

Reliability Estimates for Ivlev's Electivity Index, the Forage Ratio, and a Proposed Linear Index of Food Selection¹

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Abstract

Ivlev's electivity index and the forage ratio, two commonly used measures of food selection, are significantly biased when the sizes of the prey samples from the gut of the predator and the habitat are unequal. Approximate confidence-interval expressions are derived for these indices. A stochastic (Monte Carlo) model was used to validate these expressions and to explore the statistical properties of the indices. The statistical reliability of each index is shown to be a function of the absolute and relative sample sizes and the relative abundances of the prey species in the environment. A linear index of food selection is proposed which avoids most of the statistical and mathematical inadequacies of these indices. Regardless of the index used, however, inadequate habitat sampling, differential availability of prey to the predator, and differential digestion of prey may be significant sources of error in the interpretation of food selection data.

Ivlev's (1961) index of electivity has been widely used as a means of comparing the feeding habits of fishes and other aquatic organisms with the availability of potential food resources in natural habitats. The purpose of the index is to characterize the electivity, or degree of selection, of a particular prey species by the predator being studied. The relationship is defined as

$$E = \frac{r_i - p_i}{r_i + p_i},$$

where E is the measure of electivity, r_i the relative abundance of prey item i in the gut (as a proportion or percentage of the total gut contents) and p_i the relative abundance of the same prey item in the environment. The index has a possible range of -1 to $+1$, with negative values indicating avoidance or inaccessibility of the prey item, zero indicating random selection from the environment, and positive values indicating active selection.

Although some problems of applying the index to field data have been identified in the literature, the index has generally been assumed to be unbiased and relatively independent of sample size. On this basis it has been used and evaluated indiscriminately by many

investigators. However, these assumptions have not been empirically or theoretically confirmed and, on the basis of the known behavior of similar indices, are probably invalid.

Ivlev's index is a ratio of essentially continuous variables which have been converted to percentages or proportions. As such, an expression for its expected sampling variance cannot be derived exactly. An asymptotic estimate of the variance may be obtained if r_i and p_i are assumed to be normally or binomially distributed, in which case the sampling distribution of the ratio E is skewed (Cochran 1977). Atchley et al. (1976) have shown stochastically that ratios of this type have frequency distributions that are leptokurtotic and skewed to the right. In practical terms, this means that (1) the expected value of E under conditions of random feeding by the predator may not always be zero, and (2) a value for the variance calculated from several replicate field samples is not a good measure of the deviation of the calculated electivity index from its expected value. As a consequence, values of Ivlev's index should not be compared by use of t -statistics, which are sensitive to significant deviations from normality.

This same criticism can be applied to the so-called forage ratio, which was used in early feeding studies but has now been largely supplanted by Ivlev's index. It is treated here because it is similar in form to many other biological indices (such as sex ratios, predator

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"switching" ratios, and standardized morphometric measurements). The forage ratio (FR) is defined simply as the ratio of the relative abundance of prey item i in the gut to that in the environment:

$$FR = \frac{r_i}{p_i}$$

FR ranges from 0 to 1 for negative selection and from 1 to infinity for positive selection. This intrinsic asymmetry is a major disadvantage of the measure. However, as Jacobs (1974) has noted, it can be eliminated by applying a logarithmic transformation (to any base). Log FR is an open-ended index varying from negative infinity to 0 for prey avoidance or inaccessibility and from 0 to positive infinity for positive selection.

The purpose of this account is to (1) derive expressions giving approximate confidence intervals for Ivlev's index and the forage ratio; (2) validate these expressions and further explore their statistical properties by means of a stochastic (Monte Carlo) model; (3) document the mathematical behavior of the measures and define a linear index of food selection which avoids most of the inadequacies of these and other indices; and (4) review problems encountered in applying any measure of food selection to aquatic field studies.

