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On size ratios and sequences in ecological communities: Are there no rules?

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I critically examine the conception that pairs of similar sympatric species in a community will be separated in size by values in excess of a minimal ratio, and that sequences of such species will be regularly spaced on a size spectrum. This expectation appears to have become widely accepted in ecology as much because of its seeming agreement with the prevailing paradigm in community ecology, that communities are structured by competitive interactions, as because of its empirical support, which has eroded upon re-examination. Studies of size ratios in communities are plagued by a variety of generally neglected methodological problems: Which morphological features should be measured? Which individuals in the populations should be included in the comparisons? Which species should be compared? How should intra- and interpopulational variation in morphology within a species be considered in the determination of between-species patterns? Several assumptions are also made in the analysis and interpretation of size relationships between species. These assumptions are fragile. Together with the relaxed logical procedures that have been used in many studies, they render size-ratio patterns and their explanation by processes such as competition suspect. Several ingredients of a more rigorous approach to the study of size relationships among species in communities are developed.

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1. Introduction

In 1959, G. Evelyn Hutchinson published his "Homage to Santa Rosalia . . ." paper. This work contained many interesting and important musings, among them a preliminary analysis of ratios of the sizes of trophic structures of several pairs of bird and mammal species where they were sympatric. The average ratio (larger/smaller) of the 11 pairings he considered was roughly 1.3, and Hutchinson concluded that this value could tentatively be used "as an indication of the kind of difference necessary to permit two species to co-occur in different niches but at the same level of a food-web" (1959: 152).[1] In the same year Hutchinson & MacArthur published a more theoretical treatment of the size distributions of organisms, concluding that a size ratio of 1.3 between sympatric forms "would ordinarily prevent complete competition between species" (1959: 119). The idea rapidly gained favor among ecologists, and Hutchinson's initial suggestion was extended to include the companion idea that, in order to avert competition, sets of sympatric, similar species should be regularly spaced along a size sequence, separated by a constant ratio (1.3 for length, 2.0 for body weight). The theoretical foundation for this argument was compelling: because larger organisms require more food but feed upon larger prey that are scarce relative to smaller prey, they must utilize a broader range of prey sizes in order to meet their demands than must smaller organisms. Given that there is a limit to the overlap of the resource-utilization curves of adjacent species that is set by competition, large species must be more widely separated from their neighbors on a size sequence than small species; on a logarithmic scale the species will be evenly spaced (MacArthur 1972).

Subsequent development of deterministic theories of community assembly (Diamond 1975, Herrera 1981; but see Connor & Simberloff 1979,

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[1] Hutchinson presented his analysis in the context of character displacement, and compared measurements in sympatry and allopatry, although, of course, he calculated size ratios only between sympatric populations. Later work generally restricted attention to areas of sympatry. Thus, despite recent usage (e.g. Strong et al. 1979), most treatments of size ratios do not meet the strict sympatry-allopatry comparison criterion of character displacement (Grant 1972); this term should not be applied to the more restrictive calculations of size ratios in sympatry alone.

Wiens in press a) suggested that species should be added to a community in accordance with these competitively driven constraints on size spacing: only combinations of species exhibiting sufficient separation (or, in equilibrium communities, uniform minimal spacing in accordance with Hutchinson's ratio) should be "permitted." In an extension of this approach, Pulliam (1975) used the constant average bill-size ratio observed among granivorous sparrows to generate a sequence of expected bill sizes of hypothetical species of potentially coexisting sparrows. By then generating seed-size utilization functions from the projected bill sizes of each "species" and relating these to information on actual seed production in several locations, he produced a "coexistence matrix" that defined the permissible sets of coexisting species. Pulliam found close agreement between the predictions of this theory and the actual composition (bill-size classes) of several communities during the one winter he considered.

By the mid-1960's the reality of size ratios in communities was widely accepted and their utility in portraying competitive relationships firmly established. Why, on the basis of so little initial evidence and the tentative nature of Hutchinson's remarks, was acceptance of these ideas so rapid and widespread? Certainly, the finding that sympatric, closely related species often did seem to differ in size by ratios that were seemingly close to Hutchinson's ratios did much to solidify the ideas, but I believe that other factors contributed as well. First, it is inherent in adaptationist logic (Gould & Lewontin 1979) that the details of morphology should be closely attuned to the ecological circumstances of organisms — if resource-based competition occurs within a set of species, this selective force should be rather precisely reflected in their morphological relationships. The emergence of optimization thinking during the 1970's served to reinforce this expectation. Second, morphology is more easily measured than ecology, fostering the hope that examination of morphological features might provide a meaningful framework within which to explore community structuring (e.g. Ricklefs & Cox 1977). Third, morphological differences between species that are in general accord with the predictions of competition-based community theory were uncritically taken as clear corroboration of that theory. In the context of the widely accepted MacArthurian community paradigm, that communities are structured by means of niche differentiation between species sufficient to permit their coexistence (Wiens in press a), it was easy to accept a body of morphological data that seemed consistent with the predictions of this paradigm. Finally, modern ecology (in fact, all Western science) is conducted within a cultural framework or worldview derived from Greek metaphysics, which holds that life and the universe are ultimately deterministic and ordered. What could be more compatible with this worldview than a precise, regular ordering of species in a community along a size sequence?

