

A DISCUSSION OF AND ESTIMATION OF  
PREY PREFERENCE INDICES

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ABSTRACT

Because of the dependence of Ivlev's forage ratio index on prey concentrations several new indices of selectivity have been proposed. These new indices have a similar dependence. Because feeding rates are dependent on concentrations of all prey, an index of selectivity independent of concentrations may only be given by describing the relation between feeding rates and prey concentrations. Since all predators are not alike indices such as  $E_i$  are considered with the distinction made between preference of the population and average preference of the individuals. Statistical procedures are described for estimation of preference of the population and average preference of the individuals.

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## 1. INTRODUCTION

Numerous attempts have been made to fully describe prey selection since Ivlev's classic monograph (1961). A review of many of these attempts is given by Lechowicz (1982). The majority of the indices proposed (Vanderploeg and Savia, 1979a, 1979b; Chesson, 1978; Jacobs, 1974) are proportional to or similar to Ivlev's original forage ratio index (Lechowicz, 1982; Paloheimo, 1979); an exception to this being Strauss' (1979, 1982) linear index. The ratio type indices have been motivated primarily with the objective of producing an index independent of species densities.

In section 2 we compare Ivlev's forage ratio index with other ratio type indices of prey preference, and show that the indices referenced above are dependent on species composition (presence or absence) and thus do not achieve their goal of being independent of the community studied. We also consider an index of prey preference independent of species composition or abundance, and derive distinct measures of preference in terms of individual predators or the population as a whole, for a nonhomogeneous predator population. In part 3 we describe estimation procedures for parameters when considering preference of a nonhomogeneous population.

## 2. DISCUSSION OF PREFERENCE INDICES

Selectivity of prey may be the result of many factors such as detectability, avoidance, or palatability (Chesson, 1978). As no set of factors can be excluded *a priori*, for the present discussion, we regard preference as the result of all such factors and make no attempt to assess the relative import of the factors influencing preference.

### 2.1 Indices of Preference

Let  $E_1 = r_1/p_1$  denote Ivlev's forage ratio index where  $r_1 =$  the

proportion of prey  $i$  in the diet of the predator,  $p_i =$  the proportion of prey  $i$  in the predator's environment. Here, proportions may be defined in numbers of individuals, by mass, or any other measurement which is biologically meaningful. If no preference is exhibited  $E_i = 1$ .

We now consider a second measure of preference. Since feeding rates are dependent on concentrations of all prey (allowing 0 as a concentration) a measure of selectivity independent of prey concentrations or composition is given by the relation between rate of consumption of prey  $i$  and prey concentrations. If this relation has a specific shape or form, or belongs to a particular family of functions, the relation can be completely determined by the parameter  $\Phi_i$  which indexes this family. Thus by considering rate of consumption as a function of prey concentrations, not proportion of prey in the diet, we are able to describe preference independently of a particular community studied.

A special case where we are able to describe the relation between consumption and concentrations may be found when considering filter feeders or passive predators. If the predator consumes prey  $i$  at a rate proportional to the concentration of prey  $i$  we may describe preference by  $\phi_i = (\text{amount of prey } i \text{ consumed in } \Delta t) / (\text{concentration of prey } i \times \Delta t)$ . The proper usage of  $\phi_i$  as an index of preference rests on the assumption that consumption is proportional to prey concentration. This assumption is unlikely for active predators, especially when food is not limiting, yet common to much of the prey preference theory.

The last index of preference we consider is Vanderploeg and Scavia's  $W_i$  (1979a) which is described for filter feeders or their "leaky-sieve" model. Let  $i=1, \dots, k$  be an index of the  $i$ 'th prey species present in the

community. Then their measure is found to be  $W_i = \phi_i / \sum_{j=1}^k \phi_j$ .  $W_i$  is hence a rate of consumption adjusted for other species present. If no preference is exhibited  $W_i = 1/k$ .

