

## What's in a niche? II. Responses of trophic niche indices to simulated and actual prey distributions and sampling regimes.

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**ABSTRACT:** If data on prey in a predator's diet can be ordered so as to produce a normal or lognormal distribution, ordinary normal-curve statistics can be used to describe trophic niche breadth or position. Substitution of prey species sizes for taxon names provides a simple means of producing such an order (Pearre, 1999). Using simulated normal and lognormal prey distributions, this study examines the utility and reliability of two such statistical indices in commonly encountered situations of data acquisition and manipulation, compared to four of the most commonly used taxon-based niche-width indices. In order to illustrate the effect of prey identification level, data on three widely different predator species were also analyzed.

Although the Shannon-Weaver index standardized to its maximum value was probably the most useful of the conventional indices, the standard deviation of the logarithmically transformed prey size distribution (christened "SLH") seems overall the best of all the indices considered. However, the related and non-dimensional coefficient of variation of the normal distribution ("CVH") may be more useful under certain circumstances.

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### INTRODUCTION:

In a previous publication (Pearre, 1999), I have argued that trophic niche estimators should be based on the numbers and sizes of prey species, rather than on taxonomic categories. When using size data in an index designed for taxonomic categories, the sizes can of course be themselves regarded as taxa, as long as no two taxonomic species are of the same mean size. Thus it is feasible to examine the behaviors of such niche indices in the same analysis as niche indices based on size distributions.

By means of simulated data, this study compares two statistical measures of prey size-spectrum widths- the coefficient of variation of prey sizes ("CVH", Pearre, 1986) and the standard deviation of logarithmically-transformed prey sizes ("SLH", Pearre, 1986)- to the four most popular taxon-based trophic niche indices. First, I shall examine the responsiveness of each index to the parameters of prey distributions, including the number of prey classes, total number of prey, and degree of aggregation of the prey into the classes. Secondly, I shall demonstrate that the properties of the size-based statistical niche indices are superior to those of the four most popular taxon-based trophic niche breadth indices for practical data manipulation. Thirdly, I shall discuss examples from the recent literature, using this analysis, showing the superior utility of the statistical niche indices in ecological investigation.

For the purposes of this paper, I shall designate as "predators" all organisms being considered as consumers, whether carnivores or not, and as "prey" all those organisms which they consume.

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## MATERIALS: THE INDICES:

The most popular indices used to describe trophic niches are undoubtedly those discussed by Levins (1968): the first is generally called the inverse Simpson Index or Levins Index:

$$B_i = 1 / \sum_{j=1}^r p_{ij}^2 \quad (1)$$

where  $p_{ij} = n_{ij} / N_i$  (the frequency of utilization of resources "j" by predator species "i"), with "r" being the total number of possible resource states (prey species) and  $N_i = \sum n_{ij}$ . The second, an "information theoretic index" (Emlen, 1973), I will term the Shannon Index, and it is based on the Shannon-Weaver information theoretic, given by:

$$H_i = - \sum_{j=1}^r p_{ij} \log p_{ij} \quad (2)$$

Both of these indices are designed to vary with the number of prey classes examined, but can be misleading when class number ("species richness") is affected by sample size. For this and other reasons (see Colwell & Futuyma, 1971) they have been at least partly superseded as niche breadth measures by versions normalized to their maximum theoretical values, which are reached when all resource species are consumed equally (Pielou, 1969; Petraitis, 1979). These normalized indices are considered to measure species evenness (Pielou, 1969; Hurlbert, 1971). For the Levins index this is "r" (Levins, 1968), and the normalized Levins index has usually been symbolized by various authors as "B" or "B<sub>A</sub>". The non-normalized version has also been symbolized as "B" (also "B<sub>i</sub>", "B<sub>s</sub>", "B<sub>x</sub>", "β<sub>i</sub>", "NB", "FNB", and Δ<sub>3</sub>); B has also been used for the Shannon index and for Feinsinger *et al.*'s (1981) index, and B' for the Colwell & Futuyma (1971) and Hurlbert (1971) indices. To avoid confusion, I will refer to the two versions simply as "Levins" and "Levins-N". The Shannon index can be normalized by division by its theoretical maximum, log(r). The non-normalized version has been termed "H", "H'", "H''", "H'NGG", "PRD", "PSD", "FNB", and "B", and the normalized version "H/H<sub>max</sub>", "H1", "H'", "H'<sub>x</sub>", "h'", "e", "J" and "J'", while "H" is also used to designate the Brillouin index (Pielou, 1969). To avoid confusion, I will likewise term these two "Shannon" and "Shannon-N". These four indices will be considered as standards against which to judge other approaches to trophic niche estimation. Note that "species" as used above need not be (although it usually is) a taxonomic species: it is just as easy to use other taxa such as genera or classes (e.g. Marti *et al.*, 1993) or classification based on some other characteristic such as color, size, or ecological requirements (Ehrlich & Holm, 1962; see Pearre, 1999).

In this study, these are compared to two statistical measures of the prey-size spectrum. The first, which assumes an approximately normal distribution, is the coefficient of variation of the spectrum, that is:

$$CVH = 100(s/m) \quad (3)$$

where "s" is the parametric estimate of the standard deviation  $\sigma$  of the prey size distribution of estimated mean "m". The second, assuming an approximately lognormal distribution, is "SLH", the parametric standard deviation "s" of logarithmically-transformed prey sizes, expressed here as log<sub>10</sub>. As standard deviations are computed by a difference equation, standard deviations of logarithmic data are equivalent to ratios of the untransformed data, giving both expressions similar content (Wright, 1968; Pearre, 1986). Of course, the responses of the taxonomic indices (Levins' and Shannon's and their derivatives) to these distributions will be the same as to any other species assemblage in which each species is assigned some unique size.

