Rates of Evolution

Philip D. Gingerich[1]

[1]Museum of Paleontology and Department of Geological Sciences, University of Michigan, Ann Arbor, Michigan 48109-1079; email: gingeric@umich.edu

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Abstract

Darwin thought evolution is slow. Evolution is slow on long time scales, but the fundamental process works on a generation-to-generation scale, not long time scales. Phenotypic variation is geometric normal, with normality reflecting its underlying polygenic source; ln transformation is part of the measurement process. The natural rate unit is the haldane, particularly H_0, representing change in standard deviations per generation on a timescale of one generation. When appropriately sampled, rates calculated on longer scales can be projected to a generational timescale. Empirical studies are reviewed concerning: (*a*) rates of polygenic mutation, (*b*) rates of response to human versus natural disturbance; and (*c*) rates of change in a classic study of punctuated equilibrium. Rate studies commonly find phenotypic change on the order of $H_0 = 0.1$ to 0.3 standard deviations per generation. This is fast by any standard. Darwin was wrong on rates, but more right than we knew on natural selection.

I do believe that natural selection will always act very slowly, often only at long intervals of time, and generally on only a very few of the inhabitants of the same region at the same time. I further believe, that this very slow, intermittent action of natural selection accords perfectly well with what geology tells us of the rate and manner at which the inhabitants of this world have changed. Charles Darwin (*Origin of Species*, 1859, p. 108–9).

INTRODUCTION

Biological evolution is a process of change. Any process, by nature, moves forward in time. A gradual process, fast or slow, moves forward in steps (this is what gradual means etymologically). Steps in a process imply continuous but not necessarily constant or continual (perpetual) change. How do we measure change? How do we measure time? And how are these related? Rates are essential for understanding evolution (and any other process).

Surprisingly, 150 years after publication of the *Origin of Species* (Darwin 1859), there is little consensus on evolutionary rates. Some biologists think evolution is fast (Hairston et al. 2005, Nilsson & Pelger 1994, Palumbi 2001, Reznick et al. 1997, Thompson 1998), whereas most, like Darwin, think it is slow (see the quotation from Darwin above). The theory of punctuated equilibrium argues that evolution is both fast and slow, with nothing in between (Eldredge & Gould 1972). Fast and slow could be limits in a spectrum of rates, but arguments about fast and slow are meaningless without quantification (Gingerich 1984, 1993; Hendry & Kinnison 1999).

Rates are ratios (both have the same etymological root), and ratios are notorious in all science for confounding the effects of numerators and denominators. Rates are used and often misused in comparisons of hypotheses, and they deserve much more careful attention in evolutionary inference. There are many ways to calculate rates of evolution, but these are only useful if they relate to models of evolutionary change; the models then dictate the units of interest. When there are choices, preferred rates are those defined in units enabling broad comparisons across traits and taxa.

Darwin's fundamental contribution to science was recognizing that evolution is a population process, not a Lamarckian process focused on individuals. Darwin emphasized (*a*) population variation, and (*b*) inheritance of this variation. He then combined variation and inheritance with (*c*) differential survival in life's struggle for existence to yield (*d*) natural selection. Darwinian selection works at the level of population phenotypes, the level where species interact with each other and with their surrounding environment. To understand evolution by natural selection, we have to quantify phenotypic variation, the steps of the inheritance process, the change (if any) resulting from differential survival, and, finally, how these are related.

Rates of evolution are important in paleontology and in all of evolutionary biology including morphology, genetics, phylogeny, and increasingly ecology. Evolutionary studies are often dichotomized as microevolutionary or macroevolutionary, and biologists sometimes distinguish ecological and evolutionary scales of time. However, these are almost always aggregations of change on scales longer than the generational scale of the evolutionary process. In models and in life, we are principally interested in the fundamental generation-to-generation scale of change, one step to the next.

This review is organized in four sections: (*a*) geometric normality of phenotypic variation and ln transformation as part of the measurement process; (*b*) models for change from one generation to the next, quantified in terms of phenotypic variation; (*c*) models for change on longer scales of time, with analysis of simulated evolutionary time series to show how rates on the requisite one-generation timescale can be recovered from more coarsely sampled series; and (*d*) application of log-rate–log-interval (LRI) scaling in empirical case studies. Evolution can be slow, as Darwin thought, but changes observed in laboratory selection experiments, field studies, and fossil

sequences, projected to the generation-to-generation timescale of the process, consistently show the upper limit to be fast. High rates of evolution have special interest and importance because the response to selection, directional or stabilizing, is so much greater for one or multiple generations.

PHENOTYPIC VARIATION

Log-Normality of Phenotypic Variation

Thousands of studies of phenotypic variation, going back to Quetelet (1846) and Galton (1869), have described population variation as fitting a Gaussian normal curve. Galton (1879) and McAlister (1879) raised the question (with unimpeachable logic; see Galton 1879) of whether such a curve should be arithmetic-normal or geometric-normal (log normal). The former is the scale of counting measurement, whereas the latter is the proportional scale of biological function (Gingerich 2000). Geometric normal is the appropriate scale for comparing differences when calculating rates (Haldane 1949).

When normality versus log-normality has been a concern in the past, it has almost always been tested by treating arithmetic normality as a null hypothesis—subjecting a small sample to a goodness-of-fit test, failing to reject the null hypothesis, and then, in effect, accepting it. An alternative approach is to accord the two hypotheses equal footing and then calculate the relative likelihood of one versus the other for the empirical sample at hand. Such a test is illustrated in **Figure 1**. In this example, as whenever the difference in likelihood is significant, phenotypic measurements fit a log-normal curve better than they do a normal curve.

Natural logarithms (ln) are used for transformation of measurements because: (*a*) the standard deviation (SD) of ln-transformed measurements is mathematically the ordinary coefficient of variation (Lewontin 1966), (*b*) this is the correction to measurement used by Haldane (1949) in his rate metrics, and (*c*) use of ln distinguishes preliminary transformation related to measurement from the order-of-magnitude log transformation used later to scale differences, rates, and intervals. In the following, $\mathbf{z}$ represents a ln-transformed vector of measurements $\mathbf{x}$ for a trait, n represents the length of this, $\bar{z}$ represents the mean, s represents the SD, and var($\mathbf{z}$) represents the variance. To emphasize again, ln transformation is required to make measurements comparable, and it is not part of a rate calculation per se. The log ($\log_{10}$) transformation employed later is a transformation related to order-of-magnitude scaling and comparison. It too has nothing to do with calculation of rates, but is useful for their interpretation.

