Habitat categorization, niche overlap measures and clustering techniques

Nicola Saino* & Mauro Fasola**
* Dipartimento di Biologia, Sezione Zoologia-Scienze Naturali
  Via Celoria 26, 20133 Milano.
** Dipartimento di Biologia Animale, Università di Pavia
   Piazza. Botta 9, 27100 Pavia.

Abstract - We compared the descriptions of niche overlaps in a guild of Laridae and Sternidae, as obtained with different grains of habitat categorization, by different overlap algorithms and by different clustering techniques. All the values of niche overlap were obtained from a unique matrix of foraging habitat utilization by the eight species considered. Very dissimilar descriptions of the niche overlaps were given by the overlap algorithms and by the clustering techniques and the strongest discrepancies arose when the values obtained from different levels of grouping of the habitat categories were compared. We conclude that values of niche overlap obtained by different algorithms and levels of resource grouping differ widely. An a priori categorization of the resources should be avoided. Except in cases very general patterns of resource use are to be compared. Multivariate techniques may offer an alternative approach in studies on resource partitioning among populations in a guild.

Key word: clustering techniques, habitat categorization, niche overlap, overlap algorithms

The niche can be formalized as the n-dimensional hyperspace whose axes represent the biotic and physical factors influencing the ability of a taxonomic unit (an individual or a population) to survive and reproduce (Hutchinson 1957). The Grinnellian and Hutchinsonian concepts of niche have been extensively reviewed and debated (see for example James et al. 1984). When studying animal guilds (*sensu* Root 1967) one of the central problems is the extent to which the consumer species in the guild share and compete for the resources available. Two or more consumers may be compared on the basis of their patterns of microhabitat use, food consumed, foraging time and behaviuor (Rolando 1985, Fasola 1987). The taxonomic units may be populations of the same species in different areas, or two species in the same guild, or even a single species and an hypothetical model of random use of the available resources. The joint use of resources by two species is simply defined as niche overlap. However it is not easy to quantify the degree of overlap of their niches: the *a priori* identification of discrete resource categories, which is requested for the use of overlap indices, may be inadequate and may not reflect their distinctness to the species, thus biasing the estimate of niche overlaps. Moreover, the choice of an algorithm to calculate the overlap index is arbitrary and could itself produce differences in the description of niche relationships among species.

Many algorithms have been proposed to quantify niche overlap. Some of them (Sorenson 1948) are simply based on the enumeration of the resource states shared.

Many others require the quantification of the frequency of utilization of the resource categories (Morisita 1959, Schoener 1968, Pianka 1973 and others). Only a few algorithms combine resource use and availability (Hurlbert 1978).

Abrams (1980) pointed out that "niche overlap measures should facilitate intercommunity comparisons"; this implies that overlap values obtained by different algorithms must be comparable. Furthermore, the measure should not be changed by a different grouping of the resource states. If this requisite is not met the measure of overlap is a simple description of the interspecific niche relationships that could be drastically influenced by the arbitrary resource categorization.

However, little attention has been paid to the comparability of overlap values obtained by different algorithms in particular when resource categories of different detail are adopted (Alatalo & Alatalo 1979, Saino et al. 1988). Furthermore little, if any, attention has been paid to the distortion produced by the clustering methods used to produce similarity phenograms on the original overlap values in studies dealing with animal ecology (see Legendre & Legendre 1983).

In this paper we compare the descriptions of the foraging habitat overlap in an avian guild as obtained by three widely used overlap algorithms and by different levels of habitat categorization; we analyze the distortion of the overlap values produced by the clustering techniques employed to obtain the phenograms of overlap and we compare the descriptions furnished by phenograms obtained using different clustering techniques. The problems of multidimensionality in niche data are discussed in a companion paper (Fasola & Saino 1990).