Confidence Intervals

A number of asymptotic confidence intervals are possible depending on the method of approximation (Paulson 1942; Noether 1957; Goldstein 1964; Cochran 1977). To develop a confidence-interval expression for the forage ratio, I will utilize a large-sample confidence interval for a ratio of binomial variables which was derived by Noether (1957), based on Geary's (1930) theorem. In the following discussion I let n_r be the total number of organisms collected from the guts of all predators examined, and n_p be the total number of potential prey organisms (of all species) collected from the habitat.

Noether's (1957) expression is

$$C = \frac{u}{1 + z^2/n} \cdot \left\{ 1 + \frac{z^2}{2k} \pm z \sqrt{V_1 + V_2 + \frac{z^2}{4} \left(\frac{1}{k^2} + \frac{4V_1}{n} \right)} \right\}, \quad (1)$$

where C = the critical values for the confidence interval (the significance of which is dependent upon z);

u = the sample estimate of the ratio ($= r_i/p_i$);

n = the sample size for the numerator ($= n_r$);

k = the number of "successes" (observed occurrences of prey type i) in the n "trials" for the numerator ($= n_r r_i$);

V_1, V_2 = the sample estimates of the relative variances of the denominator and numerator, respectively, and

z = the 2-sided normal deviate at significance level α (for example, 1.96 for $\alpha = 0.05$, yielding a 95% confidence interval).

The relative variances (Edwards 1964) for the denominator and numerator of the forage ratio are, respectively,

$$V_1 = \frac{1 - p_i}{n_p p_i} \quad \text{and} \quad V_2 = \frac{1 - r_i}{n_r r_i}.$$

Once the appropriate substitutions have been made, the expression giving an approximate confidence interval for the forage ratio becomes

$$FR_c = \frac{r_i/p_i}{1 + z^2/n_r} \left\{ 1 + \frac{z^2}{2n_r r_i} \pm z \sqrt{\frac{1 - p_i}{n_p p_i} + \frac{1 - r_i}{n_r r_i} + \frac{z^2}{4} \left(\frac{1}{n_r^2 r_i^2} + \frac{4(1 - p_i)}{n_r n_p p_i} \right)} \right\}, \quad (2)$$

where the FR_c are the two critical values corresponding to a given significance level α . Unfortunately, the confidence limits for log FR are not simply the logarithms of the FR_c . Instead, reasonable upper and lower confidence limits for log FR are given by respectively adding the logarithm of the upper FR_c to, and subtracting it from, the point estimate of log FR . That is,

$$(\log FR)_c = \log FR \pm \log(\text{upper } FR_c). \quad (3)$$

The expressions for the variances of the numerator and denominator of Ivlev's index are more complex than for those of the forage ratio, and cannot be directly substituted into Equation (1). There is more than one sample size for the numerator in this case because it is a function of both r_i and p_i . If the sample sizes for the gut and habitat samples are both large enough that their reciprocals can be considered

negligible, this problem can be circumvented by using a simplified expression also given by Noether (1957):

$$C = u(1 \pm z\sqrt{V_1 + V_2}). \quad (4)$$

The relative variance of the numerator of Ivlev's index can be shown to be

$$V_2 = \frac{[r_i(1 - r_i)/n_r] + [p_i(1 - p_i)/n_p]}{(r_i - p_i)^2},$$

while that of the denominator is

$$V_1 = \frac{[r_i(1 - r_i)/n_r] + [p_i(1 - p_i)/n_p]}{(r_i + p_i)^2}.$$

Because the ratio u is used as a multiplicand in Equation (4), the expression will not yield a valid confidence interval when $E = 0$ (that is, when $r_i = p_i$). This problem can be resolved by adding 1 to the ratio (so that $E = 1$ when $r_i = p_i$) and subtracting 1 from the resulting values for the confidence limits. Adding 1 to the ratio $(r_i - p_i)/(r_i + p_i)$, reexpressing to reduce the number of terms, and then making the appropriate substitutions into Equation (4) gives

$$E_c = \left(2 - \frac{2p_i}{r_i + p_i}\right) \cdot \left\{1 \pm z\sqrt{\frac{2n_r p_i(1 - p_i)(r_i + p_i)^2 + r_i(1 - r_i)n_p + p_i(1 - p_i)}{n_r n_p (r_i + p_i)^2}}\right\} - 1. \quad (5)$$

The E_c are the two critical values corresponding to a given significance level, α .