## 2.2 Properties of Indices

We first consider  $\phi_i$  and  $W_i$  as measures of prey preference for filter feeders or predators which consume a prey at a rate proportional to the concentration of that prey. Adjusted for the species present in the predator's community Vanderploeg and Scavia's  $W_i$  is independent of concentration but dependent on presence or absence of any particular prey species.  $\phi_i$  is, however, independent of both species concentration and composition. Thus when considering filter feeders, it is  $\phi_i$ , not  $W_i$  which should be considered.

Though  $W_i$  was proposed in place of  $E_i$ ,  $W_i$  and  $E_i$  are, in fact, proportional to each other with the constant of proportionality being a function of prey concentrations (Vanderploeg and Scavia, 1979a). As neither is independent of species composition,  $W_i$  has little advantage over Ivlev's original index in practices where species composition as well as species abundances may change from community to community.

In general we wish to obtain  $\phi_i$ , the parameter which governs feeding rates in terms of prey concentrations. When this functional form is unknown we cannot obtain  $\phi_i$  experimentally, in which case inferences concerning selection cannot directly be made between communities. However, it is reasonable to consider relative preferences of different prey within a community, though this relative preference will be dependent on the specific prey concentrations. If relative preferences are compared between studies any differences are the combined effect of changes in prey

concentrations and changes of conditions apart from prey concentrations. If however prey concentrations are identical, comparisons can be made without the confounding factor of change in prey concentrations. An example where this commonly occurs is for predators of the same community. Comparison of preference for different predators will be discussed in section 2.3.

In ignorance of the functional form relating consumption of prey and prey concentrations we again consider the properties of  $E_i$  and related preference indices. When comparing prey preference focus is not the preference for one prey but rather the relative preference between prey. Consider two prey called a and b. If we let  $E'_a$  and  $E'_b$  be indices of preference, not necessarily identical to  $E_i$ , the fraction  $f_{a,b} = E'_a/E'_b$  may be of primary interest thus making it irrelevant whether  $E'_a$  and  $E'_b$  are multiplied by a constant or not. When making comparisons within or between study populations through the use of  $f_{a,b}$ , the choice of which index to use among those motivated by  $E_i$  becomes an irrelevant question when the indices differ by only a multiplicative constant. The new indices have little advantage over Ivlev's original forage ratio index when making comparisons of preferences between experiments or communities where species composition may change.

Strauss (1979) proposes the linear measure  $L_i = r_i - p_i$  in place of  $E_i$  as the estimates of  $E_i$  may, depending on  $r_i$  and  $p_i$ , have large (statistical) variances. However  $L_i$  does not have the biological motivation of  $E_i$  or  $W_i$  and its greatest value is as a second measure of selectivity, as it contains information not available in  $E_i$  alone.

However, if we are to consider a  $2k$  dimensional vector which describes preference we might consider  $(r_i, p_i)$  for the  $k$  prey species present. Both  $r_i$  and  $p_i$  have an interpretation apart from the other, and from the  $(r_i, p_i)$

we may derive different measures of preference. Practically,  $r_i$  and  $p_i$  are often estimated in a way which assures their statistical independence thus allowing behavior of estimates of functions of  $r_i$  and  $p_i$  to be more easily described. Most importantly though, by considering  $(r_i, p_i)$  for the prey present we may calculate the  $E_i$  or  $L_i$  but do not run the risk of extrapolating  $E_i$  or  $L_i$  to unobserved prey concentrations where, depending on the functional relationship between feeding rates and prey concentrations, we expect to observe different  $E_i$  or  $L_i$ .

A shortcoming of the  $(r_i, p_i)$  is dependence on species composition or concentrations. In response to this shortcoming consider  $s_i$  = rate of consumption of prey  $i$ . From the  $s_i$  we can obtain the  $r_i$ . If ignorant of the relationship between the  $s_i$  and the  $p_i$  the only comparisons possible will be between prey within communities. It is only for the filter feeder that the  $s_i$  are proportional to the  $p_i$ . Since  $r_i = s_i / \sum s_i$ ,  $r_i$  and  $s_i$  are proportional to one another and it is reasonable to consider  $r_i$  because of its natural interpretation (Ivlev, 1961; Paloheimo, 1979) and the value of 1 for  $r_i/p_i$  in the absence of preference.

