SEASONALITY AND PATTERNS OF NATURAL SELECTION FOR LIFE HISTORIES

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Meterological variation throughout the year entails climatic seasonality of temperature, humidity, rainfall, ocean currents, cloud cover, and wind patterns. These factors in turn create temporal variation in various components of the environment for most populations of organisms. One of the most significant and widespread aspects of seasonality is variation in the availability of an essential resource, e.g., food, water, nutrients, or energy (e.g., Annegers 1973; Asplund 1967; Bobek et al. 1974; Croat 1974; Fleming and Hooker 1975; Fogden 1972; Fretwell 1972; Karr 1976; Smith 1971; Emmel 1976, chap. 10). In this paper I provide a simple model which considers the effect of seasonality in resource availability on the evolution of life histories, especially in terms of r- and K-selection.

A great deal of ecological theory has focused on the classic Lotka-Volterra population equation for single species population growth, which may be written $dN/Ndt = r - (r/K)N$, where N is population size, r is the intrinsic growth rate, and K is the carrying capacity. MacArthur (1972), Roughgarden (1971), King and Anderson (1971), Pianka (1972), and others have studied this equation as a model of fitness where phenotypes are affected differently by density, i.e., different rates of $-r/K$. If two density-dependent functions intersect, the phenotype with a higher r possesses superior Malthusian fitness in low-density environments (r-selection), whereas the phenotype with the largest carrying capacity, K, has greatest fitness at high densities (K-selection).

Pianka (1970) and Southwood et al. (1974) have suggested that various life-history characteristics may be associated with r- and K-selection. At least three aspects of the Lotka-Volterra r- and K-selection model tend to limit its generality and potential for interpretation in terms of life-history evolution.

1. The linearity of the density-dependent function is not based on empirical observation. Several authors (Gadgil and Bossert 1970; Gadgil and Solbrig 1972; Hassell 1975; Pianka 1972) have suggested that a concave function is more appropriate.

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2. A variety of density-dependent mechanisms may be responsible for density-dependence, e.g., predation, competition, or emigration (Wilson 1975). Clearly an evolutionary response to density-dependent predation will probably be very different than adapatations to various levels of resource availability. MacArthur (1972) emphasized a gradient of decreasing resource availability as density increases.

3. Seasonality has been considered only as an agent imposing density-independent mortality (Cody 1966; Roughgarden 1971; King and Anderson 1971). One of the predominating aspects of seasonality in many populations is seasonal variation in the availability of or ability to exploit essential resources. I present a nonlinear model of resource density-dependence which incorporates seasonal variation in the availability of a limiting resource.

"In analyzing any complex system, the crucial decision lies in the choice of relevant variables" (Maynard Smith 1974, p. 3). I suggest that when considering evolution in seasonal environments the current theory does not contain enough relevant variables. My application of the model presented here to "real world" examples is intended as a purely heuristic approach. The precision of this model in describing life-history characteristics probably decreases as organism complexity increases. On the other hand, I feel that these applications yield insight and provide an improvement of understanding of life histories over that which has been gleaned from the Lotka-Volterra model.

THE MODEL

Population growth is a function of a large number of extrinsic factors: $dN/dt = f(N,X_i,P,Q,I,F,T , . . .)$, where N is population density, X_i is the per capita abundance of a potentially procured limiting resource i, P is the predation rate, Q is the migration rate, I is interspecific interference, F is feeding efficiency, and T is the length of the season relative to the length of the life history or breeding period of an organism (see Hutchinson 1965). The significance of time lags and T will be treated in a later paper; much of the existing literature is reviewed by May (1976), Southwood (1976), and Thompson (1975). This paper will emphasize the first two components of population growth, density and resource availability, while all other components, P, Q, I, F, T, . . . are assumed constant.

