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The pace of modern life II: from rates of contemporary microevolution to pattern and process

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Abstract

We compiled a database of microevolution on contemporary time scales in nature (47 source articles; 30 animal species), comprising 2649 evolutionary rates in darwins (proportional change per million years) and 2151 evolutionary rates in haldanes (standard deviations per generation). Here we demonstrate how quantitative rate measures can provide general insights into patterns and processes of evolution. The frequency distribution of evolutionary rates was approximately log-normal, with many slow rates and few fast rates. Net selection intensities estimated from haldanes were on average lower than selection intensities commonly measured directly in natural populations. This difference suggests that natural selection could easily accomplish observed microevolution but that the intensities of selection typically measured in nature are rarely maintained for long (otherwise observed evolutionary rates would be higher). Traits closely associated with fitness (life history traits) appear to evolve at least as fast as traits less closely tied to fitness (morphology). The magnitude of evolutionary difference increased with the length of the time interval, particularly when maximum rates from a given study were considered. This pattern suggests a general underlying tendency toward increasing evolutionary diversification with time. However, evolutionary rates also tended to decrease with time, perhaps because longer time intervals average increasingly disparate rates over time, or because evolution slows when populations approach new optima or as genetic variation is depleted. In combination, our results suggest that macroevolutionary transitions may ultimately arise through microevolution occasionally 'writ large' but are perhaps temporally characterized by microevolution 'writ in fits and starts'.

Introduction

Evolution, genetically-based change in the characteristics of populations and species over time, is fundamentally a concept of rate. Surprisingly, however, quantifying evolutionary rates has until recently remained the pursuit of paleontologists rather than biologists studying evolution on contemporary time scales. The reluctance of neontologists to calculate and compare rates may hearken back to the view, espoused by Darwin (1859), that 'we see none of these slow changes in progress until the hand of time has marked the long lapse of ages'. In recent years, however, a growing body of literature has focused on observations and experimental studies of evolution over short, sometimes directly observable, time scales (contemporary evolution; reviewed by Hendry & Kinnison, 1999). Such studies often report 'rapid' evolution and have thus altered scientific and public perceptions of how evolution relates to contemporary concerns. However, claims of 'rapid' can be misleading unless the rate is contrasted with other, presumably 'not-rapid', rates. Unfortunately, few studies of contemporary microevolution have actually quantified rates and attempted to statistically validate whether or not they are 'rapid'.

Why have rates so rarely been quantified and statistically compared in studies of contemporary microevolution? First, quantifying evolution can be a laborious task, particularly if the genetic basis for an observed change is examined (e.g., Grant & Grant 1995; Reznick et al., 1997). Second, a consensus has been slow to develop as to the best way to quantify and statistically compare rates (Simpson, 1944; Haldane, 1949; Simpson, 1953; Lerman, 1965; Gingerich, 1983; Fenster, Hecht & Sorhannus, 1992; Gingerich, 1993; Schluter, 2000, Sheets & Mitchell, 2001b). Third, rates have sometimes been considered uninformative or misleading unless they deviate from null expectations and unless a specific evolutionary mechanism has been identified (Lande, 1976; Charlesworth, 1984; Bookstein, 1987; Bookstein, 1988; Lynch, 1990). In a previous paper, we provided a review and evaluation of ways to estimate and compare rates of contemporary microevolution (Hendry & Kinnison, 1999).

Studies of contemporary microevolution in specific systems have made significant contributions to our understanding of evolution (e.g., Darwin's finches, Trinidadian guppies, *Anolis* lizards). It is also possible, however, that broad scale compilations and analyses of rates can be used to address general questions regarding patterns and processes of contemporary evolution. Hendry and Kinnison (1999) presented a preliminary compilation of rates estimated for some well-known studies of contemporary micro-evolution. General conclusions from our analysis were (1) rates of evolution often called 'rapid' may actually be quite common in nature, (2) observed rates appear slower than would be expected based on selection intensities commonly observed in nature (i.e., in comparison to Endler, 1986), and (3) evolution in contemporary populations is usually less than the theoretical maximum sustainable rate (*sensu* Bürger & Lynch, 1995; Lynch, 1996). Here, we expand the rate database of Hendry and Kinnison (1999) to a broader range of studies, taxa, traits, and time intervals. Using existing rate metrics we address four questions:

1. What is the distribution of contemporary evolutionary rates and how do estimates of net selection intensities from observed rates of microevolution match selection intensities measured directly in nature? This analysis extends that of Hendry and Kinnison (1999) by adding more data, defining the distribution of rates in more detail, and making additional comparisons to a recent review of selection intensities in nature (Kingsolver et al., 2001).
2. Do differences in the amount of genetic variation for different types of traits influence the rate at which those traits evolve? For example, life history traits may evolve more slowly than morphological traits because the former have lower heritabilities (Mousseau & Roff, 1987). Alternatively, life history traits may evolve faster because they have more additive genetic variance and therefore 'evolvability' (Houle, 1992).
3. Is the amount of evolutionary diversification positively correlated with time interval on the scale of contemporary evolution? A growing number of studies have documented 'rapid' evolution in the wild and we have argued that such change is not exceptional but rather the norm (Hendry & Kinnison, 1999). If indeed all such studies, covering a broad range of ecological and evolutionary conditions (see Reznick & Ghalambor, 2001 for conditions promoting contemporary adaptations) capture a snapshot into a general process then we would also expect a general trend between diversification and time interval within, and perhaps among, taxa.
4. Does the rate of evolution decrease with increasing time? Such a trend would be expected if populations are evolving toward adaptive peaks, if genetic variance is depleted under strong directional selection, or if evolutionary rates and trajectories vary over time (Gingerich, 1983; Hendry & Kinnison, 1999; Barton & Partridge, 2000). Changes in rates with time are important to examine because they may indicate if and how microevolutionary trends ultimately translate into macroevolutionary transitions. The traditional view is that evolutionary diversification within a given lineage increases rapidly and then comes to a halt or decreases. In contrast, Schluter (2000) has argued that within several different adaptive radiations (e.g., continental mammals and birds, *Anolis* lizards, African cichlids and foliage-gleaning warblers) evolutionary diversification shows no signs of abating over millions of years.

Our investigation is akin to other studies that have drawn broad generalizations from a diverse database gleaned from the literature. Examples include analyses of heritabilities (Mousseau & Roff, 1987), genetic and residual variance (Houle, 1992), and the strength of selection (Endler, 1986; Kingsolver et al., 2001). Our

results form an empirical test for some of the expectations and inferences derived from these earlier studies. We conclude our analysis by addressing some computational and theoretical considerations in the future use of contemporary rates to infer pattern and process.

Methods

The database

Only a small subset of studies directly estimated evolutionary rates. We therefore estimated rates ourselves using data provided by investigators or extracted from text, tables, or figures in original publications. The data usually consisted of mean trait values, sample sizes, phenotypic variation within populations (variances, standard deviations, confidence intervals), generation lengths, and time intervals for evolution (change over time within a population) or divergence (differences between populations that had a common ancestor in the recent past).

We estimated evolutionary rates (all as absolute values) using two metrics: darwins and haldanes (Haldane, 1949; Gingerich, 1993; Hendry & Kinnison, 1999). Darwins were calculated as:

$$d = \frac{\log_e x_1 - \log_e x_2}{t},$$

where $\log_e x$ is the natural logarithm of the population mean trait value at time 1 and time 2, and t is time interval in millions of years. Rates in darwins were not estimated for data not on a ratio scale (e.g., maturation date) or for composite variables, such as principle component scores (see Hendry & Kinnison, 1999). Haldanes were calculated as:

$$h = \frac{\left(x_2/s_{\mathrm{p}}\right) - \left(x_1/s_{\mathrm{p}}\right)}{g},$$

where x is the mean trait value at time 1 and time 2, s_{p} is the pooled standard deviation of trait values across time (evolution) or populations (divergence), and g is the number of generations. When variances were expected to scale with the mean (most ratio scale data), raw data were $\log_e$ transformed to standardize variances before calculating s_{p}. When raw data were not available, we estimated (1) the mean of the $\log_e$ trait values as the $\log_e$ of the mean of non-transformed trait values minus half of the square of the coefficient of variation of non-transformed values (Lynch, 1990), and (2) the s_{p} of $\log_e$ trait values as the coefficient of variation of non-transformed values (Lynch, 1990). In practice, $\log_e$ transformations had little effect on rates in haldanes (not shown).