It must be emphasized that Equations (2), (3), and (5) yield only approximate confidence intervals. In the case of an exact expression, the protection provided by the equation would be given by the confidence coefficient (α) selected by the investigator. This is often chosen to be 0.05, yielding a 95% confidence interval. However, these are approximate intervals in the sense that the actual protection may be somewhat higher or lower than that indicated by the confidence coefficient. Noether (1957) found that the protection provided by Equation (1) is usually greater than expected, while that of Equation (4) is usually less. Such biases would also apply to Equations (2) and (5). For all four expressions, the deviation from the expected protection increases as the values of the numerator and (or) denominator of the ratio decrease.

Stochastic Validation of Confidence Intervals

The confidence-interval expressions for Ivlev's index and the forage ratio are surprisingly complex in view of the simplicity of the indices themselves. The validity of these confidence-interval expressions cannot be verified directly because the distributions of these ratio estimates are intractable to analytic methods. However, sampling distributions for the indices may be examined indirectly by means of a stochastic model which presumes to mimic the relevant behavior of a randomly feeding predator. Once the distributions have been determined empirically, they can then be used to estimate confidence intervals (or, more correctly, probability intervals) to be compared with those calculated from the confidence interval expressions given in the previous section. They may also be used to explore the statistical properties of the indices.

The stochastic model used is one which assumes random sampling by a predator species from a mixed pool of prey with a fixed proportion π_i of prey species i (in terms of either numbers of individuals or biomass). No specific distribution of prey items in space or in relative importance is assumed. However, it is assumed that the capture of any given prey item is independent of the capture of any other (that is, the trials are independent). The actual proportion of species i consumed (r_i) is then binomially distributed with mean π_i and variance $\pi_i(1 - \pi_i)/n_r$ (Edwards 1964), where the sample size n_r , as before, is the total number of organisms collected from the guts of all predators. Habitat sampling by the researcher is assumed to be random and unbiased from the same prey pool. The proportion of species i collected (p_i) will have a mean π_i and variance $\pi_i(1 - \pi_i)/n_p$, where n_p is the total number of prey organisms (of all species) collected. An index value is calculated for each r_i and p_i . If the sampling distribution of the index is not skewed, its expected value under these conditions would be zero. The probability interval will then correspond to a confidence interval around zero.

Frequency distributions for given values of π_i , n_r , and n_p were constructed by randomly generating 1,000 values each of r_i and p_i from pseudorandom numbers selected from binomial distributions with the proper defining parameters, and using these values to calculate the

