.0207	2.358	0.4481
2	0.0350	0.3710	0.2870	0.2030	0.1702	0.1222	0.1010	0.0743	0.0662	0.0262	0.0158	3.078	0.2547
3	0.0262	0.1462	0.2663	0.2183	0.1543	0.1277	0.1462	0.1063	0.1190	0.0350	0.0119	4.068	0.1742
4	0.0210	0.1143	0.2077	0.1810	0.2262	0.1863	0.2870	0.2030	0.3325	0.0525	0.0101	4.787	0.1355
5	0.0	0.0	0.0262	0.2663	0.0350	0.3710	0.0525	0.6125			0.0084	5.809	0.1786
6	0.0	0.0	0.0	0.0	0.0	0.0					0.0069	7.090	0.2532
7	0.0	0.0	0.0	0.0	0.0	0.0					0.0058	8.364	0.4463

NOTE.—The values in the table describe the declining and peaked life histories used in figure 4. λ_0, The dominant eigenvalue of the average Leslie matrix; T_0, the mean generation length; D, a measure of the diversity of the life history. (See the text for further details.)

distinct ages at last reproduction (ω); and those with distinct α but identical ω. Our analytic results (see below) indicate that stochastic growth rates can be thought of as simple functions of just two parameters: the intrinsic rate of increase ($\ln\lambda_0$) and the mean generation length (T_0) of the average life history. Therefore, we focused on the greatest span of $\ln\lambda_0$ and T_0 given a value of ω. All other life histories that can be reasonably added to these sets (such as those with intermediate α and ω) have intermediate values of $\ln\lambda_0$ and T_0 relative to the life histories in the tables.

Given α and ω, the next constraint needed concerns the dependence of ϕ_i values on age. Analyses of empirical data (e.g., Murphy 1968; Caughley 1977; Leggett and Carscadden 1978; Snell 1978; Shine and Bull 1979; Taylor 1979; Itô 1980; Millar and Zammuto 1983; Begon et al. 1986) suggest that most life histories have ϕ_i values that are flat, that decline, or that have an intermediate peak with respect to age. Each "shape" represents different constraints on the average values of the vital rates in the underlying life history. Hence, flat life histories (as in table 1), for example, result if l_i and m_i do not vary with age and may also result from declining average survival rates (l_i) and increasing average fertility values (m_i). In contrast, peaked life histories (as in table 2) result from age-independent l_i and peaked average fertility values (m_i). The general analytic results (eqs. 3–6) apply to life histories with any age dependence of ϕ_i's (given one constraint noted below concerning the periodicity of reproduction).

The specific results presented here (figs. 1–9) are a subset of a large collection, since we examined analytic and numerical stochastic growth rates for all 25 life histories (9 flat, 9 declining, 7 peaked) for many patterns of random variability. We focus on presenting results for the life histories with "flat" ϕ_i's because (1) the qualitative features of interest are the same regardless of the shape of ϕ_i's (compare figs. 3 and 4), (2) our goal is to highlight conclusions that appear robust in the face of geometric changes in the life-history set, and (3) we can make coherent comparisons within the set. Accordingly, most of the results for declining and peaked life histories are omitted.

2. *Periodicity of reproduction*.—The results apply to any life history as long as it has two nonzero ϕ_i values that are not periodic (i.e., the associated ages i and j share only 1 as a divisor). This is a standard assumption (e.g., Pollard 1973). The demographic consequence of this constraint is that an appropriate time unit must be chosen for quantitative analysis such that all life histories being compared are iteroparous. Numerical analysis indicates that the calculation of growth rates for some populations may be little affected by the time unit chosen (Pollard 1973, p. 37). The biological and demographic criteria needed to make biologically realistic decisions about appropriate time units need elucidation (see Cull 1980). At present, it is known only that such time units vary among taxa (Kirkendall and Stenseth 1985).

3. *Random variation: age and environmental sensitivity*.—Our major assumption is that variability in vital rates is a function of extrinsic changes in the environment or of the way in which organisms "experience" these changes. This distinction is most apparent in the analysis of "indifference" curves (see below). Our analytic and associated numerical results relate to life histories in which

the coefficient of variation (C) of the ϕ_{it} values does not change with age. This assumption was made primarily because it simplifies the analytic calculations. (The general analytic framework can accommodate any kind of age dependence for C.) Few data are available to guide one's choice in this regard. The results of Rose and Charlesworth (1981) indicate that the coefficient of variation of daily fecundity increases with age in lines of *Drosophila melanogaster* sampled from a laboratory population. Alternatively, the data of Piñero and Sarukhán (1982) suggest that the coefficients of variation for survival rates decline with age in the palm *Astrocaryum mexicanum*. If we ignore (purely for the sake of argument) that these data do not relate directly to ϕ_{it} values, the data most likely indicate that one could find species in which C values decrease, remain constant, or increase with age. Hence, we consider our choice of an age-independent C value convenient for analysis and most likely applicable to many organisms but not the only choice one could make.

4. *Random variation: distribution of environmental states.*—Numerical calculation of stochastic growth rates requires a choice about the distribution from which random "environmental" deviates are to be sampled. In all our simulations, the underlying distribution is lognormal. Several reasons motivated this choice. The first is that a continuous distribution was deemed more biologically realistic than one with discrete states, and its use avoids possible mathematical singularities (see, e.g., Tuljapurkar 1984). Second, this distribution applies naturally to ϕ_{it} values since it arises as the limiting distribution of products of independent or weakly correlated positive random variables (see, e.g., Johnson and Kotz 1970, p. 113). Finally, it is known that a skewed environmental distribution can have an appreciable effect on the stochastic growth rate (Slade and Levenson 1984).