While amount of evolutionary time is easily defined for studies of evolution within a population (i.e., allochronic designs), divergence measured between two populations at a given point in time (i.e., synchronic design) integrates the evolutionary trajectories of the component populations (see Hendry & Kinnison, 1999) making the appropriate time measure debatable. For example, at one extreme divergence may represent primarily evolution of one population, in which case time should be measured as the period since common ancestry, whereas at another extreme divergence may represent equal and opposite evolution of the two populations, in which case time may be measured as twice the time since common ancestry. For simplicity we used the time since populations split from a common ancestor as our estimate of time interval for divergence studies, and not the sum of times down descendant branches as used by some investigators (e.g., Lynch, 1990, under a neutral model of divergence). We note in some instances how an alternative representation of time interval for synchronic designs might impact our conclusions. The number of generations was estimated as the number of years divided by generation length. Generation length was provided by authors of the original papers (published, or by personal communication), or was estimated as the age at maturation. When trait variation or generation length could not be determined, haldanes were not calculated.

Darwins specify the rate of proportional change in units of e per million years and haldanes specify rates in standard deviation units per generation. Darwins thus represent rates of change on an absolute time scale, whereas haldanes represent rates relative to the life history of the organism (note that proportional change could be specified per generation and standard deviations could be specified per year). Because darwins specify change in units of e, they are influenced by trait dimensionality (Gingerich, 1993) and are only useful for ratio scale data (Hendry & Kinnison, 1999). Haldanes, in contrast, are dimension-independent and can be applied to both ratio and interval scale data (Hendry & Kinnison, 1999). Because our goal is to draw generalizations from diverse species and traits, haldanes are used for most of our analyses. However, darwins have hitherto been used more extensively and, under certain conditions, can provide complimentary insights into evolutionary pattern and process (see below).

When possible we classified trait types according to Mousseau and Roff (1987) and Houle (1992). Mousseau and Roff's (1987) categories were: life history traits ('characters directly and invariably connected to fitness'), morphological traits (e.g., 'body size, wing size, and other metric traits'), behavioral traits (e.g., 'alarm reaction, activity level, and sensitivity to conditioning'), and physiological traits (e.g., 'oxygen consumption, resistance to heat stress, and body temperature'). Houle's (1992) categories were: traits under directional selection ('many life history traits, and traits highly correlated with size during growth') and traits subject to optimizing selection ('primarily morphological traits that are not directly a function of growth rate'). We also distinguished genetic (common-garden) versus phenotypic (wild-caught individuals) rates, and allochronic (evolution) versus synchronic (divergence) rates (Hendry & Kinnison, 1999).

Studies of contemporary microevolution are scattered across both basic and applied journals and only a limited number of studies report enough information to calculate rates. We were therefore not able to adopt a systematic search restricted to particular journals or time periods (e.g., Kingsolver et al., 2001). Instead, we used data from our previous database (Hendry & Kinnison, 1999) and added any studies we obtained since then. Our search was not exhaustive but neither was it biased, except for our focus on quantitative traits in animals (see Bone & Farres, 2001, for an analysis in plants). A few rates were excluded when associated with extremely small sample sizes (e.g., rates for Hawaiian mosquitofish with only two individuals per sample). At present, the database comprises 47 sources (publications), 30 species, 2649 rates in darwins, and 2151 rates in haldanes. The studies date from 1964 through the present, and represent change over a single generation through at most 300 generations. A bibliography of sources is provided in the appendix and an electronic copy of the database is available from the authors upon request.

Analysis

In several cases, multiple papers were published on the same populations, and we considered the data from such papers to represent a single 'study'. Some studies contributed more rates to the database than others, and so we controlled for study, trait, and time scale whenever possible. For example, we made some comparisons between different traits or time intervals within studies. We also used a hierarchical approach similar to that of Houle (1992): first including all values from the entire data set, then summary values per trait and study, and finally summary values for each study. For some analyses, we separated rates from common-garden studies (genetic) from studies of wild-caught individuals (phenotypic).

We did not perform a formal meta-analysis (Hedges & Olkin, 1985; Arnqvist & Wooster, 1995) because the necessary assumptions were not met. Foremost among these was the lack of independence among data points, which has convinced authors conducting analogous reviews to similarly eschew formal meta-analysis (e.g., Kingsolver et al., 2001). Another problem specific to our database was that we typically did not know errors or variances associated with rate estimates (because we estimated rates from mean values). Our inferences are therefore based on graphical approaches and on analyses designed to detect general trends (e.g., Mousseau & Roff, 1987; Houle, 1992; Kingsolver et al., 2001).

Our database can be used for two types of inference: what does microevolution *typically* accomplish and what can microevolution *potentially* accomplish. For the first type of inference, we used statistics considering the entire distribution of rates. This approach would be inappropriate for the second type of inference because many traits or populations are probably not evolving anywhere near their potential. For questions involving evolutionary *potential*, we therefore considered elements of the shape of the data distribution and maximum rates for combinations of traits, studies and/or time intervals.

Results and discussion

Evolutionary rates and natural selection

Medians of the absolute values for evolutionary rates in the entire database were 5.8×10^{-3} standard deviations per generation (haldanes), and 1151.3 powers of e per million years (darwins). These values are very large compared to rates observed in paleontological studies (e.g., 0.11–32.0 darwins, Gingerich, 1983) but comparisons of this nature are questionable because rates scale negatively with length of the time interval (Gingerich,1983; Gingerich, 1993; Hendry & Kinnison, 1999; Sheets & Mitchell, 2001a). Here we focus on comparisons within the time scale of contemporary microevolution ($\leq$300 years in our database).

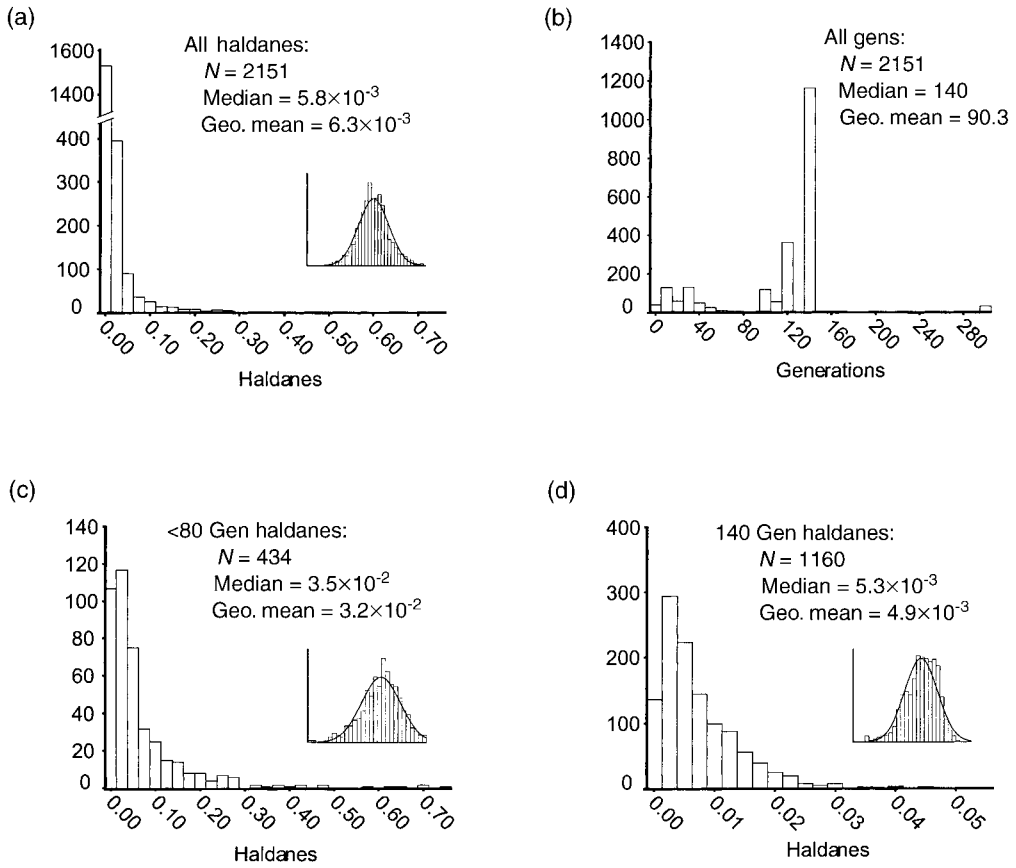

Figure 1. Histograms of contemporary evolutionary rates and associated time intervals: (a) all rates in haldanes (note break in y-axis), (b) frequency of time intervals in generations associated with haldane rates, (c) haldane rates for subset of time intervals less than 80 generations, (d) haldane rates for 140 generation interval only (divergence in Hawaiian mosquito fish: Stearns 1983a,b). Inset figures show distributions after log-transformation of rates (with curve for expected distribution under log-normality).

