Interpreting Selectivity Indices Calculated from Field Data or Conditions of Prey Replacement

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Indices of prey selection are compared empirically to clarify the kind of information each can provide and when the indices can be used appropriately. Emphasis is given to Chesson's alpha (α) and Strauss' Linear index (Li) because they are commonly used and represent two mathematically dissimilar approaches to measuring selection. Neutral selection for α and Li is not equivalent. For Li, neutral selection for a prey type occurs when selectivity equals the weighted (by relative abundance) average selectivity for all other prey types. For α, neutral selection equals the unweighted average for all prey types, which is equivalent to 1 divided by the number of prey types. Li and α respond differently to rare prey types. This is especially evident in field samples having large differences in relative prey abundances. Li values decrease as abundance of a prey type decreases in the environment. In contrast, α values often increase greatly as the proportional abundance of a prey type in the environment decreases. Consequently, α values, but not Li values, are often strongly influenced by the values for very rare prey. α values are sensitive to changes in the number of prey types, but not to changes in prey proportion. When the number of prey types is constant, α may be the most meaningful indicator of prey type preference. In contrast, Li values are sensitive to changes in prey proportions in the environment. When prey proportions are constant among experiments, Li is appropriate for measuring changes in the impact of a predator on a prey type and changes in selectivity relative to the average prey item. If number of prey types and prey proportions vary among experiments, Vanderploeg and Scavia's W or E* may be most appropriate.

On fait des comparaisons empiriques d'indices de choix de proies afin d'établir le type d'information que chaque indice peut fournir et de déterminer quand ces indices peuvent être utilisés de façon appropriée. On met l'accent sur l'indice alpha (α) de Chesson et l'indice linéaire de Strauss (Li) parce qu'ils sont communément utilisés et représentent deux approches mathématiques différentes pour quantifier le choix. Le choix neutre pour le deux indices n'est pas le même. Pour l'indice Li, le choix neutre d'un type de proie a lieu quand la sélectivité est égale à la sélectivité moyenne pondérée (en fonction de l'abondance relative) pour tous les autres types de proies. Pour l'indice α, le choix neutre est égal à la moyenne non pondérée pour tous les types de proies, soit 1 divisé par le nombre de types de proies. Les indices Li et α réagissent différemment aux types de proies rares. Ceci est surtout évident dans les échantillons recueillis sur le terrain qui montrent des différences élevées de l'abondance relative des proies. Les valeurs de Li baissent en fonction d'une baisse de l'abondance d'un type de proie dans l'environnement. Au contraire, les valeurs de α augmentent souvent fortement en fonction d'une baisse de l'abondance proportionnelle d'un type de proies dans l'environnement. Ainsi, les valeurs pour des types très rares de proies influent souvent fortement sur les valeurs de α mais non sur celles de Li. Les valeurs de α sont sensibles aux variations du nombre de types de proies mais non à des variations de la proportion de proies. Quand le nombre de types de proies est constant, α peut être l'indicateur le plus significatif de la préférence pour un type de proies. Au contraire, les valeurs de Li sont sensibles à des variations des proportions de proies dans l'environnement. Quand les proportions de proies sont constantes dans les expériences, l'indice Li est approprié pour quantifier les variations de l'incidence d'un prédateur sur un type de proies et les variations de la sélectivité par rapport à la proie moyenne. Si le nombre de types de proies et les proportions de proies varient dans les expériences, les valeurs W ou E* de Vanderploeg et Scavia seront peut-être plus appropriées.