For a wide variety of organisms, empirical observations repeatedly demonstrate that per capita population growth rate is a concave function of per capita resource availability, X_i (Cushing 1975; Droop 1968; Eppley et al. 1969; Henson 1968; Monod 1950; Titman 1976). This function is often closely described by a modification of the von Bertalanffy equation,

$$\frac{1}{N} \frac{dN}{dt} = r^*[1 - e^{-z(X_i-D)}], \tag{1}$$

where r^* is the maximum population growth rate when resources are unlimiting, D is the resource demand of an organism, i.e., the mean per capita resource availability level required to maintain a constant population size, and z is a constant for each phenotype which determines the initial slope between per capita growth rate

and X_i. Unfortunately, inadequate data are available to test the applicability of this model to large organisms, but data presented by Kilham (1975) for the diatom, *Asterionella formosa*, provide close concordance.

Changes in resource availability are a function of population density and extrinsically determined environmental variation through time, i.e., $dX_i/dt = f(N,t)$. For mathematical simplicity I will consider X_i to be a linear function of N, where resource availability decreases at a constant rate c as density increases, or $N = a - cX_i$. Substituting into equation (1), a concave density-dependent function is described asymptotic to r:

$$\frac{1}{N}\frac{dN}{dt} = r\left[1 - \exp\left(-z\frac{K-N}{c}\right)\right] \tag{2}$$

This equation closely defines the density-dependent function of the form which Gadgil and Bossert (1970, fig. 1) suggested intuitively. Defining N as a nonlinear function of X_i need not destroy the general concavity of equation (2).

If $m^* = dN/Ndt$ is used as a measure of the fitness of phenotype j (*sensu* Emlen 1975; Fisher 1958), functions of fitness dependent upon the availability of the ith resource may be defined

$$m_j^* = r_j^*[1 - e^{-z_j(X_i - D_j)}] \tag{3}$$

where r_j^*, z_j, and D_j are phenotype-specific constants as defined above.

Association of relative values for r_j^*, z_j, and D_j with specific life-history characteristics is often possible. Figure 1 describes four possible life-history dichotomies. Figure 1A illustrates two phenotypes, where phenotype 1 possesses superior r^* but also requires more resources to maintain a stable population. If i is food, an example might be a simple difference in fecundity where investment in more offspring creates greater resource demands.

In dichotomy B both phenotypes have similar resource demands. When resources are abundant phenotype 1 has a higher rate of increase r^*, but when resources are inadequate for maintenance phenotype 2 decreases less rapidly than phenotype 1. An interesting example might be the allocation of nutrient and energy resources toward the production of fat bodies or somatic tissue (rather than toward reproductive effort), which enhances survivorship during periods of resource shortage.

Figure 1C illustrates two population growth rate functions which are similar to B, but where phenotype 2 possesses greater resource demands. Again r^* and z are larger for phenotype 1. Cell size in marine phytoplankton appears to provide a possible application of this dichotomy. Eppley et al. (1969) present data which demonstrate that z values are inversely proportional to cell size in several species of phytoplankters. Larger cells usually divide at a slower rate than small ones and also require more resources for growth and maintenance. A similar heuristic analogy may be body size in homeothermic vertebrates. A larger individual requires absolutely more resources for maintenance since $M = bW^{0.75}$, where M is oxygen consumption in milliliters O_2 per hour and W is body weight in grams (Schmidt-Nielson 1975). Also, since large individuals may possess longer de-
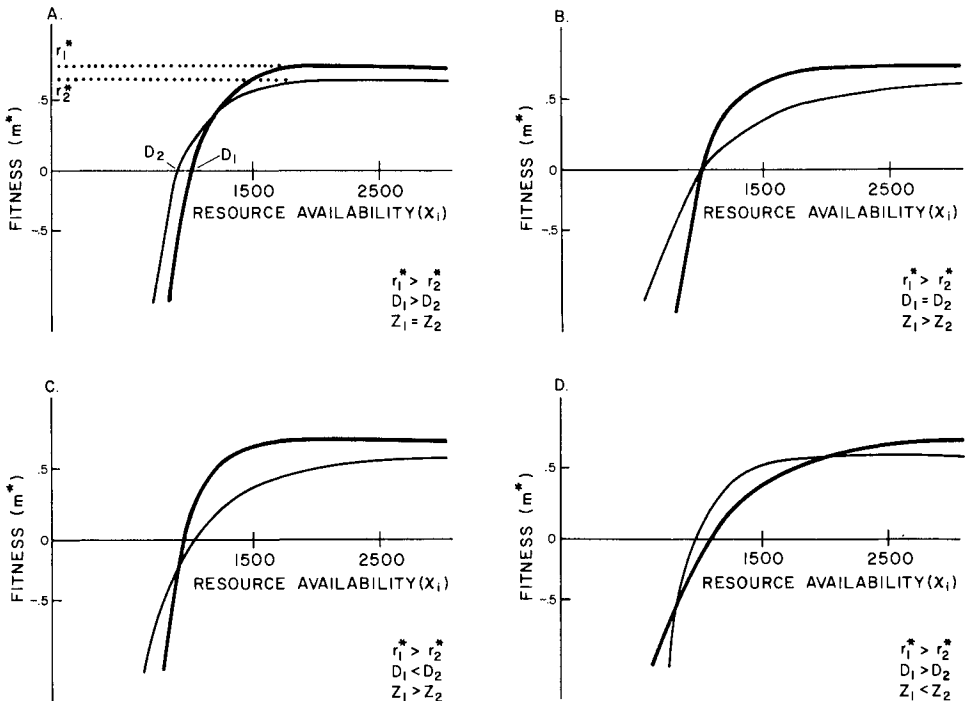
FIG. 1.—Growth rate curves for four life-history dichotomies (A,B,C,D). The heavy line represents phenotype 1, the light line phenotype 2. The units are arbitrary, values represent those used in simulations; see text.

