SOME PROBLEMS WITH ASSESSING COPE'S RULE

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Cope's Rule states that the size of species tends to increase along an evolutionary lineage. A basic statistical framework is elucidated for testing Cope's Rule and some surprising complications are pointed out. If Cope's Rule is formulated in terms of mean size, then it is not invariant to the way in which size is measured. If Cope's Rule is formulated in terms of median size, then it is not invariant to the degree of separation between ancestral and descendant species. Some practical problems in assessing Cope's Rule are also described. These results have implications for the empirical assessment of Cope's Rule.

KEY WORDS: Body size, evolutionary trend, Markov process, measurement scale.

Cope's Rule states that the body size of species tends to increase along an evolutionary lineage. There has been a continuing discussion in the literature about the validity of Cope's Rule and its possible causes. It is not our intention to review this literature here. A small sample of relevant references are Newell (1949), Stanley (1973), LaBarbera (1986), McKinney (1990), McShea (1994), Gould (1997), and Jablonski (1997). In a widely cited contribution to this area, Alroy (1998) presented a statistical analysis of Cope's Rule. Briefly, this involved collecting body mass estimates for a large number of pairs of species in which one species is known or believed to be ancestral to the other. Alroy used these data to test the two related null hypotheses that the mean and median of the difference in log body mass between a descendant species and its ancestor are 0 against the alternative hypotheses that they are greater than 0. The first hypothesis was tested via a *t* test and the second via a sign test. In both cases, the null hypothesis was rejected, confirming Cope's Rule.

The purpose of this article is to elucidate a basic framework for the statistical analysis of Cope's Rule and to point out some surprising implications of it. Specifically, we show that, if Cope's Rule is formulated in terms of mean size, then its validity does not depend on the number of speciation events separating an ancestor–descendant pair, but can depend on the way in which size is measured (e.g., body mass, body length). If instead Cope's Rule is formulated in terms of median size, then its validity does not depend on the way in which size is measured, but can depend on the number of speciation events separating an ancestor–descendant pair. We also point out some practical obstacles to assessing Cope's Rule by comparing the sizes in ancestor–descendant pairs. Although the results presented here are somewhat technical, they have important implications for Cope's Rule and its empirical assessment.

Results

A MEAN SIZE FORMULATION OF COPE's RULE

Let S denote a specific measure of size (e.g., log body mass) and let $\ldots S_{j-2}, S_{j-1}, S_j, \ldots$ be the sizes for species somewhere along an evolutionary lineage, where species $j-2$ is the direct ancestor of species $j-1$ that is the direct ancestor of species j and so on. We will use the term "degree of separation" to denote the difference in rank between species along a lineage. For example, the degree of separation between species $j-2$ and species $j-1$ is 1, whereas the degree of separation between species $j-2$ and species j is 2. We

will treat the sequence of sizes as a stochastic process and assume that it obeys the Markov property that the conditional distribution of the size of a species given the sizes of a set of its ancestors depends only on the size of the most recent ancestor in the set. The Markov property simplifies, but is not central to, the results of this article.

As in Alroy (1998), suppose that interest centers on testing the validity of Cope's Rule using the sizes in a collection of ancestor–descendant pairs. A natural formulation of the null hypothesis under which Cope's Rule does not hold is

$$E(S_j \mid s_{j-1}) = s_{j-1}, \tag{1}$$

where $E(S_j \mid s_{j-1})$ is the conditional mean of S_j given that $S_{j-1} = s_{j-1}$. The corresponding alternative hypothesis under which Cope's Rule holds is

$$E(S_j \mid s_{j-1}) > s_{j-1}. \tag{2}$$

Under the null hypothesis (1), the size of a species is, on average, equal to the size of its direct ancestor, whereas under the alternative hypothesis (2) it is, on average, larger.