Normality and Additive Genetic Variance

The normality of biological variation illustrated in **Figure 1**, arithmetic or geometric, is an indication of its source. Variation is the result of error or difference-from-expectation, and normality results from the addition of numerous small differences. This is why it is easy to generate an arithmetic-normal curve by flipping coins or rolling dice and tabulating the relative frequencies of permutations in the resulting combinations. A geometric-normal curve results from the addition of numerous small proportional differences. The SD is the only parameter of a standard normal curve (with mean $= 0$ and total density or area under the curve $= 1$); the mean and density must be specified in more general applications.

The source of the variation observed in population phenotypes is the underlying genotype. Each phenotypic trait, like brain size in **Figure 1**, is determined by additive contributions of genes and alleles and interactions. This is why additive genetic variance and the rates of polygenetic mutation generating additive genetic variance are so important. Heritability is important too

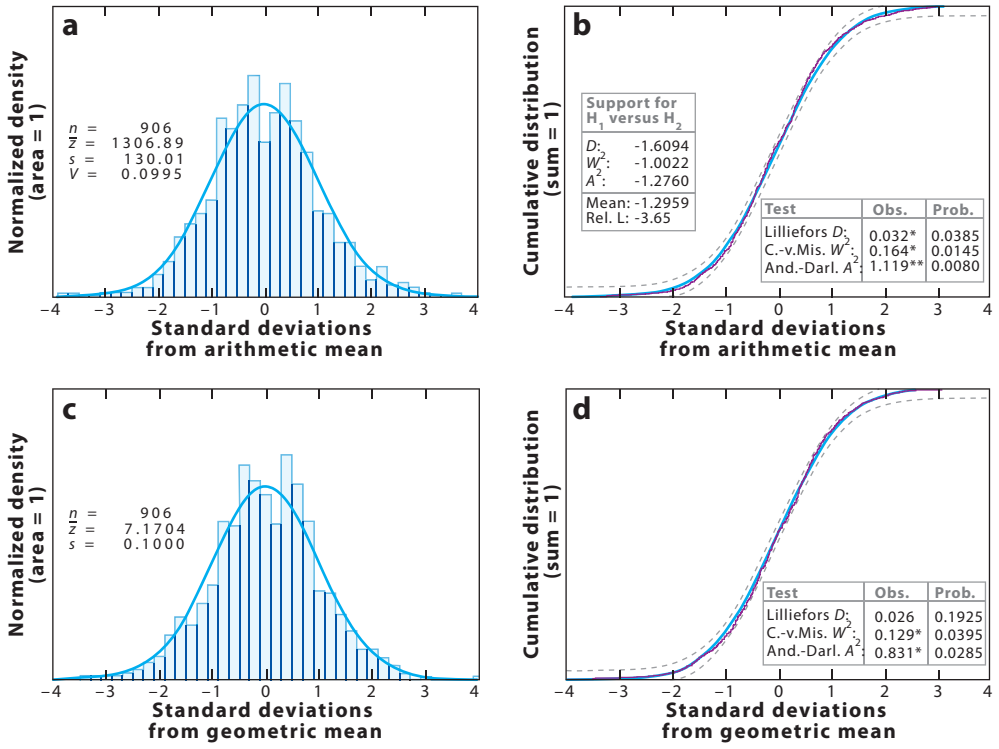

Figure 1

Likelihood comparison of arithmetic and geometric normality of human brain size. Blue lines are model curves. (*a*) Normalized density histogram of brain weight in grams. (*b*) Same measurements plotted as a cumulative empirical distribution function (EDF; *stepped line*). (*c*) Normalized density of ln-transformed stature measurements. (*d*) Same ln-transformed data plotted as a cumulative EDF. Application of goodness-of-fit statistics is explained in Gingerich (2000). These represent deviations of the observed EDF from the corresponding normalized distribution function (*smooth curve* in *b* and *d*). Mean support here, −1.2959, indicates that H_2 (geometric normality) is about 3.65 times more likely than H_1 (arithmetic normality) for these data. This case is one more added to the evidence in Gingerich (2000). Most traits of organisms should be logged as part of the measurement process, before any statistical or rate analysis. Note that the standard deviation of ln-transformed measurements here (0.1000) is almost exactly the coefficient of variation of the raw measurements (0.0995; see Lewontin 1966). Empirical data are autopsy measurements of 906 adults (Bischoff 1880).

because additive variance is never all the variance. Most evolution of morphology is not about genes, per se, but about normal distributions of phenotypic variation and how these distributions change through time.

CHANGE FROM ONE GENERATION TO THE NEXT

Rate Units

Haldane (1949) calculated rates of evolutionary change two ways, first in factors of *e* (base of the natural logarithms), and second in phenotypic SDs. He marked time in years and in generations. Haldane coined the rate unit "darwin" to represent "increase or decrease of size by a factor of *e* per million years" (Haldane 1949, p. 55). The rates of horse evolution that he calculated were on the order of 40 millidarwins (40×10^{-9}; a darwin is a factor of *e* per million years,

and 1/1000 of that is a factor of *e* per billion years). These were calculated on timescales of 5–16 million years.

Haldane wrote that "the use of the standard deviation as a yardstick has a certain interest because, on any version of the Darwinian theory, the variation within a population at any time constitutes, so to say, the raw material available for evolution" (p. 52). He calculated that horses changed by about one SD per 200,000 generations, or 5×10^{-6} SD per generation on a timescale of about 1–3 million generations.

What does change by a factor of *e* per million years on a timescale of millions of years (darwins) have to do with change in units of population variation on the generation-to-generation timescale of the evolutionary process? There is nothing intuitive about change by a factor of *e* that isn't better expressed in SD units. The timescale of interest is generations, not millions of years or millions of generations. Traits of different dimension differ in their characteristic variability (Lande 1977), and this is automatically compensated when change is quantified in SD units (ratio and shape traits of undefined dimension are similarly made comparable when represented in SD units).

The rate unit that takes account of population variation on the appropriate scale of measurement, and evolutionary time on the scale of the evolutionary process, is the "haldane" (Gingerich 1993; **Figure 2**). This was named to emphasize its difference from the darwin of Haldane (1949), while simultaneously honoring Haldane's contribution to quantification. The haldane, abbreviated H, is defined in **Table 1**. It is useful to add a subscripted log I (for interval length in generations) to H to specify the scale of the rate (scale is illustrated in the random walk model developed below). Base, step, generating, or generational rates are those on a one-generation timescale, that is, H_0 ($\log 1 = 0$). In an earlier study, I called base rates intrinsic rates (Gingerich 1993), but these neutral terms are preferable.

Table 1 explains the computation of differences and rates commonly used to represent change in morphology. The process rates are all rates per generation scaled to a timescale of one generation. Any difference between successive generations in an evolutionary time series is itself a rate of change per generation on a timescale of one generation. Thus, the so-called haldane numerators are useful as rates when scaled or projected to a timescale of one generation (see below).