METHODS

The data on foraging habitat use by eight Laridae (Mediterranean Gull *Larus melanocephalus*, Black headed Gull *Larus ridibundus*, Yellow legged Gull *Larus cachinnans*, Slender billed Gull *Larus genei*) and Sternidae (Gull billed Tern *Gelochelidon nilotica*, Sandwich Tern *Sterna sandvicensis*, Common Tern *Sterna hirundo*, Little Tern *Sterna albifrons*) species, were collected during the breeding seasons 1983 and 1984 in a 560 Km^2 area of NW Italy covering the Comacchio lagoon and the surrounding agricultural land, salt and fresh water marshes, rivers and channels and the sea. The study area was subdivided into 23 habitat categories based on position within the lagoon, and on salinity and depth of water. The sea was subdivided into three bands based on distance from the coast. Particular artificial habitats such as salt works, harbors and fish ponds were also considered. The habitats and their use by seabirds are summarized in an other paper on niche measures (Fasola & Saino 1990). The data of habitat use by the species were then grouped by means of a predator oriented criterion and referred to 16 and 10 more general habitat categories. Similar habitats with similar frequencies of utilization by the eight species were grouped thus minimizing the effect of the resource grouping. Further details on the study area and methods are given by Fasola et al. (1989). We applied three overlap algorithms:

$$W = 1-0.5 \cdot \Sigma /P_{ij} -P_{ik}/ \qquad \text{(Schoener 1968)}$$

$$\Sigma P_{ij} \cdot P_{ik} / \Sigma P_{ij}^2 * \Sigma P_{ik}^2 \qquad \text{(Pianka 1973)}$$

$$A/XY * \Sigma x_i * y_i / a_i \qquad \text{(Hurlbert 1978)}$$

where p_{ij} and p_{ik} are the frequencies of utilization of the ith category by the jth and the kth species. A is the surface of the study area, X and Y are the total populations of species x and y, xi and yi are the proportions of individuals of the species x and y exploiting the ith resource and ai is the availability of the ith category.

The values of Pianka's and Schoener's algorithms may range from 0 (no overlap) to 1 (complete overlap). Hurlbert's algorithm may range from 0 to a value > 0 depending on the sizes of a_i.

STATISTICAL ANALYSES AND CLUSTERING TECHNIQUES

The Kendall correlation coefficient was adopted to investigate the extent to which overlap values obtained by different algorithms and by different resource levels of grouping reciprocally deviate from the joint monotonicity. Linear regression analysis was performed to analyze the quantitative relations between values obtained by Schoener's and Pianka's algorithms within the same grouping level. One-way analysis of variance was used to test the difference between the overlap values obtained with different levels of resource grouping.

We applied UPGMA,WPGMA, Complete linkage and Single linkage methods which belong to a family of clustering techniques usually indicated by the acronym SAHN (Sequential, Agglomerative, Hierarchic, Nonoverlapping). The Cophenetic correlation coefficient (Sokal and Rohlf 1962) was employed to measure the agreement between the overlap values implied by the phenograms (tree matrices) and those of the original overlap matrix. The Cophenetic correlation coefficient was also used to study the similarity among phenograms obtained by the different clustering techniques, overlap algorithm and resource grouping level. Since no significance test is available for the cophenetic correlation coefficient, we followed Sneath and Sokal (1973) in considering values of cophenetic correlation coefficient > 0.9 as indicators of good correlation and values of the cophenetic correlation coefficient < 0.8 as indicators of bad correlation.

RESULTS

Levels of resource grouping

The descriptions obtained by the same algorithm at different levels of resource grouping (23, 16 and 10 categories) were compared (Tab. I). All the pairwise comparisons showed statistically significant correlation coefficients (Kendall test; p<0.01) but in no case was the condition of the joint monotonicity respected (i.e. the values of the correlation coefficient were always <1) with correlation values ranging from 0.54 to 0.82 for Schoener's and Pianka's algorithms (Tab. I) and from 0.51 to 0.73 for Hurlbert's. This means that species overlaps were never ordered in the same way by an algorithm when the grouping level was changed. The deviation from the joint monotonicity increased with decreasing number of resource categories and was higher when the overlap values obtained by 10 and 23 resources where compared for all the three algorithms. One-way analysis of variance showed significant variation among the values at different levels of grouping for Pianka's algorithm ($F_{2,81}$=4.9; p<0.01) and a borderline significance for Schoener's algorithm ($F_{2,81}$=3.0; p=0.054). The values of Schoener's and Pianka's algorithms decreased with an increase in resource categories. The values obtained by Hurlbert's algorithm did not show any clear variation ($F_{2,81}$=0.519; NS).