Despite the compelling force of these factors and the widespread acceptance of the reality and ecological interpretation of size ratios, however, challenges have recently emerged, as part of a developing dissatisfaction with the prevailing community paradigm (e.g. Connell 1975; Wiens 1977, in press a, b; Connor & Simberloff 1979.) Wiens & Rotenberry (1981a), for example, found substantial variation (and many low values) of size ratios among breeding birds in grasslands and shrubsteppe, and questioned the relationship of such ratios to the occurrence of competition in communities. Roth (1981) and Simberloff & Boecklen (1981) reviewed many of the published studies of size ratios and subjected the patterns to various statistical analyses; they found little evidence of regularity in the spacing of species along size spectra and little adherence to the Hutchinsonian ratio (1.3). And in a sequel to his 1975 study, Pulliam (in press) considered information from 3 additional years on his study areas as well as from other nearby habitats. The occurrence of sparrows of various bill sizes exhibited rather little agreement with the patterns predicted by this coexistence matrix theory, and in fact predictions based upon a model of random cooccurrence of species matched the observations about as well. Bowers & Brown (1982), on the other hand, subjected Brown's earlier studies of size ratios in desert granivorous rodent communities to new analyses, and argued strongly in support of the reality of the uniform spacing of species and of the competitive interpretation placed upon the pattern.

The issue is thus far from immediate resolution, despite strong opinions and assertions. Here, I will offer some comments on the initial conditions, methodology, and logical foundation of size-ratio studies, and explore some hypotheses that may relate to them. My concern will be with some of the problems that have beset many studies, because in order to progress toward resolving whether size-ratio patterns are real and what, if anything, they might mean, these problems must be addressed. I will not attempt to review previous studies of size ratios in communities; to do so would largely duplicate the work of Roth (1981) and Simberloff & Boecklen (1981).

2. Initial conditions for the study of size ratios

Any attempt to consider the patterning of morphology among species in a community must begin by specifying precisely the boundaries of the comparisons to be made. Unfortunately, this has not always been done; much (but by no means all) of the disagreement between Strong et al. (1979) and their critics (Grant & Abbott 1980, Hendrickson 1981), for example, relates to the definition of the initial conditions of their comparisons.

Two conditions are basic to size comparisons: the species must be sympatric and they must use generally similar resources (Roth 1981, Fox 1982). It makes little sense to calculate size ratios of species pairs or sequences that are not sympatric (except in tests of null hypotheses of random community structuring — see below), as the potential to address various hypotheses of processes underlying the size patternings is thereby destroyed. Defining sympatry is not always easy, although the persistent cooccurrence of species in a local community would seem to qualify them as sympatric. Nonetheless, if the predicted size ratios are not found among such species, one may argue that they are not in fact sympatric, thus preserving the theory. Certainly, determining sympatry on the basis of overlap of general geographical distributions derived from field guides, as Oksanen et al. (1979) did in some of their analyses, would seem an unrealistically coarse approach.

The values of size ratios are, of course, totally dependent upon the identity of the species pairs compared, and determinations of the species composition of the set to be analyzed is therefore critical. Hutchinson (1959) restricted his comparisons to congeneric pairs of species, believing that congeners were more likely to be ecologically similar (and thus potential competitors) than noncongeners (cf. Schoener 1965, Lack 1971). In subsequent studies, however, the species compared have been congeners, members of the same ecological guild, or simply taxonomically close (Roth 1981). Strong et al. (1979), for example, calculated ratios among confamilial species pairs. If one is drawn to calculate size ratios because of an anticipation that they might embody some ecological meaning, however, it is necessary to restrict the comparisons to species that are at least generally similar in ecology. As Grant & Abbott (1980) observed in their response to Strong and his colleagues, members of different genera within a family are by no means ecologically similar, even if they are sympatric. Perhaps the most appropriate framework for comparisons is the guild (Root 1967), as guild membership is defined by similarities in resource use (or other ecological attributes) independently of species taxonomy (but see Jaksić 1981, Wiens in press a for discussions of problems in defining guild boundaries and membership). Oksanen et al. (1979), for example, calculated size ratios among species within guilds (defined by general feeding position and habitat) containing representatives of different families or orders of birds. Their definition of guild membership, however, was excessively broad, and this may have produced the particular size-ratio pattern for which they then proceeded to develop a theoretical explanation (Nudds et al. 1981). Both Bowers & Brown (1982) and Chew & Chew (1980) have drawn attention to the disappearance of apparent patterns of size-spacing within guilds once other nonguild species are added to the set being compared.

