

THE STATISTICAL ANALYSIS OF SIZE RATIOS

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Ecologists have long believed that differences in the sizes of ecologically similar species may provide or reflect differences in their niches sufficient to permit coexistence (e.g., Lack 1944; Brown and Wilson 1956). Hutchinson (1959) first used the ratio of the larger to the smaller of each pair of species to characterize these differences. He suggested that, in order to coexist, species depending on size alone for niche separation must differ by ratios of at least 1.28 in some linear measurement. This was an empirically derived rule, based on the observation of a number of similar species that had apparently diverged in size in areas of sympatry. This suggestion has generated a great deal of research into questions of limiting similarity and community structure. It has also provoked a controversy whose most beneficial effect has perhaps been to illuminate the very different ways in which ecologists work (Lewin 1983*a,b*).

As reviewed by Simberloff (1983) and Simberloff and Boecklen (1981), Hutchinson's suggestion has been interpreted by various researchers to mean that similar, coexisting species differ by minimum ratios, constant ratios, or both. In most cases, these ratios have been presented to corroborate or merely act as metaphors for more-substantial characterizations of species' differences and similarities. In some cases, however, the 1.28 ratio in linear dimensions, or doubling in weight, has been used as a standard against which actual data were compared in order to make inferences about the ecology and evolution of organisms. For example, Enders (1976) concluded that successive instars of certain spiders must compete with one another for food because they differed by size ratios of less than 1.28. Oksanen et al. (1979) inferred that bird species had disappeared from particular feeding guilds because some size ratios in those guilds were much larger than 1.28. (This requires the additional, unstated assumption that species are packed tightly in niche space.) More commonly, however, authors have used ratios of between 1.2 and 1.5 or more as evidence that animals do not compete for food (e.g., Diamond 1973). These authors all may be correct in their assertions; however, we question whether they can make such inferences from size ratios alone.

There is good reason to be cautious when making inferences from size ratios.

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The size of an animal may reflect adaptation to any of a wide range of factors, of which interspecific competition for food is but one. Body sizes may also be influenced by physiological, mechanical, reproductive, behavioral, and defensive factors (Peters 1983; Calder 1984). The selective benefits that accrue from most of these mechanisms are independent of the sizes of other species in the community. Therefore, the sizes of two sympatric species may be set independently by factors other than competition, in which case their size ratio, whether large or small, would be irrelevant to questions of competition and coexistence. If size ratios are to be used as indexes of morphological, and hence ecological, displacement, then methods must be found to distinguish ratios of ranked, independent body sizes from those of species constrained from being too similar.

In this paper, we first explore the statistical properties of size ratios under the null hypothesis that the sizes of species within guilds are independent of one another. We show that this leads to predictions about ratio distributions different from those of the alternative hypothesis that species' sizes are constrained to be dissimilar. Second, we ask which of the two models better explains several large data sets. Finally, we argue that previously described tests for constant or minimum ratios in single guilds depend critically on the assumed but unknown underlying size distribution, and are therefore of little use. We conclude that size ratios alone are of limited explanatory power and that they can be used only to identify broad patterns in large data sets. If one wishes to determine the role that body-size differences play in permitting particular species to coexist, then these ratios must be supplemented, if not replaced, by more-detailed ecological data.

THE MODEL

Suppose each species in a guild has evolved to an optimal size, not dependent on the sizes of the other species in the guild. Suppose, in addition, that no two species are exactly the same size. Given these two assumptions, it is clear that the species can be ranked in order of increasing size, and the ratios of successive pairs computed. Two questions arise immediately. What distributions of ratios are generated under this simple hypothesis of independent body sizes? Does this hypothesis explain the data better than a competitive model, in which species' sizes are not independent of one another?

In order to answer these questions, we must specify some underlying distribution of species sizes from which guilds of size n are independently and randomly drawn. This underlying distribution can be viewed in either of two ways: (1) there is an actual pool of species with this size distribution; (2) species evolve to different sizes at frequencies reflected in the distribution.

In the first case, our selection of species is analogous to the colonization of an island or new habitat from some actual species pool. In the second case, the pool is not a reality, only a potentiality. Either way, body sizes can be treated as random variables independently drawn from some specified underlying distribution. The shape of this distribution subsumes all the biologically important effects of body size within it.

Suppose a guild of n species is drawn from this effective species pool. The species sizes are independent random variables, denoted by Y_1, Y_2, \dots, Y_n . We

