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Cohort-size/body-size scaling rules for stationary populations

Eric L. Charnov

Department of Biology, The University of New Mexico, Albuquerque, NM 87131-0001, USA

ABSTRACT

I derive a rule linking individual growth rate to mortality rate. It yields a power function for cohort size plotted against body size.

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Body size distributions within populations must reflect the dynamics of individual growth, recruitment and mortality. A constant recruitment rate means that there will always be fewer older, and hence larger, individuals, provided growth continues throughout life; this statement is also true as a time average for fluctuating recruitment. The rule is almost trivial and obvious; it is not obvious, however, that the number of individuals versus body size should follow any *particular* declining function. Yet, power functions are commonly found (number proportional to size to a minus power) (e.g. Enquist and Niklas, 2001). This paper asks why this might be true.

Assume that with increasing age (t) each individual increases in body size ($m(t)$, here mass) as the cohort declines in number $N(t)$. This paper asks for conditions for a graph of $\ln N(t)$ versus $\ln m(t)$ to be a power function:

$$\ln N(t) = K - \delta \ln m(t) \tag{1}$$

For a non-growing population (the stationary state), the $N(t)$ is also the standing number of individuals of age t (Charnov, 1993, p. 7), so the power function is the rule for the standing $N(t)$ versus body size.

From equation (1) we have:

$$\frac{\mathrm{d} \ln N(t)}{\mathrm{d}t} = -\delta \cdot \frac{\mathrm{d} \ln m(t)}{\mathrm{d}t} \tag{2}$$

The right-hand side is simply δ times the specific growth rate, $\mathrm{d}m/m\mathrm{d}t$. For non-growing populations, the left-hand side is the instantaneous mortality rate ($Z(t)$) appropriate for age t, size $m(t)$. Let $L(t)$ be the survival to age t; then

$$L(t) = e^{-\int_0^t Z(x)\mathrm{d}x}, \quad \ln L(t) = -\int_0^t Z(x)\mathrm{d}x \quad \text{and} \quad \frac{\mathrm{d}\ln L(t)}{\mathrm{d}t} = -Z(t)$$

Thus, the power function form of equation (1) means that

$$Z(t) = \delta \cdot \frac{\mathrm{d}m}{m \cdot \mathrm{d}t} \tag{3}$$

Enquist and colleagues (Enquist *et al.*, 1998; Enquist and Niklas, 2001) have shown for standing number in forest trees that

$$\ln N = K - 0.75 \ln m \tag{4}$$

in several large samples that pool data over species. It is straightforward to show (with $\delta = \frac{3}{4}$) that equation (3) implies equation (4) for such a pooled sample for a stationary species (and population size) composition so long as growth continues throughout life and the smallest body size counted is the same for all species. It would be very interesting to know (in trees) if relative body-size growth $\mathrm{d}m/m\mathrm{d}t$ is indeed linked to mortality by $Z = \frac{3}{4}(\mathrm{d}m/m\mathrm{d}t)$ (equation 5).

Note three additional points. First, the argument given above may not be the only path to (approximate) $N - m^{0.75}$ scaling, particularly for pooled data over several species (or for heterogeneous growth/mortality trajectories within one species). Second, the argument does not answer the deeper question as to *what forces* Z to equal $\frac{3}{4} \cdot \mathrm{d} \ln m/\mathrm{d}t$, a very specific numeric rule. Finally, the argument raises issues of how the rule could hold in the face of environmental variability. The stationary population assumption may be acceptable as an average (Charnov, 1993, p. 6), but what about factors like temperature (e.g. latitude)? Surprisingly, the rule *may be* independent of temperature *because both* Z and $\mathrm{d} \ln m/\mathrm{d}t$ are expected (an hypothesis) to change with temperature according to a Boltzmann multiplier, thus cancelling out temperature (Gillooly *et al.*, 2002; Savage *et al.*, in press).

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