

How can the functional response best be determined?

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Summary. We evaluated three methods for the analysis of functional response data by asking whether a given method could discriminate among functional responses and whether it could accurately identify regions of positive density-dependent predation. We evaluated comparative curve fitting with foraging models, linear least-squares analysis using the angular transformation, and logit analysis. Using data from nature and simulations, we found that the analyses of predation rates with the angular transformation and logit analysis were best at consistently determining the "true" functional response, i.e. the model used to generate simulated data. These methods also produced the most accurate estimates of the "true" regions of density dependence. Of these two methods, functional response data best fulfill the assumptions of logit analysis. Angularly transformed predation rates only approximate the assumptions of linear least-squares analysis for predation rates between 0.1 and 0.9. Lack-of-fit statistics can reveal inadequate fit of a model to a data set where simple regression statistics might erroneously suggest a good match.

Key words: Curve fitting – Density dependence – Functional response – Logit – Predation

The functional response describes the rate at which a predator kills its prey relative to the density of that prey. When the number of prey killed is plotted against the number of prey available, a continuum of patterns may emerge from which ecologists delimit three types. These curves may represent an increasing linear relationship (type I), a decelerating curve (type II), or a sigmoid relationship (type III). These result in a constant (I), decreasing (II), or increasing (over a limited range of prey densities) (III) rate of prey killing and yield density-independent, negatively density-dependent, and positively density-dependent prey mortality, respectively. Demographers often wish to identify predators that impose positively density-dependent mortality on their prey, because such mortality schedules can regulate prey populations (Murdoch and Oaten 1975). They usually attempt to do so by comparative curve fitting, examining whether a type-III curve best fits the observed functional response.

Statistical analysis of such data is not straightforward, and recently several papers have proposed new methods

(Livdahl and Stiven 1983; Juliano and Williams 1985; Williams and Juliano 1985). These papers have focused on the analysis of the number of prey killed per unit time relative to the number of prey available. This focus stems from theoretical and historical motivations rather than statistical ones. We argue that this focus may not always allow a demographer to determine the most appropriate general type of functional response for a given body of data.

Specifically, we argue that some popular methods of analyzing such data can inspire misleading conclusions. The predation event is a discrete one; the number of prey killed can only take integer values bounded by 0 and the number of prey available. A natural probability model to use for such a situation is the binomial. This model is appropriate as long as the predation events included in the sample were independent, i.e., could justifiably be described as a random sample of predation events from the population of inference. Nonetheless, most methods that have been employed for analyzing functional response data do not account for the specialized nature of these data.

Several problems can arise when a discrete, binomially distributed variable is analyzed as if it were continuous and normally distributed (Anderson et al. 1980; Cox 1970). These problems can accumulate quickly, causing biases in the fit of models to data and inefficiency in tests used to discriminate among competing models. In this paper we evaluate three methods of analyzing functional response data. We show how some of the methods suggest functional forms that, in reality, do not fit the data and how competing models of differently shaped functional responses cannot always be distinguished. We also illustrate how misleading conclusions about the shape of the true functional response can be readily drawn from a standard procedure. Our goal is to find how functional response data are best analyzed in order to identify the correct shape of a curve and to identify correctly the region of positively density-dependent prey mortality. Juliano and Williams (1987) compare methods for estimating parameters of foraging models of functional responses, once the correct shape of the response has been identified. It is that process of initial identification with which we are concerned.

Methods and results

Fitting mechanistic foraging equations to real data

A common practice for the analysis of functional response data is to choose two or more theoretical equations that arise from foraging theory and that describe a functional

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response and to fit them directly to data. These equations describe the number of prey killed as a function of the number of prey available and one or more deterministic parameters. The protocol of this approach invokes parsimony in accepting the equation that has the fewest biological assumptions yet adequately fits the data (Hassell et al. 1977; Akre and Johnson 1979; Livdahl and Stiven 1983).

Two typical equations are Rogers's (1972) random predator model, which describes a type-II response, and Hassell et al.'s (1977) type-III model. Roger's model is:

$$N_{ha} = N[1 - \exp\{-a'(T - T_h N_{ha})\}] \quad (1)$$

where:

N is the number of prey available,

N_{ha} is the number of prey killed,

a' is the instantaneous searching rate (the area covered by a searching predator in a given amount of time),

T_h is the handling time (the time spent dealing with each prey item), and

T is the total time spent searching in a patch of prey.

Hassell et al.'s (1977) model contains the same three parameters but allows a' to be a function of prey abundance, $a' = bN/(1 + cN)$.

This model can be written as:

$$N_{ha} = N(N - N_{ha})[c \log\{(N - N_{ha})/N\} - bT_h N_{ha} + bT] \quad (2)$$

Equations 1 and 2 are implicit formulae requiring iterative techniques for solution.

We evaluated the efficiency of this approach by fitting equations (1) and (2) along with four others to several data sets and comparing the results with the use of lack-of-fit statistics. Lack-of-fit statistics document the extent of bias in the residuals produced by comparison of the predicted values to the actual values. If the errors are normally and independently distributed, the lack-of-fit test yields an F statistic that, when significant, indicates that the model in question does not adequately fit the data (Draper and Smith 1981). A non-significant result is evidence that the model fits the data well. Ordinarily, such a test would result in rejection of those models yielding a significant "lack of fit" and subsequent analysis of the residuals of the models that were judged adequate to determine which of the "adequate" models fit best. With binomially distributed data, the lack-of-fit statistic will only have an approximate F distribution. However, as a descriptive statistic the F value is still valid; larger values indicate poorer model fit. Our goal is to evaluate how well the model-fitting method can distinguish among competing mechanistic models, not to investigate the usefulness of particular models *per se*.

