

QUANTIFYING PASSIVE AND DRIVEN MECHANISMS
IN LARGE-SCALE EVOLUTIONARY TRENDS

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ABSTRACT

We introduce a new statistical method, Analysis of Skewness, for quantifying large-scale evolutionary trends as a combination of both passive and driven mechanisms. Our approach is based on the skewness of subclades within a parent clade. We partition the total skewness of the parent clade into three components: (1) skewness between subclades, (2) skewness within subclades, and (3) skewness due to changes in variance among subclades. The third component corresponds to a new type of passive mechanism, in which overall skewness of a parent clade is due to greater variability in subclades to the right of the mean. This partitioning allows us to quantitatively decompose the mechanisms underlying trends into two components: a driven portion and a passive portion. We thus quantify the effect of small-scale dynamics on large-scale behavior of clades. Applications are given to Miocene-Pliocene rodent size and Ordovician brachiopod muscle geometry.

KEY WORDS

Analysis of Skewness, driven trend, passive trend, evolutionary trends, trend mechanisms, subclade test, skewness decomposition

INTRODUCTION

Biological systems often exhibit large-scale evolutionary trends occurring in higher taxa over geological time. Examples include increases in size and complexity over the history of life (see, for instance, Fisher 1986, McShea 1996, Alroy 1998, Adami et al 2000). It is of interest to determine whether such trends are the result of persistent directional forces (e.g., natural selection), or undirected diffusion away from a constraining boundary. McShea (1994) refers to these mechanisms as *driven* and

passive, respectively. A similar distinction is made by Fisher (1986), who refers to the alternatives as *progressivist* and *Markovian*. Wagner (1996) refers to *active* and *passive* trends, the former a more general class of mechanisms that includes McShea's driven trends.

Two existing methods for distinguishing passive and driven trends are the minimum test and the ancestor-descendant test (see, for instance, Jablonski (1987, 1997), Gould (1988, 1996), Boyajian and Lutz (1992), Wagner (1996), Alroy (1998), and Saunders, Work, and Nikolaeva (1999), among others). McShea (1994) proposes a third test, the subclade test, which uses the skewness of the distribution of a characteristic (e.g., size, complexity) in subclades of a parent clade to determine whether a trend is passive or driven. These tests attempt to categorize observed trends as either strictly passive or strictly driven. Such a dichotomous classification, however, represents the extremes of an underlying continuum (McShea 1994). Trends are likely to be not simply passive or driven, but the product of a combination of both mechanisms in varying proportions.

In this paper, we introduce a new statistical method, Analysis of Skewness, for describing a trend as a combination of both passive and driven mechanisms. Like McShea's subclade test, our approach is based on the skewness of subgroups within a larger population. We expand on this concept by partitioning total skewness of into three components: (1) skewness between subgroups, (2) skewness within subgroups, and (3) skewness due to changes in variance among subgroups. The third component corresponds to a new type of passive mechanism that we call heteroskedasticity skewness. This partitioning allows us to quantitatively decompose the mechanisms underlying trends into two components: a driven portion and a passive portion. We thus quantify the effect of small-scale dynamics on large-scale behavior of clades.

DRIVEN AND PASSIVE SYSTEMS

Mechanisms for large-scale evolutionary trends may be broadly classified as driven or passive. In a driven system, the trend occurs due to selective pressure or some other force acting in a persistent direction. Suppose the characteristic in question is body size, which, it has been argued, has (on average) increased in lineages throughout the history of life—a trend known as Cope’s Rule (see, for instance, Jablonski 1987, Gould 1996). If this trend were driven, then it would have been due to some evolutionary advantage for larger organisms.

On the other hand, such a trend could also occur in a passive system. Stanley (1973) argues that if there is a constraining boundary such as a minimum size (Gould (1996) calls such a boundary a “left wall”), and lineages originate at or near the boundary and are equally likely to grow larger or smaller, then an increase in mean size would be expected. Such a process is analogous to a random walk or diffusion process with its starting point near a lower bound. Since movement to the left is constrained, a net movement to the right is expected, even in the absence of a rightward driving force, resulting in a right-skewed distribution. Gould (1988) characterizes such a trend as an increase in variance over time, rather than an increase in the mean.

McShea (1994) draws an analogy between passive and driven trends and force fields. A driven trend is analogous to a directed external force field acting on the system, while a passive trend is analogous to a lack of a force field. Alternately, we can think of a driven system as one subject to a homogeneous force field in which lines of force point persistently in one direction. A passive system, on the other hand, is subject to a heterogeneous force field in which lines of force point in different directions, the result being no net force.

