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THE ESTIMATION AND ANALYSIS OF PREFERENCE AND ITS RELATIONSHIP TO FORAGING MODELS[1]

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Abstract. This paper summarizes methods of estimation and analysis for the measure of consumer food preferences originally derived by Manly et al. (1972) and further developed by Chesson (1978). Unlike many alternative measures this measure of preference does not change with changes in food densities unless consumer behavior also changes. This measure is shown to relate in a simple way to parameters, such as clearance and attack rates, which appear in certain commonly used models of foraging behavior.

Key words: attack rates; clearance rates; functional response; preference; selective predation.

INTRODUCTION

In an earlier paper (Chesson 1978) I showed that Manly's measure of preference (Manly et al. 1972) could be derived from a simple stochastic model which incorporated the probability of prey encounter and the probability of capture given encounter. In this paper I summarize the techniques which are available for estimating this measure of preference and indicate its relationship to some of the commonly used models of foraging behavior.

DEFINITION

Suppose a consumer has a choice of m food types, and the number of type i present is n_i, $i = 1, \ldots, m$. The probability that the next food type consumed is of type i is given by the formula

$$P_i = \frac{\alpha_i n_i}{\sum_{j=1}^{m} \alpha_j n_j}, \tag{1}$$

where the α_i are positive numbers ranging from 0 to 1. This formula is derived assuming that encounters with food items which do not result in consumption do not affect the consumer's subsequent behavior (Chesson 1978). Note that when the α_i are all equal ($\alpha_i = 1/m$, $i = 1, \ldots, m$), then

$$P_i = \frac{n_i}{\sum_{j=1}^{m} n_j},$$

and the consumer is sampling at random from the available food types.

In the simplest case, in which food consumption does not significantly reduce the abundances of each of the food types, α_i is simply estimated as the ratio

of the amount of food type i in the diet to the amount of food type i in the environment, scaled so that the α_i sum to 1 (see below). In other situations different estimation formulae are required, but they all estimate the same theoretical quantity, α_i. These α_i can be interpreted as the proportion of the diet which would consist of type i if all food types were present in equal numbers in the environment (i.e., n_i all equal). From this interpretation it is clear that the α_i are relative measures which indicate the preference of a consumer for a food type relative to the other food types present. This agrees with the intuitive meaning of the word "preference."

Using α, the vector with i^{th} component α_i, one can measure deviations of the consumer from random sampling of its food types, and then, if appropriate, investigate further which factors are responsible for this deviation (e.g., differences in ease of detection, prey escape responses, palatability, etc.). There seems to be no good a priori reason why any particular set of factors should be automatically excluded from contributing to preference. Rather than eliminating them to arrive at the ill-defined concept of "innate preference" it is much more informative to regard preference as the end result of several factors and then set about assessing the roles of these factors.

A major fault of many existing measures of preference (e.g., Savage 1931, Ivlev 1961, Rapport and Turner 1970, Strauss 1979, Freed 1980) which has been pointed out repeatedly (Jacobs 1974, Yurochko 1976, Cock 1978, Paloheimo 1979, Vanderploeg and Scavia 1979, Zaret 1980), is that their values depend not only on consumer behavior but also on the numbers of each food type present. This dependence on food density precludes comparisons between observations or experiments carried out at different food densities, and therefore such measures cannot be used to investigate the effect of food density on preference. On the other hand, α does not change with food density unless consumer behavior changes. It is the appropriate measure for detecting behavior such as "switching" (Murdoch

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1969) in which preference for a food item increases as the relative density of that food item increases.