The values of Schoener's algorithm are unchanged when categories increase in number provided that when a resource category is split in two the ratio of the frequencies is the same as in the original one. Whereas the value decreases if the ratio is different. Therefore at least the two coarser levels of grouping were inadequate and further segregation within some of the 10 or 16 resource categories was achieved between species.

Comparison between algorithms

The coefficients of correlation of the values obtained with Schoener's and Pianka's algorithms at the same levels of resource grouping (underlined values in Tab. I) showed that in no case the requisite of the joint monotonicity was respected.

TABLE I. Kendall's correlation coefficients of the values of Pianka's and Schoener's algorithms at different levels (23, 16 and 10 categories) of resource grouping.

Algorithm and number of categories	Schoener 23	Schoener 16	Schoener 10	Pianka 23	Pianka 16	Pianka 10
Schoener 23	-	0.82	0.54	0.80	0.64	0.51
Schoener 16		-	0.69	0.80	0.78	0.66
Schoener 10			-	0.57	0.66	0.83
Pianka 23				-	0.80	0.61
Pianka 16					-	0.76
Pianka 10						-

Furthermore the comparisons of Pianka's and Schoener's algorithms, regardless of the level of grouping showed an increasing deviation from monotonicity with increasing difference in the number of resource states.

The correlations of Schoener's and Pianka's with Hurlbert's algorithm within the same level of grouping showed much lower values ranging from 0.51 to 0.75.

The regression analysis of the values of Schoener's algorithm on those obtained by Pianka's algorithm for each level of grouping showed that the values of the former tend to increase at a slower rate than the latter. In particular at all three levels of grouping Schoener's algorithm, as compared to Pianka's, overestimated the overlap index for values of the index from 0 to about 0.2 (0.16-0.21) and to underestimated the overlap index for values greater than this value.

Cophenetic comparison between overlap and tree matrices

The values of the cophenetic correlation coefficient (Tab. II) indicated that the UPGMA method always gave the lowest distortion of the original overlap values. WPGMA was the second less distorting method and its associated cophenetic values were higher (except in one case) than the Single linkage and Complete linkage methods. Even the UPGMA cophenetic correlation coefficient value were always below 0.9 thus indicating a certain degree of distortion of the original overlap values. The Complete linkage and the Single linkage methods had associate cophenetic correlation coefficient values well below 0.8, in 5 and 1 cases respectively, and may thus be regarded as the least adequate methods when adherence between overlap values and graphical representation by phenograms is needed.

Cophenetic comparison among clustering methods

We applied different clustering methods to the values obtained by each algorithm at the different levels of resource grouping. Table III shows that the highest agreement between clustering methods was that of UPGMA with WPGMA with

TABLE II. Average and range of the values assumed by the cophenetic correlation coefficient for the different clustering techniques. The third column represents the mean rank of the cophenetic correlation coefficients computed over 9 combinations of three algorithms and three levels of resource grouping.

Clustering technique	Average	range	mean rank
UPGMA	0.872	0.822-0.897	1
WPGMA	0.867	0.813-0.895	1.56
Complete linkage	0.822	0.745-0.888	3.33
Single linkage	0.828	0.782-0.885	3.56

TABLE III. Average and range of the values assumed by the cophenetic correlation coefficient obtained by comparing the tree matrices derived from different clustering techniques.

Clustering technique	UPGMA	WPGMA	Single linkage	Complete linkage
UPGMA	-	0.993 (0.982-1)	0.930 (0.872-0.985)	0.914 (0.769-0.992)
WPGMA		-	0.923 (0.875-0.984)	0.905 (0.754-0.989)
Single linkage			-	0.976 (0.719-0.903)
Complete linkage				-

values ranging from 0.982 to 1; all the other comparisons had lower associated cophenetic correlation coefficients and a much higher range of variation (see for example Complete linkage and Single linkage methods) for all the algorithms and for all the levels of grouping thus indicating that important quantitative differences existed between the phenograms obtained from a overlap matrix by different clustering methods.

