

MEASURING PREFERENCE IN SELECTIVE PREDATION¹

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Abstract. Selective predation occurs when the relative frequencies of prey types in a predator's diet differ from the relative frequencies in the environment. A measure of preference is proposed which is derived from a simple stochastic model involving probability of encounter and probability of capture upon encounter. The measure is applicable to any number of prey types and methods of estimation are given for both constant and changing prey numbers. Because the measure is based on a biological model, it can be manipulated and interpreted in a meaningful way.

Key words: Estimation; preference; selective predation.

INTRODUCTION

There have been many attempts to quantify selective predation, the situation in which the relative frequencies of prey types in a predator's diet differ from the relative frequencies in the environment, e.g., Ivlev (1961), Gerald (1966), Murdoch (1969), Paulik and Robson (1969), Rapport and Turner (1970), Cook (1971), Manly et al. (1972). The measure I advocate is not new; it is in fact identical to that used by Manly (1973) for 2- and 3-prey situations and can be shown to be equivalent to measures used by other authors. However Manly et al. (1972) suggested this measure on purely intuitive grounds whereas it can be derived as a stochastic model from basic biological considerations with resulting advantages in ease of interpretation and general applicability to a wide range of circumstances.

DERIVATION OF THE MEASURE

Suppose there are m types of prey and n_i ($i = 1, \dots, m$) individuals of type i so that

$$N = \sum_{i=1}^m n_i$$

is the total number of prey. Let p_i be the probability that a predator captures an individual of type i , given it encounters this type.

If the probability, f_i , of encountering prey of type i is some function of n_1, \dots, n_m , i.e., $f_i = f_i(n_1, \dots, n_m)$ where

$$\sum_{i=1}^m f_i = 1,$$

then the probability of making a capture of any type at the first encounter is

$$\sum_{i=1}^m p_i f_i.$$

It follows that

$$\left(1 - \sum_{j=1}^m f_j p_j\right)^{l-1} \left(\sum_{j=1}^m p_j f_j\right)$$

is the probability that the first capture is made at the l th encounter and the probability that the first capture occurs at the l th encounter and is of type i is

$$\left(1 - \sum_{j=1}^m f_j p_j\right)^{l-1} p_i f_i. \quad (1)$$

Hence, the probability that the first prey captured is of type i can be found by summing over all values of l , i.e., the probability of capturing type i first is

$$\sum_{l=1}^{\infty} \left(1 - \sum_{j=1}^m f_j p_j\right)^{l-1} p_i f_i = p_i f_i \left(\sum_{j=1}^m p_j f_j\right)^{-1}. \quad (2)$$

Suppose the probability of encounter of type j is directly proportional to the relative abundance of type j , i.e., $f_j = \beta_j n_j N^{-1}$ for constant β_j , $j = 1, \dots, m$,

$$\sum_{j=1}^m \beta_j n_j = N.$$

The β_j can be interpreted as being proportional to the area about a prey of type j within which it will be detected by the predator. Then the probability of capturing type i becomes

$$p_i \beta_i n_i \left(\sum_{j=1}^m \beta_j n_j p_j\right)^{-1}$$

or when $f_j = n_j N^{-1}$, $j = 1, \dots, m$ it is

$$p_i n_i \left(\sum_{j=1}^m n_j p_j\right)^{-1}.$$

Replacing $p_i \beta_i$ with α_i , $i = 1, \dots, m$ we get the probability of a predator eating type i , P_i , as

$$P_i = \alpha_i n_i \left(\sum_{j=1}^m \alpha_j n_j\right)^{-1}. \quad (3)$$

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TABLE 1. Measures of preference and their relation to α