A common practice in this protocol is to force the functional response equation through the origin (Akre and Johnson 1979). This practice is motivated by the observation that, at zero prey available, no prey can be killed. However, in some cases the observed x intercept may be greater than zero (i.e. the y intercept is below the origin; see Fig. 3 of van Lenteren and Bakker 1976). The biased predicted values that result from forcing an equation through the origin in this situation could lead to the unnecessary rejection of a model by the lack-of-fit statistic (Draper and Smith 1981, p. 112). We have not forced our curves through the origin unless required to do so in order to obtain a solution to a particular equation.

We have analyzed four previously published data sets (Table 1; Fig. 1). In one case (*Plea atomaria*) only the mean

Table 1. Results from lack-of-fit analysis of models predicted by equations 1 through 6 to fit data sets taken from literature sources. Asterisk indicates that the iterative procedure failed to converge. F -literature are results of fitting parameter estimates (when available from published sources, F -iteration are results from iterative solutions

Data Set	Equation	F -literature	F -iteration	df
<i>Aphelinus thomsoni</i> preying	1	0.6	0.5	5,133
on <i>Drephanosiphus platanoides</i>	2	0.8	0.3	4,133
(constant-time expt.):	3		4.4	6,133
Collins et al. 1981	4		1.2	6,133
	5		0.14	4,133
	6		0.08	4,133
<i>Aphelinus thomsoni</i> preying	1		0.9	5,133
on <i>Drephanosiphus platanoides</i>	2		0.8	4,133
(variable-time expt.)	3		7.3	6,133
Collins et al. 1981	4		1.2	6,133
	5		0.7	4,133
	6		0.7	4,133
<i>Plea atomaria</i> preying	1	5.9	4.5	7,81
on <i>Aedes aegypti</i> :	2	18.7	*	6,81
Hassell et al. 1977	3		37.4	8,81
	4		5.8	8,81
	5		3.3	6,81
	6		2.3	6,81
<i>Notonecta glauca</i> preying	1		1.3	9,78
on <i>Asellus aquaticus</i> :	2		1.0	8,78
Hassell et al. 1977	3		5.3	10,78
	4		6.2	10,78
	5		1.9	8,78
	6		1.1	8,78

values of the number of prey killed were available, so we simulated the raw data by generating ten normally distributed replicates at each prey density with a mean equivalent to the mean number of prey killed at that density and a coefficient of variation (cv) at that level equal to 20% of that mean. Our literature review revealed cv values from 18% to 165%, with most data sets ranging from 30% to 90%. Our use of a 20% value is conservative. In two cases (*Aphelinus thomsoni*) the observed standard errors were available and were used. In each of these cases, sample sizes from 10 to 20 were apparently used at different levels of number of prey available. However, the specific sample sizes for each level were not given, so we used the largest sample sizes cited to simulate the raw data. In a fourth case (*Notonecta glauca*) the raw data were shared with us.

We used the two mechanistic models formulated by Rogers (1972) and Hassell et al. (1977) (equations 1 and 2 respectively) and four mathematical functions with no particular theoretical interpretation. These functions are:

$$N_{ha} = N[1 - \exp\{-P_1\}] \quad (3)$$

$$N_{ha} = N[1 - \exp\{-P_1/N\}] \quad (4)$$

$$N_{ha} = P_1 \exp\{-P_2 \exp\{-P_3 N\}\} \quad (5)$$

$$N_{ha} = P_1/[1 + P_2 \exp\{-P_3 N\}] \quad (6)$$

where P_1 , P_2 , and P_3 are parameters to be estimated. Equation 3 generates type-I curves (Nicholson and Bailey 1935), and equation 4 produces type-II curves (Thompson 1924).

