

USE OF OVERLAP INDICES AS COMPETITION COEFFICIENTS: TESTS WITH FIELD DATA

JON LOMAN

Department of Animal Ecology, University of Lund, S-223 62 Lund (Sweden)

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ABSTRACT

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The possibility of using overlap indices as competition coefficients was investigated by applying this substitution to field data on the food of a predator community.

(1) The maximum value of the carrying capacity for each predator was estimated and compared to the carrying capacity predicted from the Lotka–Volterra competition equations with overlap indices used as competition coefficients. Carrying capacities were sometimes larger when computed with the latter method. The contradiction was not resolved with the use of more complex overlap indices leading to the conclusion that overlap indices have limited use as competition coefficients if a realistic description of the dynamics of populations is required.

(2) The outcome of pairwise competition between all combinations of predators is considered. If overlap indices are used as competition coefficients, the theory of competitive exclusion tends to predict that foxes, stoats, and long-eared owls should be excluded rather than they should exclude other predators. The opposite applies to cats and buzzards. Both these results are apparently contradictions as all species were permanent members of the community studied. The pattern, however, can be explained if it is assumed that the carrying capacity of the first group has been underestimated and/or that of the second group overestimated. This could well be the case if the first group has 'food refugia' and the second is not able to fully exploit its prey populations. This is only a hypothesis suggested by the observed patterns. Even if they are not numerically equivalent to competition coefficients, overlap indices can thus be of use as a tool for hypothesis generation.

INTRODUCTION

A popular tool for analysis of ecological communities is overlap indices. These measure the similarity of two species use of resources. Such indices are undoubtedly useful as numerical representations of important properties of coexisting species (Pianka, 1973). One possible use of overlap indices is as substitutes for competition coefficients. Methods of computing overlap

indices that explicitly should make them useful as competition coefficients have been suggested by MacArthur (1972) and Schoener (1974).

Intuitively, there should be some correlation between overlap indices and competition coefficients. Measured overlap indices have been used to propose that competition for the measured resource affects the population dynamics of the species involved (Högstedt, 1980; Rusterholz, 1981). However, the substitution has often been questioned (Hespenheide, 1973; Heck, 1976; Maurer, 1983 and others). If the substitution is to be valid, then the overlap must be measured for a limiting resource (Abrams, 1980). Even after correctly identifying the limiting resource in general terms, e.g. food, it may be questioned which measure is most relevant to use, e.g. units of prey weight or prey individuals. It may also be necessary to take into account resource availability or renewability. These complications may be considered part of the concept of *limiting*. It has repeatedly been stressed that high overlap may not be indicative of competition, rather the reverse, because species may have evolved to tolerate overlap without competing (Lawlor, 1980), which may simply mean that the considered resource is no longer limiting. This may well be due previous competition for this resource. Also, if competition coefficients are to be of any use, the equations describing the dynamics of the species must be at least approximately realistic models.

To summarize, if overlap indices are used as competition indices and this produces erroneous results, it may be because (1) the whole approach is fruitless — overlap is not a measure of competition, (2) overlap has not been measured for a limiting resource, (3) the relevant properties of the resource have not been considered when computing the overlap value, or (4) the model used to describe the dynamics of the population is not realistic.

True demonstration of competition requires large perturbation experiments (MacNally, 1983). However, obtaining measurements of research overlap in field populations is much easier than carrying out experiments, usually an impossible task. This makes it important to test the interchangeability of the concepts. Despite the difficulties hinted at above, field data will, in this paper, be used to study the possibility of such a substitution.

Data from field populations can however only be approximations of parameters in formulae from idealized models. Below it is shown how I have attempted to use data from a field study to estimate these parameters. Uncertainty remains but can be considered consistent with the scope of the study. This scope is to provide a case study of the possibility of using overlap indices as competition coefficients in the study of real populations. The uncertainty involved in measuring the parameter values are a real part of the problem, the importance of which is to be evaluated.