Further assumptions about the correlation of ϕ_{it}'s among ages are discussed in the following section.

METHODS

Analytic Estimation of Stochastic Growth Rates

Calculation of stochastic growth rates requires further assumptions concerning the correlations among the ϕ_{it} values. A "small noise" approximation (Tuljapurkar 1982b) to the stochastic growth rate for a life history subject to small temporally uncorrelated environmental fluctuations is

$$a \approx \ln \lambda_0 - \frac{S^T V S}{2},$$ (3)

where λ_0 is the dominant eigenvalue of the average Leslie matrix; S is a column vector of the sensitivities of the intrinsic rate of increase to a fluctuation in the ϕ_i values (i.e., the ith component of S is $\partial \ln \lambda_0 / \partial \phi_i$); S^T is the transpose. Elements of these vectors are always nonnegative. V is a variance-covariance matrix of the ϕ_{it}'s. This approximation is very accurate at predicting a when $C \leq 0.3$. As our numerical results indicate (see below), it is even accurate to within a few percent when C is as large as 3, especially for longer life histories.

Any biologically plausible or implausible pattern of correlations can be accommodated within equation (3). To indicate the power of the method, we present three specific cases.

1. *Complete independence of ϕ_{it} values.*—In this case,

$$a \approx \ln \lambda_0 - \frac{C^2 (\Sigma G_i^2)}{2 T_0^2},$$ (4)

where G_i is $\phi_i \lambda_0^{-i}$, and T_0 is the mean generation length ($\Sigma i \phi_i \lambda_0^{-i}$) as defined by Leslie (1966). This and all subsequent sums are over all ages i ($i = \alpha, \ldots, \omega$) unless noted otherwise. This case most simply corresponds to the variability of the underlying fertility values, not to the variability of the survival rates, which are, by definition, likely to be positively correlated. In this case, one can directly see the dynamic consequences of varying degrees of "diversity" of the ϕ_i values. This follows because $\Sigma G_i = 1.0$, and therefore, $D = \Sigma G_i^2$ is a measure of the diversity of the reproductive schedule similar to Simpson's index for species abundances. This index decreases as reproduction is spread over more ages. For a life history of length ω, D has a minimum value of $1/\omega$, corresponding (if λ_0 is 1.0) to a flat ϕ_i schedule with reproduction at all ages, and a maximum value of 1.0, when reproduction occurs at one age only (see tables 1, 2).

2. *A correlation between each pair of ϕ_{it} values of $+1.0$.*—In this case,

$$a \approx \ln \lambda_0 - \frac{C^2}{2 T_0^2}.$$ (5)

Simple cases of life-history variation encompassed by this equation include variation in the first survival rate only and variation in an age-independent average fertility.

3. *An age-independent correlation r between ϕ_{it} values:*

$$a \approx \ln \lambda_0 - \frac{C^2 (\Sigma G_i^2 + r \Sigma \Sigma G_i G_k)}{2 T_0^2}$$ (6)

($i \neq k$). In this case, r may take any value between -1.0 and $+1.0$. It is important to note that life histories of different lengths must differ in the degree to which their ϕ_{it} values can be negatively correlated. In particular, it is straightforward to show that

$$r \geq \frac{-1}{n_\phi - 1}$$ (7)

is a necessary lower bound on the correlation among the ϕ_{it} values (n_ϕ is the number of varying ϕ_i values in the life history). Thus, assuming age-independent correlations, the most negative correlation for any life history with two varying ϕ_{it}'s is -1.0. In contrast, the most negative correlation possible for any life history with 10 varying ϕ_{it}'s, for example, is approximately -0.11.

Numerical Estimation of Stochastic Growth Rates

Monte Carlo simulations were performed in order to determine the accuracy of the analytic results. The life histories shown in tables 1 and 2 were used. The sum

R_0 is constrained to be 1.05 for all life histories. At each time t, vital-rate values were chosen from lognormal distributions with the appropriate means (ϕ, values), variances (calculated from C), and correlation structure. The uniform random numbers underlying the lognormal deviates were generated using the multiplicative congruential method (further details of the simulations are available upon request). Each run for a particular life history, correlation among vital rates, and coefficient of variation lasted 5000 time units. The starting population size was arbitrarily chosen to be 10, and the initial age-distribution vector was chosen to be as flat as possible, given integral numbers of individuals in each age class. All single-period growth rates ($n = 4999$) were calculated and then averaged to produce an estimate of the stochastic growth rate. Since the process is ergodic, this expectation converges to the limit in equation (1).

The generation of correlated lognormal deviates deserves comment. The correlation coefficient between lognormal deviates (r) is an exponential function of the correlation between the underlying normals and the coefficient of variation of the lognormal deviates (C). This dependence imposes a constraint on the possible values of r, in addition to relationship (7). Consider the case when n_{ab} is 2. In general, the range of possible correlations between the two random variables is -1.0 to 1.0. However, as C increases (when R_0 increases), the lower limit on r increases. Most important, for the life histories we used, some of the desired combinations of r and C cannot be achieved, including all of the combinations for $r = -0.95$, for example. Accordingly, we included numerical results for only one negative value of r, one for which we can generate the exact distributions of random variables. We have numerically explored other more-negative values of r by calculating stochastic growth rates for similar life histories with a lower R_0 (resulting in smaller C values). This approach indicates that our analytic framework accurately predicts stochastic growth rates even when the correlations of ϕ_{it} values are strongly negative, as in figure 1. For simplicity and conciseness, we have omitted these simulation results.

