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QUANTIFYING PASSIVE AND DRIVEN LARGE-SCALE EVOLUTIONARY TRENDS

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Abstract.—I introduce a new statistical method, analysis of skewness, for quantifying large-scale evolutionary trends as a combination of both passive and driven trends. My approach is based on the skewness of subclades within a parent clade. I 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 trend, in which overall skewness of a parent clade is due to greater variability in subclades to the right of the mean. Using this partitioning, I decompose an observed trend into two components: a driven portion and a passive portion, thus quantifying 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, evolutionary trends, macroevolution, passive trend, subclade test, trend partitioning.

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Biological systems often exhibit large-scale evolutionary trends in higher taxa over geological time. Examples include increases in size and complexity over the history of life (e.g., 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 as well as some trends that McShea considers passive (e.g., species selection and species hitchhiking).

Two existing methods for distinguishing passive and driven trends are the minimum test and the ancestor-descendant test (e.g., Jablonski 1987, 1997; Gould 1988, 1996; Boyajian and Lutz 1992; McShea 1994; Wagner 1996; Alroy 1998; Saunders et al. 1999). Wagner (1996) also examines shifts in distributions over time within the original morphospace. McShea (1994) proposes 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. Trends are

likely to be not simply passive or driven, but the product of both types in varying proportions.

In this paper, I introduce a new descriptive statistical method, the analysis of skewness, for describing a trend as a combination of both passive and driven components. Like McShea’s subclade test, this approach is based on the skewness of subgroups within a larger population. I 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 trend that I call heteroskedasticity skewness. This partitioning allows us to quantitatively decompose trends into two components: a driven portion and a passive portion, thus quantifying the effect of small-scale dynamics on large-scale behavior of clades. I apply the method to Miocene-Pliocene rodent size and Ordovician brachiopod muscle geometry and propose directions for placing the analysis of skewness into an inferential framework.

DRIVEN AND PASSIVE TRENDS

Large-scale evolutionary trends may be broadly classified as driven or passive. In a driven system, a trend arises 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 increased (on average) in lineages throughout the history of life—a trend known as Cope’s rule (e.g., Jablonski 1987; Gould 1996; Alroy 1998). If this

trend were driven, then it would have been due to some evolutionary advantage for larger organisms.

However, such an increase 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. Because 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, whereas 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, in contrast, is subject to a heterogeneous force field in which lines of force point in different directions, the result being no net directional force.

Diffusion away from a constraining boundary is just one of many types of passive trends. McShea (1994) considers a passive trend to be any trend that results from a heterogeneous force field. Likewise, driven trends encompass a variety of mechanisms. Wagner (1996) proposes a broader class called active trends, which includes McShea’s driven trends and also incorporates other types of mechanisms such as species selection, adaptive radiation, and species hitchhiking. In this paper, I focus primarily on bounded diffusion and selective bias as examples of passive and driven trends, respectively, but my conclusions generalize to other types of passive and driven trends as well.

TESTS FOR DRIVEN AND PASSIVE SYSTEMS

The Minimum Test and the Ancestor-Descendant Test

Two methods for distinguishing driven and passive trends 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 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 and 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.

Although 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, especially if rates of change or extinction are low.

The ancestor-descendant test is more direct and informative, but it requires detailed phylogenetic information from which a series of ancestor-descendant pairs can be inferred. Such information about ancestral conditions is unavailable for many taxa, for instance, when only sister taxa are known. Furthermore, constructing phylogenetic inferences often involves assumptions about the size or probabilities of directional changes (Sober 1988). Such assumptions can bias the resulting inferences toward finding either driven or passive trends.

The Subclade Test

McShea (1994) proposes a 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 because 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 Fig. 1).

This idea is the basis for McShea’s (1994) 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. Typically several subclades are used, and their sign and magnitude are compared to that of the parent clade. (It is useful to use a larger number of subclades if the overall trend may apply only to certain subclades, because we then have a greater chance of including those subclades. For instance, the observed trend in the parent clade could be primarily due to the effect of one particular subclade, with other subclades not reflecting the trend to the same extent.)