## Niche index simulations

## METHODS AND RESULTS: THE SIMULATIONS:

**I). Prey distributions of known characteristics: Investigation of relevant parameters and preliminary results:** In order to compare the statistical niche indices to the conventional set, simulated data of known characteristics were generated. In the interest of clarity and to save space, the results of the analyses are presented with the description of each test. Two approaches to simulation-based exploration of the indices were used:

First, distributions were generated in which all of the principal statistical functions were independently varied, in order to identify and rank the major influences on each index. Although some of the factors are more apt than others to vary in real prey spectra, all were given equal total variation (3x or 5x) for the purpose of fairly assessing sensitivity. Levels of each of these factors were chosen to bracket realistic values (Pearre, 1986). The output of the niche estimations on these distributions was analysed by forward-stepped analysis of variance (SYSTAT<sup>R</sup>, Wilkinson, 1991), with an entry tolerance level of 0.01, indicating the order in which the independent variables and their higher-order interaction terms affected the magnitude of each index. As numerical values would only refer to the particular simulation parameters, results are given simply as rankings of factors and factor interactions.

A). In the first set 4 factors (mean, standard deviation, class number and prey number) were varied over 3 levels each, in sets of both normal and lognormal distributions. The un-normalized Levins and Shannon indices responded most strongly to the number of abscissa ("prey") classes (Table Ia and b), and somewhat surprisingly, for both normal and lognormal distributions, classes remained the best predictor for the Shannon-N index as well. Except for the unmodified Shannon index (normal distributions) and Levins index (lognormal distributions), total prey number was generally the second best predictor in this group. The two important first-order interactions can be regarded as indicators of aggregation of prey into groups. In these situations, the unmodified Levins index appears superior to the other three related ones in assessing the importance of unevenness of lognormal prey distributions. In both normal and lognormal sets, CVH and SLH were most influenced, as expected, by standard deviation.

B). As the mean had generally proven a poor predictor in the four-factor simulations, a three factor, 5 level lognormal simulation was generated with only standard deviation, class number and total number varying (Table II). Class number remained the best predictor for both versions of the Levins index and the Shannon index, but was second to prey number in Shannon-N. As before, the (classes)\*(total number) interaction was also important. Standard deviation remained the best predictor for CVH and SLH.

**II). Simulations of data collection and presentation: methods and results:** Secondly, a group of distributions was generated simulating common data manipulation tasks from samples of different designs and reporting strategies: these should test how consistent the various indices are in ordinary use. Of course, many of the situations were similar to those discussed in the first sets of simulations. As these were not designed for analysis by factorial ANOVA, the results were generally examined graphically and by linear regression (SYSTAT<sup>R</sup>). The combinations used were:

A). **Increasing sample sizes:** If the prey size class interval is not permitted to vary, then as total prey number increases with a given distribution width, or distribution width increases with a given total number, the number of prey classes will increase. This simulates increasing sampling effort in assemblages of varying distribution widths (Table III). For this two-factor simulation, standard deviation and total sample size were the independent variables. All of the indices responded more strongly to the standard deviation than to total prey number. This was initially surprising, but is explained by the response of class number to these factors (Fig. 1): presumably the Levins and Shannon indices are responding to standard deviation as a proxy variable. Standardized

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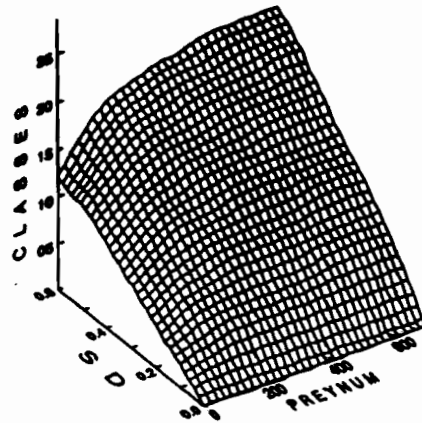


Fig. 1. Relationship of the number of classes to total prey number and standard deviation. 12 x 12 matrix, with distance-weighted least-square smoothing (SYSTAT®). Standardized to a maximum value of 25.

Table I: Identification of major sources of variation: 4-factor, 3-level series, 3<sup>4</sup> = 81 distributions: prey class interval unfixed, factorial design:

factors	levels	levels
	(a)	(b)
	<u>Normal:</u>	<u>Lognormal:</u>
mean	24, 48, 72	12, 24, 36
s.d.	4, 8, 12	0.3, 0.6, 0.9
class #	6, 12, 18	6, 12, 18
prey #	60, 120, 180	40, 80, 120

a). Normal:                      Significant (p<0.05) factors or interactions, in order<sup>1</sup>:

- Levins' Index: CLASSES, PREY, PREY\*S.D., CLASSES\*MEAN\*PREY\*S.D
- Levins-N: PREY, PREY\*S.D., CLASSES\*PREY, CLASSES\*PREY\*S.D.
- Shannon Index: CLASSES, CLASSES\*S.D., S.D.
- Shannon-N: CLASSES, CLASSES\*S.D., PREY, S.D.
- CVH: S.D., MEAN\*S.D.
- SLH: S.D., MEAN\*S.D., MEAN

b). Lognormal:

- Levins' Index: CLASSES, CLASSES\*PREY
- Levins-N: CLASSES, PREY
- Shannon Index: CLASSES, PREY
- Shannon-N: PREY, CLASSES\*PREY, CLASSES
- CVH: S.D., PREY\*S.D., CLASSES\*S.D., PREY, CLASSES
- SLH: S.D., CLASSES\*S.D., CLASSES\*PREY\*S.D., PREY\*S.D.

