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*).

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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 enough for a resting metabolic rate to be determined. The birds were trained to wear light latex masks while they walked so that all the air they exhaled could be captured. The mask was supported by a pulley system and counterweighted to minimize interference with the animal. The gas analysis system used and the calculations of the oxygen consumption have been described (*7*). Steady-state oxygen consumption was measured over the full range of speeds that the birds would maintain for at least 20 minutes. Data were used only when the bird had walked steadily and the rate of oxygen consumption had been nearly constant for at least 10 minutes. Treads were driven by variable-speed motors, which maintained constant set speeds. Tread speed was calculated from tread length and from the time elapsed for a counted number of revolutions. Systematic error and imprecision (*8*) were less than 1 percent of measured speeds. Emperor and Adélie penguins walked at air temperatures between −5° and 10°C, and white-flippered penguins at between 17° and 25°C. Air temperatures at which emperors walked are within their thermoneutral zone (*7, 9*); we assumed the same for Adélie and white-flippered penguins.

Emperor penguins were weighed with a magnetically damped beam balance (*10*) that had a systematic error of 2.5 g. Adélie and white-flippered penguins were weighed on a beam balance (Ohaus 1119D) with a systematic error of 1 g. Imprecision of both balances was less than 1 percent of any measured value.

Table 1. Comparison of E and M_t for penguins with those of other birds and mammals.

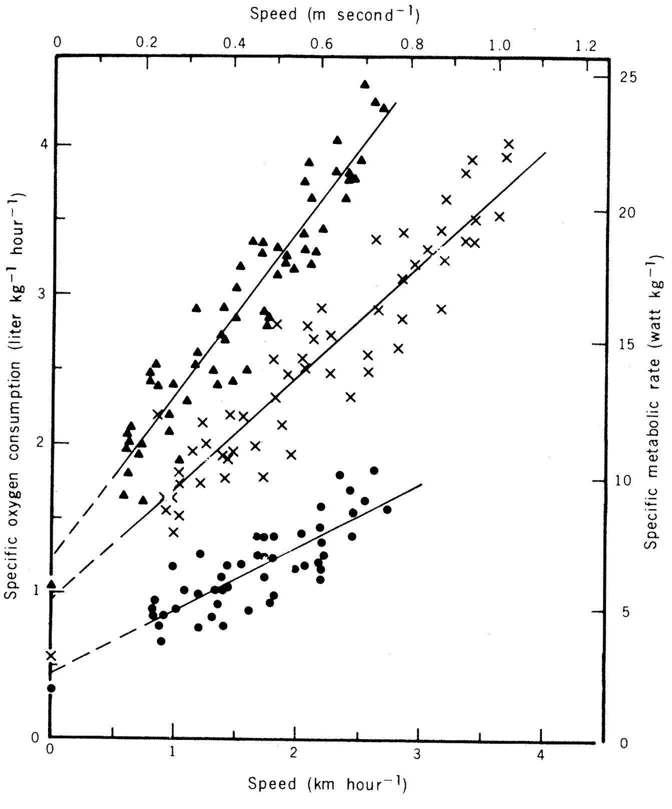
Species	Mean body mass (kg)	Mean resting $\dot{V}_{O_2}$ (liter O_2 kg^{-1} hour^{-1})	E (liter O_2 kg^{-1} km^{-1})	M_t (liter O_2 kg^{-1} km^{-1}) 2 km hour^{-1}	M_t (liter O_2 kg^{-1} km^{-1}) 3 km hour^{-1}
Emperor penguin	20.79	0.33	0.43	0.66	0.58
Rhea (*16*)	22.00	0.38	0.34	0.54	0.47
Running mammal (12)	21.00	0.29	0.16	0.41	0.32
Adélie penguin (*13*)	3.89	0.55	0.76	1.23	1.07
Goose (*5*)	3.81	0.63	0.72	0.97	0.89
Turkey (*5*)	4.31	0.56	0.41	0.71	0.61
Running mammal (12)	4.00	0.44	0.31	0.69	0.56
White-flippered penguin	1.15	1.03	1.11	1.73	1.52
Guinea fowl (*5*)	1.21	1.05	0.47	1.17	0.94
Running mammal (12)	1.00	0.62	0.53	1.07	0.89

Specific (*11*) rate of O_2 consumption, $\dot{V}_{O_2}/m$ (where $\dot{V}_{O_2}$ is the rate of O2 consumption and m is body mass) increased with walking speed (S) in all three species (Fig. 1). This increase was approximately linear over the rather limited range of speeds that the birds would maintain for 20 minutes or more.

The relation of $\dot{V}_{O_2}$ and S is similar to that found for other species, that is, $\dot{V}_{O_2}$ increases linearly with walking speed. This increase is greatest in the smallest species of penguin, and falls with increasing body mass.

We shall use two quantities derived from the relationship between $\dot{V}_{O_2}$ and walking speed to compare penguins with other walking and running animals: (i) The specific cost of transport (M_t) is defined as $\dot{V}_{O_2}/(m \cdot S)$. This is the amount of oxygen consumed per kilogram body mass while walking 1 km at a particular speed. (ii) The slope of the line (E) relating O_2 consumption to S is defined as $d\dot{V}_{O_2}/dS$. In animal species that show a linear increase in $\dot{V}_{O_2}$ with S, as do penguins and most other animals so far studied, E is constant for each species. Thus, E may be used to compare animals differing in body mass, morphology, and resting metabolic rate.