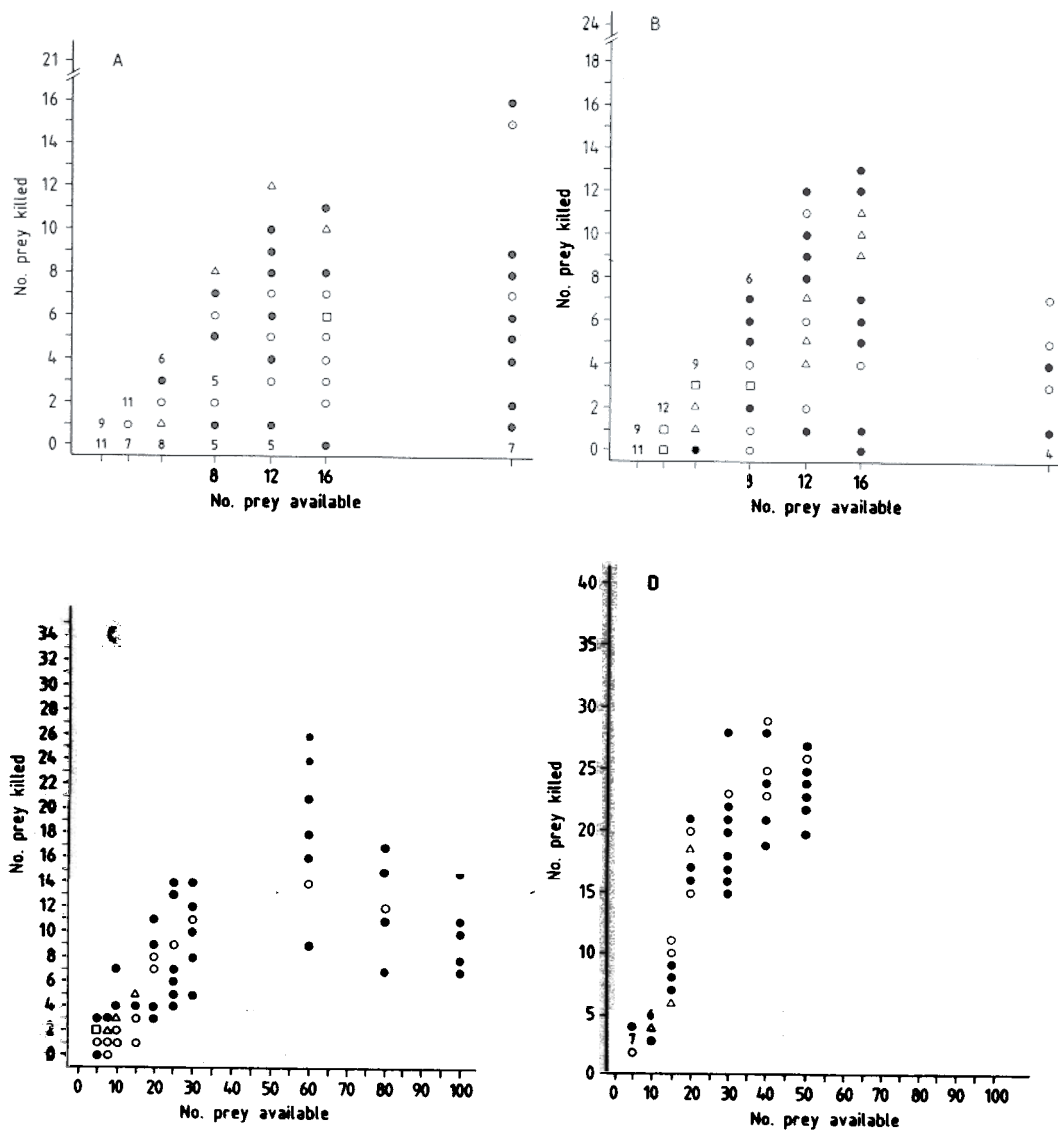


Fig. 1A–D. Plots of raw data taken from published sources: A Collins et al. 1981, *A. thomsoni* constant-time experiment; B Collins et al. 1981, *A. thomsoni* variable-time experiment; C Hassell et al. 1977, *N. glauca*; D Hassell et al. 1977, *P. atomaria*. Closed circles indicate single points. Open circles indicate two overlapping points, open triangles three, and open squares four. Numbers are plotted for respectively higher numbers of overlapping points

Equation 5 is the Gompertz equation and produces a family of sigmoid curves that resemble type-III foraging. Equation 6 is the logistic equation, which can also produce sigmoid curves. For equations 5 and 6 P_1 is the asymptote, P_2 determines the position of the curve along the x axis, and P_3 determines the rate of approach of the curves to the asymptote (Draper and Smith 1981). The logistic curve has its inflection point fixed at the midpoint of the curve. The Gompertz curve, like equation 2, does not have a fixed midpoint. Thus the Gompertz curve should be the more flexible of our type-III "empirical" curves.

The rationale for fitting these equations was to vary shape and number of parameters for competing descriptions of data. If two models with different shapes fit a data set, then the model-fitting method is not statistically powerful enough to determine the correct shape of the functional response. We use equations 5 and 6 in this context to preclude the possibility that we cannot distinguish among dif-

ferent shapes solely because of our choice of any one particular model for a sigmoid shape. Our six equations also vary in the number of parameters they contain. Equations 3 and 4 are one-parameter models. Equation 1 has two parameters, and equations 2, 5, and 6 contain three parameters. We consider T in equations 1 and 2 as a constant. Comparing the success of one-, two-, and three-parameter models allowed us to evaluate further the power of this method. If relatively higher-order models inevitably give a better fit to functional response data, regardless of shape, then the reliability of the curve-fitting approach is questionable. A three-parameter model will yield a better fit than a one- or two-parameter model by chance alone (Draper and Smith 1981). If one cannot objectively choose a sigmoid-shaped model over a type-II shape, then one cannot objectively say on the basis of the functional response alone that the predator has the ability to regulate the prey.

We employed an iterative least-squares method

(BMDPAR: Dixon and Brown 1979) to estimate the parameters that gave the best fit for each model to each data set. We set initial values for parameters from either the source of the data or from reasonable guesses. We set initial values for all but one parameter and solved for that remaining one. We ran each model with at least two sets of initial values to find the global minimum solution. In two cases we used published parameter values to fit our simulated versions of the original data and to compute lack-of-fit statistics in order to examine how precisely we reconstructed the original data.

The performance of the various models we fit to actual data sets is erratic (Table 1). Although the data on *N. glauca* can be adequately described by four models (F-values below 2), the data on *P. atomaria* is not adequately fit by any model. The data on *P. atomaria* is, on the whole, not fit as well as the data on *N. glauca* (compare F-values). The *A. thomsoni* constant-time experiment data yield quite low lack-of-fit statistics for five of six models, and the variable time experiments are well fit by four of six models. Published parameter estimates yield fits close to those obtained by the iterative solution method, suggesting that we have adequately reconstituted the original data structure.