<sup>1</sup> - order is rank of entry in forward stepped ANOVA model (SYSTAT®)

"MEAN" = arithmetic or logarithmic (as appropriate) mean of the distribution

"S.D." = standard deviation of the distribution

"CLASSES" = number of prey species or size classes

"PREY" = total number of prey

\* - denotes interaction between factors

Niche index simulations

Table II: 3-factor, 5-level series: factorial design:  $5^3 = 125$  distributions:

Lognormal: mean = 10; class interval unfixed:  
 s.d. 0.2, 0.4, 0.6, 0.8, 1.0  
 class # 5, 10, 15, 20, 25  
 prey# 50, 100, 150, 200, 250

Significant (p<0.05) factors or interactions, in order<sup>1</sup>:

Levins' Index: CLASSES, CLASSES\*PREY  
 Levins-N: CLASSES, PREY  
 Shannon: CLASSES, PREY  
 Shannon-N: PREY, CLASSES, CLASSES\*PREY  
 CVH: S.D., S.D.\*PREY, CLASSES\*S.D., CLASSES  
 SLH: S.D., CLASSES\*S.D., S.D\*PREY, CLASSES\*S.D.\*PREY

<sup>1</sup> - order is rank of entry in forward stepped ANOVA model (SYSTAT<sup>®</sup>)

\* - indicates interaction between factors

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Table III: Simulating increasing sampling effort.

Increasing sample sizes: 2-factor, 12 level series:  $12^2 = 144$  distributions:

Lognormal: fixed class interval, class number allowed to vary:

s.d. 0.05- 0.60 (+0.05<sup>a</sup>)  
 prey # 50- 600 (+50<sup>a</sup>)

Lognormal: Significant (p<0.05) factors or interactions, in order<sup>b</sup>:

Levins' Index: S.D., PREY\*S.D., PREY  
 Levins-N: S.D., PREY\*S.D., PREY  
 Shannon Index: S.D.  
 Shannon-N: S.D., PREY  
 CVH: S.D., PREY\*S.D., PREY  
 SLH: S.D., PREY\*S.D., PREY

<sup>a</sup> - increment (additive)

<sup>b</sup> - order is rank of entry in forward stepped ANOVA model (SYSTAT<sup>®</sup>)

\* - denotes interaction between factors

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response surfaces of each index are shown in Fig. 2(a-f): from these the non-normalized Levins Index and SLH appear to have the most linear responses to either factor, with CVH not far behind. The Shannon Index takes a curvilinear approach to its maxima as standard deviation increases, but appears very nearly constant as prey number (usually the more relevant variable) varies. Both the Levins-N and Shannon-N indices appear very unreliable for small samples, though of course the exact shapes of the response surfaces are influenced by the parameters and type of smoothing function used (see figure headings). Hurlbert (1971) showed that evenness (here estimated by the normalized niche indices) should decrease as sample size increases, but this is presumably offset by the concomitant increase due to increasing class number.

B). **Data summation:** Data sets often consist of samples taken at different times or places, and the researcher may wish to sum these for an overall value of the niche. Usually, there are two directions for tabular data summation. The most obvious and generally useful is summation of numbers of each prey species in the table across all of the samples in which it appears. This yields a set of data in which each species appears only once, at the total number of that species found in the whole original table, and is, of course, equivalent to increasing sample size (above). This type of summation I have termed "horizontal" (as most data tables are set up in columns each representing a