When $\log E$ is plotted against $\log m$ for quadrupeds of varying mass (Fig. 2), the values for E fall near a straight line having a slope of −0.40 (*12*). Fedak *et al.* (*5*) have shown a similar relationship for



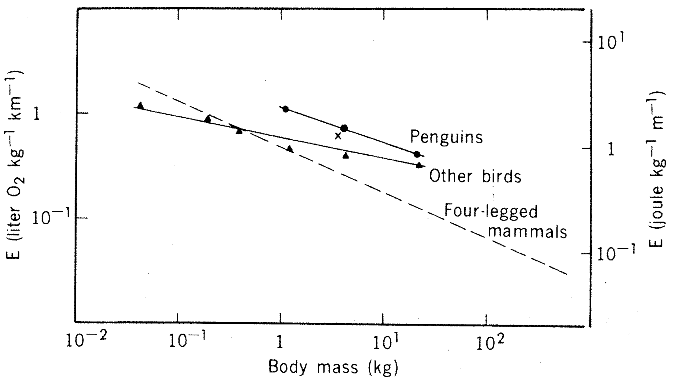


Fig. 1 (left). Oxygen consumption plotted against walking speed for three species of penguin (*14*). Oxygen consumption is plotted on the left and is converted to metabolic power input on the right under the assumption that 1 liter O_2/hour = 5.58 watt. Single symbols on the ordinate are mean resting metabolic rates (*15*). Symbols: ●, emperor penguins; ×, Adélie penguins; ▲, white-flippered penguins. Fig. 2 (right). Logarithmic plot of E against body mass for penguins, other birds, and four-legged runners. Circles represent penguins and triangles represent other birds [from (*5*)]. The × adjacent to a circle at $m \approx 4$ kg is for the goose. The dashed line is for four-legged runners [from (*12*)].

bipeds, including man and seven species of birds. The slope of the line for birds (−0.20), however, is only half as great as that for quadrupeds. The line for this relation in penguins has a slope of −0.33. The values of E for penguins are higher than would be expected for other birds or quadrupeds (Table 1).

Penguins and geese have an "awkward" gait when they walk, which we call waddling; their bodies undergo large lateral displacements. In emperor penguins the lateral and rotational movements of the trunk are large enough to cause the tail to draw a sinusoidal track in the snow. Penguins and geese have legs that are relatively short compared to those of guinea fowl, turkeys, and rheas, and their range of walking speeds is comparatively limited.

Mechanical analysis may explain why E and M_t are higher in waddling birds than in running birds. Waddling may involve large kinetic energy changes with each stride, and short legs require a higher stride frequency to walk at a given speed than do long legs. Stride frequency of emperor penguins walking at the maximum speed they can maintain (2.8 km hour^{-1}) is about 85 strides per minute (*13*). Stride frequency of a rhea at the same speed is 50 strides per minute, or only 60 percent of that of the emperors. When stride frequency of Adélie penguins is compared to that of turkeys, the difference is even greater. At 3.9 km hour^{-1}, the stride frequency of turkeys is only 50 percent of that of the Adélies. The speeds used for this comparison are the top speeds that the two species of penguin would maintain on our treadmill, but both turkeys and rheas can move much faster.

The morphology of penguins and geese may in part represent a compromise between aquatic and terrestrial locomotion. Both energy economy and speed of walking seem to suffer as a consequence.

A low walking speed probably is not a detriment to the antarctic penguins, for they have no terrestrial predators. If need be, they can travel faster by tobogganing on their bellies; this allows them to use their powerful flippers to push themselves along on the snow. In emperor penguins, however, the high energy cost of walking could have serious effects on breeding success during seasons when rookeries are separated from the sea by unusually broad sea ice (*7*).

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Selenium in the Environment

The role of methylation of selenium in the aquatic environment, as discussed by Chau *et al.* (*1*), adds to knowledge of the Se cycle in nature. Their statement, however, that Se and its compounds are carcinogens and environmental pollutants calls for correction. Evidence that Se is not a carcinogen has been summarized by many (*2*). Evidence has accumulated to indicate that the ambient unavailability of Se for uptake by plants in some areas actually increases susceptibility to cancer (*3*). The incidence of some forms of cancer appears inversely related to levels of Se in human blood, milk, and locally grown plants (*3, 4*).

As prosthetic group of the oxidoreductase glutathione peroxidase (*5*), Se functions with vitamin E in the avoidance of aberrant oxidations of lipids. Nutritional inadequacy of Se is thought to underlie various chronic diseases caused by such aberrant lipid oxidations (*6*), including cardiovascular disease (*6, 7*). The absolute essentiality of Se for animals is well established (*2*) and its essentiality for humans strongly indicated (*8*). Selenium deficiency is thought to represent far more of a problem than are any likely excesses of Se in the environment. Realistically, then, Se should be viewed not as a pollutant, but as a critically essential nutrient.

The incidence of Se-responsive diseases in livestock and even in zoo animals has increased steadily for two decades. The concept that nutrient inadequacy is a growing problem due in part to imbalance between the sulfur and selenium cycles was advanced (*6, 9*). If the availability of Se in the air-soil-plant-animal-human food chain is diminishing, what it may mean in terms of human nutrition can only be speculated upon. In any case, evidence suffices to invoke critical investigations of the possible anticancer value of Se, as well as its reported value against other chronic diseases.

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