Importantly, together with the Markov property, (1) implies that $E(S_j \mid s_{j-k}) = s_{j-k}$ for all k and similarly (2) implies that $E(S_j \mid s_{j-k}) > s_{j-k}$ for all k. These results are important in empirical work, such as Alroy (1998), where a direct ancestral relationship in an ancestor–descendant pair cannot be assumed. They ensure that the mean formulation of Cope's Rule does or does not apply to an ancestor–descendant pair of arbitrary degree of separation according to whether it does or does not apply to a direct ancestor–descendant pair. Unfortunately, as discussed below, lack of knowledge of the degree of separation poses a practical problem for assessing the mean formulation of Cope's Rule.

Consider now a nonlinear, monotonically increasing function g and let

$$T = g(S). \tag{3}$$

The function g can be thought of as a change in measurement scale, so that T is itself a measure of size. A problem with the mean size formulation of Cope's Rule is that it is not invariant to the scale at which size is measured. For example, suppose that, conditional on s_{j-1}

$$S_j = s_{j-1}\,\beta\,\varepsilon_j \tag{4}$$

where $\beta > 0$. Under this multiplicative model, to which we will return repeatedly, the size of a species (as measured by S) is equal to the product of the size of its direct ancestor, a constant factor β, and a random factor ε_j. As a concrete example, suppose that ε_j has an exponential distribution with mean 1 so that $E(S_j \mid s_{j-1}) = \beta\, s_{j-1}$. Now, take $T_j = \log S_j$. It is straightforward to show in this

case that, conditional on t_{j-1}, T_j has a Gumbel distribution with mean

$$E(T_j \mid t_{j-1}) \cong \log \beta + t_{j-1} - 0.577. \tag{5}$$

Thus, for $1 < \beta \le \exp (0.577)$, the mean size formulation of Cope's Rule holds for S but not for T. We emphasize that the exponential model is used here purely for convenience. The same kind of result can be shown to hold for other models.

More generally, suppose that Cope's Rule does not hold for some size measure S. In that case, by the so-called delta method (e.g., Oehlert 1992)

$$E(T_j \mid t_{t-j}) \cong t_{j-1} + \frac{g''(s_{j-1})}{2}\sigma^2, \tag{6}$$

where $g''(s_{j-1})$ is the second derivative of g evaluated at s_{j-1} and σ^2 is the conditional variance of S_j given s_{j-1}. Thus, if the function g is concave (i.e., $g'' > 0$), then Cope's Rule will hold for the size measure T. A similar argument shows that, if Cope's Rule holds for size measure S, then there exist functions g that are convex (i.e., $g'' < 0$) for which Cope's Rule does not hold for T.

At a theoretical level, it seems natural to require that Cope's Rule (or any general statement about body size) should be invariant to monotonically increasing transformations of a measure of size, such transformations being themselves measures of size. The mean formulation of Cope's Rule does not exhibit this invariance. As a consequence, whether this formulation holds can depend on the way in which size is measured. This is not simply a question of whether a logarithmic transformation is applied, for the question remains: applied to what?

It would be useful to have a real example in which Cope's Rule holds for one measure of size, but not for another. Unfortunately, published datasets of the kind needed to show this (i.e., multiple size measurements for each of a collection of ancestor–descendant pairs) do not seem to be available. However, the following real situation is one in which this problem could arise. Two measures of body size that have been used to investigate Cope's Rule are log body mass (e.g., Alroy 1998) and log body length (e.g., Hone et al. 2005). MacFadden (1986) found that, for fossil horses, head–body length is linearly related to log body mass. In terms of the previous notation, this implies that $T = \exp (S)$ where T denotes log body mass and S denotes the log of (linearly rescaled) length. Suppose that Cope's Rule does not hold for S. In that case, (6) implies that the conditional mean of T_j given t_{j-1} is approximately $t_{j-1}(1 + \sigma^2/2)$ where σ^2 is the conditional variance of S_j given s_{j-1}, so that, in contrast to S, Cope's Rule holds for T. To be sure, we are making no claim about fossil horses, but merely pointing out a real situation in which a nonlinear relationship between equally reasonable measures of size raises the possibility of contradictory results regarding Cope's Rule.

