MATTERS OF THE RECORD

Accounting for unequal variances in evolutionary trend mechanisms

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Evolutionary trends seemingly abound throughout the history of life. Perhaps the best-known example is Cope's rule, the tendency for lineages to increase in size over time. Other examples include hypothesized trends toward increasing complexity and fitness. What kinds of mechanisms cause such large-scale trends—trends occurring in higher taxa over geological time spans—and how can we effectively visualize them?

In a seminal paper, Stanley (1973) proposed that apparent directional trends such as Cope's rule can result from unbiased change away from small initial values, analogous to diffusion away from a lower bound. Fisher (1986) generalized this idea, and Gould (1988, 1996) argued that such trends are properly viewed as increases in variance rather than trends in the average. These types of trend mechanisms were labeled by McShea (1994) as *passive,* in contrast to *driven* mechanisms in which change is biased in a particular direction because of (for instance) adaptive benefit or ontogenic constraint.

In McShea's usage (McShea 1994, 1998b, 2000), the passive and driven categories include a broad range of evolutionary dynamics, of which unbiased diffusion and biased change are the simplest. More generally, McShea defines a driven trend mechanism as one resulting from an unstructured state space in which rates of change, speciation, and extinction are constant for all lineages. In contrast, a passive trend mechanism is one in which change among lineages follows a state space in which the rates vary in a structured way (McShea 2000). A similar distinction is the passive/active classification proposed by Wagner (1996), although Wagner's active trends constitute a broader category than McShea's driven trends.

Much empirical and methodological work has been devoted to distinguishing passive and driven trends. Some recent papers in the paleontological literature include those of Carlson (1992), Boyajian and Lutz (1992), McShea (1993, 1994, 1996, 1998a,b, 2000, 2001), Arnold et al. (1995), Wagner (1996), Saunders and collaborators (1996, 1999), Dommergues et al. (1996), Jablonski (1996, 1997), Trammer and Kaim (1997), Alroy (1998, 2000), Renaud et al. (1999), Wang (2001), Sidor (2001), Norris and Nishi (2001), and Carrano (2005). Biologists have explored the issue as well; see, for instance, papers by Maurer (1998), Bokma (2002), and Knouft and Page (2003).

In a recent Matters of the Record article, Alroy (2000) argued that the passive/driven distinction should be superseded by a complexity-based classification based on ancestor-descendant data. To visualize such data, he advocated a powerful graphical tool, the change-vs.-ancestor plot, and showed how it can effectively discern a variety of complex trend mechanisms. In this paper, I expand upon the change-vs.-ancestor plot and its use in classifying trend mechanisms. In particular, I show that the variance as well as the average of ancestor-descendant transitions must be taken into account, because (1) unbiased mechanisms (having zero average change) can generate complex evolutionary trends as a result of having unequal variances, (2) mecha-

nisms with the same average behavior can produce dissimilar evolutionary trends if their variances differ, and (3) mechanisms with dissimilar average behavior can produce similar evolutionary trends if their variances differ.

The Change-vs.-Ancestor Plot and Trend Classification

The change-vs.-ancestor or ''branch-breaking'' plot (Wagner 1996; Alroy 1998, 2000; so named because it ''breaks'' the branches of a phylogenetic tree) is a valuable tool for visualizing within-lineage trends, particularly complex and subtle ones. In such a plot, the x-axis represents the ancestral value of some state variable, and the y-axis represents the change or transition in that state variable between its ancestral and descendant values (i.e., descendant value minus ancestral value). The plot thus shows how different types of ancestors differ in their degree of change. The state variable may represent any quantitative characteristic, but because this methodology is most often used to study body size or other morphological characteristics, I will henceforth refer to the state variable as ''morphology'' for the sake of simplicity.

Why use a change-vs.-ancestor plot rather than a simple plot of descendant vs. ancestral morphologies? The weakness of the latter plot is that subtle patterns may be obscured when the descendant and ancestral morphologies are strongly correlated, as is often the case. The change-vs.-ancestor plot does not suffer from this problem, because it portrays first differences in morphology. It is thus similar to the residuals-vs.-predicted plot commonly used when checking the fit of a linear regression model. Taking first differences can also be seen as analogous to subtracting sister species in comparative studies using phylogenetic independent contrasts (Felsenstein 1985).

