

The Sampling Characteristics of Electivity Indices

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Summary. Electivity indices measure the utilization of food types (r) in relation to their abundance or availability in the environment (p). Foods that constitute a larger proportion of the diet than of the available foods are considered preferred; conversely those proportionately underrepresented in the diet are avoided. A food is eaten at random if its proportion in the diet equals its proportion in the environment. A family of electivity indices stemming from Ivlev's (1961) classic monograph exist and differ only in the particular algorithm used to calculate electivity from r and p .

For each available index I graphed the values of electivity as contours for all combinations of r and p . These graphs are compared to illustrate the strengths and weaknesses of each index on the basis of the following criteria: 1) the value of the index when $r=p$ for a food, 2) the symmetry of the electivity value as feeding deviates from random, 3) the possible range of index values, 4) the linearity of changes in electivity over the full range of r and p , 5) the sensitivity of the index to sampling errors, 6) the statistical testability of the electivity, and 7) the stability of the electivity value for a food type that changes relative abundance or occurs in combination with different food types. No one index ideally satisfies all the criteria.

The host preferences of gypsy moth, *Lymantria dispar*, feeding on tree foliage in an undisturbed deciduous forest in southwestern Quebec, Canada were used to compare the available indices: Ivlev's electivity, E ; Ivlev's forage ratio, E' ; Jacob's modified electivity, D ; Jacob's modified forage ratio, Q ; Chesson's alpha; Strauss' linear index, L ; and Vanderploeg and Scavia's relativized electivity, E^* . The electivity values calculated by each index differ one from another; host trees shown as preferred by one index will frequently appear avoided according to an alternative index. The rank order electivities for the 19 available host trees, however, are remarkably similar for all but Strauss' linear index, L . *Populus grandidentata*, *Quercus rubra*, *Ostrya virginiana*, and *Amelanchier* were the most preferred host trees in the sampled forest; *Prunus serotina*, *Acer pensylvanicum*, *A. rubrum*, *Betula lutea*, and *Fraxinus americana* were most avoided. The use of Vanderploeg and Scavia's E^* index is recommended.

The general problem of quantifying feeding preferences has continued to be of special concern in two related areas of ecological research: 1) tests of optimal foraging theory and 2) quantitative descriptions of feeding ecology. Optimal foraging theory has attempted to predict food choice as a function of

food quality and related characteristics (Pyke et al. 1977). Cock (1978) found the majority of preference indices inappropriate for testing the predictions of optimal foraging theory. Another large literature, derived from Ivlev's (1961) classic study on the feeding of fishes, attempts to quantify an organism's preference or electivity for the host of available foods in its environment. Such a quantitative description of food choice is often a necessary prerequisite to studies of predator-prey or plant-herbivore interactions. This paper considers the value of available electivity indices from this point of view.

Ivlev compared the relative availability of food types in the environment (p) and their relative utilization in the diet (r). If r and p are equal for all food types, the organism is choosing food types wholly at random – that is in direct proportion to the relative abundance or likelihood of encountering the food types. If r and p differ for a food type, an algorithm is used to calculate a quantitative measure of the deviation from random feeding; it is this algorithm which has undergone extensive modification from Ivlev's original proposals (see Table 1). Despite the frequent use of one or another of these electivity indices, no comprehensive comparison of their characteristics is available.

Table 1. Various indices of electivity or feeding preference based on the proportions of food i in the diet (r_i) and in the environment (p_i)

Algorithm	Comment	Reference
1) $E_i = (r_i - p_i) / (r_i + p_i)$	Ivlev's electivity index	Ivlev (1961)
2) $E'_i = r_i / p_i$	Ivlev's forage ratio	Ivlev (1961)
3) $D_i = \frac{r_i - p_i}{r_i + p_i - 2r_i p_i}$		Jacobs (1974)
4) $Q_i = \frac{r_i(1 - p_i)}{p_i(1 - r_i)}$	Use of $\log_{10} Q$ recommended	Jacobs (1974)
5) $L_i = r_i - p_i$		Strauss (1979)
6) $\alpha_i = W_i = \frac{r_i/p_i}{\sum_i r_i/p_i}$	Chesson's alpha, Vanderploeg and Scavia's selectivity coefficient	Chesson (1978); Vanderploeg and Scavia (1979a)
7) $E_i^* = [W_i - (1/n)] / [W_i + (1/n)]$	n = number of kinds of food items	Vanderploeg and Scavia (1979b)

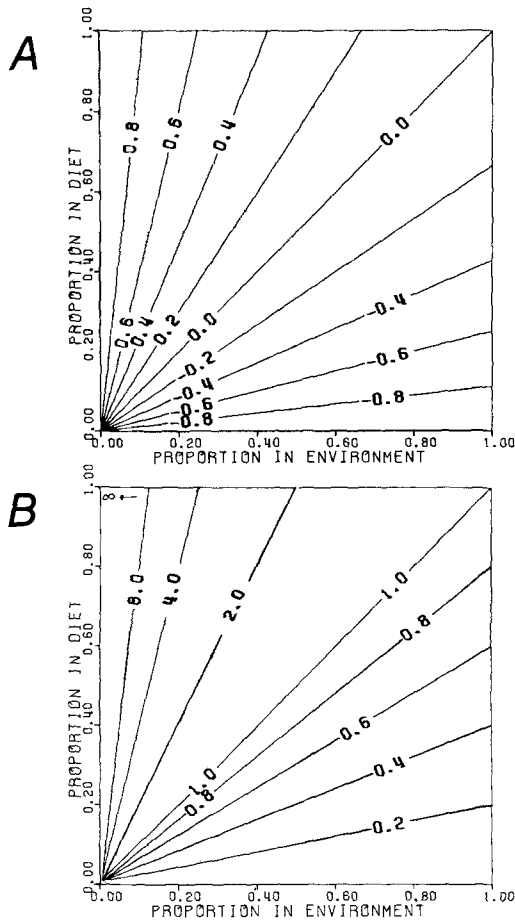


Fig. 1. The values of Ivlev's electivity index E (A) and the forage ratio E' (B) as functions of availability and utilization of a food item