velopmental periods or lower age-specific reproductive effort, they often have a lower potential rate of increase, r^* (Bonner 1968).

Lastly, dichotomy D as shown in Figure 1D describes phenotype 1 as possessing larger values of r^* and D, but with z lower than for phenotype 2. Phenotype 1 might possess rapid somatic growth to a larger size with concomitant high resource demands (i = food, nutrients). A rapid growth rate may confer a decreased age at first breeding (e.g., mountain sheep [Geist 1971] or fish [Alm 1959]), increased age-specific fertility rates (e.g., oviparous fishes [Weatherley 1972], urodeles [Tilley 1973], and reptiles [Tinkle 1969]), or some other function which enhances r^*. Nevertheless, the larger age-specific size may still provide advantages to survivorship during periods of resource shortage as in dichotomy C.

EVOLUTION IN CONSTANT ENVIRONMENTS

In an environment with unchanging levels of resource availability, an argument similar to the r- and K-selection model may be constructed for dichotomies A and D, assuming approximate niche identity of phenotypes (thus $K_1 = \alpha_{12}K_2$, $K_2 = \alpha_{21}K_1$ where α is an intraspecific heterotypic competition coefficient [see Emlen 1975]). When resources are abundant phenotype 1 wins, and when resources are

barely adequate to maintain population growth phenotype 2 possesses superior fitness. Applications of this model have been suggested as determining competitive outcomes between species of aquatic bacteria (Jannasch 1967) and algae (Liere et al. 1975) grown in chemostat cultures. Dichotomies A, B, and D permit polymorphism if $X_i = D_1 = D_2$. In dichotomy C, phenotype 1 wins for all values of X_i adequate to maintain the population. Similar to the r- and K-selection model, the graphical models in figure 1 suggest that natural selection favors high r^* when resources are abundant and low D in resource-limited populations.

SEASONALITY

As mentioned above, resource availability often changes seasonally in some extrinsically deterministic manner, often a result of meteorological variation throughout the year. Figure 2a depicts a seasonal regimen of resource availability with symmetrical sine-wave variation around a mean $\bar{X}_i$. Figure 2b illustrates a seasonal pattern with a short growth period during the summer. Seasonal patterns in X_i may assume an infinite variety of distributions. Assuming that the shape of the seasonality function remains constant, a seasonality index S may be defined

$$S = n^{-1} \int_{t=0}^{n} \frac{\bar{X}_i(t) - \bar{X}_i^2}{\bar{X}_i} \, dt \tag{4}$$

for n complete seasonal cycles in time t. This simply describes the normalized deviation from the mean (without the stochastic implications of the coefficient of variation).