Rates in units appropriate for testing null hypotheses of random change are listed in **Table 1**, but here too calculating per-generation rates is not enough, and the per-generation rates must be scaled to a one-generation time interval before they can be compared or employed as generating rates in models of evolutionary change. Random change implies a neutral mixture of directional and stabilizing selection: genetic drift is a trivial part of a neutral model because drift is so sensitive to effective population size.

Darwins and darwin numerators are included in **Table 1** because they are descriptive. Given that they are not process rates, it does not matter that they be projected to a timescale of one generation, but, whether darwins or darwin numerators, these must be projected to the same timescale for comparison. Some researchers prefer the rate unit darwin because no knowledge of variation or generation time is required, but this is no advantage if resulting rates cannot be related to evolutionary change. It is best to study large samples where variation can be quantified directly, but variation tracks trait size and dimension closely enough for common traits that variation can often be estimated with reasonable accuracy. It is best to study lineages where generation times are known, but generation times also track body size in some groups of organisms sufficiently that these, too, can be estimated with reasonable accuracy.

Metrics involving squared difference and squared change, as in the Δ of Lynch (1990), advocated as a general rate unit by Bell et al. (2006) and Hunt (2008), are quadratic and not on the scale of measurement.

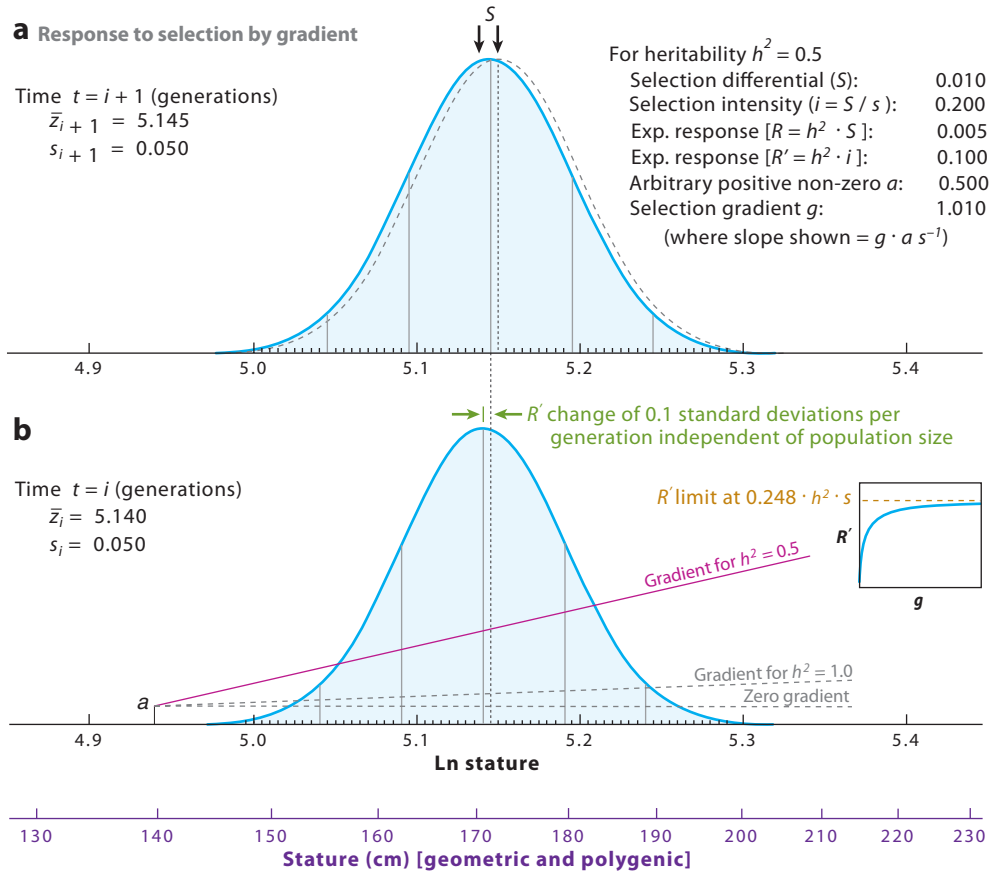

Figure 2

Change in human stature (*a* and *b*) as a model for evolution in successive generations. Blue normal curve in *b* represents generation $t = i$, and blue normal curve in *a* represents succeeding generation $t = i + 1$. Gradient of selection (*pink solid line*) superimposed in *b* favoring larger individuals explains the response R′ graphed in *a* for heritability $h^2 = 0.5$ (drawn to scale). Population samples have means $\bar{z} = 5.140$ and 5.145 (corresponding to statures of 170.7 and 171.6 cm, respectively), and a common standard deviation $s = 0.05$. Vertical lines within normal curves are standard deviation (SD) units. Selection differential $S = 0.01$, equivalent to a selection intensity $i = 0.2$ yielding dashed normal curve in *a*, is required to achieve a response $R = 0.005$. This is equivalent to the response of 0.1 SD shown here (*blue curve* in *a*), independent of population size (*areas under blue curves*). Selection and response follow Falconer (1981; see Gingerich 2001). Example could be continued to a third generation $t = i + 2$ (not shown), with evolution from $t = i$ to $t = i + 1$, and then $t = i + 1$ to $t = i + 2$, but not from $t = i$ to $t = i + 2$ directly. The timescale of the evolutionary process is generation to generation, not longer. Rate of change shown here is representative of the observed secular trend in human stature (Bowles 1932). Recent change in human stature is not necessarily evolution, but it is not too fast to be evolution.

Selection versus Drift

Selection, artificial or natural, is a powerful force for change because it affects the additive genetic variance of a population whether the population is large or small. The same selection gradient or point of truncation will produce the same response regardless of the size of the population. For a population of any reasonable population size, rate of polygenic mutation, heritability, fecundity, and gradient of selection, the geometric relationships shown in **Figure 2** will hold regardless of population size (regardless of the area under the normal curve). The expected response *R*, where $R = 0.005$ in ln stature units, is the product of the selection differential *S* and heritability h^2; and

