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A likelihood approach for functional response models

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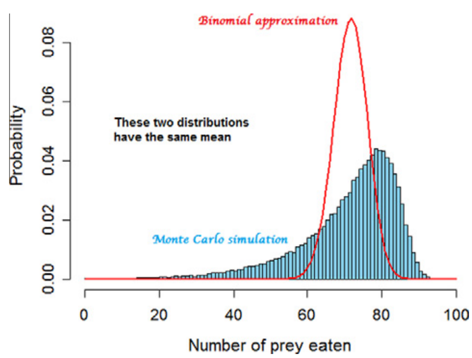
HIGHLIGHTS

- ▶ A likelihood method for estimating parameters of functional response models is described.
- ▶ The method allows researchers to examine a variety of functional response models with flexible choices of probability distributions.
- ▶ A computer function for facilitating the application of the method to model estimation is provided.

GRAPHICAL ABSTRACT



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ABSTRACT

Functional response is an important determinant of community dynamics, and thus empirical methods for characterizing functional responses are as important in understanding ecological processes. The most commonly used method is based on the sum of squares, and the maximum likelihood method is rarely used. When the likelihood method is used, potentially inappropriate probability distributions such as binomial distributions are typically assumed for the number of prey eaten in experiments. In this study, I present a likelihood approach in which the probability distributions are generated by mechanistic understanding of predation processes using Monte Carlo simulations. An example is given on the Holling type II functional response model, but the method is flexible and allows characterization of a wide variety of functional response models. In the example, the likelihood method consistently resulted in superior estimates than the least squares method.

1. Introduction

The functional response of predators is an important determinant of community dynamics (Turchin, 2003). It describes the rate at which a predator consumes prey, commonly as a function of prey densities. Because of its importance, functional responses have been characterized for a wide variety of consumer-resource pairs (e.g., Hassell, 1978; Dale et al., 1994; Pitt and Ritchie, 2002; Vonesh and Bolker, 2005; Stillman and Simmons, 2006; Fussmann et al., 2007). In biological control, the efficiency of pest management strongly depends on the functional responses of predators and parasitoids (Chen et al., 2006; Timms et al., 2008). To make reliable inferences about consumer-resource/pest interactions, it is important that the method for characterizing functional responses is also reliable.

A widely used experimental method for the characterization of functional responses is to record the number of prey eaten Y in a given time interval T under conditions of variable initial prey density N. Thus, the number of prey is depleted during the experiment. The expected number of prey consumed can be derived for a given functional response model by accounting for the depletion. For example, if a predation rate follows the Holling type II functional response (i.e., $aN/(1+ahN)$), the expected number of prey eaten in time T is the solution of

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$$Y = N(1 - e^{ahY - aT}) \quad (1)$$

where a is the attack rate and h is the handling time per prey (Royama, 1971; Rogers, 1972). Thus, the solution $\widehat{Y}$ depends on the parameters a and h and on the experimental conditions given by N and T. Similarly, the expected number of prey consumed can be derived for many other functional response models (Okuyama and Ruyle, 2011).

The least squares estimates for the parameters a and h are the values of a and h that minimizes the sum of squares,

$$\sum_{i=1}^{n}(Y_i - \widehat{Y}_i)^2 \quad (2)$$

where Y_i is the observed number of prey consumed for a given initial density N_i, and $\widehat{Y}_i$ is the expected number of prey consumed for a, h, and N_i (for the ith sample of the n experimental samples). Although this is a common method, large uncertainly may be associated with estimates. For example, it is known that the least squares method may produce undesirable results such as a negative handling time (e.g., Song and Heong, 1997; Wanink and Zwarts, 2004; Kratina et al., 2009). Some studies have used likelihood models that assumed the number of prey consumed followed binomial distributions whose probability parameter was $\widehat{Y}_i/N_i$ (e.g., Vonesh and Bolker, 2005). However, although the number of prey eaten given an initial number of prey is a binomial-like process, it is not precisely so (e.g., the mean–variance relationship is not restricted as in a binomial process, further discussed below).