Diffusion away from a constraining boundary is just one of many types of passive mechanisms. McShea (1994) considers a passive trend to be any trend that results from a heterogeneous force field. Likewise, driven mechanisms encompass a variety of mechanisms. Wagner (1996) proposes a broader class of mechanisms called active

trends, which includes McShea's driven trends as a particular case. In this paper, we will focus primarily on bounded diffusion and selection-produced bias as examples of passive and driven trends, respectively, but our conclusions generalize to other types of passive and driven trends as well.

TESTS FOR DRIVEN/PASSIVE SYSTEMS

The Minimum Test and the Ancestor-Descendant Test

Two standard methods for determining the driven or passive cause of a trend are the minimum test and the ancestor-descendant test. The minimum test examines the behavior of the minimum of a system over time. In a driven system with directed selection pressure, the minimum should increase over time. In a passive system analogous to diffusion, the minimum is likely to remain roughly constant over time.

The ancestor-descendant test uses comparisons between ancestors and descendants in lineages located away from any constraining boundary. For each pair, we can record the direction and magnitude of change in the characteristic being studied (e.g., size). In a passive system, we expect that the average change between pairs of lineages will be close to zero, or that the number of increases will roughly equal the number of decreases. In a driven system, we expect that the average change between pairs will be significantly positive or negative, and that either increases or decreases predominate.

While both of these tests are useful, both also have drawbacks. The minimum test uses information only from trends in the minimal taxa (e.g., the smallest or least complex) through time; this constitutes but a small part of the information in the entire system. Also, a lack of increase in the minimum does not uniquely identify a passive system; it could indicate a driven system in which sufficient time has not passed for the minimum to have changed. The ancestor-descendant test is more direct and

informative, but it requires detailed phylogenetic information — a series of ancestor-descendant pairs — that is not available for many taxa.

The Subclade Test

McShea (1994) proposes an elegant test that does not require extensive phylogenies or paleontological time series. In many systems, whether passive or driven, the distribution of a characteristic such as size or complexity will be skewed, usually to the right. Suppose we examine a subgroup or subclade from the tail of the overall (“parent”) clade’s distribution. Here a subclade is defined as a monophyletic subset of the parent clade, consisting of an ancestral taxon and all of its known descendants (or a random sample thereof). If the trend is the result of passive diffusion away from a constraining boundary, then a subclade in the tail of the parent distribution should exhibit no tendency to be skewed, since it lies far from the constraining boundary. If the trend is a driven one, however, we expect the subclade to mirror the parent distribution, and thus be skewed in the same direction (although perhaps not to the same extent). See Figure 1.

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Figure 1. *McShea’s subclade test*. In a passive system (left), a subclade in the right tail is symmetric. In a driven system, a subclade in the right tail is skewed since it is subject to the same forces as the parent clade.

This idea is the basis for McShea's subclade test. In a driven system we expect to see significantly positive or negative skewness in subclades drawn from the tail of the parent distribution; in a passive system we expect skewness not significantly different from zero. The subclade test has also been used by Maurer (1998) in analyzing body size in birds, and by Saunders, Work, and Nikolaeva (1999) in analyzing suture complexity in ammonites.

The subclade test has the advantage that it requires only an ancestral distribution and a descendant distribution; information about the intervening history of the system is not needed. The test does assume that the system's parameters (such as speciation and extinction rates) are stochastically constant over time.

Combinations of Passive and Driven Trends

All three of the above methods attempt to label a trend as strictly passive or driven. These categories, however, represent extremes of a continuum. In reality, trends are likely to be the product of a combination of both passive and driven forces in varying proportions. McShea (1994) writes that "Most large-scale trends are probably quite complex.... Given this complexity, the prior expectation was that most trends would not be readily classifiable as either purely driven or purely passive, but rather that most would lie somewhere in between or share features of both." Furthermore, he notes that "homogeneity and heterogeneity are continuous variables... real spaces need not be completely one or the other."

In this paper, we introduce a method we call the Analysis of Skewness that is conceptually analogous to the Analysis of Variance. Like McShea's subclade test, our approach is based on the skewness of subgroups within a parent distribution. However, the Analysis of Skewness accounts for the contribution of both passive and driven forces and allows us to quantify the extent to which a trend is passive, driven, or some

combination of both. Using this approach, we can allocate the causes of a trend to some proportion due to “passiveness” and some proportion due to “driveness”.