Such differences among data sets in the capacity to be fit by a unique model, or any model, may be based in differences in the relative amount of variance in number of prey killed (y). The greater the variance in y , the less power we will have to distinguish among competing models. The lower the variance in y , the more likely we are to reject particular models. These principles are illustrated in our results: four models fit the *N. glauca* data adequately, whereas no models fit the *P. atomaria* data adequately. The coefficients of variation in y at the various numbers of prey available (x) range from 32% to 77% in the *N. glauca* data, 53% to 165% for the *A. thomsoni* constant-time experiment, and 31% to 138% for the *A. thomsoni* variable-time experiment, but are only 20% of the mean in the *P. atomaria* data.

For none of our data sets could we arrive at an unambiguous, objective choice of a model. The *P. atomaria* data, as we have simulated them, have a high "signal-to-noise ratio," suggesting that, had a clearly appropriate model been among those tested, we should have been able to recognize it. However, our conclusion in this case must be tempered by the fact that we imposed an arbitrary variance structure on the data that was conducive to rejecting inappropriate models. Other reconstructions could have different variance structures (within-level or "pure error" vs a lack-of-fit component) that might permit a choice of model. Each of the other three data sets, "noisier" than our version of the *P. atomaria* data, were fit well by several models, precluding an objective choice. Thus the model-fitting approach was unable to help us discriminate objectively among functional response types and was thus inadequate for deciding whether predators could regulate prey.

Fitting mechanistic foraging equations to simulated data

Would better data, with less variation or with a simple pattern of variation, allow more accurate discrimination of competing descriptions of functional responses, or is the protocol itself really inadequate? The "true" functional response of data from nature can never be determined beyond doubt. We simulated data from predetermined functional

responses to evaluate whether the model-fitting method can discriminate accurately among response curves and predict correctly the positively density-dependent regions. If we can succeed with simulations where we could not with real data, then the problem lies in the way experiments are designed. If we fail with simulations, then the problem of discrimination is certainly based in the protocol.

We generated three pairs of functional responses, labelled pairs A, B, and C (Fig. 2). One member of each pair was a type-II curve in which the "true" number killed was generated with equation 1. The other member was a type-III curve in which the "true" number killed was generated with equation 2. We used parameter values for these models from Hassell et al. (1977, their Table 7) and set them to be as similar as possible for the members of each pair so that we had three pairs of functional response curves whose two members differed only in shape. Differences among the three pairs of curves reflected different parameter values. The three pairs were constructed to differ in the rate at which they approach the asymptote and in the height of that asymptote. As a result, the three pairs display, in general, different killing rates. Pair B curves show extremely low killing rates, pair A curves show intermediate rates, and pair C curves show very high killing rates. Those curves identified as "2" are all decelerating curves (type II), and "3" are sigmoid curves (type III). The "2" and "3" versions of each curve (A, B, or C) are similar with regard to the rate at which they approach the asymptote and the height of the asymptote. We constructed the simulated data sets by generating ten normally distributed replicates whose mean equalled the value of the true functional response at each of several levels of prey abundance (9–11 levels were used). The coefficient of variation of the number of prey killed was set at approximately 20% at all levels of prey abundance.

We fit equations 3–6 to these six simulated data sets using the iterative-solution method. This procedure is the same as our previous analyses of real data, except that here we know the correct shape of the functional response. Thus we can evaluate the accuracy and precision of the iterative method *vis a vis* curve shape. In addition, we "re-fit" equation 1 to the data generated from equation 1 and "re-fit" equation 2 to the data generated from equation 2, using the usual iterative method. We compared the lack-of-fit statistics and parameter estimates from the "re-fitting" to the lack-of-fit statistics calculated from the true predicted values and the true parameters themselves. This procedure calibrated the accuracy of the model-fitting method *vis a vis* alternative models of the same shape.

The performance of our models with our simulated data was erratic (Table 2). Curves A2, A3, B2, and B3 were adequately described by both Gompertz and logistic equations (5 and 6 respectively). Thus the type-II and type-III versions of curves A and B are both fit well by the sigmoid, higher-order *ad hoc* equations. This result is not surprising because the extra parameter in these equations allows increased flexibility. For curves A3 and B3, the generating equation (2) fit as well as the two *ad hoc* equations with the same numbers of parameters. If these were real data, and our three equations all mechanistic foraging models, we would not be able to choose among them objectively. For curve A2, the generating equation has two parameters, yet it fits the data as well as or better than the three-parameter *ad hoc* models. This result represents a success for the curve-