If the diet of a consumer consists entirely of food type i, then $\alpha_i = 1$. Conversely, if food type i is not represented in the diet, then $\alpha_i = 0$. Strauss (1979) criticizes this property of α because it does not distinguish between the situation in which food type i is very abundant and the consumer does not eat any of it, and the situation in which food type i is very rare and may be absent from the diet by chance. However, it is necessary to distinguish between the measure of preference and the ability of a situation to produce accurate estimates. In both of the above situations the best estimate of α_i is 0. There is no reason to assign any other particular value to α_i since the consumer did not include any of food type i in its diet. It is clear that the second situation, in which food type i was very rare, provides a poor opportunity for estimating the preference for that food type; therefore we cannot have much confidence in this zero value. If a more accurate estimate is required, then many repeated observations must be made or a higher food density used. Strauss's measure of preference, which increases as the density of the food type decreases even when the predator consumes none of that food type, results in a biased measure which confounds the actual preference value with a measure of the degree of confidence one has in the estimation of it. His measure will suggest changes in the behavior of the predator when in reality all that have changed are the relative densities of the food types.

Optimal foraging theory in its simplest form (e.g., Charnov 1976) predicts an abrupt change from a consumer including none of a particular food type in its diet (i.e., $\alpha_i = 0$), to the consumer eating every item of that food type which it encounters (i.e., a fixed α_i determined by relative encounter rates), depending on the absolute abundance of more valuable food types. More recent modifications to the theory take into account factors such as exploitation of the food supply by the consumer, and predict a more gradual change in preference as food densities change (e.g., Hubbard et al. 1982). These changes in preference can be conveniently measured by α since the measure itself does not change with food density.

ESTIMATION

Case 1. No food depletion (n_i assumed constant)

If food densities do not change appreciably during an experiment or observational period, either because food items are replaced by the experimenter as they are eaten, or due to reproduction or immigration of the food item, or because reduction in food density due to consumption is insignificant compared to the total amount of food available, then α_i is estimated by the maximum likelihood (ML) estimator

$$\hat{\alpha}_i = \frac{r_i/n_i}{\sum_{j=1}^{m} r_j/n_j}, \quad i = 1, \dots, m \quad \text{(Chesson 1978)} \quad (2)$$

where r_i is the number of items of food type i in the consumer's diet. The r_i and n_i can be expressed as the proportion or the percentage of food type i in the diet and environment, respectively, without affecting the value of $\hat{\alpha}_i$. Manly (1974) provides approximate formulae for the bias, variance, and covariances of the $\hat{\alpha}_i$, and describes methods for constructing confidence intervals and testing various hypotheses.

Case 2. Food depletion (n_i not assumed constant)

Except in the special circumstances described in Case 1 above, feeding by the consumer will reduce the amount of food available. In this situation an approximate moment estimator of α_i is

$$\hat{\alpha}_i = \frac{\ln((n_{i0} - r_i)/n_{i0})}{\sum_{j=1}^{m} \ln((n_{j0} - r_j)/n_{j0})}, \quad i = 1, \dots, m$$

$$\text{(Manly et al. 1972)} \quad (3)$$

where n_{i0} is the number of items of type i present at the beginning of a foraging bout. The actual ML estimator can be found by numerical integration but Eq. 3 appears to be adequate in most cases (Chesson 1978). Again, bias, variance, covariance, and statistical tests are described by Manly (1974).

Case 3. Order of selection known

In some situations it is possible to observe not only the number of each food type eaten but also the order in which the items are eaten (e.g., Freed 1980). This extra information can be used to obtain a more precise estimate of α_i (Manly 1980). A straightforward computer program is required to perform the necessary iterative procedure.

For the special case in which only the first item eaten by a consumer is recorded, and the observation is repeated for K consumers, the ML estimator of α_i, obtained by maximizing the likelihood function based on Eq. 1, is

$$\hat{\alpha}_i = \frac{k_i/n_i}{\sum_{j=1}^{m} k_j/n_j}, \quad i = 1, \dots, m, \quad (4)$$

where k_i is the number of consumers whose first food item was of type $i \left(\sum_{i=1}^{m} k_i = K \right)$.

Cases 1, 2, and 3 above (with the exception of the special case in 3) provide estimates of α for a single consumer individual.

In practice it is common to replicate feeding trials by using a different consumer individual each time, or by making field observations on several individuals

with a view to characterizing preference values for the consumer population as a whole. This results in a sample of K values of α, where K is the total number of consumers observed. Note that a value of α is estimated for each individual consumer. If different individuals have different preferences and only a single value of α is calculated by lumping the data for several individuals, then this will give a different result from that obtained by averaging the K values of α and phenomena such as negative switching may appear, even though individual behavior remains constant (Chesson 1983).