McShea (1994) uses the subclade test to analyze rodent molar size, brachiopod muscle geometry, and chordate vertebral complexity. The test has also been used by Maurer (1998) to analyze body size in living birds and by Saunders et al. (1999) to analyze 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.

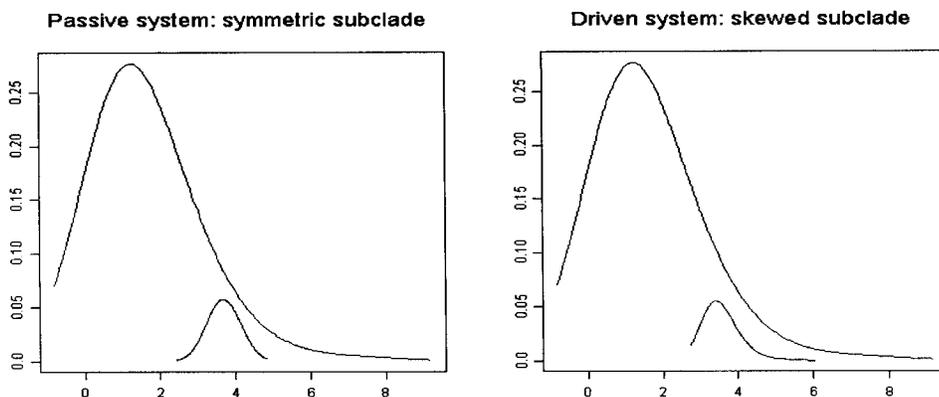


FIG. 1. McShea’s (1994) subclade test. In a passive system (left), a subclade in the right tail is symmetric. In a driven system, a subclade in the right tail is skewed because it is subject to the same forces as the parent clade.

It should be noted that higher-level trends, such as species selection, species hitchhiking, and adaptive radiations, may produce patterns similar to those seen in Figure 1. Alroy (2000) argues that several distinct situations may produce similar patterns when only cross-sectional, or “time-slice,” data are used. However, McShea (2000) maintains that given the current limitations of phylogenetic inference, time-slice-based tests such as the subclade test are nonetheless useful in differentiating between passive and driven trends, if not necessarily in distinguishing among the wide variety of passive mechanisms.

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 components in varying proportions. McShea (1994, p. 1751) 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, McShea (1994, p. 1752) notes that “homogeneity and heterogeneity are continuous variables . . . real spaces need not be completely one or the other.”

In this paper, I introduce a method I call the analysis of skewness that is conceptually analogous to the analysis of variance. Like McShea’s subclade test, this 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 components and allows us to quantify the extent to which a trend is passive, driven, or some combination of both. By using this approach, we thus allocate the causes of a trend to some proportion due to “passiveness” and some proportion due to “drivenness.” The method as proposed here is strictly descriptive and is analogous to the use of R^2 in the analysis of variance, which is also used descriptively. Extensions to an inferential framework are discussed at the end of the paper.

ANALYSIS OF VARIANCE

I first briefly review the analysis of variance (ANOVA) and introduce notation to be used throughout the paper. The methodology for skewness (below) will be developed in an analogous manner.

Suppose our data consists of observations belonging to k different subgroups (hereafter “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 $\bar{y}_{..} = 1/N \sum_{i=1}^k \sum_{j=1}^{n_i} y_{ij}$, and the sample mean in group i be denoted by $\bar{y}_{i.} = 1/n_i \sum_{j=1}^{n_i} y_{ij}$. 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 ($SSTot$):

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

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):

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

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):

$$SSW = \sum_{i=1}^k \sum_{j=1}^{n_i} (y_{ij} - \bar{y}_{i.})^2. \tag{3}$$

It is straightforward to show the identity $SSTot = SSB + SSW$ by writing

$$SSTot = \sum \sum [(y_{ij} - \bar{y}_{i.}) + (\bar{y}_{i.} - \bar{y}_{..})]^2 \tag{4}$$

and expanding the square. This gives us three terms: SSB , SSW , and a cross-product term that is always zero (because it is a sum of deviations from a mean). Thus, we partition