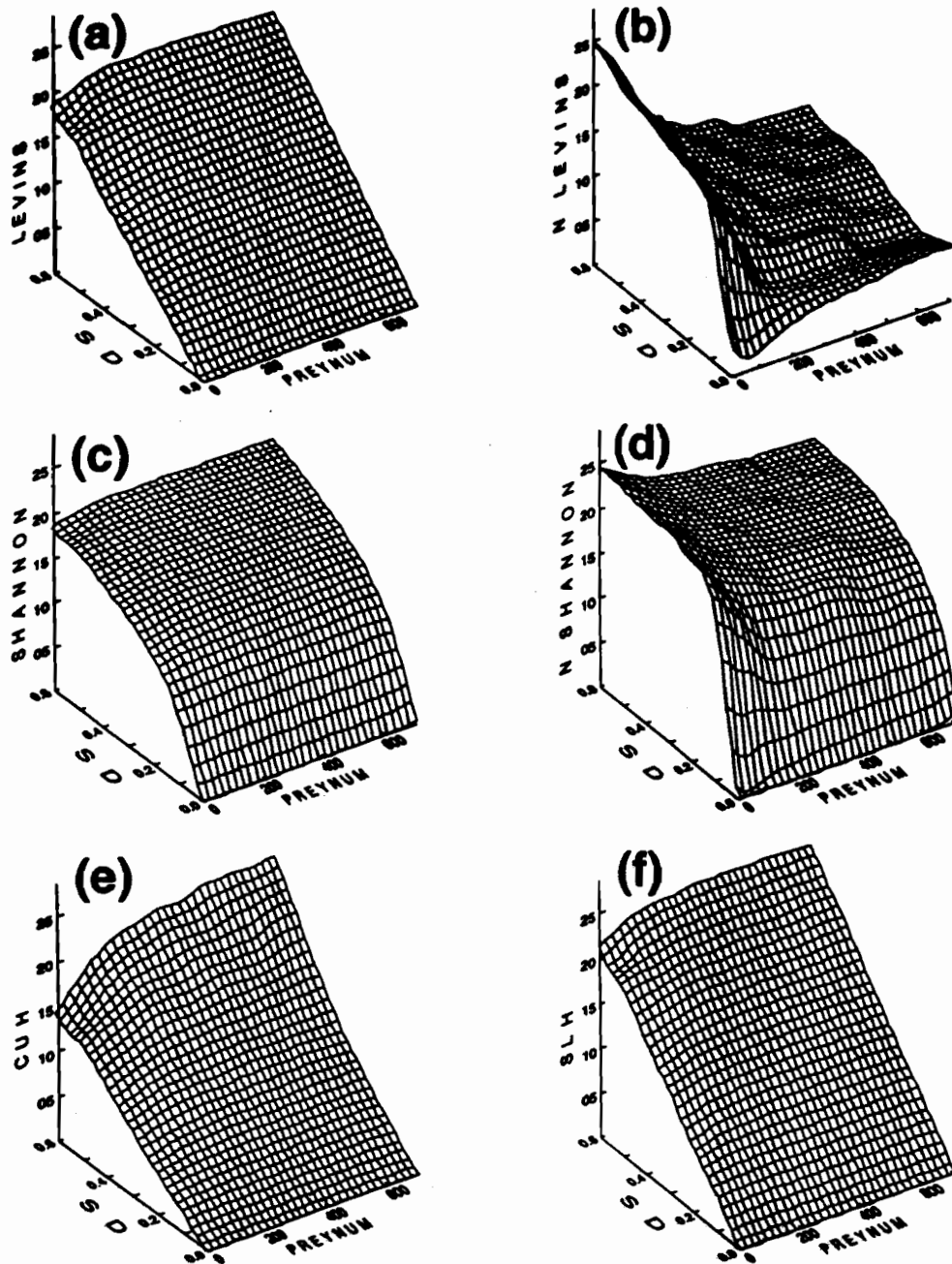


Fig. 2: Relationships of each of the niche breadth indices to total prey numbers and standard deviations of the distributions. 12x12 element matrices, using distance-weighted least-square smoothing (SYSTAT<sup>®</sup>). All indices standardized to a maximum value of 25.

a). Levens' Index.

b). Levens-N (as "N Levens") Index: Levens' Index normalized to "r", the number of resource states ("prey species", "prey sizes", or classes).

c). Shannon's Index: the Shannon-Weaver or information theoretic index.

d). Shannon-N (as "N Shannon") Index: Shannon's index normalized to log "r".

e). CVH: the coefficient of variation (standard deviation/mean, x100) for the distributions.

f). SLH: the standard deviation of the distributions of log-transformed "prey sizes".

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whole sample grouping, e.g. by date or locale), and horizontal summation must be the standard. The other, and often more convenient way of summing data is to "stack" or append data sets end-to-end. This results in many species appearing more than once in the final data set: I have called this "serial" summation. Regardless of how any index changes as more distributions are added, in an ideal index the changes resulting from horizontal and serial summation should be identical. To examine this, each succeeding data set was made cumulative of all the previous ones. Useful summation is thus testable by a regression of the results in serial summation against those in horizontal summation. Details of the distributions and probabilities of the regressions are provided in Table IV. For visual presentation, the results were arranged as the ratio of the value under serial summation to the value under horizontal summation, plotted against the number of summed distributions.

1). The first test was summation of identical distributions. As would be predicted from their forms, the Levins and Shannon indices and their normalized variants were constant-valued in horizontal summation of identical distributions, but all except the normalized Levins index increased as distributions were added serially (Fig. 3a and Table IV). In Levins-N, each generated value was divided by the number by which the class number was incremented, which meant that Levins-N was the only index in which serial summation was exactly equivalent to horizontal summation. The non-normalized Levins and Shannon indices again responded mainly to class number, which in serial summation, increases as more distributions are summed. In horizontal summation, of course, the class number is constant, as were the indices. Note that Levins' Index corresponded absolutely to this factor. CVH and SLH declined slightly as distributions were added:

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Table IV: Data summation:

Lognormal distribution types; 10 of each: fixed class intervals. These were added cumulatively to track the results of horizontal and serial summation.

	<u>Identical</u>	<u>Varying s.d.:</u>	<u>Varying mean:</u>
mean	25	10	2.5-30 (+2.5 <sup>a</sup> )
s.d.	0.2	0.05-0.6 (+0.05 <sup>a</sup> )	0.15
class #	13	15	12
prey #	50	101	101

<sup>a</sup> - increment (additive)

Regressions: Cumulative serial summation (dependent) vs. cumulative horizontal summation (independent):  
Form: INDEX = a + b (# summed distributions): values of "a" omitted.

<u>SERIES:</u>	<u>index:</u>	<u>b</u>	<u>F-ratio</u>	<u>p</u>
a). Identical:	Levins	1.0	-	0.0
	Shannon	0.098	76.8	0.00002
	Shannon-N	0.004	27.1	0.0008

Levins-N was constant: CVH and SLH declined slightly (see text).

b). Varying s.d.:	Levins	0.441	392.3	<0.0001
	Levins-N	0.076	191.8	<0.0001
	Shannon	0.028	10.9	0.008
	Shannon-N	0.008	8.83	0.014

CVH and SLH had identical values under both types of summation.

c). Varying mean:	Levins	0.094	36.6	0.00012
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Levins-N, Shannon's and Shannon-N had no significant relationships.  
CVH and SLH had identical values under both types of summation.