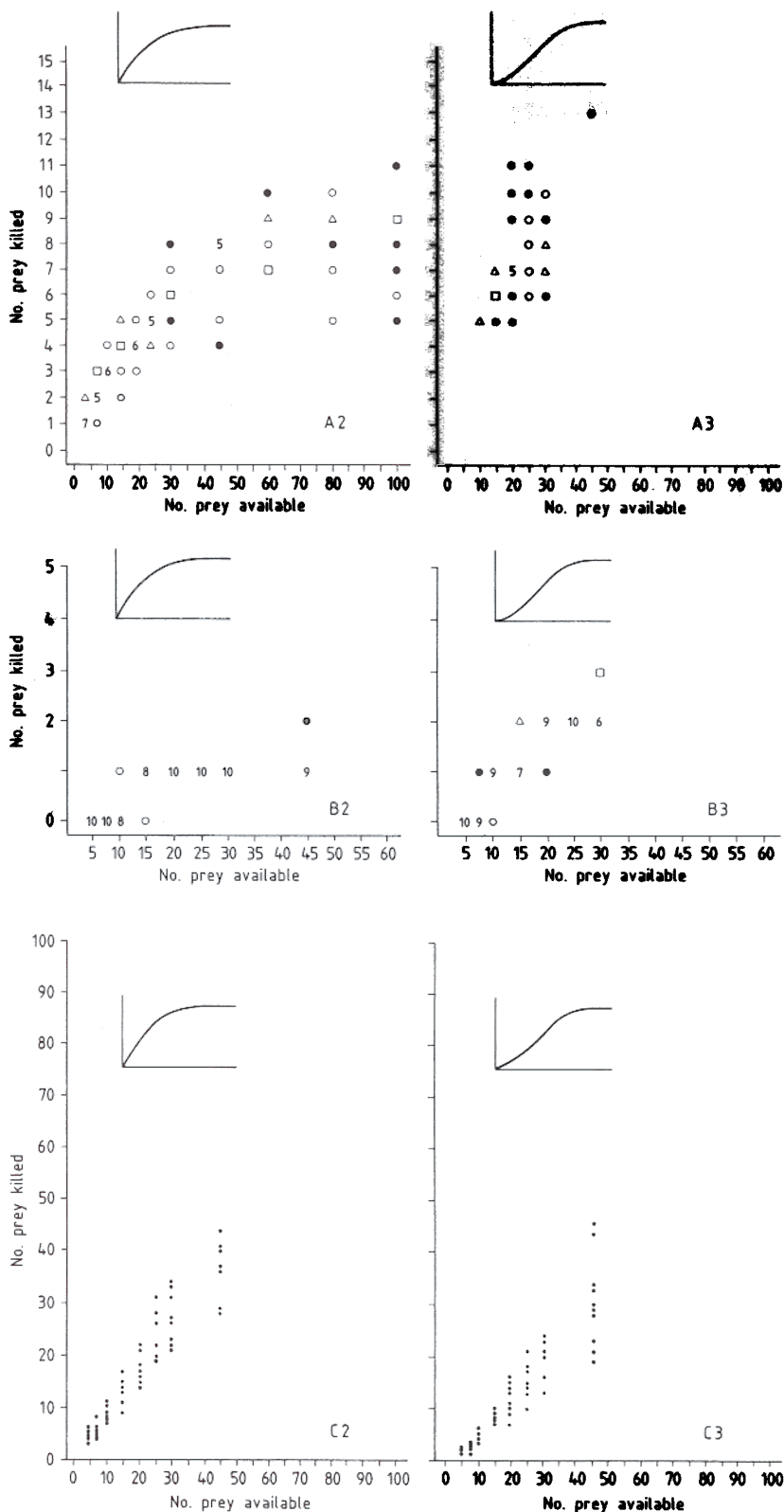


Fig. 2. Plots of raw data generated by simulations. Curves are identified on each plot; "2" corresponds to type-II form and "3" to type-III. Closed circles indicate single points. Open circles indicate two overlapping points, open triangles three, and open squares four. Numbers are plotted for respectively higher numbers of overlapping points

fitting approach. The situation is reversed for curve B2; the generating equation fits worse than *ad hoc* models. Only the generating equation fit curve C2, another success for the approach. Curve C3 was fit well by its generating equation (2) and by equations 3 and 6. Equation 6 fit less well

than equations 2 and 3; if we consider parsimony important we might choose equation 3 as the "correct" model because it fits almost as well with one parameter as equation 2 does with three parameters. A strict curve-fitting approach would thus fail here.

Table 2. Results from lack-of-fit analysis of true functional responses, fit predicted by models used to generate data sets, and equations 3 through 6 to data sets generated by simulation. F-true are data for fit of true functional response, and F-iteration are results of iterative parameter estimation for indicated models

Data Set	Equation	F-true	F-iteration	df
A2	1	1.2	1.2	9,99
	3		41.9	10,99
	4		20.2	10,99
	5		1.1	8,99
	6		1.3	8,99
A3	2	1.2	1.0	8,99
	3		10.3	10,99
	4		12.3	10,99
	5		1.5	8,99
	6		1.3	8,99
B2	1	6.4	6.4	7,81
	3		9.1	8,81
	4		42.5	8,81
	5		0.8	6,81
	6		0.6	6,81
B3	2	2.4	1.8	6,81
	3		9.1	8,81
	4		42.9	8,81
	5		1.6	6,81
	6		1.0	6,81
C2	1	1.5	0.4	9,99
	3		5.8	10,99
	4		2.4	10,99
	5		3.5	8,99
	6		2.3	8,99
C3	2	0.8	0.5	8,99
	3		0.9	10,99
	4		11.4	10,99
	5		2.8	8,99
	6		1.4	8,99

These results illustrate the potential inadequacies of the curve-fitting approach for distinguishing among competing models. In the two cases that represented moderate to high killing rates and a type-II curve (A2 and C2), the curve-fitting approach performed as one would hope, distinguishing the "correct" model from all others. In the two cases that represented very low to moderate killing rates with a type-III curve (B3 and A3), the curve-fitting method found the correct shape but did not allow an objective choice to be made among three similarly shaped descriptors. In the difficult case of very low killing rates and a type-II response (B2), only the incorrectly shaped curves appear to fit well. This data set displayed a positive x intercept; our stochastic realization of this curve "killed" no prey at the lowest densities, and the left-hand tail of a sigmoid curve fits this pattern very well. This observation (positive x intercept) also explains the unlikely-appearing lack-of-fit values for the generating equation. On the whole, this example illustrates the problems for the curve-fitting approach that can be produced by a binomial random variable (number killed) when the probability of success is very small. This situation will arise often in experiments designed explicitly to minimize the level of exploitation during a trial (e.g. Akre and Johnson 1979). In the other difficult case (C3), that of high killing and a type-III response, different shapes fit equally well, and parsimony might have led us

to choose the incorrect shape. This example illustrates in some sense the problem that is the converse of that of B2. In case C3, the high killing rates, along with the variance-mean dependence, produce such a scatter at the high densities that the curve-fitting approach loses power to distinguish among shapes. Increased sample sizes at each level might have enhanced our power; alternatively, our 110 "trials" in this case (11 levels of prey density \times 10 replicates per level) represent the upper end of what can usually be accomplished in a real experiment.

