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Mono-dimensional and multi-dimensional niches in a Mediterranean seabirds community

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Abstract - The overlaps in the food and in the habitat niche components, between 8 species of sympatrically breeding gulls and terns, were inversely correlated. The indexes of the multidimensional (food and habitat) niche were compared with the estimates generated by summation (Σ) and by product (π) of the monodimensional parameters. Although the results may not be applied quantitatively to other cases, they show that monodimensional approaches only describe the selection of single resources by the consumers, without in any way offering inference about the absolute amount of complete ecological overlap. Overlap values between species, obtained by the Σ and the π methods, are subject to very large errors; contrary to previous suggestions, the π method approximates the complete niche better than does the Σ method, even when the use of differing resources is dependent. Both Σ and π methods in most cases estimated correctly the rank, but not the absolute value, of niche breadth. The rank of complete overlap between species was correctly estimated only when the average overlap of one species with all the other species in the community was considered.

Key words: community, competition, food, Laridae, habitat, niche.

The ecological niche is envisaged as multidimensional in theory (Hutchinson 1957, Vandermeer 1972, Pianka 1976, Blondel & Bourlière 1979), but in the practice of field research only a single niche dimension is usually measured. In some studies this niche component is foraging habitat (e. g. Saether 1982, Jenssen et al. 1984), in others it is food type (Wiens & Rotenberry 1979, Griffiths 1986), or activity time (Ortega et al. 1986). In other studies the authors described both habitat and food, but they treated each component separately (Rosenberg et al. 1982, Mittelbach 1984, Glanz 1984, Fasola 1986, Harris 1986, Griffiths & Mylotte 1987, and studies reviewed by Toft, 1985 and by Ross, 1986).

What we consider the "complete" multidimensional niche includes major "components", each of which consists of one or more "dimensions". For instance, the complete "trophic" niche of a given species is made up by a "food" component that is related to the types of food taken, by a "temporal" component that accounts for the rhythm of the trophic activities, and by a "habitat" component that is related to the habitats utilized. This last component may include several spatial dimensions, horizontal, vertical or vegetational. The gradient along each dimension may be subdivided into discrete "resource states" (e.g. prey types or vagetational layers).

The unidimensional approach in many niche studies is justified by the actual difficulty of measuring simultaneously the use of different resources in nature. However, monodimensional studies do not measure ecological segregation: species are segregated from each other in their complete niche space, but they may overlap considerably along a given dimension, as shown by Cody (1974), May (1975), Pianka (1976) and by others.

Few studies have endeavoured to describe complete multidimensional niches in animal species. Alatalo & Alatalo (1979) and Alatalo (1982) studied various dimensions of foraging niches for passerine birds, but they did not consider possible segregation along other components. Crowley and Johnson (1982) analized the two-dimensional niches of an Odonate community; Hulsman (1987) studied the contribution of body size, foraging zones, and prey type to the niche segregation of terns. Other authors investigated both food and habitat components; the multidimensional overlap was estimated by the product π (Gladfelter & Johnson 1983), by the summation Σ of monodimensional overlaps (Meserve 1981, Reynolds & Meslow 1984, Monda & Ratti 1988), or by both methods (Brown 1982). The choice of method was suggested by (undemonstrated) assumptions about whether resource dimesions are independent (in which case the π method would be appropriate) or dependent of each other. May (1975) made it clear that overlap in the complete niche of two species cannot be inferred by the Σ or by the π methods applied to the utilization functions of each niche dimension; however, his warnings have often been overlooked, and the subject still awaits tests that are based on field data. To our knowledge, Hanski's (1978) study is the only one that compares the estimates obtained by the π and the Σ methods with a direct measure of the complete overlap; however, its results are probably influenced by the peculiarity that resource dimensions were completely independent of each other.

The goal of this paper is to discuss the problems of multidimensionality in niche studies; a multidimensional calculation of the complete trophic niches in a community of breeding seabirds is compared with estimates derived from a combination of monodimensional niches. The problems related to the categorization of resource states and the comparability of the different indexes in niche studies, are discussed in a companion paper (Saino e Fasola 1990).