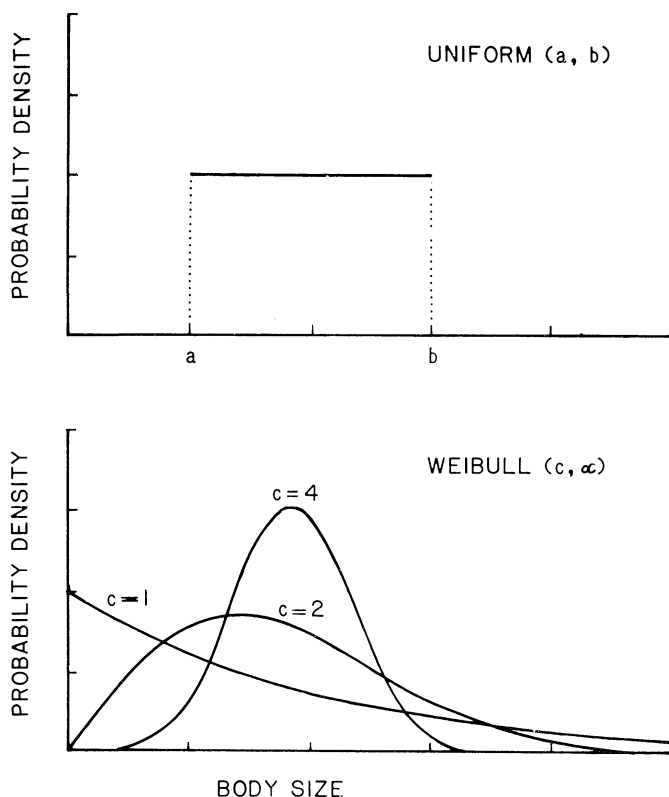


FIG. 1.—Assumed distribution of body sizes in the species pool. *Above*, all body sizes between two values are equally likely or common, as represented by the uniform (a, b) distribution. *Below*, small- or intermediate-sized species are more likely, as described by some Weibull (c, α) distribution.

define a new set of statistics, the order statistics, such that $X_1 = \min(Y_i), \dots, X_n = \max(Y_i)$. These are the species sizes ranked in increasing order, which are no longer independent of one another. The variables of interest are the size ratios, defined as $Z_i = X_{i+1}/X_i$, for $i = 1, 2, \dots, n - 1$. If a large number of guilds of size n were drawn from the pool, it is clear that a sampling distribution would be obtained for each ratio Z_i . Rather than perform such repeated sampling, we have obtained exact analytic solutions for two cases (fig. 1).

1. Uniform distribution.—All size classes between some upper and lower limits are equally represented in the actual species pool, or are equally likely to evolve from selection on size-related aspects of physiology, behavior, etc.

2. Weibull distribution.—Small- or intermediate-sized species are either more abundant in the pool or more likely to evolve.

The Weibull distribution is defined by a shape parameter c and a scale parameter α (Johnson and Kotz 1970), where c and α are both positive. At $c = 1$, the distribution reduces to the negative exponential distribution; as c increases, it

becomes first approximately lognormal and then increasingly symmetrical about a single mode (fig. 1). Distributions of species' sizes from higher taxa can easily be fit by this distribution (e.g., Schoener and Janzen 1968; Van Valen 1973; May 1978). Given the flexibility of the two-parameter Weibull distribution, and the likely paucity of bimodal size distributions in nature, we believe the two cases above cover most biologically plausible possibilities for a species pool.

In Appendix A, we derive the probability density function for ratio values, assuming that the underlying species' sizes are uniformly distributed. If a and b are the smallest and largest sizes attainable and $Z_{i,n} = X_{i+1}/X_i$, the ratio of the $(i + 1)$ th-smallest to the i th-smallest species out of n , then the probability density function of $Z_{i,n}$ is given by

$$h(z_{i,n}) = [(b - az)^{n-1}/(b - a)^n z^i] [(ib/z) + a(n - i)], \tag{1}$$

where z ranges from 1 to b/a .

If the species pool can be approximated by some Weibull (c, α) distribution, then the probability density of ratios of successive, randomly selected species is given by

$$h(z_{i,n}) = \frac{n! c z^{c-1}}{(n - i - 1)! \prod_{r=1}^i [z^c(n - i) + r]} \sum_{s=1}^i \frac{1}{z^c(n - i) + s} \tag{2}$$

(Appendix B). Notice that only the shape parameter c is important; the scaling parameter α is eliminated when ratios are taken. When the derivation is repeated for a Weibull distribution truncated at a and b , the relevant parameters are $c, a/\alpha$, and b/α ; only the positions of the endpoints relative to the scaling parameter, not their absolute values, are important. The following discussion is based on the non-truncated distribution, since for c much larger than 2, the probabilities of very large and very small species become very small.

By taking the appropriate derivatives of equations (1) and (2), it is possible to show that they share three qualitative features (see the appendixes). Distributions or histograms of ratios of ranked independent variables (1) decrease monotonically from a peak at the lower limit, $z = 1$, and (2) are concave upward. Furthermore, (3) the average value of all ratios decreases as the number of species per guild increases. These three patterns do not depend on particular parameter values, but they are true for all ratios z_1, \dots, z_{n-1} , in all uniform (a, b) and Weibull (c, α) distributions, provided that $c = 1$ (exponential) or $c > 1$ (unimodal) in the latter case. These three features are illustrated in figure 2.

These results can be generalized immediately. It is clear that any (finite) unimodal size distribution yields relatively more small ratios in random draws than does a uniform distribution. Therefore, ratios of ranked independent variables from any unimodal size distribution should have frequency distributions that decline monotonically (feature 1). Feature (3) is also general; if species are added to a guild independently of their sizes, their average similarity must increase. We have not been able to extend feature (2) to all unimodal distributions, but it should not be affected by small deviations from a uniform or Weibull size distribution.