The paper has two parts. First, 18 different methods of computing overlap indices are tested. Predictions of carrying capacity made by using these

NOMENCLATURE

A_i	Number of prey specimens consumed by predator i per unit time
a_{ij}	Index of resource overlap between species i and j
b_{ik}	Value (e.g. weight or caloric content) of an individual or unit of prey kind k for predator i
f_k	Relative abundance of prey individuals of kind k in the environment
g_k	Relative weight abundance of prey kind k in the environment.
K_i	Carrying capacity of the environment for predator i
N_i	Number of individuals of predator i
\bar{N}_i	Number of individuals of predator i in a stable community
n	Number of competing predators
p_{ik}	Proportion, by individuals, of prey kind k in the diet of predator i
q_{ik}	Proportion, by weight, of prey kind k in the diet of predator i
r_i	Maximum rate of increase for predator i (at low density of this population and of its competitors) in the considered environment
V_i	Weight of prey consumed by predator i per unit time
α_{ij}	Coefficient of competition (impact of species j on species i)

indices as competition coefficients are compared with an independent estimate of carrying capacity (see below). Contradictions observed are considered evidence of unsuitability of the substitution. In the second part of the paper no attempt is made to separate the usefulness of different indices. It is assumed that there is a correlation but not necessarily a numerical correspondence, between overlap indices and competition coefficients and this is used for a biologically meaningful analysis.

METHODS

Population dynamics

Competition coefficients are components in equations that represent the dynamics of populations. These can take the form of differential equations. In this study I chose to test the use of overlap indices as substitutes for competition coefficients in one particular differential equation system, viz. the Lotka–Volterra competition equations. This is one of the most commonly used and simple ones. It is given by the following equation:

$$\frac{dN_i}{dt} \frac{1}{N_i} = r_i \left(1 - \frac{\sum \alpha_{ij} N_j}{K_i} \right); \quad j = 1, 2, 3, \dots, n \quad \alpha_{ii} = 1.0 \quad (1)$$

The competition coefficients (the α -values) thus give the effect on population growth from an individual of another species (j) compared to the

effect from an individual of the same species (i), the species of the affected population.

Overlap indices

Three commonly used measures of overlap are:

$$a_1 = \sum_k \min(q_{ik}, q_{jk}) \quad (2a)$$

which is equivalent to

$$a_1 = 1 - 0.5 \left(\sum_k |q_{ik} - q_{jk}| \right) \quad (2b)$$

$$a_2 = \sum_k q_{ik}q_{jk} / \sum_k q_{ik}^2 \quad (3)$$

$$a_3 = \sum_k q_{ik}q_{jk} / \sqrt{\sum_k q_{ik}^2 q_{jk}^2} \quad (4)$$

The first of these was originally suggested by Renkonen (1938) and has later been used by others (e.g. Schoener, 1970). It has the advantage of being very easy to compute. The second was suggested by MacArthur and Levins (1967) and the third is a symmetric version of this that is due to Pianka (1973) These measurements could possibly be made more useful as competition coefficients by adding a correction for the relative food intake of the competing species; equations (5), (6), and (7) do this for a_1 , a_2 , and a_3 :

$$a_4 = A_j a_1 / A_i \quad (5)$$

$$a_5 = A_j a_2 / A_i \quad (6)$$

$$a_6 = A_j a_3 / A_i \quad (7)$$

The six indices can alternatively be computed for relative weight intake (instead of relative number of individuals of different prey kinds). Doing this gives a_7 to a_{12} . When correcting for relative food intake ($a_{10} - a_{12}$), W is used instead of A (which was used when computing $a_4 - a_6$). An overlap index that was intended explicitly to measure competition has been suggested by MacArthur (1972) and reformulated by Schoener (1974):

$$a = \frac{A_j \sum_k \left((p_{ik} p_{jk} / f_k^2) (b_{ik} K_k / r_k) \right)}{A_i \sum_k \left((p_{ik}^2 / f_k^2) (b_{ik} K_k / r_k) \right)} \quad (8)$$