MATERIAL

A detailed account of the trophic ecology of these seabirds is presented elsewhere (Fasola et al., 1988). The study area (560 km ^{2}) included a lagoon (the "Valli di Comacchio", near the Adriatic Sea, North-Western Italy), and all the main foraging zones (categories listed in Tab. II) used by the seabirds that bred in the lagoon: Mediterranean Gull *Larus melanocephalus* , the Black-headed Gull *Larus ridibundus*, the Slender-billed Gull *Larus genei*, the Yellow-legged Gull *Larus cachinnans*, the Gull-billed Tern *Gelochelidon nilotica*, the Sandwich Tern *Sterna sandvicensis*, the Common Tern *Sterna hirundo* and the Little Tern *Sterna albifrons*. Data were collected from 9 to 24 June 1983 and from 19 May to 11 June 1984, on the three relevant components of the trophic niche (food, foraging habitat, diel activity) of the breeding seabirds.

The distribution of foraging gulls and terns (results summarized in Tab. I) was recorded throughout the study area. Seabirds were counted within zones with homogeneous habitat; the average density of each species in each habitat was calculated, and these densities were extrapolated to the total surfaces of all the study area (measured on 1:10,000 scale maps), in order to estimate the total number of foraging birds. Only adult gulls, which were feeding actively during the counts, were considered; immature gulls, and adults resting in groups far from the colonies (all of which were presumably non-breeders) were excluded.

The food of the chicks (Tab. II) was recorded for each species by direct observation of prey carried in the bill of adult terns or regurgitated by adult gulls; by the collection of the spontaneous regurgitations of handled chicks; by the collection of food samples from chicks that were fitted with collars. Prey items were identified as precisely as possible; size was measured or was estimated by comparison with the bill of the adult bird. The weight of each food category was estimated from equations relating the length to the weight of Adriatic fish, or from the weight of invertebrates and of terrestrial vertebrates captured in the study area. Direct observations of the feeding success and of prey type were performed on the foraging adult seabirds.

NICHE METRICS

Breadth in the use of resources was estimated by the index $B = 1 / R \sum p_i^2$ (Levins, 1968), where p is the proportion of resource i (out of all those used by the population), and R is the number of available resources. Resource overlap was estimated by the Proportional Similarity Index: $O = 1 - 0.5 \sum |p_{xi} - p_{yi}|$ (Schoener 1970) where p are proportions of resource i that are respectively used by the two consumers x and y.

The complete trophic niche was calculated from the food and the habitat components. The data on feeding activity, obtained by direct observation of the adults, were insuffícent to implement the food-habitat matrix (160 resource states, deriving from 10 prey types and 16 habitats) that was needed to calculate complete trophic niche. We adopted the alternative of estimating this matrix from its two dimensions, total number of birds in each habitat and proportion of each prey type in the diet, supplemented by 1) information about the habitats where each prey was available (personal observations on the feeding seabirds, and Callegarini et al. 1983): certain prey types were restricted to one habitat (e.g. terrestrial vertebrates and arthropods exclusively taken on cultivated land), fish species were placed into categories (open sea, coast, lagoons, canals, freshwater) that could be confidently assigned to the appropriate habitat, and special cases were considered (e.g. eels that were captured only in fish ponds); 2) the assumption that those prey that were available in more than one habitat were captured in each habitat in amounts proportional to the number of birds foraging there. In practice, for each species of seabird we first defined prey-habitat availability, and then for each bird species we assigned its prey to the habitat where it was available; prey that was present in more than one habitat was subdivided in proportion to the number of birds that foraged in each habitat. Albeit indirect, this estimate of the food and habitat matrix provides a realistic description of the bidimensional resource utilization by the seabirds.

MONODIMENSIONAL NICHES

Food niche

Food niche overlap identified a guild of strictly piscivorous species (the 5 species on the left of Fig. 1 A) whose overlap exceeds 0.5. The remaining species differed considerably (overlap < 0.3); the Gull-billed Tern specialized in terrestrial vertebrates; the Little Tern on small fish (length < 6 cm); the Slender-billed Gull fed on small and medium fish. The high segregation of the Slender-billed Gull may be partially due to the incompleteness of our data (see sample-size in Tab. II), and its diet was certainly broader than the diet recorded.