Frequency histograms of all observed rates (absolute values) revealed a distribution in which the vast majority of rates were very slow and only a few were very fast (Figure 1(a)), approximating a normal distribution after logarithmic transformation (i.e., log-normal: geometric mean haldane $= 6.3 \times 10^{-3}$).

Rates are known to correlate negatively with time interval, even on contemporary scales (Hendry & Kinnison, 1999). This effect might have influenced the observed distribution in Figure 1(a) because studies over relatively long time intervals contributed the most rates to our database (Figure 1(b)). Despite this effect, however, the many-slow/few-fast pattern seems robust. First, haldane rates over 80 or fewer generations were still distributed in an approximately log-normal fashion, although with a slightly greater skew toward larger values (Figure 1(c)). Second, a similar distribution characterizes analyses restricted to a common time interval; for example, the 1160 pair-wise rate estimates for mosquitofish populations 140 generations after their introduction to Hawaii (Stearns, 1983a, b, Figure 1(d)). For darwins, a similar many-slow/few-fast pattern was evident but log-transformed data did not as closely approximate normality as they did for haldanes (a tendency for more large darwin rates than expected under log-normality; geometric mean darwin rates = 964.7).

Are these results at odds with our previous assertion that 'evolution hitherto considered rapid may often be the norm and not the exception' (Hendry & Kinnison, 1999)? Yes and no. Yes, because exceptionally rapid rates are truly rare. No, because many of the studies falling into the unexceptional part of the distribution have called the evolution they documented 'rapid.' This serves to illustrate our point that 'claims of rapid evolution mean little without specifying what rapid actually means' (Hendry & Kinnison, 1999). Perhaps the appellation 'rapid' should be re-

served for the subset of rates that exceed the median (or some other standard) for a specified time scale (or after temporal scaling). A caveat associated with identifying truly rapid evolution is that investigators should be particularly suspicious of high rates for studies with small sample sizes. By analogy, Kingsolver et al. (2001) found that the strongest selection often coincided with the smallest sample sizes in a review of studies of the magnitude of selection in the wild.

A haldane rate is equivalent to a standardized response to selection (standardized by s_p) averaged over the time interval. Dividing a haldane rate by the trait's heritability, thus provides an estimate of the net (or effective) selection intensity (assuming heritability remains roughly constant). The net intensity of selection is the hypothetical amount of constant directional selection per generation that would produce the observed amount of difference. Over a single generation of selection in a population, or when selection is constant over time, the net selection intensity will equal the actual selection intensity (barring measurement error).

We examined whether observed evolutionary rates were consistent with intensities of directional selection commonly documented in nature by converting haldane rates to estimates of net selection intensity. We did not have direct estimates of trait heritabilities for most studies in the database, and so we employed two general narrow-sense heritability estimates, one that was decidedly low (0.10) and one that was rather high (0.40; Mousseau & Roff, 1987). The resulting distributions of net selection intensities were then compared to selection intensities measured directly in nature. These comparisons were made to two different databases of selection: 262 estimates published prior to 1984 (from Figure 7.2 in Endler, 1986); and 753 estimates published between 1984 and 1997 (from Kingsolver et al., 2001; raw data provided by J. Kingsolver).

Directly-estimated selection intensities reported in the literature followed asymmetric distributions similar to the many-slow/few-fast pattern observed for evolutionary rates. Endler (1986) emphasized the high selection intensities found in the tail of the distribution, whereas Kingsolver et al. (2001) emphasized the large number of small values. Part of this difference in emphasis arises because Kingsolver et al. (2001) found a higher proportion of small intensities than did Endler (1986). Perhaps early studies were more likely to focus on systems and traits where selection was exceptionally strong, with authors and editors recently becoming more receptive to publishing estimates of weak selection. Additionally, early studies focused on a few traits expected to be under strong selection during specific periods (e.g., droughts and Darwin's finches), whereas recent studies often report selection on large suits of traits over many time intervals, where strong selection is not necessarily expected.

Cumulative frequency distributions were roughly similar in shape for net selection intensities estimated from evolutionary rates and selection intensities measured directly in nature (Figure 2(a)). The main difference was that net selection intensities were substantially more skewed toward smaller values. Assuming all traits had a heritability of 0.10, over 70% of the net selection intensities were smaller than the median selection intensity of 0.13 in Kingsolver et al.'s (2001) database. Assuming a heritability of 0.40, over 90% of the net selection intensities were smaller than 0.13. The differences were even greater in comparison to Endler's (1986) database. Furthermore, had we estimated divergence times as twice the time since common ancestry, the majority of our net intensities would have been even smaller than the values we estimated.

The difference between net intensities and directly-estimated intensities may partly result from biases that act differently in the two types of studies. As noted above (and in Kingsolver et al., 2001), studies of selection may be biased against low values. Perhaps more so than in our database, because we estimated rates without regard to their magnitude, thus generating many very slow rates, particularly in multiple pair-wise comparisons, such as for Hawaiian mosquitofish populations(Stearns, 1983a,b). Indeed, if we exclude the many pair-wise comparisons resulting from Hawaiian mosquitofish the difference in distributions between net intensities and directly measured intensities is reduced (Figure 2(b)). It is also feasible that net selection evaluated from divergence studies could be biased toward values lower than those measured in individual populations if a component of parallel evolution commonly occurs in diverging lineages with common ancestry.

A second potential bias may arise when estimating the time interval for evolution. For instance, overestimating the number of generations will underestimate the true net selection intensity. The majority of generation lengths in our database were estimated as age at first maturation. Because many of the species are iteroparous, actual generation lengths were sometimes underestimated, numbers of generations overestimated, and net selection intensities perhaps underestimated. If large enough this bias might account for

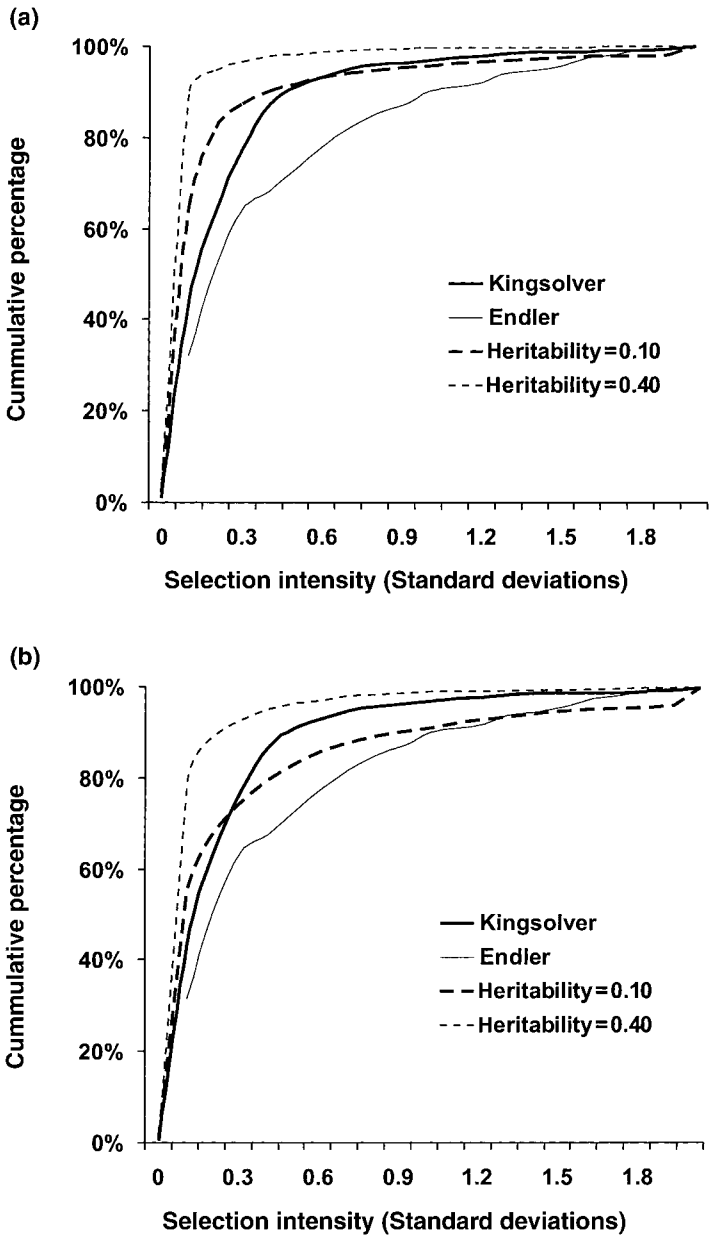

Figure 2. Cummulative frequency distributions for selection intensities measured directly in the wild (Endler, 1986, Kingsolver et al., 2001), and for net selection intensities estimated from haldane rates for studies of contemporary microevolution assuming overall heritabilities of 0.10 and 0.40. (a) all rates in databae, (b) excluding rates for Hawaiian mosquito fish (Stearns, 1983a,b).