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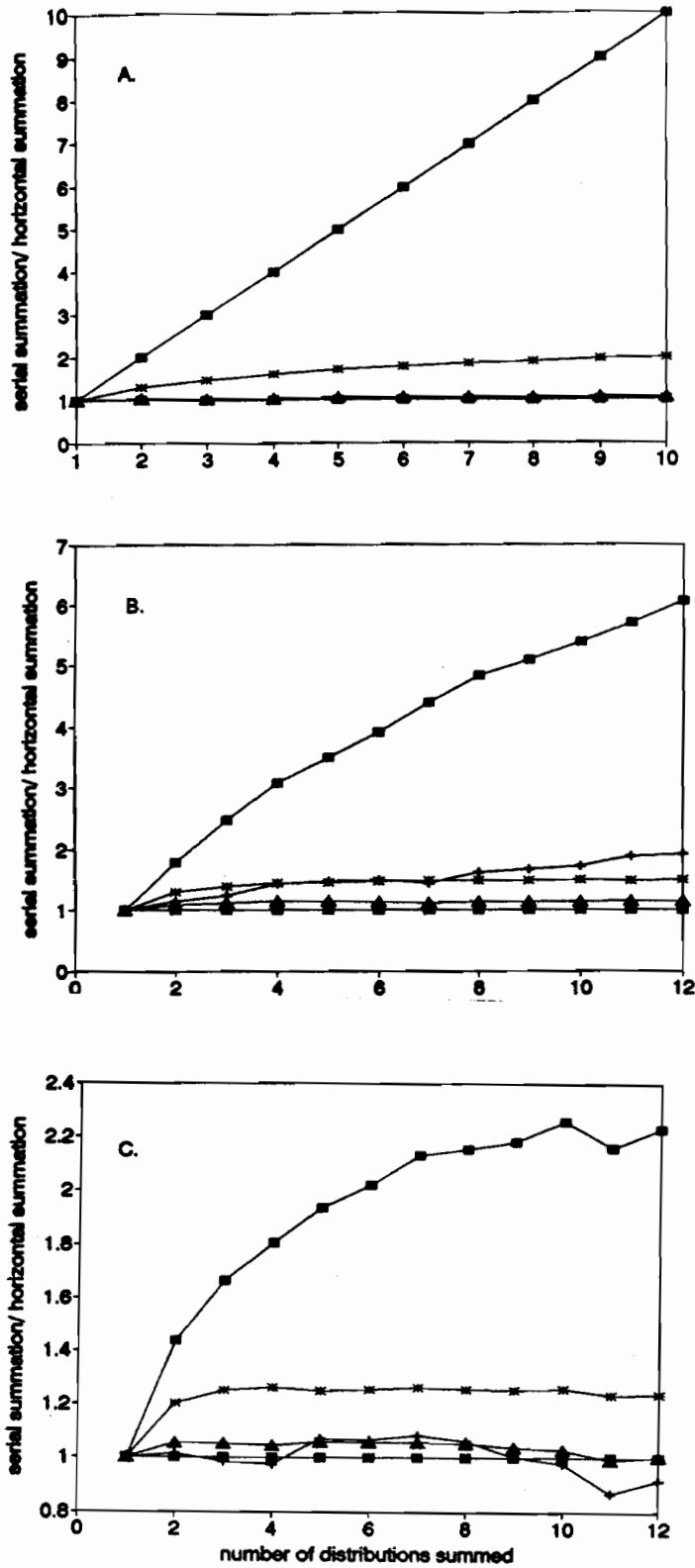


Fig. 3. Ratio of each index as determined by serial addition within data tables to its value from horizontal addition.

- a). Identical data sets.
- b). Data sets with variable standard deviation.
- c). Data sets with variable means.

Symbols: ■ Levens Index; + Levens-N; \* Shannon Index; ▲ Shannon-N; x CVH; □ SLH



Niche index simulations

this is expected because of relative restriction of the tails of the cumulative (finite) distributions. However, from Fig. 3a, it appears that the non-normalized Levins and Shannon indices are by far the worst performers.

When differing distributions (the general case) are summed, the results are quite different. As neither the prey sizes (or taxa) nor total class number was necessarily identical between distributions, both forms of summation should generate changing class numbers.

2). When distributions of either varying standard deviations (Fig. 3b) or of varying mean ("niche position") (Fig. 3c) were summed, all indices also changed: only CVH and SLH changed identically under both forms of summation in both sets of simulations, but Shannon-N varied relatively little. It appears that class number, which necessarily increases as distributions are added by either method, again mainly controlled the magnitudes of all versions of the Levins and Shannon indices in both cases, but as expected, less drastically in the normalized versions. As opposed to that, CVH and SLH responded mainly to the broadening of the cumulative distributions.

C). **Addition of information on within-size-class variability:** The niche breadth estimated by a finite number of weighted prey size classes should always be an underestimate of the true niche breadth, as grouping prey into prey size classes always hides some within-class variance (see Pearre, 1999: "Limitations"). If the distribution of prey sizes within each prey size class is added to the spectrum, the true niche width should be approached. No index should decrease under these circumstances, but the indices should be asymptotic as increased information about the variation is added, and clearly, vary as little as possible. This was tested by adding normally distributed size data in increasing numbers of classes to a framework of a basic lognormal distribution. This simulates the frequently encountered case where prey sizes and standard deviations are supplied along with the total numbers per size class; it is assumed that most authors supplying such data have used normal approximations for their data variability estimation. For taxon-based niche indices, this is equivalent to adding prey species information to data originally presented only as genera or higher taxa (see Greene and Jaksić, 1983). Details of the generated distributions are provided in Table Va, and the behaviors of the indices are shown in Fig. 4. Shannon-N varied least, followed closely by SLH and CVH, and all three appeared to

Table V:

a). Addition of information on within-size class variability:

Lognormal.

The first step up in class number is made by substituting a normal distribution having the same mean and prey number as each class in the original lognormal distribution, but with 3 prey sizes instead of the original one. Each subsequent step is made by substituting a normal distribution of the same characteristics but with the prey size classes further subdivided. Seven distributions. (see Fig. 4)

mean	20
s.d.	0.2
Prey #	480
subclasses/class	1, 3, 4, 5, 6, 7, 9
total class #	7, 21, 28, 35, 42, 49, 63

b). Variable spacing on the prey-size axis: This involved a single value per size class, but with the intervals between the size classes varying. Distribution 1 was approximately normal but very tightly aggregated, while Distribution 2 had a larger variance. Distribution 3 was uniform, while Distribution 4 was essentially a normal distribution split in half and reassembled with the peaks at the extremes.