Table 1 Rate computation

Term	R code	Reference
Number of successive samples	**N** = length (t.yr [i]) = length (z [i])	
Time or age of successive samples (years)	**t.yr [i]** vector with i = 1, 2, . . . N and N > 1	
Generation time (years)	**t.gen or t.gen [i]**	
Sample size for successive samples	**n [i]**	
Sample means	**zbar [i]** (all measurements ln-transformed before analysis)	
Sample variances	**zvar [i]**	
Sample standard deviations	**zsd [i] = sqrt (zvar [i])**	
Pooled within-sample variance (i = 2, 3, . . . N)	**zvar.w [i] = ((n [i-1] – 1) • zvar [i-1] + (n [i] – 1) • zvar [i]) / (n [i-1] + n [i] – 2)**	Lynch (1990)
Denominator n_0 (i = 2, 3, . . . N)	**n0 = n [i-1] + n [i] – (n [i-1]^2 + n [i]^2) / (n [i-1] + n [i]))**	Lynch (1990)
Between-sample variance (i = 2, 3, . . . N)	**zvar.b [i] = (((n [i-1] • n [i] • (zbar [i-1] – zbar [i])^2) / (n [i-1] • n [i])) – zvar.w [i]) / n0**	Lynch (1990)
Difference between successive means	**zdiff [i] = zbar [i] – zbar [i-1]** for i = 2, 3, . . . N	
Time intervals between samples (years)	**tdiff [i] = t.yr [i] – t.yr [i-1]** for i = 2, 3, . . . N	
Rate in units appropriate for study of the evolutionary process (when scaled to one-generation time interval; H_0)		
Rate in haldanes	**H [i] = (zdiff [i] / sqrt (zvar.w [i]) / (tdiff [i] / t.gen)** for i = 2, 3, . . . N	Gingerich (1993)
Difference appropriate for study of the evolutionary process (when scaled to a one-generation time interval; H_0)		
Haldane numerator	**Hn [i] = zdiff [i]/sqrt (zvar.w [i])** for i = 2, 3, . . . N	
Rates in units appropriate for testing null hypotheses of random change (when scaled to a one-generation time interval)		
Polygenic mutation rate	**mvar [i] = 0.5 • zvar.b [i]/(tdiff [i]/t.gen)** for i = 2, 3, . . . N	Lynch (1988)
Expected rate of phenotypic divergence	**D [i] = sqrt (2 • (tdiff [i]/t.gen) • mvar [i])** where tdiff [i] is time since divergence	Lynch (1990)
Delta	**Δ = zvar.b [i]/((tdiff [i] / t.gen) • zvar.w [i])** for i = 2, 3, . . . N	Lynch (1990)
Rate appropriate for comparing change on a graph of morphology versus time on a geological timescale (when scaled to a common interval)		
Rate in darwins	**D [i] = zdiff [i] / tdiff [i] • 10^6** for i = 2, 3, . . . N	Haldane (1949)
Difference appropriate for comparing change on a graph of morphology versus time on any timescale (when scaled to a common interval)		
Darwin numerator	**Dn [i] = zdiff [i]** for i = 2, 3, . . . N	

the expected response R', where $R' = 0.10$ in SD units, is the product of the selection intensity i and heritability h^2 (Falconer 1981). These are independent of population size, and selection from generation to generation will produce a sustained trend.

The same cannot be said for random genetic drift. Drift is very sensitive to population size. There is a very small chance of achieving a response equal to or greater than the response diagrammed in **Figure 2** by random drift. The probability of achieving $R' \geq 0.10$ SD by drawing a single founder for the second generation is 0.411. This goes down to 0.255 for $n = 10$; to 0.017 for $n = 100$; and to 0.000 for $n = 1000$. With positive and negative change being equally likely, the chance of producing a sustained trend from generation to generation by drift is vanishingly small.

Haldane (1949) calculated very low rates of evolution by averaging small changes observed in fossil lineages spanning long intervals of geological time. He then assumed that these very low rates were equivalent to the per-generation rates of a geneticist and recognized that only the weakest natural selection would be required. More recent studies use similar reasoning, concluding that drift might be important (Bell et al. 2006, Charlesworth 1984, Lande 1976, Lynch 1990, and others). The fallacy, reviewed here, lies in equating rates per generation calculated on timescales of tens, hundreds, thousands, or millions of generations in the laboratory, field, and fossil record, with the rates of evolutionary theory, which are rates per generation on a timescale of one generation. Rates are not comparable when their scales are different.

MODELS FOR CHANGE ON LONGER TIMESCALES

Random Walk Simulation

The easiest way to understand an evolutionary time series, and the rates and patterns generated by the evolutionary process, is through computer simulation (see sidebar, Why Use Simulations to Study Rates?). Definitions and calculations used in rate computation are listed in **Table 1**. The point in what follows is, first, that net rates of any time series calculated on aggregate timescales can be very different, systematically different, from the base rate used to generate the time series; and second, a sample of net rates on different timescales can be used to recover the base rate and say something about the mode of the process.

Any random walk is informative. Here we focus on a single walk, but it is best to study these in families to understand their behavior. In the simulation of **Figure 3**, a series of $n = 200$ random

WHY USE SIMULATIONS TO STUDY RATES?

The simulations in **Figures 3** and **4** provide visual images of time series, but the real reason for simulation is to confirm that all parameters required to model a process are known. Here we must know: (*a*) the time step (a step in evolution is a generation); (*b*) the rule for generating step values or deviates (here random sampling from a normal distribution, with the SD adjusted to make the mean deviation $m = 1$); and (*c*) additional optional constraints on values. Signs of the random deviates are unconstrained in **Figure 3** (random time series). All signs are constrained to be positive in **Figure 4** (positive or negative runs generate directional time series). Alternatively, signs could be constrained to fluctuate, making, for example, every odd-numbered step negative and every even-numbered step positive (generating stasis). Models can be mixed, but there are no mixed models. For empirical evolutionary series, points b and c are unknown a priori and have to be recovered by sampling and analysis. LRI plots in **Figures 3*d*** and **4*b*** illustrate successful recovery of m and the optional constraint. Skeptical readers should try this with their own simulations.

