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"Predation in Food Webs"

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PREDATION IN FOOD WEBS

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ABSTRACT

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For the case when the specific predation is a hyperbolic function of prey concentration in one-predator–one-prey systems, expressions are derived for predation rate in food webs for both nonselective and selective predation. These expressions can readily be applied to ecosystem models of food webs.

INTRODUCTION

One of the long-standing problems in nonlinear models of food webs is how to calculate the balance of energy or biomass. Since transfers of energy and food are often nonlinear, predators usually consume more than one prey and also share prey populations, the problem cannot be solved by simply adding nonlinear expressions derived from feeding experiments involving one-prey–one-predator populations. Furthermore, the problem cannot be solved satisfactorily by lumping many populations together and assuming that they have the same population-specific parameters. This approach has never been justified theoretically, and experimental evidence (for example Vidal, 1980, and references therein) does not, in general, support it.

In this paper, expressions for calculating transport of energy or matter in a food web are given based on hyperbolic dependence of the specific predation rate on prey concentration. In the case where predators do not actively select prey, experimental evidence on a complete series of one-predator–one-prey systems is sufficient for quantifying the food web.

If selective feeding is taking place, results of a complete series of pairwise experiments will not suffice to calculate balance of neither energy nor matter correctly. In this case, either additional experiments or field monitoring must be performed to measure selectivity functions.

Determination of parameters from field observations is treated elsewhere (Legović, 1987).

PREDATION IN THE ONE-PREDATOR ONE-PREY SYSTEM

Experimental studies on feeding of one predator population on one prey population often show that specific predation can be described by a simple hyperbolic function, called the Michaelis–Menten or Monod function:

$$s^{11} = \frac{vN}{k + N} \tag{1}$$

where s^{11} denotes the specific predation in a system where one predator and one prey population are present, v is maximum predation rate of prey per predator, k is the half-saturation constant, and N is density of the prey population. It is sometimes convenient to express s^{11} as the number of prey caught per unit of time and per number of predators, so the dimensions of v and k are:

$[\text{number of prey } T^{-1} \text{ (number of predators)}^{-1}]$

and

$[\text{number of prey } L^{-3}]$

respectively, where T is time and L^3 volume. When working with biomass density, prey and predator density should be replaced by respective biomass densities. Predation rate, p^{11}, by the predator population is:

$$p^{11} = s^{11}P$$

where P is predator density. If the predator population is measured as biomass density [predator biomass L^{-3}], then the dimension of p is:

$$[p^{11}] = [\text{prey biomass}/T^{-1}L^{-3}]$$

PREDATION IN THE ONE-PREDATOR–n-PREY SYSTEM

Assume that one has performed n experiments. In each experiment, the same predator and a different prey population was present so that each experiment was a one-predator–one-prey experiment. Let results of each of n hypothetical experiments support the expression (1), where each experiment gives a different v_i constant ($v_i \neq v_j$, for $i \neq j$), but the same k constant.

The quantity offered to the predator population when all prey populations are present is:

$$N_t = \sum_{i=1}^{n} N_i$$

Hence the specific predation rate on the ith prey in the one-predator–n-prey system is:

$$s_i^{n1} = \frac{v_i N_i}{k + N_t} \tag{2}$$

The total specific predation rate by the predator is simply the sum of specific predation over all prey:

$$s_t^{n1} = \sum_{i=1}^{n} s_i$$

i.e.

$$s_t^{n1} = \frac{\sum_{i=1}^{n} v_i N_i}{k + N_t} \tag{3}$$

Expressions (2) and (3) are most often used in nonlinear models of food webs. In some models:

$$s_t' = \sum_{i=1}^{n} [v_i N_i/(k + N_i)]$$

is used as supposedly the true total predation. However, the true predation is smaller and is actually given by expression (3). If one lets $n = 2$ and $N_1 = N_2 = N > k$, then expression (3) gives:

$$\frac{(v_1 + v_2)\, N}{(k + 2N)}$$

which is smaller than s_t' ($s_t' = (v_1 + v_2)N/(k + N)$). ~~Since~~ Let $N \gg k$ and $v_1 = v_2 = v$ it follows that $s' > v$, and this contradicts experimental evidence that v is the maximum specific predation rate. Using expression (3), as $N \to \infty$, ~~$s_t^{n1} \to (v_1 + v_2)$~~/2, as expected.