An obvious way to avoid this problem is to narrow the statement of the mean formulation of Cope's Rule to a specific size measure, recognizing that the results may be different for other measures. Unfortunately, a practical problem remains. Suppose that the multiplicative model in (4) holds for size measure S and that the measure of interest is taken to be log S. Consider an ancestor–descendant pair with degree of separation k. It is straightforward to show that, conditional on s_{j-k}

$$\log S_j - \log s_{j-k} = k \log \beta + \sum_{i=j-k+1}^{j} \log \varepsilon_i. \qquad (7)$$

Finally, suppose that $\log \varepsilon_i$ is normally distributed with mean 0 and variance σ^2 for all i. Under the null hypothesis that Cope's Rule does not hold, the mean of the difference $\log S_j - \log s_{j-1}$ is 0. If the degrees of separation between all ancestor–descendant pairs in a collection are the same, then the null hypothesis can be tested by the one-sample t test as in Alroy (1998).

The situation is different if, as in practice, the degrees of separation between the ancestor–descendant pairs in a collection cannot be assumed to be the same. Let k_j be the degree of separation in pair j. In this case, (7) has the form of a regression (through the origin) of $\log S_j - \log s_{j-1}$ on k_j with nonconstant variance $k_j \sigma^2$. The previous t test is not valid in this case because it fails to account for nonconstant variance. The degree to which this is a problem will depend on how variable the degrees of separation are. If the degree of separation is known for each pair, then a valid test can be carried out via weighted least squares (Seber 1977). In practice, the degrees of separation are not known. One option in this case is to use the estimated age difference between the ancestral and descendant species as a proxy for the degree of separation. However, this approach is certainly quite crude and cannot be recommended without further study.

A MEDIAN SIZE FORMULATION OF COPE's RULE

A formulation of Cope's Rule that does not depend on the way in which size is measured can be based on the conditional median of the size of a species given the size of its direct ancestor. Under this formulation, the null hypothesis under which Cope's Rule does not hold is

$$\text{med}(S_j | s_{j-1}) = s_{j-1} \qquad (8)$$

where med denotes the median. This is equivalent to the condition prob $(S_j > s_{j-1}) = 1/2$. The alternative hypothesis under which Cope's Rule holds is

$$\text{med}(S_j | s_{j-1}) > s_{j-1} \qquad (9)$$

or equivalently prob $(S_j > s_{j-1}) > 1/2$. This formulation underlies the sign test used by Alroy (1998) and others.

Because

$$\text{med}(g(S_j) | g(s_{j-1})) = g(\text{med}(S_j | s_{j-1})) \qquad (10)$$

for any monotonically increasing function g, this formulation of Cope's Rule is invariant to monotonically increasing transformations of a measure of size. There is, however, a different problem with the median size formulation of Cope's Rule. Surprisingly, the null hypothesis in (8) does not guarantee that med $(S_j | s_{j-k}) = s_{j-k}$ for $k > 1$, nor does the alternative hypothesis in (9) ensure that med $(S_j | s_{j-k}) > s_{j-k}$ for $k > 1$. That is, in general, the median formulation of Cope's Rule is not invariant to the degree of separation in an ancestor–descendant pair.

