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## HOW TO MEASURE ECOLOGICAL HOST SPECIFICITY

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HOST RANGE  
HOST SPECIFICITY  
PARASITES  
HERBIVORES  
SYMBIONTS  
COMMENSALS  
HOST ECOLOGY  
PARASITE ECOLOGY

**ABSTRACT.** – Rohde's original host specificity index and the modified index correcting for number of host species are discussed, using some arbitrary examples. The indices can be applied to address ecological questions involving parasites, herbivores, symbionts and commensals, where phylogenetic relationships of hosts are irrelevant.

### INTRODUCTION

Parasites do not infect all host species they utilize equitably, and this does not only apply to parasites *sensu strictu*, but also to herbivores, commensals and symbionts. For example, *Toxoplasma* infects a wide range of vertebrates, *Enterobius vermicularis* infects only humans. Fig wasps (Hymenoptera, Agaonidae) show remarkable specificity for their host plants, the common honey bee (*Apis mellifera*) pollinates a wide range of them. Rohde (1994) has discussed niche including host restriction in parasites. An important problem in parasite ecology is how to measure the degree of host restriction. It is useful to distinguish host range and host specificity and refer to the number of host species infected as the host range. In contrast, host specificity considers the abundance and/or prevalence of infection of each host species as well. The first index proposed specifically to measure host specificity of parasites is that by Rohde (1980). Later indices have attempted to incorporate phylogenetic relationships of host species (e.g., Caira *et al.* 2003, Poulin & Mouillot 2003, 2005). However, for ecological studies, they are not necessarily more useful and the phylogenetic relationships of hosts are often not important. In doubtful cases, both indices without and with correction for host phylogeny could be used. For a detailed discussion of the various indices proposed and their advantages and disadvantages see Rohde & Rohde (2005). This discussion is restricted to the measurement of ecological host specificity using Rohde's index and its modification as proposed by Rohde & Rohde (2005). The aim is to make the index better known among parasitologists, since – at present – it is mainly accessed by marine parasitologists. In order to avoid ambiguity, we also update the equations such that:

$$\frac{1}{j} \sum_j \frac{1}{j} \text{ is replaced with } \frac{1}{j} \sum_{k=1}^j \frac{1}{k}$$

### ROHDE'S ORIGINAL INDEX

Rohde's original host specificity index is defined as follows:

$$S_i = \frac{\sum_j \frac{x_{ij}}{n_{ij} h_{ij}}}{\sum_j \frac{x_{ij}}{n_{ij}}}$$

If intensity is considered, the various parameters are:

$x_{ij}$  = number of parasite individuals of *i*th species in *j*th host species,  $n_{ij}$  = number of host individuals of *j*th species examined,  $h_{ij}$  = rank of host species *j* (species with greatest intensity has rank 1),

$$\frac{x_{ij}}{n_{ij}} = \text{intensity of infection.}$$

The index can also be based on prevalence (frequency) of infection, the various parameters now are:

$x_{ij}$  = number of host individuals of *j*th species infected with parasite species *i*,  $n_{ij}$  = number of host individuals of *j*th species examined,  $h_{ij}$  = rank of host species based on prevalence of infection (species with highest prevalence has rank 1),

$$\frac{x_{ij}}{n_{ij}} = \text{mean prevalence of infection.}$$

Numerical values for the indices range from close to 0 to 1; the closer to 1, the higher the degree of host specificity.

The index can also be used for measuring preferences for microhabitats. The parameters now are:  $x_{ij}$  = number of parasite individuals of *i*th species in *j*th microhabitat,  $n_{ij}$  = number of microhabitats of type *j* examined,  $h_{ij}$  = rank of microhabitat *j*.

## THE INDEX CORRECTED FOR NUMBER OF HOST SPECIES

As pointed out by Poulin (1998), the minimum value of  $S_i$  depends on the number of host species used (Poulin 1998). For example, for 5 hosts the minimum value is greater than 0.3, for 50 hosts it is less than 0.05. Therefore, large  $S_i$  values do not necessarily indicate narrow host specificity. This problem is removed by using Rohde's modified host specificity index (Rohde K, Rohde PP 2005):

$$S_i = \frac{\frac{\sum_j \frac{x_{ij}}{n_{ij} h_{ij}}}{\sum_j \frac{x_{ij}}{n_{ij}}} - \frac{1}{j} \sum_{k=1}^j \frac{1}{k}}{1 - \frac{1}{j} \sum_{k=1}^j \frac{1}{k}}$$

where  $\frac{1}{j} \sum_{k=1}^j \frac{1}{k}$  is the minimum possible  $S_i$ ;

it is used to normalise  $S_i$ . This equation is based on the assumption that for minimum possible  $S_i$  all species have *approximately* the same value of

$$\frac{x_{ij}}{n_{ij}}$$

and maintain unique ranks. The possible ranges of all values are now equal (0 to 1), irrespective of the number of host species, with the exception of species with  $j = 1$ , in which case  $S_i = 1$ .  $j$  is the number of host species,  $n_{ij}$  is the number of host individuals of host species  $j$  examined for parasite species  $i$ ,  $k$  is a summation variable. All other symbols are as in the original index (see above).