I illustrate the change-vs.-ancestor plot with a simple example (Fig. 1A, adapted from Alroy 2000: Fig. 2A). The horizontal line represents the average morphological change from one time step to the next. (Here the units for morphology are arbitrary.) For any ancestral morphology, the average change is zero, and therefore the trajectory followed by each individual lineage is an unbiased random walk.
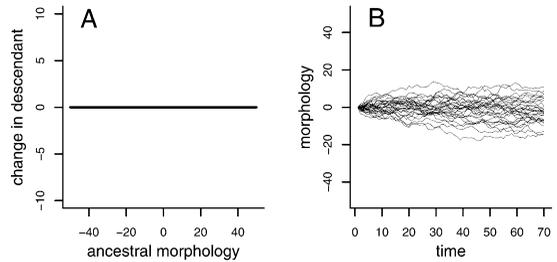

FIGURE 1. A simple evolutionary trend mechanism, equivalent to an unbiased random walk. A, Change-vs.-ancestor plot. Horizontal line represents average change from ancestral to descendant morphologies and is zero for all ancestral morphologies. B, Morphology-vs.-time plot showing evolutionary trajectories for 30 lineages over 70 simulated time steps. See the Figure 3 caption for details on the simulation methodology.

The corresponding morphology-by-time plot, showing simulated trajectories for 30 lineages over 70 time steps, is shown in Figure 1B (adapted from Alroy 2000: Fig. 3A). All lineages are assumed to persist through the entire time interval, with no speciation or extinction. After 70 simulated time steps (see the Fig. 3 caption for details on the simulation methodology), the lineages maintain the same average morphology but their range has increased, as one would expect. At the last time step shown, the distribution of morphologies is roughly symmetric. (The symmetry or skewness of such ''time-slice'' distributions is used by methods such as the subclade test (McShea 1994) and the Analysis of Skewness (Wang 2001) to classify trend mechanisms as passive or driven.) The change-vs.-ancestor plot provides a concise description of the dynamics generating these trajectories.

Figure 1 represents the simplest example of an evolutionary trend. The power of the change-vs.-ancestor plot, however, lies in its ability to depict and discern complex trends. Alroy (2000: Fig. 2) gave a variety of trends involving stable and unstable equilibria, saddle points, and other features; four examples are redrawn here in my Figure 2. Suppose the morphological variable represents size, measured in arbitrary units. Figure 2A shows a simple driven trend toward unlimited increasing size; all taxa have identical positive average change. Figure 2B shows a stable equilibrium (a ''point attractor'') at size = 0 units. Taxa below this size have positive av-
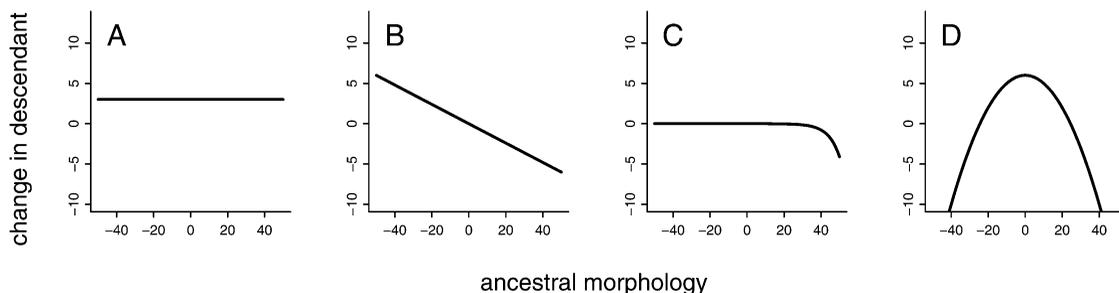
FIGURE 2. Examples of change-vs.-ancestor plots. A, A system exhibiting a simple driven trend. Average ancestor-descendant change is positive and constant for all ancestral morphologies. B, A system exhibiting a stable equilibrium (a ''point attractor'') at size = 0 units. Taxa below this point tend to increase on average, and taxa above this point tend to decrease. C, A system exhibiting an upper bound. All taxa have zero average change except taxa with the largest morphologies, which tend to decrease on average. D, A system exhibiting two equilibria at size = ±30. An unstable equilibrium (a ''repeller'') occurs at size = −30; taxa below this point tend to decrease on average, and taxa slightly above this point tend to increase. A stable equilibrium (a ''point attractor'') occurs at size = +30; taxa slightly below this point tend to increase on average, and taxa above this point tend to decrease.