Consider again the multiplicative model (4), but now suppose that the random factor ε_j has median 1, so that med $(S_j | s_{j-1}) = \beta s_{j-1}$. The median formulation of Cope's Rule holds if $\beta > 1$. It follows from (4) that conditional on s_{j-k}

$$S_j = s_{j-k} \beta^k \prod_{i=j-k+1}^{j} \varepsilon_i \qquad (11)$$

so that med $(S_j | s_{j-k}) = \beta_{sj-k}^k$ med $(\prod_{i=j-k+1}^{j} \varepsilon_i)$. What can be said about med $(\prod_{i=j-k+1}^{j} \varepsilon_i)$? It is straightforward to show that, if the distribution of $\log \varepsilon_j$ is symmetric (by assumption, the point of symmetry being 0), then the median of $\prod_{i=j-k+1}^{j} \varepsilon_i$ is 1 and the median formulation of Cope's Rule is invariant to the degree of separation. That is, under this symmetry assumption, the median formulation of Cope's Rule does or does not apply to an ancestor–descendant pair of arbitrary degree of separation according to whether it does or not apply to a direct ancestor–descendant pair.

Beyond the symmetric case, general results regarding the median of the product of random variables are not available (e.g., Rathie and Rohrer 1987). To illustrate what can happen, suppose that ε_j has an exponential distribution with median 1. The corresponding Gumbel probability density function of $\log \varepsilon_j$, which is shown in Figure 1, is mildly negatively skewed. Numerical calculation shows that in this case med $(\varepsilon_{j-1} \varepsilon_j) \cong 0.82$ and med $(\varepsilon_{j-2} \varepsilon_{j-1} \varepsilon_j) \cong 0.67$. So, for example, if $\beta = 1.1$, the conditional median size of a species is 10% greater than the size of its direct ancestor, equal to the size of its ancestor of degree 2, and 12% smaller than the size of its ancestor of degree 3. It follows that size will tend to increase in a collection of direct ancestor–descendant pairs, tend to remain constant in a collection of pairs of degree 2, and tend to decrease in a collection of pairs of degree 3.
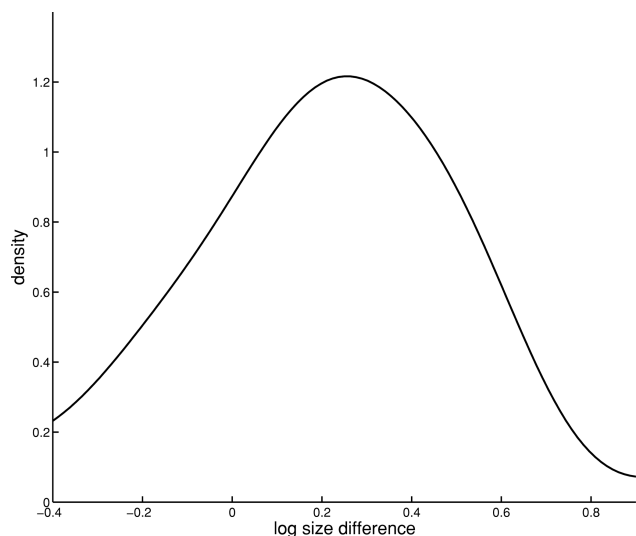
As before, the exponential model is used here solely for its convenience. In this case, it is also possible to show some results based on real data. Figure 2 shows a kernel estimate (Silverman 1986) of the probability density function of the difference in log body mass for 24 ancestor–descendant pairs of fossil horses provided by MacFadden (1986). The estimated density, which was based on a Gaussian kernel with bandwidth 0.125, is
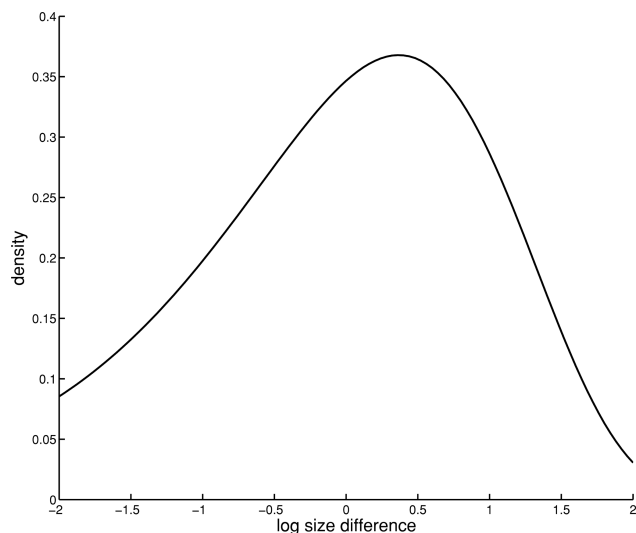
Figure 1. Probability density function of the logarithm of an exponential random variable with median 1.