Importantly, the modified index is not sensitive to the number of host species evaluated, i.e., it can be reliably applied even if parasite species using different numbers of host species are compared.

We give some arbitrary examples in two tables to show applications of the index. In order to make it easier to see the meaning of the  $S_i$  value at one glance, we assume that the same number of individuals of each host species (i.e., 100) has been examined for all host species. In Table I, 0-values are included in the calculations, in Table II, they are excluded. Both approaches are useful, depending on the question asked. The first approach should be used if we are interested in how parasite infections are spread over the entire community of possible hosts. The second approach should be used if we are interested in how para-

site infections are spread in the host community actually infected. The difference is made clearer by the example of parasite species 6: the normalized index has a value of 0.53 in Table I (because only 3 of the 20 host species are infected), it has a value of 0 in Table II (because the parasites are evenly spread over the few host species infected). The  $S_i$  values show that the normalized index gives far more realistic results than the original one. For example, parasite species 8 in Table I is spread evenly over all host species, and parasite species 6, 8, 9 and 10 in Table II are spread evenly over all host species infected, host specificity should therefore be 0 for all of these, which it is with the normalized but not the original index (because the lower value of  $S_i$  can never be 0 in the original index).

As pointed out in the Introduction, other indices incorporating host phylogeny are available, which may be more relevant for examining particular problems. However, often host phylogeny may not be important, and in these cases the index discussed here is sufficient. In doubtful cases both the index discussed here, as well as indices incorporating host phylogeny could be applied (Rohde & Rohde 2005). An example of the index applied to "real" data was given by Rohde & Rohde (2005).

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- The program for the index can be found at:  
<http://www-personal.une.edu.au/~krohde/files/hsi.m>

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Table I. - Host specificity indices of 12 parasite species infecting up to 20 host species, based on the number of parasites found per host species. 100 individuals of each host species were examined. Uninfected host species are included in the calculations. Both the original and the modified indices are given.

HOST SPECIES	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<b>Par. Species 1</b>																				
X	5000	500	5	4	3	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Original index	0.95																			
Normalized index	0.94																			
<b>Par. Species 2</b>																				
X	5000	500	5	4	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Original index	0.95																			
Normalized index	0.94																			
<b>Par. Species 3</b>																				
X	500	500	5	4	3	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Original index	0.73																			
Normalized index	0.68																			
<b>Par. Species 4</b>																				
X	500	500	5	4	3	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Original index	0.74																			
Normalized index	0.69																			
<b>Par. Species 5</b>																				
X	50	50	50	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Original index	0.56																			
Normalized index	0.46																			
<b>Par. Species 6</b>																				
X	50	50	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Original index	0.61																			
Normalized index	0.53																			
<b>Par. Species 7</b>																				
X	10	10	10	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Original index	0.43																			
Normalized index	0.30																			
<b>Par. Species 8</b>																				
X	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
Original index	0.18																			
Normalized index	0																			
<b>Par. Species 9</b>																				
X	5	5	5	5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Original index	0.46																			
Normalized index	0.34																			
<b>Par. Species 10</b>																				
X	5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Original index	0.75																			
Normalized index	0.70																			
<b>Par. Species 11</b>																				
X	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Original index	1																			
Normalized index	1																			
<b>Par. Species 12</b>																				
X	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Original index	1																			
Normalized index	1																			

Table II. - As in Table I, but uninfected host species not included in the calculations.

Host species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<b>Par. Species 1</b>																				
X	5000	500	5	4	3	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Original index	0.95																			
Normalized index	0.94																			
<b>Par. Species 2</b>																				
X	5000	500	5	4	3	2	1													
Original index	0.95																			
Normalized index	0.92																			
<b>Par. Species 3</b>																				
X	500	500	5	4	3	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Original index	0.73																			
Normalized index	0.68																			
<b>Par. Species 4</b>																				
X	500	500	5	4	3	2	1													
Original index	0.74																			
Normalized index	0.60																			
<b>Par. Species 5</b>																				
X	50	50	50	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Original index	0.56																			
Normalized index	0.46																			
<b>Par. Species 6</b>																				
X	50	50	50																	
Original index	0.61																			
Normalized index	0																			
<b>Par. Species 7</b>																				
X	10	10	10	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Original index	0.43																			
Normalized index	0.30																			
<b>Par. Species 8</b>																				
X	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
Original index	0.18																			
Normalized index	0																			
<b>Par. Species 9</b>																				
X	5	5	5	5	5															
Original index	0.46																			
Normalized index	0																			
<b>Par. Species 10</b>																				
X	5	5																		
Original index	0.75																			
Normalized index	0																			
<b>Par. Species 11</b>																				
X	5																			
Original index	1																			
Normalized index	1																			
<b>Par. Species 12</b>																				
X	1																			
Original index	1																			
Normalized index	1																			