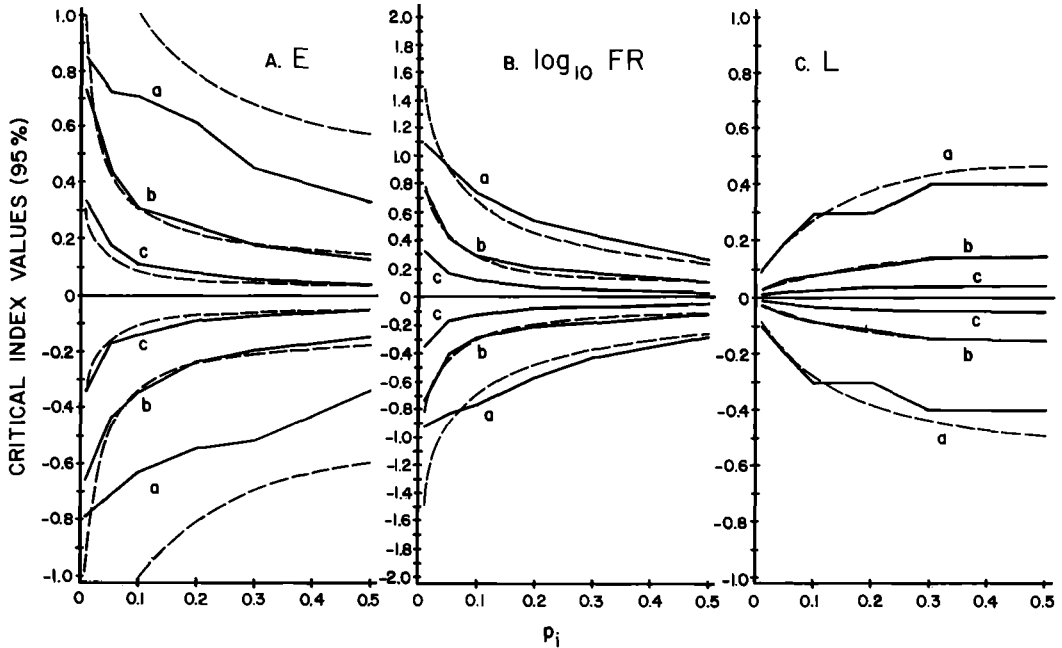


FIGURE 1.—Ninety-five percent confidence intervals around zero derived from the stochastic model (solid lines) and confidence-interval expressions (dotted lines, where different from the solid lines) for the three indices, as a function of the relative occurrence of the prey species in the habitat (π_i) and three arbitrary levels of sample size: a. $n_r = n_p = 10$; b. $n_r = n_p = 100$; c. $n_r = n_p = 1,000$. Panel A: Ivlev's electivity index (E); Panel B: \log_{10} (forage ratio, FR); Panel C: linear index (L).

same number of index values. For each frequency distribution generated, the mean (\bar{x}), variance (s^2), skewness (g_1), and kurtosis (g_2) were calculated (Selby 1964). To estimate pertinent probability intervals, the 1,000-entry array of generated index values was sorted into ascending sequence and the values of array positions 5, 10, 25, 50, 951, 976, 991, and 996 were recorded. These correspond to α levels of 0.005, 0.01, 0.025, 0.05, 0.95, 0.975, 0.99, and 0.995, respectively. Distributions were generated for $\pi_i = 0.01, 0.05, 0.10, 0.20, 0.30$, and 0.50 and for values of n_r and n_p ranging from 10 to 1,000. All computations were programmed in FORTRAN IV.

For both indices the fit of the calculated confidence intervals (from Equations 3 and 5) to those determined stochastically is excellent when the sample sizes are reasonably large (Fig. 1, A and B). Some important trends which are not immediately obvious from Equations (3) and (5) are evident in these figures. In relation to the possible range of -1 to $+1$, the confidence limits of Ivlev's index for reasonable val-

ues of α are quite wide and highly dependent on π_i , the proportion occurrence of the prey species in the environment. As expected, progressively larger sample sizes are needed to maintain a constant confidence-interval length as the relative abundance of the prey type decreases. For scarce prey species (for example, $\pi_i < 0.05$) and small sample sizes the 95% confidence interval for the point $E = 0$ might include 70% or more of the entire range of the index. This means that a calculated value of $E = 0.5$, for example, which would normally be considered indicative of active prey selection, may be a reasonable sampling value to expect under these conditions even if the predator is acquiring prey randomly from the environment. Such wide confidence intervals would obviously negate the usefulness of the index for prey species that are not dominant in the environment unless the samples from the predators and the habitat are large, containing thousands of individuals. The confidence intervals for more abundant prey species are much more reasonable even for moderate sample sizes. Confi-