ANALYSIS OF VARIANCE

We first briefly review the Analysis of Variance (ANOVA) and introduce notation to be used throughout the paper. Our methodology for skewness (below) will be developed in an analogous manner.

Suppose our data consists of observations belonging to k different subgroups (from now on we refer simply to “groups”), with the i th group having n_i observations. We denote the total number of observations as $N = \sum_{i=1}^k n_i$. We label each observation as y_{ij} , with $i = 1 \dots k$ denoting group membership and $j = 1 \dots n_i$ denoting the particular observation in each group. Let the overall sample mean be denoted by $\bar{y}_{..} = \frac{1}{N} \sum_{i=1}^k \sum_{j=1}^{n_i} y_{ij}$, and the sample mean in group i be denoted by $\bar{y}_{i\cdot} = \frac{1}{n_i} \sum_{j=1}^{n_i} y_{ij}$. As in standard statistical notation, the dot symbol “.” indicates summation over the replaced subscript.

The total variability of the y_{ij} (without regard to group membership) is measured by the Total Sum of Squares (SSTot):

$$\text{SSTot} = \sum_{i=1}^k \sum_{j=1}^{n_i} (y_{ij} - \bar{y}_{..})^2$$

Part of the total variability is due to the fact that the group means differ. This variability between groups is measured by the Between-Group Sums of Squares (SSB):

$$\text{SSB} = \sum_{i=1}^k \sum_{j=1}^{n_i} (\bar{y}_{i\cdot} - \bar{y}_{..})^2$$

Another part of the total variability is due to the fact that the observations within each group differ. This variability within groups is measured by the Within-Group Sums of Squares (SSW):

$$\text{SSW} = \sum_{i=1}^k \sum_{j=1}^{n_i} (y_{ij} - \bar{y}_{i\cdot})^2$$

It is straightforward to show the following identity:

$$SST_{\text{ot}} = SSB + SSW$$

by writing SST_{ot} as $\sum [(y_{ij} - \bar{y}_{i\bullet}) + (\bar{y}_{i\bullet} - \bar{y}_{\bullet\bullet})]^2$ and expanding the square. This gives us three terms: SSB, SSW, and a cross-product term that is always zero (since it is a sum of deviations from a mean). Thus we partition the total variability of the y_{ij} into two disjoint and exhaustive components: that due to the variability between the different group means, and that due to the variability within the groups.

To determine the proportion of the total variation due to the variation between group means, we use the ratio SSB/SST_{ot} , which is known as the coefficient of determination and is denoted R^2 . Similarly, the proportion of the total variation due to the variation within groups is $SSW/SST_{\text{ot}} = 1 - R^2$.

ANALYSIS OF SKEWNESS

In biological applications, the overall distributions of many datasets are skewed. This skewness may result from three possible causes: (1) the skewness of individual subclade means, (2) the skewness of the observations in each subclade, and (3) the change in variance between the subclades. High values of the first and last quantity correspond to a passive mechanism, while high values of the second quantity correspond to a driven mechanism. The Analysis of Skewness partitions the proportion of the overall skewness that is attributable to each of these causes. In this way, we quantitatively partition overall skewness into proportions due to driven and passive causes. We develop the Analysis of Skewness in a manner analogous to ANOVA, decomposing the overall skewness (as measured by sums of cubes) into three sources analogous to the three causes above: (1) sums of cubes due to the skewness between group means, (2) sums of cubes due to skewness within individual groups, and (3) sums of cubes due to heteroskedasticity (i.e., changing variances) between groups.

Sums of Cubes

The standard statistical measure of the skewness of a random variable Y is the third central moment of its distribution, $E[(Y - E(Y))^3]$. (Often this is scaled by dividing it by $[\text{Var}(Y)]^{3/2}$, making the resulting number dimensionless.) For observed sample data, this is a function of sums of cubes. In particular, we can measure the total skewness of a dataset as the Total Sums of Cubes (SCTot):

$$\text{SCTot} = \sum_{i=1}^k \sum_{j=1}^{n_i} (y_{ij} - \bar{y}_{\bullet\bullet})^3$$

We will use the fact that

$$\text{SCTot} = \text{SCB} + \text{SCW} + \text{SCH}$$

where each of the terms on the right-hand side is a sum of cubes corresponding to the three possible sources of skewness.