$s_t^{n1} = (v_1 + v_2)/2$

and when $v_1 = v_2$ we recover:

$s_t^{n1} = v$.

With one modification:

$$N_i = N_i^c - N_0$$

where N_i^c is the actual concentration of prey and N_0 is the threshold concentration of prey, the expression (3) has been used in many ecosystem models (Park et al., 1974; Canale et al., 1976; for other literature, see Scavia, (1976; Baretta and Ruardij, 1988).

One step further toward reality is to assume that both maximum specific predation and half-saturation constant are not just a characteristic of the predator but also of the prey population, and this is apparent from many experimental studies.

If two prey populations having the same concentrations $N_1 = N_2$ are offered to the predator while $v_1 = v_2$ and $k_1 < k_2$, we expect that the predation rate on the first prey will be greater. Expression (3) cannot be used to calculate the predation rate in the presence of both prey populations, because $k_1 \neq k_2$.

In order to calculate the correct predation rate in one-predator–n-prey system, the model underlying expression (1) must be known. Holling (1959) and Rashevsky (1959) developed such a model based on predator behavior. They postulated that the number of prey eaten, S, in time interval T per one predator is the product of prey density, N, rate of capturing one unit of prey, a, while the predator is searching, and search time. Time interval T is then split into two parts: consuming and searching. An extension for prey of differing palatability is given in Harris (1974). Time spent consuming is proportional to prey caught in T. Hence:

$$S = (T - bS)aN$$

or

$$S/T = aN/(1 + abN) \tag{4}$$

where bS is time spent consuming prey captured in time-interval T. By passing to the limit, expression (4) becomes identical to (1), where $v = 1/b$ and $k = 1/(ab)$. Murdoch (1973) used model (4) to calculate predation in one-predator–two-prey systems. Assuming predation rates a_1, a_2 and handling times per unit of prey b_1, b_2, Murdoch stated:

$$S_1 = (T - b_1S_1 + b_2S_2)a_1N_1$$
$$S_2 = (T - b_1S_1 + b_2S_2)a_2N_2 \tag{5}$$

Solving for S_1 and S_2 and passing to the limit, one obtains:

$$s_i^{21} = \frac{a_iN_i}{1 + a_1b_1N_1 + a_2b_2N_2} \qquad i = 1, 2 \tag{6}$$

For the case of a one-predator–n-prey system, a straightforward generalization of (6) in terms of v_i and k_i is:

$$s_i^{n1} = \frac{v_iN_i/k_i}{1 + \sum_{j=1}^{n} N_j/k_j} \tag{7}$$

Total specific predation rate of the predator is:

$$s_i^{n1} = \frac{\sum_{i=1}^{n} v_iN_i/k_i}{1 + \sum_{j=1}^{n} N_j/k_j} \tag{8}$$

In expressions (7) and (8) constants v_1 and k_1 are obtained from the ith of n one-predator–one-prey experiments, which gave:

$$s_i^{11} = \frac{v_iN_i}{k_i + N_i} \tag{9}$$

Nonselective predation

Expressions (7) and (8) will be valid for all the predators that conform to the hyperbolic relationship in one-predator–one-prey experiments but do not actively select their prey when a mixture of prey populations is offered. A typical example of a nonselective feeder is that zooplankton species which is unable to change the inclination of its sieve during predation.

It has been a practice to assign selectivity coefficients defined by O'Neill (1969) as soon as one discovers that the predator feeds unequally on any two prey populations having the same concentrations. Expression (7) shows that unequal predation will result almost always when $k_i \neq k_j$ or $v_i \neq v_j$ or both, for $i \neq j$, even without any selection from the predator's side.