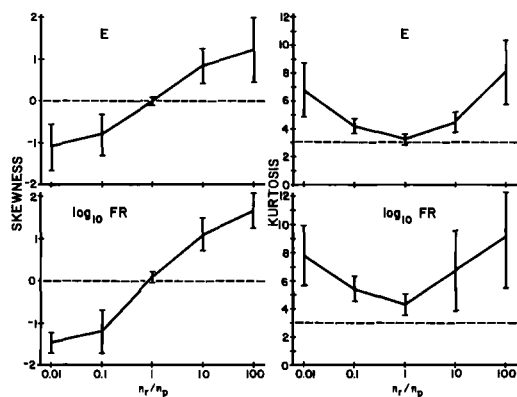


FIGURE 2.—Mean values ± 2 SE of skewness and kurtosis for Ivlev's index (E) and the \log_{10} -transformed forage ratio (FR), as a function of the ratio of the sample size of prey organisms collected from the gut (n_r) to that from the environment (n_p). Dotted lines indicate the skewness and kurtosis values of a normal distribution.

dence intervals for $\log_{10}FR$ behave similarly to those of Ivlev's index, but in practice are more difficult to evaluate because the index is open-ended.

The skewness and kurtosis of the sampling distributions are highly dependent upon the relative equality of the gut and habitat sample sizes (Fig. 2). When the two sample sizes are equal, the distributions of E and $\log_{10}FR$ approach normality and are essentially unbiased. With increasing sample size inequality, skewness and kurtosis in general become increasingly significant. For any given ratio of n_r to n_p , however, the actual deviation from normality is dependent upon the magnitudes of the sample sizes. Small sample sizes result in greater skewness and kurtosis than larger ones. In practical terms, these findings demonstrate that (1) the expected value of either index is not zero (that is, the index is biased) when the sample sizes are not equal, and (2) the variance alone is usually not a sufficient measure of deviation from the expected value.

Inadequacies of the Indices

The results of the stochastic analysis have indicated that these indices are neither unbiased nor relatively independent of sample size, as has been assumed. Rather, the sampling distributions are significantly skewed and highly kurtotic when sample sizes are unequal, and the statistical reliabilities of the measures are de-

pendent upon both the absolute and relative sample sizes as well as the relative rarity or abundance of the prey species in the environment.

The rather wide confidence intervals of these indices are significant in relation to the amount of assurance that various investigators have placed in electivity values of relatively small magnitude. The application of these findings to diet studies reported in the literature is difficult to assess properly because the original sample sizes of prey items are usually not reported. Index values calculated for planktivores may be sufficiently reliable for proper evaluation because the sample sizes involved can easily be on the order of several thousand. Electivity values calculated for predators of larger and less abundant prey should be assessed more critically.

An additional factor which makes difficult the proper quantitative evaluation of electivity values is the intrinsic nonlinearity of the indices with respect to their defining parameters. In his discussion of the formulation of his index, Ivlev (1961, pages 43–45) listed as an advantageous property that the measure is linearly related to the series of ratios of the proportions of prey in the environment and predator diet (that is, 9/1, 8/2, 7/3, . . .). While this characteristic may be desirable in experimental feeding situations, it is not expedient for comparing measures of prey selection calculated from field data. Ratio linearity results in a nonlinear relationship of the index with interval changes in r_i when p_i is held constant (and vice versa). Thus, for constant changes in r_i or p_i , E varies least rapidly near zero and most rapidly toward the extremes of -1 and $+1$. The exact formulations for the partial derivatives of E are

$$\frac{\partial E}{\partial r_i} = \frac{2p_i}{(r_i + p_i)^2} \quad \text{and} \quad \frac{\partial E}{\partial p_i} = \frac{-2r_i}{(r_i + p_i)^2}.$$

Ivlev (1961, pages 73–74) discussed these derivatives (without stating them explicitly) and recognized the complexity of any mathematical analysis due to nonlinearity.