Natural selection will favor those phenotypes with the greatest fitness averaged over a continuous time interval. Thus when fitness is largely a function of resource availability the mean fitness of phenotype j may be defined as

$$\overline{m_j^*} = n^{-1} \int_{t=0}^{n} r_j^* \{1 - e^{-z_j[X_i(t) - D_j]}\} dt. \tag{5}$$

If deterministic variation occurs over periods greater or less than one annual cycle, n may define the end of any number of complete cycles.

A computer expedited the simulation of the effect of various seasonal regimes on the fitness of each phenotype for the dichotomies in figure 1. The effect of simple sine-wave seasonality on the fitness of the phenotypes in dichotomy C is illustrated in figure 3. Note that phenotype 2 possesses superior positive fitness at high seasonality levels, whereas it had fitness inferior to phenotype 1 in a constant environment. Different seasonality schedules, e.g., as in figure 2b, produce qualitatively similar results, simply scaling the axes. By considering a continuous time model of fitness, both losses as well as growth are essential determinants of phenotypic fitness. Thus, gains attained during a summer growth period offer little selective advantage if the losses are excessive during the winter. The problem is analogous to maximizing long-term monetary gains in economics.

The effect of seasonality varies with $\bar{X}_i$ in the fashion shown by figure 4. As $\bar{X}_i$ increases for a constant S, the limiting effect of a shortage in X_i is never realized.
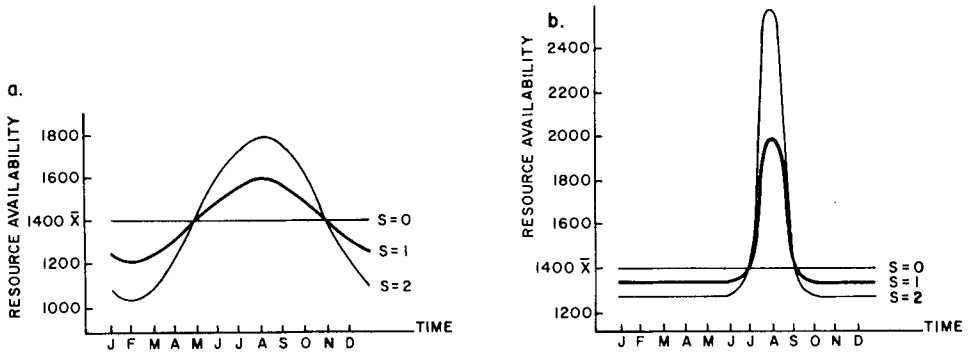
FIG. 2.—Seasonal functions of resource availability for two seasonality regimens. Seasonality, S, increases with deviations from a mean. a, Sine-wave variation with a period of one year; b, A more complex function with a short summer period of high resource abundance. The wavelength of various regimes is constant, with seasonality affecting only the amplitude of fluctuations.
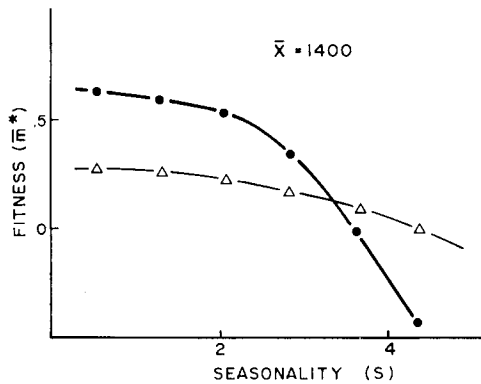

FIG. 3.—The effect of seasonality on the fitness of phenotype 1 (●) and phenotype 2 (△) in dichotomy C. Note that phenotype 2 possesses superior positive fitness for a range of high seasonality levels.
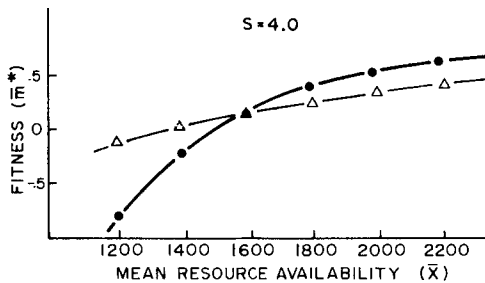