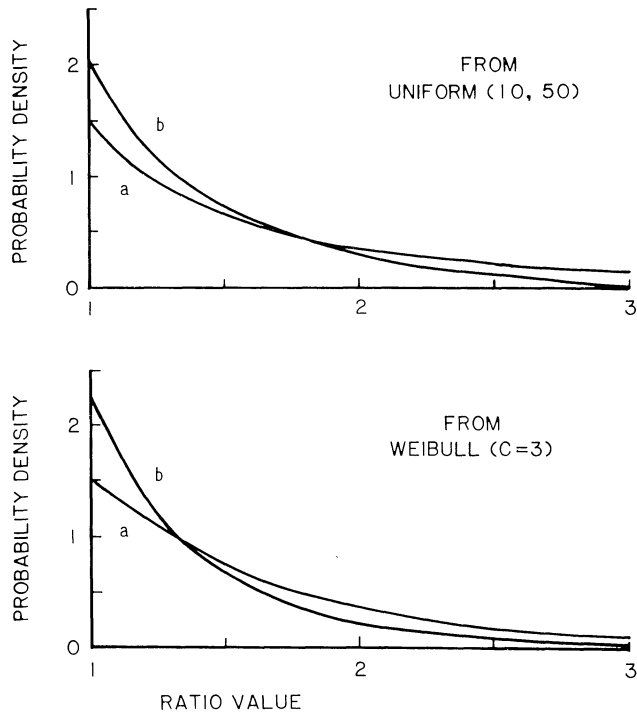


FIG. 2.—Distribution of ratios of the second-smallest to the smallest species, assuming that sizes are independent random draws from a uniform probability density (*above*) and from a Weibull probability density (*below*). *a*, Two-species guilds; *b*, four-species guilds.

Finally and most important, all three properties of the curves are additive. If species' sizes within different guilds are drawn independently from different uniform and Weibull distributions, the summed distribution of ratios from these guilds still displays the same three properties. The converse, of course, is not necessarily true.

Therefore, we make the following general predictions. Suppose that actual or potential species pools are uniform or unimodal in shape. If the sizes in subsets of this pool (e.g., those that are sympatric) are independent of one another, then distributions of their ratios will be monotonically declining and concave upward (i.e., approximately negative exponential in shape), and the average value of all ratios will decrease as the number of species per guild increases.

These predictions can be contrasted with those expected when species' sizes within guilds are not independent of one another but exhibit minimum or constant ratios. When ratios are constrained to differ, frequency distributions of ratios are unimodal, with a peak at 1.2, 1.3, or some other intermediate value; they are therefore neither monotonically declining nor concave upward. Furthermore, ratios in larger guilds should be the same as those in smaller guilds, if not larger owing to increased levels of diffuse competition (Pianka 1974). The two sets of

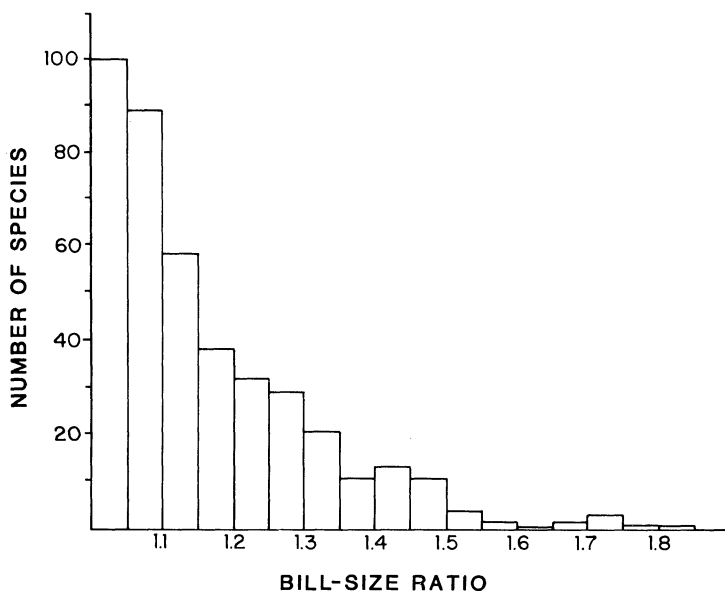


FIG. 3.—Frequency distribution of bill-size ratios for sympatric, congeneric bird species listed by Schoener (1965). The total number of ratios is 410.

predictions, based on a large role for Hutchinson's rule in the one case and a complete independence of species' sizes in the other, are quite different from one another. It is now a straightforward matter to compare distributions of real ratios with these two models.

COMPARISON WITH DATA

Schoener (1965) analyzed the bill lengths of 684 species of birds. He divided the birds into guilds, that is, groups of two to six sympatric congeners. These data were biased both from the inclusion in guilds of congeners that really do not belong and from the exclusion of non-congeners that do belong in the guilds. These factors tend to bias ratios to smaller and larger values, respectively, and may cancel each other. In any case, there is no way to correct these problems. It should be pointed out that, by presenting all sets of sympatric congeners he could find, Schoener was unbiased in his selection process, and that these data represent a sizable fraction of the world avifauna.