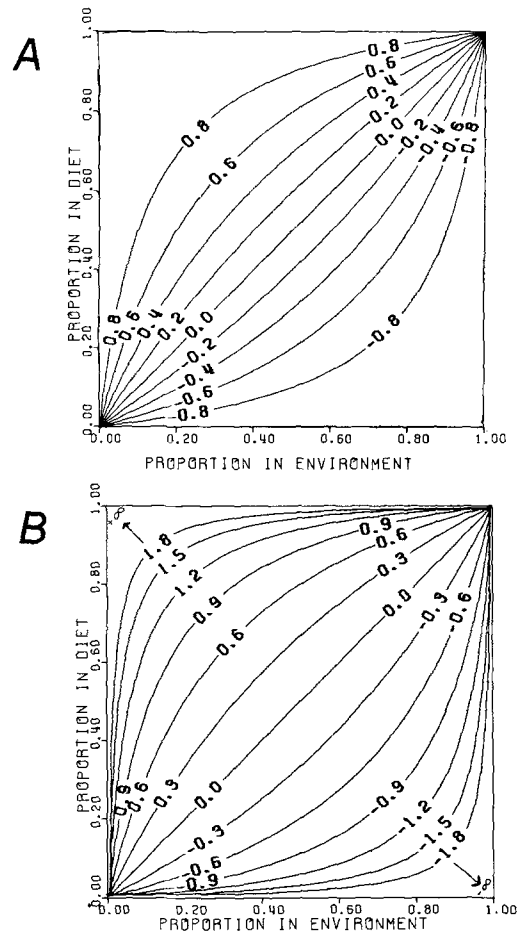


Fig. 2. The values of Jacob's modified electivity D (A) and modified forage ratio, $\log Q$ (B) as functions of availability and utilization of a food item

The following characteristics, desirable in any index of electivity, provide a basis of comparison:

1) *random model*, $f(r, p) = 0$ if and only if $r = p$: an index should take the value 0 if a food is taken simply in proportion to its abundance.

2) *symmetry*, if $r = p$ then $|f((r + c), p)| = |f((r - c), p)|$ where c is a constant: a particular deviation from random feeding should result in the same magnitude of change in the index regardless of its sign.

3) *range*, for any p , $\text{MAX } f(r, p) \equiv f(1.0, p)$ and $\text{MIN } f(r, p) \equiv f(0.0, p)$: a food is maximally preferred when all that is available is utilized; conversely a food is maximally avoided when none is taken regardless of its abundance. At the extreme of only one food type in the environment it is logically impossible to satisfy both criterion 1 and criterion 3. This is of little concern, however, since the concept electivity need not apply in this situation.

4) *linearity*, $[f(r, p) - f((r + a), p)] = b$ for any r, p where a and b are constants: any unit change in food availability or utilization should have the same effect on the index regardless of the levels of availability and utilization.

5) *robustness*: the index should not be markedly sensitive to sampling errors, particularly for rare or little used foods.

6) *testability*: the index should be amenable to statistical comparisons between species or between samples.

7) *stability*: the index should give comparable, but not necessarily identical, results for samples from diverse sites

that may differ in types or relative abundances of available food.

No user of electivity indices is likely to agree completely with these particular criteria nor does any existing electivity index satisfy all of them. My goal in this paper is not to choose any "ideal" electivity index, but rather to alert would-be users to the particular sampling characteristics of the electivity indices in the literature. The choice of an appropriate index in a particular study or the interpretation and comparison of results in the literature both require a clear understanding of the available indices. Each index, as a unique transformation of the raw data, results in a distinctive measure of electivity. As a basis of comparison, graphical analyses of the indices for the full range of possible availabilities and utilization levels are presented and illustrated with reference to a particular data set on the feeding of the gypsy moth, *Lymantria dispar*, in a deciduous forest.

Graphical Analysis of Available Indices

To compare the commonly used electivity indices I graphed the value of the index for all combinations of r and p . These graphs of the sampling characteristics of an index illustrate its behavior under all possible feeding patterns. Such graphs have been constructed for each algorithm using a contour plotting routine (Figs. 1 to 5). The contours give the value of the index at a particular combination of r and p ; the spacing

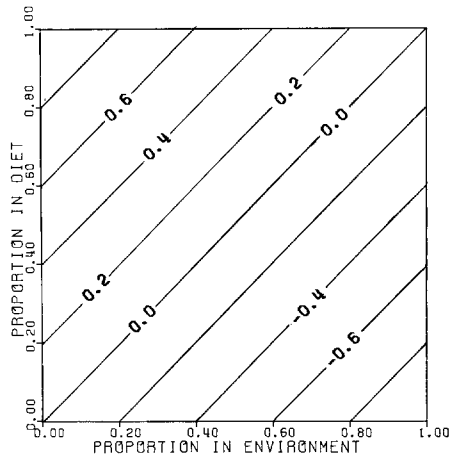


Fig. 3. The values of Strauss' linear preference index L as a function of availability and utilization of a food item

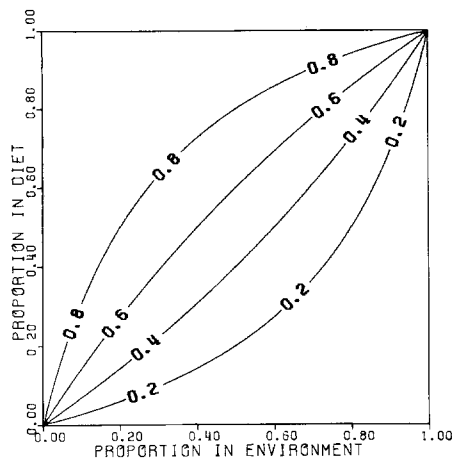


Fig. 4. The values of a relativized forage ratio (Chesson's α , Vanderploeg and Scavia's W) as a function of availability and utilization of a food item when two food types are available

between contours indicates how rapidly the index changes in response to changes in r and p . With these contour graphs the characteristics of each index under the listed criteria can be more effectively judged than by the selected numeric examples that prevail in earlier and less comprehensive comparisons (Cock 1978; Jacobs 1974; Strauss 1979; Paloheimo 1979).