Since ML estimators are asymptotically distributed as normal random variables and the preferences of individual consumers are likely to vary about a population mean, the K values of $\hat{\alpha}$ obtained in cases 1 or 3 above can be regarded as a sample from a multivariate normal distribution, provided K is sufficiently large. The same result holds for the moment estimator in case 2 (Manly 1974). This means that standard statistical tests can be used to test hypotheses involving the α's. For example, when there are only two food types ($m = 2$), the null hypothesis of no preference (i.e., $\alpha_1 = \alpha_2 = 0.5$), against the alternative, $\alpha_1 \neq \alpha_2$, can be tested by calculating the t statistic,

$$ t = \frac{\bar{\alpha}_i - 0.5}{\sqrt{s^2/K}} \quad \text{for either } i = 1 \text{ or } 2, \quad (5) $$

where $\bar{\alpha}_i$ is the sample mean and s^2 is the sample variance of the K estimates of α_i. The null hypothesis is rejected if $|t|$ exceeds the appropriate critical point of the t distribution on $K - 1$ degrees of freedom. Similarly, two samples of α_1 or α_2 obtained from different populations of consumers or under different experimental conditions but with the same two food types present can be compared using the standard t test for the difference between two means.

When there are more than two food types ($m > 2$) the multivariate analogues of the above methods can be used to test hypotheses about the column vector $(\alpha_1, \alpha_2, \ldots, \alpha_{m-1})'$ (see Anderson 1958). A vector of length $m - 1$ rather than m is used because α_m is determined by the remaining $m - 1$ values ($\alpha_m = 1 - \sum_{j=1}^{m-1} \alpha_j$), and therefore the variance-covariance matrix of α would be singular.

PREDICTION

An added advantage of using α as a measure of preference is that it can be used to predict consumer preference in situations other than the ones in which the estimates of α were originally obtained. These predicted values can be used as a null hypothesis against which actual experimental values can be compared. An example is provided in Chesson (1978) using data from Ivlev (1961) on the preference of fish for four species of prey. Given $\alpha = (\alpha_1, \alpha_2, \alpha_3, \alpha_4)'$ one can

predict the preference for any subset of the four prey species, assuming predator behavior does not change with changes in the number of prey types available. The predicted preference vector (α^*) for the two-species system obtained by eliminating, say, species 2 and 4 would be $\alpha^* = [\alpha_1/(\alpha_1 + \alpha_3), \alpha_3/(\alpha_1 + \alpha_3)]'$. A significant difference between preference estimated in an experiment involving only species 1 and 3, and the predicted preference vector α^*, would indicate that the predator exhibited different behavior towards particular prey types depending on which other prey types were present.

A second example is the use of preference values to infer the relative preference of a consumer for two food types, given the consumer's preference for each of them relative to a third food type. Scott and Murdoch (1983) estimated the preference of the aquatic bug *Notonecta hoffmani* for *Daphnia* relative to *Ceriodaphnia* to be 0.81 (i.e., $\alpha_{DC} = (0.81, 0.19)'$) and its preference for *Ceriodaphnia* relative to *Moina* to be 0.09 (i.e., $\alpha_{CM} = (0.09, 0.91)'$). The predicted preference for *Daphnia* relative to *Moina* is

$$ \alpha_{DM}^* = \frac{\alpha_{DC}\alpha_{CM}}{\alpha_{DC}\alpha_{CM} + (1 - \alpha_{DC})(1 - \alpha_{CM})} = 0.29 $$

(Appendix 1).