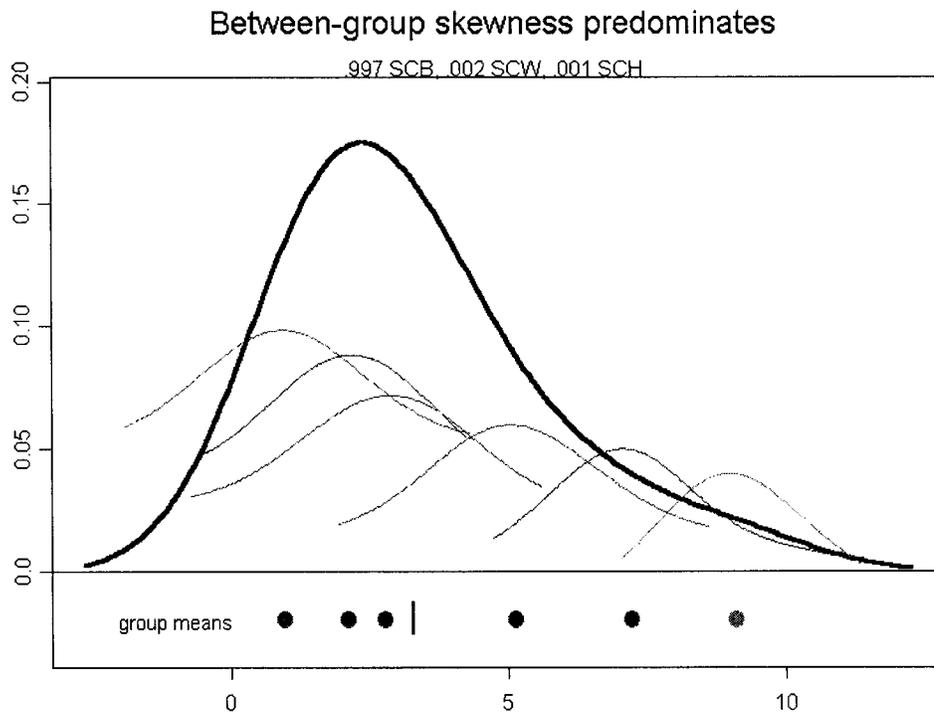


FIG. 2. Total skewness due to between-group skewness. Each individual group (small curves) is symmetric, indicating a passive system. (Individual group curves are shown with heights offset to minimize overlap. The dotplot at the bottom of the graph shows the locations of individual group means, with the vertical black line indicating the overall mean.) The skewness of the overall distribution (large 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.

the total variability of the y_{ij} into two disjoint and exhaustive parts: 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/SS_{Tot} , which is known as the coefficient of determination and denoted R^2 . Similarly, the proportion of the total variation due to the variation within groups is $SSW/SS_{Tot} = 1 - R^2$.

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 third quantity correspond to a passive trend, whereas high values of the second quantity correspond to a driven trend. 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 components. I 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., unequal variances) between groups. This idea of partitioning skewness is similar in spirit to the logic

of Foote (1993), who examines disparity between and within 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 ($SCTot$):

$$SCTot = \sum_{i=1}^k \sum_{j=1}^{n_i} (y_{ij} - \bar{y}_{..})^3. \quad (5)$$

We will use the fact that $SCTot = SCB + SCW + SCH$, where each of the terms on the right 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 . Figure 2 illustrates an extreme situation of what I call between-group skewness, with $k = 6$ groups or subclades. As is common in biological applications, the overall distribution (large curve) is skewed. This overall skewness can be attributed to the fact that the six group means (i.e., the centers of gravity of the small curves, indicated by the dotplot) are skewed about their overall mean. However, each individual group (small curve) is symmetric, indicative of a passive system. This is an extreme situation in which the overall

