



100 YEARS AGO

The majority of deep-sea species are mud eaters; some are of gigantic size; some are armed with peculiar tactile, prehensile, and alluring organs; some are totally blind, whilst others have large eyes and are provided with a kind of dark lantern for the emission of phosphorescent light. The deep-sea fauna does not represent the remnants of very ancient faunas, but has rather been the result of migrations from the region of the mud-line in relatively recent geological times. The *Challenger* investigations show that species are most abundant in the shallow waters near land, decreasing in numbers with increasing depth, and especially with increasing distance from continental land. This is true as a general rule, especially of tropical waters, but in polar regions there are indications of a more abundant fauna in depths of 50 to 150 fathoms than in shallower water under 50 fathoms. The various points touched upon regarding the distribution of marine organisms, might be explained on the hypothesis that in early geological times there was a nearly uniform high temperature over the whole surface of the globe, and a nearly uniformly distributed fauna and flora; and that with the gradual cooling at the poles, species with pelagic larvæ were killed out or forced to migrate towards the tropics, while the great majority of the species which were able to survive in the polar areas were those inhabiting the mud-line. The uniform physical conditions here referred to might be explained by adopting the views of Blandet as to the greater size and nebulous character of the sun in the earlier ages of the earth's history.

From *Nature* 25 March 1897.

50 YEARS AGO

The advantages of hydrogen cooling for large high-speed electrical machines have not up to now been exploited in Great Britain. Several manufacturers are at present engaged on the construction of turbo-alternator units employing hydrogen as a cooling agent. In a report on work and progress in 1946 issued by the Metropolitan-Vickers Electrical Co., Ltd., it is stated that a 60,000 kW., 3,000 r.p.m. set is approaching completion and will be ready for testing shortly. — "Hydrogen-cooled turbo-alternators."

From *Nature* 29 March 1947.

Evolutionary ecology

The right size for a mammal

Andy Purvis and Paul H. Harvey

Elephants live slow lives, voles fast lives — vole populations may pass through 50 generations while an elephant grows up. Many facets of mammalian life history combine in this slow-fast continuum: species with long generation times produce small litters of large offspring who wean late, mature late and live longer after maturity¹. Why do these components of life history co-vary as they do? In a paper in *American Naturalist*², Kozłowski and Weiner propose an elegant and comprehensive model of life-history evolution for animals, such as mammals, that stop growing when they reach reproductive maturity. Their model accords with the comparative patterns and may, as a bonus, resolve another knotty problem — the skewed frequency distribution of body sizes among species, whereby far more species are small than large (Fig. 1).

The study of mammalian life-history evolution gained impetus from the demonstration of impressively tight scaling relationships between life-history attributes and body size among species³ — large species lead slow lives and small species fast ones. However, the fast-slow continuum cannot be just a side-effect of natural selection on size because it exists independently of size differences: voles are fast, for example, but bats are slow. Empiricists and theoreticians have batted alternative explanations back and forth, setting each other ever more demanding challenges^{4,5}. Ironically, in Kozłowski and Weiner's explanation, the interspecies scaling relationships that sparked the whole debate turn out to be red herrings.

Kozłowski and Weiner's new model assumes that, within a species, the rates of energy assimilation, respiration and mortality scale with body size according to simple power laws, yielding straight lines on double-logarithmic plots. Further, differences in ecology cause both the slopes and the intercepts of these lines to vary among related species (Fig. 2). Within a species, these six

parameters — the three slopes and three intercepts — are facts of life. Evolution responds to them by optimizing the timing of the switch from investing energy in growth to investing in reproduction⁶. Optimal size varies among species because of ecological differences. But various combinations of parameter values can yield the same optimum adult size for different species and, when this happens, one species matures later than the other and lives longer afterwards: the model captures the slow-fast continuum.

For each species, the optimal size corresponds to a particular growth rate, age at maturity, adult mortality rate and so on. In simulations, these life-history traits scale as power functions of adult body size among species. The exact scalings depend upon the distributions of the six ecologically determined parameters that went into the model but, for some realistic choices at least, the likeness to observed interspecies scalings is uncanny. However, the scaling relationships carry no functional significance — the slopes are not the same as within-species slopes, but are statistical consequences of body-size optimization. Another finding deserves special mention. In Kozłowski and Weiner's simulations, each ecological parameter is assumed to be normally distributed among species. The resulting distribution of optimal body sizes, however, is skewed to the right even when body size is logarithmically transformed. Actual body size distributions are often this shape too⁷, and a long search for the reason has hitherto proved inconclusive.

Kozłowski and Weiner are not the first to tackle life-history evolution by combining optimality theory with body-weight scaling of life-history variables. Charnov^{4,8} produced a model having many of the same predictions which tightly couples size to age by assuming a growth law, with all species growing along parallel trajectories. His model, which also features optimization of adult size, successfully recovers both the slow-fast continuum and the scaling relationships between life history and adult size, and has led to insights into bird life-history too⁹. However, tests of the model against real data have found flaws: most importantly, body weight at weaning is not, as Charnov assumes, a constant proportion of adult weight⁷. As Kozłowski and Weiner point out, the assumption is illogical: it precludes the existence of an optimum size, because delaying reproduction would incur the double whammy of lower survivorship to maturity and lower fecundity once mature.

Kozłowski and Weiner's model is an advance over Charnov's, but how good is it?

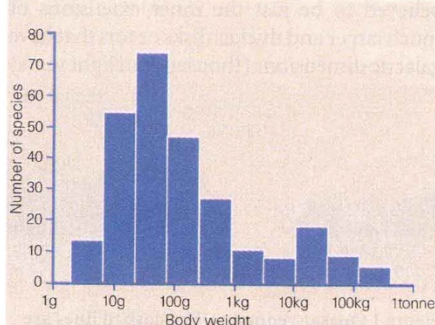


Figure 1 Distribution of adult body weights among Palaearctic terrestrial mammals, which is skewed so that it has a long right-hand tail¹³. The shape is typical of other plots for other areas.