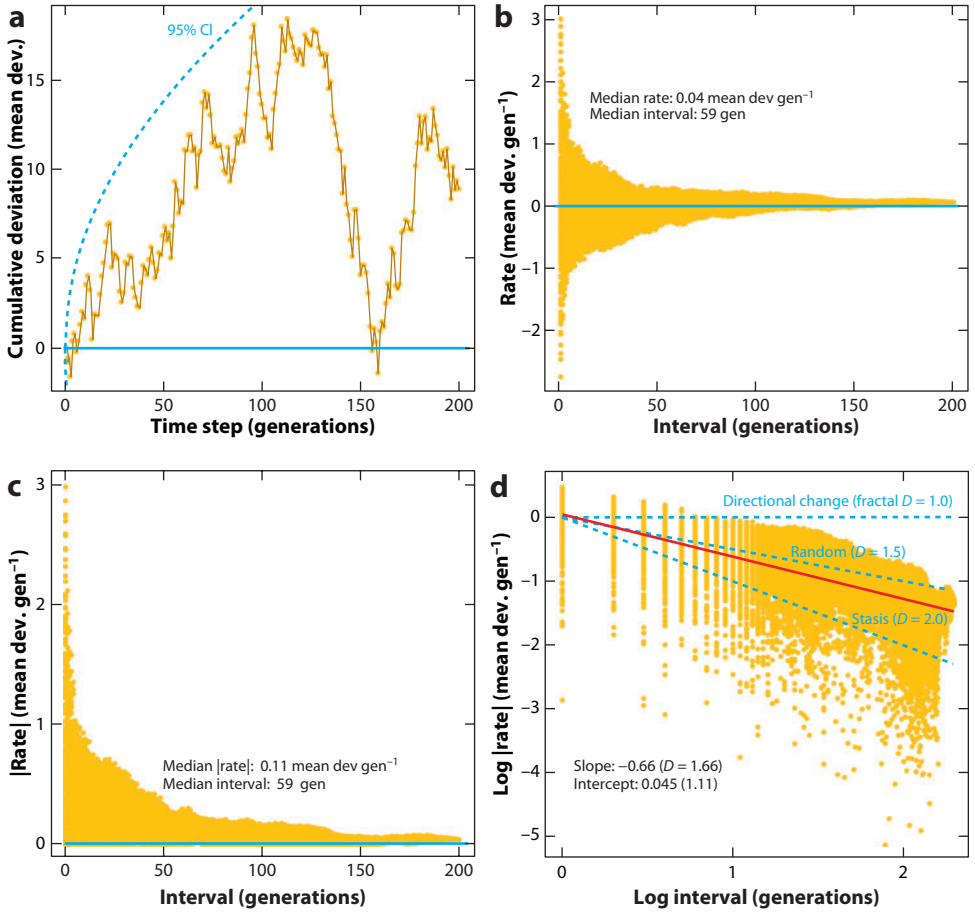

Figure 3

Rate analysis of a simulated evolutionary time series, here a random walk of 200 steps (generations). (*a*) Cumulative deviation of a random walk starting at zero, with deviates for each step generated from a normal distribution with $\bar{z} = 0$ and $s = 1.25$. Expected mean base or step rate is $m = 1$ (base rate for the series shown is 0.92). Blue dashed lines ($\pm 1.96 \cdot m \cdot \sqrt{t_i}$) enclose a 95% confidence region for all random walks with $\bar{z} = 0$ and $s = 1.25$. (*b*) Rate-interval plot of all 20,100 possible rates of cumulative change for pairwise combinations of steps in *a*; note that the variance is much less for longer intervals. (*c*) Absolute values of rates in *b*. (*d*) Log-rate–log-interval (LRI) plot of all rates in *c*. Regression of log rate on log interval is shown with a red line. The intercept ($10^{0.045} = 1.11$ mean deviations per generation) is close to the base rate for the series ($10^{-0.036} = 0.92$, within 0.1 orders of magnitude). Blue dashed lines of different slope show expected scaling of rates for directional time series (fractal $D = 1.0$), random change ($D = 1.5$), and stasis ($D = 2.0$).

deviates was generated from a standard normal distribution ($\bar{z} = 0$ and $s = 1.25$). The expectation for the mean of the absolute value of the 200 deviates is $m = 1$ (where $m = s \cdot \sqrt{2/\pi}$, Pearson & Hartley 1966). In **Figure 3**, there are 94 positive deviates ($m_p = 1.03$), and 106 negative deviates ($m_n = -0.83$). These can be pooled by taking absolute values, and the pooled mean for the particular sample analyzed here is $m_a = 0.92$. The random deviates were added in sequence, starting with zero, to form the time series **z** of $n = 200$ steps illustrated in **Figure 3*a*** (step number $i = 1, 2, \ldots, n$).

Figure 3*b* is a graph of the $(n^2 + n)/2 = 20{,}100$ rates representing change between all possible pairs of values in the 200-step walk of **Figure 3*a***. This is an exhaustive survey, and all rates calculated from any subsample of **z** necessarily lie within the distribution shown here. Time series with gaps, sometimes large gaps, and time series with time-averaged measurements are common in evolutionary studies, and one advantage of simulation is that all samples and all rates are known. The distribution in **Figure 3*b*** shows high and low rates, positive and negative, calculated on short timescales, but only low rates calculated on long timescales. The median rate for the distribution in **Figure 3*b*** is 0.04, again close to expectation (0) for a time series generated with $\bar{z} = 0$ and positive and negative rates cancelling each other over time. The median interval for the rates shown here is 59 generations, which is much longer than the timescale of the simulation process repeated to generate the time series.

We can also consider the distribution of absolute values of the rates, shown in **Figure 3*c***. Here, again, the distribution shows high and low rates calculated on short timescales, but only low rates calculated on long timescales. The median rate calculated from the absolute values is 0.11 on a median interval of 59 generations.

To understand evolutionary dynamics we have to be able to estimate the mean rate of the generating process. This is easiest when the distribution in **Figure 3*c*** is transformed by logging both axes ($\log_{10}$ to represent rates and intervals on an order-of-magnitude scale). The resulting LRI distribution is more linear, shows the inverse relationship of rates and intervals, and shows the substantial dependency of rates on their intervals (that is, dependency of ratios on their denominators as well as numerators).

The intercept of the regression of rate on interval is 0.045 (**Figure 3*d***). Exponentiated, this yields $10^{0.045} = 1.11$ as a prediction of the mean deviation per generation in our model, on a timescale of one generation. On an order-of-magnitude scale, this is close to the expected mean rate of 1.00 for the deviates used to generate the random walk model in the first place. We use the intercept to estimate this because $10^0 = 1$ generation is the timescale of interest here. Precision can be estimated by bootstrapping (Gingerich 1993). An LRI distribution provides a simple and direct approach to base rate estimation when rates are sampled on longer scales of time.

Fractal Dimension of a Time Series

Regression of log rate on log interval for the time series studied in **Figure 3*d*** yields a slope of −0.66, which is a measure of the fractional (fractal) dimension, complexity, or roughness of the series (Gingerich 1995). For evolutionary series, fractal dimension D is calculated as 1 plus the absolute value of the slope on an LRI plot. Here $D = 1 + |-0.66| = 1.66$. A smooth line has dimension 1 and a smooth area has dimension 2. A linear time series with dimension $D = 1.66$ is complex enough to begin to fill an area. The expected fractal dimension for a random walk is $D = 1.5$ (Mandelbrot 1983), and $D = 1.66$ is close to this value. The comparability of evolutionary time series to fractal coastlines and a host of other complex curves is clear (Mandelbrot 1967), and the LRI framework provides a parallel approach to analysis.