There are some advantages for using parametric methods (e.g., likelihood method) as opposed to nonparametric methods (e.g., least squares method). For example, parametric models are generally superior (e.g., more powerful) provided that assumed distributions are reasonable. Furthermore, parametric approaches allow us to investigate variation characteristics in data. For example, two different predator species may have an identical functional response in expectation, but the variance around the expectation may vary. Differences in variance can also be important in ecological processes (Okuyama, 2008, 2011; Bolnick et al., 2011). Likelihood approaches explicitly consider probability distributions and can extract more information (e.g., variation and parametric distributions) from data.

Despite the utility of likelihood methods, the distribution of the number of prey consumed in the common experimental design is not obvious. In fact, the distribution would vary depending on predation behavior (e.g., search and handling processes). One way to understand the distribution is to simulate it. For example, because the Holling type II functional response was mechanistically derived (Holling, 1959), it is possible to simulate the predation processes according to the mechanism and generate the distribution of the number of prey eaten. In this study, I develop a likelihood model for the predation process using Monte Carlo simulations and show that the method consistently produces parameter values that are more accurate than those obtained by means of the conventional methods.

2. Methods

Here I describe a method for obtaining the maximum likelihood estimates of functional response parameters. To evaluate the performance, maximum likelihood estimates and least squared estimates were compared based on simulated data.

2.1. Simulation

The predation process of functional response experiments can be considered to be a sequence of prey capturing and prey handling. That is, a predator needs to capture a prey first, and the captured prey must be handled to be consumed. After a predator finishes handling a prey, it starts searching for a new prey. If the prey capture rate is λ, and the handling time is h, the predation rate is,

$$\frac{\lambda}{1 + \lambda h}. \quad (3)$$

For example, the Holling type II functional response assumes that prey capture rate increases linearly in the prey density, $\lambda = aN$ where a is the attack rate and N is the prey density, and the handling time h is static. When there are N prey, the expected time to capture a prey is $1/(aN)$. (Generally, the expected time to capture a prey is λ^{-1}.) After a predator finishes handling a prey (i.e., after h time units on average), the expected time to capture the next prey is $1/(a(N-1))$ because the number of prey decreases by one after each predation event. In this study, I assumed that the time to capture a prey followed an exponential distribution with mean $1/(aN)$ when there are N prey in the environment (Okuyama, in press), and the handling time was assumed to follow a gamma distribution with a specified mean μ and variance σ^2 (shape parameter $= \mu^2/\sigma^2$ and scale parameter $= \sigma^2/\mu$). The simulation algorithm for obtaining the number of prey consumed u in time interval T is as follows:

(1) Set $t = 0$, $u = 0$, and the initial prey number N.
(2) Generate a search time t_s and a handling time t_h from specified distributions.
(3) Set $t = t + t_s + t_h$, $N = N - 1$, and $u = u + 1$.
(4) If $t < T$ repeat (2) and (3).

Thus, this procedure assumes that if a predator is in the middle of handling a prey at T, the prey individual is not counted as eaten.

In this simulation it is evident that the distribution for the number of prey consumed u is flexible and depends on the distributions of search time and handling time. For example, suppose both search time and handling time are static (i.e., zero variance). Then the outcome in u also has no variance. Likewise, large variance in search time and handling time would result in large variance in the number of prey eaten. In other words, for a given mean number of prey eaten, variance can vary. On the other hand, if we assume a binomial distribution, it assumes a specific mean–variance structure. That is, for a given mean pN where p is the probability of capture, it has the fixed variance $pN(1-p)$. Thus, binomial distributions would not be able to accommodate general predation patterns in functional response experiments.

2.2. Likelihood construction

The likelihood model consists of three parameters: a (attack rate), μ (mean handling time), and σ^2 (variance handling time). These parameters correspond to the parameters used in the simulation described above. To obtain accurate likelihoods of data, we need to know accurate probability distributions of the number of prey eaten. To accomplish this, the simulation model described above can be used. Suppose we simulate the number of prey consumed for q trials, there are q realizations of the number of prey consumed $(u_1, u_2, \ldots, u_q)$. Then, the probability mass function for observing y prey consumed is,

$$f(y; a, \mu, \sigma^2) = \frac{1}{q}\sum_{i=1}^{q} I_y(u_i) \quad (4)$$

where I_y is the indicator function. The indicator function $I_y(x)$ is 1 if $x = y$ and is 0 otherwise $(x \neq y)$. Increasing the number of