### 2.3 Preference of the Population vs. Average Preference of Individuals

Preference may be described for the population or the individual. A distinction between these two preferences is usually not made; an exception is found in Chesson (1983). As we expect at least some differences between individuals, these preferences will not in general be the same for preferences defined in terms of the proportions  $r_i$  and  $p_i$ , such as  $E_i$ . When considering preference for the population, interest may center on preference of the population as a whole, or the average of the preferences of the individual predators. Unless each predator feeds at the same rate when considering total consumption, these preferences will not be the same.

For population studies the former is appropriate and for behavior studies the latter may be of interest.

Let  $j=1, \dots, N$  index the predator population. To describe preference of the population consider

$$\begin{aligned} \omega_i &= \text{proportion of prey taxa } i \text{ in the diet of the predator population} \\ &= (\text{amount taken of taxa } i) / (\text{amount taken of all prey}) \\ &= N\mu_i / N\mu_{(n)} = \mu_i / \mu_{(n)}, \text{ where } N \text{ is the predator population size,} \end{aligned}$$

$\mu_i = E[T_{i,j}] = \text{average amount of prey } i \text{ taken by the predators and}$   
 $\mu_{(n)} = E[n_j] = \text{average amount of all prey taken by the predators.}$  The amount of prey taken by a predator is defined for a predescribed length of time over which, for statistical considerations, we assume change in prey abundance to be negligible. The expectations are taken both over predator (over  $j$ ) and over conceptual replications of the feeding of the individual predators. To describe average preference of individuals define  $\theta_i = E[r_{i,j}]$  where  $r_{i,j}$  is the expected proportion of taxa  $i$  in the diet of the  $j$ 'th predator. The  $\omega_i$ ,  $\theta_i$  and the  $p_i$  can then be used to describe preference of the population and average of individual preferences.

When considering preference defined by  $\phi_i$  the ambiguity between preference of the population and average of individual preferences is avoided. Let  $\mu_{i,j}$  = amount of prey  $i$  taken by the  $j$ 'th member of the predator population, and let  $c_i$  = concentration of prey  $i$ . If  $\phi_{i,j}$  represents  $\phi_i$  for the  $j$ 'th predator, and if  $\psi_i$  = preference of the population, then  $\psi_i = N\mu_i / c_i = \sum_{j=1}^N \mu_{i,j} / c_i = \sum \phi_{i,j} = N\bar{\phi}_i$  where  $\bar{\phi}_i = \sum_{j=1}^N \phi_{i,j} / N$ .

*Note.* Though we will almost always be interested in the preference for many prey, when considering the behavior of the indices we often, for the sake of simplicity of presentation, consider only one prey taxa and without

confusion leave off the subscript  $i$ . We may then, depending on our biological motivation, express preference (for a particular prey) in terms of  $\omega$ ,  $\theta$ ,  $r_j$  and  $p$ , or  $\phi_j$  and  $\psi$ .

### 3. ESTIMATION

We now consider the estimation of  $\omega$ ,  $\theta$ ,  $r_j$  and assume  $p$  is estimated by an independent measurement. In Strauss (1982) the total amount of prey taken was considered as a fixed quantity for each predator though this quantity was allowed to vary between fishes. Feeding rates are in general random and for either a homogeneous or heterogeneous predator population, a source for different observed feeding rates for different predators. Here we assume that feeding rates are random.

Consider a study in which we observe the consumption for a fixed period of time for  $k$  independent predators. This may be accomplished experimentally by placing  $k$  fish in tanks for a fixed amount of time and analyzing gut contents. The assumption of independence may be made more just if fish are placed in separate tanks. Observations may be made in the field, though our ability to observe a predator may be dependent upon the choice of prey thus introducing an unknown bias in any measure of selectivity. Therefore In both the field and the lab, our estimates apply to parameters of hypothetical populations which are determined by the scientist's sampling scheme, as in practice we are not able to sample all individuals with equal probability. As the deviation from the assumption of equal probability sampling is unknown to the scientist we are not able to eliminate any biases introduced. Hence our indices of preference lose their strength as absolute measures of preference and their primary value occurs when making comparisons between or within communities.