The utility of fractal dimension for studying evolutionary series is illustrated in **Figure 4**, which was generated by adding the absolute values of the random deviates studied in **Figure 3** rather than the deviates themselves. As shown in **Figure 4*a***, this makes the resulting time series smooth and unidirectional. It leaves the 95% confidence envelope for a random walk within a few steps. A regression fit to the LRI distribution of all rates for the series (**Figure 4*b***) yields a slope of 0.025 and a fractal dimension of $D = 1.025$. This is close to $D = 1.0$, which is expected for directional change, and much less than $D = 1.5$, which is expected for a random walk, or $D = 2.0$, which is expected for stasis.

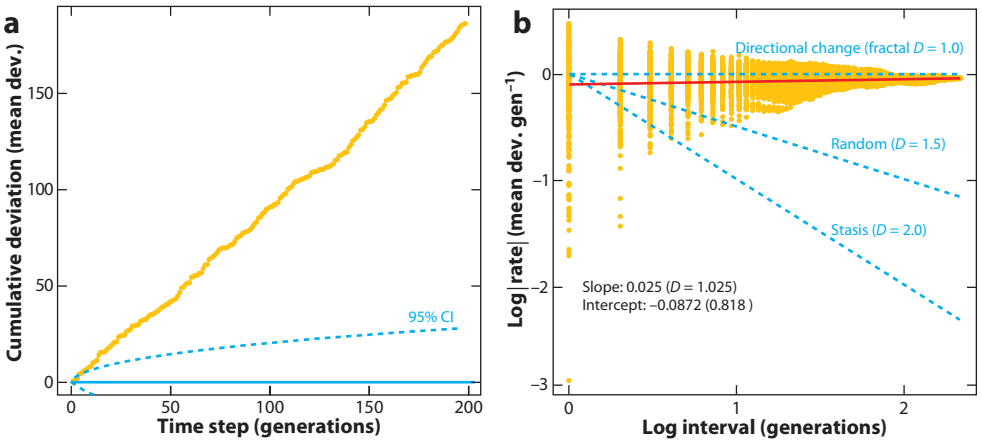

Figure 4

Rate analysis of a simulated evolutionary time series, here a directional series of 200 steps (generations). (*a*) Cumulative deviation constructed from absolute values of the same deviates used in **Figure 3**. Blue dashed lines enclose the same 95% confidence region as that in **Figure 3**, but most of the directional series lies outside this envelope. (*b*) Log-rate–log-interval (LRI) plot of all 20,100 possible rates of cumulative change for pairwise combinations of steps in *a*; note that the variance is, again, much less for longer intervals but the scaling of rates with interval is different. Regression of log rate on log interval is shown with a red line. The intercept ($10^{-0.087} = 0.82$ mean deviations per generation) is close to the base rate for the series ($10^{-0.036} = 0.92$; again, within 0.1 orders of magnitude).

Interpretation of evolutionary series as directional or static is beyond this review, but distributions like those in **Figures 3*d*** and **4*b*** generated for empirical evolutionary series can be used to compare hypotheses of directional change and stasis in terms of relative likelihood.

Critiques of the LogRate–Log Interval Framework for Study of Rates

I introduced the LRI framework studying rates in 1983 (Gingerich 1983), and several critics have been influential. Gould (1984) had many concerns (numbered here and quoted verbatim). Hopefully, focusing on these explicitly will clarify some misconceptions concerning measurement and rates.

1. "Comparison of rates in darwins is valid regardless of the time interval if the organisms' rate of change is exponential.": Gould interpreted the ln transformation of Haldane (1949) as a transformation related to rates rather than a transformation related to measurement (see empirical evidence and discussion above).
2. Gingerich "plotted time (on the abscissa) against its own reciprocal ($1/t$) on the ordinate, and his negative slope arises necessarily from this artificial redundancy.": My investigation was not about plotting time against its reciprocal, but about testing the independence of rates and their denominators. Contra Gould, these are rarely independent.
3. "But why should a numerator, a measure of absolute evolutionary change in a lineage, be constant? Surely this invariance cannot be a property of the world.": Constraint is a property of biology because, empirically, a relatively narrow range of variation is viable for any morphological trait, and, again empirically, the history of life has been very long (see Gingerich 2001).
4. "The fastest rates are for populations when they change, and do not include the millions of natural populations that are not evolving and would display rates . . . of flat zero.": How,

after Darwin, can a biologist think there are (or have ever been) millions of populations that are not evolving?

5. "Finally, the artificial character of Gingerich's curve refutes his general conclusion that its smoothly linear character demonstrates that microevolution and macroevolution are different manifestations of a common underlying process.": The inverse relationship of rate and interval has been duplicated many times in many contexts (including the simulations above and empirical studies below), reinforcing each time the idea that microevolution and macroevolution, on different scales, are manifestations of a common underlying process (Simons 2002).

Bookstein (1987) stated repeatedly that "random walks have no rates" (p. 458), and "evolutionary rates exist only when the hypothesis of symmetric random walk can be refuted" (p. 446). Bookstein did concede (p. 447) that a random walk has a parameter, which he called the step variance (the parameter is actually proportional to the square root of the step variance). Thus, random walks do have a rate. There is no random walk without a step, base, or generating rate of some kind. In addition, random walks have clouds of net rates on the full range of scales from 1 to n generations, and the scaling of all of these rates contains information about the series represented.

It is true, as Bookstein may have intended, that evolutionary rates representative of directional or stabilizing selection are meaningful only when a null hypothesis of random change or random walk can be rejected. Note that the null hypothesis is not just any random walk of any rate, but the particular set of random walks with the base rate of the empirical series being tested.

Bookstein (1987) argued, obliquely, that rates do not exist because the underlying time series are fractal, and the rates do not approach a limit as the interval over which they are calculated approaches zero. Evolutionary time series are fractal, however, the timescale of interest is not zero but one generation. Bookstein's study was at least, in part, a response to Charlesworth (1984), who proposed testing evolutionary time series against linear null models.

Sheets & Mitchell (2001a) and Roopnarine (2003) considered the inverse dependency of rate on interval to be an artifact produced by spurious self-correlation predictable in random walks. Dependence, whatever the explanation, is a failed test of independence. I would say rather that this inverse relationship is a property, not an artifact, of random walks (and indeed any nondirectional time series).

Sheets & Mitchell (2001b) characterized LRI as comparing change or rate in an observed series to the maximum change expected in a random walk. It would be more accurate to say that LRI is a carefully controlled comparison of the scaling of rate in an observed series to the scaling of rate in a random walk, which involves more than comparison of the maximum.

EMPIRICAL CASE STUDIES

Rates of Polygenic Mutation

The variation observed in population phenotypes is determined by additive contributions of genes, alleles, and interactions, as explained above. Natural selection reduces genetic variation, and the rate of phenotypic evolution ultimately depends on the generation of new variance by mutation (Lynch 1988). Lynch compiled tables of estimates of V_m, the new genetic variance introduced each generation by polygenic mutation, expressed as a proportion of V_E, the environmental variance for the same trait. The estimates are derived from measures of divergence in highly inbred lines divided and reared separately. Here, I develop one of Lynch's examples to show how temporal scaling affects interpretation of polygenic mutation rates.