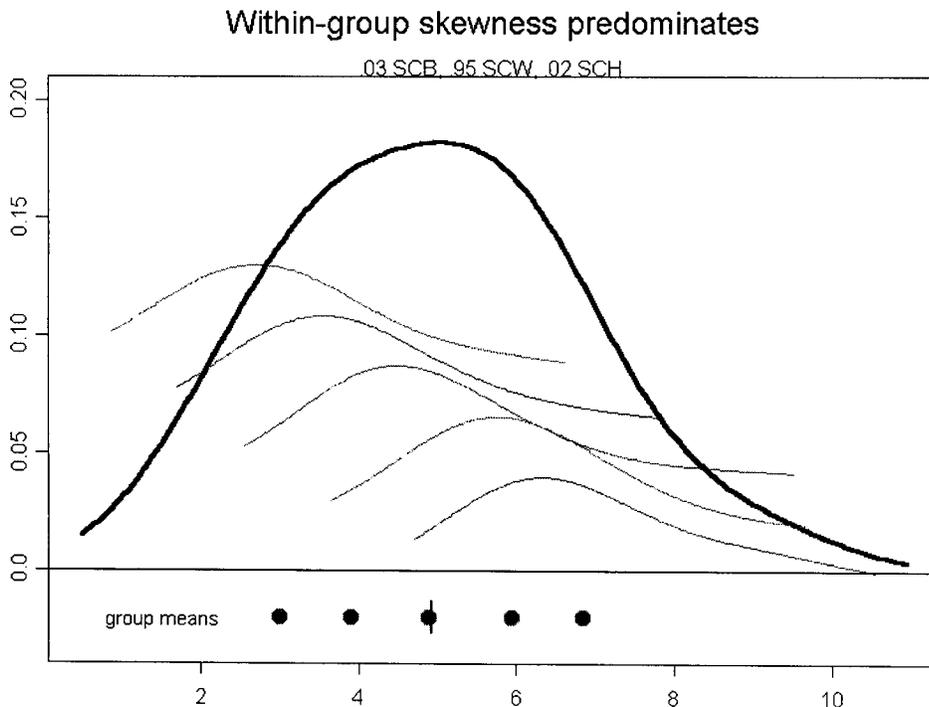


FIG. 3. Total skewness due to within-group skewness. Although the group means are distributed symmetrically, the individual groups are skewed, indicating a driven system. Note that the group means themselves are symmetric about the overall mean, which can be seen in the dotplot, so the overall skewness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

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*):

$$SCB = \sum_{i=1}^k \sum_{j=1}^{n_i} (\bar{y}_i - \bar{y}_{..})^3. \tag{6}$$

Figure 3 illustrates an extreme situation of what I call within-groups skewness, with $k = 5$ groups. Again, the overall distribution (large curve) is skewed. This overall skewness can be attributed to the fact that each of the five groups (small curves) is itself skewed, indicative of a driven system. However, the locations of the five 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*):

$$SCW = \sum_{i=1}^k \sum_{j=1}^{n_i} (y_{ij} - \bar{y}_i)^3. \tag{7}$$

Recall that in ANOVA we have the identity $SSTot = SSB + SSW$, with the cross-product term in the expansion of $SSTot$ equaling zero. At this point, the analogy to ANOVA no longer holds because it is not true that $SCTot = SCB + SCW$. Instead, there are two cross-product terms in the expansion of $SCTot$, only one of which equals zero. The other cross-product term is the following, which I will call the heteroskedasticity sums of cubes (*SCH*):

$$\begin{aligned} SCH &= 3 \sum_{i=1}^k \sum_{j=1}^{n_i} (\bar{y}_i - \bar{y}_{..})(y_{ij} - \bar{y}_i)^2 \\ &= 3 \sum_{i=1}^k (\bar{y}_i - \bar{y}_{..}) \sum_{j=1}^{n_i} (y_{ij} - \bar{y}_i)^2. \end{aligned} \tag{8}$$

The $\sum (y_{ij} - \bar{y}_i)^2$ term in *SCH* measures the variability of the i th group about its mean, and each such term is weighted by $(\bar{y}_i - \bar{y}_{..})$, 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 means 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 because the individual groups are symmetric. Figure 4 below illustrates an extreme situation of what I call heteroskedasticity skewness, with $k = 5$ groups.

Combining the three sums of cubes, we have the identity $SCTot = SCB + SCW + SCH$. 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, I will use this fact to partition a trend into passive or driven causes. Table 1 summarizes the characteristics of the individual group distributions and group means corresponding to each source of skewness.