As above, suppose that our dataset consists of observations belonging to k groups, with the i th group having sample mean $\bar{y}_{i\bullet}$. Figure 2 below illustrates an extreme situation of what we call *between-group skewness*, with $k = 6$ groups or subclades. As is common in biological applications, the overall distribution (large black curve) is skewed. This overall skewness can be attributed to the fact that the six group *means* (i.e., the peaks of the small colored curves, indicated by the dotplot) are skewed about their overall mean. However, each individual group (small colored curve) is symmetric, indicative of a passive system. This is an extreme situation in which the overall skewness is due almost entirely to the skewness between the individual group means — hence the name “between-group skewness”. We measure between-group skewness by the Between-Group Sums of Cubes (SCB):

$$\text{SCB} = \sum_{i=1}^k \sum_{j=1}^{n_i} (\bar{y}_{i\bullet} - \bar{y}_{\bullet\bullet})^3$$

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Figure 2. *Total skewness due to between-group skewness.* Each individual group (small colored curves) is symmetric, indicating a passive system. (Individual group curves are shown with heights offset in order to minimize overlap. The dotplot at the bottom of the graph shows the locations of individual group means, with the vertical black line indicating the overall mean.) The skewness of the overall distribution (large black curve) is a result of the relative locations of the group means. This can be seen from the dotplot, which is right-skewed about the overall mean.

Figure 3 below illustrates an extreme situation of what we call *within-groups skewness*, with $k = 5$ groups. Again, the overall distribution (large black curve) is skewed. This overall skewness can be attributed to the fact that each of the six groups (small colored curves) is itself skewed, indicative of a driven system. However, the locations of the six group *means* are symmetric. This is an extreme situation in which the overall skewness is due almost entirely to the skewness within the individual groups — hence the name *within-group skewness*. We measure within-group skewness by the Within-Group Sums of Cubes (SCW):

$$SCW = \sum_{i=1}^k \sum_{j=1}^{n_i} (y_{ij} - \bar{y}_{i\bullet})^3$$

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Figure 3. *Total skewness due to within-group skewness.* Although the group means are distributed symmetrically, the individual groups are skewed, indicating a driven system. Note that the group means themselves are symmetric about the overall mean, which can be seen in the dotplot, so the overall skewness does not result from between-group skewness.

Recall that in ANOVA, we have the identity $SST_{\text{Tot}} = SSB + SSW$, with the cross term in the expansion of SST_{Tot} equaling zero. At this point, the analogy to ANOVA no longer holds since it is not true that $SCT_{\text{Tot}} = SCB + SCW$. Instead, there are two cross-product terms in the expansion of SCT_{Tot} , only one of which equals zero. The other cross-product term is the following, which we will call the Heteroscedasticity Sums of Cubes (SCH):

$$SCH = \sum_{i=1}^k \sum_{j=1}^{n_i} (\bar{y}_{i\bullet} - \bar{y}_{\bullet\bullet})(y_{ij} - \bar{y}_{i\bullet})^2 = \sum_{i=1}^k (\bar{y}_{i\bullet} - \bar{y}_{\bullet\bullet}) \sum_{j=1}^{n_i} (y_{ij} - \bar{y}_{i\bullet})^2$$

The $(y_{ij} - \bar{y}_{i\bullet})^2$ term in SCH measures the variability of the i th group about its mean, and each such term is weighted by $(\bar{y}_{i\bullet} - \bar{y}_{\bullet\bullet})$, the distance from the i th group mean to the overall mean. Therefore SCH increases when groups in the right tail of the overall distribution are more variable than groups near the center. In this way SCH measures *heteroskedasticity*, or unequal variances among groups. Intuitively, this tells us that increasing variance among groups in the right tail contributes to the overall skewness, even if such groups are not themselves skewed. In a biological system, this corresponds to larger or more complex subclades being more variable, and smaller subclades being more uniform. This is indicative of a passive system, since the individual groups are symmetric. Figure 4 below illustrates an extreme situation of what we call *heteroskedasticity skewness*, with $k = 5$ groups.

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Figure 4. *Total skewness due to heteroskedasticity skewness (increasing variance among groups in right tail). Each individual group is symmetric, indicating a passive system. Note that the group means themselves are*

symmetric about the overall mean, which can be seen in the dotplot, so the overall skewness does not result from between-group skewness. Nor does it result from within-group skewness, since the individual groups themselves are symmetric.