The behavior of the index can more readily be appreciated from a matrix of E values corresponding to various levels of r_i and p_i (Table 1). Although it is often stated that a value of $+1$ indicates complete selection of a prey species, this value is actually attained only when

TABLE 1.—Values of Ivlev's electivity index E corresponding to interval values of the relative abundances r_i (food item i in the gut) and p_i (food item i in the environment).

p_i	r_i										
	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
0		1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
0.1	-1.00	0	0.33	0.50	0.60	0.67	0.71	0.75	0.78	0.80	0.82
0.2	-1.00	-0.33	0	0.20	0.33	0.43	0.50	0.56	0.60	0.64	0.67
0.3	-1.00	-0.50	-0.20	0	0.14	0.25	0.33	0.40	0.45	0.50	0.54
0.4	-1.00	-0.60	-0.33	-0.14	0	0.11	0.20	0.27	0.33	0.38	0.43
0.5	-1.00	-0.67	-0.43	-0.25	-0.11	0	0.09	0.17	0.23	0.29	0.33
0.6	-1.00	-0.71	-0.50	-0.33	-0.20	-0.09	0	0.08	0.14	0.20	0.25
0.7	-1.00	-0.75	-0.56	-0.40	-0.27	-0.17	-0.08	0	0.07	0.13	0.18
0.8	-1.00	-0.78	-0.60	-0.45	-0.33	-0.23	-0.14	-0.07	0	0.06	0.11
0.9	-1.00	-0.80	-0.64	-0.50	-0.38	-0.29	-0.20	-0.13	-0.06	0	0.05
1.0	-1.00	-0.82	-0.67	-0.54	-0.43	-0.33	-0.25	-0.18	-0.11	-0.05	0

the prey species is not present in the habitat sample (that is, $p_i = 0$). Any occurrence of the prey item in the habitat sample will give a maximum electivity value less than +1, with a zero value being reached when only that prey species occurs in the sample. This behavior is actually desirable, because the greater the relative abundance of the prey in the environment, the more likely it is that its sole occurrence in the diet is a matter of random selection. In contrast, the index shows two undesirable traits. Absence of the prey item in the habitat sample yields an electivity value of +1 regardless of the relative proportion of the prey in the gut. Similarly, the absence in the diet of any prey which occurs in the habitat sample will result in a value of -1, no matter how scarce or abundant the prey is in the environment. These are unrealistic reflections of the behavior of a predator because the rarer a prey species is in the environment, the more likely its lack in the diet is due to chance.

Similar criticisms hold for the forage ratio and for several other indices of food selection (for example, Jacobs 1974; Chesson 1978) which I will treat elsewhere in more detail. The transformed forage ratio (Table 2) possesses the additional disadvantages of being open-ended and undefined when either r_i or p_i is equal to zero.

A Linear Food Selection Index (L)

These remarks on the inadequacies of the two indices lead to the consideration of an alternative measure of prey selection which preserves many of the desirable properties of the others while avoiding their shortcomings. This

index, which apparently has not been previously proposed, is simply the unweighted difference in proportions

$$L = r_i - p_i,$$

where r_i and p_i , as before, are the relative abundances (expressed in this case as proportions) of prey item i in the gut and habitat, respectively. Its properties include the following. (1) It ranges from -1 to +1, with positive values indicating preference and negative values indicating avoidance or inaccessibility. (2) The expected value of the index for random feeding is zero under all conditions. (3) The measure takes on extreme values only when the prey item is rare but consumed almost exclusively, or is very abundant but is rarely consumed. (4) It is defined for all values of r_i and p_i . (5) It is linear in terms of r_i and p_i . (6) The index is distributed approximately normally. (7) The sampling variance is defined so as to allow statistical comparison of two calculated values or of a calculated value and a null-hypothesis value (such as zero). The characteristics of a fixed range and linearity in terms of the defining parameters are valuable properties because, in conjunction with an estimate of the sampling variance, they allow a better judgment of the significance of a calculated value in terms of the range of possible values.