All numerical data in figures 1, 2, 3, 5, and 6 are obtained from polynomial equations fitting the relation between the numerically estimated stochastic growth rates and the associated coefficients of variation. For a set of simulation data involving a given life history, polynomial curves of various degrees (≤ 4) were fitted and one chosen depending upon the general fit of the curve, regardless of the degree of the polynomial. Almost all chosen curves are cubics, and for almost all, R^2 is greater than 0.90.

RESULTS

Application to Specific Life Histories

Stochastic growth rates for specific cases of correlation among ϕ_{it} values are shown in figures 1–6, most of which contain both analytically and numerically derived "indifference" curves. (The lines in these figures are not meant to imply intermediate life histories; i.e., the abscissa represents a categorical variable.) Such curves indicate life histories that are selectively neutral with respect to one another. It is clear that very distinct life histories can be so classified. For ex-
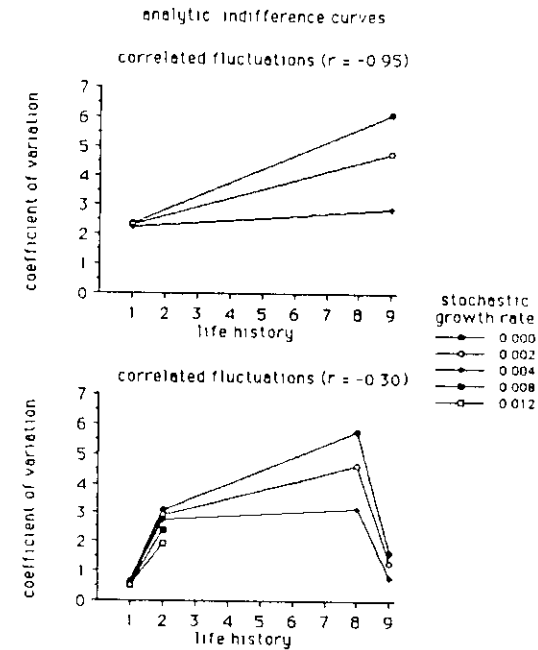
FIG. 1.—Analytic indifference curves when net fertilities have correlations of -0.95 (*top*) and -0.30 (*bottom*). Analytic values from equation (6) using the flat average life histories in table 1.

ample, when a equals 0.002, a life history with early reproduction and short lifetime ($\phi_i = 0.525$, $i = 1,2$) has no selective advantage over a life history with delayed reproduction in a long lifetime ($\phi_i = 0.0$, $i = 1,\ldots,8$; $\phi_j = 0.525$, $j = 9,10$) if it *differs* in the amount of environmental variability it experiences. In particular, the values of C producing neutrality when ϕ_{it}'s are completely correlated (fig. 6, *top*) are approximately 0.37 and 0.75 for the early- and late-reproducing life histories, respectively. This result indicates that it is important to determine whether life histories are differentially sensitive to a given amount of environmental variability. Acquisition of such data and information on temporal variability of vital rates (for a rare example, see Baker et al. 1981) should be an important goal of experimental evolutionary genetics.

There is no consistent relation among life histories with respect to the coefficients of variation (C's) allowing neutrality: C can increase (fig. 1, $r = -0.95$, $a = 0.0$), have an intermediate peak (fig. 3, $a = 0.0$), or decrease (fig. 5, $a = 0.014$). The consequence is that predictions about the direction of life-history evolution must also be based on adequate quantitative information about the quality of the environment (as indexed here by the stochastic growth rate).
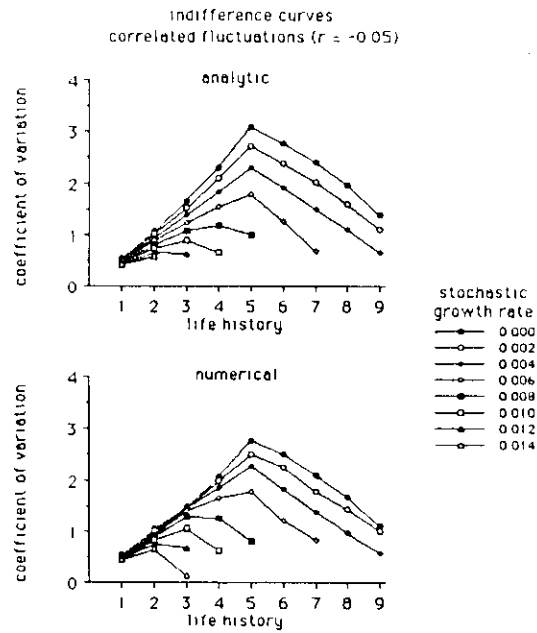
Fig. 2.—Indifference curves when net fertilities have a correlation of −0.05. *Top.* Analytic values from equation (6) using the flat average life histories in table 1. *Bottom.* Numerical estimates from polynomial fit to simulation data.
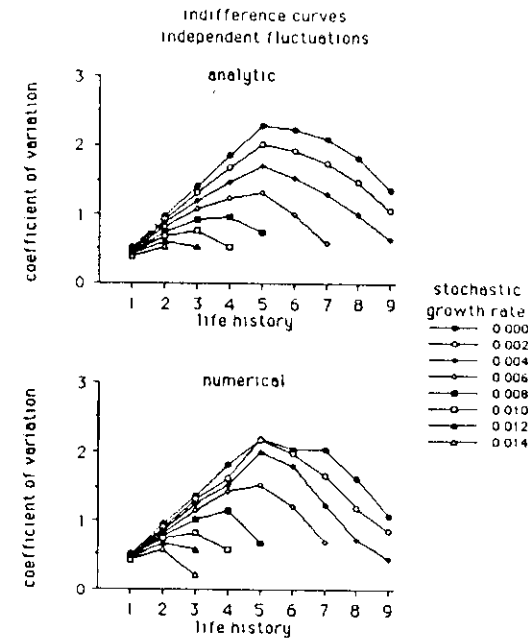

Fig. 3.—Indifference curves when net fertilities are independent. *Top.* Analytic values from equation (4) using the flat average life histories in table 1. *Bottom.* Numerical estimates from polynomial fit to simulation data.