FIG. 4.—The relationship between mean resource availability and fitness of phenotypes 1 (●) and 2 (△) of dichotomy C for a constant seasonality level. This suggests that the effects of seasonality on relative fitness cannot be realized if $\overline{X}$ is so large that resources are seldom limiting.
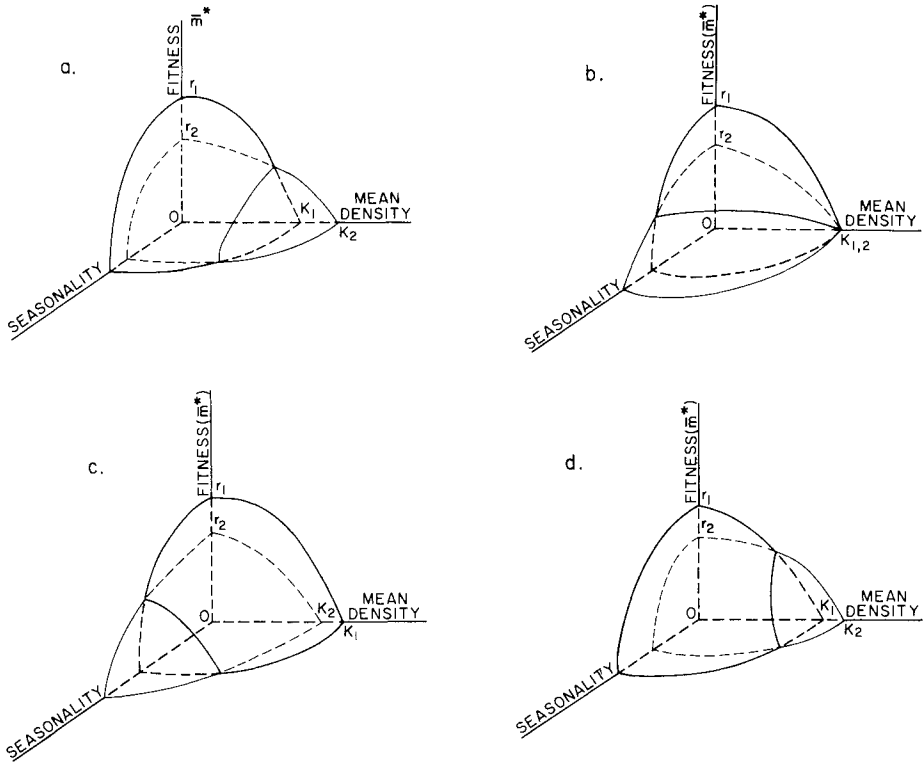
FIG. 5.—The relationship between mean fitness ($\overline{m}^*$), mean population density ($\overline{N}$), and seasonality (S) for four life-history dichotomies. The surface outlined by the heavy lines represents phenotype 1 and the light lines phenotype 2 in each of the corresponding dichotomies in fig. 1; e.g., fig. 5a corresponds to dichotomy A, 5b to B, etc.

For large X_i variance in X_i must be concomitantly very large if there is to be any temporal restriction in the growth rate of a population.

In figure 5 the interrelationships between fitness, resource-limited density-dependence (see eq. [2]), and seasonality are depicted by three-dimensional diagrams for each of the four dichotomies in figure 1. In all cases fitness decreases as seasonality becomes high, as does the carrying capacity, K. Harsh periods of low resource availability lower the carrying capacity of a given environment, but by reducing competition increase the resource availability for the survivors during the periods of resource abundance.