(see Fig. 5): 4 distributions:

mean	12.5
minimum	1
maximum	25
class #	49

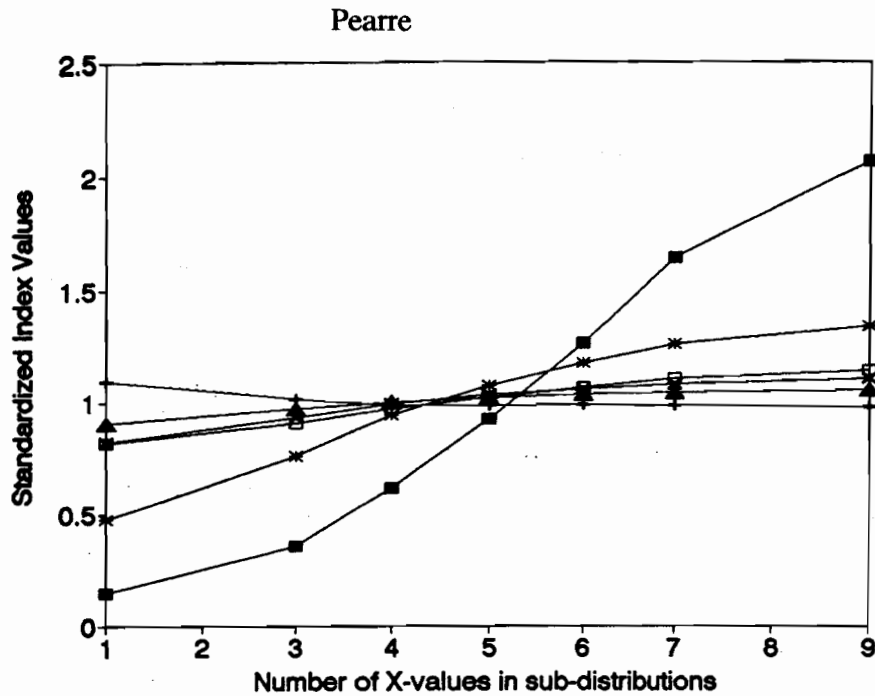


Fig. 4. Response of each index as supplementary data (ordinates of normal sub-distributions: see text) are added to an original lognormal "prey size" distribution with 7 classes. Abscissa values are the maximum number of classes inserted at the original prey size class in each run. Indices are standardized to their means for presentation on the same ordinate scale. Symbols as in Fig. 3.

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 approach asymptotes, as desired. Levins' Index increased most and did not appear to be approaching an asymptote, and Levins-N actually decreased.

D). **Variable spacing on the prey-size axis:** Thus far, spacing on the prey-ranking axis has been held constant within any distribution, as the Levins and Shannon indices cannot respond to this as a factor. However, an ideal index should reflect such changes in clustering, allowing use of and comparisons with data of this type (see Pearre, 1999: "The question of incorporating resource availability"). Four such distributions were generated, each with a single "prey" per ordinate location. These are illustrated in Fig. 5, and the parameters of the distributions are given in Table Vb. Because equal representation per prey group defines the maximal evenness for Levins or Shannon indices, all of these take their limiting constant values for this type of simulation.

For a taxon-based index, such clustering might reflect species relatedness if appropriate coefficients were available (see Pearre, 1999: "Taxonomic relatedness"). For a size-based index, this clustering represents the between prey-size spacing of the size groups, even if the range and all other statistics remain constant. These distributions also simulate unweighted scattergram data in which each point represents a single predator/prey interaction in some predator size group (e.g. Pearre, 1986). Despite the gross violations of normal distributional assumptions in the last two cases, CVH and SLH produced useful indices, being lowest-valued when the sizes were most strongly aggregated, and maximal when the distributions were broadest (bimodal).

#### EXAMPLES AND DISCUSSION OF FIELD DATA ANALYSIS:

A). Mauchline and Gordon (1985) estimated cumulative Shannon indices for groups of deep-sea fish. They found that the index was very sensitive to sample size at small sample sizes, but reached asymptotic values fairly early (c.f. Fig. 2c).

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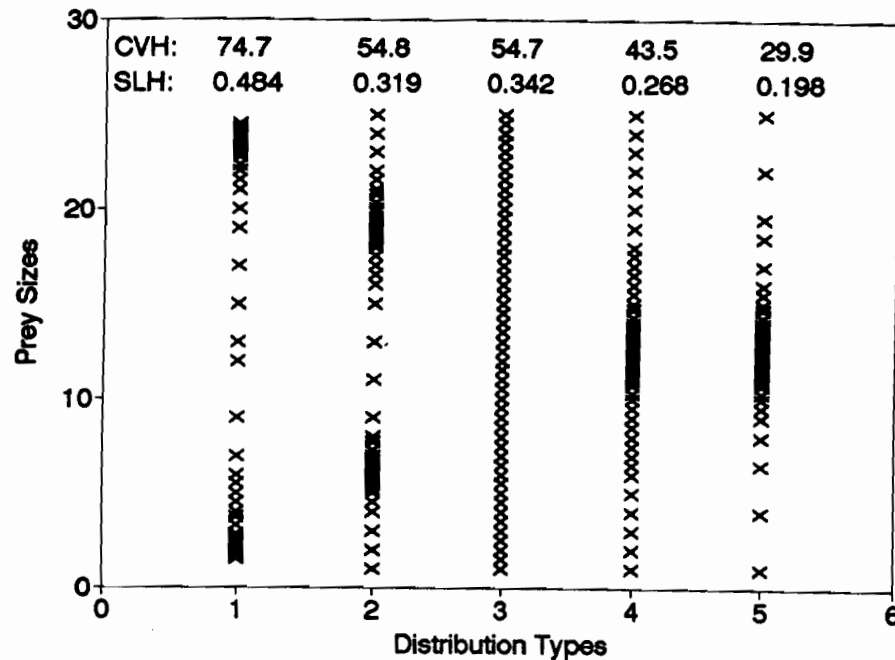


Fig. 5. Distributions of 49 single points ("prey") on size axes, illustrating types and degrees of clustering. Levins' niche index = 49.0 (the number of size classes) and the Shannon index = 3.89 (ln number of size classes) for all distributions. Levins-N and Shannon-N = 1.0 (see text).