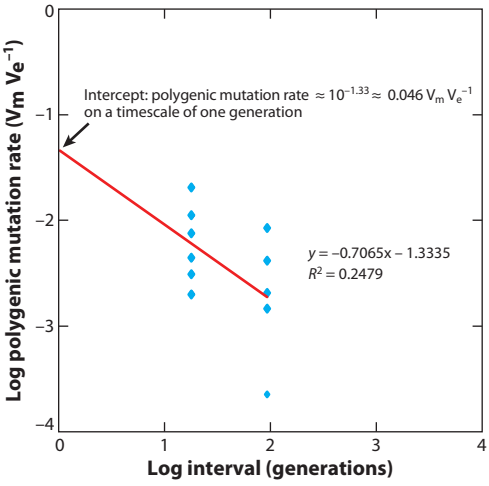

Figure 5

Temporal scaling of the rate of polygenic mutation calculated from analysis of variance in divergent lines of inbred mice studied by Bailey (1959) and Lynch (1988). One line was studied after 9 generations (18 generations of divergence; 1.26 on a log scale) and the other after 46.5 generations (93 generations of divergence; 1.97 on a log scale). All are per-generation rates (calculated on timescales of 18 or 93 generations). Note that the intercept of a linear model fit to the rates calculated by Lynch (1988; *red line*) is about an order of magnitude greater than the average of the rates of polygenic mutation calculated on longer scales of time. The intercept represents the expected value of per-generation rates of polygenic mutation on a timescale of one generation. This is the rate of interest for comparison and incorporation in genetic models.

Bailey (1959) studied rates of divergence in highly inbred strains of mice. Two sublines of one line were allowed to diverge for 9 generations (18 generations of separation) and two sublines of another line were allowed to diverge for an average of 46.5 generations (93 generations of separation). Bailey measured four cranial traits and two postcranial traits (ulna length and ilium length) to compare sublines in each line. Lynch (1988, his table 2) calculated V_m/V_E and averaged the results for the four cranial traits in the two lines (mean $0.0046 = 10^{-2.34}$), ulna traits in the two lines (mean $0.0311 = 10^{-1.51}$), and ilium traits in the two lines (mean $0.0158 = 10^{-1.80}$). He then treated each replicated line as an independent study deserving equal weight in the resulting interpretation.

We can test this by plotting the 18-generation results and the 93-generation results on an LRI plot, as shown in **Figure 5**. The studies are independent, but the results are highly dependent on interval and, in fact, no interval studied reflects the timescale of interest. The intercept, representing a summary scaling of all of the results, is $V_m/V_E = 0.046 = 10^{-1.33}$, which is approximately an order of magnitude higher than the rate of polygenic mutation calculated by Lynch for the same data. Scaling yields a rate that is not only per-generation but on the generation-to-generation timescale of interest. Rates calculated over two or more generations almost always go up when projected to a one-generation timescale.

It is true that calculation of polygenic mutation rates requires study of long lineages because it takes time for mutations to accumulate and yield measurable differences. But then the aggregate of per-generation rates must be projected to a one-generation timescale for comparison and incorporation in genetic models. Projection would not be possible if all rates were calculated on the same timescale. Two or more intervals, like the 18 and 93 generation intervals studied here, are required to estimate a rate for a timescale that cannot be studied directly.

Rates of Phenotypic Change in the Laboratory and Field (Microevolution)

Hendry et al. (2008) posed and tested the proposition that phenotypic change associated with human disturbance is greater than change in a natural context. In a carefully controlled study, they found that rates of phenotypic change are higher in anthropogenic contexts than in natural contexts, and phenotypic changes associated with human disturbance often exceed the baseline typical of natural environmental variation. Hendry and colleagues were concerned that rates of phenotypic change are lower when calculated over longer intervals, so they scaled absolute phenotypic change, the haldane numerator, rather than rate, against interval length (advocated elsewhere by Kinnison & Hendry 2001, and Estes & Arnold 2007). Hendry et al. (2008) published their data, which are reanalyzed here in an LRI framework to test the interpretation that rates are higher in a human context, and to show how haldane numerators scale to yield the same base rates as haldanes do on the generation-to-generation timescale of interest.

Temporal scaling of the haldane numerator, reflecting change as a difference in SD units, yields an intercept of $10^{-0.49} = 0.32$ SD per generation on a one-generation timescale (**Figure 6*a***). This difference, on this timescale, is the base rate H_0 of interest for understanding the generating process. The alternative, scaling haldane rates rather than numerators, yields the same intercept of $10^{-0.49} = 0.32$ SD per generation on a one-generation timescale (**Figure 6*b***). This too, on this timescale, is the base rate H_0 of interest. It does not matter which way the rate is calculated as long as the focal timescale is generation to generation.

A rate $H_0 = 0.3$ SD per generation on a timescale of one generation is high and, if humans are responsible, such a high rate might be cause for concern. However, analysis in an LRI framework shows rates of phenotypic change in a natural context ($H_0 = 10^{-0.36}$ or 0.44) to be higher than those in anthropogenic contexts ($H_0 = 10^{-0.44}$ or 0.37). The data were divided as Hendry et al.