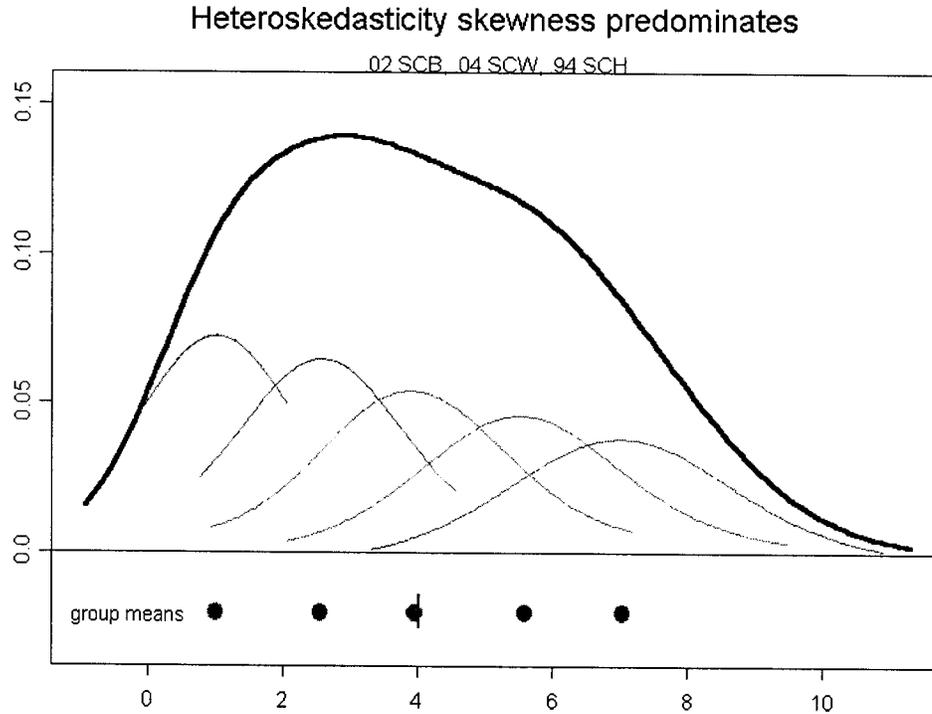


FIG. 4. Total skewness due to heteroskedasticity skewness (increasing variance among groups in right tail). Each individual group is symmetric, indicating a passive system. Note that the group means themselves are symmetric about the overall mean, which can be seen in the dotplot, so the overall skewness does not result from between-group skewness. Nor does it result from within-group skewness, because the individual groups themselves are symmetric.

Partitioning Skewness

Ideally, we would like to be able to say that the proportion of total skewness attributable to skewness between group means is $SCB/SCTot$, the proportion of total skewness attributable to skewness within groups is $SCW/SCTot$, and the proportion of total skewness attributable to heteroskedasticity among groups is $SCH/SCTot$. Large values of SCW (relative to SCB and SCH) provide evidence for a driven system, because 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, because they indicate a high degree of symmetry within subclades. Thus, we may consider $SCW/SCTot$ to be the proportion of total skewness due to driven trends, and $1 - SCW/SCTot = (SCB + SCH)/SCTot$ 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 trends.

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 and larger groups are skewed right; these negative and positive group skewnesses could cancel and result in SCW being close to zero. Similar issues may arise 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, and the last has very high variability. To avoid such an ambiguity, we usually make the assumption in ANOVA that groups are sampled from populations with

TABLE 1. Summary of properties for the three sources 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

equal variances. In the analysis of skewness, we will make a roughly analogous assumption: that groups are 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 (e.g., size or complexity), which are often strongly right skewed, even after logarithmic transformations (Brown 1995, ch. 5).

A further assumption is necessary for ensuring that SCH is nonnegative. In theory it is 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, I 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, $SCW/SCTot = 0.002$, $SCB/SCTot = 0.997$, and $SCH/SCTot = 0.001$. In Figure 3, representing a driven system having skewed groups with nearly constant variance, $SCW/SCTot = 0.95$, $SCB/SCTot = 0.03$, and $SCH/SCTot = 0.02$. In Figure 4, representing a passive system having symmetric groups with increasing variance, $SCW/SCTot = 0.04$, $SCB/SCTot = 0.02$, and $SCH/SCTot = 0.94$.