Figure 4 contains analytic indifference curves for the declining and peaked life histories when the ϕ_i's are independent. (The numerical indifference curves are omitted for reasons of space but indicate that the analytic curves are quantitatively accurate.) Comparison with figure 3 indicates the general similarity of indifference curves despite changes in the geometries of the life histories. Similar results hold for other values of correlation between the ϕ_i's. Accordingly, further analysis will focus on the flat set of life histories in table 1.

The analytic data in figures 1, 2, 3, 5, and 6 can be plotted in a different manner, as in figures 7–9, to reveal how natural selection acts upon life histories with the *same* sensitivity to environmental fluctuations (a given value of C). (The numerical results are omitted since they are clearly redundant.)

We can identify three dynamic regimes associated with small, intermediate, and high levels of environmental variability, as defined by different values of C. We define these terms relative to the correlation structure. Accordingly, for a given C value, a life history with completely correlated ϕ_i's experiences more variation than one with independent ϕ_i's. Consider, for example, the latter case (fig. 8, $r = 0.0$).

Small variability.—When C is relatively low (e.g., ≤ 0.5), there is a clear selective advantage to a type of semelparity: reproducing early in a short lifetime. This is basically Cole's result in an age-structured, stochastic context.

Intermediate variability.—Life histories with various types of iteroparous reproductive schedules have an advantage relative to genotypes with larger $\ln \lambda_0$ or T_0 values. For example, when $C = 0.75$, life history 3 can invade as a heterozygous mutant into a monomorphic population composed of any other life history. Note that the entire set of life histories has similar stochastic growth rates when C is approximately 1.0–1.5, and the outcome of life-history evolution depends closely on the details.

High variability.—For larger C values (≥ 1.5), there is an advantage to the most iteroparous life history. Note that when ϕ_i's are positively correlated, long-lived, late-reproducing genotypes can also (depending on the value of r) have the highest stochastic growth rates, since their long mean generation lengths allow them to "miss" much of the variability (e.g., $C \geq 1.0$ in fig. 9, $r = 1.0$). Consequently, selection may favor dispersed or delayed reproduction in highly variable environments.
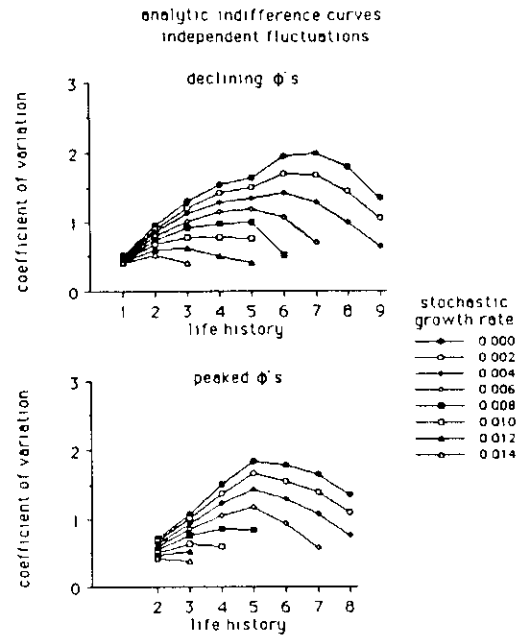
analytic indifference curves
independent fluctuations

Fig. 4.—Analytic indifference curves when net fertilities are independent. Values from equation (4) using the declining (top) and peaked (bottom) average life histories in table 2. Compare with the curves in figure 3.

It is clear that knowing the absolute amount of environmental variability and the correlation of ϕ_a's can be critical to predicting the direction of life-history evolution in a particular instance. Note, for example, that when $C = 1.0$, the life history from table 1 with the highest value of a is 1 when $r = -0.95$, 2 when $r = -0.30$, 3 when $r = -0.05$, 4 when $r = 0.0$, 8 when $r = 0.50$, and 9 when $r = 1.0$. When $C = 0.25$, life history 1 has the highest value of a regardless of the value of r.

General Features

Only the analysis of population dynamics allows one to determine the way in which $\ln \lambda_0$ and T_0 jointly determine evolutionary success (see also Cohen 1979b). A static approach might identify a large value of $\ln \lambda_0$ or T_0 as advantageous and thereby predict selective differences among the life histories on an indifference curve. Values of a are determined by the balance between their growth potential in the average environment $(\ln \lambda_0)$ and the level of environmental variability discounted by T_0. A "crossover" value of C distinguishes environments with low and intermediate variability. A lower bound on this value (regardless of correla-
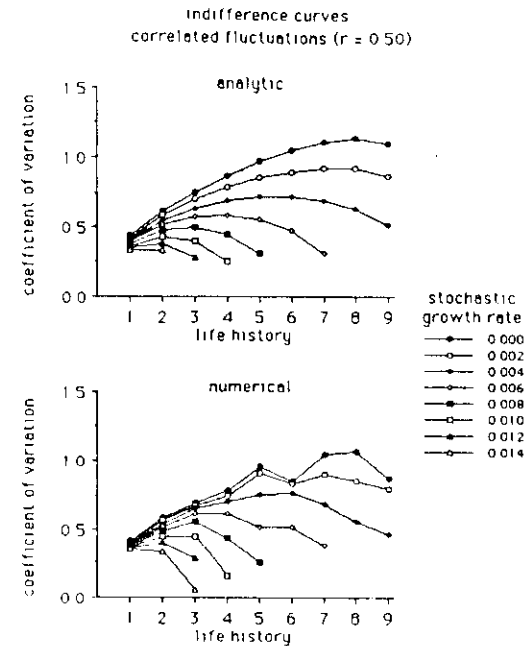
indifference curves
correlated fluctuations (r = 0.50)