In Figure 5a phenotype 2 (e.g., small clutch or litter size) is favored in high density (low resource availability) environments with low seasonality. In low density or highly seasonal environments, phenotype 1 (e.g., large clutch or litter size) dominates. This result provides interesting semblance with Cody's (1966) observation that smaller clutch sizes in birds are found in environments with low seasonality and high density, whereas races of birds breeding in more seasonal regions (e.g., high latitudes, high altitudes, continental vs. coastal, savanna vs. rain forest) exhibit larger clutch sizes. Lord (1960) observed a similar relationship

between latitude and mammalian litter size. Ashmole (1961) and Ricklefs (1977) have suggested that the flush of food resources experienced during the breeding season in highly seasonal climates may permit the observed high reproductive effort.

Figure 5*b* may help in understanding the evolution of nutrient or fat storage mechanisms in many taxa. For example, Benson et al. (1972), Lee (1975), and Lee et al. (1971) discovered that marine zooplankton in seasonal environments allocate considerable resources of nutrients and energy into wax ester storage which is later used slowly during periods of resource shortage. In less seasonal regions, zooplankton storing wax esters are seldom found, and potential rates of population increase are greater as resources may be more rapidly converted into offspring. Similarly, Parnas and Cohen (1976) discuss the optimal "strategy" for the metabolism of reserve materials for microorganisms.

Dichotomy C was suggested above to provide a possible analogy to a food-limited body size dichotomy in homeotherms. Figure 5*c* suggests that large size will be favored in seasonal environments, but not in constant ones. Brodie (1975) observed precisely this phenomenon in cetaceans. Several geographic patterns of body size variation suggest that body size is larger in more seasonal regions, but many of these patterns cannot be explained by the classic thermoregulatory explanation of Bergmann (1847). It is probably more than a coincidence that precisely the same correlates have been observed with homeotherm body size as Cody (1966) observed for avian clutch size, i.e., larger size with increasing latitude (Rensch 1960; James 1970) and altitude (Mayr 1944; Rummler 1938; Schafer and Schauensee 1939; Traylor 1950), continental versus coastal (Palmer 1937; Pitelka 1951; Wolters and Clancey 1974), and savanna versus rain forest at the same latitude (Clancey 1974; Bouliere 1973). McNab (1971) criticized the traditional thermoregulatory explanation of Bergmann's rule, but unfortunately never discussed the potential importance of a larger body size in enhancing survival through periods of resource shortage (see Morrison 1960; Brodie 1975; Downhower 1976). Large size may be envisioned as effectively buffering the seasonality of the environment, and may be important in determining patterns of body size variation in taxa other than homeotherms (Lindsey 1966; Ray 1960; Thomas 1968).

Seasonality is probably an important aspect accounting for size variation in the fossil record. Larger forms often existed during highly seasonal glacial versus interglacial periods (Kurten 1968) and were often associated with savanna or grassland steppe habitats; modern counterparts are very seasonal (Guthrie 1968; Guilday 1967).

Figure 5*d* suggests that slow growth is favored in environments with high densities or low resource availability. Slow development is adaptive under conditions of low resource availability as fewer resources are required for normal growth and maintenance (Ealey 1967) and the probability is lower that limiting resources will be overexploited (Parsons 1968). White (1974) observed that nestling tropical birds grow more slowly than those from more seasonal environments, even when resources are adequate for more rapid growth. Ricklefs (1972) observed that somatic growth rates in birds usually increase with increased availability of food for the young during the growth season. In highly seasonal environ-

ments the short high-quality growth season favors those individuals with the highest growth rates, which are capable of securing the maximum somatic gain to enhance survival through the forthcoming period of resource shortage. Seasonality reduces K, and thus should result in reduced competition and increased resource availability for the survivors during the growth period. Further gains may be realized through the increased fecundity often associated with rapid growth to a large size, e.g., in fishes and urodeles.

It should be apparent from these results that z is a very important variable determining fitness in seasonal environments. The rate at which populations will decrease during periods of resource shortage is largely determined by the magnitude of z. Consequently it may well be that natural selection is acting principally on z in regions experiencing pronounced seasonality or other types of resource shortages. As I have discussed above, life-history characteristics most likely associated with low z values are large body size and resource storage mechanisms, but also a variety of more specialized functions such as hibernation, aestivation, and resource storage behavior.