Ivlev's Electivity, E

Ivlev's original electivity index, E , takes a value of zero for random feeding and deviates symmetrically from zero between plus and minus one as an item is, respectively, preferred or avoided (Fig. 1A). The index does not, however, take its extreme values at intermediate values of r and p ; that is, for example, a food type that represents 0.20 of the possible diet can give an electivity of only 0.67 even if it constitutes the entire diet ($p=1.00$). Deviations from the random model, while symmetrical, are not linear – for a small change in either r or p , the index changes very rapidly at any value of r or p below about 0.3. These changes are extremely rapid below any r or p less than 0.1. Sampling errors in estimating such low levels of food utilization or availability are likely and will result in marked errors in the estimated electivity.

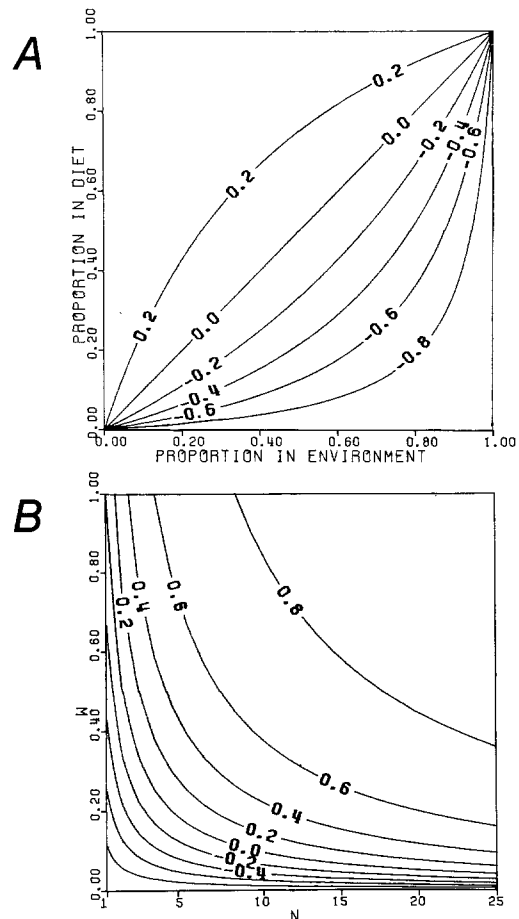


Fig. 5. The values of Vanderploeg and Scavia's relativized electivity index, E^* , as a function of availability and utilization of a food item when the number of items in the diet, n , is two (A). The E^* index varies as a function of the relativized forage ratio (α , W) and the number of items in the diet (B)

This weakness in Ivlev's E algorithm necessitates large sample sizes to assure accurate estimation of availability and utilization but as sample size increases still rarer food types are likely to be discovered in natural communities. No matter how large the sample there will thus always be some rare food types whose electivity cannot be effectively assessed with Ivlev's E index.

This sampling problem is compounded by the statistical properties of the index. Strauss (1979) points out that since the index is a ratio: 1) the expected value of E under random feeding will not be zero for all values of r and p , and 2) any deviation from the expected cannot be simply tested by using the variance estimated from replicate samples. Strauss derives estimates of the confidence interval about E and shows by Monte Carlo methods that even at large sample sizes the confidence interval becomes excessively large at $p \leq 0.1$. This result reaffirms the inappropriateness of Ivlev's E in estimating electivity for rare food types. Finally Ivlev's E has been criticized as unstable under changes in relative abundance of the food types (Jacobs 1974). This problem arises because the range of possible index values is not $-1 \leq E \leq 1$ for all values of r and p and is aggravated by the nonlinearity of the index. Jacobs correctly concludes that a sound quantitative comparison of selection between different food types requires that the

food types have the same relative abundance. This does not, however, prevent rank order comparisons of electivities within multispecies samples which in many ecological contexts can be appropriate and useful.

Ivlev's Forage Ratio, E'

As originally proposed Ivlev's E' (Fig. 1B), which is usually called the forage ratio, took a value of 1.0 for random feeding and deviated asymmetrically for $r \neq p$. It has a range from 1.0 to infinity for preferred food items and from 0.1 to 1.0 for avoided items. These undesirable characteristics can be avoided by taking the $\log E'$ as the index (Jacobs 1974; Cock 1978). Like Ivlev's E neither the original E' nor $\log E'$, however, can attain maximal values of preference or avoidance for intermediate values of r or p . Again like Ivlev's E , the forage ratio inevitably suffers from asymmetry over the full range of r and p . The sensitivity to sampling error for rare or little utilized foods remains problematic as does the low statistical estimability for $p \leq 0.1$ (Strauss 1979). Similarly, strictly quantitative comparisons between forage ratios derived from samples differing in relative abundances are inappropriate.