Fig. 5.—Indifference curves when net fertilities have a correlation of 0.50. Top, Analytic values from equation (6) using the flat average life histories in table 1. Bottom, Numerical estimates from polynomial fit to simulation data.

tion among fluctuations) is

$$ C = \left[\frac{2(\ln \lambda_0 max - \ln \lambda_0 min)}{1/T_0^2 min - 1/T_0^2 max} \right]^{1/2} , $$

where max and min refer to the smallest and largest values among the life histories being analyzed. This crossover value is obtained by equating the analytic approximation (5) for stochastic growth rates of the two extreme phenotypes in the life-history set and solving for C. Comparison of this estimate with the C value associated with a particular life-history polymorphism may help determine whether the polymorphism is transitory or stable.

Selection between genotypes can be based purely on the sign of the covariances between vital rates. For example, assume that environmental variability affects only fertilities but does so equally for all genotypes. Then, a mutant heterozygote with negative correlations among fertilities can enter a population composed of a genotype with identical average fertilities that are independent or positively correlated. This point underscores the multivariate nature of "fitness" in age-
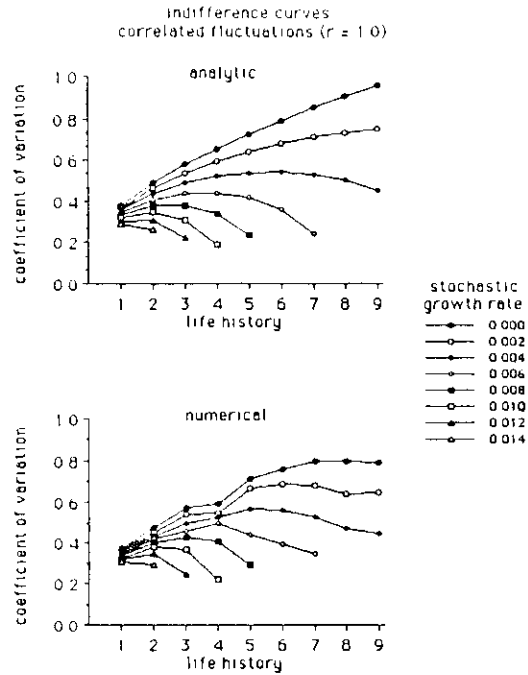
Indifference curves
correlated fluctuations (r = 1 0)

FIG. 6.—Indifference curves when net fertilities have a correlation of 1.0. *Top*, Analytic values from equation (5) using the flat average life histories in table 1. *Bottom*, Numerical estimates from polynomial fit to simulation data.
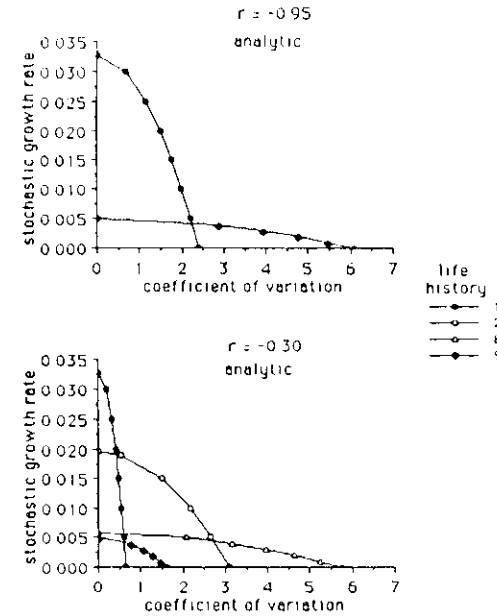

FIG. 7.—Analytic stochastic growth rates versus coefficient of variation when net fertilities have correlations of -0.95 (*top*) and -0.30 (*bottom*). Values from equation (6) using the flat average life histories in table 1.

structured populations and is also a reminder that negative correlations between life-history components can be selectively advantageous. Hence, care must be taken when analyzing "costs" of reproduction (for a general discussion, see Reznick 1985) to separate such correlations from those caused by a nonselective constraint on reproduction and survival.

One evolutionary implication to be drawn from indifference curves concerns the comparative analysis of life histories within or between conspecific populations or between closely related species. There is clearly the potential for the nonselective (and probably transitory) coexistence of distinct life histories, say, within a population as a result of mutational accumulation. One consequence of this accumulation is that even a marked differentiation of life histories between populations or between closely related species may be caused by the random fixation of alleles resulting from stochastic fluctuations in population size or genetic drift. It is not appropriate to assume, a priori, that such differentiation

reflects adaptation to different environments (see, e.g., Gadgil and Bossert 1970; Schaal 1984; the same point is made using a different approach in Schaffer 1974a).

