fluids were mainly glucidic (a mixture of glucose, vitamins, salts, and a commercial amino acid mixture, Trophysan, yielding 1.0 kcal/ml), and some recent success was obtained with a lipid emulsion (Trivé 1000). The results are similar for all solutions and have thus been combined in the data presentation.
7. Body weight is a convenient index of energy balance, but we do not imply it is a regulated variable. The intravenous intakes were controlled almost immediately despite considerable weight loss for the first 1 to 2 weeks, and decreasing weight did not significantly augment the intake. Set point concepts for body weight are unnecessary here, as elsewhere [for example, Booth (*3*); J. W. Peck, in *Hunger—Basic Mechanisms and Clinical Implications*, D. Novin, W. Wyrwicka, G. Bray, Eds. (Raven, New York, 1976), pp. 297–311].
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Evolution in a Time-Varying Environment

Abstract. *A simple model of competition in a time-varying environment was developed and used to discuss the evolution of life-history strategies.*

The concept of *r* and *K* strategies has been popular with ecologists for some time (*1–6*). The concept dates to a suggestion by Dobzhansky (*1*) that populations in frequently disturbed environments will tend to have higher maximum rates of increase *r* than will populations whose densities are more nearly constant. Conversely, MacArthur (*2*) showed that in undisturbed environments phenotypes which can maintain denser equilibrium populations (that is, those with higher "carrying capacities" *K*) will be selectively favored. The idea that species can be classified in terms of their positions along an *r-K* continuum was first proposed by MacArthur and Wilson (*3*). This idea has since become the subject of considerable debate (*4–8*).

We first develop a simple model of competition in a time-varying environment. This model extends the Volterra (*9*) competitive exclusion proof to a certain class of time-dependent environments (*10*). We then use this model in discussing the utility of *r-K* theory (*3–6*).

Consider a set of *m* populations growing according to the equations

$$\frac{1}{N_i}\frac{dN_i}{dt} = r_i - \gamma_i F(N_1,\ldots,N_m) - f_i(t) \qquad (1)$$

for $i = 1,\ldots,m$. Here N_i is the density of population (haploid phenotype) i, r_i is its maximum rate of increase, γ_i is a positive constant, and t is time. All species are limited by the same "limiting factor" $F(N_1,\ldots,N_m)$ (*11*). The function $F(N_1,\ldots,N_m)$ is assumed to be an increasing function of the N_i, with $F(0,\ldots,0) = 0$. The function $F(N_1,\ldots,N_m)$ summarizes the effects of population densities on population growth rates; the values of the γ_i reflect the sensitivities of the various phenotypes to these density effects. The functions $f_i(t)$ are externally imposed, time-varying rates of density-independent mortality (*12*).

We inquire as to which phenotype is most fit. In other words, we ask: After a long time has elapsed (mathematically, as $t \to \infty$), will one phenotype come to predominate? And if so, which one?

A straightforward extension of the Volterra (*9*) competitive exclusion proof yields the answer. Consider two phenotypes growing according to Eq. 1, which can be rearranged as

$$\frac{1}{\gamma_1}\left[\frac{1}{N_1}\frac{dN_1}{dt} - r_1 + f_1(t)\right] = -F(N_1,\ldots,N_m)$$

$$\frac{1}{\gamma_2}\left[\frac{1}{N_2}\frac{dN_2}{dt} - r_2 + f_2(t)\right] = -F(N_1,\ldots,N_m) \qquad (2)$$

Since the right-hand sides of these equations are equal, Eq. 2 can be combined and rearranged to yield

$$\frac{dN_1}{\gamma_1 N_1} - \frac{dN_2}{\gamma_2 N_2} = \{[r_1 - f_1(t)]/\gamma_1 - [r_2 - f_2(t)]/\gamma_2\}\, dt$$

integration of which from time 0 to time τ yields

$$\frac{N_1^{1/\gamma_1}(\tau)}{N_2^{1/\gamma_2}(\tau)} = \frac{N_1^{1/\gamma_1}(0)}{N_2^{1/\gamma_2}(0)} \times \exp\left\{\left[r_1 - \frac{1}{\tau}\int_0^\tau f_1(t)dt\right]/\gamma_1 - \left[r_2 - \frac{1}{\tau}\int_0^\tau f_2(t)dt\right]/\gamma_2\right\}\tau \qquad (3)$$

We now define the average values $\bar{f}_i$ of the removal functions $f_i(t)$ by

$$\bar{f}_i \equiv \lim_{\tau \to \infty} \frac{1}{\tau}\int_0^\tau f_i(t)dt \qquad (4)$$

If the removal function is periodic, $\bar{f}_i$ is the average value of this function over one time period. Alternatively, if $f_i(t)$ is determined by some stochastic process, then $\bar{f}_i$ is viewed as the expected value of $f_i(t)$ over a randomly chosen interval (or at a randomly chosen point). In any case, we assume that the limits in Eq. 4 are well defined.