Aquatic ecologists use a variety of selectivity indices to quantify consumer food preference (Lechowicz 1982). β (Manly et al. 1972), α (Chesson 1978), W (Vanderploeg and Scavia 1979a, 1979b), and SFR (Paloheimo 1979) are mathematically equivalent and widely employed by aquatic ecologists and fishery biologists (e.g. Butler and Bence 1984; Schmitt and Holbrook 1984; Li et al. 1985; McClintock and Lawrence 1985; Stemberger 1985; Govoni et al. 1986). These indices are nonlinear in the sense that changes in the index value for a prey type are not linearly related

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to changes in the proportion of that prey in the diet. Among these indices, β was derived first and then extended (Manly 1974) to apply to conditions with or without prey replacement. These nonlinear indices compare the relative abundance of food types in the environment (p_i) with their relative abundance in the diet (r_i). α and its equivalents are a function of the forage ratio, (r_i/p_i) (Ivlev 1961), for each prey type. Specifically:

$$\alpha_i = \frac{r_i/p_i}{\sum_{i=1}^{n} r_i/p_i}$$

whereby the sum of all α for a predator is normalized to 1. W' (Vanderploeg and Scavia 1979a) and E^* (Vanderploeg and Scavia 1979b) are both derived from the forage ratio and have been recommended (Lechowicz 1982; Horn 1985). Recently, use of Strauss's (1979) Linear index (Li) was advocated for certain population studies (Ready et al. 1985). Li, which cannot be derived from the forage ratio, is described by

$$\text{Li}_i = r_i - p_i.$$

We have quantified prey selection by a fish and an insect on prey from field samples. These samples had many prey types of very unequal abundance, and the prey type experienced very unequal selectivity as is common for field samples. We have used α and Li to express selectivity and have noted empirical attributes of these indices which, to us, did not seem clearly described in preceding, more theoretical treatments. Herein we describe several qualitative attributes of these indices for conditions of prey replacement: (1) neutral or random selection; (2) the response of the indices to uncommon prey; (3) inferences from selectivity values; and (4) mean and variance estimates of selectivity.[1]

Neutral Selection

The concept of neutral selection differs for α and Li. α, for neutral or random selection, equals 1 divided by the number of prey types. α is neutral when the forage ratio for a prey type equals the mean forage ratio for all other types. A neutral value for α can be perceived as indicating type-neutral selection. This gives equal weight to all prey types regardless of differences in abundance of prey types.

In contrast, neutral or random selection for Li occurs when $\text{Li}_i = 0$ or $r_i = p_i$. If the visibility and ease of capture for all prey types is equal, neutral selection for an item occurs when the probability of pursuit equals the average probability for all prey items rather than prey types. Such behavior can be perceived as item-neutral selection. Positive and negative Li values suggest selection or avoidance relative to the average for all items.

Response of Indices to Uncommon Prey

Indices derived from the forage ratio are particularly sensitive to consumption of rare prey. For example, in a two-prey system, if p_i and $r_i = 0.01$, α_i will equal 0.50 so that half of the sum of all α is due to 1% of the diet (Fig. 1). Rare prey are a common feature of field studies. Our field samples show that rare prey tend to have larger than average forage ratios (Fig. 2, 3). For

[1]Computer programs for IBM-PCs or "look-alikes" that enter data on prey frequency in the environment and diet, and calculate the Li and its variance, are available at cost from the senior author.
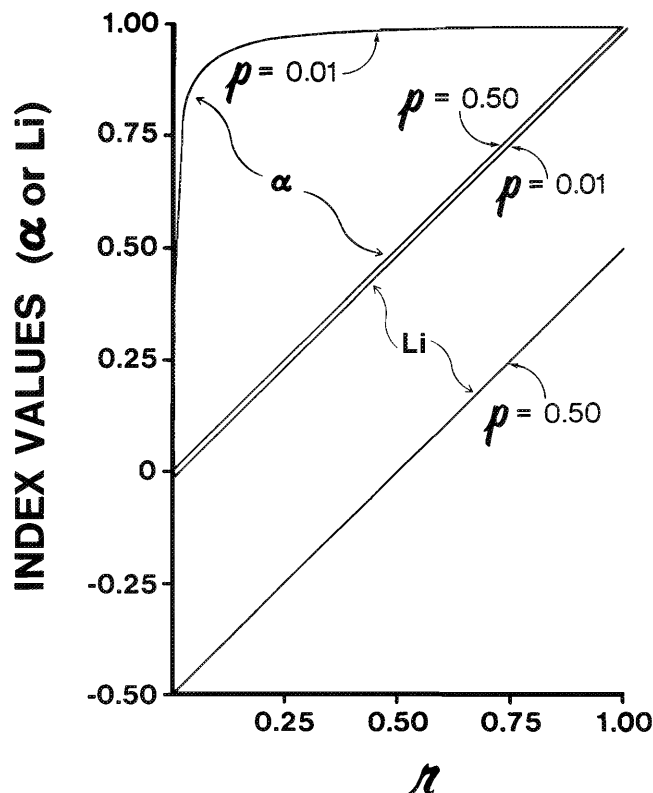
TWO-PREY SYSTEM