The frequency distribution of all ratios in this data set, 410 in all, is plotted in figure 3. There is no tendency for ratios to predominate in any band between 1.15 and 1.40; in fact, the median value is only 1.10. The distribution is essentially monotonically decreasing and concave upward, fitting the null model quite well.

The third prediction of the null model, that ratio values decrease with guild size, is also satisfied. Table 1 shows the mean and median values for each of the ratios for each guild size. Note that when all the ratios in each guild size are combined,

TABLE 1
MEAN (AND MEDIAN) RATIO FOR GUILDS OF DIFFERENT SIZES (FROM SCHOENER 1965)

NO. OF SPECIES IN GUILD	SIZE RANKING OF SPECIES IN RATIO					N
	2:1	3:2	4:3	5:4	Combined	
2	1.20 (1.14)	—	—	—	1.20 (1.14)	181
3	1.17 (1.10)	1.17 (1.13)	—	—	1.17 (1.12)	122
4	1.13 (1.06)	1.07 (1.06)	1.11 (1.08)	—	1.10 (1.06)	69
5	1.06 (1.01)	1.10 (1.08)	1.08 (1.06)	1.12 (1.10)	1.09 (1.05)	28
6	—	—	—	—	1.04 (1.03)	10

NOTE.—Only summary statistics are presented for the two six-species guilds.

their mean values decrease from 1.20 in two-species guilds to 1.04 in six-species guilds. This is a consistent trend with no reversals. There is significant variation among the medians (*K*-sample-median test, $P < 0.001$), and their ordering is significantly correlated with guild size, in the direction predicted (Kendall rank correlation, $P < 0.05$). The same trend is clear if one looks only at the ratios of the second-smallest to the smallest across different guild sizes (*K*-sample-median test, $P < 0.05$), but it cannot be detected in the other ratios.

In summary, the distribution of ratios is monotonically decreasing and concave upward, and ratios tend to be smaller in larger guilds. We conclude that, if constant ratios do occur as some sort of ecological law among certain kinds of guilds, these guilds are poorly represented in Schoener's data. Competition may still be important in many or all of these guilds; however, it has not typically led to minimum differences in bill sizes. An alternative hypothesis, that birds' bill sizes respond to selective factors that are independent of the sizes of other guild species, appears to explain the evidence much better.

T. Tomasi (in prep.) has presented 62 body-size ratios for sympatric species of insectivorous bats. The distribution of the data is shown in figure 4. Here, also, the distribution appears to conform to the null expectations.

The only other analysis of a large set of size ratios illustrates the power of our approach. Schoener (1984) showed that the distribution of wing lengths for all 47 species of *Accipiter* hawks in the world is unimodal. Furthermore, by drawing species pairs, trios, and quartets at random from this pool, he showed that wing-length ratios of sympatric species should be more or less negative exponential in form, if species associate independently of size. Since the actual ratios of sympatric *Accipiters* are distributed unimodally, he concluded that there are often limits to similarity among these birds. Here the null distribution was derived from the observed distribution, not independently of it, and the observed distribution may have been altered by the competitive processes being tested for. Schoener

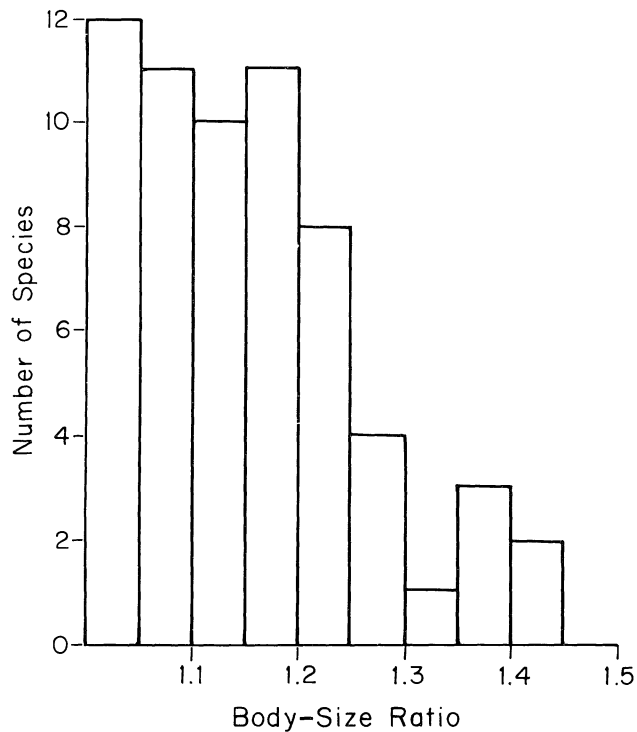


FIG. 4.—Frequency distribution of body-size ratios for sympatric, insectivorous bats from T. Tomasi (in prep.). The total number of ratios is 61.

was well aware of this potential problem (considered a fatal flaw by some; e.g., Gilpin and Diamond 1984). Indeed, he suggested that “a better approach would be somehow to deduce a null expectation from knowledge of evolutionary and ecological processes” (Schoener 1984, p. 275). Although we cannot offer such a model, we can state on statistical grounds that almost any species pool will yield the predicted null distribution of ratios, so that Schoener’s conclusions are unaffected by these concerns.