Substituting Eq. 4 into Eq. 3, we find that as $\tau \to \infty$

$$N_1^{1/\gamma_1}/N_2^{1/\gamma_2} \to \infty$$

if

$$(r_1 - \bar{f}_1)/\gamma_1 > (r_2 - \bar{f}_2)/\gamma_2$$

and

$$N_1^{1/\gamma_1}/N_2^{1/\gamma_2} \to 0$$

if

$$(r_1 - \bar{f}_1)/\gamma_1 < (r_2 - \bar{f}_2)/\gamma_2$$

The proof is extended to include all phenotypes by considering them pairwise (*9*). As $\tau \to \infty$, that phenotype with the largest value of

$$(r_i - \bar{f}_i)/\gamma_i \qquad (5)$$

will become infinitely more common than any other phenotype. Since the total density of all phenotypes must remain finite, only the most favored phenotype will be retained at substantial densities (provided $r_i > \bar{f}_i$ and $N_i(0) \neq 0$ for that phenotype); all other phenotypes must approach extinction (*13, 14*).

Equation 5 provides a useful focus for discussing the utility of *r-K* theory (*3–6*). We first identify

$$F(N_1,\ldots,N_m) = \sum_{i=1}^{m} N_i$$

the total density of all phenotypes, and $\gamma_i = r_i/K_i$, where K_i is the carrying capacity of phenotype i (*15*). With this identification, which transforms Eq. 1 into time-dependent logistic equations (*2, 3*), we see from Eq. 5 that the phenotype with the largest value of

$$K_i(1 - \bar{f}_i/r_i) \qquad (6)$$

will replace all others.

Assume now that the various phenotypes do not differ in their susceptibility to externally imposed mortality, so that $\bar{f}_i = \bar{f}$ for all i. Assume further that there exists some trade-off between the ability to reproduce at high population densities and the ability to reproduce at low densities. That is, assume that if phenotype A has higher fitness than phenotype B in one density range, then A will be less fit than B in the opposite density range. As a concrete example, let the admissible pairs of values of r_i and K_i for the various phenotypes lie on the line defined by

$$r_i/r_{\max} + K_i/K_{\max} = 1$$

where $r_{\max}$ and $K_{\max}$ are the largest possible values of r_i and K_i, respectively. In this case, the best possible (optimal) phenotype will have values of r_i and K_i given by

$$r_{\mathrm{opt}}/r_{\max} = (\bar{f}/r_{\max})^{1/2}$$
$$K_{\mathrm{opt}}/K_{\max} = 1 - (\bar{f}/r_{\max})^{1/2}$$

This example illustrates the posited trend (*1–3*), that in harsh (high $\bar{f}$) environments, a large value of the intrinsic rate of increase r will be favored. Conversely, large values of K will be favored in benign (low $\bar{f}$) environments.

Such an approach is a consistent extension of standard *r-K* theory (*3–6*). The emphasis is on the trade-off between fitness in rarefied environments (r selection) and fitness in saturated environments (K selection). The choice of an *r-K* parameterization (that is, choosing to consider Eq. 6 rather than Eq. 5 as the basic relationship) focuses our attention on this one trade-off.

Other trade-offs are also taking place, however. For example, if we write $r_i = b_i - d_i$, where b_i is the birth rate and d_i the death rate in the most favorable rarefied circumstances (*12*), and substitute this relationship into Eq. 5, we find that the phenotype with the largest value of

$$(b_i - d_i - \bar{f}_i)/\gamma_i \qquad (7)$$

will replace all others.

Equation 7 yields a different perspective on what is evolutionarily important. In the *r-K* parameterization (Eq. 6), the $\bar{f}_i$ were assumed to be given, externally imposed death rates. But Eq. 7 emphasizes the trade-off between birth rate b_i, total average death rate $d_i' = d_i + \bar{f}_i$, and a parameter γ_i which reflects sensitivity to density effects. This parameterization focuses on the fact that the magnitudes of the $\bar{f}_i$ may not be characteristics of environment alone, but rather are characteristic of species-environment interactions. Desert annuals and cacti employ strikingly different life-history strategies, even though faced with the same physical environment.