Furthermore, as a result of the discrepancies which emerged between overlap values obtained by different algorithms and levels of resource grouping and of the distortion produced by the clustering techniques, the phenograms gave very different quantitative representations of the overlap between the species. In particular 4 of the 12 comparisons between phenograms obtained by Pianka's and Schoener's algorithms within the same level of resource grouping and clustering method had associated cophenetic correlation coefficients below 0.8 and 5 above 0.9.

The discrepancies are much bigger if the phenograms obtained by the same clustering method and algorithm are compared at different levels of resource grouping. Twenty four of the 36 comparisons had values below 0.8 and just 4 above 0.9 thus again showing that the main source of disagreement is the level of resource grouping.

DISCUSSION

Our results may be summarized as follows:
- Different patterns of the niche overlap were described by the same algorithm when the grouping level changed
- Different algorithms gave different descriptions of the overlap relationships both when the grouping level was different or held constant
- UPGMA was the least distorting clustering method
- UPGMA and WPGMA were the most concordant clustering techniques of the four techniques considered
- Tree matrices and phenograms obtained by different algorithms with the same grouping level and clustering technique are to a certain extent quantitatively different. The tree matrices and phenograms obtained by the same algorithm and clustering technique for different levels of grouping gave strikingly different descriptions of the interspecific overlap relationships.
The ecologist attempting to quantify and represent the niche overlap in a guild graphically will face at least four problems.
1) the problem of resource categorization (the problem of "spacing" in Colwell & Futuyma 1971).
    Our data clearly showed that the problem of spacing is a real one in at least two respects. First, when simply comparing the values obtained by an algorithm at different resource levels of grouping the differences observed are probably of the same order of magnitude as those attributable to ecological phenomena such as niche compression or widening due to intra- or inter species competition. For Pianka's and Schoener's algorithms the values of overlap decreased with increasing number of resource states thus suggesting that habitat segregation between species is achieved in a finer scale than is usually adopted for habitat categorization. The extent to which the true habitat segregation is obscured by inadequate habitat categorization is, obviously, unknown.
    Second, the phenograms may depict very different patterns of inter species relationships even when the same clustering technique and the same algorithm are adopted. Always adopting the same algorithm and clustering technique may avoid discrepancies but this does not solve the problem of habitat categorization.
2) the difficulty in choosing an algorithm to calculate an overlap index because of the differences in estimates of the overlap furnished by the algorithms.
    The adequacy of the different algorithms in describing the niche overlap has been extensively discussed by Linton et al.(1981), by Smith and Zaret (1982).
    There is no agreement on which algorithm is preferable (Hurlbert 1978,1982, Abrams 1980, Linton et al. 1981). Our results showed that there is a significant correlation between the overlap values obtained by different algorithms, but that the deviation from the joint monotonicity between Pianka's and Schoener's algorithms is notable. The fact that a significant correlation always existed may be regarded as a necessary rather than a sufficient condition in order to consider the values comparable.
3) the degree of agreement between the original overlap matrix and the similarity matrices (tree matrices) implied by the phenograms.
    UPGMA method produced the least distortion in the original overlap data for all the levels of grouping and for all the overlap algorithms considered. The representation obtained by WPGMA is very similar to that of UPGMA, although

the former produces a slightly greater distortion of the overlap values. The complete linkage method leads to tight and discrete clusters which join others only at low levels of overlap values whereas the Single linkage method leads to long and dispersed clusters (Sneath and Sokal 1973). In cases in which adherence between the phenograms and the original overlap values is needed, the UPGMA method is to be preferred.

4) the differences among the graphical representations of the overlap relationships obtained by the phenograms deriving from different clustering techniques.