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B). Greene and Jaksić (1983) compared the niche breadths and overlaps generated by the Levins Index (non-normalized) for eight studies of sympatric predators, as influenced by the level of prey identification. They found that for every study, "lower" identification (*i.e.* to higher taxa only) produced smaller niche estimates, hence with smaller overlaps, than did identification to species (although they could only identify insects to orders). To illustrate this point, I analyzed three data sets in which a large range of prey taxa were found, and for which mean prey species sizes were supplied by the authors. Hiraldo *et al.* (1975) examined the diets of the Eagle Owl (*Bubo bubo*), which spanned 24 orders in 8 classes of two phyla. Heidemann (1973) examined the diets of feral cats (*Felis catus*), in which a smaller total variety of prey were found (10 orders in 5 classes), but in three phyla. Cockcroft & Ross (1990) examined the diets of stranded bottlenose dolphins (*Tursiops truncatus*); these contained only three prey classes (two phyla) but in 13 orders and with a number of multispecies genera. These are analyzed by the six methods used here, with prey sizes expressed in equivalent spherical diameters (ESD, mm: see Pearre, 1999: Appendix) and SLH expressed in logarithms to the base 10. Mean sizes of higher taxa were estimated by weighting the species means by the numbers consumed. Variability was examined by estimating the coefficient of variation (C.V.) of each index over the various taxonomic levels, with each index weighted for the number of taxa included at each level. This also tests "**Addition of information on within-size-class variability:**", above. The results of this analysis are presented in Table VI. As can be seen, the niche estimates from SLH tend to vary least with taxonomic level, while CVH is slightly higher. As in the simulations (Fig. 4), Shannon-N also is relatively constant and Levins-N actually decreases as taxonomic levels are added.

C). Pearre (1986) estimated size-based trophic niche breadths (CVH and SLH) of fish species, both within species as they grew larger and between species of differing mean size. This analysis used both "histogram" type data (abundances of different mean prey sizes within predator size classes, often presented as tables) and "scattergram" data (individual predator and prey sizes, weighted or unweighted; as in "**Variable spacing on the prey-size axis :**", above). The ability to

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utilize these various types of data- and to obtain consistent niche estimates per predator species (e.g. see Pearre, 1986: Fig. 5)- demonstrates the value of this type of index in comparative studies.

D). Krzysik (1979) examined the overall niche structure (microhabitat + diet) of a salamander community, and concluded that food size (as CVH) was more valuable than taxa (Levins Index) for describing diet segregation in that context. Pearre and Maass (1998) analyzed diets of feral domestic cats (*Felis catus*) around the world, comparing SLH to Levins-N and Shannon-N, the two best overall of the conventional indices, above. Using SLH, trophic niches were found to expand as prey became more available on two time scales (seasonal and decadal) and as latitude decreased. This supports Zaret and Rand's (1971) hypothesis, rather than that of Ivlev (1955) and Schoener (1971), who

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Table VI. Variation of niche estimates with taxonomic level: field data.

1). Eagle Owl (*Bubo bubo*), Spain.

Levins	Levins-N	Shannon	Shannon-N	CVH	SLH	# taxa	taxonomic level
2.02	0.253	0.95	0.458	27.3	0.231	8	classes
3.04	0.126	1.69	0.532	31.6	0.239	24	orders
3.20	0.059	2.09	0.523	34.6	0.255	54	families
4.25	0.052	2.50	0.568	36.0	0.264	82	genera
4.25	0.048	2.56	0.571	36.1	0.265	89	species
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3.85	0.065	2.31	0.553	35.0	0.259		mean
0.60	0.040	0.37	0.026	1.92	0.0093		s.d.
15.6	61.7	16.1	4.8	5.5	<u>3.6</u>		C.V.

2). feral cat (*Felis catus*), Germany.

Levins	Levins-N	Shannon	Shannon-N	CVH	SLH	# taxa	taxonomic level
1.03	0.343	0.084	0.077	8.9	0.076	3	phyla
1.14	0.228	0.301	0.187	23.2	0.098	5	classes
1.26	0.126	0.526	0.228	31.3	0.105	10	orders
1.36	0.085	0.724	0.261	31.6	0.106	16	families
3.52	0.130	1.797	0.545	31.9	0.108	27	species
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2.27	0.136	1.100	0.366	29.9	0.104		mean
1.13	0.060	0.645	0.166	5.36	0.0070		s.d.
50.0	43.9	58.6	45.2	17.9	<u>6.7</u>		C.V.

3). bottlenose dolphin (*Tursiops truncatus*) off Natal, South Africa.

Levins	Levins-N	Shannon	Shannon-N	CVH	SLH	# taxa	taxonomic level
1.30	0.434	0.403	0.366	20.1	0.073	3	classes
1.52	0.117	0.761	0.297	24.0	0.087	13	orders
3.98	0.097	2.048	0.552	33.7	0.126	41	families
4.19	0.069	2.279	0.554	36.0	0.133	61	genera
4.72	0.066	2.422	0.566	38.4	0.140	72	species
<hr/>							
4.12	0.083	2.150	0.538	35.3	0.130		mean
0.856	0.048	0.466	0.070	4.10	0.015		s.d.
20.8	57.5	21.7	13.0	11.6	<u>11.4</u>		C.V.