Recently, it has become fashionable to conduct tests to determine whether the particular community pattern observed differs significantly from that generated using some randomized algorithm to generate the community membership (e.g. Strong et al. 1979, Connor & Simberloff 1979, Simberloff & Boecklen 1981). If such tests are to be conducted, a third initial condition becomes critical: specification of the species pool from which the "random" community is to be generated. Simberloff and his colleagues have determined the species pools for their analyses in various ways, and it is apparent from the criticisms of some of this work (Strong et al. 1979) by Grant & Abbott (1980) and Hendrickson (1981) that this may influence tests of such null models, although perhaps not very greatly (Strong & Simberloff 1981). At the least, it would seem that a legitimate source pool for such tests should contain only species of the appropriate guild (or other category) that are geographically accessible to a given local community, have the dispersal ability to invade the community, and occupy similar environmental settings. Grant & Abbott (1980) have suggested that an appropriate null model should also take into account differences in the dispersal probabilities of species in the source pool. Inadequate development of procedures for objectively specifying the composition of realistic source pools of species remains one of the major hindrances to testing such null hypotheses.

3. The methodology of size-ratio studies

Once the initial conditions for an investigation of size patterning within some set of species are specified, one must determine which features of morphology to measure, which individuals to include in the sample, and how the measures should be analyzed to derive size-ratio values. As I develop elsewhere (Wiens in press a), close attention to the details of sampling, measurement, and methodology is not a conspicuous element of the research tradition that has developed within the MacArthurian community paradigm, so it is not surprising that such details have received little attention in size-ratio studies. This is unfortunate, as the ratio values that are obtained (and therefore the explanations that are offered for their patterns) are quite sensitive to several methodological features.

3.1 Which morphological features should be measured?

Investigations of the size-sequence structuring of communities have relied on measurements of a wide array of morphological characters — skull length, head width, bill length, jaw length, carapace width, ovipositor length, proboscis length, wing length, body weight, total body length, and so on. More often than not it seems that characters have been selected for their ease of measurement or because data are already available for them rather than because they are precisely related to a specific hypothesis of size relationships among species. Usually, the selection of a character for analysis is justified on the basis of some purported ecological relevance, although evidence supporting such contentions is rarely supplied. Features of feeding morphology, such as bill length or proboscis length, may have an intuitively apparent ecological relevance, but the ecological significance of size spacing in, say, wing lengths (e.g. Grant 1968) is less clear (Strong & Simberloff 1981), although an association with overall body size has often been claimed. Selection of a character or set of characters for analysis is not trivial, for, as Fig. 1 demonstrates, ratios calculated for different characters for a set of species not only produce different spacing patterns but in some cases different sequences of species. If such varying patterns of morphological relationships among coexisting species are to be interpreted ecologically, a clear notion of the ecological relevance of each of the characters (or whatever character is finally chosen) is required.