the differences between net selection intensities and directly-measured selection intensities. However, for net intensities to have a geometric mean comparable to that of the intensities reported by Kingsolver et al. (2001), generation lengths would need to be between 1.8 (at $h^2 = 0.10$) and 7.1 times (at $h^2 = 0.40$) greater on average than were used in our analyses (with Hawaiian mosquitofish excluded: between 1.3 and 5.3 times greater respectively). Though perhaps feasible this seems unlikely. Still excluding such biases could potentially bring net selection intensities inferred from contemporary rates more in line with expectations based on intensities measured in natural populations over short time scales.

Assuming the difference between net selection intensities and directly-estimated selection intensities is

real and not the result of biases, what conclusions can we draw? First, directional selection would seem powerful enough to explain most contemporary evolution, without the need to invoke special mechanisms. Second, strong and consistent directional selection is not likely indefinitely maintained in most natural populations, even over contemporary time intervals. Most direct estimates of selection are obtained over short intervals, often less than a generation, and thus belie variation in the magnitude and direction of selection that likely contribute to evolution over multiple generations (e.g., Grant & Grant, 1995), and even over a single generation (e.g., Schluter, Price & Rowe, 1991). Moreover, persistent and strong selection are likely rare in nature because the associated high mortality would put such populations at risk of extinction (Lynch, 1996). As a result, the strength of selection measured over short intervals will often not be representative of net selection driving longer-term evolutionary outcomes. Moreover, factors such as density-dependence, genetic correlations, and gene flow can allow directional selection in the absence of evolutionary change (e.g., Larsson et al., 1998; Merilä, Sheldon & Kruuk, 2001).

Evolutionary rates and genetic variation

One of the questions motivating surveys of genetic variance is what influence will this variation have on evolutionary potential, or 'evolvability' (Mousseau & Roff, 1987; Houle, 1992; Merilä & Sheldon, 1999)? Traits more closely associated with fitness might posses less genetic variation, as has been suggested to follow from Fisher's (1930) fundamental theorem of natural selection: 'the rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time'. Several reviews have indeed found that traits assumed to be under strong directional selection, such as life history traits, typically have lower heritabilities than traits assumed to be under weak stabilizing selection, such as morphological traits (Mousseau & Roff, 1987; Roff & Mousseau, 1987; Falconer, 1989). This could cause an evolutionary limitation for populations exposed to changing environmental conditions (including introduced populations). Under these circumstances, life history traits may be subject to the strongest selection and yet be fettered with the least genetic variation.

It is also possible, however, that the lower heritability of traits closely associated with fitness is not caused by diminished additive genetic variation but instead by more phenotypic variation (V_p). Higher V_p could be caused by higher residual variation resulting from non-additive genetic variation, environmental variation, or measurement error (Price & Schluter, 1991; Houle, 1992; Hoffman, 2000). In support of this view, recent reviews and empirical studies have found that the lower heritabilities of life history traits are not necessarily associated with lower additive genetic variation (Houle, 1992; Merilä & Sheldon, 1999; Merilä & Sheldon, 2000; Kruuk et al., 2000). The evolvability of life history traits may therefore not be compromised and they may be able to evolve as fast as other types of traits.

The relationship between levels of genetic variation and evolutionary potential is best addressed empirically: do traits closely associated with fitness evolve at different rates than traits less closely associated with fitness? We addressed this question using a simple 'vote counting' procedure based on which type of trait had the maximum evolutionary rate (darwins and haldanes analyzed separately) within a given study or study/interval combination (some studies had rates over several intervals). Counting the results of these contests formed our basis for inference and controlled for time interval and taxon. Our first level of comparison included phenotypic (measured on wild-caught individuals) and genetic (common garden) rates for each study/interval combination. Our second level of comparison included only genetic study/interval combinations. Our third level of comparison was based on an overall vote for each study (i.e., count of the number of intra-study cases supporting one trait type or the other). Our fourth level of comparison used an overall vote for each study based on genetic comparisons only. Sample sizes restricted our analyses to contrasts of life history versus morphological traits (using the categories of Mousseau & Roff, 1987, Roff & Mousseau, 1987) and traits under directional versus weak optimizing selection, (using the categories of Houle, 1992).

The use of darwins versus haldanes generated different results. Using haldanes, we found no evidence that either morphological or life history traits evolved faster (Table 1). Using darwins, however, life history traits appeared to evolve faster than morphological traits at each comparison level (Table 1). The difference between rate measures was particularly striking when only genetic rates were considered: life history traits won contests nearly as often as morphological traits using haldanes but life history traits were always faster using darwins (Table 1). With a vote counting

Table 1. Counts of contest winners in comparison of maximum rates for life history (L)and morphological (M) traits. Results are tabulated from a nested analysis, first considering all contrasts in the dataset by species, time, and genetic basis, the subset of those cases using a 'genetic' (common garden) design, and then the overall evidence by entire study (evaluated in each study on the basis of number of contest wins for all rate contrasts and just genetic contrasts)

Type of comparison	Haldanes			Darwins		
	L	M	Binomial	L	M	Binomial
All cases	8	7	0.500	16	5	0.013
All 'genetic' cases	4	4	0.637	9	0	0.002
By study*	1	2	0.500	6	2	0.145
By 'genetic' study	2	3	0.500	6	0	0.016

*studies with equal numbers of cases where L and M won are excluded as inconclusive.
Binomial: binomial probabilities of obtaining the observed number, or less, of life history or morphological losers under a null probability of 0.5 per contest.

procedure based on maxima, trait types with more estimated rates would be expected to win more often by chance alone. To examine if this was responsible for the observed patterns, we tabulated the number of rate estimates (N_r) used in obtaining the maxima for all haldane and darwin contests. The trait type with the larger N_r won the vote in 20 out of 33 contests where a disparity existed (across both rate types combined: $p = 0.150$), suggesting that while N_r may have some impact on winning a contest, it is not likely to have accounted for our results. Indeed, N_r was more often larger for morphological darwins than for life history darwins, and yet life history rates rates clearly won out most of the time.

The difference between life history and morphological rates in darwins versus haldanes presumably arises because haldanes are standardized by larger phenotypic standard deviations. In 11 out of the 15 contests for haldanes (all study and level combinations available: $p = 0.042$) life history traits had larger s_p estimates consistent with this explanation, and in all cases where life history traits won for darwins but lost for haldanes s_p was larger for life history traits. Regardless of the rate measure, the lower heritability of life history traits does not seem to impede their evolution, at least relative to morphological traits. Perhaps life history traits tend to be under stronger directional selection in new environments, which would compensate in the short term for their lower heritabilities. Alternatively, perhaps additive genetic variation is more important than heritability in determining evolutionary potential (Houle, 1992).

Our intra-study contrasts for traits under directional versus weakly optimizing selection (using Houle's, 1992, categories) did not suggest a significant difference between trait types with our limited sample sizes for such contrasts (e.g., four directional versus nine optimizing wins for haldanes; nine directional versus six optimizing wins for darwins for all study/interval contests combined). Indeed, at no level in our hierarchy of contrasts (same as those in Table 2) were proportions significantly different from chance. This result might be construed as consistent with no difference in response of trait types, perhaps due to stronger selection compensating for any diminished genetic variation in directionally selected traits. However, a slight tendency for directional wins for darwins to become optimizing wins with haldanes (3 out of 3 cases where winner changed with rate metric) would again suggest that relative amounts of s_p, and perhaps residual variation, played a role in differences between rate measures in quantifying the realized evolutionary potential of nominative directional and weakly optimizing characters. Indeed the s_p of directional traits was larger than that of optimizing traits in 12 out of the13 cases where haldanes were estimated ($p = 0.002$).