Jacob's Modified Electivity, D

In an analysis based on mortality rates for food types, Jacobs (1974) derived a modification of Ivlev's E which he said was independent of food relative abundance (Fig. 2A). His index, D , takes a value of zero under random feeding and deviates symmetrically from zero between plus and minus one for preferred and avoided items, respectively. In an environment with only two food types, Jacob's index can potentially give the full range of values ($-1 \leq D \leq 1$) for any particular value of r or p . This desirable property, however, does not hold for samples with greater than two food types (Vanderploeg and Scavia 1979b; Paloheimo 1979). Jacob's D is only slightly less sensitive to sampling errors for rare species than is either Ivlev's E or E' . The statistical comparison of D values is beset by the problems common to ratio data but these are not wholly insurmountable (Strauss 1979). Despite his intentions, Jacob's D is also inappropriate for quantitative comparison of index values from different samples except in the unusual situation where the same and only two food types are under consideration.

Jacob's Modified Forage Ratio, $\log Q$

Jacob's (1974) preferred modification of Ivlev's forage ratio, $\log Q$, has essentially the same advantages and disadvantages as D , his modification of Ivlev's electivity index E (Fig. 2). The $\log Q$ index, however, has a range from plus to minus infinity. Jacob's $\log Q$ is also unusually sensitive to sampling error when either r or p is less than about 0.1. Again, despite Jacob's intentions, $\log Q$ can potentially assume maximal values for preference or avoidance at any value of r or p only in the two-food case.

Strauss' Linear Index, L

After a review of the statistical shortcomings of Ivlev's electivity indices, E and E' , Strauss (1979) proposed a simple linear index L (Fig. 3). Strauss' index has the following desirable properties: 1) a range of preference and avoidance from +1 to -1 centered on zero (for random feeding), 2) linear and symmetrical deviation of the index for all $r \neq p$, and 3) a normal distribution of the index which readily allows statisti-

cal comparisons between samples or against a null hypothesis. Strauss recognizes that the index, like any other, is vulnerable to sampling error for items rare in the environment or in the diet. His Monte Carlo analyses, however, indicate that the effects of sampling error at low r or p values are less than in either Ivlev's E or E' indices. Ironically, Strauss' index becomes more vulnerable to sampling error as p increases. Despite its generally favorable properties, Strauss' L retains a characteristic fault of Ivlev's and Jacob's indices. The full range of index values ($-1 \leq L \leq 1$) cannot potentially be attained under all values of r or p . Maximum avoidance obtains when $r=0$ and $p=1$, and maximum preference could only obtain when $r=1$ and $p=0$ - an unlikely contingency! The index values for intermediate r or p depend on the relative abundance of other items in the environment or in the diet. Thus Strauss' index also is not amenable to comparison of electivity for an item sampled at sites with differing abundances of items in the environment or diet. This essentially precludes any field comparisons of electivity.

Chesson's α ; Vanderploeg and Scavia's Selectivity, W

A number of authors have independently proposed an alternative electivity index (Fig. 4) to overcome the problem of variation with the relative abundance of other items in the sample (Chesson 1978; Paloheimo 1979; Vanderploeg and Scavia 1979a). The index is essentially an Ivlev forage ratio normalized so that the sum of all such ratios in a sample equals one (see Vanderploeg and Scavia 1979a). The biological import of this normalization is not easily appreciated but the index can be thought of as representing the feeder's perception of the value of a food item in relation to both its abundance and the other food types available. Alternatively the index can be derived from a stochastic model of prey encounter and capture (Chesson 1978). The expected value for random feeding with this index is a function of number of food items: $1/n$ where n is the number of types of food in the sample. The index varies between 0 and 1 with values above $1/n$ indicating preference, those below $1/n$ indicating avoidance. The index is nonlinear, that is a change in r or p does not have the same effect at all values of r and p . The index is symmetrical only for the two-food case. Moreover the pattern of asymmetry will shift as the number of food types changes. The statistical characteristics of this ratio of ratios are open to criticisms such as those Strauss (1979) levelled against Ivlev's E and E' and it is vulnerable to sampling error for items rare in the environment or in the diet. The α or W index does have the advantage of being unaffected by the relative abundance of food types which allows meaningful between sample comparisons.

*Vanderploeg and Scavia's Relativized Electivity, E^**

Vanderploeg and Scavia (1979b) proposed a relativized electivity index, E^* , which is analogous to Ivlev's E but based on the selectivity coefficient W_i and the number of available food types (Fig. 5). The E^* index has the convenient properties of a zero value for random feeding and a possible range between plus and minus one. But the maximum preference value ($E^*=1$) can be attained only under the unrealistic conditions that $r=1.0$, $p=0.0$ and the number of food types is infinite. In practical terms it is important that the maximum attainable preference is an increasing function of the number of food types. The index is markedly nonlinear and asymmetrical, but these properties are a necessary adjunct to stabilizing the

index under changes in relative abundance in food types. As the number of food types increases, the index does become vulnerable to sampling errors for foods that are rare in the diet and rare to only moderately common in the environment. The E^* index is not amenable to parametric statistical analyses. Vanderploeg and Scavia (1979b) proposed this index on the grounds of convention to achieve a possible range from plus to minus one. This property is indeed advantageous, but direct comparisons of electivities must be limited to samples with the same food types. Like the selectivity coefficient, E^* embodies a measure of the feeder's perception of a food's value as a function of both its abundance and the abundance of other food types present. In addition E^* includes a measure of the deviation from random feeding that makes rank order comparison of electivities from diverse sites meaningful. Overall the E^* index provides the single best, but not perfect, electivity index.

The Electivity of Gypsy Moth Larvae Feeding on the Foliage of Forest Trees

Most previous workers have used only one or another of these indices to study feeding ecology. For example, Kitting (1980) used the forage ratio in analyzing the diets of limpets feeding on intertidal algae. Skogland (1980) compared the food preference of arctic and alpine caribou using Ivlev's electivity. Jenkins (1979) used Jacob's log Q to analyze feeding preferences in beaver. Newsome and Gee (1978) studied food selection in creek chubs using Ivlev's electivity index. Erlinge (1981) used Chesson's index to analyze the preferences of stoats for a number of vole species. It is more instructive to compare the behavior of all these diverse electivity indices in the context of a single, real example: feeding by the gypsy moth, *Lymantria dispar*.