The simulation results show that our inability to fit the *P. atomaria* data with any equation was not due only to a low cv or the problem of our inability to pinpoint a pure error term. Four of our six simulated data sets were fit by three equations, despite having cv's similar to that of the *P. atomaria* data. The low cv values increase our ability to detect a significant lack of fit (Draper and Smith 1981) and should allow us greater power to discard an inappropriate model. If we had used higher cv values, we would have had to accept more models as fitting adequately, and consequently have been unable to choose among them objectively. If the model-fitting approach is inadequate for distinguishing among models of very different shapes at low cv values (equations 2, 3, and 6 with curve C3), it will be grossly inadequate at the higher values more typical of real data. It seems clear that the curve-fitting approach will be inadequate for many types of data sets that are encountered.

Those equations that adequately fit our 6 artificial data sets did not necessarily predict correctly the range and location of the regions of prey density in which the predation rate is positively density-dependent (Table 3). No equation predicted the narrow positive density-dependence manifested in the "observed data" in data set A2. The Gompertz model came the closest to predicting correctly the density-dependent regions and did so perfectly in one of the three cases, curve B3 (Table 3). In the remaining two cases, however, it underestimated the range of the density-dependent region. Because the actual observations were generated by Monte Carlo methods, the observed average proportions killed often deviate from the "true" functional response. The inaccuracies in predicting the density-dependent region do not necessarily correspond with instances where, by chance, the "true" and observed density-dependent regions do not correspond (Table 3: curves A2, A3, B2).

Analysis of predation rate

Predation rate is the ratio of number of prey killed per unit time to number available. The slope of the predation rate relative to prey abundance can be used to discriminate among the three functional response types. A positive slope observed over any range of prey abundances is indicative of positive density-dependent prey killing, no slope indicates type-I responses, and a negative slope type-II. More critically, the predicted values from a regression analysis of predation rate would reveal immediately the regions of positive density-dependent predation without recourse to diagnosis of curve shape.

There is no real danger with a ratio correlation *per se*. The danger in some situations lies in improperly interpreting a ratio correlation as due to some biological mechanism rather than due to independence. In our case independence of number of prey killed and number of prey available

Table 3. The "true", observed, and predicted proportions of prey killed relative to number of prey available for simulated data. Predicted proportions reported for all models yielding adequate fit of data. Asterisks mark density-dependent portions of curves

Number avail- able	"True"	Ob- served	Models			
			Logistic	Gom- pertz	Logit anal- ysis	Angular trans- form
Curve A2						
	0.340	0.260*	0.402	0.369	0.392	0.334
	0.321	0.329*	0.323	0.311	0.343	0.301
10	0.297	0.320	0.270	0.270	0.295	0.270
15	0.262	0.260	0.231	0.238	0.245	0.234
20	0.234	0.200	0.214	0.220	0.214	0.210
25	0.211	0.196	0.203	0.206	0.191	0.192
30	0.192	0.197	0.193	0.193	0.174	0.177
45	0.150	0.151	0.160	0.157	0.141	0.148
60	0.123	0.135	0.129	0.127	0.121	0.127
80	0.099	0.099	0.099	0.099	0.103	0.108
100	0.083	0.079	0.080	0.080	0.091	0.095
Curve A3						
	0.298*	0.300*	0.428	0.377	0.349*	0.316*
7	0.345*	0.329*	0.387	0.375*	0.374*	0.351*
10	0.381*	0.430*	0.371	0.382*	0.381*	0.367*
15	0.385*	0.387	0.371	0.381	0.367	0.364
20	0.358	0.380	0.361	0.359	0.341	0.347
25	0.322	0.324	0.334	0.327	0.314	0.326
30	0.287	0.267	0.299	0.293	0.288	0.301
45	0.209	0.200	0.212	0.212	0.222	0.237
60	0.161	0.163	0.160	0.161	0.172	0.181
80	0.123	0.134	0.120	0.121	0.126	0.123
100	0.099	0.097	0.096	0.097	0.094	0.080
Curve B2						
	0.045	0.000	0.005*	0.001*	0.004*	0.000*
7	0.044	0.000*	0.008*	0.006*	0.011*	0.002*
10	0.043	0.020*	0.020*	0.024*	0.021*	0.013*
15	0.040	0.053*	0.051*	0.048*	0.035*	0.028*
20	0.038	0.050	0.054*	0.051*	0.042*	0.035*
25	0.036	0.040	0.045	0.045	0.043*	0.038*
30	0.034	0.033	0.038	0.039	0.042	0.039*
45	0.030	0.024	0.025	0.026	0.031	0.031
60	0.026	0.025	0.019	0.020	0.020	0.022
Curve B3						
	0.044*	0.000*	0.065	0.040*	0.016*	0.000*
7	0.058*	0.014*	0.061*	0.049*	0.032*	0.012*
10	0.072*	0.090*	0.064*	0.063*	0.055*	0.044*
15	0.084*	0.087 (*)	0.075*	0.081*	0.081*	0.079*
20	0.086*	0.095*	0.085*	0.089*	0.091*	0.093*
25	0.084	0.080	0.089*	0.089	0.092*	0.096*
30	0.079	0.080	0.086	0.084	0.088	0.092
45	0.063	0.071	0.065	0.065	0.067	0.068
60	0.050	0.048	0.049	0.050	0.048	0.042
Curve C3						
	0.313*	0.260*	0.638	0.721	0.243*	0.243*
	0.381*	0.343*	0.638	0.615	0.343*	0.349*
10	0.455*	0.460*	0.638	0.551	0.447*	0.453*
15	0.535*	0.533*	0.638	0.528*	0.543*	0.547*
20	0.586*	0.575*	0.638	0.541*	0.595*	0.597*
25	0.620*	0.612*	0.638	0.566*	0.624*	0.628*
30	0.643*	0.637*	0.638	0.594*	0.642*	0.646*
45	0.678*	0.680*	0.638	0.661*	0.662*	0.668*
60	0.683*	0.693*	0.638	0.686*	0.661	0.669*
80	0.665	0.606	0.638	0.665	0.647	0.658
100	0.630	0.639	0.638	0.611	0.627	0.641