DISCUSSION

Individual guilds catalogued by Schoener (1965) or T. Tomasi (in prep.) may maintain minimum or constant ratios as a result of interspecific competition; however, their presence could easily be masked by a large number of guilds that do not show this pattern. How can one detect these guilds, on the basis of their size ratios alone? The only possibility is to devise a statistical test for use on individual guilds. Several authors have proposed such tests (e.g., Roth 1981; Simberloff and Boecklen 1981), and other tests could be imagined, based for example on tests for the nonrandom division of the unit interval (e.g., Poole and

Rathcke 1979; for a review, see David 1981). We believe that these tests are unsuccessful and, furthermore, that their deficiencies cannot be corrected with current knowledge. This places a limit on the use of size ratios alone to make inferences about the role of size differences in permitting coexistence. We present some general criticisms below. These criticisms apply with equal force to tests for nonrandom flowering times in plant communities, since these tests are also based on (unreplicated) order statistics.

First, when dealing with a few species in a single guild, the determination of whether body sizes are more different than one would expect by chance alone depends inherently on what one would expect by chance alone. A guild that appears to be significantly displaced toward constant ratios, under the null model that body sizes are uniformly distributed, may be indistinguishable from random when large body sizes are assumed to be less common than small ones. Unfortunately, we do not know what the distribution of body sizes would be in the absence of competition. To determine this, we need a greater knowledge of how various factors affect the evolution of body size. (If we had that information, the sort of analysis discussed here would be unnecessary.)

Researchers have typically assumed that, in the absence of competition, all body sizes between two limits are equally likely or common; the analogue for the analysis of community flowering patterns is that, in the absence of competition for pollinators, all days in the season are equally likely to be the dates of peak flowering. This assumption simplifies the statistical analysis, but it is hardly realistic. We know of no biological data that are uniformly distributed, nor have we any reason to expect that here. Seasonal and developmental factors conspire to make very early and very late dates less desirable for flowering (Stiles 1979), just as diminishing returns and various physiological and biomechanical constraints render very small and very large body sizes less desirable. The statistical comparison of data against this unrealistic null hypothesis seems an empty enterprise, though we cannot specify precisely a better null distribution.

A second, related problem is that the statistical significance of observed sizes in single guilds depends on the range of body sizes possible. To use a different example, suppose that five plant species flower at precise 5-day intervals starting on July 6 and ending on July 26. If the season during which flowering is possible runs from July 1 to July 31, then the species have spaced themselves perfectly through the season. On the other hand, if the season lasts from March to October, then the peak flowering dates are markedly clumped in time. An intermediate-length season could lead one to conclude that flowering times are essentially random. Until we better understand the factors determining flowering times, or body sizes, we cannot determine what the possible endpoints are; yet our conclusions depend on what we assume these endpoints to be. To overcome this difficulty, researchers have taken the first and last species in the sequence, be it in flowering times (Poole and Rathcke 1979; Cole 1981) or in body size (Simberloff and Boecklen 1981), as the endpoints. They have then asked the slightly altered question of whether the remaining $n - 2$ species are placed nonrandomly between the first and last in the sequence. Unfortunately, this apparently commonsense solution introduces several new problems that further weaken the statistical analysis.

The most obvious difficulty with using the first and last species in the sequence as the endpoints is that one loses two data points. Since guilds are typically small to begin with, one has little information left with which to draw any conclusions. In the limit, one is testing the statistical significance of a single data point, the second of three species (e.g., Simberloff and Boecklen 1981, table 1).

The second difficulty with this approach has not been discussed before. If one wishes to treat body sizes as independent random variables in some null model, it is inconsistent to treat the sizes of intermediate-ranked species as statistically independent of the endpoints, the first and last species. As pointed out earlier, once the body sizes are ranked in the order of increasing size, they are no longer independent of one another; the fact that a species is the second smallest in a series presupposes that one other species in the draw is smaller, and the rest are larger. A proper null model would not ask whether the intermediate-sized species are, for example, uniformly distributed between the largest and the smallest species; rather, it would compare their values against a more complex null distribution that reflects this interdependence.