Combining the three sums of cubes, we have the following identity:

$$SCT_{ot} = SCB + SCW + SCH.$$

That is, the total skewness can be decomposed into three constituent parts or sources of skewness, each suggesting either a passive or driven trend. Below, we will use this fact to apportion the causes of a trend to passive or driven mechanisms. Table 1 summarizes the characteristics of the individual group distributions and group means corresponding to each source of skewness.

Category	Individual group distributions	Location of group means	Trend indicated	Figure
Between-group skewness	symmetric	skewed	passive	Figure 2
Within-group skewness	skewed	symmetric	driven	Figure 3
Heteroskedasticity skewness	symmetric	symmetric	passive	Figure 4

Table 1. Summary of properties for the three sources of skewness.

Apportioning Skewness

Ideally, we would like to be able to say that the proportion of total skewness attributable to skewness between group means is SCB/SCT_{ot} , the proportion of total skewness attributable to skewness within groups is SCW/SCT_{ot} , and the proportion of total skewness attributable to heteroskedasticity among groups is SCH/SCT_{ot} . Furthermore, large values of SCW (relative to SCB and SCH) provide evidence for a driven system, as they indicate a high degree of skewness within subclades. Conversely, large values of SCB and SCH (relative to SCW) provide evidence for a passive system, as they indicate a high degree of symmetry within subclades. Thus we may consider SCW/SCT_{ot} to be the proportion of total skewness due to driven trends, and $1 - SCW/SCT_{ot} = (SCB + SCH)/SCT_{ot}$ to be the proportion of total skewness due to passive trends. Therefore, a driven system is characterized by high values of

SCW/SCTot, and a passive system by low values of SCW/SCTot [or equivalently, by high values of (SCB + SCH)/SCTot]. This interpretation is roughly analogous to that of the ANOVA quantity R^2 for partitioning the proportion of variance explained.

Such an interpretation is not possible, however, when the sums of cubes are negative (a problem that does not arise with sums of squares in ANOVA). It is possible, for instance, to have SCTot = 100, SCB = 110, SCW = 120, and SCH = -130. In this case, both SCB/SCTot and SCW/SCTot would exceed one. It is difficult to give an intuitive meaning to such a result in terms of passive or driven systems.

Negative sums of cubes can also cause a problem with identifiability or uniqueness. Suppose SCW is close to zero. This may indicate that the groups are symmetric, but it may also indicate a systematic trend in skewness. For instance, suppose smaller groups are skewed left, while larger groups are skewed right; these negative and positive group skewnesses could cancel and result in SCW being close to zero. Similar issues may occur in ANOVA, even though sums of squares are always positive. Suppose, for instance, that SSW is large, which presumably indicates that there is high variability in each group. But it is also possible that all groups but one have low variability, while the last has very high variability. To avoid such an ambiguity, we usually make the assumption in ANOVA that groups are randomly sampled from populations with equal variances. In the Analysis of Skewness, we will make a roughly analogous assumption: that groups are randomly sampled from populations with nonnegative skewnesses. In fact, this is a less restrictive assumption than the assumption of equal group variances in ANOVA; here, we assume only that the population skewnesses have the same sign (or have zero skew), not necessarily the same value. This assumption should be reasonable for many biological characteristics (for instance, size or complexity), which are often strongly right-skewed, even after logarithmic transformations (Brown 1995, chapter 5).

A further assumption is necessary for ensuring that SCH is nonnegative. It is in theory possible that small subclades have more variability and large subclades less

variability, in which case SCH will be negative. To avoid this, we make the assumption that variances are nondecreasing as a function of the characteristic in question. This assumption should also be reasonable for many biological characteristics. For instance, we would expect that larger animals display more size variation (on an absolute scale) compared to small animals, rather than vice-versa.

Even if these assumptions hold, however, it is still possible that some of the sums of cubes could be negative simply due to sampling variation. One possible remedy is to take absolute values of the sums of cubes, but then SCB, SCW, and SCH would no longer necessarily sum to SCTot. With biological data, however, we believe this problem should be rare in practice.