The gypsy moth is a polyphagous folivore that in laboratory feeding trials has accepted 458 out of 477 proffered host plants (Forbush and Fernald 1896). In the forests of eastern North America gypsy moth larvae are reported to feed primarily on the leaves of deciduous trees, especially *Quercus* and *Populus* species (Mosher 1915; Campbell and Sloan 1977). Host selection is mediated by wind-rafting of early instar larvae. Soon after eclosion, which occurs in late April or early May, larvae begin to feed on foliage (Leonard 1970). Part of the larval population spins silk threads and release from the host tree to be carried by wind currents to another tree (Leonard 1971). Within limits of food reserves, this rafting continues through the early instars until a suitable host is found. Larval development then generally continues on that same host tree to pupation unless exhaustion of the food supply forces larval migration. Unless population density is very high, the later instar larvae feed at night and rest by day under bark flaps and similar shelters on or near the host tree (Leonard 1970). By late June or early July pupation occurs in these same diel shelters although there is limited migration by late instar larvae to alternate host trees, especially conifers (Rossiter 1980). A few weeks later the female moth, which is incapable of flight, lays her eggs near the pupation site (Doane 1976). The population overwinters in the egg stage until the next spring when dispersal can again occur through wind-rafting of the early instar larvae. The extensive literature on the gypsy moth has been recently summarized in bibliographies by Campbell et al. (1978) and Griffiths (1980).

We obtained estimates of r and p for a gypsy moth

population occurring on the southern faces of Lake Hill, Mont St. Hilaire, Quebec (Maycock 1961). The population sampled in 1979 had only been present on Mont St. Hilaire since about 1977 (Dr. Luc Jobin, personal communication). The larvae on Lake Hill were feeding in a *Quercus-Acer-Fraxinus* forest with 769 stems/hectare having an average diameter at breast height ($dbh=1.3$ m) of 16.3 cm. Using a stratified random grid scheme, we sampled 922 trees in 24500 m² circular quadrats; the total area of the sampled forest was about 1600 hectares. Each tree ($dbh \geq 8.0$ cm) was identified and its diameter at breast height was measured. This dbh measurement provides a reasonable estimate of the relative amounts of foliage biomass for each of the 19 tree species in our random sample (Madgwick 1970; Whittaker and Marks 1975). Thus p was estimated as:

$$p = \frac{\sum_{j=1}^{n_i} d_{ij}}{\sum_{i=1}^m \sum_{j=1}^{n_i} d_{ij}} \quad (1)$$

where d_{ij} is the dbh in cm for the j th of n_i trees of the i th among m tree species. To estimate the relative proportion of larvae feeding on each tree species we counted numbers of larvae congregated by day under tarpaper skirts around each tree trunk (Weseloh 1974). We counted the larvae on each of our 922 sample trees on two occasions: June 26–27 and July 3–4, 1979. These sampling dates were coordinated with larval development on the diverse tree species to provide a sound comparative estimate of larval numbers (Lechowicz and Mauffette 1980). Thus r could be calculated as:

$$\frac{\sum_{j=1}^{n_i} l_{ij}}{\sum_{i=1}^m \sum_{j=1}^{n_i} l_{ij}} \quad (2)$$

where l_{ij} is the mean number of larvae found on the j th of n_i trees of the i th among m tree species. These data on summed dbh and mean larval numbers for each tree species appear in Table 2.

The various electivity indices, with a single exception, arrive at remarkably similar rank ordered estimates of gypsy moth feeding patterns (Tables 3 and 4). The exceptional index is Strauss' L which has very low rank correlation with any of the other indices. In practical terms this suggests that despite their various advantages and disadvantages all the indices but Strauss' L give comparable rankings of gypsy moth host preferences. Even Strauss' L , with notable exceptions like *Acer saccharum*, identifies similar rankings for reasonably abundant host trees; the low correlations with other indices arise in part from numerous tied ranks among rarer species ($0.001 \leq L \leq 0.004$). It appears that the linearity which sets this index apart from the others may inevitably result in confounded estimates of electivity for rare and little-used tree species.

These similar rank order preferences obtained with all the indices except Strauss' L do not obviate the very real differences which arise in comparing the absolute values of electivity obtained with each index. Differences in the ranges, symmetry and linearity of the various indices makes any comparison of their absolute values meaningless. Strauss (1979) has contended that even the values of a single index for two different tree species cannot be validly compared.

Table 2. Data on the distribution of gypsy moth larvae, *Lymantria dispar*, feeding in a deciduous forest in southwestern Quebec, Canada