If $k_1 \neq k_2$ and $v_1 = v_2$, then for the same concentrations of prey, $N_1 = N_2$, one expects that the two prey populations are caught according to proportions:

$$s_1^{21}/s_2^{21} = k_2/k_1 \tag{10}$$

In the n-prey–one-predator system, when $k_i \neq k_j$, $v_i \neq v_j$ for $i \neq j$, and if all prey populations are present in equal concentrations, it follows from (7) that prey populations will be caught in the following proportions:

$$s_1^{n1} : \ldots : s_n^{n1} = v_1/k_1 : \ldots : v_n/k_n \tag{11}$$

It is difficult to keep all the prey in equal concentrations during experiments, and it is also an unnecessary restriction in order to measure whether nonselective predation takes place or not. If concentrations of prey populations are unequal, then:

$$s_1^{n1} : \ldots : s_n^{n1} = v_1N_1/k_1 : \ldots : v_nN_n/k_n \tag{12}$$

Selective predation

In experiments or in the field, when a system with one predator and more than one prey is investigated, if the prey populations are not taken by the predator according to proportions (12), and yet experiments with one-predator–one-prey demonstrate that expression (9) holds, then this is an indication that either the predator selects some prey or an interference is taking place.

In the case of selective feeding, the true predation rate on the ith population will be smaller or larger than in nonselective predation, but it will be smaller or equal to predation in the one-predator–one (ith)-prey population system.

To account for selectivity it has been a custom to assign a constant w_i so that instead of rate of capture a_i one would have $w_i a_i$. Constants w_i have been termed selectivity constants. Obviously, $w_i \leq 1$.

Unfortunately, selectivity constants are not sufficient to take care of selection processes even in the most simple case. To show this let us choose two prey and one predator populations. Let us assign two constants: $w_1 = 1$ and $w_2 = 0.5$. If for some other reason the prey population 1 disappears i.e. $N_1 = 0$, one would be left with:

$$s_2^{21} = \frac{0.5 v_2 N_2}{k_2 + 0.5 N_2}$$

which obviously contradicts expression (9). It follows that the selection process cannot be resolved with a set of constants. Instead, one should consider selection by a predator as a function of prey density, hence w_i should be a function of prey density specific to each predator. Denote selectivity functions with $w_i(\cdot) = w_i(N_1, \ldots, N_n) \leq 1$.

When this substitution is made in expressions (7) and (8), expressions for specific predation on the ith prey and a total specific predation of the predator in case of selective predation become:

$$s_i^{n1} = \frac{w_i(\cdot)\ v_i N_i/k_i}{1 + z} \tag{13}$$

and

$$s_t^{n1} = \frac{\sum_{i=1}^{n} w_i(\cdot)\ v_i N_i/k_i}{1 + z} \tag{14}$$

where

$$z = \sum_{i=1}^{n} w_i(\cdot)\ N_i/k_i$$

and $w_i(\cdot), \ldots, w_n(\cdot)$ are selectivity functions. The functions have the property that $0 < w_i(\cdot) \leq 1$ if the predator feeds on the ith prey and $w_i(\cdot) = 0$ otherwise. We shall also adopt the convention that when $w_i(\cdot) = 0$ then $w_i(\cdot)/k_i = 0$.

It is clear that most often $w_i(\cdot) < 1$ and $\sum_{i=1}^{n} w_i(\cdot) < n$. In case $w_i = 1$ for all i, the predation is nonselective. Thus, nonselective predation is the special case of selective predation. Interpretation of the condition $w_i(\cdot) \leq 1$ for $i = 1, \ldots, n$ is as follows. In the one-predator–one-prey system, the predator population tries to get the maximum number of prey per unit of time, hence $w(\cdot) = 1$. In this case the predator has no choice. When there is more than one prey population available the predator may select, and in comparison to nonselective feeding it will get more of populations that it favors and less of the one that it does not. However, without some additional mode of behaviour, the specific feeding on the prey population that predator favors can not be greater than in the corresponding one-predator–one-prey population experiment.

Assuming $w_i(\cdot) > 1$ for some i would mean that some other population, say the jth, serves as a pilot that allows the predator to get more of the ith prey than in the one-predator–one-prey system. In such a case $w_i(\cdot)$ has the added property that:

$$\lim_{N_i \to 0} w_i(\cdot) \leq 1$$

Although it is known that some predators use other populations as pilots, this is relatively rare. Hence, $w(\cdot) > 1$ will also rarely occur in food web models.

Using expression (13), relative rates in which different prey populations will be predated can easily be calculated. The proportions are:

$$p_1^{n1} : \ldots : p_n^{n1} = s_1^{n1} : \ldots : s_n^{n1} = w(\cdot) v_1 N_1/k_1 : \ldots : w(\cdot) v_n N_n/k_n \tag{15}$$

Expression (15) may be called the law of selective predation.