However, this includes the prey parameters r and K which are difficult to measure, especially the K 's. Following Schoener's suggestion (I) cancel

these: if this is acceptable it considerably increases the practical utility of the formula:

$$a_{13} = \frac{A_j \sum_k (p_{ik} p_{jk} b_{ik} / f_k^2)}{A_i \sum_k (p_{ik}^2 b_{ik} / f_k^2)} \quad (9)$$

A further simplification of this measure is obtained by assuming that the densities of the available resource types are equal. This is done because resource densities are usually unknown. The simplification is:

$$a_{14} = \frac{A_j \sum_k (p_{ik} p_{jk} b_{ik})}{A_i \sum_k (p_{ik}^2 b_{ik})} \quad (10)$$

If weight ingested of different resource types rather than numbers ingested is considered, a_{13} is replaced by:

$$a_{15} = \frac{V_j \sum_k (q_{ik} q_{jk} / g_k^2)}{V_i \sum_k (q_{ik}^2 / f_k)} \quad (11)$$

a_{14} is correspondingly replaced by a_{11} (see above). Another measure of overlap has been suggested by Hurlbert (1978):

$$a_{16} = \frac{\sum_k (p_{ik} p_{jk} / f_k)}{\sum_k (p_{ik}^2 / f_k)} \quad (12)$$

If this is modified by introducing a correction for the relative food intake of the two predators and a correction for the abundance of the different resource types we obtain:

$$a_{17} = \frac{A_j \sum_k (p_{ik} p_{jk} b_k / f_k)}{A_i \sum_k (p_{ik}^2 b_k / f_k)} \quad (13)$$

Basing the measure on relative resource weight rather than individuals gives

$$a_{18} = \frac{V_j \sum_k (q_{ik} q_{jk} / g_k)}{V_i \sum_k (q_{ik}^2 / g_k)} \quad (14)$$

Carrying capacities

The carrying capacities for different predator populations cannot usually be measured directly. Removing all species but one and observing the new equilibrium density could give an estimate. This is quite difficult to do and involves the same kind of manipulations as a direct measure of competition coefficients. For the purpose of this study an estimate is made of the maximum level of the carrying capacity for each predator species in the study area.

The estimate is based on the following assumptions. In a non-competitive situation it is unlikely that any predator population could consume more of one resource than the entire guild does in the competitive situation (which is the one we measure). In fact, it is likely that the non-competitive consumption by one species is less because a multispecies community will probably be able to utilize the available resources more efficiently. Two alternative restrictions will be made in order to partially mimic this effect. The first and most obvious is that prey types not utilized by a predator population in the competitive situation are not assumed to be utilized in the non-competitive situation either. For example, cats are not supposed to eat frogs even if they are the sole predators in the area. This gives a 'maximum' estimate of the carrying capacity. If certain prey types are utilized only occasionally, this may be because the predator is competitively excluded from taking more. However it is more likely that the considered resource, for reasons unrelated to competition, is normally not available to the predator. This consideration leads to a more realistic 'minimum' estimate made by assuming that only prey types that make up more than 5% of the predator's diet (by weight) in the competitive situation are further utilized in the non-competitive one. Table 1 gives an example of the estimation procedure.

Limiting season

One possible cause for contradictory results is, as stated in the introduction, that the limiting resource has not been measured. Even if this is food, as assumed in the present study, it is quite possible that food is limiting only during part of the year. To try to eliminate this variable, all computations were made for data from two seasons that I considered possibly limiting, winter (October–March) and the breeding season (April–June). Computations were also made from feeding data from the whole year as it is possible that compensating mechanisms make this the most relevant measure. Only conclusions (contradictions, see below) reached for all three periods were considered valid.