erage change, and taxa exceeding this size have negative average change, so that over time lineages converge toward size = 0. Figure 2C shows unbiased change with an upper bound. All taxa have zero average change except the largest taxa, which have negative average change, forcing lineages to stay below a maximum size. Figure 2D shows a complex double-equilibrium dynamic, with equilibria at size = ±30, where the curve would intersect the $y = 0$ line (not shown). An unstable equilibrium (a ''repeller'') occurs at size = −30 because taxa diverge away from this point: taxa below this size have negative average change, and taxa exceeding this size have positive average change, until a stable equilibrium is reached at size = +30. Taxa slightly below this stable equilibrium have positive average change, and taxa exceeding this stable equilibrium have negative average change, so that lineages near this size converge toward size = +30. Patterns similar to these have been found in real paleontological data: Wagner (1996: Fig. 9B,C) found morphological trends in Paleozoic gastropods similar to that shown in Figure 2B, and Alroy (1998: Fig. 4) found body mass trends in Cenozoic mammals similar to that shown in Figure 2D.

Rather than use McShea's (1994) passive/driven distinction, Alroy (2000) argued that a trend mechanism be classified according to the number of parameters needed to describe its average change in a change-vs.-ancestor plot. For instance, an unbiased random walk

(Fig. 1A) requires no parameters. A simple driven trend (Fig. 2A) requires one parameter, representing the height of the line. A trend that is a linear function of morphology (Fig. 2B) requires two parameters, representing the slope and the intercept of the line. A trend that is an exponential function of morphology (Fig. 2C) requires at least two parameters, representing the location and scale (rate of decay) of the curve, and possibly another parameter representing its height. A trend that is a quadratic function of morphology (Fig. 2D) requires three parameters, representing the location, scale, and height of the curve. According to Alroy, such a parameter-counting classification scheme describes trend mechanisms better than the broad passive/driven distinction.

Accounting for the Variance

Change-vs.-ancestor plots provide a powerful tool for discovering, portraying, and classifying within-lineage trends. However, I propose that the methodology be improved by explicitly accounting for an important aspect of trends—the variability around the average. Alroy's (2000) classification takes into account only the *average* change; variation about this average is not accounted for. In most of Alroy's plots (e.g., 1998: Fig. 4B; 2000: Fig. 2A–L), only the linear or polynomial trend is shown, omitting the scatter of points about the average. (An exception is Fig. 4A of Alroy

1998.) This omission is a conscious choice by Alroy, who wrote (2000: p. 324):

> Note that in computing these counts of parameters, I have simply omitted the extra term that would summarize the error [i.e., variability] in the model. As an example, in the case of random evolution at least one parameter would be needed to describe the change variable's variance around its mean value of zero. So this distribution does require descriptive parameters in a trivial sense, but none that have anything to do with explaining the relationship between the changes and ancestral states. Because the whole point of the exercise is to see how far a given dynamic departs from randomness, excluding the error term only makes sense.

However, the variance around the average need not be trivial or irrelevant. Alroy has made the implicit assumption that the variance is constant for all ancestral morphologies. What happens if this simplifying assumption is not satisfied? If instead the variance differs among ancestral morphologies, interesting within-lineage trends can result—*even when the average change within each lineage is zero.* Furthermore, as a result of unequal variances, systems with the same average change can give rise to dissimilar evolutionary trends, and systems with different average change can give rise to similar evolutionary trends.