Tree species	Number of randomly sampled individuals	Summed diameters at breast height, cm	Summed numbers of larvae ^a	<i>r</i>	<i>p</i>
<i>Acer pensylvanicum</i>	1	8.5	0.5	2.86×10^{-5}	5.66×10^{-4}
<i>A. rubrum</i>	3	67.7	5.0	2.86×10^{-4}	4.51×10^{-3}
<i>A. saccharum</i>	158	2,344.0	1,342.0	7.68×10^{-2}	1.56×10^{-1}
<i>A. spicatum</i>	4	39.2	23.5	1.34×10^{-3}	2.61×10^{-3}
<i>Amelanchier</i> sp.	3	27.4	25.5	1.46×10^{-3}	1.82×10^{-3}
<i>Betula papyrifera</i>	47	696.3	69.0	3.95×10^{-3}	4.64×10^{-2}
<i>B. lutea</i>	4	60.7	4.5	2.57×10^{-4}	4.04×10^{-3}
<i>Carya cordiformis</i>	2	35.6	8.0	4.58×10^{-4}	2.37×10^{-3}
<i>Fagus grandifolia</i>	77	1,366.4	538.0	3.08×10^{-2}	9.10×10^{-2}
<i>Fraxinus americana</i>	56	778.5	58.0	3.32×10^{-3}	5.18×10^{-2}
<i>Juglans cinerea</i>	2	71.8	42.0	2.40×10^{-3}	4.78×10^{-3}
<i>Ostrya virginiana</i>	181	1,835.3	1,937.0	1.11×10^{-1}	1.22×10^{-1}
<i>Pinus strobus</i>	4	92.4	23.5	1.34×10^{-3}	6.15×10^{-3}
<i>Populus grandidentata</i>	11	206.1	382.5	2.19×10^{-2}	1.37×10^{-2}
<i>Prunus pensylvanica</i>	3	27.2	3.5	2.00×10^{-4}	1.81×10^{-3}
<i>P. serotina</i>	2	29.0	0.5	2.86×10^{-5}	1.93×10^{-3}
<i>Quercus rubra</i>	341	6,963.8	12,896.5	7.38×10^{-1}	4.64×10^{-1}
<i>Ulmus rubra</i>	1	15.4	2.5	1.43×10^{-4}	1.02×10^{-3}
<i>Tilia americana</i>	22	357.5	123.5	7.06×10^{-3}	2.38×10^{-2}
Totals	922	15,022.8	17,485.5	1.00×10^0	1.00×10^0

^a Mean of two larval counts taken June 26–27, 1979 and July 3–4, 1979

Table 3. Electivities of gypsy moth larvae for host tree species calculated with all the commonly used electivity indices (see Table 1 for algorithms)

Tree species	E_i	E'_i	D_i	$\log Q_i$	L_i	$\alpha_i = W_i$	E_i^*
<i>Acer pensylvanicum</i>	-0.904	0.050	-0.904	-1.297	-0.001	0.006	-0.787
<i>A. rubrum</i>	-0.881	0.063	-0.881	-1.199	-0.004	0.008	-0.739
<i>A. saccharum</i>	-0.341	0.492	-0.380	-0.347	-0.079	0.061	0.075
<i>A. spicatum</i>	-0.320	0.515	-0.321	-0.289	-0.001	0.064	0.098
<i>Amelanchier</i> sp.	-0.111	0.800	-0.112	-0.097	-0.000	0.099	0.308
<i>Betula papyrifera</i>	-0.843	0.085	-0.849	-1.089	-0.042	0.011	-0.665
<i>B. lutea</i>	-0.880	0.064	-0.881	-1.198	-0.004	0.008	-0.738
<i>Carya cordiformis</i>	-0.676	0.193	-0.677	-0.715	-0.002	0.024	-0.373
<i>Fagus grandifolia</i>	-0.494	0.338	-0.518	-0.499	-0.060	0.042	-0.111
<i>Fraxinus americana</i>	-0.880	0.064	-0.885	-1.215	-0.049	0.008	-0.737
<i>Juglans cinerea</i>	-0.331	0.503	-0.332	-0.300	-0.002	0.063	0.086
<i>Ostrya virginiana</i>	-0.049	0.907	-0.055	-0.048	-0.011	0.113	0.364
<i>Pinus strobus</i>	-0.641	0.218	-0.643	-0.663	-0.005	0.027	-0.319
<i>Populus grandidentata</i>	0.229	1.595	0.223	0.206	0.008	0.198	0.581
<i>Prunus pensylvanica</i>	-0.801	0.111	-0.801	-0.957	-0.002	0.014	-0.586
<i>P. serotina</i>	-0.971	0.015	-0.971	-1.830	-0.002	0.002	-0.932
<i>Quercus rubra</i>	0.228	1.591	0.530	0.512	0.274	0.198	0.580
<i>Ulmus rubra</i>	-0.755	0.140	-0.755	-0.856	-0.001	0.017	-0.504
<i>Tilia americana</i>	-0.542	0.297	-0.548	-0.535	-0.017	0.037	-0.175

Great import, for example, should not be given to the avoidance of *Acer saccharum* according to Ivlev's electivity index ($E = -0.341$) versus its preference according to Vanderploeg and Scavia's index ($E^* = 0.075$). The most meaningful and useful observation is that in both cases *Acer saccharum* ranked seventh among foods utilized by gypsy moth larvae. If preference ranks rather than absolute values are interpreted then all the indices except Strauss' L provide comparable and useful measures of electivity.

In some studies such as quantification of feeding responses to food abundance, simple rank preferences may

prove inadequate. In such studies the use of absolute preferences calculated with one of these indices can be misleading since all the indices purposely subsume a measure of food abundance. In these instances it is generally worthwhile to simply examine an appropriate direct measure of utilization for each food type (Downing 1981). For gypsy moth this might be the number of larvae per cm dbh of each tree species. In this example this utilization measure has high rank correlations ($0.992 \leq r \leq 1.000$, $p < 0.0001$) with all the preference indices except Strauss' L . This high correlation between the absolute measure of utilization and the various preference

Table 4. Spearman rank correlation between the electivities calculated by the diverse algorithms (lower half matrix) and their significance levels (upper half matrix). Based on electivities for gypsy moth larvae feeding on 19 tree species (Table 3) in an undisturbed native forest; Table 1 gives the electivity algorithms. Italicized entries are *not* significant

	E_i	E'_i	D_i	$\log Q_i$	L_i	$\alpha_i = W_i$	E_i^*
E_i		0.0001	0.0001	0.0001	0.264	0.0001	0.0001
E'_i	1.000		0.0001	0.0001	0.273	0.0001	0.0000
D_i	0.994	0.992		0.0001	0.235	0.0001	0.0001
$\log Q_i$	0.995	0.993	1.000		0.235	0.0001	0.0001
L_i	0.270	0.265	0.286	0.286		0.252	0.273
$\alpha_i = W_i$	0.998	0.998	0.998	0.998	0.276		0.0001
E_i^*	1.000	1.000	0.992	0.993	0.265	0.998	

indices will not, however, necessarily prevail for organisms other than gypsy moth. The correlation depends on exactly how the relative abundance of food types affects food choice. An absolute measure of utilization has the advantage that it will usually be amenable to analysis by regression or ANOVA. These utilization measures do not, however, measure the electivity for a food type. If interest centers on food utilization relative to food availability the various electivity indices provide a more appropriate summary of the feeding ecology.