FIG. 1. Two examples each for α and Li response curves for changes in the diet proportion of one prey type, r_i, in a two-prey system. With prey relative abundance, p_i, of 0.01 and 0.50 and r_i varying from 0 to 1.00, the response curve for Li is linear. With $p_i = 0.01$ the response curve for α is nonlinear. With the special case of $p = 1.0$ over the number of prey types, the response curve of α is linear.

prey that comprised 1–0.01% of the available prey, forage ratios were frequently in the range of 5–10 and occasionally in the 100's. In several samples the forage ratio for a very rare prey type exceeded the sum of the ratios for all other types. These values for very rare prey had a major effect on α values for all other prey. This effect could accurately reflect the predator's preferences, or result from chance ingestion by the predator, or be an artifact of small sample size. It must be remembered that a high α value does not mean the prey type is numerically important in the predator's diet.

Li values for rare prey are usually small even if the predator has a high forage ratio for that prey type. For example, if $p_i = 0.01$ and $r_i = 0.05$, which produces a relatively high forage ratio of 5, Li would equal 0.04. This is a small value, since Li values can approach 1.0.

Inferences from Selectivity Values

Studies of predation frequently focus on diet composition and, consequently, the impact of the predator on the prey. Often, changes in a predator's effect are deduced from a change in an index value. α may be more suitable for comparisons of the predator's selectivity among prey types, but with appropriate restrictions Li is more suitable for describing the impact of predation on a prey population as described in the following.
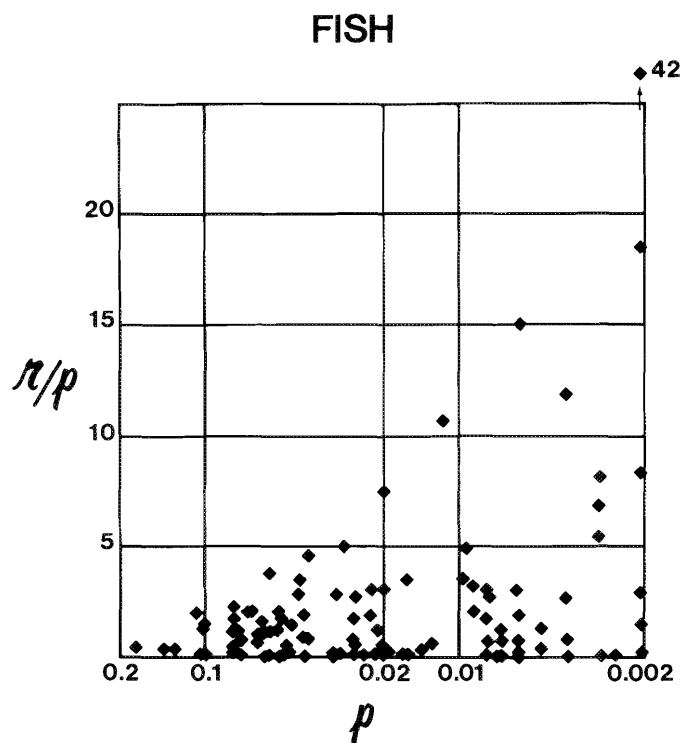
FISH

FIG. 2. Relationship between r_i/p_i and p_i from several laboratory experiments where *Perca flavescens* (30–60 mm) were offered a natural mixture of cladoceran and copepod prey.