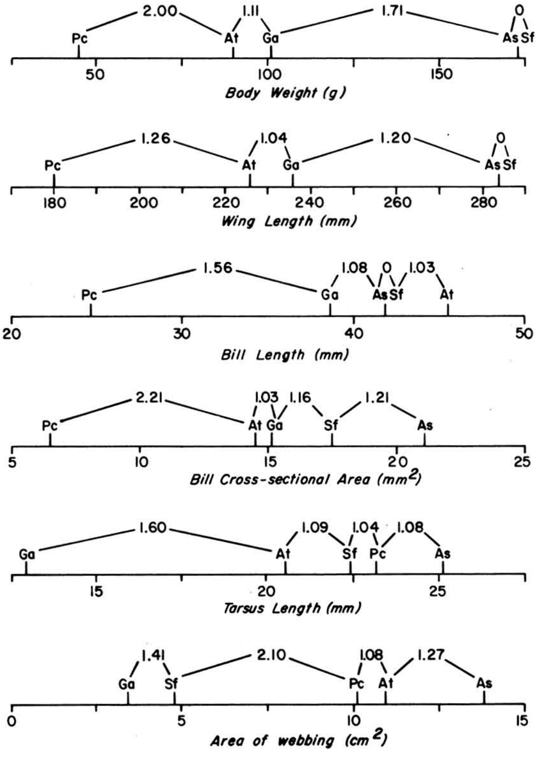

Fig. 1. Species sequences and size ratios of five species of tropical terns with respect to several morphological features. Values are from Ashmole (1968). As = *Anous stolidus* (Brown Noddy), At = *Anous tenuirostris* (= *A. minutus*) (Black Noddy), Ga = *Gygis alba* (Fairy Tern), Pc = *Procelsterna cerulea* (Blue-gray Noddy), and Sf = *Sterna fuscata* (Sooty Tern). Bill cross-sectional area is measured at the proximal end of the gonys; area of webbing represents the approximate area of the lower surfaces of the two feet when the toes are fully spread.

Character comparisons between organisms spanning a spectrum of overall sizes are also complicated by the interrelationship of the shape of features to size (Fagerstrom 1978, Mosimann & James 1979). Because these relationships are often allometric, the absolute linear measurement of a character may vary as some function of overall size of the organisms, and different characters are likely to follow different allometric functions. This is undoubtedly one factor contributing to the discrepancies apparent in Fig. 1. It means, of course, that the size ratios themselves are size-dependent, but in different ways for different characters.

Because so many features of morphology often covary (Wiens & Rotenberry 1980), one potential way to circumvent some of the problems posed by the selection of single variables and by their allometric patterns might be to record measures of a large number of morphological features and then subject these to some form of multivariate analysis. Rather than calculating ratios between adjacent species on a single size dimension, one determines the distances separating species in this multivariate morphological space; these are the multidimensional analog of size ratios (e.g. Findley 1973, 1976; Gatz 1979, 1980; Ricklefs & Travis 1980; Ricklefs et al. 1981; James & Boecklen in press). While such multivariate approaches lend themselves to the testing of null hypotheses of random or independent assignment of species to morphological space, they are still sensitive to most of the problems I discuss in this paper. If anything, ecological interpretation of the positioning of species in multivariate morphological space is often more difficult.

3.2. The influence of age

By convention, the measures from which size ratios are calculated are usually obtained from adult individuals. For forms with determinate growth in which the adult size is rapidly reached and in which this age class is readily recognizable, there is little difficulty. Subadults of various ages are not always distinguishable from adults, however, and if size is age-dependent in a population, inclusion of such individuals in a sample will bias measurements toward lower values.[2] Size ratios between adjacent species may thus be distorted, especially if this sampling bias is unequal for the different species. If growth is indeterminate, the average size of the "adult" age class of a population will depend upon the specific age (size) structure of that age class. Comparisons of two species with different age structure will again produce distorted size ratios.

These problems aside, the ecological justification for restricting size ratio determinations to adults is not entirely clear (unless one assumes that the only interactions of any ecological and evolutionary significance occur among adults). Hines (1982) demonstrated that almost all species pairs in a five-species assemblage of spider crabs had size ratios of carapace width greater than the Hutchinsonian ratio value. He also found, however, that recruitment into the populations was more or less continuous, and in only one species was there any apparent separation of the recruitment zone from the area of adult sympatry. Thus, the zone of coexistence of these species included individuals covering a much more continuous array of sizes than the adult size ratios alone would suggest.

3.3. Sexual dimorphism

Like age, morphological variation associated with sex is usually ignored in the determination of size ratios. Measurements are usually simply averaged for males and females combined (often without standardization of sample sizes for each sex), or presented for only one sex (usually males; e.g. Karr & James 1975). There is little biological justification for either procedure — the first assumes that sexual differences in size or shape do not matter in potential ecological interactions, while the second assumes that only individuals of one sex participate in such interactions (the other presumably being ecologically neutered). The spider crabs studied by Hines (1982), for example, displayed pronounced sexual dimorphism within species. Hines recognized this, but presented size-ratio calculations only for females and for the population (sexes combined). It is not clear how the inclusion of males as separate entries in the size sequencing would affect the overall pattern, as Hines did not provide the data that would permit this calculation.

In some forms the extent of sexual dimorphism in size is so great that it is not readily ignored. Hutchinson (1959) recognized this problem for the mustelids (but not for the other species) he considered, and calculated interspecific size ratios separately for males and females. The data presented by Moors (1980), however, suggest that intersexual size ratios within the smaller mustelid species may be fully as great as Hutchinson's interspecific ratios. Further, the magnitude of size dimorphism in these animals is less in the larger species, so if one were to combine sexes for interspecies comparisons, the resulting bias would not be constant over the entire size spectrum.