PREDATION IN THE ONE-PREY–m-PREDATOR SYSTEM

Assume that m experiments are performed, each involving the same prey and a different predator population. Let the result of each experiment be given as a Michaelis–Menten–Monod function (1). In that case all the predators have equal specific predation rates.

If each of the predators that feed on the same prey has a different pair of v and k constants, the specific predation rate of each predator is:

$$s_j^{1m} = \frac{v_j N}{k_j + N} \tag{16}$$

The predation rate by all predators, or total predation rate, is:

$$p_t^{1m} = N \sum_{j=1}^{m} \frac{v_j p_j}{k_j + N} \tag{17}$$

Expressions (13), (14) and (16), (17) can be applied to a general food web. Consider a food web with r populations. Let some populations serve as prey to others. There could be m trophic levels in the food web, where $m \le r$ (in case $m = r$, one deals with a food chain).

Define the $r \times r$ matrix W whose matrix element $w_{ij}(\cdot)$ denotes a preference of the jth predator for the ith prey as follows:

$$w_{ij}(\cdot)\begin{cases} \le 1 & \text{when the } j\text{th predator feeds on more than } i\text{th prey population} \\ = 1 & \text{when the } j\text{th predator feeds only on the } i\text{th prey} \\ = 0 & \text{otherwise} \end{cases}$$

In addition, define $r \times r$ matrices V and K whose elements v_{ij} and k_{ij} denote maximum specific predation rates and half-saturation constants of the jth predator on the ith prey population, respectively.

Let each experiment, involving only the ith prey and jth predator population, result in the following Michaelis–Menten function:

$$s_{ij}^{11} = \left[\begin{array}{c}\text{specific predation rate of } j\text{th} \\ \text{predator on } i\text{th prey when only} \\ \text{two populations are present}\end{array}\right] = \frac{v_{ij}N_i}{k_{ij}+N_i} \tag{18}$$

Specific predation rate of the jth predator on the ith prey, when all predator and prey populations are present and a selection takes place, is given by:

$$s_{ij}^{rr} = \frac{w_{ij}(\cdot)\; v_{ij}N_i/k_{ij}}{1 + \sum_{i=1}^{r} w_{ij}(\cdot)\; N_i/k_{ij}} \tag{19}$$

Total predation rate of the jth predator is:

$$p_{ij}^{rr} = N_j \frac{\sum_{i=1}^{r} w_{ij}(\cdot)\; v_{ij}N_i/k_{ij}}{1 + \sum_{i=1}^{r} w_{ij}(\cdot) N_i/k_{ij}} \tag{20}$$

If the jth population does not feed on the ith population, then $w_{ij}(\cdot) = 0$, $v_{ij} = 0$ and $k_{ij} = 1$, so that $w_{ij}(\cdot)v_{ij}/k_{ij} = 0$ and $w_{ij}(\cdot)/k_{ij} = 0$.

Predation rate on the ith prey, when all m predators are present, is:

$$p_{ii}^{nn} = N_i \sum_{j=1}^{r} \frac{w_{ij}(\cdot)\; v_{ij}N_j/k_{ij}}{1 + \sum_{i=1}^{r} w_{ij}(\cdot) N_i/k_{ij}} \tag{21}$$

The total predation rate (predation rate by all predators) is:

$$p_{ii}^{nn} = \sum_{j=1}^{r} N_j \frac{\sum_{i=1}^{r} w_{ij}(\cdot) v_{ij}N_i/k_{ij}}{1 + \sum_{i=1}^{r} w_{ij}(\cdot) N_i/k_{ij}} \tag{21}$$

The above expressions allow one to calculate energy and mass balance in animal food webs in cases of nonselective and selective predation. In case the kth predator does not select prey, then $w_{ik}(\cdot) = 1$ for all i that the kth predator consumes and $w_{ik}(\cdot) = 0$ for those populations that are not prey to the kth predator.

In order to calculate energy (or biomass) transfer, the experimental parameters v_{ij} and k_{ij} need to be converted into units expressing maximum specific energy (biomass) flux per prey and per predator, and half saturation density of energy (biomass), respectively. In case, each prey population consists of a continuum of possible sizes in which prey could arise, to correctly calculate energy (biomass) flux, an integration over the respective size distributions must be performed in the above expressions (see Eggers, 1977).

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