TABLE 1

An imaginary example demonstrating the method to compute estimated maximum carrying capacities from population densities and food spectra

	Prey 1	Prey 2	Prey 3	Prey 4	Total
<i>Competitive situation</i> (the measured data)					
Predator population A	150 kg (75%)	45 kg (22.5%)	5 kg (2.5%)	0 kg (0%)	200 kg
Predator population B	800 kg (40%)	400 kg (20%)	400 kg (20%)	400 kg (20%)	2000 kg
<i>Non-competitive situation</i> (the estimated food spectra)					
'Conservative estimate'					
Predator population A	950 kg	445 kg	405 kg	0 kg	1800 kg
Predator population B	950 kg	445 kg	405 kg	400 kg	2200 kg
'Realistic estimate'					
Predator population A	950 kg	445 kg	5 kg	0 kg	1400 kg
Predator population B	950 kg	445 kg	405 kg	400 kg	2200 kg
				Predator A	Predator B
<i>Measured population sizes in the competitive situation (\hat{N}):</i>					
		50 ind.		20 ind.	
Carrying capacities (estimated non-competitive population sizes)					
'Conservative estimate'		$50 \times 1800 / 200 = 450$		$20 \times 2200 / 2000 = 22$	
'Realistic estimate'		$50 \times 1400 / 200 = 350$		$20 \times 2200 / 2000 = 22$	

The upper part of the table give the total consumption by two predator populations of five different prey types. In the lower part of the table the food spectrum data are used to compute carrying capacities according to two methods.

Population densities

The \hat{N}_j -values (equation 15) represent populations in equilibrium. It is difficult to assess if this is the case for the studied populations. However, Levins (1979) has shown that if N (as a function of time) is a bounded function in some domain, then the average change in population density is zero. The condition can be considered fulfilled for populations that are permanent members of a community. This is the case with the populations used in this study. It is, therefore, assumed that the measured densities, which represent mean values for the 4 years 1975-1978, are estimates of the populations' equilibrium densities.

Data sources

Studies of predators and their prey in an area in southern Sweden (55°40'N, 13°30'E) provided data used in the analysis below (Erlinge, 1981;

Erlinge et al., 1983, Hansson, personal communication; Högstedt, personal communication; Jeppsson, personal communication; Liberg, 1981; Nilsson, 1981; von Schantz, 1981; Sylvén, 1982). Predator species studied were fox (*Vulpes vulpes*), domestic and feral cats (*Felis catus*), polecat (*Mustela putorius*), stoat (*M. erminea*), common buzzard (*Buteo buteo*), kestrel (*Falco tinnunculus*), tawny and (*Strix aluco*), and long-eared owl (*Asio otus*). The studied prey species were field hare (*Lepus europeus*), rabbit (*Oryctolagus cuniculus*), field vole (*Migrotus agrestis*), water vole (*Arvicola terrestris*), wood mouse (*Apodemus sylvaticus*), bank vole (*Clethrionomys glareolus*), common shrew (*Sorex araneus*), mole (*Talpa europea*), and frogs, mainly *Rana* spp. The information used include: (1) the food spectra, measured as percentages of different prey species by individuals or weight, (2) food intake per predator individual and day, (3) number of predator individuals (measured before breeding in the spring), and (4) number of prey individuals in the study area, measured before breeding in the spring and in the autumn. Number of bank voles and moles were only estimated but these species were of minor importance so this should not significantly influence the results. Percentages of birds and invertebrates in the food were determined for all predators but the prey species consumed could usually not be determined. However, all methods of computing overlap indices have the property that low percentages can be approximated by zero (as they appear in second-degree terms) without much effect on the final results. It was thus assumed that the categories 'birds' and 'invertebrates' were made up of several species, each in a small fraction, and these were excluded.