Measure	Definition	Relation to α	Comments
Described by Ivlev (1961)	$E_i = r_i n_i^{-1}$	$\alpha_i = E_i \left(\sum_{j=1}^m E_j \right)^{-1}$	n_i assumed constant $0 \leq E_i \leq \infty$
Forage ratio, Gerald (1966)	$FR_i = r_i n_i^{-1}$ where r_i and n_i are proportions	$\alpha_i = FR_i \left(\sum_{j=1}^m FR_j \right)^{-1}$	n_i assumed constant $0 \leq FR_i \leq \infty$
Electivity index, Ivlev (1961)	$E_i = (r_i - n_i)(r_i + n_i)^{-1}$ where r_i and n_i are percentages	$\alpha_i = \left(\frac{1 + E_i}{1 - E_i} \right) \left(\sum_{j=1}^m \frac{1 + E_j}{1 - E_j} \right)^{-1}$	n_i assumed constant $-1 \leq E_i \leq 1$
Operational measure of preference, Murdoch (1969)	c such that $r_1/r_2 = c n_1/n_2$ where r_1, r_2, n_1, n_2 are proportions	$c = \alpha_1/\alpha_2$	n_i assumed constant 2-prey case only
Instantaneous selective coefficient, Cook (1971)	$y = 1 - (r_1 n_2 / r_2 n_1)$ where r_1, r_2, n_1, n_2 are proportions	$1 - y = \alpha_1/\alpha_2$	n_i assumed constant 2-prey case only
Survival ratio, Paulik and Robson (1969)	$s_1/s_2 = (r_1 n_2)/(r_2 n_1)$	$s_1/s_2 = \alpha_1/\alpha_2$	n_i assumed constant 2-prey case only
Preference coefficients, Rapport and Turner (1970)	p_i such that the proportion of time devoted to capturing type i is $p_i m^{-1}$, $i = 1, \dots, m$	not directly comparable	assumes unlimited number of prey
Manly et al. (1972)	α such that the probability of next prey eaten being type 1 is $P_1 = n_1/(n_1 + \alpha n_2)$ and being type 2 is $P_2 = \alpha n_2/(n_1 + \alpha n_2)$	$\alpha_1 = 1(1 + \alpha)^{-1}$ $\alpha_2 = \alpha(1 + \alpha)^{-1}$	n_i not assumed constant, 2-prey case only

The α_i are a measure of the deviation of the probability of eating type i from

$$n_i \left(\sum_{j=1}^m n_j \right)^{-1}.$$

Thus, they are a measure of relative preference. Since only their relative values are of consequence, it is convenient to normalize the α_i so that

$$\sum_{i=1}^m \alpha_i = 1.$$

(This is essentially what Manly [1973] does when he defines his

$$\beta_i = \alpha_i \left[\sum_{j=1}^3 \alpha_j \right]^{-1},$$

$i = 1, 2, 3$.) In cases in which the probability of encounter of type i is directly proportional to the relative abundance of type i , the α_i represent the product of a measure of the probability of encounter, β_i , and a measure of the probability of capture given encounter, p_i . One can also think of the predator behaving as if there were $\alpha_i n_i$ individuals of prey type i instead of n_i and that P_i is the probability of selecting, at random, a prey of type i from this distorted population. This is the intuitive reasoning on which the α_i were originally based (Manly et al. 1972).

For the m -prey case, we have an m -dimensional vector

$$\underline{\alpha} = \begin{bmatrix} \alpha_1 \\ \vdots \\ \alpha_m \end{bmatrix}$$

representing relative preferences such that

$$\sum_{j=1}^m \alpha_j = 1.$$

When selective predation does not occur, $\alpha_i = m^{-1}$, $i = 1, \dots, m$. If $\alpha_i > m^{-1}$, then more of species i occurs in the diet than expected and if $\alpha_i < m^{-1}$, less occurs than expected.

Many measures used previously can be regarded as variations of $\underline{\alpha}$, although they often apply only to restricted cases (Table 1).

Preference, as defined by $\underline{\alpha}$, reflects any deviation from random sampling of the prey and therefore depends on a multitude of factors such as prey distribution in space, prey escape mechanisms, predator hunger, and many others. It is a somewhat arbitrary decision to select 1 group of factors as appropriate to a measure of preference and try to eliminate the effect of the remaining. In eliminating "capturability" from Rapport and Turner's (1970) measure of preference one might eliminate the main reason why a predator prefers a particular prey, i.e., it is easier to catch. Ivlev (1961:50) remarks that preference (when prey

TABLE 2. Preference vectors for 4 species of fish. (Data from Ivlev 1961.) α : estimated from data with all 4 prey types present. α' : calculated from α by eliminating α_1 . α'' : estimated from the experiment in which chironomid larvae were absent