An example is useful here. Suppose the sizes of four species are independent random variables from a uniform (a, b) distribution. Then, by equation (1), the ratio X_3/X_2 of the third to the second species will have the probability density

$$h(z_{2,4}) = [(b - az)^3 / (b - a)^4 z^2] (2b/z + 2a). \tag{3}$$

However, if one doesn't know the values of a and b , but treats the sizes of the second and third species as independent random variables from a uniform distribution defined over the interval $[X_1, X_4]$, one expects the probability density of X_3/X_2 to be

$$h(z_{1,2}) = [(x_4 - x_1z) / (x_4 - x_1)^2 z] (x_4/z + x_1), \tag{4}$$

where $a \leq x_1 \leq x_4 \leq b$. Clearly, the two equations are not the same, and it would not be valid to compare statistically the observed ratio of the third-smallest to the second-smallest species against the latter distribution. However, this is precisely what Poole and Rathcke (1979), Simberloff and Boecklen (1981), and others have done when they chose the first and last species in a sequence as endpoints for the underlying distribution. The first-order and last-order statistics are the maximum-likelihood estimates of the low and high endpoints in random samples from a uniform distribution, but they are biased estimates (Carlton 1946). Furthermore, it seems unreasonable to try to estimate the endpoints and the significance of observed ratios from the same limited data. This seems an insoluble problem.

The statistical analysis of size ratios within individual guilds depends on the shape of the underlying size distribution, and on its endpoints. Neither of these is known, and the assumptions that authors have made about them are probably wrong and internally inconsistent. Unfortunately, these problems are inherent, and we see no way around them. This places a severe limit on the inferences that can be made from size ratios alone.

There is one circumstance in which we could envision the possibility of drawing inferences about ratios from a single or few guilds. This is the case of island colonization from a known source in which there has been no subsequent size

change (Schoener, in prep.). In this event the possible sizes are known and the problem becomes one of simple combinatorial mathematics.

We have assumed merely that species' sizes can be approximated by some uniform (a, b) or unimodal Weibull (c, α) distribution, and that the sizes of sympatric species are independent of one another. Given only this, we can make three qualitative predictions about distributions of large numbers of ratios, and these predictions are nearly independent of the form of the underlying species pool. This independence should not be surprising. From a statistical point of view, size ratios are ratios of order statistics. Order statistics such as the minimum, median, and maximum are relatively distribution-free; this explains their widespread use in nonparametric statistics. In taking ratios of order statistics, we eliminate even further any "memory" of the distribution from which they were drawn.

This reveals both the strengths and the weaknesses of our approach. Our predictions are nearly independent of the actual form of the underlying species pool. If they are not met, as in the world's *Accipiters*, then we have strong evidence that species are constrained to be dissimilar. In answer to our original question, such ratios could be considered reasonable evidence of the nonrandom structuring of guilds due to competition or other factors.

However, if the data do not differ from our predictions under the general null model, this does not tell us much. There may be individual guilds of species whose sizes are strongly influenced by competition, but whose presence is masked. Our method cannot detect such guilds, if they are rare. If we were to make stronger assumptions about the underlying species pool, we could define more clearly the null distribution and obtain better resolution in these tests for "nonrandomness." Unfortunately, we do not know enough about the determinants of body size to make these stronger assumptions.

The only way to identify individual "competitive" guilds is to devise a statistical test for constant or minimum ratios that can be used with single guilds. We have argued that any such test is necessarily sensitive to assumptions of the underlying size distribution, about which nothing is usually known. This is in direct contrast to our results for large sets of ratios, which are insensitive to the underlying size distribution. We question whether one can ever determine if the sizes of species within single guilds are independent of one another, on the basis of size ratios alone. It is important to note that most of the controversy over the ecological significance of size ratios has concerned ratios in single, often small guilds. We submit that neither side has a case, in these instances, if it relies solely on size-ratio data. One can no more assert that the ratios are structured by competition than assert that they are not.

Empirical laws concerning the relative sizes of ranked objects abound in biology (for reviews, see Horn and May 1977; Roth 1979; Cole 1980). They include the notions that successive instars of arthropods differ by ratios of either 1.26 or 1.6 in linear dimensions, the observation that cell nuclei increase in size by a factor of the square root of two between different tissues, and the discredited ideas that brain volumes and body volumes increase by a factor of two in stepwise fashion in evolution. We suspect that the ubiquity of such rules is not accidental. To the extent that humans classify objects into groups of relatively small numbers of

similarly sized objects, the ratios of the ranked sizes of these objects will be a little larger than one and will readily appear to obey such laws. It is not easy statistically to distinguish real patterns of this sort from ones that would be generated entirely at random in taking ratios of order statistics.

SUMMARY

Size ratios are convenient indexes of the morphological differences between species. They have been variously used to predict multidimensional niche separation, explain coexistence, and even indicate "missing species," depending on whether they are small, moderate, or large. From a statistical viewpoint, ratios of ranked species' sizes are ratios of successive order statistics, which are largely independent of the underlying size distribution. We derive probability density functions for these ratios, assuming that species' sizes are independently drawn from uniform or unimodal distributions. In the absence of frequent character displacement, distributions of ratios should be negative exponential in form, with average values decreasing with increasing guild size. These predictions, which differ from those under a purely competitive model, are tested with several large data sets. In contrast, the statistical analysis of ratios in small data sets, such as individual guilds, depends on arbitrary assumptions about the shape and endpoints of the underlying size distribution. We conclude that size ratios alone are of limited explanatory power and should be supplemented with other data in studies of character displacement and community structure.