- 1). Hiraldo, F., J. Andrada, & F.F. Parreño, 1975. Diet of the Eagle Owl (*Bubo bubo*) in Mediterranean Spain. Doñana, Acta Vertebrata 2: 161-177.
- 2). Heidemann, G. 1973. Weitere Untersuchungen zur Nahrungsökologie "wildernder" Hauskatzen (*Felis sylvestris* f. *catus* Linné, 1758). Z. Säugetierkunde 38: 216-224.
- 3). Cockcroft, V.G., & G.J.B. Ross, 1990. Food and feeding of the Indian Ocean bottlenose dolphin off southern Natal, South Africa. ch. 15: 295-308 In: Leatherwood, S.; Reeves, R.R. (eds.) The bottlenose dolphin. Academic Press, N.Y.

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proposed that niches should expand as prey becomes scarcer. While both Levins-N and Shannon-N varied substantially between studies, neither exhibited any trends consistent with predator, prey, or environmental characteristics; thus SLH proved a much more powerful tool for this investigation.

### DISCUSSION:

There are a number of factors which might affect the way in which these indices react. For the simulations, the factors examined were the width of the distribution (as standard deviation), the position of the distribution (as mean), the "prey size" class interval, the number of "prey size" classes, and the total number of "prey". These are, of course, interrelated. It is perhaps worth reiterating that estimating Levins and Shannon-Weaver indices using prey size data is identical to doing so with taxonomic data, as long as each named species is of a different mean size (i.e., there is a unique name for each species, in words or numbers). Thus, the simulations used in this way reflect how these types of index respond to changes in degrees of aggregation into species classes. However, estimating means and standard deviations per se is only relevant if the species data are ordered into approximately normal distributions (see Pearre, 1999: "EVOLUTION OF A SIZE-BASED TROPHIC NICHE INDEX"). If different ordering criteria lead to different prey-abundance spectra, different statistical indices will be needed. The original Levins and Shannon-Weaver indices, which are independent of ordering, were designed to grow larger as more prey species (size classes) were added, so should be sensitive to the number of such classes. Analysis of the multi-factor simulations confirms this and that they are less influenced by the manner in which prey are distributed into the classes. This is reflected in the fact that SLH and CVH generally vary less than the others with taxon level in real data (Shannon-N also generally varied little). This could be a disadvantage if one wished to look separately at "species diversity" vs. "trophic diversity" (e.g. Greene & Jaksić, 1983: see Pearre, 1999: "TAXON-BASED NICHE METRICS vs. SIZE-BASED ONES: **Advantages of taxon-basing:**"), but is an obvious advantage in estimating a niche breadth from small samples and/or mixed taxonomic levels.

The normalized versions react more to the evenness of the distribution of prey among classes, so they should not respond as strongly to class number, but should and do respond to the interaction between class number and total prey. The normalized versions are superior for certain purposes, such as manipulation of data tables, but appear unreliable in assessing niche widths for small sample sizes. Of the four, only the normalized Shannon-Weaver Index ("Shannon-N") performed well at either serial data addition or addition of extra distributional information to species tables. Overall, Shannon-N was probably the most useful of the four variants: usually, the non-normalized Levins Index was the most variable.

Although Levins' and Shannon's indices are sometimes used with size data instead of taxonomic species (Pearre, 1999: "PREY-SIZE BASED NICHE INDICES: **Approaches**"), doing so wastes size and size increment information contained in the data. These indices, by their nature, react alike to a perfectly even distribution of sizes (or other ordering information, such as relatedness) and to a highly clumped distribution (e.g. around a central "optimal" size value, or perhaps to a prey species most closely related to the predator), as long as the number of distinguishable size classes is constant. However, ability to utilize this type of data is a useful attribute of a niche index, and both CVH and SLH do so. For brevity, other types of imaginable data manipulations were omitted, and of those examined, clearly, some of the simulated problems are more serious than others. The judgement of seriousness will probably vary with the researcher and with the type of problem under investigation.

## CONCLUSIONS:

In general, SLH and CVH were the best or near the best performers on all tasks on both simulated and real data. From Figures 3 and 4, it is clear that their values very closely track each other in the simulated data, confirming expectation (Wright, 1968; Lewontin, 1966) and the results from fish trophic niche analyses (Pearre, 1986). Because both SLH and CVH are statistical measures, it is also simple to test for the reality of differences between niche widths (Alevizon, 1975; Krzysik, 1979; Pearre, 1986), which may be important in comparative studies. As we may expect prey size distributions to approach lognormality (see Pearre, 1999: "EVOLUTION OF A SIZE-BASED TROPHIC NICHE INDEX"), SLH should in principle be more useful, and indeed appears slightly superior to CVH with simulated lognormally distributed data. In practice, it was found less variable than CVH and less subject to biases (Pearre, 1986) in comparisons of fish predator species. Also, as it describes a section of a logarithmic biomass spectrum (e.g. Sheldon *et al.*, 1972; Kerr, 1974; Platt & Denman, 1978; Peters, 1983) the trophic niche breadth thus obtained can be used to predict energy flow or relative population size (Pearre, 1986). However, because the numerical value of SLH will change depending on the prey size units and logarithmic base chosen, the non-dimensional CVH may sometimes be more appealing. Also, as many published prey size spectra are presented only as means and standard deviations, CVH may be superior if one wishes to compare them to new results.

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DEDICATION:

This paper is based on a presentation made at a special symposium held in honor of Peter J. Wangersky at Dalhousie University, Halifax, N.S., in July 1994, a year after his formal retirement from the Department of Oceanography at Dalhousie University. Because his academic career and interests have spanned so many fields, discussions with him in various contexts have been direct progenitors for many of the ideas expressed here.

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