Conclusions regarding different rates of evolution for different classes of traits depended on whether or not rates were standardized by the phenotypic standard deviation (i.e., haldanes vs. darwins). Perhaps the same is true for analyses of selection. In their review, Kingsolver et al. (2001) found that selection was nearly twice as strong on morphological traits as on life history traits. As they noted, this is counterintuitive to the idea that life history traits are more closely tied to fitness and therefore under stronger selection. However, the observed difference may arise in part because selection gradients and standardized selection differentials (i.e., selection intensities) are standardized by the phenotypic standard deviation (s_p). For a single trait, uncorrelated with other traits, evolution should proceed according to $R = h^2 S$ on a non-standardized scale and $R/s_p = h^2(S/s_p)$ on a variation-standardized scale. If life history traits have

Table 2. Evolutionary difference relative to time within species and study systems

Species	Study*	Type	Difference		
			Increase	Other	Net
Anolis sagrei	Losos et al., 1997	Pop.	3	0	+
Bronta leucopsis	Larsson et al., 1998	Pop.	2	0	+
Oncorhynchus gorbuscha	Bigler et al., 1996	Time	1	0	+
Oncorhynchus keta	Bigler et al., 1996	Time	3	0	+
Oncorhynchus kisutch	Bigler et al., 1996	Time	1	0	+
Oncorhynchus nerka	Bigler et al., 1996	Time	2	1	+
Oncorhynchus nerka	Cox & Hinch, 1997	Time	2	0	+
Oncorhynchus tshawytscha	Bigler et al., 1996	Time	3	0	+
Passer domesticus	Baker, 1980	Pop.	2	0	+
Peromyscus maniculatus	Pergams and Ashley, 1999	Pop.	9	7	+
Poecilia reticulata	Reznick et a1., 1990, 1997 Reznick, et al., 1987	Pop.	9	3	+
Poecilia reticulata	Margurran et al., 1992, 1995	Pop.	1	0	+
Salmo salar	Beliak and Powers, 1986	Time	2	0	+
Thymallus thymallus	Haugen and Vøllestad, 2000	Pop.	17	7	+
Thymallus thymallus	Haugen and Vøllestad, 2001	Time	2	1	+
Zosterops lateralis	Clegg et al., 2001	Pop.	4	6	−

*Studies cited are listed in the appendix.

Two types of studies are tabulated 1) contrasts among populations diverging or evolving for different periods of time (pop.), and 2) time series trends within populations (time). In the case of the former, counts represent number of traits suggesting increase or decrease (other) in maximum rate numerators (haldane or darwin) with increasing time interval. For the latter, counts represent the number of traits showing a significant trend in trait value over time (increase) or no statistically significant trend with time (other). A '+' indicates net tendency for increasing difference with time. Both genetic and phenotypic comparisons are tabulated.

a greater s_p they may be characterized by smaller selection intensities (S/s_p) and slower evolution on a haldane scale (R/s_p), despite greater additive genetic variation, larger selection differentials (S), and larger evolutionary responses on an absolute scale (R).

As an alternative to standardizing by s_p it may be possible to create a rate measure that standardizes evolutionary difference by a measure of mean trait size, creating a metric with analogy to the coefficient of additive genetic variation that is at times used as an alternative to heritability in evaluating evolvability (e.g., Houle, 1992; Merilä & Sheldon, 1999; Kruuk et al., 2000; Merilä & Sheldon, 2000). Though such an alternative metric could provide further insights into the factors impacting evolutionary response, our goal here was to make use of existing rate measures.

What are the implications of our finding that traits with low heritabilities (life history) evolve just as fast as (or faster than) traits with high heritabilities (morphology)? First, life history traits, which are closely associated with fitness and presumably evolved under strong directional selection, retain considerable potential for microevolution. Second, conclusions regarding evolutionary rates and the strength of selection for different types of traits depend on standardization by the phenotypic variation. Rates of evolution on a non-standardized scale (darwins) are higher for life history (and directionally selected) traits but this is not because they have higher heritabilities (they don't) or only because they have higher additive genetic variance (they often do), but probably because they experience stronger selection differentials (not variation standardized).

Contemporary diversification and time interval: a positive correlation?

The trajectory of evolutionary diversification through time is an issue of great importance because it may indicate how microevolutionary processes (selection, micromutation, drift, gene flow) translate into macroevolutionary events (e.g., speciation). The trajectory of evolution thus remains a central question of evolutionary biology (e.g., Jablonski, 2000; Schluter, 2000). Studies on time scales of thousands to millions of years have been used to argue that evolutionary rates

do or do not decline with time, and the answer obtained depends on the methods of analysis and the perspective of the investigator (Gingerich, 1983; Gould, 1984; Lynch, 1990; Schluter, 2000). A pattern that does seem universal on these time scales is that the amount of evolutionary diversification within a lineage increases with time (Schluter, 2000), although not necessarily indefinitely or at a constant rate. In this section, we test whether the amount of microevolutionary change increases on contemporary time scales.

Before answering this question, we must address the root cause of negative relationships (i.e., slope = negative) between evolutionary rate and time interval (Gingerich, 1983, Sheets & Mitchell, 2001a). Part of this pattern reflects autocorrelation brought about by regressing rates, in which time is in the denominator, against time itself (Gingerich,1983; Gould, 1984; Sheets & Mitchell, 2001a). This autocorrelation can be revealed by randomizing evolutionary rate numerators (trait difference) with respect to denominators (time interval). When these randomized rates are plotted versus their time intervals on a log-log scale, a strong negative correlation, approximating the actual pattern is often evident (Sheets & Mitchell, 2001a). This autocorrelation is strong within our dataset (Figure 3). Nonetheless, an underlying evolutionary trend in diversification can still be examined using these log-rate versus log-interval plots by assessing whether the slope and intercept of the actual data set differ from those obtained under many randomizations. The actual slope in our database was significantly flatter than the slopes of 1000 randomizations ($p = 0.01$), and the actual intercept was correspondingly smaller ($p = 0.01$), which would tend to occur when shorter time intervals are associated with smaller amounts of trait change.

To further examine evolutionary trajectories independent of artefactual autocorrelation, we examined the absolute amount of evolutionary diversification (i.e., difference or change in trait values) relative to the time interval. For this analysis, we used haldane numerators (difference/s_p) as our measure of evolutionary difference. Several studies contributed a disproportionate number of rate estimates to our database, which might skew any regression so that the line would have to pass through the points for that study. To avoid this problem, we also analyzed maximum values by study, trait, and time interval, and then by study and time interval. For this analysis we also only included studies in which evolutionary differences likely arose

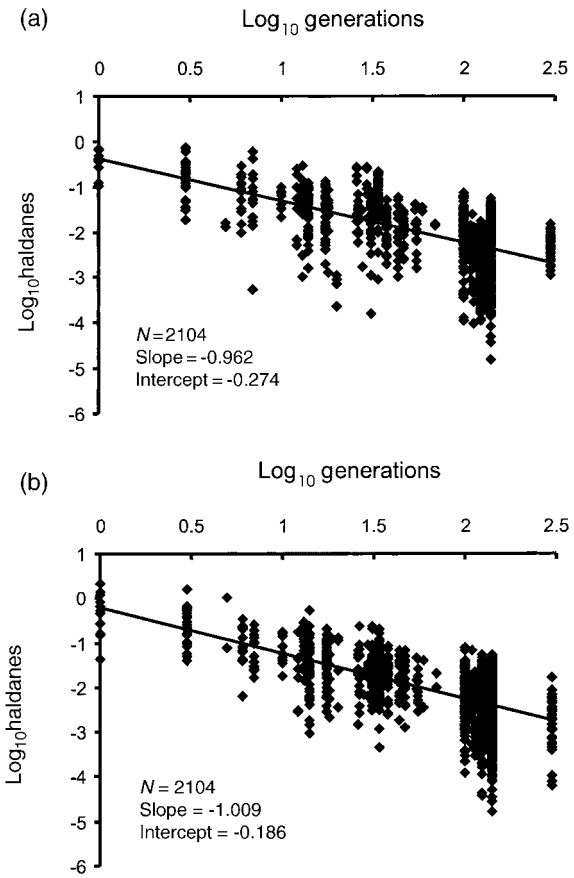

Figure 3. Actual and randomized log-rate versus log-interval (LRI) distributions for studies of contemporary microevolution. (a) actual data, for which an LRI analysis has been performed (in the manner of Gingerich, 1993), (b) example of a randomized dataset in which actual haldane numerators have been randomized with respect to time intervals in our dataset.

de novo over a defined time period, and excluded a few cases in which evolutionary difference was measured at an undefined point in the evolution or divergence of the populations (e.g., allochronic evolution in deer mice, *Peromyscus maniculatus*: Pergams & Ashley, 1999).