Same Average, Different Trends.—Two change-vs.-ancestor plots are shown in Figure 3A,C (adapted from Alroy 2000: Fig. 2E). Both plots exhibit the same average behavior (represented by the heavy line): most lineages have zero average change except the smallest lineages, which have positive average change. In addition to the average change, the variance of ancestor-descendant changes is also shown, represented by light lines two standard deviations above and below the average (the standard deviation is the square root of the variance). For simplicity, I assume here that the distribution of ancestor-descendant changes is symmetric about the mean; later I discuss the effects of asymmetry. In Figure 3A the standard deviation is constant for all ancestral morphologies, whereas in Figure 3C
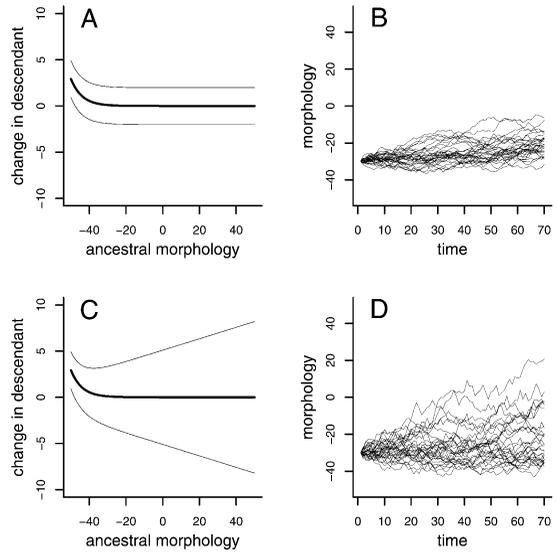

FIGURE 3. Two systems with the same average behavior but different evolutionary trends. A, C, Change-vs.-ancestor plots. Heavy line represents average change from ancestral to descendant morphologies; light lines represent ±2 standard deviations from the average. The average change is the same in both plots. In A, the standard deviation is constant; in C, larger morphologies vary more in ancestor-descendant transitions. B, D, Morphology-vs.-time plots, each showing evolutionary trajectories for 30 lineages over 70 simulated time steps. Trajectories were simulated as follows: At each time step, the change in morphology for each lineage was randomly drawn from a normal distribution with mean and standard deviation given by the corresponding change-vs.-ancestor plot. This value was added to the ancestral morphology to arrive at the descendant morphology. For the next time step, this descendant morphology was used as the new ancestral morphology, and the process was repeated. All lineages were assumed to persist through the entire time interval, with no speciation or extinction. Simulations were run using the software R (version 1.6.2) on a Macintosh. Both sets of trajectories have a lower bound or ''left wall'' resulting from positive average change at small values. However, the maximum and the average morphology increase more quickly in D than in B, as a result of unequal variances in the corresponding change-vs.-ancestor plots. The system portrayed in C, D resembles that found by Wang (2001) for North American Cenozoic rodent sizes.

the standard deviation increases for larger ancestral morphologies. The latter situation would be expected for variables such as body mass when raw data are used without taking logarithms, but it can occur even with log-transformed data, as in the Cenozoic rodents example cited below.

The systems shown in Figure 3A,C give rise to a lower bound or ''left wall,'' because line-

ages with the smallest morphologies tend to increase. In Alroy's (2000) classification, both systems would be summarized by the same two-parameter model, because their average change is identical. However, because their variances differ, these two systems can give rise to qualitatively different evolutionary trends. For the system in Figure 3A, the corresponding morphology-vs.-time plot (Fig. 3B) shows that the average and the maximum morphologies increase slowly over time, as does the range. The increase in morphology is relatively small, however, and as a result these lineages could appear to be in stasis, especially if their fossil record is poor. At the last time step shown, the distribution of morphologies is roughly symmetric, so that this system qualitatively resembles the unbiased system shown in Figure 1B.

For the system in Figure 3C, the corresponding morphology-vs.-time plot (Fig. 3D) shows that the average value and the maximum values increase to a greater extent than in Figure 3B. If this increase in morphology is sufficiently large, this trend mechanism could be mistaken for directional selection. At the last time step shown, the distribution of morphologies is skewed, which would cause the subclade test (McShea 1994) and the Analysis of Skewness (Wang 2001) to classify this mechanism differently from the mechanism producing the symmetric distribution in Figure 3B. Thus, even though the systems depicted in Figure 3A and C share the same average change, they may generate qualitatively different evolutionary trajectories solely because their variances differ.