The obvious importance of the trade-off between b_i and d_i' led Hairston *et al.* (*7*) to suggest that "*b* and *d* selection" may be more fundamental than "*r* and *K* selection." Pianka (*5*) responded that the use of such a conceptual scheme would tend to mask the importance of density effects. Both positions have merit; what they ultimately show, however, is that no two-parameter trade-off scheme can be satisfactory in all cases. Trade-offs will occur simultaneously among fecundity and mortality rates at low population densities, the sensitivity of fecundity and mortality rates to density, resistance to a harsh environment or to predators, adaptation to the pattern of fluctuations (*16*), and other traits which affect individual fitness; which of these trade-offs are most important will depend on the case at hand.

These considerations lead us to suspect that, although *r-K* patterns do exist (*4*), the *r-K* trade-off might not be the most interesting, or most important, trade-off in many cases. An *r-K* continuum may provide one major axis along which life-history strategies can be ordinated. But a simple *r-K* continuum cannot provide an inclusive classification of life-history strategies. In many, if not most, cases, a detailed analysis of relevant ecological factors will be required to explain observed life-history patterns (*8*).

ROBERT A. ARMSTRONG
MICHAEL E. GILPIN
Department of Biology, University of California, San Diego, La Jolla 92093

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12. We define r_i to be the density-independent growth rate of phenotype i under the very best conditions (for phenotype i) that ever occur in the environment under consideration. Under these conditions, $f_i(t) \equiv 0$. At all other times, $f_i(t) > 0$. We further assume that the γ_i are time-invariant (*10*).
13. Because we assumed a simple model of population growth and haploid genetics, we were able to obtain a simple relation (Eq. 5) for optimality. In more complicated models employing diploid genetics and age-structured populations (*14*), or in which growth rates are not linear functions of the limiting factor (R. A. Armstrong and R. McGehee, in preparation), or in which phenotypes are different enough that they are not all limited by the same limiting factor, polymorphisms may be maintained [see also (*10*)].
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15. That is, we define the carrying capacity K_i of phenotype i by $K_i = r_i/\gamma_i$, with r_i defined as in (*12*).
16. In the simple Volterra model (Eq. 1), temporal fluctuations in mortality enter only as mean harshness $\bar{f}_i$, rather than depending on the pattern of fluctuations. Our model thus suggests that in some cases "fluctuating" or "unpredictable" environments may have evolutionary effects similar to those produced by "harsh" constant environments. In many, if not most, cases, however, temporal patterns of harshness (seasonal temperature or rainfall patterns) will themselves be of ecological and evolutionary importance.
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Terrestrial Locomotion in Penguins: It Costs More to Waddle

Abstract. *The energetic cost for walking is relatively higher for penguins than for other birds or for quadrupeds of similar body mass. The morphology of penguins seems to represent a compromise between aquatic and terrestrial locomotion wherein both energy economy and speed suffer when the birds move on land.*

Penguins are highly adapted to movement in water. Some species, however, spend a great deal of time walking about on land, and two antarctic species, the emperor penguin (*Aptenodytes forsteri*) and the Adélie penguin (*Pygoscelis adeliae*), are prodigious walkers.

Every year, emperor penguins trek over the antarctic sea ice to their rookeries, which may be as much as 120 km from open water (*1*). Adélie penguins may walk more than 100 km from the sea to their rookeries (*2*), and there are records of Adélie tracks on the Ross Ice Shelf at least 100 km from the sea (*3*). In addition, Sladen and Ostenso have reported emperor tracks and what were probably Adélie tracks at least 300 km from the nearest known open water (*4*).

Because both of these species must fast while they are out of the water, the energetic cost of walking is of special interest to our understanding of their life histories. Furthermore, because the morphology of penguins is very different from that of other birds in which the energetics of locomotion have been studied, we can test the generality of conclusions drawn about the energetics of locomotion in birds (*5*).

We determined the energetic cost of walking in three species, emperor penguins ($N = 4$), Adélie penguins ($N = 3$), and white-flippered penguins (*Eudyptula albosignata*) ($N = 3$) (*6*). (These species include the largest and the smallest penguins.) The number of experimental sessions with each species was 48, 56, and 60, respectively.

Oxygen consumption was determined while the penguins walked on a treadmill at various constant speeds and while they rested on the stationary tread. Adélie penguins would not remain still long