During our studies (Mills et al. 1984; Moore-Rodenhouse 1986) of prey selection on natural prey mixtures, we estimated predation intensity at constant prey proportions while prey density or light intensity was varied. Sometimes the proportion of a prey type in the diet, r_i, increased while α_i decreased. At other times, α_i changed even though r_i and p_i were constant as illustrated by the following. In Table 1 the forage ratio and total consumed for prey type 1 remain constant in samples A and B, yet α_1 varies from 0.33 to 0.19. This occurs because of the increase in α_3 in sample B. In these samples, Li_1 for prey type 1 remains constant. Because of their discordance, α values are inappropriate for estimating a predator's impact on prey populations.

Changes in diet proportions produce a linear response in Li_i as long as p_i remains constant (Fig. 1). Consequently, when p_i for all prey types can be held constant while other experimental conditions are varied, then changes in Li_i always directly reflect changes in predation intensity. For α, if prey types have unequal abundance, changes in diet proportions produce a nonlinear response. This was particularly evident in our field samples where very rare prey had large forage ratios and a major effect on the calculation of all α values.

It is commonly said that α is insensitive to variations in p (Lechowicz 1982; Chesson 1983). This is true only when the number of prey types is constant. However, field samples collected on different dates or at different sites often have different numbers of prey types, and on average, p and α will decrease as the number of prey types increases. For example, if selection is type-neutral in two samples with three or five prey types, the α values would be 0.33 or 0.20, respectively. The use of relativized indices such as (Chesson 1983) or E^* (Vanderploeg and Scavia 1979a, 1979b) corrects for differences in number of prey types among samples. Chesson (1983) and

TABLE 1. α and Li values for a three-prey system given a constant forage ratio (r_i/p_i) for prey type 1 and a constant total number of prey consumed in sample A and sample B.

		Prey type		
		1	2	3
Sample A	r_i	0.50	0.40	0.10
	p_i	0.50	0.40	0.10
	r_i/p_i	1.00	1.00	1.00
	α_i	0.33	0.33	0.33
	Li_i	0.00	0.00	0.00
Sample B	r_i	0.50	0.10	0.40
	p_i	0.50	0.40	0.10
	r_i/p_i	1.00	0.25	4.00
	α_i	0.19	0.05	0.76
	Li_i	0.00	−0.30	+0.30

Lechowicz (1982) remarked that the statistical properties of these indices are not given and Chesson advocated the use of α values for statistical comparisons. However, Vanderploeg et al. (1984) did describe a procedure for parametric tests of E^*.

Mean and Variance Estimates of Selectivity

Parametric tests can be conducted with α values for a particular prey type using independently derived values from replicate predators (Manly 1974). This assumes that replicate α asymptotically approach a normal distribution around the mean for individual predators (Chesson 1983). This mean is an estimate of the average predator behavior. The degrees of freedom associated with this estimate relate to the number of sampled predators. As illustrated earlier, α changes in a nonlinear fashion as diet changes when prey types are of unequal abundance. Consequently, the average predator α_i seldom equals the population α_i when the latter is calculated from data pooled for all predators.

Estimating the variance of the index of selection from field samples involves two sources of variability: (1) r_i variance caused by individual variability of consumer feeding and (2) p_i variance resulting from the patchy distribution of food types in the environment and/or sampling error. Murtaugh (1981) attempted to solve this problem for a field study of mysid predation by constructing empirical distributions for r_i and p_i and using two Monte Carlo simulations to independently select r_i and p_i values. α was calculated for 500 pairs of r_i and p_i from which α_i and variance were estimated.

Variance estimates for Li have been described (Ready et al. 1985, after Strauss 1982). The mean and variance apply to the pooled population. This variance includes contributions from estimates of the prey eaten and from estimates of the prey available. The degrees of freedom associated with this variance relate to the total number of prey in the predator and environment samples (Ready et al. 1985). For a constant p, Li_i values from pooled populations determined with different experimental conditions can be compared by parametric tests.