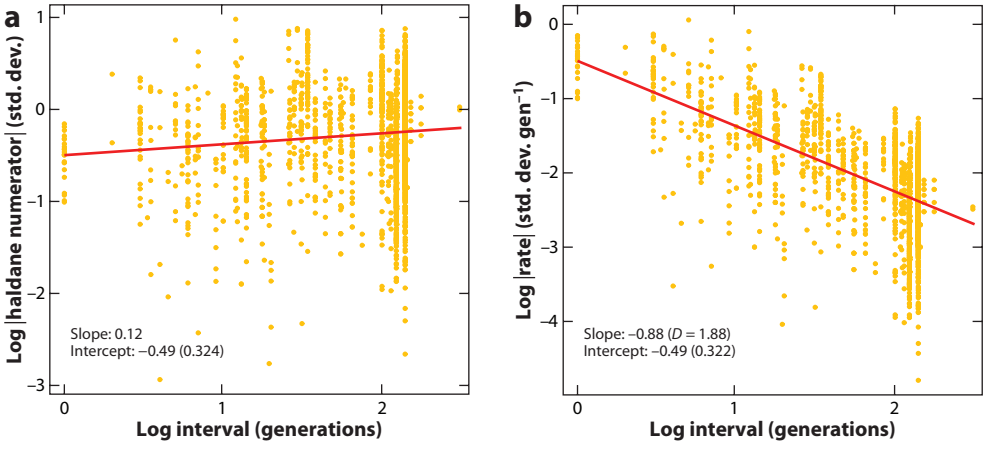

Figure 6

Two ways to recover the generation-to-generation base or step rate representative of evolutionary change from generation to generation in nature. (*a*) Prediction using the haldane numerator [difference in standard deviation (SD) units] advocated by Kinnison & Hendry (2001). Intercept is $10^{-0.49} = 0.32$ SD per generation on a one-generation timescale. (*b*) Prediction using the haldane rate unit (SD per generation) advocated by Gingerich (1993, 2001). Intercept is, again, $10^{-0.49} = 0.32$ SD per generation on a one-generation timescale. Both approaches to quantification, applied to the same data (from Hendry et al. 2008), yield the same prediction on a generation-to-generation timescale. Microevolutionary change and rates, like macroevolutionary change and rates, must be projected to a generational timescale to recover rates representative of the generation-scale process. Change at a rate H_0 of 0.3 SD per generation is fast compared to the narrow range of possible phenotypes in any taxon and the long history of most taxa through ecological and geological time.

(2008) did, with their category 6 considered natural. Based on experience with bootstrapping, it is unlikely that such rates are different from each other or from the rate of the combined samples. Selection, it appears, is equally potent with us or without us.

Rates of Phenotypic Change in the Fossil Record (Macroevolution)

Temporal scaling of evolutionary rates in the fossil record of the 54–55 million-year-old dawn horse *Hyracotherium grangeri*, sampled on a median interval of 100,000 generations, indicates a base rate $H_0 = 0.2$ SD per generation on a timescale of one generation (Gingerich 1993; compare with Haldane's low rates for horses discussed above). Some other mammalian lineages contemporary with *Hyracotherium*, sampled on the same range of scales, yield lower rates (Clyde & Gingerich 1994), but the upper limits of per-generation rates on a generation-to-generation timescale found in the fossil record are consistent with what we find in the field and laboratory today.

I end with a study by Cheetham (1986) that is widely cited as compelling documentation of punctuated-equilibrium evolution in the fossil record (Foote & Miller 2007). Cheetham, following Charlesworth (1984), modeled the rate of change within a species as the slope of a linear trend-with-error fit to within-species samples, yielding a rate on the timescale of the whole trend. Cheetham then modeled change between species pairs as a ratio of the difference in species morphologies, divided by the difference in their times of origin, yielding a rate on the timescale of the difference in times of origin. Cheetham found, in every case studied, that the between-species rate is signficantly higher than can be explained by variation in the within-species rate, and he labeled the categories punctuation and stasis, respectively.

However, the rates were compared on long and often different timescales. It would be more appropriate to calculate all possible pair-wise rates of change on all observed timescales within each species lineage. An LRI plot could then be used to project each array of within-species rates on their different scales of time for comparison with the corresponding between-species rates on their scales of time. I expect that all of the rates calculated by Cheetham on differing long timescales can be explained by change at the appropriate base rate when this is known.

A Big-Picture Perspective

Why is $H_0 = 0.1$ to 0.3, mentioned above, a high rate of evolution? Modern mammals span something like 10^2 SD or 10^3 0.1 SD units (comparing the least shrew to the great blue whale), and these diverged from each other something like 10^7 generations ago (Gingerich 2001, p. 141). At $H_0 = 0.1$, a rate found commonly in rate studies, a mammal could conceivably change from the size of a shrew to the size of a whale in 10^3 generations, and with suitable selection do this back and forth as many as $10^4 = 10{,}000$ times in the geological span of known insectivores and whales. At such high rates, ecosystems stabilize rapidly with the passage of time and then change only when perturbed (Stenseth & Smith 1984). The fossil record is punctuated, yes, but the punctuations are reasonably interpreted as pulses of rapid evolutionary response to environmental change or other perturbations (Brett et al. 1996; Gingerich 2001, 2006; Vrba 1993), not a distinct and unexplained mode of evolution.

SUMMARY POINTS

1. To understand and relate processes underlying polygenic mutation, microevolution, and macroevolution, we have to understand their rates. All are generated by parents giving rise to offspring, but routinely studied on much longer timescales. Laboratory settings

enable rates to be studied on a generation-to-generation timescale, but investigations of mutation, microevolution, and macroevolution are generally studied opportunistically on longer timescales. These must then be rescaled to the generation-to-generation timescale of interest.

2. Simulations like those in **Figures 3** and **4** (and many empirical studies) show that the relationship of rates to their intervals is linearized in a log-rate–log-interval proportional framework. This is the context in which rates are most easily rescaled to the interval of interest.
3. Empirical studies in all settings—laboratory and field studies of change from one generation to the next, laboratory and field studies of microevolution on scales of two or more generations, and paleontological studies of macroevolution on scales of thousands and millions of generations—project to yield the same spectrum of rates on a generation-to-generation timescale, suggesting that all can be explained by the same process.
4. The mean deviations per generation required to model the phenotypic change we see in empirical studies, whether estimated by rescaling differences (haldane numerators) or estimated by rescaling rates (haldanes), are on the order of 0.1 to 0.3 SD per generation on a timescale of one generation, meaning that evolution is much faster than generally conceived.
5. Haldane (1949, p. 56) wrote that "slowness of the rate of change ... makes it clear that agencies other than natural selection cannot be neglected." Many researchers have amplified this message. Now we understand that evolution is also often very fast, and we can turn Haldane's reasoning around. We see that natural selection is much more powerful than generally conceived, both in shifting populations to track opportunities, and in curbing their stochastic wanderings (Grant & Grant 2002, 2006; Hoekstra et al. 2002).
6. Darwin was wrong on rates of evolution, but more right than we knew on the power of natural selection.

FUTURE ISSUES

1. Univariate studies are easiest to visualize and quantify, but there is a need for further development of parallel quantification and comparison of rates in a multivariate morphometric context (Lerman 1965). Much has been done to quantify the underlying genetic basis of multivariate change (Hansen & Houle 2008, Lande 1979, Lande & Arnold 1983) and to develop measures of multivariate phenotypic difference (Loy et al. 2004, Slice 2005, Zelditch et al. 2004). Applied multivariate studies of rates include studies by Cheetham (1986) (discussed above), Gingerich (2003), and Polly (2004, 2008), among others, but more work remains.
2. Temporal scaling is especially important when comparisons involve cladistic relationships of multiple species because the resulting rates will depend on the positions in time of taxa and hypothesized branching nodes in ways that are sometimes unanticipated (Martins 1994, O'Meara et al. 2006, Revell & Harmon 2008).

3. There is a small literature on temporal scaling and time dependency of rates in molecular evolution (Gingerich 1986, Ho et al. 2005), and this too is a potential avenue of important research.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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