Experiments were subsequently carried out with only *Daphnia* and *Moina* present, and the estimated mean preference of *Daphnia* relative to *Moina* ($\bar{\alpha}_{DM} = 0.37$) was not significantly different from the predicted value using the test statistic

$$ Z = \frac{\alpha_{DM}^* - \bar{\alpha}_{DM}}{\sqrt{V(\alpha_{DM}^*) + V(\bar{\alpha}_{DM})}} $$

where $V(\alpha_{DM}^*)$ is the variance of α_{DM}^* estimated by (A2) (Appendix 1) and $V(\bar{\alpha}_{DM})$ is the sample variance of α_{DM} divided by the sample size. Under the null hypothesis of no difference between observed and predicted values, Z will be approximately normally distributed with mean 0 and variance 1. A nonsignificant value of Z indicates that *N. hoffmani* does not change its behavior towards these prey types in response to the presence of different alternative prey.

Chesson (1981) was able to predict the preference of *N. hoffmani* for small mosquito larvae relative to *Daphnia*, given the preference for small mosquito larvae relative to medium mosquito larvae and the preference for medium mosquito larvae relative to *Daphnia*.

It must be stressed that the tests described in this and the preceding section are large-sample tests and their validity for small sample sizes is unknown. Therefore inferences based on them should be made with caution. However, in situations where sample sizes are reasonably large and the α_i values are not

too close to 0 or 1, such tests provide a useful tool for analyzing preference.

RELATIONSHIP TO FORAGING MODELS

Clearance rates

Studies on zooplankton grazing often involve the calculation of the "clearance rate." This quantity is based on the model

$$n_{it} = n_{i0}e^{-c_it} \quad \text{(Dodson 1975)}, \tag{6}$$

where n_{it} is the number of items of food type i which are left after the animal has been feeding for t time units, n_{i0} is the number of items of that type which were originally present, and c_i is the clearance rate. c_i is estimated by

$$\hat{c}_i = -\frac{1}{t} \ln \frac{n_{it}}{n_{i0}} \tag{7}$$

and is regarded as a measure of the volume of water which an animal clears of food type i per unit time. It is immediately apparent that when m food types are present, the quantity

$$\frac{\hat{c}_i}{\sum_{j=1}^{m} \hat{c}_j} \tag{8}$$

is identical to $\hat{\alpha}_i$ in Eq. 3. In other words, this estimate of the relative clearance rates is equivalent to the moment estimate of the relative preference of the animal for each food type. This relationship has been used by Vanderploeg and Scavia (1979). Clearance rates can be found for each of the food types presented singly and then combined as in Expression 8 to predict the relative preference when all prey are present simultaneously. Deviations from these predicted α values would indicate that the animal was not behaving in the same way in the many-food-type situation as it was when only a single food type was present.

The relationship between food consumption per unit time and food density, called the "functional response" (Solomon 1949) has been categorized into three basic types (Holling 1965). Eq. 6 is a version of the Type I functional-response curve (Holling 1965), taking into account food depletion. Jacobs (1974) used the same model, assuming no food depletion, to derive his preference index, D. D is defined only for the case of two food types ($m = 2$). If $\hat{\alpha}_1$ is calculated using Eq. 2 (the equation for estimating α when there is no food depletion) then $2\hat{\alpha}_1 - 1$ is identical to D. This rescaling of α_i is discussed below.

From these examples we can see that the estimates of α in both the no depletion and depletion cases (Eqs. 2 and 3, respectively) can be interpreted in terms of the Type I functional response model or the clearance-rate model.

Type II functional response

The Type II functional response for m food types, also known as the "disc equation," is given by

$$r_i = \frac{a_in_i}{1 + \sum_{j=1}^{m} a_jn_jh_j}, \quad i = 1, \ldots, m$$

$$\text{(Murdoch 1973)} \tag{9}$$

where a_i and h_i, $i = 1, \ldots, m$, are constants referred to as the "attack rate" and "handling time," respectively. This equation describes the number of food items eaten in one time unit when food depletion does not occur. Applying Eq. 2, we get

$$\hat{\alpha}_i = \frac{a_i}{\sum_{j=1}^{m} a_j}, \quad i = 1, \ldots, m, \tag{10}$$

i.e., $\hat{\alpha}_i$ can be interpreted as the attack rate on food type i relative to the attack rates on the other food types present.