Given the assumptions of nonnegative group skewnesses and nondecreasing variances, and with all sums of cubes positive, our interpretation of SCW/SCTot as the proportion of total skewness due to within-group skewness is valid. In Figure 2, representing a passive system having symmetric groups with nearly constant variance, $SCW/SCTot = .002$, while $SCB/SCTot = .997$ and $SCH/SCTot = .001$. In Figure 3, representing a driven system having skewed groups with nearly constant variance, $SCW/SCTot = .95$, while $SCB/SCTot = .03$ and $SCH/SCTot = .02$. In Figure 4, representing a passive system having symmetric groups with increasing variance, $SCW/SCTot = .04$, while $SCB/SCTot = .02$ and $SCH/SCTot = .94$.

Note that skewness depends on the scale on which data are measured; distributions that are skewed on a raw scale may be symmetric on a logarithmic scale. Since a single appropriate scale may not be known or may not even exist, we cannot always know whether skewness is inherent in the data or is an artifact of the chosen scale. Even in the latter situation, though, our methodology is useful for distinguishing homogeneity and heterogeneity of forces in different regions of the state space.

TWO EXAMPLES

Figures 2–4 represent idealized situations in which a system is dominated by only one source of skewness. Real biological systems will generally result from a combination of all three sources in varying proportions. Here we analyze two datasets discussed by McShea (1994) to show how the Analysis of Skewness quantifies the joint effects of passive and driven trends.

Rodent size

McShea (1994) analyzed a dataset on anterior-posterior length of the first lower molar in North American rodents of the Miocene and Pliocene (this dimension is used as a proxy for size). These data were originally presented by Stanley (1973), who found that the minimum size decreased over time, thus supporting a passive trend. McShea, using an augmented dataset, found that the subclade test also supported the conclusion of a passive trend: the mean skewness in six subclades was not significantly greater than zero. Renaud et al (1999) find a similar passive trend in size among European Miocene murine rodents.

In an Analysis of Skewness of these data, we use rodent family as the group variable [families are taken from Carroll (1988)]. Using the formulas given for SCB, SCW, SCH, and SCTot, we find that the total skewness can be decomposed as 35% due to skewness between groups, 10% due to skewness within groups, and 55% due to increasing heteroskedasticity among groups. See Figure 5. The figure shows the entire dataset plotted with a thick curve and the five families (*Geomyidae*, *Heteromyidae*, *Cricetidae*, *Sciuridae*, and *Castoridae*) plotted with light curves. (Each curve is a kernel density estimate, a smooth curve estimating the underlying population from which the subclade observations are drawn. See Silverman 1986.) From the graph, we can see that each group is roughly symmetric; the overall skewness is primarily a result of the increasing variance of the two largest groups, *Sciuridae* and *Castoridae*. This supports

the conclusion of a passive trend for rodent size. Using SCW/SCTot, we apportion this trend as 10% driven and $(35\% + 55\%) = 90\%$ passive.

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Figure 5. *Analysis of Skewness for the rodent size data of Stanley (1973) and McShea (1994)*. The groups consist of five rodent families and are reasonably symmetric, suggesting a passive system. The group means are somewhat skewed about the overall mean, as can be seen from the dotplot, indicating moderate between-group skewness. Overall skewness is primarily due to heteroskedasticity among groups, further suggesting a passive system. Quantitatively, SCB accounts for 35% of total skewness, SCW for 10%, and SCH for 55%. We conclude that the trend is 10% driven and $(35\% + 55\%) = 90\%$ passive.

Brachiopod muscle geometry

McShea (1994) also analyzed a dataset on muscle geometry in Ordovician deltidiodont brachiopods. These data were originally collected by Carlson (1989, 1992); the data used here are measurements of the angle formed by the hinge axis, the cardinal process, and the diductor muscle, which Carlson (1992) calls “HBPM”. Carlson (1992)

found that the minimum increased over time, thus supporting a driven trend. McShea found that the subclade test also supported the conclusion of a driven trend: all four subclades had a positive skewness.

In an Analysis of Skewness of these data, we will use the same subclades (*Pentamerida*, *Entelacea*, *Orthacea*, and *Strophomenida*) used by McShea. (Recent work in brachiopod taxonomy suggest that some of these groups may not be monophyletic (SJ Carlson, pers. comm. 2000), but we use these groups to maintain comparability with McShea's analysis.) Using the formulas given for SCB, SCW, SCH, and SCTot, we find that the total skewness can be decomposed as 1% due to skewness between groups, 83% due to skewness within groups, and 16% due to increasing heteroskedasticity among groups. See Figure 6. The figure shows the entire dataset plotted with a thick curve and the four orders (from left to right, *Pentamerida*, *Entelacea*, *Orthacea*, and *Strophomenida*) plotted with light curves. (As in Figure 5, each curve is a kernel density estimate.) From the graph, we can see that three of the four groups are skewed, particularly *Orthacea* and *Strophomenida*; the overall skewness is primarily a result of the skewness within groups. This supports the conclusion of a driven trend for brachiopod muscle geometry. Using SCW/SCTot, we apportion this trend as 83% driven and $(1\% + 16\%) = 17\%$ passive.