Habitat niche

Habitat overlap (Fig. 1 B) identified three species-pairs with overlaps that exceed 0.5: the Mediterranean Gull and the Gull-billed Tern foraged mainly on land; the Black-headed Gull and the Little Tern foraged mainly in the lagoons; the Yellow-legged Gull and the Common Tern primarily at sea around fishing boats, and secondarily in many of the other habitats (Tab. I).

MULTIDIMENSIONAL TROPHIC NICHE

The eight seabirds differed more evenly in their complete niches (Fig. 1 C) than when their segregation was judged from the monodimensional niches (Fig. 1 A, B). Some species-pairs seem to overlap considerably when we only consider their food (Mediterranean and Yellow-legged Gulls, Black-headed Gulls and Sandwich Terns, Fig. 1 A), or their foraging habitat (Black-headed Gulls and Little Terns, Yellow-legged Gulls and Common Terns, Mediterranean Gulls and Gull-billed Terns, Fig.

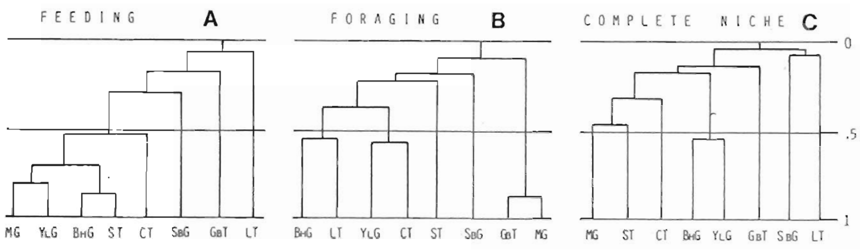

FIGURE 1. Dendrograms of overlap in food (a), habitat (b), and complete trophic niche (c) of the 8 seabirds. MG = Mediterranean Gull, BhG = Black-headed Gull, SbG = Slender-billed Gull, YlG = Yellow-legged Gull, GbT = Gull-billed Tern, ST = Sandwich Tern, CT = Common Tern, LT = Little Tern.

TABLE I. Habitat distribution of the 8 species of seabirds during foraging. The figures are percentages of the average total number of birds of each species, that were estimated to be foraging in the entire study area.

	Mediterranean Gull	Black-headed Gull	Slender-billed Gull	Yellow-legged Gull	Gull-billed Tern	Sandwich Tern	Common Tern	Little Tern
Sea coast	1	6	42	1	0	18	14	2
Open sea	5	6	0	5	0	71	13	0
Fishing boats	5	0.5	0	56	0	1	26	0
Docks	0.03	0.3	0	2	0	0	0.3	0
Large lagoons, open waters	0	16	42	4	0	0	7	23
Large lagoons, among islets	0	0	0	6	0	0	2	18
Small lagoons, Brackish	0	10	0	1	0	5	3	10
Small lagoons, Freshwater	1	15	0	9	4	0	3	19
Ponds, brackish	2	5	0	4	0	0	3	22
Ponds, freshwater	0	2	0	2	5	0	4	0
Canals, brackish	0	8	0	1	0	0	18	1
Canals, freshwater	1	9	0	8	7	5	3	1
River	0	0.5	0	0.2	0	0	3	1
Saltpans	0	0.3	16	0	0	0	0.1	1
Fishponds	0	0.8	0	2	0	0	0.2	0.3
Cultivated lands	86	21	0	0	83	0	0	0

1 B), but their complete niches reveal wide segregation. The food and the habitat overlaps of the seabirds were inversely correlated (Fasola et al. 1988). In other words two species that overlapped broadly in one component were widely segregated in the other component; this inverse correlation resulted in low overlap values of their complete niche.

TABLE II. Food brought to the chicks by the 8 species of seabirds. The figures are percentages of each prey type (dry weight) in the diet of the species.