RESULTS AND DISCUSSION

Comparing different overlap indices

In a community of competing species in equilibrium there is no change in numbers ($dN/dt = 0$) and from equation (1) we have:

$$K_i = \sum_{j=1}^n \alpha_{ij} \hat{N}_j; \quad j = 1, 2, 3, \dots, n \quad (15)$$

Density values and food overlap indices from the studied field populations are used as the \hat{N} and α -values in this equation. This gives estimates of K_i which are compared to the 'maximum' and 'minimum' estimates of K_i computed according to the methods described in a previous section. If the K_i values computed from (15) exceed the estimated K_i -values this is considered to be a contradiction, possibly due to an illegitimate use of an overlap value (from (2) to (14)) as a competition coefficient in (15)). For all

TABLE 2
 Characteristics of the different overlap indices and the number of contradictions yielded by the analysis of each index

	a_1	a_2	a_3	a_4	a_5	a_6	a_7	a_8	a_9	a_{10}	a_{11}	a_{12}	a_{13}	a_{14}	a_{15}	a_{16}	a_{17}	a_{18}		
Characteristics of the overlap index																				
Proportions based on prey individuals	×	×	×	×	×	×							×	×		×				
As above plus information on the weight of individual prey items																				
Proportions based on prey weight				×	×	×	×	×	×	×	×	×	×	×	×					
Prey weight intake by individual predators considered				×	×	×														
The relative abundance of different prey species considered													×		×	×	×	×		
Number of contradictions yielded by the index																				
<i>Data from the whole year</i>																				
'Realistic estimate' of K	1	3	2	2	3	3	1	1	1	1	3	2	1	3	2	1	1	1	1	1
'Conservative estimate' of K	1	1	2	2	2	3	1	1	1	1	3	2	1	2	2	1	1	1	1	1
<i>Data from winter months only</i>																				
'Realistic estimate' of K	1	3	2	2	3	3	1	1	1	1	2	4	3	3	2	3	3	3	3	3
'Conservative estimate' of K	1	1	1	2	2	2	1	1	1	1	1	4	2	2	2	1	2	2	2	2
<i>Data from spring months only</i>																				
'Realistic estimate' of K	1	2	2	2	2	3	1	1	1	3	3	4	3	2	3	2	2	2	2	2
'Conservative estimate' of K	1	1	2	2	2	3	1	1	1	2	3	4	2	2	3	1	2	2	2	2

The maximum number of contradictions is eight (one per species) for data from the whole year and spring and six for data from winter (when the migrant species (kestrel and long-eared owl) were not tested).

the described methods of computing overlap indices, this comparison yields contradictions for one or more predator species (Table 2).

In a comparison of overlap indices computed according to the most simple methods, those based on relative weight intake (indices a_7 – a_9) seem to perform better than those based on relative intake of prey individuals (a_1 – a_3) (Table 2).

Intuitively, taking the relative food intake of individual predators (indices a_4 – a_6 , a_{10} – a_{12} compared to a_1 – a_3 , a_7 – a_9) and the relative density of the different prey categories (indices a_{13} , a_{15} – a_{18} compared to the rest) should considerably add to the indices' use as competition coefficients. This result was not obtained. On the contrary, using the more complex methods to compute overlap indices increased the number of contradictions. Interpreting this result is difficult. I am inclined to take a pessimistic stand and regard the test presented here as one-tailed, thus considering the more successful performance of the simple indices as a random effect. One to three errors out of eight (or six) appears to be a valid generalisation for all indices, regardless of how many aspects of the prey populations are taken into account. This suggests that the relationship between overlap and competition is too complex for an explicit or general solution. Also, the addition of further factors when computing the indices does not seem to lead us closer to the goal.

It was assumed that the factor limiting the populations in ecological time is food. Some of the studied predator species are probably socially limited to densities below the 'minimum' estimate of K (e.g. the tawny owl, I. Nilsson personal communication). This increases the number of contradictions (Table 2). This is not a theoretical critique because the use of food overlap indices clearly assumes the competing species to be food limited. It does however decrease the practical utility of overlap indices as competition coefficients further, especially if social regulation is common.