3.4. Abundance

The consequences of competitive interactions between species are usually thought to be density-dependent. If the size structuring of communities is to be viewed as an expression of competitive interactions, it would therefore seem necessary to consider the size ratios between species in the context of their relative densities. This is rarely done. "Species," not populations, are the entities compared, and it is therefore tacitly assumed that abundances do not matter. Slatkin's (1980) theoretical treatment of character displacement, however, clearly shows the central importance of relative abundances of species to understanding the possible mechanisms underlying such differences.

Some authors have considered abundances in at least a general way in their analyses. Brown (1973, 1975; Bowers & Brown 1982), for example, restricted his calculations of size spacings among granivorous rodents to those species accounting for more than 5 % of the trap captures, arguing that the rarer species were not likely to be important constituents of the community. This

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[2] Maiorana (1978) and others have suggested that sequential age classes (e.g. instars) within a species may differ in size by a "developmental constant" whose value approximates that of the Hutchinsonian constant. Bruce (1982), however, has noted that this requires that growth of individuals be exponential, which it rarely is; size ratios between age classes may instead be age-dependent in their values.

restriction, however, was applied only to the smaller species; two large species were included in the analyses despite their rarity in the samples. Brown rationalized that they were probably undersampled by the trapping and, in any case, were obviously important members of the community. Ranta & Tiainen (1982) analyzed the spacing of species in communities (bumblebees sequenced by proboscis length) using both the entire community and just the common species. Their comparisons of actual size ratios with those generated for random bee communities revealed no significant differences for either the total community or the common species alone. Hanski (1982a) approached the same question in the context of his distinction between "core" (abundant and widespread) and "satellite" (uncommon and localized) species in communities (1982b). With attention restricted to the "core" species in bumblebee communities, his tests revealed a significantly greater spacing of proboscis lengths among species than expected by chance, although much of the pattern was determined by the inclusion of one species with a long proboscis in the analysis. Hanski's (1982a) reanalysis of the data of Ranta & Tiainen led him to conclude that the "core" species in their community were also more widely separated than randomly selected species, although in fact the difference was not statistically significant. In any event, Hanski's distinction between "core" and "satellite" species is potentially important. Hanski argues that the "core" species are equilibrial, competitive, and separated in niche space, while the "satellite" species in a local community may be nonequilibrial and noncompetitive. If this is so, it provides some justification for restricting attention in size-ratio studies to the "core" species, *if* (and only if) such studies are conducted within the framework of competition theory.

3.5. Intraspecific variation in morphology

Calculations of size ratios between species pairs are usually made by dividing the mean value of a morphological measure for the larger species by that of the smaller. Thus, most individuals in the local population of a species are implicitly assumed to be reasonably close to the mean value for the species as a whole. In fact, if interspecific competition is driving the size spacing of species, variance about the mean value for the morphological trait should be severely constrained in each species in order to preserve the necessary spacing between them. Such logic has perhaps justifield the use in many ecomorphological studies (e.g. Grant 1968, Pulliam 1975, Ricklefs & Cox 1977, Ricklefs & Travis 1980) of values of morphological features obtained from general sources such as Ridgway (1901—1918) or from museum collections. But such sources inevitably represent a heterogeneous sampling of individuals from various areas, times, and habitats, and ignore the fact that morphology may vary substantially within and between local populations of a species (James 1970, Wiens & Rotenberry 1980, Ulfstrand et al. 1981, Barbault & Maury 1981). Further, the degree of morphological variation within a species or population may be influenced in both proximate (James MS) and ultimate (Pachut & Anstey 1979) manners by features of the environmental setting. Variation in morphology within and between local populations (beyond that directly attributable to age or sex) may thus be significant. The use of mean values of morphological measures for a species as a whole in the calculation of size ratios within local communities thus obscures much of the rich texture of intraspecific variation in morphology, and permits detection of patterns only at a coarse level of resolution.

4. Assumptions, logic, and hypotheses

4.1. The assumptions of competition-based size-ratio theory

The patterns of size ratios between members of a community are usually interpreted as indirect measures of competitive interactions. Such reasoning involves several assumptions (Wiens in press a, b). First, resources are assumed to be limiting in relation to the demands of the organisms; this is what prompts the competition that, ultimately, produces the patterns of size spacing between community members. This, in turn, leads to the assumption that the community is at or close to an equilibrium determined by resource limitation. Such equilibrium communities are assumed to be "saturated", that is, they contain the maximum number of species that can subdivide and coexist upon the resource base. If discontinuities or "gaps" appear in a size sequence, they must be explained in a way that is compatible with the equilibrium assumption. One source of such "gaps" might be an absence in the regional species pool of forms of an appropriate size to occupy a certain position in the local community array (Wiens & Rotenberry 1981a) — the expectation of constant spacing of species thus also assumes that the overall species pool contains representatives of all of the size classes necessary to assemble a local community, and that all species have the opportunity to colonize the local community (e.g. Brown 1973). The shufflings of species produced by colonization and local extinction resulting from competition can then be expected to produce the optimal spacing patterns predicted by theory.