The linear behavior of L can be observed from a matrix of values corresponding to fixed levels of r_i and p_i (Table 3). For reasonably large sample sizes, where

$$n_p \geq \frac{3}{p_i(1-p_i)} \quad \text{and} \quad n_r \geq \frac{3}{r_i(1-r_i)}$$

TABLE 2.—Values of the \log_{10} -transformed forage ratio corresponding to interval values of the relative abundances r_i (food item i in the gut) and p_i (food item i in the environment).

p_i	r_i										
	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
0											
0.1	0		0.30	0.48	0.60	0.70	0.78	0.85	0.90	0.95	1.00
0.2	-0.30	0	0.18	0.30	0.40	0.48	0.54	0.60	0.65	0.70	
0.3	-0.48	-0.18	0	0.12	0.22	0.30	0.37	0.43	0.48	0.52	
0.4	-0.60	-0.30	-0.12	0	0.10	0.18	0.24	0.30	0.35	0.40	
0.5	-0.70	-0.40	-0.22	-0.10	0	0.08	0.15	0.20	0.26	0.30	
0.6	-0.78	-0.48	-0.30	-0.18	-0.08	0	0.07	0.12	0.18	0.22	
0.7	-0.85	-0.54	-0.37	-0.24	-0.15	-0.07	0	0.06	0.11	0.15	
0.8	-0.90	-0.60	-0.43	-0.30	-0.20	-0.12	-0.06	0	0.05	0.10	
0.9	-0.95	-0.65	-0.48	-0.35	-0.26	-0.18	-0.11	-0.05	0	0.05	
1.0	-1.00	-0.70	-0.52	-0.40	-0.30	-0.22	-0.15	-0.10	-0.05	0	

(Sokal and Rohlf 1969), both r_i and p_i will be distributed approximately normally. Because r_i and p_i are statistically independent, L will also be approximately normal. The estimated sampling variance s^2 of L is then

$$s^2(L) = \frac{r_i(1-r_i)}{n_r} + \frac{p_i(1-p_i)}{n_p}$$

and t -statistics can be used for evaluation and statistical comparison (with $n_r + n_p - 2$ degrees of freedom).

As in the case of Ivlev's index and the forage ratio, the reliability of the proposed index is dependent upon the relative abundance of the prey in the environment (Fig. 1, C). However, in this case the widths of the confidence intervals are smaller for less frequent prey species than for more abundant ones.

In general, then, this proposed measure of prey selection should be preferable in most sit-

uations to the other indices. It should be noted that Jacobs' (1974) criticism of Ivlev's index and the forage ratio, that is, that their values depend upon both the degree of selection and the relative abundance of the food type in the environment, holds for this measure as well. However, any index which would fulfill Jacobs' criterion must be nonlinear and would therefore have a more complex variance structure, and thus be less reliable, than the measure proposed here.

Problems of Application

Regardless of the statistical reliability of the index used, there are several serious problems to consider when any measure of prey selection is to be used to evaluate the feeding habits of a predator in terms of availability of potential food resources. These can be reduced to two principal concerns: (1) obtaining an unbiased

TABLE 3.—Values of the proposed electivity index L corresponding to interval values of the relative abundances r_i (food item i in the gut) and p_i (food item i in the environment).

p_i	r_i										
	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
0	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
0.1	-0.1	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0.2	-0.2	-0.1	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8
0.3	-0.3	-0.2	-0.1	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7
0.4	-0.4	-0.3	-0.2	-0.1	0	0.1	0.2	0.3	0.4	0.5	0.6
0.5	-0.5	-0.4	-0.3	-0.2	-0.1	0	0.1	0.2	0.3	0.4	0.5
0.6	-0.6	-0.5	-0.4	-0.3	-0.2	-0.1	0	0.1	0.2	0.3	0.4
0.7	-0.7	-0.6	-0.5	-0.4	-0.3	-0.2	-0.1	0	0.1	0.2	0.3
0.8	-0.8	-0.7	-0.6	-0.5	-0.4	-0.3	-0.2	-0.1	0	0.1	0.2
0.9	-0.9	-0.8	-0.7	-0.6	-0.5	-0.4	-0.3	-0.2	-0.1	0	0.1
1.0	-1.0	-0.9	-0.8	-0.7	-0.6	-0.5	-0.4	-0.3	-0.2	-0.1	0