	Carp	Bream	Roach	Tench
Chironomid larvae	.412	.275	.143	.437
Amphipods	.306	.381	.407	.259
Fresh water isopods	.241	.308	.331	.297
Molluscs	.041	.036	.119	.007

	α'				α''			
	Carp	Bream	Roach	Tench	Carp	Bream	Roach	Tench
Amphipods	.547	.628	.625	.482	.520	.526	.475	.460
Fresh water isopods	.378	.322	.161	.513	.410	.425	.386	.528
Molluscs	.075	.050	.214	.005	.069	.050	.139	.012

are "equally accessible") and accessibility of prey cannot be clearly distinguished as they may both be simultaneously influenced by the same feature. The derivation of α in terms of encounter and capture upon encounter does provide a distinction between factors affecting encounter, e.g., prey distribution, predator searching behavior, and those affecting capture upon encounter, e.g., ability of prey to escape, the amount of effort expended by the predator. The simple model discussed in this paper shows how the effects of these factors can be combined to describe the result of predation.

Thus far we have seen the role of α as a parameter in the model for consumption of a single prey. By assuming that successive prey are captured according to the same model, we can obtain stochastic models for the composition of the diet after r prey have been consumed. These models, which are discussed in the next section, allow us not only to predict dietary composition given values of α but also to estimate α from field or experimental data.

ESTIMATION OF α

Suppose we obtain data on the composition of a predator's diet and the food available in the environment either by observation or experimentation. Let r_i be the number of prey type i in the diet ($\sum_{i=1}^m r_i = r$) and n_i be the number of prey type i in the environment, $i = 1, \dots, m$. We will see below that often r_i and n_i need only be relative proportions or percentages (i.e., $r = 1$ or 100). Denote the random vector with i th element representing r_i , $i = 1, \dots, m$ by \underline{R} . To estimate the α_i we distinguish 2 situations:

1) The n_i are constant over time or very nearly so. This is the case in which the number of prey eaten is extremely small compared to the number available (e.g., Ivlev's selective feeding experiments [1961]) or

replacement prey are added (e.g., Murdoch et al. 1975). Then \underline{R} has a multinomial distribution

$$P(\underline{R} = \underline{r}) = \frac{r!}{m! \prod_{i=1}^m r_i!} \left[\alpha_i n_i \left(\sum_{j=1}^m \alpha_j n_j \right)^{-1} \right]^{r_i}$$

and the maximum likelihood estimate of α_i , α_i , normalized to give

$$\sum_{i=1}^m \alpha_i = 1 \text{ is } r_i n_i^{-1} \left(\sum_{j=1}^m r_j n_j^{-1} \right)^{-1}, \quad i = 1, \dots, m.$$

Ivlev (1961) pointed out that the use of $r_i n_i^{-1}$ is meaningless as a measure of selectivity, but once it is normalized, it is immediately interpretable as an estimate of α_i . Another measure described by Ivlev (1961), the percentage of type i in the diet divided by the percentage of type i in the environment, also becomes identical to α_i after normalization, since the same estimate of α_i is obtained whether the r_i and n_i are numbers of prey or percentages.

The measure of "electivity" (Ivlev 1961),

$$E_i = (r_i - n_i)(r_i + n_i)^{-1}, \quad (4)$$

where r_i and n_i are percentages, was proposed to avoid the undesirable property of a measure ranging from 0 to infinity. This is not a problem with normalized measures. The main criticism of E is that it is not easily interpretable in biological terms. It compares prey type i with "the rest" whatever "the rest" may be and depends only on the ratio r_i/n_i . Consider the following 2 cases: (1) 25% of the diet and 50% of available food is contributed by prey type 1; and (2) 40% of diet and 80% of available food is contributed by prey type 1. The value of E_1 is -0.33 in both cases. Regarding all other prey types as "type 2," the estimate of α ,

$$\begin{bmatrix} \hat{\alpha}_1 \\ \hat{\alpha}_2 \end{bmatrix}, \text{ is } \begin{bmatrix} 0.250 \\ 0.750 \end{bmatrix} \text{ in case 1 and } \begin{bmatrix} 0.143 \\ 0.857 \end{bmatrix}$$

in case 2. Considering a value of E in isolation can be misleading as it suggests the predator's behavior towards prey type 1 is unchanged. However, the values

of α show that the predator's behavior is different in the 2 cases. In the first case, it is acting as if the prey were in the ratio $.25 \times n_1$ prey of type 1 to $.75 \times n_2$ prey of type 2, whereas in case 2 it is acting as if the ratio was $.143 \times n_1$ to $.857 \times n_2$.