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APPENDIX A

Let $f(x)$ be some continuous probability density on the interval $[a, b]$, and let $F(x) = \int_a^x f(t)dt$ be the corresponding cumulative distribution function. Suppose n numbers are drawn at random from this distribution and then ranked in order of increasing size to yield the order statistics $X_1 < X_2 < \dots < X_n$. (In the continuous case, ties $X_i = X_{i+1}$ occur with probability 0 and can be ignored.) If $j = i + 1$, then the joint density of X_i and X_j is given by

$$g_{ij}(x_i, x_j) = [n! / (i - 1)!(n - j)!] [F(x_i)]^{i-1} [1 - F(x_j)]^{n-j} f(x_i) f(x_j)$$

(Hogg and Craig 1970). The probability that the ratio X_j/X_i will be less than or equal to Z is given by a new cumulative distribution function $H(z)$, where $H(z) = \iint_D g_{ij}(x_i, x_j) dx_i dx_j$ and the domain D is defined by $1 \leq x_j/x_i \leq z$ (fig. A1). This integral has two parts:

$$H(z) = [n! / (i - 1)!(n - j)!] \int_a^{az} [1 - F(x_j)]^{n-j} f(x_j) \int_a^{x_j} [F(x_i)]^{i-1} f(x_i) dx_i dx_j + [n! / (i - 1)!(n - j)!] \int_{az}^b [1 - F(x_j)]^{n-j} f(x_j) \int_{x_j/z}^{x_j} [F(x_i)]^{i-1} f(x_i) dx_i dx_j.$$

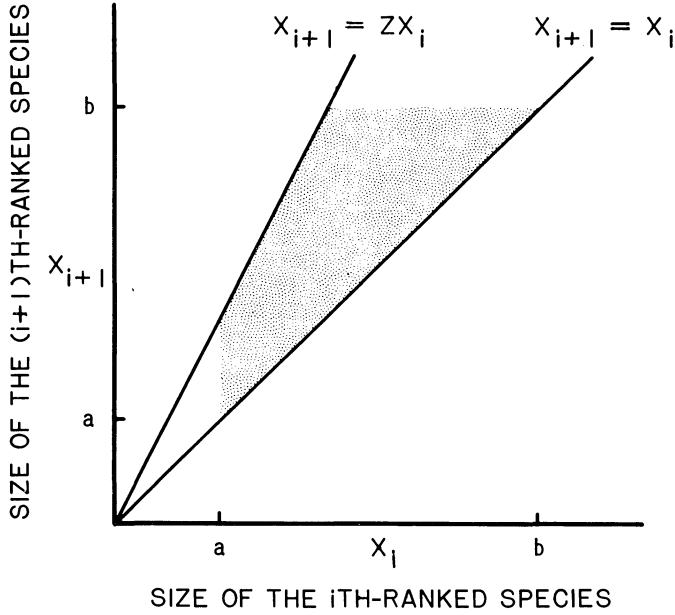


FIG. A1.—The stippled area is the domain D in which the order statistics X_i and X_{i+1} ($a \leq X_i \leq X_{i+1} \leq b$) satisfy the relation $1 \leq X_{i+1}/X_i \leq Z$. The cumulative distribution function of z is obtained by integrating the joint density $g(X_i, X_{i+1})$ over D .

Integration over x_i yields

$$H(z) = [n! / i!(n - j)!] \int_a^b [1 - F(x_j)]^{n-j} [F(x_j)]^i f(x_j) dx_j - [n! / i!(n - j)!] \int_{az}^b [1 - F(x_j)]^{n-j} [F(x_j/z)]^i f(x_j) dx_j.$$

The first integral is simply the beta function $B(i + 1, n - i) = i!(n - j)!/n!$, and the equation simplifies to

$$H(z) = 1 - \frac{n!}{i!(n - j)!} \int_{az}^b [1 - F(x_j)]^{n-j} [F(x_j/z)]^i f(x_j) dx_j.$$

We have not yet specified the underlying distribution of species' sizes; the relation above is a general one.

If species' sizes are uniformly distributed over the interval $[a, b]$, then $f(x) = 1/(b - a)$ and $F(x) = (x - a)/(b - a)$. Substituting into the formula above (and omitting subscripts) yields

$$H(z) = 1 - [n! / i!(n - j)!] [1 / (b - a)^n z^i] \int_{az}^b (b - x)^{n-j} (x - az)^i dx$$

or

$$H(z) = 1 - (b - az)^n / (b - a)^n z^i.$$

The probability density of z is simply the derivative $h(z) = dH(z)/dz$:

$$h(z) = [(b - az)^{n-1} / (b - a)^n z^i] [(ib/z) + a(n - i)].$$

It is tedious but straightforward to demonstrate that $h'(z) < 0$ and $h''(z) > 0$ for all $1 < z < b/a$, such that $h(z)$ is a monotonically decreasing function of z and is concave upward.