Alternatively, when food is not replenished as it is eaten, Eq. 9 can be regarded as the instantaneous rate of food consumption (i.e., equal to $-dn_i/dt$), and solving the appropriate differential equation produces the multi-species version of the "random predator equation" (Rogers 1972),

$$r_i = n_i\left\{1 - \exp\left[-a_i\left(1 - \sum_{j=1}^{m} r_jh_j\right)\right]\right\}. \tag{11}$$

Eq. 11 describes the number of individuals of food type i eaten in one time unit when food is not replenished as it is eaten. Cock (1978) and Hassell (1978) suggest that in this case preference becomes much more complicated and involves handling times as well as attack rates. However, application of Eq. 3 (the equation for estimating α when food depletion occurs) yields the same result as before,

$$\hat{\alpha}_i = \frac{a_i}{\sum_{j=1}^{m} a_j}, \quad i = 1, \ldots, m.$$

This is an intuitively reasonable result, since it would be undesirable for a measure of preference to change merely because food densities were kept constant in one case and allowed to decline in the other. When food is not depleted, then Eq. 2 should be used to estimate α, whereas when food densities do decline, Eq. 3 provides the appropriate estimate. A measure of preference should reflect changes in animal behavior, not changes in the experimental conditions, and α has this desirable property. Provided the values of a_i, $i = 1, \ldots, m$, remain constant, α will not change.

Type III functional response

The third basic category of functional response curves is the Type III curve, which is sigmoid in shape. There are several formulae which can be used to describe a sigmoid curve (e.g., Real 1977, Hassell 1978). I will use the equation

$$r_i = \frac{b_i n_i^2}{(1 + c_i n_i)\left(1 + \sum_{j=1}^{m} \frac{b_j n_j^2 h_j}{1 + c_j n_j}\right)}, \quad i = 1, \ldots, m.$$

(12)

which is obtained from Eq. 9 by replacing a_i by $\dfrac{b_i n_i}{1 + c_i n_i}$, where b_i and c_i are constants, $i = 1$, $\ldots$, m. In other words the attack rate is no longer a constant, but depends on food density. As the density of food type i increases, the attack rate on it also increases up to a maximum value b_i/c_i. A large value of c_i indicates a rapid rise to the maximum value, suggesting that the attack rate is near the maximum for all but very small food densities, whereas a small value of c_i represents the situation in which the attack rate continues to rise over a broad range of food densities. A large value of b_i relative to c_i indicates a high maximum attack rate.

Assuming no food depletion, we can obtain $\hat{\alpha}_i$ from Eq. 2,

$$\hat{\alpha}_i = \frac{n_i b_i/(1 + c_i n_i)}{\sum_{j=1}^{m} n_j b_j/(1 + c_j n_j)}.$$

(13)

In contrast to the Type I and II functional response models, preference, as defined by α, does not remain constant with a Type III response but changes with food density. This is not surprising since preference was determined by relative attack rates in the Type II model, and in the Type III model attack rates depend on food density. Examination of Eq. 13 reveals that changes in either absolute or relative food densities cause a change in preference. The direction and magnitude of the change depends on the values of the b_i's and c_i's.

For example, if the c_i's are all very small, then preference is determined mainly by the b_i's and n_i's. In this particular case changes in absolute food density will have little effect, but α_i will range from 0 to 1 as the relative density of food type i increases. Conversely, if the b_i's are all very small, both absolute and relative food densities are important in determining preference. Keeping total density constant and varying relative densities, one finds that increasing the relative density of type i may result in a decrease in the preference for that food type ("negative switching," Chesson 1983).