When determining maximum rates, we grouped the data into four-generation time intervals within studies to prevent excessive representation of studies reporting rates over multiple, but very similar, time scales. We then performed least squares ANCOVA and regressions (when significant interaction term) for divergence versus time on raw and $\log_{10}$-transformed values (with genetic and phenotypic studies as a fixed factor and time as a covariate). Though $\log_{10}$-transformed data is probably more appropriate from the standpoint of assumptions for regression, we

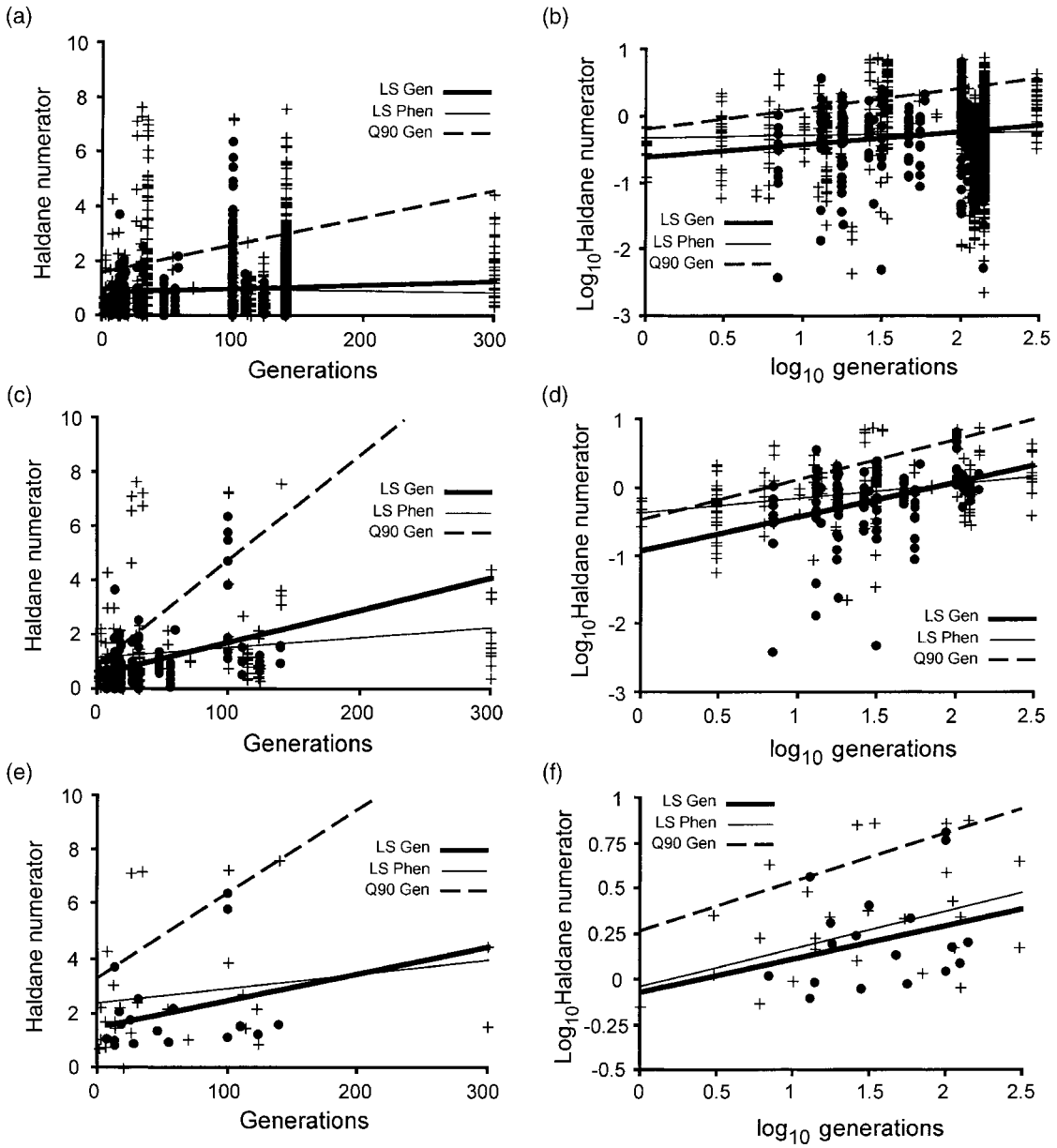

Figure 4. Plots of evolutionary difference relative to interval on non-transformed (on left) and log-transformed (on right) scales. Least squares regression lines and equations are shown for genetic and phenotypic study designs, along with the 90th quantile least absolute deviations regression for genetic studies. (a) and (b) all rates by time frame, (c) and (d) maximum rates by study, trait and time frame, (e) and (f) maximum rates by study and time frame. A single point occurs below the x-axis in (f) ($x = 1.30$, $y = -1.65$)

feel that examination of such a relationship on the natural scale of the data is also informative given that log-log relationships are by nature heavily influenced by trends on the shortest time intervals. We characterized the upper bounds of the relationship (90th quantile regression) using a least absolute differences algorithm (Scharf, Juanes & Sutherland, 1998) in a manner analogous to the least squares procedures described above. *P*-values for slopes are for one-tailed hypotheses (i.e., H_o: slope $= 0$, H_a: slope > 0).

Examination of all haldane numerators plotted against their time interval (generations) showed little evidence of a general trend toward increasing evolutionary diversification (slope $\leq 1.4 \times 10^{-3}$; $p = 0.267$; Figure 4(a)). The 90th quantile regression for genetic studies had a notably steeper slope that neared

significance (slope = 0.010; $p = 0.031$). Transforming evolutionary differences and time intervals onto log scales tended to linearize the relationship and homogenized variances (Figure 4(b)). These log-log plots revealed a slight trend toward larger evolutionary differences over longer time intervals for genetic studies (slope = 0.191; $p = 0.005$) but not phenotypic studies (slope = 0.037; $p = 0.126$). The upper 90th quantile regression was also significant for genetic studies (slope = 0.309; $p = 0.002$) but not for phenotypic studies (slope = 0.023; $p = 0.178$).

When focusing specifically on maximum rates for each trait, species, and time scale, evolutionary difference was significantly related to time interval for genetic and phenotypic least-squares and 90th quantile analyses, for both raw (Figure 4(c)) and log-transformed (Figure 4(d)) data ($p \leq 0.012$ for all). In each of the least squares cases, slopes for genetic rates (raw: slope = 0.012; $\log_{10}$: slope = 0.494) were steeper than those for phenotypic rates (raw: slope = 0.004; $\log_{10}$: slope = 0.218; $p \leq 0.050$ for all contrasts). Upper 90th quantile slopes for genetic and phenotypic studies were significant ($p \leq 0.025$) and tended to be higher than the least squares values (Genetic: raw: slope = 0.039; $\log_{10}$: slope = 0.570; Phenotypic: raw: slope = 0.007; $\log_{10}$: slope = 0.201). At the most conservative level of analysis (i.e., maximum among all traits within a study: Figures 4(e),(f)), genetic and phenotypic least-squares slopes no longer differed ($p \geq 0.331$), and the combined slope for raw data was suggestive ($p = 0.086$). A positive combined slope was found for the least-squares (slope = 0.203; $p = 0.036$) and 90th quantile (slope = 0.224; $p = 0.028$) ANCOVAs of $\log_{10}$-transformed data. Our results suggest that over a wide range of studies, taxa, and traits, evolutionary difference accumulates with time, particularly when considered on a log scale, although a large amount of variation remains unexplained. Most data points in our analyses were for synchronic designs so the effect of doubling divergence time was largely just an increase in the temporal spread in the dataset with little impact on the observed pattern (beyond changes in slope estimates).

We also looked within studies to see if the maximum amount of difference increased with time. For this analysis, we used 16 independent study systems that included either among-population comparisons on different time scales (different population pairs representing different intervals) or time series within populations (Table 2). In the latter case, we interpreted a statistically significant correlation between trait values and time (as reported by the authors) as evidence of increasing difference with time. Evolutionary difference increased with time interval in 15 of the 16 studies (Table 2). Only one study showed a greater tendency for decreases in evolutionary amount with time and the six traits showing this trend in that study were all measurements of head and beak dimensions.