APPENDIX B

Let $f(x)$ and $F(x) = \int_0^x f(t)dt$ define a probability function as before, except that x ranges from 0 to infinity. The joint density of the order statistics X_i and $X_{i+1} = X_j$ is the same, and the probability that the ratio X_j/X_i is less than or equal to Z is given by

$$H(z) = 1 - [n! / i!(n - j)!] \int_0^\infty [1 - F(x_j)]^{n-j} [F(x_j/z)]^i f(x_j) dx_j,$$

where only the limits of integration are altered. Again, this equation is a general one, and it applies to all continuous probability densities $f(x)$ defined on $[0, \infty)$. Suppose $f(x)$ is the Weibull probability density

$$f(x) = (c/\alpha)(x/\alpha)^{c-1} \exp[-(x/\alpha)^c]$$

$$F(x) = 1 - \exp[-(x/\alpha)^c], \quad c, \alpha > 0.$$

Substituting these terms, and making the change of variable $U = F(x/z)$, yields

$$H(z) = 1 - [n! / i!(n - j)!] z^c \int_0^1 U^i (1 - U)^{z^c(n-i)-1} dU$$

$$= 1 - [n! / i!(n - j)!] \left\{ z^c \Gamma(i + 1) \Gamma[z^c(n - i)] / \Gamma[z^c(n - i) + i + 1] \right\}$$

$$= 1 - n! / \left\{ (n - i)! [z^c(n - i) + i] \cdot \dots \cdot [z^c(n - i) + 1] \right\}.$$

Again, differentiation with respect to z yields the probability density of z ,

$$h(z) = \frac{n! c z^{c-1}}{(n - j)! \prod_{r=1}^i [z^c(n - i) + r]} \sum_{s=1}^i \frac{1}{z^c(n - i) + s}.$$

Determining the signs of $h'(z)$ and $h''(z)$ is a little more complex here. Consider first the case in which the underlying distribution of body sizes is negative exponential, in which $c = 1$. If we substitute u for z , and write

$$A_r(u) = 1 / [u(n - i) + r], \quad dA_r(u) / du = -(n - i)[A_r(u)]^2,$$

then

$$h(u) = [n! / (n - j)!] \prod_{r=1}^i A_r(u) \sum_{s=1}^i A_s(u),$$

$$h'(u) = -[(n - i)n! / (n - j)!] \prod_{r=1}^i A_r(u) \left\{ \left[\sum_{s=1}^i A_s(u) \right]^2 + \sum_{s=1}^i [A_s(u)]^2 \right\},$$

$$h''(u) = [(n - i)^2 n! / (n - j)!] \prod_{r=1}^i A_r(u) \left\{ \left[\sum_{s=1}^i A_s(u) \right]^3 + 3 \sum_{s=1}^i A_s(u) \sum_{s=1}^i [A_s(u)]^2 \right.$$

$$\left. + 2 \sum_{s=1}^i [A_s(u)]^3 \right\}.$$

Clearly, $h'(u) < 0$, and $\overline{h''(u)} > 0$ when $c = 1$. Next, let $u = z^c$, for $z \geq 1$, $c > 1$. Then, by the chain rule

$$\begin{aligned} dh(u)/dz &= h'(u) du/dz = h'(u) cz^{c-1} \\ d^2h(u)/dz^2 &= h'(u) d^2u/dz^2 + h''(u) (du/dz)^2 = cz^{c-2} [(c-1)h'(u) + cz^c h''(u)]. \end{aligned}$$

The first derivative is negative for all $z \geq 1$. The second derivative is positive if and only if the term in brackets is positive. After replacing z^c with u , and factoring out common elements, this reduces to the requirement

$$\begin{aligned} cu(n-i) \left\{ \left[\sum_{s=1}^i A_s(u) \right]^3 + 3 \sum_{s=1}^i A_s(u) \sum_{s=1}^i [A_s(u)]^2 + 2 \sum_{s=1}^i [A_s(u)]^3 \right\} \\ > (c-1) \left\{ \left[\sum_{s=1}^i A_s(u) \right]^2 + \sum_{s=1}^i [A_s(u)]^2 \right\}. \end{aligned}$$

Using the relationships

$$\sum_{s=1}^i [A_s(u)]^2 \geq A_i(u) \sum_{s=1}^i A_s(u) \quad \text{and} \quad \left[\sum_{s=1}^i A_s(u) \right]^2 \geq i A_i(u) \sum_{s=1}^i A_s(u),$$

we can show that the left side of the inequality is greater than or equal to

$$cu(n-i)(i+2)A_i(u) \left\{ \left[\sum_{s=1}^i A_s(u) \right]^2 + \sum_{s=1}^i [A_s(u)]^2 \right\}.$$

Therefore, a sufficient condition for $h''(u) > 0$ is that this term exceeds the right side of the inequality, that is, if

$$cu(n-i)(i+2)A_i(u) = \frac{cu(n-i)(i+2)}{u(n-i)+i} > c-1.$$

This simplifies to

$$u(n-i) > (ci-i)/(ci+c+1),$$

which is always true, since $u(n-i) \geq 1$, and the right side is always less than one. Therefore, $h'(z) < 0$ and $h''(z) > 0$, for all $z > 1$, $c \geq 1$.

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