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[2] *School of Biological Sciences, University of Kentucky, Lexington, Kentucky 40506 USA.*

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NOTES ON THE MEASUREMENT OF OVERLAP[1]

Stuart H. Hurlbert[2]

Many formulae have been put forward in recent years which lead to precise definition and quantification of concepts such as association, niche overlap, and competition. The value of the whole enterprise is open to debate, as are the assumptions and philosophies underlying each formula that has been recommended. Some of the existing range of opinion arises, however, not from philosophical differences but rather from simple misunderstandings or technical errors, such as those in three recent papers on overlap (Petraitis 1979, Abrams 1980, Linton et al. 1981). Succinct correction of these may permit a clearer view of the larger issues. An element of self-defense also is involved, as the papers by Abrams and Petraitis misinterpret my earlier one on the topic (Hurlbert 1978).

Abram's (1980) concern that Hurlbert (1978) "will only aggravate the confusion" reflects the disparateness of our views on such matters as: (1) how niche overlap should be defined, (2) whether the measurement of niche overlap should utilize information on resource abundances, (3) how niche overlap should relate to the 'compettition coefficient' (sensu Levins 1968), and (4) the feasibility of constructing realistic consumer resource models. Our respective views on these items mostly can be ascertained from our original papers and need not be restated here, though they are more fundamental than the more technical points discussed below.

In his penultimate section (1980:48) Abrams lists four reasonable criteria for judging the suitability of a niche overlap index and states that my overlap index, L (Hurlbert 1978: Eq. 11), meets none of them. In fact, it meets all of them. (1) Ease of calculation is no problem; I doubt if there exists a data set for which L could not be calculated on a pocket calculator in less than 30 seconds. (2) None of the indices I proposed are based on "assumptions about the nature of the competitive process"; they do not presume any particular definition of competition, nor does their use presume that competition is occurring. (3) Intercommunity comparisons will always pose interpretation problems, but no more so for my indices than for the older ones. The problems are simply different. For an index such as Schoener's (1970; Eq. 1 in Hurlbert 1978), the risk lies in the implicit assumption that available but unutilized resource states are irrelevant, and equally so in both communities, to the ecological phenomenon we are trying to quantify. For an index such as L, risk lies in the possibility that the particular way the index is applied may be inappropriate in some way. That is, for some indices the problems arise at the time of index selection; for others they arise at the time of index application. (4) Despite Abrams' contention to the contrary, neither L nor the competition coefficient (either in its original form [Levins 1968] or as modified to incorporate resource abundance data [Hurlbert 1978]) will "be changed by the subdivision of resource states which are not distinguished by the competitors."

In the last paragraph of his section titled "A critique of Hurlbert's formulas," Abrams (1980:48) sets up a straw man by incorrectly guessing the "basic motivation" behind the development of my overlap index, and demolishes it with a puzzling geometric analogy. Three points may be made. First, the simple conceptual basis for my index was given in the original article; Abrams need not have guessed. Second, the question of whether two "similar" (in resource use) specialists exhibit more overlap than do two "similar" generalists has no meaning until, among other things, an index or definition of similarity is specified; Abrams does not specify one. And third, it is not clear what the size difference between his smaller and larger geometric figures represents. Resource utilization spectra or histograms are usually standardized so that the total area of each is 100% or 1.00; that is, so that they are all the same size.

Petraitis (1979) makes the minor slip of confusing "All men are gentlemen" with "All gentlemen are men." He states (1979:706): "When $L = 1$, Hurlbert asserted, 'both species utilize each resource state in proportion to its abundance'. . ." and then demonstrates, with an example, that the proposition is not always true. However, I did not put forward *that* proposition but rather its converse ("L assumes . . . a value of 1.0 when both species utilize each resource state in proportion to its abundance" [Hurlbert 1978: 70]), which *is* always true. If $L = 1$, this means only that the frequency of interspecific encounter (or a conceptually equivalent parameter) is the same as it would be if the two species utilized each resource state in proportion to its abundance; there is no implication that the two species *are* such perfect generalists.

Linton et al. (1981) usefully demonstrate with Monte Carlo methods that four of the most commonly used overlap indices (those of Schoener, Horn, Pianka, and Morisita), when calculated using sample data, frequently yield highly biased estimates of actual population overlap (which each index defines differently). These results should be heeded. However, their comparative evaluation of the four indices is faulty. They define 'true overlap' as the area of intersection of two resource utilization curves, and end up concluding that generally "Schoener's index produces estimates which are most consistent with the true overlap" (Linton et al. 1981:287) and that "Horn's, Morisita's and Pianka's equations produced substantial misrepresentation of the data" (1981:290). Such are the foregone conclusions of a circular argument. Linton et al. (1981) seem unaware (1) that Schoener's index was devised specifically to measure what they call 'true overlap' (hence its predictable "success"), and (2) that the other three indices were devised specifically to measure properties other than 'true overlap' (hence their predictable "failure"). In other words, they show that Schoener's index usually gives a better estimate of Schoener's index than do the three indices unrelated to Schoener's index. Their conclusions as to the relative merits of the four indices are thus not useful.