would induce a negative correlation of predation rate with prey density, analogous to a case of negative allometry in morphometrics (Mosimann and James 1979). This result could also be properly (and perhaps importantly) interpreted as a negative density dependence (although we recognize that this is not the meaning used by biologists in this context). The problem would arise only if the negative density dependence were considered to be due to some causal factor other than the independence of number killed and number available. To continue our morphometric analogy, positive density dependence is akin to positive allometry, and ratio-correlation methods are quite powerful for detecting this pattern (Mosimann and James 1979).

The predation rate (p) can be analyzed as a function of prey density using weighted regression analysis of angularly transformed values ($\arcsin \sqrt{p}$). This technique is not effective over all ranges of predation rates and densities. The angular transformation approximates the binomially distributed variance of a discrete variable as $1/(4n)$. The true binomial variance is given by $p(1-p)/n$. Thus the angular transformation is effective when n is large (Cox 1970). When n is small, the approximation overestimates the variance; the severity of the problem increases as p deviates from 0.5. For example, $n=5$ yields a variance estimate of 0.05 for the angular transformation, whereas the true value ranges from 0.018 to 0.05 as p goes from 0.1 to 0.5. The angular transformation also loses information at extreme values of p ($P < 0.10$ or $P > 0.90$) (Cox 1970).

The most desirable method of analysis should behave similarly at all levels of predation rate and prey density. Logit analysis is a statistical technique formulated for the analysis of the relationship between a dichotomous dependent variable and a continuous independent variable. It uses the logit transformation to expand the range of potential values taken by the dependent variable from a range of 0 to 1 to a range of $-\infty$ to $+\infty$ and provides an exact estimate of the binomial variance. It does not lose information at extreme values of p . Thus, it is appropriate for all values of p and n . The statistical model employed by logit analysis is:

$$\ln \left[\frac{p}{1-p} \right] = \alpha + \beta N + \epsilon$$

where p is the proportion of available prey killed. This model may be fitted to data with maximum likelihood techniques (BMDPLR, Dixon and Brown 1979, and SPSS X, Nie 1983, include this method) and evaluated with a valid lack-of-fit test. An alternative method for the use of this model, called empirical logistic regression, is to use logit-transformed values of predation rate as the dependent variable in weighted least-squares regression on prey density. The logit transform is:

$$y_j = \ln \left[\frac{R_j}{N_j - R_j} \right]$$

where R_j is the number of prey killed at the j th level of prey available (N_j). The weights are $N_j/(R_j(N_j - R_j))$. Empirical logistic regression requires repeated observations at each level of the independent variable. Where R_j is 0 or N_j , the logit transform must be modified to (Snedecor and Cochran 1980: 429):

$$y_j = \ln \left[\frac{R_j + \frac{1}{2}}{N_j - R_j + \frac{1}{2}} \right]$$

and used with weights

$$\frac{N_j + 1}{(R_j + \frac{1}{2})(N_j - R_j + \frac{1}{2})}$$

When many zeros are present, this transformation can lead to incorrect conclusions and it is wise to use a maximum likelihood method instead of a weighted least-squares regression.

We used the BMDPLR package to analyze our simulated data sets (curves A, B, and C) with the logit regression model via maximum likelihood. In this procedure, we used logit-transformed predation rates as the dependent variable and the log-transformed prey density as the independent variable. We began with a model whose highest-order term was the log of prey density cubed and used backward elimination of the highest order term until the lack-of-fit statistic became significant. We then selected the model with the fewest terms that gave a non-significant lack-of-fit chi-square statistic. This procedure invokes parsimony to decide among competing models that fit the data and generally results in selecting the "worst fit" of all models that "do fit" (because higher-order models tend to fit better than lower-order models). We used a similar procedure with angularly transformed predation rates for comparison. In this case we employed lack-of-fit F tests. The flexibility of these statistical models ensures that one can almost always get an adequate fit. One can evaluate their performance by examining whether they predict correctly the regions (if any) of positively density-dependent mortality.