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Figure 6. *Analysis of Skewness for the brachiopod geometry data of Carlson (1989, 1992) and McShea (1994).* The groups consist of four brachiopod subclades. Overall skewness is primarily due to skewness within groups, suggesting a driven system. The group means are roughly symmetric about the overall mean, as can be seen from the dotplot, indicating low between-group skewness. Quantitatively, SCB accounts for 1% of total skewness, SCW for 83%, and SCH for 16%. We conclude that the trend is 83% driven and $(1\% + 16\%) = 17\%$ passive.

DISCUSSION

In summary, we propose a new method for quantifying the extent to which a trend is passive or driven. We introduce the Analysis of Skewness to partition the overall skewness of a system into components due to between-group skewness, within-group skewness, and heteroskedasticity skewness. These components are measured using sums of cubes, and the proportion of passiveness or drivenness of a trend is calculated from

ratios of these sums of cubes. The method is applied to examples involving trends in rodent size and brachiopod muscle geometry.

In both examples, the Analysis of Skewness reached the same conclusions as the minimum test and the subclade test. Since large-scale trends are the result of a complex set of interacting forces, and each test is sensitive to a different aspect of these forces, it is not inevitable that three tests would agree. That they do suggests that (as McShea (1994) observes) the distinction between driven and passive trends is a reasonable one, and furthermore, that the tests work.

As noted in Alroy (2000) and McShea (2000), the labels passive and driven are broad categories, each encompassing a variety of mechanisms. The latter observes that “with so many types of passive mechanism possible, a subdivision of the passive category into subcategories would seem to be desirable.” One benefit of our methodology, then, is that a distinction between two types of passive mechanisms emerges from the Analysis of Skewness. What we have called heteroskedasticity skewness, corresponding to the SCH term in our decomposition of total skewness, is a route to overall skewness that is new to the literature. In a system exhibiting heteroskedasticity skewness, overall skewness arises from greater variability in subclades to the right of the mean. This can occur even if both the subclade means and the subclade distributions are symmetric. Such a system may arise for several reasons: a constraining boundary may limit variation in subclades to the left of the mean, or a heterogeneity in the space may result in increased variability in subclades to the right of the mean even when no constraining boundary exists. In either case, the trend is passive, as it results from a heterogeneous force field and exhibits symmetry within subclades. Such a trend is suggested in the rodent size example, raising the possibility that overall skewness in size distribution is the primarily the result of greater diversification in larger subclades.

In addition to the categorization into types of passive or driven trends, the Analysis of Skewness also quantifies the extent to which a system is due to each mechanism.

McShea (1998) observes that large-scale dynamics of a system are often difficult to deduce from its small-scale dynamics alone, and vice-versa. In our case, the large-scale dynamics corresponds to the overall skewness of a system, and the small-scale dynamics corresponds to the skewness of the individual subgroups. The Analysis of Skewness quantifies the relationship between these large- and small-scale dynamics. It is hoped that such information will lead to new avenues of research. For example, the degree to which a system is driven may be used as a covariate in studies of properties of passive and driven systems. One could also study variation in SCW/SCTot among various taxa or among various characteristics. Quantification could also be helpful in investigations of whether passive or driven trends are more common.

The discussion here has focused on the use of Analysis of Skewness as a purely descriptive tool. An important benefit of the ability to quantify mechanisms of trends is that we may address random sampling variation or attempt inference to a larger population. In an inferential setting, it is natural to test the null hypothesis of a passive trend against the alternative hypothesis of a driven trend, with SCW/SCTot being the test statistic. In order to interpret a value of SCW/SCTot as being large enough to reject the null hypothesis, we would need to know the sampling distribution of SCW/SCTot under the null hypothesis of a passive system. Since the null hypothesis is consistent with a broad class of stochastic models, simplifying assumptions will likely be necessary in order to determine a null distribution. Applying the Analysis of Skewness in an inferential setting is an area of current research.

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