	Mediterranean Gull	Black-headed Gull	Slender-billed Gull	Yellow-legged Gull	Gull-billed	Sandwich Tern	Common Tern	Little Tern
Fish < 3cm	0	0	33	0	0	0.02	0	12
Fish 3-6cm	2	6	0	0	3	3	8	81
Fish 6-9cm	5	11	67	1	13	16	50	1
Fish 9-15cm	58	74	0	56	8	67	41	0
Fish 15-25cm	24	7	0	43	0	15	0	0
Brackish-water crustaceans	0	0.2	0	0	0	0	1	6
Freshwater anellids	2	2	0	0	0	0	0	0
Terrestrial arthropods	9	0.06	0	0	6	0	0	0
Lizards, frogs, small mammals, birds	0.2	0	0	0	71	0	0	0
Total number of prey items	6378	722	14	76	385	371	347	1116

MULTI- VS. MONO- DIMENSIONAL ESTIMATES OF THE COMPLETE NICHE

May (1975) suggested that the complete niche cannot be inferred simply from monodimensional components. In the special case when the utilization functions along differing resource dimensions are fully independent of each other, complete overlap could be approximated by multiplying the monodimensional overlaps (product a); when two resources are completely dependent the complete overlap of two species in some cases could be approximated by averaging their monodimensional overlaps (summation a). In most cases, however, the dimensions will not be completely dependent or independent, and there is no way to calculate complete overlap from monodimensional overlaps; summation a is believed to constitute an upper bound on true overlap.

In order to test the above predictions, we compared the complete multidimensional niche of the 8 seabirds with the estimates generated by summation (Σ) and product (π) of the parameters of their monodimensional food and habitat niches (Fig. 2). The technique proposed by Slobodchikoff & Schulz (1980) to test the degree of dependence of two resources was applied to our data and indicated a high dependence between food and habitat resources.

The breadth of the complete niche was largely overestimated by the Σ method, whereas it was closely approximated by the π method (Fig. 2 A, B). The ranks of breadth of the multidimensional niche and of both the Σ and the π methods coincided in 6 species out of 8. Hanski (1978), who studied the temporal and spatial niches of dung-inhabiting beetles, obtained the opposite result in that the Σ method approximated complete breadth better than did the π method.

Complete niche overlap was influenced by monodimensional food overlap (Fig. 2 C), while it was not related to the monodimensional habitat overlap (Fig. 2 D). This