The statistical models using the angular transformation and logit analysis gave similar predictions (Table 3). This result was not unexpected; the proportion of prey killed was generally between 0.1 and 0.9 for data sets A and C. In two cases (A3 and C3), the density-dependent regions and predicted values estimated by the logit analysis correspond to the "true" functional responses as well as or better than the predictions derived from the subset of equations 3-6 that actually fit the data (Table 3). In one case (B3), the Gompertz equation performed best. In data set A3, the logit's prediction missed the "true" range by one level of the independent variable; however, the observed average predation rate also declined at this point and the logit's prediction matches the observed region of density dependence perfectly. In data sets B3 and C3, the logit's predictions also missed the "true" and "observed" ranges by one level of the independent variable, but its incorrect predictions are only tenths of a percentage point in the wrong direction.

The logit and the angular transform did a poor job of predicting predation rates for curve B2, in which "true" predation rates were very low. The "incorrectly shaped" Gompertz equation performed well on this curve. This paradox arises because the "observed" values display a positive x intercept (Fig. 2). The Gompertz model passes through the origin, and its left-handed tail provides a good mimicry of the zero predation rates at low densities. Had we "shifted" the start of our Gompertz model to the x intercept of the data, the fit would have been very poor, and the logit and angular transforms would have out-performed the Gompertz.

Discussion

We have tried to show that curve-fitting methods can perform poorly on some kinds of functional response data.

By "perform poorly" we mean that one often cannot use these methods to distinguish among competing models of similar shapes, and one can inadvertently select an incorrect shape for some data. Although it may appear amusing to be unable to choose between a legitimate theoretical model (equation 2) and a "nonsense equation" (equation 3), it is by no means amusing to be unable to distinguish between competing legitimate models of different shapes. If one wishes to identify a predator or parasitoid that can regulate a prey population, one wants to be able to recognize positive density dependence when it occurs. We argue that logit analysis of predation rate using maximum likelihood is the best way to do so. This method performs reliably, especially at lower levels of prey density (Cox 1970), and does not depend on any particular foraging model. Logit analysis should be used as the primary tool for diagnosing a functional response possessing a region of positively density-dependent prey mortality. Retention of a quadratic term in the regression (log prey density squared) could be used as the diagnostic for distinguishing between type-II and type-III shapes if an investigator wishes to use that terminology.

Although our results were equivocal concerning the superiority of logit analysis over least-squares with the angular transform, we suggest that logit analysis will be a superior method. Functional response data meet the assumptions of logit analysis more closely than least-squares analysis with the angular transform. Although we did not generate data for which incorrect results were obtained by use of the angular transformation, functional response experiments frequently generate predation rates on the order of 10% (Murdoch and Oaten 1975), a region in which the angular transformation loses its effectiveness, especially at lower prey densities.

We did not use either weighted least squares or a maximum-likelihood method of curve-fitting to fit each model to each data set. The heteroscedasticity of nearly all functional response data violates assumptions of least-squares analysis and would seem to require one of these two alternative approaches. These methods are not generally employed in practice (see list of studies in Juliano and Williams 1987). We argue that logistic regression is best suited statistically to functional response data, is easy to use, and performs at least as well as the methods currently in use. Thus we evaluated the performance of curve-fitting methods *as they are commonly used*. It is possible that non-linear maximum-likelihood methods or the use of weighted non-linear least squares would cause the curve-fitting method to perform more accurately. We suspect that they will not outperform the logit method consistently, and the simplicity of the logit method relative to the others favors its use.

Our results suggest that very high levels of replication may be necessary in situations in which observed killing rates are less than 10%. In data set B2 the observed killing rate increased over a range of prey densities when the "true" rate did not. This result arose because the "true" killing rate was very low, and at low prey abundances (e.g. 5), the number of prey killed was usually zero. As the abundance of prey increased, the probability of a predation event did not change, but the increased number of "trials" (potential prey) produced an increase in the "observed" killing rate. Stochastic effects produced a predation refuge at low prey abundance and density-dependent predation at higher abundances. High levels of replication will be necessary in

such instances in order to diagnose the correct functional response. Even those models that fit these data yielded poor predictions; in addition, the supposed "good fit" of the Gompertz model in such a case (B2) shows how misinformative simple curve-fitting techniques can be.

Acknowledgments. We thank Donald Strong and Daniel Simberloff for discussions and encouragement throughout the course of this study. Duane Meeter cheerfully provided expert statistical advice. We are especially grateful to John Lawton for sharing his raw data with us. We thank Kermit Rose for helping us to complete this project despite the active efforts of the FSU Computing Center. We thank Melanie Trexler for drawing the figures. Steve Juliano and Robert Taylor provided thoughtful comments on previous drafts. Joel Trexler and J. Travis acknowledge the support of grants DEB 81-02782 and BSR 84-15529 to J. Travis and BSR 83-05823 to J. Travis and J.A. Farr during the development of this project.

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Received January 17, 1987

Erratum

How can the functional response best be determined?

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Oecologia (1988) 76:206–214

Two equations in our paper were inverted. These were the weights for empirical logistic regression reported on the bottom of page 212 and top of page 213. The corrected weight from the bottom of page 212 is:

$$(R_j(N_j - R_j))/N_j.$$

When R_j equals 0 or N_j the weight, incorrectly given on top of page 213, is:

$$(R_j + 1/2)(N_j - R_j + 1/2)/(N_j + 1).$$

These changes have no effect on the results we report as these equations were not used in our analyses. We opted for the more accurate maximum likelihood solution to logistic regression, which we continue to advocate over the empirical logistic approach.

Ms. No. 990	Author Erratum	Ms. 1	Pages 1
Springer-Verlag, Heidelberg / H. Stürtz AG, Würzburg		Korr. (F)	Date 25.1
Provisorische Seitenzahlen / Provisional page numbers		 f..