The outcome of natural selection for various life-history characteristics depends not only upon the shape of the life history–specific population growth functions, but also upon the form of the seasonality function. My model suggests that the severity of the resource shortage period may often be a very important selecting component of the environment. This observation is compatible with the maximin model of Templeton and Rothman (1974), where the greatest fitness is realized by the genotype that maximizes minimum fitness. This notion is only valid in environments where selective forces of a harsh period dominate. A continuous time model of inclusive fitness (e.g., eq. [5]) must weigh the gains during good times against the losses during the bad times. This model of evolution by selection on average fitness is again distinct from Levins' (1968) notion of adaptation to average conditions (see discussion by Templeton and Rothman 1974).

STOCHASTIC VARIATION IN RESOURCE AVAILABILITY

Pianka (1970), MacArthur and Wilson (1967), and Southwood et al. (1974) emphasize the importance of environmental predictability in determining r- versus K-selection, as populations in unpredictable environments are probably exposed to greater density-independent mortality. Indeed, climatic predictability usually decreases with seasonality (Trewartha 1954; see Slobodkin and Sanders 1969 for discussion).

I incorporated normally distributed random variation in resource availability into the continuous time model of fitness (eq. [5]). The results of discrete difference equation approximations for a type C life-history dichotomy are presented in table 1. These data follow several of the same general patterns as the effect of seasonality, i.e., (1) fitness for both phenotypes decreases as predictability decreases. This was also shown, but for different models, by Leigh (1975) and Boyce (1977). (2) The carrying-capacity, where $dN/dt = 0$, decreases as the predictability of resource availability decreases. (3) The phenotype with the lowest rate of decrease during the worst conditions possesses superior fitness in environments

TABLE 1

RESULTS OF MONTE CARLO SIMULATIONS ILLUSTRATING EFFECT OF NORMALLY DISTRIBUTED
RANDOM VARIATION IN RESOURCE AVAILABILITY ON FITNESS

	$\bar{X} = 1,400$			$\bar{X} = 1,800$		
	$S = 1$	$S = 2$	$S = 4$	$S = 1$	$S = 2$	$S = 4$
$\sigma = 25$						
$\bar{m}_1^*$	.6249	.5695	−.1963	.7306	.7068	.4022
	±.0091	±.0751	±.1210	±.0019	±.0036	±.0473
$\bar{m}_2^*$	.2702	.2305	.0628	.4621	.4333	.2899
	±.0108	±.0170	±.0297	±.0044	±.0059	±.0147
$\sigma = 50$						
$\bar{m}_1^*$	.6206	.5261	−.2114	.7299	.7043	.4003
	±.0209	±.0642	±.2010	±.0038	±.0126	±.1144
$\bar{m}_2^*$	.2659	.2263	.0554	.4613	.4324	.2885
	±.0213	±.0260	±.0612	±.0085	±.0103	±.0271
$\sigma = 100$						
$\bar{m}_1^*$	.6110	.4970	−.3340	.7268	.7024	.3601
	±.0507	±.1217	±.4673	±.0071	±.0263	±.2270
$\bar{m}_2^*$	.2670	.2206	.0477	.4562	.4288	.2877
	±.0484	±.0488	±.0935	±.0196	±.0292	±.0609

NOTE.—The values represent the mean fitness ($\bar{m}_i^* \pm 1$ SD, $n = 30$) of phenotypes 1 and 2 of a type C life-history dichotomy at seasonality levels (S) 1, 2, and 4 (see eq. [5]); σ = standard deviation in $X_i(t)$; $\bar{X}$ = mean resource availability.

with the lowest predictability in resource availability (*sensu* Templeton and Rothman 1974). (4) The variance in fitness increases with the variance and seasonality in resource availability.

In the theory of stochastic processes, the first two observations are as predicted by Jensen's inequality (Karlin and Taylor 1975); i.e., for a concave function the expected value of the function Φ of a random variable is always less than or equal to the expected value of the deterministic case, $E[\Phi(x)] \leq \Phi[E(x)]$.

