Quantitative Measurement of Food Selection

A Modification of the Forage Ratio and Ivlev's Electivity Index

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Summary. The forage ratio and Ivlev's electivity index are common measures to quantify food selection but the values of both indices depend not only on the extent of selection but also on the relative abundances of the food types in the environment. They are therefore useless when food types with different relative abundances are compared, or when the relation between selection and relative abundance is studied. Modified versions of both indices are proposed which are based directly on the rates of decrement (mortality) of the food due to feeding, and are independent of the relative abundance.

Selective feeding takes place if a feeder consumes co-occurring food sources at different rates. If m_A and m_B are the rates of mortality (or decrement) of food A and food B due to feeding, N_A and N_B the numbers of items (or any other quantities) of A and B in the environment, and t is time, then positive selection of A occurs if

$$m_A = \frac{dN_A}{dt \cdot N_A} > m_B = \frac{dN_B}{dt \cdot N_B}.$$

Negative selection occurs if $m_A < m_B$. There is no selection if $m_A = m_B$. Depending on the desired comparison, A and B may be specific food types or groups of food types; of course, B may also be the sum of all food types in the environment except A. Different m-values reflect different selection coefficients concerning mortality, the principle of selection is the same as that considered in classical population genetics.

A number of indices are in use to measure selective feeding. The most common measures are the so-called Forage ratio FR, and Ivlev's electivity index E (Ivlev, 1961; Edmondson, 1971). FR is defined as the ratio of the fraction r of a given food type in the feeders ration, to the fraction p of the same food in the environment:

$$FR = \frac{r}{p}. \tag{1}$$

FR varies from 0 to 1 for negative selection, from 1 to ∞ for positive selection. E is defined as the relative difference between r and p:

$$E = \frac{r-p}{r+p}. \tag{2}$$

E varies from -1 to 0 for negative selection, from 0 to $+1$ for positive selection.

It is easily shown that

$$FR = \frac{r}{p} = \frac{m_A}{m_T} \tag{3}$$

and

$$E = \frac{r-p}{r+p} = \frac{m_A - m_T}{m_A + m_T} \tag{4}$$

where m_T is the total mortality rate of A plus B,

$$m_T = \frac{d(N_A + N_B)}{dt \cdot (N_A + N_B)}.$$

The total number of items eaten per unit time is

$$\frac{d(N_A + N_B)}{dt} = m_A N_A + m_B N_B.$$

Hence,

$$m_T = \frac{m_A N_A + m_B N_B}{N_A + N_B}. \tag{5}$$

The fraction of food A in the environment is

$$p = \frac{N_A}{N_A + N_B}, \tag{6}$$

the fraction of food B in the environment is

$$1 - p = \frac{N_B}{N_A + N_B}. \tag{7}$$

The fraction of food A in the ration is

$$r = \frac{m_A N_A}{m_A N_A + m_B N_B}. \tag{8}$$

Dividing (8) by (6), the expression

$$\frac{r}{p} = \frac{m_A (N_A + N_B)}{(m_A N_A + m_B N_B)}$$

is obtained. Recalling Eq. (5), it follows that

$$FR = \frac{r}{p} = \frac{m_A}{m_T}.$$

For E, the calculation is analogous.

Both FR and E have a serious disadvantage: at constant mortality rates of A and B, their values change with the relative abundance p

of the food in the environment: Recalling Eqs. (6) and (7), Eq. (5) may be rewritten as follows:

$$m_T = m_A\,p + m_B\,(1-p)$$
$$= p\,(m_A - m_B) + m_B.$$

Thus, if both m_A and m_B stay constant, and $m_A \neq m_B$, then m_T and hence FR must change if p changes. As p changes from 0 to 1, m_T changes from m_B to m_A, FE approaches 1.—For E the situation is analogous, E approaches 0 as p changes from 0 to 1.

Therefore, FR and E cannot be used if one wishes to study the correlation between the relative abundance of food and food selection, which is, for instance, an important aspect in the establishment and maintenance of homeostasis in multiple predator-prey relations. Strictly speaking, a quantitative comparison of selection between different food types with the aid of FR or E can only be made if the food types have the same relative abundance.

To eliminate this disadvantage, I propose modified versions of the forage ratio and Ivlev's index which are independent of the relative abundance, and reflect directly differential mortality rates. In analogy to FR and E, I define the indices
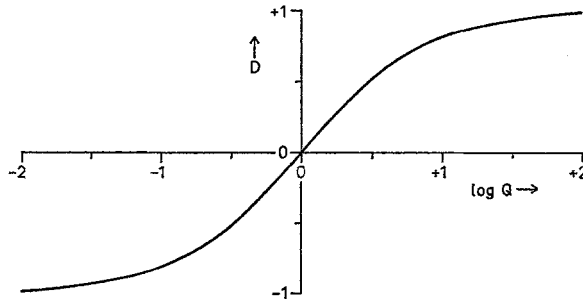
$$Q = \frac{m_A}{m_B} \tag{9}$$

and

$$D = \frac{m_A - m_B}{m_A + m_B}. \tag{10}$$

Analogous to FR, the quotient Q varies from 0 to 1 for negative selection, from 1 to ∞ for positive selection. The disadvantage of unequal ranges for negative and positive selection is eliminated if $\log Q$ is used. $\log Q$ varies symmetrically from $-\infty$ to 0 for negative selection, from 0 to $+\infty$ for positive selection. The relative difference D varies from -1 to 0 for negative selection, from 0 to $+1$ for positive selection. In contrast to FR and E, Q and D are immune to changes of food composition in the environment.

Mortality rates are difficult to determine in the field, usually one has to rely on the measurements of r and p. It is therefore useful to express Q and D in terms of r and p:

Since $m_B = m_A/Q$ [Eq. (9)], and $N_B = N_A(1-p)/p$ [Eqs. (6) and (7)], Eq. (8) may be rewritten as follows:

$$r = \frac{m_A N_A}{m_A N_A + m_A N_A (1-p)/Q\,p}$$

Fig. 1. The relation between log Q and D

or

$$r = \frac{Qp}{Qp+1-p}.$$

Solving for Q, the expression

$$Q = \frac{r(1-p)}{p(1-r)} \tag{11}$$

is obtained. Q is thus identical to FR except for the factor

$$(1-p)/(1-r).$$

The calculation of D is analogous: Since $m_B = m_A(1-D)/(1+D)$ [Eq. (10)], and $N_B = N_A(1-p)/p$ [Eqs. (6) and (7)], Eq. (8) may be rewritten as follows:

$$r = \frac{m_A N_A}{m_A N_A + m_A N_A (1-p)(1-D)/p(1+D)}$$

or

$$r = \frac{p(1+D)}{p(1+D)+(1-p)(1-D)}.$$

Solving for D, the expression

$$D = \frac{r-p}{r+p-2rp} \tag{12}$$

is obtained which is very similar to Ivlev's index E.

I recommend the use of log Q or D instead of FR and E whenever food selection is to be quantified. Comparing log Q and D, there does not appear to be any *a priori* preference of one index over the other. Fig. 1 shows the relation between log Q and D. Within the range of log Q from -0.6 to $+0.6$ there is almost proportionality between both indices, however, log Q has the advantage to be unlimited in both directions.

If $\log Q > 1$, i.e. if the mortality rate of A is ten times that of B or more, then $\log Q$ is a more sensitive indicator of selection changes than is D. In general, both indices should be tested when a relation is studied between food selection and variables such as the relative abundance of food, light conditions, hunger, or size of the feeder. The types of relations might indicate whether the quotient or the difference of mortalities is a biologically more meaningful parameter of selection.

References

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