Given α for m prey types, it is easy to eliminate 1 or more types and obtain a relative preference measure for those remaining. For example, if we have

$$\begin{bmatrix} \alpha_1 \\ \alpha_2 \\ \alpha_3 \\ \alpha_4 \end{bmatrix}$$

for 4 prey types, the new preference vector, after eliminating type 3, will be

$$\begin{bmatrix} \alpha_1 \\ \alpha_2 \\ \alpha_4 \end{bmatrix} = \begin{bmatrix} \alpha_1 (\alpha_1 + \alpha_2 + \alpha_4)^{-1} \\ \alpha_2 (\alpha_1 + \alpha_2 + \alpha_4)^{-1} \\ \alpha_4 (\alpha_1 + \alpha_2 + \alpha_4)^{-1} \end{bmatrix}.$$

Ivlev (1961:52, Table 9) collected data for 4 species of fish preying on 4 prey types. He repeated the experiment omitting 1 prey type, Chironomid larvae, (Ivlev 1961:54, Table 11) and commented on the difficulty of comparing values of E for the 2 experiments. Table 2 gives α estimated from the first set of data and then reduced to a 3-dimensional vector α by eliminating α_1 . Comparison of α' and α'' estimated from the second experiment shows quite good agreement allowing for experimental variation (Table 2). Thus, the measure proposed here is both more meaningful biologically and more flexible than Ivlev's (1961) index of electivity.

2) The n_i are changing. When a predator consumes a substantial proportion of the prey available (e.g., a predator feeding on an isolated patch of prey such as an aphid colony in which aphid instars could be regarded as types) or when it is not possible to replace prey as they are consumed (e.g., Manly et al. 1972), the changing numbers of prey must be taken into account. In this case, \mathbf{R} has a noncentral multivariate hypergeometric distribution with

$$P(\mathbf{R} = \mathbf{r}) = \prod_{i=1}^m \binom{n_i}{r_i} \int_0^1 \prod_{i=1}^m (1 - t^{\alpha_i})^{r_i} dt, \quad (5)$$

$$\text{where } c = \left(\sum_{i=1}^m \alpha_i (n_i - r_i) \right)^{-1} \quad (\text{Chesson 1976}).$$

An approximate moment estimator for α has been found (Manly 1974) and tables of standard errors are available for the 2-prey case (Manly 1972).

In general, maximum likelihood estimates for α can be found from the likelihood function (Eq. 5) by non-linear optimization techniques. Estimates from artificial data using the subroutines DCADRE (integration) and ZXMIN (optimization) from the International Mathematical and Statistical Library (IMSL) (1975) agreed quite well with Manly's (1974) estimator. (To use Manly's [1974] formula, the single observation was regarded as an estimate of the mean.)

A further advantage of the measure α proposed here is that it can be estimated directly from investigation of the probabilities of encounter and capture upon encounter. Such estimates can be compared with those obtained by the methods described above. Also, knowledge of how factors such as temperature, density of prey, density of predators, etc., affect encounter and capture can be used to predict changes in the composition of the predator's diet. In deriving the measure, the probability of encounter was assumed to be directly proportional to relative density. If this is not the case, or if the probability of capture on encounter varies with relative density of prey types, then "switching" could result (see Murdoch 1969, Murdoch and Marks 1973, Murdoch et al. 1975). Various modifications such as these will probably make analytic development impossible but the measure can be incorporated readily and manipulated in simulation models because of its obvious biological interpretation.

CONCLUSION

α is a useful measure for quantifying predator preference in selective predation because it can be derived from a stochastic model based on simple biological considerations. It encompasses an arbitrary number of prey types of both constant and changing prey densities. It can be modified to cater for special mechanisms and can be incorporated readily into mathematical models. The fact that it is based on a biological model indicates that it is useful in prediction as well as estimation, a property lacking in many selectivity measures.

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