

# QUANTIFICATION AND COMPARISON OF EVOLUTIONARY RATES

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**ABSTRACT.** Calculation of evolutionary rates in phenotypic standard deviations per generation (haldanes) has several advantages over conventional calculation in factors of  $e$  per million years (darwins). Rates in haldanes are independent of dimension in a way that rates in darwins are not, making them more widely comparable, and rates in haldanes are more readily interpretable in terms of quantitative evolutionary genetics. Evolutionary rates are inversely related to time scale, and this must be considered when rates are compared. The slope of a log rate versus log interval [LRI] distribution is important for distinguishing significant directional change or stasis from a null expectation of random change, and the intercept of an LRI distribution provides an estimate of the average intrinsic generation-to-generation rate of an evolutionary time series. The intrinsic rate is important as the upper limit of possible long-term rates of evolution. Evolutionary lineages in the fossil record yield intrinsic rates similar to those observed in laboratory selection experiments and natural selection in the wild. Intrinsic rates for lineages in stasis lie within the range of rates for lineages undergoing directional change. Significant long-term stasis and evolutionary change do not differ intrinsically, which means change and stasis are determined by extrinsic environmental factors.

## INTRODUCTION

Evolution in plants and animals is driven by a set of interacting component processes (including mutation, recombination, selection, and random drift) that simultaneously produce and limit genetic and phenotypic change over time. The relationship of phenotypic change to genetic change and the relative importance of different component processes in producing and limiting change are still poorly understood. Evolutionary change is rarely quantified in terms of rate in any standard way, which inhibits comparison of evolution in different species, or in the same species on different time scales, and precludes comparative evaluation of the contribution components make to the general process.

Here I want to review developments in the study of evolutionary rates, introduce a new rate unit, outline a new approach involving analysis of the structure of log rate versus log interval distributions, test the approach by investigation of simulated time series generated as random walks, and finally apply this in selected empirical studies.

## BACKGROUND

George Gaylord Simpson was the first to make broad comparisons of evolutionary rate in his classic book *Tempo and Mode of Evolution* (1944), which opens with a chapter entitled "Rates of Evolution." Much of the chapter is concerned with survivorship ("group rates") of mammalian

and pelecypod genera, and the section on morphological rates (“character change”) is largely concerned with allometric change of one characteristic relative to another. Meaningful quantification of long-term evolutionary change requires radiometric calibration of the geological time scale, and in 1944 Simpson was able to provide only tentative estimates of the durations of eras and epochs: he published a single graph relating molar morphology in horses to geological time (his fig. 4). Simpson showed that different characteristics of teeth evolved at different rates at the same time, while the same characteristics evolved at different rates at different times. A key feature of Simpson’s graph was use of a logarithmic scale to plot measures of morphology in terms of *proportion*. Nature knows nothing of meters or liters or grams, and organisms necessarily experience and compare form in terms of proportion.

A few years later J. B. S. Haldane (1949) reconsidered rates of change in Simpson’s horses and proposed a convenient unit of proportional change, the *darwin*, which he defined as evolutionary change by a factor of  $e$  (the base of natural logarithms) per million years. This is practically equivalent to an increase or decrease of  $1/1000$  per 1000 yrs. Factors of  $e$  are easily calculated by subtracting natural logarithms of the measurements of interest. Haldane mentioned standard deviations as an alternative to factors of  $e$  and generations as an alternative to years for quantifying evolutionary rates, but he did not develop either of these possibilities. Haldane found Simpson’s Tertiary horses to have evolved at about 0.04 darwins [d], while recognizing that domestic animals probably changed at rates of thousands of darwins.

Björn Kurtén (1959) took study of evolutionary rates a step further in quantifying and comparing rates for mammals in different environments at different times. He discovered that change in post-glacial Holocene mammals averaged 12.6 d, change in Pleistocene mammals averaged 0.5 d, and change in Tertiary mammals averaged 0.02 d. Kurtén suggested two possible explanations: (1) high rates of evolution in Pleistocene and Holocene mammals may reflect rapid and “revolutionary” changes of climate and sealevel characteristics of these intervals, while earlier low rates of evolution may reflect slow and gradual environmental change in the Tertiary; or (2) low Tertiary rates may be partially or wholly spurious, being based on samples millions of years apart while intervening histories may have contained any amount of fluctuation at higher rates. Subsequent study of evolutionary rates calculated over a broader range of time intervals and representing a broader range of organisms confirmed the second of Kurtén’s two explanations (Gingerich, 1983): most evolutionary rates, like sediment accumulation rates (Schindel, 1980; Sadler, 1981), are strongly dependent on the interval of time over which change is measured. Time scale is an integral component of evolutionary rates for all but the simplest of special cases (fig. 1), and rates can only be meaningfully compared when change is measured on the same scale or rates are projected to a common scale for comparison.