mildly negatively skewed and, indeed, is similar in shape to the Gumbel density in Figure 1. However, as discussed below, there is a problem in interpreting this result.

Suppose again that the multiplicative model in (4) holds for a specific size measure S and that med $(\varepsilon_j) = 1$. As noted, the problem with the median size formulation of Cope's Rule is avoided if it can be assumed that $\log \varepsilon_j$ has a symmetric distribution. It may seem at first glance that this assumption can be checked through the empirical distribution of the differences in log size in ancestor–descendant pairs as in Figure 2. This would be true if the degree of separation in all such pairs was 1. In that case, it follows from (7) that $\log S_j - \log s_{j-1} = \log \beta + \log \varepsilon_j$, so that the density of this difference is symmetric around $\log \beta$ if and only if the density of $\log \varepsilon_j$ is symmetric around 0. Otherwise, the situation is more complicated. For example, suppose that the degree of separation in all ancestor–descendant pairs is equal to k with $k > 1$. Provided k is not too small, the Central Limit Theorem ensures that the distribution of $\log S_j - \log s_{j-k}$ is approximately normal (and therefore symmetric) with mean $k \log \beta$ and variance $k \sigma^2$ irrespective of the distribution of $\log \varepsilon_j$. Thus, it is not possible to infer symmetry of $\log \varepsilon_j$ from symmetry of $\log S_j - \log s_{j-k}$. On the other hand, because the sum of independent random variables each symmetric around 0 is also symmetric around 0, asymmetry of this difference does imply asymmetry of $\log \varepsilon_j$. The situation is worse in the realistic case in which the degree of separation varies among the ancestor–descendant pairs. Briefly, in this case, the distribution of log size differences follows a mixture of distributions that differ in mean, variance, and possibly shape. In this case, the shape of the distribution of the log size differences cannot be assumed to provide any information about the shape of the distribution of $\log \varepsilon_j$.

Discussion

Existing methods for assessing Cope's Rule appear to be based implicitly on the following argument. There is a correct size measure S that follows the multiplicative model in (4) with ε normal (or symmetric) with mean 0. Moreover, this measure is known. It then follows that the difference in log size is also normal, so that either a t test or sign test can be used to assess the validity of Cope's Rule. In the context of this argument, which is not on its face unreasonable, we have pointed out (1) that the assumption that the correct size measure is known is not innocuous because the result of the t test can be different for other size measures; (2) that even if the assumptions are valid, the t test is not valid if the degree of separation in the ancestor–descendant pairs varies; (3) that the assumption that ε is normal (or symmetric) is not innocuous because the result of the sign test can depend on the degrees of separation among the ancestor–descendant pairs; and (4) that it is not possible to assess normality (or symmetry) from the empirical distribution of the differences in log size when the degree of separation varies among the ancestor–descendant pairs.

As a practical matter, where does this leave the assessment of Cope's Rule? Arguably, among existing methods, the best case can be made for testing the median formulation via the sign test assuming that the multiplicative model in (4) holds with symmetry at the log scale. Under this assumption, the results are invariant both to nonlinear transformation of the measurement scale and to the degree of separation in the ancestor–descendant pairs. It needs to be recognized, however, that the symmetry assumption—which is not invariant to nonlinear transformation of the measurement scale—cannot be checked.

Figure 2. Kernel estimate of the probability density function of the difference in log body mass for fossil horses.

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