The system portrayed in Figure 3C,D exhibits heteroskedasticity skewness (from the Greek; ''hetero-'' = different, ''-skedasticity'' = scatter), a concept introduced by Wang (2001) to describe a passive mechanism in which the average and maximum increase as a result of greater variability among larger clades. Wang (2001) gives an example in which such a mechanism is inferred for a data set of North American Cenozoic rodent sizes, so trends such as that shown in Figure 3C,D do occur in real paleontological data.

Different Averages, Same Trend (1).—Figure 3 showed two systems with lower bounds aris-
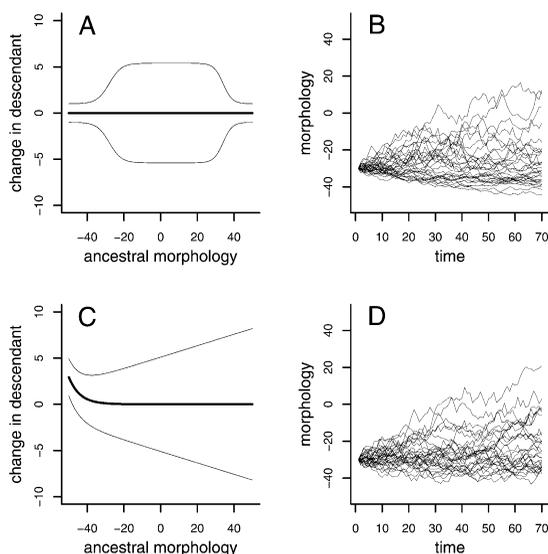

FIGURE 4. Two systems with different average behavior but similar evolutionary trends. (C, D are redrawn from Fig. 3C,D for ease of comparison.) A, C, Change-vs.-ancestor plots. Heavy line represents average change from ancestral to descendant morphologies; light lines represent ±2 standard deviations from the average. In A, the average change is zero but the standard deviation varies according to a combination of two logistic functions. In C, the average change is an exponential function and the standard deviation is a linear function of morphology. B, D, Morphology-vs.-time plots, each showing evolutionary trajectories for 30 lineages over 70 simulated time steps. Details of the simulation methodology are given in the Figure 3 caption. The two sets of trajectories appear qualitatively similar; in both sets the maximum and the average morphology increase, but the minimum stays near a lower bound. Despite differences in the average change, the trajectories appear similar, as a result of unequal variances in the corresponding change-vs.-ancestor plots. The system portrayed in A, B resembles that found by Wagner (1996) for Paleozoic gastropod shell torques.

ing because lineages with smaller morphologies tend to increase. However, a lower bound can arise even when the average change is zero for all morphologies. Figure 4A portrays a system with zero average change whose standard deviation varies according to a combination of two logistic functions, with extreme morphologies having less variation. The corresponding morphology-by-time plot in Figure 4B shows that such a system gives rise to a lower bound with an increasing mean and maximum, and the distribution of morphologies at the last time step is again skewed. These features are similar to those seen in Figure 3C,D (redrawn as Fig. 4C,D for ease of

comparison), even though the average behavior of the two systems is different. Thus, qualitatively similar evolutionary trajectories can be generated by systems with dissimilar average behavior, solely because of differences in variance. Furthermore, note that Alroy's classification would group the system in Figure 4A,B together with the system in Figure 1 (the unbiased random walk) because both have an average change of zero, even though they generate evolutionary trajectories that are quite different.

The system in Figure 4A,B is biologically plausible as well. A qualitatively similar mechanism was inferred by Wagner (1996: Fig. 9A) to have caused trends toward increasing shell torque in Paleozoic gastropods.

Different Averages, Same Trend (2).—Here I give a more dramatic example of similar trends arising from systems with dissimilar averages. In fact, even very complex trends with multiple equilibria can be generated by mechanisms having zero average change.