### 3.1 Estimation for Population Preference

Ignoring unknown biases due to the sampling scheme or redefining the parameters governing the feeding rates to include this bias we assume we have  $k$  independent, identically distributed observations. Then the ratio estimate for  $\omega$ , is

$$\hat{\omega} = (\sum_{j=1}^k T_j / k) / (\sum_{j=1}^k n_j / k) \text{ and is distributed approximately}$$

$$N(\mu_\omega, \sigma_\omega^2) \text{ where } \mu_\omega = \mu_t / \mu_n,$$

$$\sigma_\omega^2 = (\mu_t / \mu_n)^2 (CV(T)^2 + CV(n)^2 + CV(T)CV(n)\rho(T,n)) / k,$$

$CV(X) = \text{var}(X)^{1/2} / E[X]$  and  $\rho(X,Y)$  is the correlation between  $X$  and  $Y$

(Cochran, 1977). As  $\hat{\omega}$  is a ratio estimate it will be biased, especially for small  $k$ .

### 3.2 Estimation of Individual Preferences

We now consider the estimation of  $\theta = E[r_j]$  and  $\sigma_r^2 = \text{var}(r_j)$ . If we assume the time period over which we observe the predators is a random sample of all such periods possible, and predators are sampled at random, then  $\hat{r}_j$  = observed proportion of prey of interest in the diet of the  $j$ 'th predator is unbiased for  $\theta$ . Hence

$\hat{\theta} = \sum_{j=1}^k \hat{r}_j / k$  is unbiased for  $\theta$  with an unbiased estimate of  $\text{var}(\hat{\theta})$  being  $\hat{\sigma}_{\hat{\theta}}^2 = (1/k) \sum (\hat{r}_j - \theta)^2 / (k-1)$ . Note that  $\hat{\omega} = \sum n_j \hat{r}_j / \sum n_j$ , a weighted average of the  $\hat{r}_j$ , and hence the weighted and unweighted means of the  $\hat{r}_j$  estimate different parameters because of the randomness of  $n_j$ , or the observed feeding rates.

To estimate  $\text{var}(r_j)$  we could repeat the observations for the individual predators. We then could estimate  $\text{var}(r_j)$  as a standard problem in analysis of variance components (Snedecor and Cochran, 1980). This however requires the assumption that feeding rates for different time periods are independent and identically distributed, which may or may not

be reasonable depending on the organisms being studied. A similar assumption is that the identity of the next prey consumed is independent of the prey consumed before. If such an assumption is reasonable the waiting times between the consumption of prey may be interpreted as the waiting times in a renewal process, and the identification of the prey eaten as an associated random variable (Karlin and Taylor, 1975). Since observations stop at a predetermined time we do not observe the "terminal observation" and hence unbiased estimates in the fixed sample case will be unbiased here as well (Kremers, 1984).

To estimate  $\text{var}(r_j)$  observe

$$\begin{aligned}\text{Var}(\hat{r}_j) &= \text{var}(E[\hat{r}_j | j]) + E[\text{var}(\hat{r}_j | j)] \\ &= \text{var}(r_j) + E[\xi_j^2]\end{aligned}$$

where  $\xi_j^2$  is measurement error variance of  $\hat{r}_j$  for  $r_j$ . Hence

$$\text{var}(r_j) = \text{var}(\hat{r}_j) - E[\xi_j^2].$$

If  $r_j$  is defined by number of organisms eaten  $\hat{r}_j$  is the mean of Bernoulli random variables, and  $\hat{\xi}_j^2 = \hat{r}_j(1-\hat{r}_j)/(n_j-1)$  is unbiased for  $\xi_j^2$ . Hence

$$\hat{\sigma}_r^2 = \sum(\hat{r}_j - \theta)^2 / (k-1) - (1/k) \sum \hat{r}_j(1-\hat{r}_j) / (n_j-1)$$

is unbiased for  $\text{var}(r_j)$ . An estimate of  $\text{var}(\hat{\sigma}_r^2)$  is

$$\text{vâr}(\text{vâr}(r_j)) + (1/k) \text{vâr}(\hat{\xi}_j^2) - 2\text{cov}(\hat{\xi}_j^2, \sum(\hat{r}_j - \theta)^2 / (k-1))$$

and is described further in the Appendix.