Our analyses showed that different phenograms may be obtained by different algorithms, but the lowest cophenetic correlations resulted when different levels of grouping were adopted. This introduces the possibility that the researcher *a posteriori* chooses the phenogram that most resembles his image of the structure of the guild. Such a choice obviously reduces the heuristic value of overlap index use and introduces some elements of circular reasoning.

Niche overlap indices aim to represent species relationships synthetically, in order to compare the same guild in different geographical areas, or to study the seasonal changes in guild structure in temporally varying environments. Our results suggest that in this respect they are of little use. Research operating in different geographical areas will presumably face partly different environments in which the same resource categorization is difficult. Furthermore the same resource states (such as geomorphological or physiognomic vegetational units) will have different ecological meanings in different geographical areas since food availability, intra species competitive pressure and competitive pressure by consumers not belonging to the guild are generally different.

Discrepancies produced by different algorithms or clustering techniques may be circumvented by always choosing the same methods but, as we showed, the most important source of variation is probably the grain of habitat categorization.

In conclusion we think that overlap indices produce a loss of information which is not offset by gains in comparability of data from different geographical areas or seasons, since the results from a matrix of resource use are heavily affected by the habitat categorization and by the overlap algorithm adopted. In agreement with Thomson and Rusterholz (1982), if the problem is to describe habitat use data one should not calculate indices at all and the original data set should be detailed. In cases in which a synthetic description of niche overlaps in one guild is needed, very general patterns of resource use are to be compared, or a precise hypothesis on niche relationships can be formulated, an index is of use. An alternative approach would be to adopt multivariate techniques such as Principal Component Analysis, Discriminant Function Analysis, Polar Ordination etc. All these techniques imply the selection of environmental variables which will be sampled at sites determined randomly or uniformly or recorded only when individuals of a studied species, their nests, the estimated center of their territories are individuated. These techniques and their correct use has been reviewed and discussed in many papers (Green 1971, Rotenberry & Wiens 1980, Carnes & Slade 1982, Williams 1983).

SOMMARIO

Categorizzazione delle risorse, misure di sovrapposizione di nicchia e tecniche di "clustering"
- Abbiamo confrontato le descrizioni delle sovrapposizioni delle nicchie di foraggiamento in una comunità di Laridi e Sternidi ottenuta utilizzando:
1) categorizzazione degli habitat di differente dettaglio
2) diversi algoritmi per calcolare l'indice di sovrapposizione
3) differenti tecniche di clustering
- Le descrizioni delle sovrapposizioni delle nicchie sono discrepanti quando ottenute con diversi algoritmi e tecniche di clustering. Tuttavia le discordanze maggiori risultano quando si confrontino i valori dell'indice di sovrapposizione ottenuti con differenti gradi di accorpamento delle categorie di ambienti di foraggiamento.
- Si conclude che l'uso di indici di sovrapposizione di nicchia nel valutare le relazioni frra nicchie di popolazioni simpatriche può risultare fuorviante e che la categorizzazione a priori delle risorse dovrebbe, quando possibile, essere evitata.
- Tecniche di analisi statistica multivariata consentono un approccio alternativo allo studio della ripartizione delle risorse per specie.
TAB. I. Coefficiente di correlazione non parametrica (Kendall τ) dei valori dell'indice di sovrapposizione di nicchia ottenuti mediante gli algoritmi di Schoener (1968) e Pianka (1973) a diversi livelli di accorpamento delle risorse.
TAB. II. Media e intervallo di variazione dei valori assunti dal coefficiente di correlazione cofenetica per le diverse tecniche di clustering . La terza colonna rappresenta il rango medio dei valori del coefficiente di correlazione cofenetica calcolati sulle 9 combinazioni di 3 algoritmi e 3 livelli di accorpamento delle risorse.
TAB. III. Media e intervallo di variazione dei valori assunti dal coefficiente di correlazione cofenetica ottenuti confrontando le matrici "tree" derivate da differenti tecniche di clustering.
APP. A. Valori dell'indice di sovrapposizione ottenuti mediante i tre algoritmi a tre diversi livelli di accorpamento delle risorse. MG=Gabbiano corallino, BG=Gabbiano comune, SG=Gabbiano roseo, YG=Gabbiano reale, GT=Sterna zampenere, ST=Beccapesci, CT=Sterna comune, LT=Fraticello.