The preference rankings achieved by all the indices except Strauss' L for gypsy moth larvae on Mont St. Hilaire, Quebec are comparable. The leaves of *Quercus rubra*, *Populus grandidentata*, *Ostrya virginiana* and *Amelanchier* consistently rank high as foods preferred by gypsy moth larvae in this forest. *Prunus serotina*, *Acer pensylvanicum*, *A. rubrum*, *Betula lutea*, and *Fraxinus americana* consistently rank as strongly avoided foods.

With the notable exceptions of *Ostrya virginiana* and *Populus grandidentata* these field results are in general accord with Mosher's (1915) classic laboratory study of gypsy moth feeding. Barbosa (1978) calls attention to factors that can lead to such differences in laboratory versus field determined feeding preferences in gypsy moth. Mosher's laboratory trials could not, for example, allow for effects of relative host abundance and are largely based on his ability to rear larvae to adulthood on fresh foliage samples. Foliage samples for rearing the larvae were from few trees and he did note tree to tree variation in food quality. Larvae fed on foliage from two adjacent *Salix alba* trees had a threefold difference in fecundity. The only quantitative and comprehensive field assessment of gypsy moth feeding preferences is that of Campbell and Sloan (1977). They calculated a defoliation ratio comparing a species potential for defoliation by gypsy moth to that of white oak for forests in eastern New England. Unlike Mosher they found high preference for *Ostrya* and *Populus*. Both Mosher (1915) and Campbell and Sloan (1977) report low preference for *Acer saccharum* which in Quebec appears to be moderately preferred. This difference may well reflect real alteration of gypsy moth feeding preferences at the northern edge of its North American range. *Acer saccharum* is also near its northern range limit at our site (Little 1971) and may have reduced resources available for defense against folivores. Overall, the various electivity indices, with the exception of Strauss' L , give rankings of gypsy moth food preference in reasonable agreement with other observations from eastern North America.

While electivity indices can help discern and quantify broad patterns in the feeding ecology of an organism, it is

also desirable to be able to draw three sorts of statistical inferences about the observed feeding preferences: 1) does the organism feed at random on available foods, 2) do feeding preferences differ between two sites or at two times, and 3) is there any difference in the preference for two food types? Quantitative descriptions of gypsy moth feeding preferences in a particular forest, for example, are interesting and informative in themselves, but will be most useful if statistically sound answers to these questions are available. These answers are best obtained by an ancillary analysis of the data using the nonparametric statistic χ^2 or its maximum likelihood analog.

The larval population in a given forest can be tested for significant deviation from random feeding using a χ^2 test for goodness of fit (Sokal and Rohlf, 1969). If the larvae are feeding at random, the null hypothesis is that the numbers on a given tree species should be directly proportional to the relative contribution of that species' foliage biomass to the total forest canopy biomass. Taking *dbh* as an approximation to foliage biomass for each tree the expected number of larvae feeding on a species is:

$$\hat{l}_i = p_i \sum_{j=1}^m \sum_{i=1}^{n_i} l_{ij} \quad (3)$$

where the variables are as defined in Eq. 1 and 2. The χ^2 is calculated as:

$$\chi^2 = \sum_{i=1}^m \frac{(l_i - \hat{l}_i)^2}{\hat{l}_i} \quad (4)$$

with $(m-1)$ degrees of freedom and where l_i is the total number of larvae observed on the n_i trees of species i . It is noteworthy that each cell's χ^2 essentially includes another variant on an Ivlev-type electivity index:

$$\chi^2_i = G \frac{(r_i - p_i)^2}{p_i} \quad (5)$$

where G in this example is the total number of larvae in the sampled forest. An alternative maximum likelihood estimate of the test statistic can also be calculated and the nature and source of any significant deviation from the random model can be further analyzed (Reynolds 1977).

The feeding patterns at two sites or the same site at two times can be most readily compared by a χ^2 test of independence in the $2 \times m$ contingency table for the 2 sites by m tree species (Reynolds 1977). Only sites with the same food types present can be compared. Any electivity measure intrinsically assesses utilization in relation to the total available food types; it is only appropriate to compare electivities from

sites with the same available food types. Within this constraint the analysis can be readily extended to more than 2 sites. The null hypothesis can be thought of as the utilization of food types does not depend on the site. Sample sizes should be sufficiently large that no cell's expected value falls below 5; if this is not possible, the rarer food types should be combined or eliminated (Reynolds 1977). A significant χ^2 by itself does not indicate the food types contributing significantly to deviation from the null hypothesis. The methods of Haberman (1973) involving standardized and adjusted residuals for each cell in the contingency table may be used to assess the significant deviations from expectation. To some extent this provides a test of the significance of the electivity for a particular food type.

The difference in electivity for a pair of food types may be tested by partitioning the site by food type contingency table. Reynolds' (1977) provides a detailed discussion of this approach.

Johnson (1980) provides an alternative test of significant differences in electivities for different food types. It requires, however, that the rank order preferences of *individual* animals are available. These individual preference rankings provide the replication necessary to calculate a minimum significant difference in average preference rank for any two foods. In many ecological situations, such as in the gypsy moth example discussed here, it is not possible to monitor the feeding preferences of individuals. It may, however, be possible and appropriate to compare the feeding preferences of populations at different sites that have the same tree species present. Taking the population of larvae at each site as a statistical analog to an individual, Johnson's methods may then be used to test for significant differences between larval preference for different host trees.