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. Because 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. Of course, the choice of an appropriate scale of measurement is an important factor in all statistical analyses.

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, I analyze two datasets discussed by McShea (1994) to show how the anal-

ysis 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 Fig. 5). Figure 5 shows the entire dataset plotted with a heavy curve and the five families (*Geomysidae*, *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, *Scuridae* 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.

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 suggests that some of these groups may not be monophyletic (S. J. Carlson, pers. comm.), but we use these groups to maintain comparability with McShea’s analysis. (Even if the groups are not monophyletic, the analysis will likely be valid as long as they are paraphyletic, as appears to be the case, rather than polyphyletic.)

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 Fig. 6). Figure 6 shows the entire dataset plotted

Analysis of Skewness: Mio-Pliocene Rodent sizes

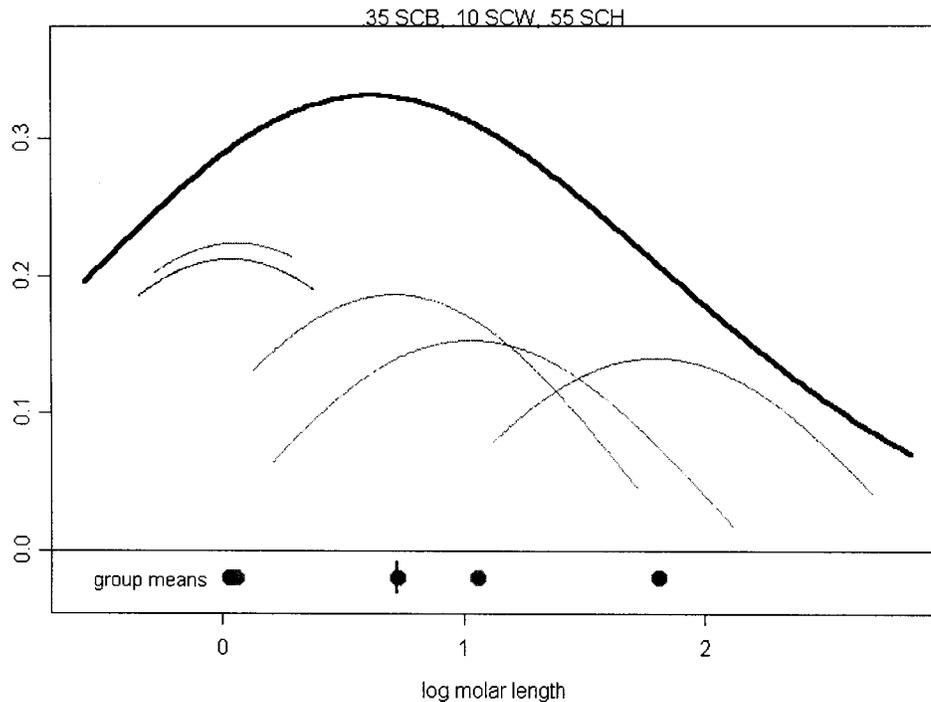


FIG. 5. Analysis of skewness for the rodent size data of Stanley (1973) and McShea (1994). The groups consist of five rodent families and are reasonably symmetric, suggesting a passive system. The group means are somewhat skewed about the overall mean, as can be seen from the dotplot, indicating moderate 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%. Thus, we conclude that the trend is 10% driven and $(35\% + 55\%) = 90\%$ passive.

with a heavy curve and the four orders (from left to right, *Pentamerida*, *Entelacea*, *Orthacea*, and *Strophomenida*) plotted with light curves. (As in Fig. 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.