The morphology-by-time plot in Figure 5B depicts a complex pattern of trajectories in body mass among North American Cenozoic mammals (reprinted with permission from Alroy 1998: Fig. 1). The range of body masses expands after the Cretaceous/Tertiary boundary, after which a lower bound is maintained but the mean steadily increases. In the Eocene a gap in mid-sized mammals appears, which persists to the present. The corresponding change-vs.-ancestor plot is shown in Figure 5A (reprinted with permission from Alroy 1998: Fig. 4B). Here the average change is described by a cubic polynomial, with two stable equilibria (closed circles) and one unstable equilibrium (open circle). The stable equilibria give rise to "point attractors" within the groups of small and large mammals, and the unstable equilibrium gives rise to a "repeller" within the gap at middle sizes. (Note that the two thin lines around the average in this plot do not represent the standard deviation of ancestor-descendant changes, but rather a confidence interval for estimating the average.)

The complex trend shown in Figure 5B results from a pattern of non-zero average change acting to create multiple equilibrium points. Surprisingly, a qualitatively similar
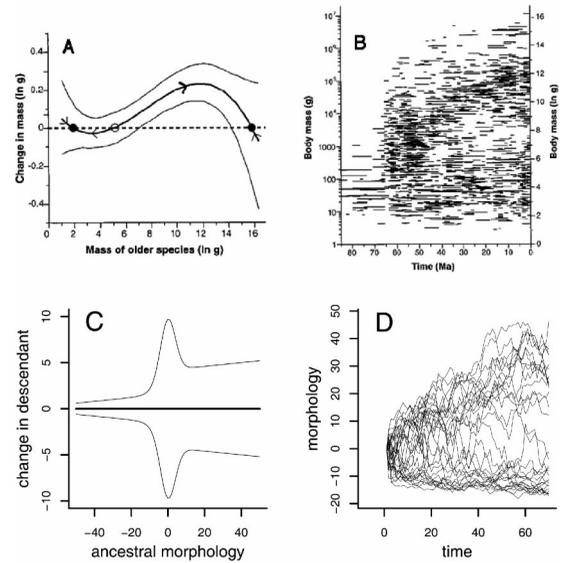

FIGURE 5.   Two systems with different average behavior but similar evolutionary trends. 5A and B reprinted with permission from Figures 4B and 1, respectively, of J. Alroy, 1998, Cope's rule and the dynamics of body mass evolution in North American fossil mammals, *Science* 280:731–734. Copyright 1998 AAAS. A, Change-vs.-ancestor plot for North American Cenozoic mammal body masses. Heavy line represents average change from ancestral to descendant morphologies and follows a cubic polynomial. Light lines represent confidence interval for the average, not variability around the average as in other change-vs.-ancestor plots in this paper. Stable equilibria (closed circles) give rise to "point attractors" for small and large mammals; the unstable equilibrium gives rise to a "repeller" for mid-sized mammals. B, Morphology-vs.-time plot. The range of body masses expands after the Cretaceous/Tertiary boundary. The average body mass continues to increase to the present, whereas the minimum stays near a lower bound. A gap in mid-sized mammals appears in the Eocene and continues to the present. C, Change-vs.-ancestor plot for simulated lineages. Heavy line represents average change from ancestral to descendant morphologies and is zero for all ancestral morphologies; light lines represent ±2 standard deviations from the average. The standard deviation is a nonlinear function of ancestral morphology and is small for small morphologies, large for large morphologies, and highest for morphologies near zero. D, Morphology-vs.-time plot with 30 simulated lineages showing major features similar to those in B, including a lower bound, increasing average, and mid-sized gap. Details of the simulation methodology are given in the Figure 3 caption. Even though the system in C, D has zero average change, complex evolutionary trends are generated by the pattern of variances in the change-vs.-ancestor plot.

trend can be generated by a system with a very different average behavior, one whose average change is zero. Figure 5D shows a morphology-by-time plot whose major fea-

tures are similar to those of Figure 5B: there is an initial expansion, an increase in the mean while a lower bound is maintained, and then a mid-sized gap. However, the change-vs.-ancestor plot generating these trajectories is altogether unlike the one in Figure 5A. Instead, this change-vs.-ancestor plot (Fig. 5C) has zero average change, but its variance increases nonlinearly with a spike near zero, and it is this variance that generates the trend. Because the average change of this system is zero, under Alroy's classification it would be grouped with the systems in Figures 1 and 4A,B—even though these three systems generate very different evolutionary trajectories.