Conclusion

The various permutations (Table 1) of Ivlev's electivity and forage ratio measures of feeding preference all give broadly comparable results with the exception of Strauss' *L*. The indices differ in the absolute values calculated for particular combinations of *r* and *p* but give essentially identical rank order preferences. The variations in absolute index values arise from the unique sampling characteristics of each index, especially differences in the range, symmetry, and linearity of responses elicited by changes in *r* and *p*. With the exception of Strauss' *L*, all the available indices provide useful measures of feeding preference. Vanderploeg and Scavia's *E** index provides the single most useful electivity index. Data used to calculate electivity are amenable to complementary statistical analyses to compare feeding preferences at spatially or temporally different sites which have the same food types available. When absolute levels of feeding on a particular food type need be predicted, direct measures of food utilization may be more appropriate. Preference indices are primarily useful in discerning and comparing feeding patterns rather than in predicting levels of food utilization.

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References

- Barbosa P (1978) Host plant exploitation by the gypsy moth, *Lymantria dispar*. Ent Exp Appl 24:28-37
- Campbell RW, Sloan RJ (1977) Forest stand responses to defoliation by the gypsy moth. Forest Science Monograph 19 34 pages
- Campbell RW, Levitan LC, Sobecki ER, Tardiff MF (1978) Population dynamics of the gypsy moth: an annotated bibliography. USDA Forest Service, General Technical Report NE-48
- Chesson J (1978) Measuring preference in selective predation. Ecology 59:211-215
- Cock MJW (1978) The assessment of preference. J Anim Ecol 47:805-816
- Doane CC (1976) Flight and mating behavior of the gypsy moth, pages 127-136 In: JF Anderson, HK Kaya, (eds), Perspectives in forest entomology. Academic Press, NY
- Downing JA (1981) In situ foraging responses of three species of littoral cladocerans. Ecol Monog 51:85-103
- Erlinge S (1981) Food preference, optimal diet and reproductive output in stoats, *Mustela erminea*, in Sweden. Oikos 36:303-315
- Forbush EH, Fernald CH (1896) The gypsy moth. Wright and Potter, Boston
- Griffiths KJ (1980) A bibliography of gypsy moth literature. Can For Service, Sault Ste Marie, Ontario Report 0-X-312
- Ivlev VS (1961) Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut
- Jacobs J (1974) Quantitative measurement of food selection. Oecologia (Berl) 14:413-417
- Jenkins SH (1979) Seasonal and year-to-year differences in food selection by beavers. Oecologia (Berl) 44:112-116
- Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71
- Kitting, CL (1980) Herbivore-plant interactions of individual limpets maintaining a mixed diet of inter-tidal marine algae. Ecol Monog 50:527-550
- Lechowicz MJ, Mauffette Y (1980) Feeding preferences of the gypsy moth (*Lymantria dispar*) in the forests of southern Quebec. Laurentian Forest Research Centre, Environment Canada, Ste. Foy, Quebec, unpublished research report
- Leonard DE (1970) Feeding rhythm in larvae of the gypsy moth. J Econ Entom 63:1454-1457
- Leonard DE (1971) Air-borne dispersal of larvae of the gypsy moth and its influence on concepts of control. J Econ Ent 64:638-641
- Little EL Jr (1971) Atlas of United States trees. Vol 1. Conifers and important hardwoods. USDA Forest Service, Miscellaneous Publication 1146, Washington, DC
- Madgwick HAI (1970) Biomass and productivity models of forest canopies, pp 47-54. In: DE Reichle (ed), Analyses of temperate forest ecosystems. Springer-Berlin Heidelberg New York
- Maycock PF (1961) Botanical studies on Mont St. Hilaire, Rouville County, Quebec. Can J Bot 39:1293-1325
- Mosher FH (1915) Food plants of the gypsy moth in America. USDA Bulletin 250, Washington, DC pages 39
- Newsome GE, Gee JH (1978) Preference and selection of prey by creek chub, *Semotilus atromaculatus*, inhabiting the Mink River, Manitoba. Can J Zool 56:2486-2497
- Paloheimo JE (1979) Indices of food preference by a predator. J Fish Res Board Can 36:470-473
- Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. Quar Rev Biol 52:137-154
- Reynolds HT (1977) The analysis of cross-classifications. Free Press, NY
- Rossiter MC (1980) Enhanced pathogen resistance as a result of a host shift by the gypsy moth. Second International Congress of Systematic and Evolutionary Biology, Vancouver, British Columbia. Abstracts: p 328
- Siegel S (1956) Nonparametric statistics for the behavioral sciences. McGraw Hill, NY

- Skogland T (1980) Comparative summer feeding strategies of arctic and alpine rangifer. *J Anim Ecology* 49:81–98
- Sokal RR, Rohlf FJ (1969) *Biometry: the principles and practice of statistics in biological research*. Freeman, San Francisco
- Strauss RE (1979) Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Trans Am Fish Soc* 108: 344–352
- Vanderploeg HA, Scavia D (1979a) Two electivity indices for feeding with special reference to zooplankton grazing. *J. Fish Res Board Can* 36:362–365
- Vanderploeg HA, Scavia D (1979b) Calculation and use of selectivity coefficients of feeding: zooplankton grazing. *Ecol Modelling* 7:135–149
- Weseloh RM (1974) Relationships between different sampling procedures for the gypsy moth, *Porthetria dispar* (Lepidoptera: Lymantriidae) and its natural enemies. *Can Ent* 106:225–231
- Whittaker RH, Marks PL (1975) Methods of assessing terrestrial productivity, pp 5–118. In: H Lieth and RH Whittaker (eds) *Primary productivity of the biosphere*. Springer-Berlin Heidelberg New York

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