The situation becomes much more complicated when food is not replenished as it is eaten. If we assume that the attack rate is determined by the initial food densities (i.e., n_{i0}) and does not change again during the experiment, then

$$r_i = n_{i0}\left(1 - \exp\left\{-\frac{b_i}{c_i}\left(1 - \sum_{j=1}^{m} r_j h_j \right.\right.\right.$$
$$\left.\left.\left. - \frac{r_i}{b_i n_{i0}(n_{i0} - r_i)}\right)\right\}\right)$$

(Hassell 1978)   (14)

is the Type III analogue of the random predator equation, and using Eq. 3 we get the same result for $\hat{\alpha}_i$, namely

$$\hat{\alpha}_i = \frac{n_{i0} b_i/(1 + c_i n_{i0})}{\sum_{j=1}^{m} n_{j0} b_j/(1 + c_j n_{j0})}.$$

However, if the attack rate changes instantaneously with every change in food density, then there is no single measure of preference, since preference is also changing throughout the experimental period.

Greenwood and Elton (1979) discuss the analysis of experiments in which preference depends on relative food densities, but they consider only the case in which food depletion does not occur. The estimation of preference when it changes instantaneously with the reduction in food density remains an unsolved problem. However, in the real world it is unlikely that abrupt changes in preference will occur. In almost all situations there will be time lags. The question is, does the experiment occur within this lag time?

Stochastic waiting time model

Suppose that the consumer searching time, X, required to locate a particular food item of type i has an exponential distribution with mean λ_i [$P(X \leq t) = 1 - \exp(-t/\lambda_i)$] and that this distribution is independent of the searching time required to locate any other particular food item. The exponential distribution and the independence between waiting times is a model of random search. Each type i food item, until it is consumed, has a constant probability per unit time of being located.

Whenever a food item is located but not consumed, then it is assumed that the searching time required to locate it again is also exponentially distributed with parameter λ_i. If the probability that a food item of type i is consumed (given it has been located) is ρ_i, then the waiting time (in terms of consumer searching time) for the food item to be removed by the consumer has an exponential distribution with mean $\lambda_i \rho_i^{-1}$ (Appendix 2). It is easily shown (Appendix 3) that if there are n_i food items of type i, $i = 1, \ldots, m$, then the prob-

ability that the next food item consumed is of type i is

$$P_i = \frac{\rho_i \lambda_i^{-1} n_i}{\sum_{j=1}^{m} \rho_j \lambda_j^{-1} n_j}.$$

The $\rho_i \lambda_i^{-1}$, once they have been normalized to sum to 1, are equivalent to the α_i in Eq. 1 and therefore can be interpreted as a measure of preference. The measure is inversely proportional to the mean searching time to locate a food item of type i (λ_i) and directly proportional to the probability of consumption given it has been located (ρ_i). Given that r_i individuals of type i, $i = 1, \ldots, m$ have been consumed in time t, then the ML estimator of $\rho_i \lambda_i^{-1}$ is $(\widehat{\rho_i \lambda_i^{-1}}) = (-1/t)\ln((n_{i0} - r_i)/n_{i0})$. Note that this is the same as the estimate of clearance rate described above and is also equivalent to the estimate of the "area of discovery" in the Nicholson-Bailey host-parasitoid model (Hassell 1978: 17). Normalizing the estimates gives

$$\frac{\widehat{\rho_i \lambda_i^{-1}}}{\sum_{j=1}^{m} \widehat{\rho_j \lambda_j^{-1}}} = \frac{\ln((n_{i0} - r_i)/n_{i0})}{\sum_{j=1}^{m} \ln((n_{j0} - r_j)/n_{j0})},$$

which is identical to Eq. 3 for estimating α_i. Manly (1975) developed a similar argument for relating measurements of natural selection to individual survival.

There is a subtle difference between this model and the situation for which Eq. 3 was originally developed. In this model the amount of searching time (t) is fixed and both the total number of food items eaten and the number of each type eaten are random variables. The situation for which Manly et al. (1972) derived Eq. 3 is when the total number of food items eaten is fixed and only the number of each type eaten is allowed to vary. It is interesting to find that Eq. 3, which is an approximate estimator in the latter case, is also the exact ML estimator for the waiting time model.