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[1] *Manuscript received 7 October 1980; revised 24 March 1981; accepted 14 April 1981.*

[2] *Department of Biology, San Diego State University, San Diego, California 92182 USA.*

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REPLY TO A COMMENT BY HURLBERT[1]

Peter A. Abrams[2]

In an earlier article (Abrams 1980), I argued that niche overlap data are most useful if used in conjunction with a consumer-resource type of model to estimate relative intensities of inter- and intraspecific competition. If this approach is not possible, and a general niche overlap measure is used for descriptive purposes, I argued that Schoener's (1970) geometric overlap formula is preferable to others that had been proposed, including Hurlbert's L (1978). Hurlbert's reply disagrees with this conclusion. This note is intended to answer his objections.

I claimed that Schoener's index was easier to calculate than Hurlbert's. Hurlbert does not argue with this point, but claims that his measure is also easy to calculate. If one already has data on resource abundances this is true (although the claim that L could be calculated in <30 s for any data set is no doubt an exaggeration). If such data are not available, L will be much more difficult to determine. To quote Hurlbert (1978), ". . . in most studies of dietary overlap it is very difficult to determine a_i (abundance of food type i)."

I argued that a descriptive niche overlap measure should be free of assumptions about the nature of the competitive process, and that Hurlbert's measures have such assumptions. L weights the product of the proportionate use of resource state k by species i and j by the inverse of the relative abundance of resource 1 k. This is also true of Hurlbert's competition coefficient. This represents an assumption that rare resources are relatively more important in determining overlap. Hurlbert's rationale for this seems to be that if competition is occurring, overlap in the use of rare resources contributes more to the process than overlap for common ones. Thus, although use of L does not necessarily mean one is assuming that competition is occurring, the form of L is based on an assumption which I earlier (1980) argued was invalid.

I argued that the fact that unused resources affect L would make comparisons of overlaps in different areas or different communities very difficult. Hurlbert does not argue with this point; instead, he claims that Schoener's overlap formula has a related problem, because it assumes that unused resource states are equally irrelevant in the communities. This is not a 2 problem, because unused resources are irrelevant. Unused resources do not affect competition between two species. Unused resources are also irrelevant to overlap by any previous usage, either ecological or common. One would not want a measure of the 3 amount of overlap of two pieces of paper on a tabletop to depend on the size of the table.

I was mistaken in claiming that Hurlbert's formulae would be altered by resource state subdivision. Contrary to Hurlbert's claim, however, Mac Arthur and 4 Levins' formula is altered by subdivision. Because Schoener's measure is not altered by subdivision, this criterion alone does not provide a ground for choosing between overlap measures. The previous three arguments seem to me to be sufficient grounds for preferring Schoener's over Hurlbert's measure.

Hurlbert also makes one point related to the general argument in my original paper. I argued that two similar specialist species should not be considered to overlap more than two similar generalists. The question of whether having this property was a "basic motivation" behind the form of Hurlbert's L is irrelevant to the question of whether a niche overlap measure should have this property. Hurlbert objects that "similar" is a nebulous term, but my original argument could have been made using "identical" instead of 5 "similar." The competition coefficient between two identical species, each of which uses one resource, is unity. The competition coefficient between two identical species each of which uses n resources is unity. Therefore, consideration of the biological consequences of overlap (competition) provides no justification for distinguishing these two cases. In addition, common usage of the word overlap would not distinguish between these cases. (This is what my geometric analogy attempted to show.) If resource utilization histograms (normalized or unnormalized) of two identical species are superimposed on one another, they overlap completely (by the dictionary definition of overlap) regardless of whether the species are specialists or generalists.

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[1] *Manuscript received 7 May 1981; accepted 25 June 1981.*

[2] *Department of Ecology and Behavioral Biology, University of Minnesota, Minneapolis, Minnesota 55455 USA.*

<u>Further comments by S. Hurlbert:</u> Numbers correspond to those on margins of Abram's note; equation numbers to those in Hurlbert (1978)

1. That is to say, L (Eq. 11) and $S_{x(y)}$ (Eq. 34) give equal weight to each unit of resource; other indices do not.
2. They do affect competition in the sense that if an "unused" resource came to be used by one or both species, competition between them probably would be altered. Unused resources also are reasonably taken into account when overlap is being measured for many species pairs, e.g. all those possible in an assemblage of *n* species that collectively use a wider range of resources than does any single pair.
3. Perhaps not. Nor would one necessarily want to measure niche overlap in the same manner as one would measure "paper overlap."
4. This is true of the original MacArthur-Levins formula but not, I believe, of my modification of it (Eq. 34).
5. The "original argument" is greatly modified when "similar" is replaced by "identical." Overlap, however defined, does not necessarily lead to competition, nor does a competition coefficient necessarily measure the intensity of competition. The suggestion that two species pairs having the same "competition coefficient" must also exhibit the same degree of niche overlap seems unwarranted and conflicts with Abram's recommendation of Schoener's index as an overlap index.