Since a is defined solely in terms of numbers of individuals and has no phenotypic dimension, it is not a fitness by itself (except in a tautological sense). As shown above, radically different life histories can have identical values of a. Hence, it is inappropriate to make inferences about the evolution of phenotypes except by using approximations such as (4), (5), and (6), which connect the life history to a.

Our dynamic analysis of life-history evolution using a is generally distinct from an optimization analysis based on a Taylor-series expansion of $\ln \lambda_0$. For example, in our analysis, the first-order structure of a life history (e.g., $\partial \ln \lambda_0 / \partial \phi_i$) modifies the contributions of variances and covariances of vital rates to stochastic growth rate. In a Taylor-series expansion, the second-order structure of a life history (e.g., $\partial^2 \ln \lambda_0 / \partial \phi_i^2$) acts in this manner. (For a more extensive discussion, see Tuljapurkar 1988.) An optimization analysis also fails to account for the effects of environmental autocorrelation, which can be appreciable (e.g., Orzack 1985). All of these considerations (and several noted in the Discussion) make clear that a is
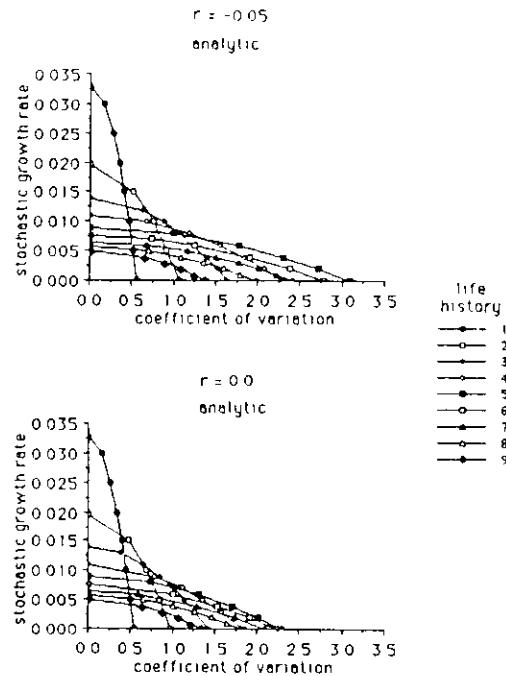
FIG. 8.—Analytic stochastic growth rates versus coefficient of variation when net fertilities have correlations of -0.05 (*top*) and 0.0 (*bottom*). Values from equations (6) and (4) using the flat average life histories in table 1.
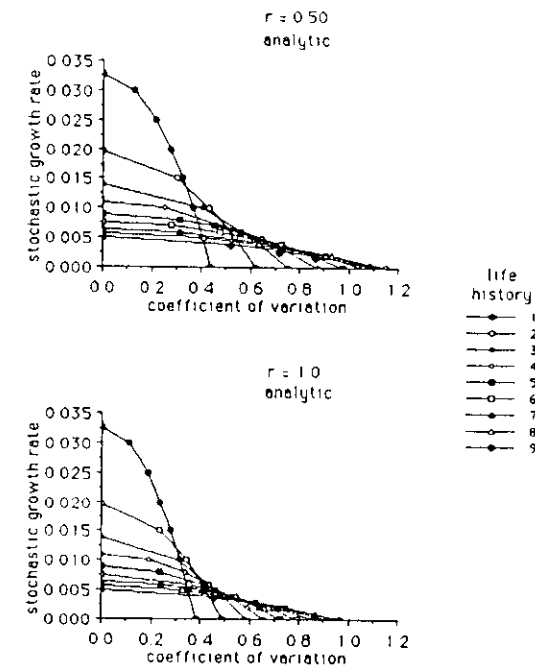

FIG. 9.—Analytic stochastic growth rates versus coefficient of variation when net fertilities have correlations of 0.50 (*top*) and 1.0 (*bottom*). Values from equations (6) and (5) using the flat average life histories in table 1.

the only adequate descriptor of density-independent growth in age-structured populations.

DISCUSSION

Context of Results

Where do these results fit in? We find ourselves in the unusual position of simultaneously agreeing and disagreeing with previous theoretical treatments. These may be roughly divided into "$r - K$" theory (based on extrapolation of deterministic theory to variable environments) and "bet-hedging" theory (the analysis of simplified stochastic dynamics for particular life histories; see below). The dichotomy between the predictions of the theories (see Stearns 1976, table 4) implies that the incorporation of environmental variation per se accounts for the differences. The more general analysis of dynamics used here clearly shows instead that the magnitude of variation and the correlation structure of ϕ_{ii}'s are

critical in determining the direction of evolution. In passing, we note that this general analysis would not be possible without the considerable mathematical and demographic achievements of Furstenberg and Kesten (1960) and Cohen (1977, 1979a,b), which form the underlying framework of our results.

In order to highlight the value and distinctiveness of our approach, consider Schaffer's (1974b) important attempt to understand life-history evolution in variable environments. He analyzed how dichotomous variation in an age-independent average litter size (B) or average adult survival rate (P) affects the geometric mean of the growth rates ($B + P$). If variability affects B, the optimal life history spreads reproduction over many ages (i.e., the life history is more iteroparous). This case includes the consequences of variable juvenile survival rates since B is the "effective litter size," a product of adult fertilities and juvenile survival rates (as is a ϕ_{ii} value). Conversely, if P is affected by variability, the optimal life history has more-concentrated early reproduction (i.e., is more nearly semelparous).