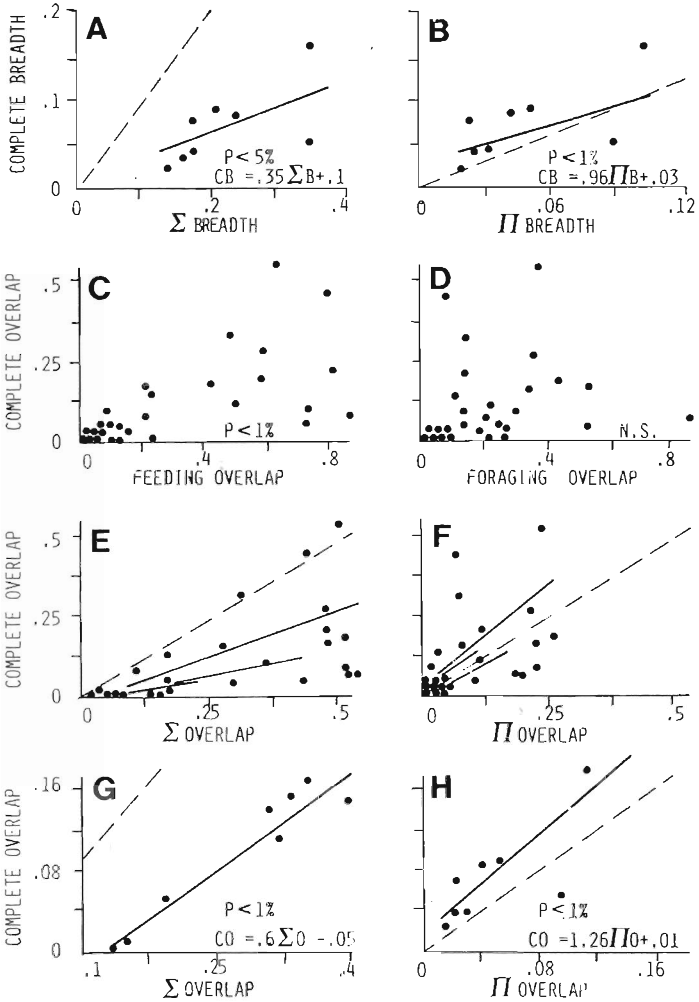

FIGURE 2. Relationships between the parameters of complete trophic niche, and: A) the summation (Σ) of monodimensional breadths; B) the product (π) of breadths; C) monodimensional food niche, each species with another; D) monodimensional habitat niche, each species with another; E) the summation of monodimensional overlaps, each species with another (the 3 lines show the regressions for the Slender-billed Gulls, the Yellow-legged Gulls and the Little Terns, the only species whose correlations were significant, and whose overlaps are not shown as points). F) the product of overlaps, each species with another, and regression lines for the same 3 species as in the previous figure; G) the summation of overlaps, species to community (average overlap of each species with the other 7); H) the product of overlaps, species to community. The significance of each correlation (tested by Pearsons'r) is indicated, N.S. = non significant. Least-squares regressions (thick lines, and their respective equations) are shown for the variables that are significantly related. Segmented lines mark equal-values diagonals.

was because the species that foraged in the same habitat (e.g. Gull-billed Terns and Mediterranean Gulls) often captured completely different prey (lizards and arthropods, respectively).

When the overlaps of each species with the others are compared, the Σ method overestimated complete overlap (Fig. 2 E), while the π method achieved very rough approximation (Fig. 2 F). However, both for the Σ and the π methods, in only 3 species (Slender-billed Gull, Yellow-legged Gull, Little Tern) out of 8 was the correlation complete - estimated overlap was significant (regression lines in Fig. 2 E, F). Neither method can be confidently adopted to assess complete overlap, or even its order of magnitude. Complete overlap was lower than π overlap in 10 cases; intermediate between π and Σ overlaps in 15 cases; slightly higher than Σ overlap in 3 cases. These latter cases show that it is the overlap in one of the dimensions that constitutes the upper bound to multidimensional overlap, and not the average (Σ) overlap, as asserted by May (1975).

Although in Hanski's (1978) study niche dimensions were independent (Hanski and Koskela 1977), whereas in our study they were dependent, the π method better approximated complete niche in both studies. This agreement is contrary to the suggestion (Cody 1974, Slobodchikoff & Schulz 1980) that the Σ method is preferable when resource dimensions are "dependent". The Σ method will approximate complete overlap, when resources are dependent, only in particular cases; in other cases (e. g. the example given by May, 1975), complete overlap is zero. In nature, resource utilizations will most frequently be intermediate between these two extreme utilizations, and complete overlap will be less than Σ overlap, as witnessed in this community of seabirds.

When the average overlaps of each species with the other 7 species of the community were compared, the correlations between complete overlaps and the estimates by the Σ and π were methods highly significant (Fig. 3 G, H). As for niche breadth, the ranks of the overlap of complete niche and from both the Σ and the π methods, coincided in 6 species out of 8; the method approximated the absolute values of complete niche better than did the Σ method. Averaging the overlaps of one species with the others seems to smooth the random variations that disturb the correlation of the overlaps of one species with each of the others (Fig. 3 E, F).

CONCLUSIONS

Neither the relations found in our study, nor those found by Hanski (1978) could be applied quantitatively to other communities. The general conclusions are that monodimensional approaches only describe the selection of single resources by the consumers, but in no way can they give inferences about ecological overlap. Estimates of the overlap between two species by the Σ or the π methods (as undertaken by Meserve 1981, Brown 1982, Gladfelter & Johnson 1983, Reynolds & Meslow 1984, Monda & Ratti 1988) are subject to very large errors, and to know whether the resources are dependent or independent does not enable one to select the appropriate method. Both the Σ and the π methods in most cases seem to estimate the rank of niche breadth of the species; the rank of their complete overlap may be estimated only when the average overlap of one species with the other species in the community is considered. The absolute values of overlap cannot be estimated from monodimensional overlap, yet the π method should approximate the complete niche better than does the Σ method, both when resoure use is dependent and when it is independent. Multidimensional studies that include the relevant niche components are needed, because they are the only approach to describe the overlap in resource use within communities.