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APPENDIX A. Overlap values obtained by the 3 algorithms used at different levels of resource grouping. MG = Mediterranean Gull, BG = Black-headed Gull, SG = Slender-billed Gull, YG = Yellow-legged Gull, GT = Gull-billed Tern, ST = Sandwich Tern, CT = Common Tern, LT = Little Tern.

	MG	BG	SG	YG	GT	ST	CT	LT
			Schoener's algorithms, 23 resources					
MG		.29	.01	.11	.86	.05	.11	.03
BG			.07	.31	.31	.14	.31	.45
SG				.01	0	.21	.17	.05
YG					.1	.06	.41	.20
GT						.02	.1	.05
ST							.34	.05
CT								.22
LT								
			Schoener's algorithms, 16 resources					
MG		.3	.01	.12	.85	.08	.14	.04
BG			.22	.36	.34	.21	.43	.52
SG				.05	0	.19	.22	.26
YG					.13	.14	.52	.27
GT						.05	.1	.06
ST							.35	.08
CT								.25
LT								
			Schoener's algorithms, 10 resources					
MG		.35	.07	.14	.85	.12	.14	.05
BG			.47	.48	.38	.21	.47	.53
SG				.53	.04	.24	.49	.53
YG					.13	.36	.75	.3
GT						.09	.14	.07
ST							.42	.09
CT								.25
LT								

Pianka's algorithms, 23 resources

	MG	BG	SG	YG	GT	ST	CT	LT
MG		.55	.0	.03	.99	.02	.03	.02
BG			.09	.2	.59	.08	.31	.57
SG				.02		.16	.25	.1:
YG					.02	.02	.48	.18
GT							.02	.04
ST							.29	.02
CT								.24
LT								

Pianka's algorithms, 16 resources

	MG	BG	SG	YG	GT	ST	CT	LT
MG		.6	.0	.07	.99	.06	.07	.02
BG			.44	.18	.63	.23	.41	.6
SG				.06	.0	.14	.35	.46
YG					.02	.12	.75	.2
GT						.0	02	.03
ST							.43	.03
CT								.25
LT								

Pianka's algorithms, 10 resources

	MG	BG	SG	YG	GT	ST	CT	LT
MG		.45	.05	.08	.99	.08	.08	.02
BG			.74	.45	.49	.21	.5	.85
SG				.76	.04	.18	.69	.78
YG					.03	.39	.92	.36
GT						.0	.03	.05
ST							.5	.06
CT								.35
LT								

Hurlbert's algorithms, 23 resources

	MG	BG	SG	YG	GT	ST	CT	LT
MG		1.35	.26	3.44	1.8	0.35	1.23	0.36
BG			1.41	4.83	2.42	1.62	4.7	6.77
SG				0.26	0	4.63	3.5	0.85
YG					1.13	0.91	7.15	2.44
GT						0.16	0.7	1.12
ST							3.09	0.3
CT								2.64
LT								

Hurlbert's algorithms, 16 resources

	MG	BG	SG	YG	GT	ST	CT	LT
MG		0.64	0.24	1.18	1.58	0.36	0.62	0.31
BG			1.18	3.61	2.52	2.01	5.78	3.98
SG				0.27	0	3.65	3.06	1.86
YG					1.79	1.4	6.55	6.66
GT						0.74	1.15	0.82
ST							2.54	0.54
CT								3.1
LT								

Hurlbert's algorithms, 10 resources

	MG	BG	SG	YG	GT	ST	CT	LT
MG		0.55	0.43	0.77	1.55	0.43	0.58	0.24
BG			1.51	2.48	1.48	1.07	5.35	2.4
SG				4.12	0.9	1.4	3.03	2.48
YG					0.99	2.94	5.9	1.58
GT						0.32	1.02	0.33
ST							2.39	0.35
CT								1.66
LT								