Schaffer's results are most usefully viewed as applying to a special kind of life

history in which the average effective litter size and age-specific survival rate are age-independent in a long lifetime (see Tuljapurkar 1982b, p. 162). However, his results are not general because the geometric mean he used does not equal the stochastic growth rate for other kinds of life history. Cohen (1977) has shown that such means do not predict the stochastic growth rate of age-structured populations in variable environments. This raises a key question: what results does our more general analysis produce that are not seen in Schaffer's special analysis?

Variance only in B corresponds to a life history in which all nonzero ϕ, values vary temporally but decline with age because of the fixed average survival rates (p_i). Hence, the results in figure 4 concerning declining life histories apply. So, for example, when $C = 2.0$, life history 7 (see table 2) has the highest value of a. When $C = 1.4$, life histories 4 and 8 have nearly identical a values. It is clear that variance in B does not necessarily select for dispersed reproduction.

Variance only in P corresponds to life histories in which ϕ_{ai} is nonzero but does not vary. All other ϕ_{ii}'s vary. Therefore, equations (4), (5), and (6), which assume that all ϕ_{ii}'s vary, do not apply. The effect of this difference for a given life history is to increase the coefficient of variation necessary to achieve a particular stochastic growth rate, but the qualitative results of the analysis remain unchanged. Hence, variance in P does not necessarily select for concentrated reproduction.

Our conclusion is that Schaffer's results do not carry over to more-general classes of life history.

Schaffer's results using geometric means have been criticized by Hastings and Caswell (1979), who noted that natural selection may maximize either the arithmetic mean or the geometric mean of a variable trait linearly affecting fitness. There are significant differences in the predictions of the theory depending on which mean is used (see their table 1). In response, Bulmer (1985) has correctly noted that the arithmetic mean is useful in a scalar model only if the fitnesses are independent over time (i.e., if there is density independence), whereas the geometric mean does not have this restriction. One need not resort to density dependence to justify the use of the geometric mean. Cohen (1979a) showed that a is the geometric mean of the overall rate at which individuals are contributed to the population at the next time interval. However, one cannot equate a to a simple arithmetic-mean rate of contribution because matrices do not generally commute. Commutativity is necessary for the analogue of equation (5) in Hastings and Caswell to hold for age-structured populations. Finally, it is clear that both the geometric and arithmetic means of the eigenvalues of the vital-rate matrices are not good predictors of a (Cohen 1977). Indeed, one can construct examples in which such means are negative when $a > 0$ (Tuljapurkar 1988).

Hastings and Caswell (1979) also noted that the direction of evolution differs depending on how variance affects a life-history trait. Consider survival rate to age 1, for example, having value p_{1t} at time t with mean p_1 and variance $s^2(p_{1t})$. Consider also a temporally variable force of mortality for age class 1, say μ_t, where $p'_{1t} = \exp(-\mu_t)$. Given the mean and variance of μ_t, one can then compute the resulting mean and variance of p'_{1t}, say, p'_1 and $s^2(p'_{1t})$. Statements about the consequences of variation in the survival rate (i.e., p_{1t} or p'_{1t}) are well defined in their respective contexts. However, unless $p_1 = p'_1$ and $s^2(p_{1t}) = s^2(p'_{1t})$, the two stochastic models must differ because "survival rate" and "variation" have dif-

ferent definitions. To compare their respective theoretical predictions requires only that one remember the distinct nature of the life-history traits involved. The models are in no sense contradictory.

An additional feature of biological note is that a is equal to an arithmetic average of the geometric-mean growth rates of individual sample paths of the process (e.g., Tuljapurkar 1982b, p. 157). Since the process is ergodic, the same decomposition can be applied to a single sample path divided into sequences of fixed length. This decomposition serves as a reminder that a single measure of population growth rate can have an arithmetic-mean and a geometric-mean character.

Goodman (1984) argued that iteroparity is advantageous in a variable environment because a long reproductive span reduces the disparity between the stochastic growth rate and the growth rate associated with the average Leslie matrix. This conclusion matches the results we obtain for certain types of random variation. It is important to note that Goodman's focus on the average Leslie matrix and on density dependence accounts for the generally distinct character of his results and ours.

Extensions

The results presented here are not, of course, a complete analysis of the dynamics of life-history evolution. At least two potentially important elements of a general theory are not directly included in this analytic framework. They are density dependence and "complex" genetics. We consider them in order.

Density-dependent interactions constitute a grab bag of biological phenomena. For example, N_t might be affected by density in a manner dependent on or independent of age. When the effect is independent of age, one can construct a model in which the population age structure has density-independent dynamics and a final population size adjusted by the product of all scalar density-dependent multipliers occurring in the sample path (Desharnais and Cohen 1986). Our results apply to a population obeying such dynamics. The more complicated (and more realistic) case of age specificity in sensitivity to density is not encompassed by our results. Such effects can, if appreciable, produce chaotic dynamics and could lead to a different picture of life-history evolution.