Assumptions must also be made about the resource base of the community. For equilibrium to hold, the resource base must be stable in its configuration or, if varying, must be closely tracked by changes in the composition of the community so that an optimal spacing pattern is maintained. The prediction of constancy of size ratios separating species further rests on the assumption that resources are evenly available over the entire spectrum used by the community. If bill size ratio constancy, for example, is to be interpreted as optimal spacing of species in relation to prey-size utilization, the frequency distribution of available prey sizes must follow some continuous function (e.g. lognormal; Oksanen et al. 1979).

Although they are rarely stated explicitly and even less often tested, such assumptions are necessary if one is to infer that competition underlies the size patterns observed in communities. If they are met, they permit one to interpret the patterns as a final result of the process of species assembly, and they absolve one of the responsibility of repeatedly sampling the community to determine whether the size patterns are stable (Wiens 1981). They allow one to neglect detailed direct measurements of the resources, as the resource states can be inferred indirectly from the morphological relationships among the species. To the degree that these assumptions are violated in nature, however, neither the predicted patterns nor (especially) the proposed mechanism (competition) is likely to hold true. There is mounting evidence that the conditions required by these assumptions may not obtain in some (perhaps many?) communities. Our work with shrubsteppe and grassland bird communities (Wiens 1977; Rotenberry & Wiens 1980; Wiens & Rotenberry 1981b; Wiens in press a, b), and that of others with, for example, assemblages of birds (Pulliam & Parker 1979), lizards (Dunham 1980), intertidal organisms (Sousa 1979), or parasites (Price 1980), suggests that resource limitation may be sporadic in its occurence and resource distributions quite uneven, and the communities may often be nonequilibrial and not fully saturated with species. This renders interpretation (as well as measurement) of size patterns in communities substantially more difficult.

Size-ratio studies also rest upon the somewhat separate assumption that there is a direct, quantitative relationship between morphological features and resource use (Ricklefs & Cox 1977). It is this assumption that allows one to infer variability in resource use from morphological variation or separation in resource use from morphological spacing between species. This assumption, like the others, has not often been directly tested. Smartt (1978) did find a clear relationship between the spacing of *Peromyscus* species in multivariate morphological space and the degree of difference in their diets, and Baker (1977) concluded that larger-bodied forms among a set of 10 shorebird species consumed larger prey (although his analysis used relatively coarse rank-correlation statistics, thus obscuring several species pairings for which the relationship did not hold). Others (e.g. Pulliam & Enders 1971, Wiens & Rotenberry 1980), however, failed to find clear associations between measures of trophic morphology and food size or type. Levinton (1982) recently subjected the body size-food size relationship in mud snails (Fenchel 1975) to experimental analysis. He found that the snails were quite flexible in their choice of food particle sizes, and that growth rates of individual snails were unrelated to food particle size.

The degree of coupling of resource use to morphology has remained somewhat enigmatic because of the difficulty of specifying exactly what constitutes the "resource" (Wiens MS). Consider, for example, seed-eating rodents. Brown & Lieberman (1973) and Brown (1975) suggested that coexistence among such forms in North American deserts was strongly influenced by seed-size selection associated with differences in body sizes among the species. Lemen (1978), however, demonstrated that when weight rather than linear dimensions was used to index seed size, Brown's seed size—body size correlation disappeared. M'Closkey (1978) and Stamp & Ohmart (1978) also were unable to demonstrate a clear relationship between these variables; the latter authors suggested instead that the body-size differences between the rodents might be associated with differences in microhabitat use, a suggestion reinforced by Price's (1978) experiments.

4.2. Logical problems

The foregoing comments relate to problems posed by various assumptions underlying the classical interpretations of size ratios, but two additional problems have more to do with the logical operations used in such studies. The first concerns the detection of a pattern in size relationships. What ratio value is to be used to specify the minimal size separation between species that will permit coexistence, and what amount of variation in ratio values between species along a size sequence is permitted in a pattern of constant or uniform spacing? Hutchinson's minimal ratio value for body weights of similar species, for example, was 2.0.