The actual underlying increase in evolutionary diversification with increasing time interval may be greater than what we could demonstrate here because of imprecise estimation of generations (see below) and sampling (i.e., measurement) error. If sampling error is roughly constant over time but true evolutionary difference is accumulating, error will contribute most strongly to differences on the shortest time scales. Even in the theoretical case of no true difference in the means of two populations, measurement error will still result in a non-zero estimate. Sampling error will thus increase the apparent intercept and decrease the apparent slope of the difference versus interval relationship.

Our results suggest some caution is merited when comparing rates obtained using 'genetic' versus 'phenotypic' methods. In most cases, the slope for phenotypic studies was at least qualitatively lower than that for genetic studies (Figure 4). Phenotypic rates integrate genetic change and any phenotypic plasticity (genotype-by-environment interaction). Substantial phenotypic shifts may occur in a single generation and the magnitude of such effects would remain relatively constant even over longer time intervals (Trussell & Etter, 2001). As a result, the relationship between trait difference and time interval will be less steep for phenotypic studies. Future studies should place even greater emphasis on quantifying the actual genetic basis for differences: after all, this is one of the special opportunities afforded by the study of contemporary evolution.

What are the implications of our finding that evolutionary change increases with time, and potentially does so more strongly for genetic rates than for phenotypic rates? First, phenotypic plasticity may make an important contribution to the earliest stages of population divergence or evolution. This matches the expectation that plasticity may be one way in which new colonists can persist in an environment that might otherwise drive them to extinction (Losos et al., 2000, 2001). Second, a general evolutionary trend toward increasing diversification seems to characterize evolutionary potential (particularly for maxima). Even

though most evolutionary alterations are fairly small, and many studies show only minor differences over long time intervals, the maximum amount of evolution that can be accomplished increases with time even on contemporary time scales and across a broad range of species, traits and selective regimes. We are left with the conclusion that at least some evolution measured over a few generations contributes to larger differences over tens of generations, and a few of these in turn contribute to even larger changes over hundreds of generations.

Contemporary rates and time interval: do rates decrease with time?

Evolutionary diversification clearly increases with time (Lynch, 1990; Schluter, 2000; above) but does the *rate* of diversification decrease with time? This is an important issue because if rates decrease substantially, microevolutionary trends may not add up to macroevolutionary events in a gradual fashion. We might theoretically expect rates to decrease with time if populations evolve toward adaptive peaks, if genetic variation becomes depleted under directional selection, or if evolutionary rates vary through time. Empirical results from laboratory studies often show an asymptotic pattern of evolutionary change (e.g., Lenski & Travisano, 1994), and a similar pattern is suggested by at least one experimental introduction in the wild (Reznick et al., 1997). Moreover, ample evidence suggests that natural selection and evolutionary rates vary considerably within and between generations (Schluter, Price & Rowe, 1991; Grant & Grant, 1995). We attempted to evaluate whether evolutionary rates decrease with time interval in our database.

The shape of the relationship between evolutionary diversification and time interval should reveal whether evolution is slowing with time. For instance, if evolution is slowing, the slope of a log-diversification versus log-interval plot should be less than one (Lynch, 1990; Gingerich, 1993). It is worth noting that interpretation of the pattern of rate relative to time is dependent on the dimensionality of the metric used to quantify diversification. While a number of authors have measured diversification in terms of among-group variance (standardized by within-group variance: e.g., Lynch, 1990; Schluter, 2000), our measure, the haldane numerator, quantifies between-group difference (standardized in units of s_p). Dimensionality effects make it quite possible that a constant rate of diversification in variance units (square difference) would actually reflect a decrease in the rate of diversification measured as difference between two groups. All of the slopes from our log-difference versus log-interval plots were less than one (Figure 4). There are, however, limits to this method of inference because log-log plots heavily weight in favor of evolution over short time intervals and because the intercept of a log-log plot will be particularly sensitive to error (Schluter, 2000). As described above, measurement error may even impact the intercept of untransformed data.

It may hence also be informative to consider the pattern of diversification relative to time on the natural scale of the data (rather than log-log) after accounting for impacts on the y-intercept due to measurement error (i.e., 'error divergence'). We simulated the effect of sampling error by drawing pairs of samples, with replacement, from a single population (mean trait value $= 0$ and SD $= 1$). Sample sizes for the studies in our database ranged from less than 10 to over 600 individuals (or families). For simplicity and to be conservative, we used 20 individuals per population in 10,000 simulations. Median divergence due to measurement error was thus estimated to be 0.213 standard deviations. This value was surprisingly high, actually exceeding 20% of the haldane numerators in our database. We then plotted the maximum haldane numerators per study relative to time interval, with the intercept of our linear regression constrained to pass through 0.213. For this analysis, we excluded the 300-generation values from Diamond (1989) because they had very high leverage. The regression was positive and significant (slope $= 0.031$, $p < 0.001$) further confirming a trend toward increasing diversification with time.

Further analyses based on regressions with a constrained intercept showed that the rate of diversification clearly decreases with time. First, most haldane numerator estimates on short time intervals lie above the regression line described above. Conversely a regression using only the data from 1 to 20 generations generates a line that, after extrapolation, most of the points over longer intervals fall below. Second, regressions run from the origin through generations 1–40, 1–60, 1–100, 1–120 and 1–140 (no rates were available for 60–80 generations) tended to have progressively shallower slopes (Figure 5(a)). Third, we partitioned the 35 maximal estimates into three groups of 11–12 rates (short, medium, and long intervals) and calculated linear regressions for each, forcing the first through 0.213 and subsequent regressions to start where the previous ones ended. This analysis revealed

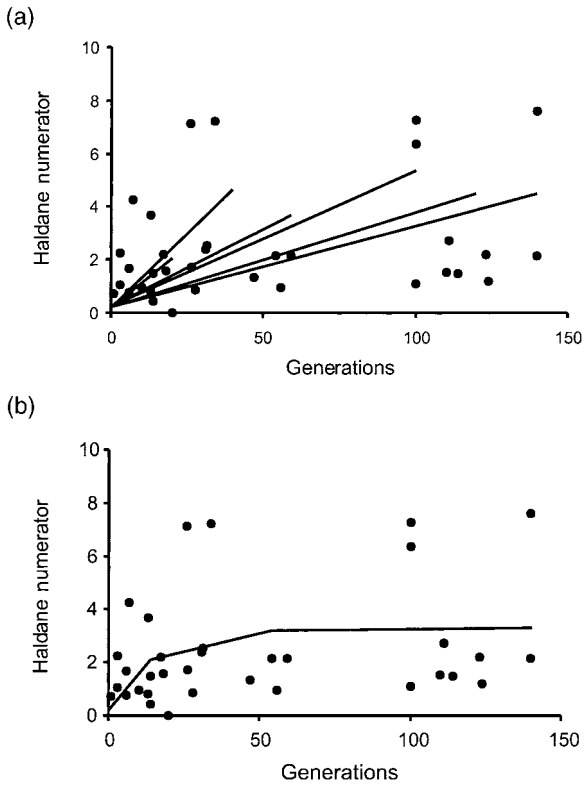

Figure 5. Two methods for graphically depicting a decline of maximum evolutionary difference (for maxima by study) with increasing time intervals with y-intercept constrained at 0.213 (simulated 'error divergence'). (a) regression lines from origin through progressively larger components of dataset (1–20, 1–40, 1–60, 1–100, 1–120 and 1–140 gens), and (b) segmented regression through three temporal subsets of maximum rates by study (11–12 rates each) starting at the origin.

an initially fast positive rate, followed by a declining rate over subsequent intervals (Figure 5(b)).

Gingerich (2001) performed his log-rate versus log-interval (LRI) analysis on a subset of studies from our current dataset (i.e., that from Hendry & Kinnison, 1999). He obtained a least absolute deviations slope of -1.046 with an intercept of -0.163, which is consistent with a 'stabilizing process' (slope $= -1.0$, Gingerich, 2001). If we perform the same analysis on our current dataset, the relationship is similar (slope $= -0.962$, intercept $= -0.274$). It is important to recognize, however, that testing for a 'stabilizing process' is not the same as testing for a slowing rate of diversification. In typical LRI tests for a stabilizing process, many pair-wise estimates of rates are made using a chronoseries within an evolutionary lineage, and both short and long time intervals are as likely to derive from early in the chronoseries as late. In this case, 'stabilizing' refers to a pattern of multiple reversals of short-term rates such that the expectation is little to no net change over longer intervals (Gingerich, 1993, 2001, Sheets & Mitchell, 2001b). Many of the studies in our database, however, were for introductions and other cases that considered evolutionary differences measured at a defined point in time following establishment or alteration of selective regimes. As a result, short time intervals tend to come from early in divergence and long time intervals integrate later periods in the divergence process. In this situation, a 'stabilizing' LRI slope may still reflect a preponderance of generally directional processes with initially rapid evolution (perhaps in response to new selection pressures), followed by a slowing of rates over time as populations approach equilibria.