DISCUSSION

In summary, I propose a new descriptive method for quantifying the extent to which a trend is passive or driven. I have introduced 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. Because 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 agree. That they do suggests that the distinction between driven and

passive trends is a reasonable one (as observed by McShea 1994), 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. McShea (2000, p. 331) 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 my methodology is that a distinction between two types of passive patterns emerges from the analysis of skewness. What I have called heteroskedasticity skewness, corresponding to the *SCH* term in the 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 two 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 because 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

Analysis of Skewness: Brachiopod geometry

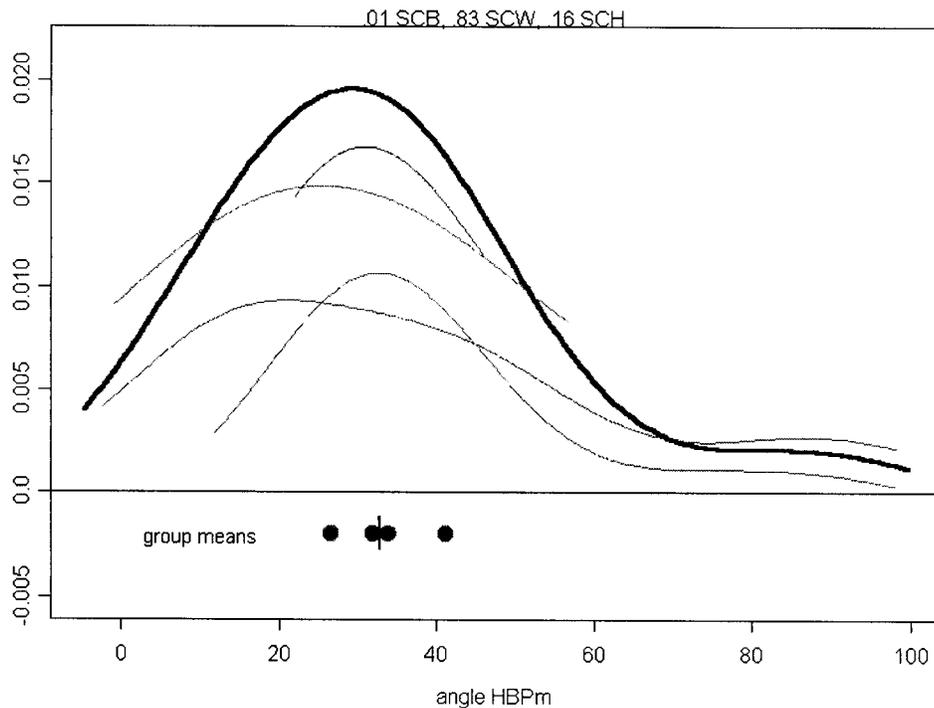


FIG. 6. Analysis of skewness for the brachiopod geometry data of Carlson (1989, 1992) and McShea (1994). The groups consist of four brachiopod subclades. Overall skewness is primarily due to skewness within groups, suggesting a driven system. The group means are roughly symmetric about the overall mean, 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%. Thus, we conclude that the trend is 83% driven and (1% + 16%) = 17% passive.

driven trends, the analysis of skewness also quantifies the extent to which a system is generated by each type of trend. McShea (1998) observes that large-scale dynamics of a system are often difficult to infer from its small-scale dynamics alone and vice versa. Here, the large-scale dynamics correspond to the overall skewness of a system, and the small-scale dynamics correspond 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 the quantitative information provided by the analysis of skewness 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.

Clearly, results from the analysis of skewness depend on the phylogenetic structure assumed for the clades under analysis. The sensitivity of the analysis to clade structure is a topic that may merit further study. For example, are there particular aspects of the clade structure that most affect the results? Also, the clade structure may not be independent of the variable being analyzed. If the variable under study was used in generating the clade structure, the results of the analysis of skewness may be biased. However, phylogenetic trees are usually based on a variety of data and are not likely to be dictated solely by a single variable. It is important to keep

in mind, though, that confidence in the results of the analysis of skewness depends on the validity of the phylogenetic tree, as is true of all historical analyses.

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 types 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. To interpret a value of *SCW/SCTot* as being large enough to reject the null hypothesis, one would need to know the sampling distribution of *SCW/SCTot* under the null hypothesis of a passive system. Because this null hypothesis is consistent with a broad class of stochastic models, however, simplifying assumptions will likely be necessary to determine the null distribution. Furthermore, applying standard sampling-based methods (e.g., bootstrap, permutation tests) is challenging due to the hierarchical and historically contingent nature of clades. Developing an inferential framework for the analysis of skewness would also allow us to calculate confidence intervals about observed values of *SCW/SCTot* to quantify our uncertainty in these estimates. Addressing inferential issues such as these is an area of current research.

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