Bowers & Brown (1982), however, used a value of 1.5 in their analysis of rodent body-size patterns, suggesting that this was a conservative estimate of Hutchinson's ratio. They concluded that the ratio was exceeded by more species pairs than expected by chance, but in fact 1.5 is not a conservative estimate of 2.0, and one fully expects more ratio values to exceed the lesser value. Other studies (e.g. Ashmole 1968, Wiens & Rotenberry 1981 a, Barbault & Maury 1981; see Fig. 1) have demonstrated substantial variation in ratio values along size sequences. Maiorana (1978) attempted to reconcile such variation with the idea of constant Hutchinsonian size ratios by developing an argument based upon increasing variance in resource use among larger organisms; this view, and that of Oksanen et al. (1979) regarding the explanation of "gaps" in community size sequences, have been addressed elsewhere (Wiens & Rotenberry 1981a).

The problem, of course, is that procedures for determining patterns in size ratios have been rather relaxed and often post-hoc, so that whatever values are obtained may be termed a "pattern," even if the "constant" ratio is in fact variable or if the minimal ratio value bears little resemblance to Hutchinson's original values. Both Roth (1981) and Simberloff & Boecklen (1981) have criticized such practices and suggested ways of determining the statistical reality of such "patterns."

A second logical difficulty involves the failure in many studies to recognize pattern detection and process explanation as separate phases of scientific activity (Wiens in press a). *If* a pattern of uniform size spacing of larger than minimal size ratios is established among a set of species following rigorous procedures, one has really done nothing more than documented the pattern. To claim or infer that a given size pattern in a community is evidence of the role of competition (or any other process) in causing the pattern is fallacious logic. Simple consistency of a pattern with the predictions of some favored hypothesis (such as competition) in no way represents verification of that hypothesis, especially when the predictions are quantitatively fuzzy and the hypothesis supported by untested assumptions. Patterns of size differences among organisms do not of necessity indicate the occurrence of present or past competition, as they may be equally consistent with the predictions of other hypotheses (Ashmole 1968, Hairston 1980, Strong & Simberloff 1981, Wiens in press a). Logically, then, the investigation of size relationships among organisms in a community must involve two successive operations: the initial detection of pattern (or the testing of pattern hypotheses) and the subsequent evaluation of hypotheses regarding processes that might have acted to produce the observed pattern.

4.3. Developing hypotheses of size relationships in communities

The theory of size relationships that developed from Hutchinson's early musings made qualitatively specific predictions of size relationships in sets of similar species: size ratios should not be less than some minimal value, and the spacing of species along a size sequence should be relatively regular. Obviously, a wide array of other size relationships among community members is possible, but the dominance of the competition paradigm in community ecology has stifled interest in other, inconsistent size patternings. As Simberloff & Boecklen (1981) and Roth (1981) have observed, inconsistent data may simply not have been reported in the literature, or when they have been published "they are frequently accompanied by explanations of coexistence which involve differences other than size. When ratios resemble Hutchinson's (1959) average, however, a citation replaces an explanation" (Roth 1981: 396).

Size, of course, is related to a great many features of the life history of organisms: clutch size, age at maturity, gestation time, growth rate, lifespan, foraging behavior, predation vulnerability, thermal tolerance, energy demands, and so on (e.g. Blueweiss et al. 1978, Case 1979, Western 1979, Clutton-Brock & Harvey 1979). Moreover, although many of these attributes covary, not all follow the same allometric relationships. Larger organisms are thus not simply quantitatively bigger versions of smaller organisms within a set of similar species, but may differ qualitatively in important ways. Given this, it would seem naive to expect the size relationships among species in a community to reflect only (or primarily) the influences of competition; this is tantamount to saying that competition overrides all other selective forces on size and its associated life history attributes.

The complexity of features associated with size variations, however, renders the generation of realistic process hypotheses to explain size patterns in communities quite difficult. Several other suggestions relating to size ratios in communities merit brief mention. Perhaps most basic is a null hypothesis that states that the patterns of species composition, size spacing, or resource utilization in a community do not differ from random. Tests of community "patterns" against such null models have become increasingly frequent (e.g. Gatz 1979, Connor & Simberloff 1979, Strong et al. 1979, Ricklefs & Travis 1980, Ricklefs et al. 1981, Ranta & Tiainen 1982, Bowers & Brown 1982). Although few deny the importance of attempting to determine whether there is in fact a nonrandom pattern to some set of community attributes before launching into more involved tests of pattern or process hypotheses, there is substantial disagreement regarding the procedures that are used (Grant & Abbott 1980, Hendrickson 1981, Pulliam in press). As Bowers & Brown (1982: 399) have noted, "there are numerous tests of null hypotheses that might reasonably be applied to almost any community. Failure to reject one or more of these is hardly evidence that the community is not structured by deterministic biological forces such as interspecific competition. The kinds of information used in the test and the statistical form of the test itself strongly influence the sensitivity of the test to nonrandom patterns and hence its capacity to reject the null hypothesis." There is considerable truth to this statement, but unfortunately it can be applied with equal force to the competition (or any other) hypothesis.