What are the implications of our finding that the rate of contemporary diversification apparently declines with time? The first is that most short-term microevolutionary trends, arising under novel conditions (e.g., colonization or altered selective regime), do not accumulate indefinitely at a steady rate (not likely in terms of difference or variance). A slowing rate of evolution with increasing time is a standard finding over macro-scales (Gingerich, 1983; Lynch, 1990) but has been challenged as a possible analytical artifact of log analyses and sampling error (e.g., Schluter, 2000). We have performed analyses that help obviate some such artifacts, and confirmed that evolutionary rates still decrease with time across a wide range of study systems. Additional studies of genetically-based alteration over time series within populations (allochronic) will be needed before we can accurately assess to what extent evolutionary rates decrease with time. However, even if nearly all rates slow to a standstill over contemporary time frames, such an observation cannot be used to argue for a disjunction between microevolution and macroevolution. With so many populations (e.g., 1.1–6.6 billion globally by estimation of Hughes, Daily & Ehrlich, 1997), and so much evolutionary time, even exceptionally rare sustained trends could easily explain most or all of the history of life on earth. New species probably arise only rarely and we are unlikely to sample a microevolutionary trend that is on its way to creating a full-fledged new species. Moreover, microevolutionary trends that ultimately lead to macroevolutionary events are unlikely to be constant in direction and rate. We argue that although macroevolution may often ultimately be the result of microevolution 'writ large' (Losos et al., 1997), from a temporal sense it may

better be characterized as the result of microevolution 'writ in fits and starts'.

Further considerations

Our analyses indicate that rates of evolution (and divergence) offer useful insights into evolutionary pattern and process. By no means do we regard our treatment as definitive but rather suggestive of general trends and instructive regarding potential analytical considerations. The major determinants of evolution will be the strength and consistency of evolutionary mechanisms (e.g., $\boldsymbol{\beta}$, vector of selection gradients) and additive genetic variance/covariance ($\mathbf{G}$-matrix). The integration of these factors determines the rate of evolution in natural populations ($\boldsymbol{\Delta z} = \mathbf{G}\boldsymbol{\beta}$; Endler, 1986; Falconer, 1989; Roff, 1997; Schluter, 2000; Arnold, Pfrender & Jones, 2001). As such, rates allow us to extend our interpretations beyond theory and into the real world. Here we discuss a few of the challenges that should be addressed in the future quantification of rates.

The conclusions we have drawn are robust to how synchronic time was specified (time from common ancestry or twice that value), largely because our analyses either considered rate pattern in a database consisting mostly of synchronic measures or controlled for time interval. Still, synchronic rates of divergence pose an interpretive challenge because they integrate the evolutionary trajectories of two populations in a single measure, which brings to question how comparable such rates are to allochronic values. The challenges posed by synchronic designs weigh heavily in favor of more analyses of allochronic rates (when they become available) and consideration of intra-lineage evolutionary alteration separate from evolutionary diversification among populations.

Measurement error in time estimation is an important issue for both synchronic and allochronic designs. Time has a disproportionate effect on rate values, and two forms of temporal error impede rate comparisons. One form of temporal error can occur when estimating the time since common ancestry or between two samples over time. Although such errors certainly exist and should be minimized, a more insidious error comes when estimating generation lengths, which is necessary when converting intervals in years to intervals in generations (i.e., for the haldane). Generation length is most commonly estimated as age at first maturity but this will consistently underestimate generation lengths for iteroparous organisms. A better alternative is to estimate generation length as the average age of breeders, preferably weighted by their relative reproductive output at age (e.g., life table approach; Reznick et al., 1997; Haugen & Vøllestad, 2001).

Error in time interval estimation also increases uncertainty in the independent variable for analyses of rate or difference versus time, causing linear regression to underestimate the true slope. The modest regression slopes we have presented should not be surprising given the often informal manner in which time interval and generation length have been specified and estimated. Such error may even factor into the impression of slowing rates with time. Some amelioration for temporal error may be possible through the use of reduced major axis regression, which allows for error in the x-axis (Sokal & Rohlf, 1995), or some similar approach.

A second important issue surrounds sampling error (see above). In many cases, differences among populations and any corresponding rate estimates may be well within the range of typical sampling error. Differences between samples (synchronic or allochronic) should therefore be examined using statistical tests. Confidence boundaries and statistical tests should also be employed when comparing evolutionary rates themselves, with one approach being randomization and bootstrapping (Hendry & Kinnison, 1999). Fortunately, rates are usually only significantly different from zero when the mean values between samples are also significantly different. Another step, not yet attempted, is to consider and quantify error in time interval estimation. We expect such error can be quite high but its direct computation will generally not be possible. It may be advantageous, however, for investigators to estimate a set of bounds within which they believe the true time interval resides. It would then be a simple matter to approximate how those time interval bounds would impact confidence in estimated rates.

Two other problems arise when accounting for error. The first is that very small evolutionary rates could conceivably lead to very large changes *if* they are consistently maintained for many generations. Thus, small evolutionary rates should only be rejected from consideration if the sample size is large enough to provide a high power when testing for differences of that magnitude. The second problem is that errors may not be randomly distributed among observed evolutionary rates. In fact, the largest rate estimates on a

given time frame (those of potentially most interest) may include contributions from errors that magnify the true difference. The single best way to minimize these problems is to have large sample sizes, but at present many sample sizes available for rate estimates are notably small (e.g., often < 10 individuals per sample).

Conclusions

We propose that contemporary rates are distributed in the following manner. Differences at any given time interval are skewed toward many slow and few fast rates. The magnitude of these differences, and the variation among them, increases with longer time intervals, leading to an increasing spread in the distribution of rates. Most short-term evolutionary trends are likely fleeting or 'dead-ends' (i.e., reach their optima with minimal change), whereas a few persist for longer periods. When conditions change, rapid evolution may begin anew in populations that had formerly ceased directional evolution. We should therefore expect occasionally fast short-term directional evolution interspersed by periods of apparent quasi-stasis in most populations. Indeed this was Darwin's (1872) view of temporal pattern in species evolution:

> "Many species when once formed never undergo any further change but become extinct without leaving modified descendants; and the periods, during which species have undergone modifications, though long as measured by years, have probably been short in comparison with the periods during which they retain the same form".

Our results also confirm that life history characters appreciate no less evolutionary potential than morphological traits, but posses larger amounts of phenotypic variation relative to additive genetic variation. Indeed life history triats appear to evolve faster than morphological traits when rates are measured in darwins. Ultimately, the class of a trait (life history or morphological; directionally or optimally selected) may pose little limitation to its short-term rate of evolution when a population is exposed to new conditions.

Is macroevolution simply microevolution writ large? Perhaps ultimately, but probably not often as a result of consistent gradual change over time. We found that although evolutionary diversification increases with time, the number of rates potentially associated with sustained change over long (but contemporary) time frames was small. The vast majority of microevolutionary changes, although surely of significance to the populations experiencing them, are unlikely to initiate macroevolutionary events in a single persisting transition. This conclusion is consistent with the observation by Kingsolver et al. (2001) that very strong directional selection is actually rare in nature. Despite these generalizations, microevolutionary trends clearly have the potential to lead to macroevolutionary events given vast numbers of populations and lengths of time. Thus over extended time frames macroevolution may be accomplished by a combination of 'microevolution writ large' and 'microevolution writ in fits and starts'.

Our database and approach does not currently fulfill the great inferential potential of evolutionary rates. Increasingly refined insights may come when many more contemporary rates are computed by original investigators with greater precision and more detailed knowledge of their respective study systems. With this study we have begun to consider elements of both what studies of 'rapid' evolution imply about the norm and the potential of contemporary evolution. While many rates may reflect evolution *par usuel*, not all reflect it *par excellence*. We believe that further attempts to understand the pattern and process of evolution require analytical approaches that become increasingly adept at focusing on both of these aspects of evolution. To neglect either would be akin to attempting to understand the scientific and artistic progress of our own species without appreciating the occasional dramatic advances made by an inspired few as well as the more common and gradual advances of the many.

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Appendix. Studies used to develop the database used in the present paper

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