Niche studies face many other methodological problems (catagorization of the resources, comparability among indexes), that are discussed in our next paper (Saino e Fasola 1990).

RIASSUNTO

Nicchie monodimensionali e multidimensionali in una comunità di uccelli marini mediterranei

- Abbiamo analizzato le relazioni tra le componenti monodimensionali (cibo e habitat) e la nicchia bidimensionale complessiva, in 8 specie di gabbiani e sterne nidificanti sintopiche nelle Valli di Comacchio.
- La sovrapposizione tra cibo e habitat erano inversamente correlate.
- Gli indici di ampiezza e di sovrapposizione bidimensionale sono stati paragonati con le stime generate dal metodo del prodotto e della somma dei parametri monodimensionali. I risultati sono solo esemplificativi, e non possono essere estesi quantitativamente ad altri casi; essi mostrano che gli approcci monodimensionali della nicchia descrivono soltanto l'utilizzo di una risorsa da parte di un consumatore, ma non permettono di concludere nulla riguardo alla sovrapposizione ecologica complesssiva tra specie. I valori di sovrapposizione tra specie, ottenuti con il metodo del prodotto e della somma sono soggetti ad errori ampi; il metodo del prodotto si avvicina alla sovrapposizione bidimensionale più del metodo della somma, anche nel caso in cui due risorse sono consumate in modo dipendente l'una dall'altra.
- Sia il metodo del prodotto che quello della somma riescono a stimare correttamente il rango, ma non il valore assoluto dell'ampiezza di nicchia; la sovrapposizione bidimensionale è stimata correttamente solo come rango e solo considerando la sovrapposizione media di una spesie con il resto della comunità.

FIG. 1. Dendrogrammi della sovrapposizione nel cibo (A), nell'habitat (B) e nella nicchia trofica complessiva (C) delle 8 specie. MG = Gabbiano corallino, BhG = Gabbiano comune, SbG = Gabbiano roseo, YlG = Gabbiano reale GbT = Sterna zampenere, ST = Beccapesci, CT = Sterna comune, LT = Fraticello.

FIG. 2. Relazioni tra alcuni parametri della nicchia trofica complessiva e A) la somma (Σ) delle ampiezze monodimensionali; B) il prodotto (π) delle ampiezze; C) la nicchia monodimensionale del cibo, ciascuna specie confrontata con un'altra; D) la nicchia monodimensionale dell'habitat, ciascuna specie confrontata con un'altra; E) la somma delle sovrapposizioni monodimensionali, ciascuna specie con un'altra (le tre linee mostrano le regressioni per Gabbiano roseo, Gabbiano reale e Fraticello, le sole specie per le quali le correlazioni sono significative, e per le quali le sovrapposizioni non sono raffigurate come punti); F) il prodotto delle sovrapposizioni, ciascuna specie con un'altra, e le 3 rette di regressione per le stesse specie della figura precedente; G) la somma delle sovrapposizioni tra ciascuna specie e la comunità (sovrapposizione media di ciscuna specie con le altre 7); H) il prodotto delle sovrapposizioni tra ciascuna specie e la comunità. E'indicata la significatività di ciascuna correlazione , N.S. = non significativo. Le rette di regressione (linee spesse) e le rispettive equazioni sono mostrate per le variabili significativamente correlate. Le linee tratteggiate indicano le diagonali con valori uguali su entrambi gli assi.

TAB. I. Distribuzione in diversi ambienti delle 8 specie durante l'alimentazione. Sono indicate le percentuali nel numero totale di uccelli di ciascuna specie, per l'intera area di studio.

TAB. II. Cibo portato ai pulcini dagli adulti delle 8 specie. Sono indicate le percentuali in peso secco di ogni tipo di prede.

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