Another possibility is that the particular size relationships among a set of species are not selected consequences of species interactions at all, but are unselected epiphenomena resulting from the cooccurrence in a location of species whose autecological requirements and restrictions are met there. Each species responds to the climatic constraints, resource characteristics, predator pressures, etc. of an environment independently of the occurrence there of other species, and whatever size patterning exists among these species may simply be a reflection of the underlying environmental features. If small food items are substantially more abundant in an environment than larger foods (and if body or bill size has anything to do with food-size selection), for example, there may be a closer packing of species at the small end of the size spectrum (see Simberloff & Boecklen 1981), while discontinuities in the resource base may produce "gaps" in the size array of consumers. Further, resource heterogeneity in time and space may alter the coexistence patterns predicted by simple competition theory (Ranta & Vepsäläinen 1981, Tilman 1982), distorting size ratio sequènces in rather unpredictable manners. Of course, the species that colonize a local environment (independently of one another or not) are drawn from a regional species pool, and Hanski (1982a) has suggested that the structuring of at least the core species component of that regional pool may have been determined by competition in the past, even if competition is not directly (proximately) involved in the structuring of local communities. Unfortunately, this seems more an assertion than a testable hypothesis.

Species *do* differ in size and shape, however, and several authors have suggested that this may be a reflection of general evolutionary trends or of the form of the speciation process. Within at least some phylogenetic branchings there is a trend of increasing specialization and size through time (e.g. Stanley 1973a, 1979; Vrba 1980). Stanley (1979) has concluded that such evolutionary size increase is generally attributable to phyletic (gradualistic) evolutionary change, perhaps fostered by sexual selection. Løvtrup (1976, Løvtrup et al. 1974), however, argued on the basis of size discontinuities within lineages in the fossil record that body size evolves by discrete, quantum steps (although his procedures were criticized by Roff 1977). Stanley (1973a) also espoused this view, and in his 1979 book he developed a hypothetical argument relating morphological changes in evolution to a punctuational model, with competition as a major driving force (see Stanley 1973b). One might anticipate a greater degree of morphological diversification within a lineage to result from punctuational evolution than from gradualistic phyletic change, although exactly how this might affect size ratio values between species in the lineage is unclear. Fagerstrom (1978) suggested that punctuational evolution might produce fairly constant character displacement through time, but this depends upon a high degree of constancy in the amount of morphological divergence accompanying speciation events. In a gradualistic model, morphological differences might be expected to be least at branch points in the phylogeny, increasing with time since divergence of the species. Thus, at a given point in time the species within a lineage might differ by varying amounts, reducing the likelihood of constancy of size ratios. While some understanding of phylogenetic patterns is essential to an overall explanation of size patterns in communities, it is apparent that little progress is likely to be made until the issues surrounding the gradualistic versus punctuational models of evolution are somewhat better resolved.

5. Concluding comments

Investigations of size ratios in natural communities have been plagued by a variety of methodological and logical problems, and the hypotheses that have been erected to explain them are resistant to testing in rigorous manners. Despite this, a great deal has been made of these Hutchinsonian ratios in the literature and textbooks of ecology. Increasingly, however, the very reality of the size-ratio patterns is being questioned (Roth 1981, Simberloff & Boecklen 1981). If the patterns in fact do not adhere to the sorts of values envisioned by Hutchinson and others or, worse, cannot be distinguished from a random array of ratios, they are obviously of little use as evidence of competition or any other process (Roth 1981, Bruce 1982), much less as a foundation from which to launch community studies (Maiorana 1978). Perhaps all this discussion of size ratios represents much ado about nothing.

This is not to say that hypotheses relating to the distributions of sizes of organisms are unimportant —size arrays in communities may have interesting ecological consequences. But a new approach is required, one that shuns the methodology and logic that has characterized many previous studies and that adopts an agnostic attitude toward the competition community paradigm. If size patternings in assemblages of organisms are to be studied, the initial conditions of the investigation must be clearly specified. The precise nature of the pattern (if one exists) must be determined. Morphological characters whose ecological significance is or can be established should be emphasized. The influences of population structure and abundance on the patterns, and the extent of intra- and inter-populational variation in morphology, should be considered. Alternative hypotheses of pattern and process that are well-structured and falsifiable, and whose underlying assumptions are clearly stated and evaluated, should constitute the framework of such investigations. And the temptation to infer a causal process solely on the basis of documentation of a pattern must be avoided. This is not an easy recipe to follow, but I believe such considerations are essential if investigations of community ecology are to become less religious and more rigorous.

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