Summary Comparison of Selectivity Indices

Nonlinear (α and its equivalents) and linear indices (Li) provide different kinds of information and are appopriate for different goals and situations. An α value can be calculated for a

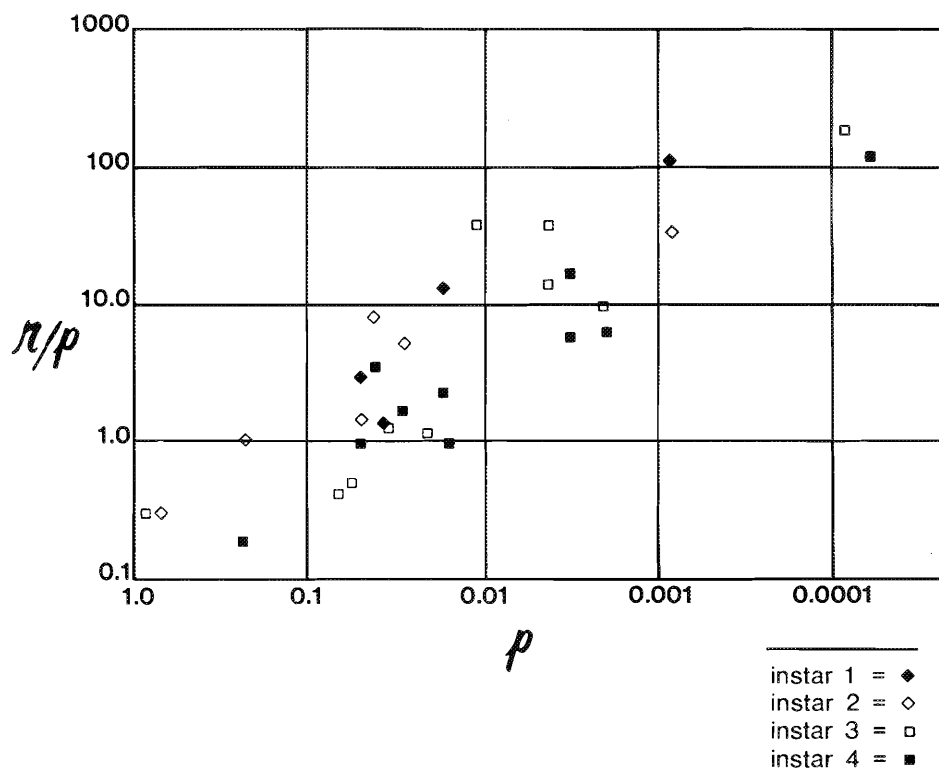*Can. J. Fish. Aquat. Sci., Vol. 44, 1987*

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CHAOBORUS

FIG. 3. Relationship between r_i/p_i and p_i derived from crop-content analyses of *Chaoborus punctipennis* instars I–IV collected at the same time (2400) and same depth (2–4 m) in a New Hampshire lake. Prey taken included large, flagellated phytoplankton, rotifers, and crustaceans.

population from pooled data or from individual α values for replicate consumers when predators eat the same number of prey types. Values of neutral selection relate to the average prey type. The statistical procedure for calculating the mean and variance of α, as recommended by Chesson (1983), describes the average predator and not the population. A distinct advantage of α is that it is insensitive to changes in p_i, if the number of prey types is constant, allowing among-sample comparisons when the relative abundance of prey varies. α is an indicator of relative prey preference, but is not a measure of diet proportion. α and all other indices derived from the forage ratio can be strongly influenced by sampling errors for rare prey.

For Li, zero represents neutral selection relative to the average prey item. The variance calculations for Li consider the number of samples and the number of items in each sample for both the environment and the predator. The mean Li_i, weighted by number of prey per predator, and calculated from replicate predators, equals the pooled or population Li_i. When p_i is constant, Li_i responds linearly to changes in r_i for all prey. Thus, changes in the mean Li_i are directly equated to changes in r_i, and changes in Li_i are a direct measure of changes in the impact of the predator on the prey population. This index has the large disadvantage of being sensitive to p_i, which produces low index values for rare prey in the environment, and prevents comparisons of most field samples collected on different dates when the relative abundance of prey changes. In the field, both the number of prey types and the relative abundances of prey often vary among samples. In such situations the indices W' and E^* seem to be most appropriate.

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