sample from the habitat which accurately represents the relative abundances of the various potential prey species as they are encountered by the predator; (2) obtaining an unbiased sample which accurately represents the relative abundances of the prey species as they are consumed.

The first of these problems is a particular difficulty in aquatic systems, for which Ivlev's index has most often been used. It has repeatedly been demonstrated that routine sampling by traditional methods to determine relative abundances and biomass of benthic invertebrates is unreliable (Leonard 1939; Needham and Usinger 1956; Longhurst 1959; Albrecht 1961; Chutter 1972). The variability of numbers and proportions of species in benthic samples is generally much greater than that of total weights. Much of this inconsistency is due to patchy (contagious) distributions of individuals, which also significantly affect the accuracy of plankton abundance estimates (Wiebe and Holland 1968; Wiebe 1971).

Selection index values represent the availability or inaccessibility of prey items as much as actual preference or avoidance. The microhabitat occupied by a prey species may be an important influence on its susceptibility to predation and accessibility to sampling, but the degree of influence may be very difficult to determine in a field study. Patchiness of prey organisms, in addition to affecting sampling estimates, may also affect the susceptibility of the prey to predation (O'Brien and Vinyard 1974). Ivlev (1961) experimentally demonstrated that the degree of clustering of food items is equally as important in determining feeding success as is food abundance.

Another aspect of habitat sampling involves the underlying assumption in food selection studies that predation does not substantially alter the relative abundances of prey organisms in the environment. This obviously may not always be the case. A particular prey item may be greatly preferred (or at least differentially selected) and may be consumed to the extent that it becomes rare in the predator's habitat. For example, planktivorous fishes have been known to significantly reduce populations of large zooplankton species (see studies cited in Allan 1974 and Gannon 1976). Once the prey population is depressed, it will seldom be encountered by the predator, and so will have a low proportion

of occurrence in the gut. A selection index calculated under these conditions may well approach zero.

The second principal problem encountered in food selection studies involves obtaining an unbiased sample which accurately represents the relative abundances of the prey as they are consumed. A gut sample is unbiased in this respect only if all prey items are digested at equal rates. A digestion rate higher than average for a particular prey type will tend to underrepresent that species in the gut sample, while a rate lower than average will have the opposite effect. Hess and Rainwater (1939), for example, demonstrated that brook trout (*Salvelinus fontinalis*) digest soft-bodied organisms such as dipteran larvae much more rapidly than heavily chitinized forms such as stonefly nymphs and caddisfly larvae. They noted also that the absolute digestion rate differences are temperature dependent. In like manner, Gannon (1976) showed that an apparent avoidance of *Daphnia* by alewife (*Alosa pseudoharengus*) could be accounted for by the relatively rapid digestion of these organisms. To compensate for differential digestion, Hess and Rainwater (1939) suggested that relative values could be experimentally assigned to each prey species. Such values could be calculated as the reciprocal of the time required for half the individuals in a sample of predators to completely digest the prey type, and could be standardized in relation to some soft-bodied species. The standardized values multiplied by the actual numbers of organisms of each species found in the gut would then give the relative numbers eaten.

In summary, the particular index chosen for a quantitative food selection study should be one which is easily interpreted and compared and which has a known statistical reliability. The linear index described in this paper is suggested as one which fulfills these criteria. However, it must also be recognized that inadequate habitat sampling, differential availability of prey to the predator, and differential digestion of prey may be significant sources of error in the interpretation of food selection data.

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