To be clear, I do not claim that the mechanism shown in Figure 5C is a biologically plausible one, nor that it is the mechanism responsible for size increase in North American Cenozoic mammals. (Alroy's data [1998: Fig. 4A] show roughly constant variances.) Rather, I use this example to emphasize two points: First, mechanisms with the same average change—even zero average change—can produce biologically dissimilar trends if their variances differ (Figs. 1, 4, and 5). Second, mechanisms with dissimilar average change can produce biologically similar trends if their variances differ (Fig. 5A,B and 5C,D). Thus, in models of evolutionary trend mechanisms, the variance of ancestor-descendant changes is an important quantity that must explicitly be taken into account.

Classifying Trends

Alroy's parameter-counting classification scheme can easily be modified to include not only the number of parameters needed to describe the average change, but also the number of parameters needed to describe the variability. In this context, it is often more straightforward to use the standard deviation as a measure of variability rather than the variance, because the latter has squared units and can be awkward in practice (e.g., in a dataset consisting of body sizes measured in grams, the variance will have units of grams^2). The standard deviation, on the other hand, has the same units as the original data.

For example, we can classify Figure 3A not simply as a 2-parameter system, but rather a 2/1-parameter system: two parameters are needed to describe the average (an exponential function), and one to describe the standard deviation (a constant function). In Figure 3C, the standard deviation is a linear function of the ancestral variable, so two parameters (the slope and the intercept) are needed to describe the standard deviation, resulting in a 2/2-parameter model.

Alroy (2000) advocated abandoning McShea's (1994) passive/driven terminology, arguing that this dichotomy is too crude to capture the range of mechanisms in Figure 2 and other possibilities as well. McShea (2000) responded that Alroy's nomenclature can easily be integrated with the passive/driven terminology, resulting in, for instance, a "1-parameter driven mechanism," a "2-parameter passive mechanism," and so on. I find this approach to be reasonable, as McShea's passive/driven terminology and Alroy's parameter-counting terminology reflect subtly different aspects of evolutionary trends. The passive/driven classification describes the *structure* of the state space, whereas Alroy's classification measures the *complexity* of the state space. Although these aspects are related, they are sufficiently different so that it makes sense to retain both forms of terminology. In that case, the additional parameters proposed here for describing the standard deviation can be incorporated as well, so that we might speak of, for instance, a "2/2-parameter passive mechanism."

I have thus far assumed that the distribution of ancestor-descendant transitions for any ancestral value is symmetric about its average. This need not be the case: it is possible, at least in theory, for the distribution of transitions to be skewed about its average. This possibility was raised by McShea (1994) and investigated by Wagner (1996). Furthermore, the direction and degree of skewness could differ for different ancestral morphologies. In that case, additional parameters would be required to describe the skewness, adding another level of intricacy to the trend classification. Whether accounting for skewness or other properties is necessary, or whether summarizing the average and variance will suffice for most real trends, is an open question—one whose an-

swer cannot be deduced from elementary principles, but instead must be found empirically.

Conclusion

The change-vs.-ancestor plot is a powerful tool for investigating within-lineage trends using ancestor-descendant data. To depict trend mechanisms completely, however, change-vs.-ancestor plots must explicitly portray not only the average ancestor-descendant change, but also the variance of such changes. This conclusion echoes the work of Gould (1988, 1996), who argued that the variance is an essential feature of evolving systems, no less important than the average or the maximum. In the case of change-vs.-ancestor plots, we have seen that the average cannot sufficiently summarize the variety of trend mechanisms found in paleontological data, because similar trends can have different averages, and dissimilar trends can have the same average. By accounting for unequal variances, we can better depict and classify large-scale evolutionary trends.

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