It should also be stressed that I have only tested for errors in one direction. If K -values predicted from (15) are too low this will not be detected.

A pattern revealed by contradictions

It can be shown (e.g. Roughgarden, 1979) that if two competing species obey the dynamics of equation (1), a sufficient condition for the competitive elimination of species i is:

$$\alpha_{ij} > K_i/K_j \quad (16)$$

The order of the indices is the same as in (1). All pairwise combinations of the eight studied predator species were tested for this inequality. If the inequality in (16) is found to hold, this is considered a contradiction as the

TABLE 3

Total number of comparisons for which the different species were predicted to be excluded or to exclude their competitor

	Analysis based on the whole year		Winter		Spring	
	<i>i</i> -species (excluded)	<i>j</i> -species (excludes)	<i>i</i> -species (excluded)	<i>j</i> -species (excludes)	<i>i</i> -species (excluded)	<i>j</i> -species (excludes)
Fox	69	1	69	1	88	2
Cat	3	60	13	55	13	56
Polecat	0	19	8	12	14	13
Stoat	33	21	42	28	54	25
Buzzard	6	60	34	40	1	67
Kestrel	35	16	0	83	50	22
Tawny owl	35	9	50	6	6	60
Long-eared owl	27	23	43	29	37	19

The total number of comparisons for each season and rôle (*i*-species or *j*-species) was 126.

species *i* is present in the studied system, despite competition from species *j* as well as diffuse competition from all other predators. The test is made by replacing the alfa-values with, in turn, the 18 overlap indices mentioned above. Each predator is thus part of 18×7 (= 126) tests as species *i* (the victim) and 126 tests as species *j* (the 'competitor'). The *K*-values were computed according to the 'minimum' method above. The analysis was repeated for overlap indices and *K*-values computed on the basis of data from the whole year, winter only, and spring only.

According to this analysis and regardless of season, foxes, stoats, and long-eared owls were more often predicted to be competitively excluded than to exclude the other species. The reverse was true for cats and buzzards (Table 3). The contradiction is resolved if it can be shown that the assumed *K*-values of foxes, stoats, and long-eared owls are too low and/or the *K*-values of cats and buzzards are too high. This would be the case if the former have "food refugia", i.e. part of their prey populations that are less available to their competitors. Observations of the predators in the study area give some support to such an explanation. Foxes are, apart from cats and to some extent polecats, the only predators that feed on adult rabbits. Stoats are able to exploit voles in their runways and are therefore, in winter, almost the only predators feeding on water voles. The last fact should be accounted for by the analysis but winter is the season when the pattern is least clear with respect to stoats. Long-eared owls exploit voles on open fields, away from fences, poles, and other travelling lines. Buzzards and cats, on the other hand, are rather restricted in their use of the prey populations. Buzzards hunt mainly from trees and poles. They thus exploit, at least in the

short run, only part of the prey populations. Also, cats, at least when hunting voles, stay close to fences and similar paths, only rarely hunting in dense grass. Domestic cats represent the majority of the cats in the study area and these mainly hunt in the vicinity of their homes.

The contradictions could have been resolved by computing a composite overlap index for several independent niche dimensions;

$$a_{ij} = \sqrt{a'_{ij}a''_{ij}} \quad (17)$$

a'_{ij} refers to overlap in the food niche and a''_{ij} to another niche (e.g. hunting mode or hunting time) (May, 1975). This could decrease the overlap value and thus eliminate most of the contradictions against eq (16). However, doing this would not teach us much more as the inclusion of almost any new niche could decrease the overlap indices.

CONCLUDING REMARK

This study shows that overlap indices cannot be equated with competition coefficients. The nature of the contradictions found in the last section suggests that this is because details in the biology of the different species make it difficult to calculate overlap for a relevant set of resources. It does not seem that the indices can easily be improved (in the sense of being more usable as competition coefficients) by simply including more factors that are measured on a scale common to all species (like prey weight and prey abundance).

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