DISPLAYING PREFERENCE

The value of α_i that would obtain if the consumer were selecting food at random ($\alpha_i = 1/m$) varies with the number of food types available (m) and it is therefore not easy to see if the strength of preference for a particular prey item is changing when selection is nonrandom, but different numbers of alternative food types are present in different experiments. It may sometimes be more convenient, particularly when there is a large number of types of food items, to display preference as an electivity index which ranges from -1 to $+1$, with 0 representing no preference.

This can be done with α_i, $i = 1, \ldots, m$, by calculating the preference for food type i relative to the average preference for all other food types (i.e., $\alpha_i/(\alpha_i + \Sigma_{j \neq i} \alpha_j/(m - 1))$), then multiplying the result

by 2 and subtracting 1. In terms of the α_i this electivity value, ϵ_i, is given by

$$\epsilon_i = \frac{m\alpha_i - 1}{(m - 2)\alpha_i + 1}, \quad i = 1, \ldots, m \qquad (15)$$

When $m = 2$, ϵ_1 is exactly equal to Jacob's D described above. If $\alpha_i = 0$, then $\epsilon_i = -1$; if $\alpha_i = 1/m$, then $\epsilon_i = 0$; and if $\alpha_i = 1$, then $\epsilon_i = 1$. Unlike Ivlev's index of electivity, ϵ_i can take any value between -1 and 1 irrespective of food densities in the environment. It also has a natural interpretation in terms of the preference of food type i relative to the average preference for the alternative food types, rather than being merely an arbitrary quantity ranging between -1 and 1.

Since the statistical properties of ϵ_i are not given, it should be used only for display purposes. For statistical analysis and for predicting preferences the ϵ_i should be converted back to α_i.

CONCLUSIONS

As a measure of preference α has many advantages. It can be interpreted as the relative contribution of each food type to the diet if all food types were equally abundant. Methods of estimation are available for a number of different situations, and standard methods of analysis can be used when sample sizes are sufficiently large. In contrast to the majority of existing measures it does not vary with food density unless consumer behavior also changes with food density. Therefore it can be used to detect such changes in behavior. Values of α obtained in one or several experiments can be used to predict expected values of preference for other food-type combinations. α also relates in a biologically reasonable way to existing foraging models and provides a unifying link between clearance rates, attack rates, and consumer preference.

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APPENDIX 1.

Predicting preference values for one food type relative to another, given the preference for each of them relative to a third food type.

Let α_{ij} represent the preference of a consumer for food type i in the presence of food type j only, $i = 1, 2, 3; j = 1, 2, 3; j \neq i$. ($\alpha_{ij} + \alpha_{ji} = 1, i \neq j$) and let $\alpha_i (i = 1, 2, 3)$ represent the preference of the consumer for food type i relative to all three food types ($\alpha_1 + \alpha_2 + \alpha_3 = 1$). If predator behavior is independent of the number and types of food present, then

$$\alpha_{12} = \alpha_1/(\alpha_1 + \alpha_2),$$
$$\alpha_{23} = \alpha_2/(\alpha_2 + \alpha_3),$$
$$\text{and } \alpha_{13} = \alpha_1/(\alpha_1 + \alpha_3).$$

Given values for α_{12} and α_{23} and these relationships, simple algebraic manipulation yields

$$\alpha_{13} = \frac{\alpha_{23}\alpha_{12}}{\alpha_{23}\alpha_{12} + (1 - \alpha_{23})(1 - \alpha_{12})}. \quad (A1)$$

If α_{23} and α_{12} are estimates obtained from samples of size K_{23} and K_{12}, respectively, then the approximate variance of α_{13} is given by

$$V(\alpha_{13}) \approx [\alpha_{23}(1 - \alpha_{23})D]^2 V(\alpha_{12})$$
$$+ [\alpha_{12}(1 - \alpha_{12})D]^2 V(\alpha_{23}) \quad (A2)$$

(Rao 1973:387), where $D^{-1} = \alpha_{12}\alpha_{23} + (1 - \alpha_{12})(1 - \alpha_{23})$. Under the assumption that all consumers have the same preference, $V(\alpha_{12})$ and $V(\alpha_{23})$ are estimated using Manly's formulae (Manly 1974, 1980). When consumers differ in their preference, $V(\alpha_{12})$ and $V(\alpha_{23})$ can be estimated by the sample variances of α_{12} and α_{23} divided by their respective sample sizes (K_{23} and K_{12}).