May (1975*a*, 1975*b*) stated that r-selected organisms view their environment as unstable and unpredictable, and selection favors large r to exploit the transient "good times." However, in an environment that is unpredictable natural selections is just as likely to favor those genotypes that sacrifice high r to allocate resources to functions which enhance survival through the unpredictable "bad times." Schaffer (1974*a*) achieved a similar result using a different rationale when he showed that increased environmental uncertainty need not necessarily select for increased reproductive output.

DISCUSSION

The effect of seasonality on the type C dichotomy provides a distinct exception to the r- and K-selection model (see fig. 5*c*). Note that phenotype 2 possesses both a lower r and a lower K than phenotype 1, and thus is neither an r- nor a K-strategist (*sensu* MacArthur 1972; Pianka 1970, 1972), but nevertheless possesses superior fitness in seasonal or unpredictable environments. Large body size

in homeotherms is generally associated with low fecundity, long developmental periods, a delayed age at first reproduction (Bonner 1968) and thus a low intrinsic rate of increase, r. Larger individuals require more resources for maintenance and thus, if resource-limited, cannot sustain higher population densities, K, on a given set of resources. Rather than being a response to K-selection as claimed by Pianka (1970), Southwood (1976), and Southwood et al. (1974) large body size, especially in homeotherms, may often be the result of selection imposed by seasonality.

Age-specific mortality aspects of seasonal environments may also enhance selection for large body size in iteroparous organisms. As noted above, climatic predictability is often inversely related to seasonality. If this consequently lowers the probability of successfully reproducing in any one year, selection will favor individuals exhibiting low age-specific reproductive effort and allocating more resources to functions, such as body size, which can enhance survival for future reproductive attempts (Hirshfield and Tinkle 1975; Schaffer 1974a, 1974b).

Several recent discussions of life-history evolution have taken a demographic approach (Schaffer 1974a, 1974b; Taylor et al. 1974; Charlesworth 1973). This approach is more precise for handling age-specificity patterns, but has yet to adequately incorporate specific environmental limitations such as seasonal variation in resource availability. I maintain that seasonal patterns of demography and resource limitation are impossible to interpret solely in terms of density-dependence versus density-independence ($sensu$ Roughgarden 1971; King and Anderson 1971; Pianka 1970; Gadgil and Solbrig 1972). More important is whether environmental seasonality affects the organism's life history in a genotype-dependent manner. Whittaker (1975), Southwood (1977) and Wilbur et al. (1974) have already suggested additional axes to the r-K model. Hopefully, with precise analyses of the density-dependent phenomena of competition, predation, and migration the concepts of r- and K-selection will not degenerate into arguments of "worthless semanticism" as suggested by Dawson (1975).

SUMMARY

I present a model to investigate the effects of density-dependent resource availability on per capita population growth rate. By considering a continuous time model of inclusive fitness, population losses as well as growth are essential determinants of phenotypic fitness. The outcome of natural selection for various life-history characteristics is dependent upon not only the shape of the life history–specific population growth curves, but also upon the form of the seasonality function. As the magnitude and length of a resource shortage period increases, the rate of decrease becomes a more important component of fitness.

Seasonality is often characterized by (1) a period of population decrease, when natural selection favors functions which minimize somatic or embryonic mortality, and (2) a period of high resource availability when high somatic and gametic productivity are favored. Assuming that mean resource availability remains constant, seasonally deterministic and/or random variation in the availability of an essential resource lowers mean fitness and carrying capacity. Life histories differ considerably in adaptedness to various levels and seasonal fluctuations in re-

source availability. Clearly life histories must assume a compromise between "good" and "bad" times.

In resource-limited populations, large body size in homeotherms represents an example of an evolutionary "strategy" which can be neither r- nor K-selected. The usual low fecundity and late maturity of large homeotherms establishes a low r, but larger individuals require more resources for maintenance and thus cannot sustain higher carrying capacities on a given set of resources. Seasonality appears to be a very important factor in the evolution of large body size, especially in homeothermic vertebrates. Seasonality is also suggested as an important factor in the evolution of (1) fat and resource storage mechanisms, e.g., wax ester production in marine zooplankton, (2) geographic variation in clutch or litter size, and (3) rapid seasonal somatic growth patterns.

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