There is, however, another sense in which the linear dynamic system analyzed in this paper may describe the dynamics of some natural populations. Assume that the vital rates of a homogeneous population are such that it has no long-term tendency to increase or decrease, that is, that $a = 0.0$. Even so, the probability of passing an extinction boundary is 1.0 (Tuljapurkar and Orzack 1980, p. 332). Does inevitable extinction somehow invalidate this picture of life-history evolution? We think not, given present information concerning population longevity. The picture arising from these data (e.g., Schoener and Spiller 1987, fig. 2) is that local populations may have high "short-term" extinction probabilities (>50%), although some may survive for "a long time." Just such a distribution of extinction times is associated with our linear model. This can be seen by looking at the first-passage-time distribution for the Wiener process, which approximately describes the dynamics of total population size (Tuljapurkar and Orzack 1980; Lande and Orzack 1988). This distribution has the form of an inverse Gaussian distribution

(Cox and Miller 1965; Johnson and Kotz 1970). It is straightforward to show that, when $a \geq 0$, the cumulative extinction probability at a given time and the mode of the first-passage-time distribution are increasing and decreasing functions, respectively, of $\ln \lambda_0$. Assuming $a = 0.0$, an extinction boundary of, say, 10 individuals, and $\ln \lambda_0 = 1\%-2\%$, populations may have modal times to extinction that are relatively small ($\approx 50-100$ years). However, the distribution of first-passage times is such that populations may have long lifetimes relative to the typical value. For example, approximately 13.5% (4.38%) of the lifetimes are greater than 100 (1000) times the value of the mode. Hence, populations may survive for times commensurate with a time scale over which appreciable life-history evolution can occur ($\approx 10^4$ years?). Indeed, the moments of the first-passage-time distribution do not exist when $a = 0.0$ because some sample paths become extinct only after infinite time.

We use this argument to show that, in an abstract sense, linear population models in stochastic environments may provide a sufficient biological framework for understanding life-history evolution. Whether they are biologically complete can be resolved only with better information about the distribution of population longevity and the nature of population regulation. In the absence of such data, we regard statements stressing the exclusive necessity of density dependence (or for that matter, density independence) as statements of faith. More generally, we find it odd that asymptotic stability of population number (not seen in a density-independent model) is regarded as an essential feature of models of life-history evolution. Indeed, given the empirical observations that many populations are ephemeral in the "short term" and that all species are so in the "long term," one might regard instability as essential. We wonder why life-history theory should differ from many other areas of ecological and evolutionary theory in which stability is not regarded as necessary. Imagine a model of clade diversity with the assumption of stable species number or an analysis of genetic variation based on the assumption that a polymorphism must be stable! Clearly, stability of population number will be important for the analysis of life-history evolution in some populations. This does not imply, however, that linear models are biologically irrelevant. As our numerical example demonstrates, a linear model may be generally compatible with the available data about extinction probabilities of populations, just as it may be for species' longevity data (Levinton and Ginzburg 1984). A linear model may also serve as the best null hypothesis for explaining population extinction data and, thereby, allow one to determine whether density-dependent interactions do act to stabilize populations. We regard both types of models as biologically relevant and worthy of study.

The positive dependence of the cumulative extinction probability on $\ln \lambda_0$ when $a \geq 0$ also implies that a population with higher average vital rates (say, life history 1 relative to life history 9) has a higher probability of extinction after a fixed time, assuming equal stochastic growth rates. (For a related conclusion based on a different approach, see Holgate 1967.) Given that higher average vital rates might arise from selection within a population, this point illustrates that in this dynamic system the interaction between selection processes operating at different levels can be understood both qualitatively and quantitatively.

The genetic basis of the present analysis is one locus with two alleles. This is, of

course, unrealistic as a complete model for the genetic basis of life-history traits. However, Lande (1982) has shown in a constant-environment polygenic model that natural selection maximizes the intrinsic rate of increase of an age-structured population just as in the single-locus case (Charlesworth 1980). These results assume the existence of a stable age distribution. This assumption is almost always inappropriate in a variable environment except when the time scale for fluctuation is much longer than the time scale over which demographic equilibrium is attained. We note the Charlesworth and Lande results because we suspect that an analogous concordance of results may occur when polygenic models of life-history evolution in variable environments are investigated. Whether or not this surmise is correct, our results represent the beginnings of the general dynamic framework by which life-history evolution in changing environments can be analyzed.

Conclusions

Finally, to come full circle, one can appropriately ask how our results relate to Cole's paradox. His biological conclusion was that short-lived early-reproducing semelparous life histories should overrun the world. Why haven't they? We have two nonexclusive answers. Reasoning from the results in figures 7–9, it may be that the magnitude of environmental variability and the correlation structure of vital rates are such that this type of semelparous life history is often selectively disadvantageous. Reasoning from the results on extinction dynamics, populations with such life histories have higher extinction rates, if a values are equal and nonnegative. Determining the truth obviously depends on (1) better data about the magnitude of environmental variability experienced by natural populations, (2) better data about the temporal variability and correlation structure of life histories, and (3) better data about the extinction dynamics of different life histories. It is our hope that the present results provide a motivation for such empirical studies and demonstrate their necessity for future gains in the understanding of life-history evolution.

SUMMARY

A dynamic analysis is presented of the manner in which survival rates and reproductive schedules evolve in variable environments. This approach accounts for (1) age structure, (2) density-independent fluctuations in vital rates, (3) life histories of arbitrary length, (4) variance and covariance of vital rates, and (5) an incorporation of genotypic differences in life history. The results indicate that there is no general advantage to a more iteroparous life history in a variable environment and that the direction of evolution depends on the absolute amount of environmental variation and the correlation structure of the vital rates. Analysis of "indifference" curves also indicates that there is considerable potential for neutral evolution with respect to life history, given genotypic differences in environmental sensitivity. We suggest two nonexclusive partial answers to Cole's paradox. One is that the magnitude of environmental variability and the correlation structure of vital rates cause short-lived, early-reproducing semelparous life histories to be disadvantageous within populations. The other answer is that, if

stochastic growth rates are nonnegative, such life histories have higher extinction rates when their stochastic growth rates equal those of more-iteroparous life histories, given that all the life histories share a constraint on the average life history.

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