This example is clearly only one of an unlimited number of manipulations which can be performed to predict one set of preference values from another, using the fact that the α_i's must sum to one and that only their relative values are relevant.

APPENDIX 2.

The distribution of the searching time required before consuming a particular food item of type i.

Let $\tau_1, \ldots, \tau_s$ be successive inter-encounter times with a particular food item of type i. The food item is finally consumed at the Sth encounter after $S - 1$ unsuccessful encounters. It is assumed that the τ_i are independent and identically distributed exponential random variables with mean λ_i, and that the conditional probability of consumpiton, given encounter, is ρ_i. It follows that $S - 1$ has a geometric distribution with parameter ρ_i (i.e., $P(S = s) = (1 - \rho_i)^{s-1}\rho_i$). To find the distribution of the total searching time required to consume the particular food item of type i (i.e., $\sum_{j=1}^{S} \tau_j$) we derive its moment-generating function ($E \exp(\sum_{j=1}^{S} \tau_j u)$), where E means the expection or theoretical mean value and u is the argument of the generating function. Since $E[\exp(\sum_{j=1}^{S} \tau_j u) | S] = (1/(1 - \lambda_i u))^S$, and the probability-generating function of S is

$$E\theta^s = \theta\rho_i/(1 - (1 - \rho_i)\theta),$$

then

$$E \exp\left(\sum_{j=1}^{S} \tau_j u\right) = 1/(1 - \lambda_i\rho_i^{-1}u),$$

which is the moment-generating function of an exponentially distributed random variable with mean $\lambda_i\rho_i^{-1}$. Thus $\sum_{j=1}^{S} \tau_j$ has an exponential distribution with mean $\lambda_i\rho_i^{-1}$.

APPENDIX 3.

The probability that the next food item eaten by a consumer is of type i.

Suppose there are n_j items of food type j, $j = 1, \ldots, m$, and let T_{ik} be the total searching time required to locate and consume a particular food item (k) of type i. Let A be the event that this particular food item is eaten next. The probability of A given that $T_{ik} = x_{ik}$ is given by the probability that all other food items have a longer searching time, i.e., $P(A \mid T_{ik} = x_{ik}) = P(T_{il} > x_{ik}$, for all $j \neq i$, $l = 1, \ldots, n_j \cap T_{il} > x_{ik}$, $l \neq k)$. Since the T_{il} are independently and identically distributed as exponential random variables with mean $\lambda_j\rho_j^{-1}$ (Appendix 2) we have

$$P(A \mid T_{ik} = x_{ik}) = \prod_{\substack{j=1 \\ j \neq i}}^{m} \left(\int_{x_{ik}}^{\infty} \rho_j\lambda_j^{-1}\exp(-\rho_j\lambda_j^{-1}t)\,dt\right)^{n_j}$$

$$\left(\int_{x_{ik}}^{\infty} \rho_i\lambda_i^{-1}\exp(-\rho_i\lambda_i^{-1}t)\,dt\right)^{n_i-1}$$

$$= \exp\left\{\left(-\sum_{j=1}^{m} \rho_j\lambda_j^{-1}n_j + \rho_i\lambda_i^{-1}\right)x_{ik}\right\}.$$

Hence

$$P(A) = \int_0^{\infty} \rho_i\lambda_i^{-1}\exp(-\rho_i\lambda_i^{-1}x_{ik})P(A \mid T_{ik} = x_{ik})\,dx_{ik}$$

$$= \rho_i\lambda_i^{-1}/\left(\sum_{j=1}^{m} \rho_j\lambda_j^{-1}n_j\right).$$

Since there are n_i food items of type i, the probability that the next item eaten is of type i is

$$\rho_i\lambda_i^{-1}n_i/\left(\sum_{j=1}^{m} \rho_j\lambda_j^{-1}n_j\right).$$

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