If  $\hat{r}_j$  is defined in amounts other than number of organisms,  $\hat{r}_j$  is a ratio of random variables in the fixed sample size case and hence we do not in general have an unbiased estimate of  $\xi_j^2$ . However we may use the somewhat *ad hoc* procedure of applying the approximate formula for the variance of a ratio from the fixed sample size setting, to this setting where sample size is random.

*Remark.* To make the discussion of the concept of preference and the statistical analysis clearer we have frequently considered only one prey species at a time. In practice we will likely consider preference for many or all of the prey present. When considering preference for all prey present the estimates of  $r_{i,j}$  and  $r_{h,j}$ , and  $\mu_{n_i}$  and  $\mu_{n_h}$  will be dependent. This dependence must be considered when making any comparisons between preferences for different prey.

#### 4. CONCLUSION

Many indices of prey preference have been proposed since Ivlev's forage ratio index in attempts to eliminate dependence on species abundance but, as shown above and in Paloheimo(1979), these indices are dependent on species composition. However this difficulty is only minor in that we are usually interested in comparing preferences for different prey.

If the functional form relating prey consumption and concentration is known we may fully describe selection by the parameter governing this relation. In the case of filter feeders the parameter is  $\phi_i$ .

While all indices proposed are a reduction of the 2-dimensional vectors  $(r_i, p_i)$  to scalars, preference is most fully described by the  $(r_i, p_i)$ , when the relation between prey consumption and concentrations is unknown. From the  $(r_i, p_i)$  we may derive either the ratio type or linear indices. Further by considering the  $(r_i, p_i)$  the dependence of preference on concentrations is described and there is not the risk of incorrectly extrapolating the index of preference to other concentrations. Also if the  $(r_i, p_i)$ , or more correctly  $(s_i, p_i)$ , are described for a range of concentrations we may begin to empirically describe a relation between prey consumption and concentration.

Also fundamental to the concept of preference is the distinction between preference by the population and preference by individuals, as these are different biological, mathematical and statistical problems.

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## 6. APPENDIX

$$\text{var}(\hat{r}_j) = \text{var}\left(\frac{\sum(\hat{r}_j - \theta)^2}{(k-1)}\right) + \frac{1}{k}\text{var}(\hat{\xi}_j^2) - 2\text{cov}\left(\frac{\sum(\hat{r}_j - \theta)^2}{(k-1)}, \frac{\sum\hat{\xi}_j^2}{k}\right)$$

An unbiased estimate of  $\text{var}\left(\frac{\sum(\hat{r}_j - \theta)^2}{(k-1)}\right)$  is

$$\left(\frac{2}{(k+1)}\right)\left(\frac{\sum(\hat{r}_j - \theta)^2}{(k-1)}\right)^2 + \left(\frac{k+3}{(k+1)}\right) \left\{ \frac{k(k+1)}{(k-1)(k-2)(k-3)}\sum(\hat{r}_j - \theta)^4 - \frac{3}{(k-2)(k-3)}\left(\sum(\hat{r}_j - \theta)^2\right)^2 \right\},$$

(Cramer, 1946).

An unbiased estimate of  $\text{var}(\hat{\xi}_j^2)$  is  $\frac{\sum(\hat{\xi}_j^2 - (\sum\hat{\xi}_j^2/k))^2}{(k-1)}$ , and of

$$\text{cov}\left(\frac{\sum(\hat{r}_j - \theta)^2}{(k-1)}, \frac{\sum\hat{\xi}_j^2}{k}\right),$$

$$\frac{1}{k} \left\{ \frac{k}{(k-1)(k-2)}\sum(\hat{r}_j - \theta)^2\left(\theta_j^2 - \frac{\sum\hat{\xi}_j^2}{k}\right) \right\}.$$