CAN THE FUNCTIONAL RESPONSE BE DETERMINED?

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ABSTRACT

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) (fig. 1a). These result in a constant (I), decreasing (II), or increasing (over a limited range of prey densities) rate of prey killing (III) (fig. 1b) and yield density-independent, inversely density-dependent, and positively density-dependent prey mortality, respectively.

A diverse array of techniques have been employed to analyze functional response data. We report the evaluation of several of them: curve fitting by eye, fitting of mechanistic foraging models, linear least-squares analysis using the angular transformation, and logit analysis. We have evaluated various methods of analyzing the functional response by asking whether they fulfill two criteria. First, can they discriminate among functional responses by correctly determining which type of functional response curve a predator produces? Second, can they accurately identify regions of positive density dependence in functional response data?

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) (fig. 1a). These result in a constant (I), decreasing (II), or increasing (over a limited range of prey densities) rate of prey killing (III) (fig. 1b) and yield density-independent, inversely density-dependent, and positively density-dependent prey mortality, respectively.

Two different types of research programs may include studies of the functional response. Demographers 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). Ethologists wish to estimate parameters that describe predator foraging and explore their dynamics (Hassell 1978). These parameters are supposed to reflect the biological mechanisms through which the various functional response forms arise. Murdoch and Oaten (1975:35) give a clear description of how experiments are performed to determine the functional response.

Analysis of functional response data is not a straightforward statistical problem, 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 a historical motivation rather than a statistical one. Holling's (1959a, b) studies of the functional response analyzed the number of prey killed, and all subsequent modelling has concentrated on this dependent variable (Hassell 1978). The number of prey killed presents problems for statistical analysis, however. The predation event is a discrete one; prey are killed or they are not, and no more prey can be killed than are available. Therefore, the number of prey killed is bounded by 0 and the number of prey available and can only take integer values, counts of the number of successful predation events. A natural probability model to use for such a situation is the binomial. This model would be appropriate as long as the predation events included in the sample were independent, i.e., could be justified as a random sample of predation events from the population of inference.

What problems arise when a discrete, binomially distributed variable is analyzed as if it were continuous (Anderson _et_ _al_. 1980; Cox 1970)?

1. Most statistical procedures assume that the variance in the dependent variable is the same no matter what the value of its mean. The mean and variance of a binomially distributed random variable are related: the variance is np(1-p) and the mean is np, where n is the number of prey available, and p is the proportion of prey killed.
2. Most statistical procedures assume that errors are normally distributed and therefore can take on a continuum of values. In analyses of predation, the errors can only take on a limited range of values, corresponding to the limited possible combinations of predation and no predation.
3. The statistical power of hypothesis-testing techniques designed for normally distributed variables can be poor for non-normal data. This problem leads to the use of inefficient tests compared with procedures based on more appropriate statistical models.

In the specific case of the functional response, the responses are bounded by 0 and n (when number of prey killed is analyzed) or 0 and 1 (when proportion of prey killed is analyzed), and the fitting of linear or polynomial normal-theory models to such data may cause the following problems:

4. Predicted values may fall outside the range of possible values for the dependent variable, regardless of whether that variable is predation rate or simply the number killed. Figure 2a illustrates a simple case in which the predicted values from an ordinary least squares regression become negative.
5. The fitted line may be very sensitive to the specific range of prey densities used. Compare figures 2a and 2b. Figure 2b is figure 2a with additional data points added beyond 24 prey available. They convey essentially the same information about functional response, yet their fitted lines differ greatly.

The problems illustrated in figure 2 stem from inappropriate statistical methods, not an inappropriate descriptive model.

A diverse array of techniques have been employed to analyze functional response data. We report the evaluation of several of them: curve fitting by eye, fitting of mechanistic foraging models, linear least-squares analysis using the angular transformation, and logit analysis. We have evaluated various methods of analyzing the functional response by asking whether they fulfill two criteria. First, can they discriminate among functional responses by correctly determining which type of functional response curve a predator produces? Second, can they accurately identify regions of positive density dependence in functional response data?

METHODS AND RESULTS

Curve-fitting by eye

Several authors have determined a predator's functional response by visual examination of plots of the number of prey killed relative to number of prey available (e.g. Hassell et al. 1977; cf. Livdahl and Stiven 1983). To examine the accuracy and precision of this method, we asked a group of biology faculty and graduate students to choose which of the three types of functional response best fit four data sets. These data sets were photocopied from a paper in which the authors had described all four sets as demonstrating type-III functional response curves (figure 1 in Hassell et al. 1977). The authors' proposed best fit lines were obliterated with liquid paper. The three type responses, copied from a standard textbook (Ricklefs 1979), were shown at the top of the survey form. The resulting data were the percentage of people choosing type-I, II, or III curves as best fitting each data set. The response was analyzed by chi-square tests for independence of proportions (table 1).

Eighty-one biologists responded to the survey, though some chose not to evaluate all four data sets. Of the four data sets presented, only for data set D was a clear preference for one type of curve evident. Data set D was most likely to be described as a type-III curve. In the other three data sets, there was no evidence that biologists chose one type of functional response curve as best fitting more frequently than another. There were no differences in curve fitting choices related to biological discipline (ecology, physiology, and cell biology) or status (faculty or graduate student). These results indicate that functional response data sets do not yield patterns so clear that statistical analysis is unnecessary; visual examination does not allow unambiguous discrimination among functional response types.

Fitting mechanistic foraging equations

A common practice for the analysis of functional response data is to fit mechanistic equations that describe foraging patterns resulting in one of the three functional responses. These models describe the number of prey killed as a function of the number of prey available and one or more deterministic parameters. The protocol is to invoke parsimony in accepting the foraging model that has the least biological assumptions and adequately fits the data (Hassell *et al*. 1977; Akre and Johnson 1979; Livdahl and Stiven 1983). Two typical models are Rogers's (1972) random predator model, which describes a type-II forager and Hassell *et al*.'s (1977) type-III model. Rogers's model is:

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

where: N is the number of prey available,

N_{ha} is the number of prey killed,

a' is the instantaneous seaching 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 may be written as:

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

Equations 1 and 2 are implicit formulae; iterative techniques are required for their solution.

We evaluated this common method of analysis by fitting these 2 models and 4 others to several data sets and comparing the success of each model with the use of lack-of-fit statistics. Lack-of-fit statistics document the extent of bias in the residuals produced by comparing the predicted values to the actual values. These statistics do not function analogously to measures of explained variation such as coefficients of determination or Mallows' statistic. If the errors are normally and independently distributed, this statistical 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, with larger values indicating poorer model fit. Because our goal is to compare the adequacy of fit of a range of models rather than find the best-fitting model, the F-statistic serves well as an objective measure.

A common practice in fitting mechanistic foraging models to functional response data is to force the equation through the origin of the graph of number of prey killed versus number available (Akre and Johnson 1979, for example). This practice is motivated by the observation that, at zero prey available, no prey can be killed. However, this practice denies the biological possibility that the x-intercept may be greater than zero (see figure 3 in van Lenteren and Bakker 1976). There is no a priori statistical reason to force the fit through the origin; such forcing does not necessarily circumvent our problem number 4. The biased predicted values that result could lead to the unnecessary rejection of a model by the lack-of-fit statistic. In addition, forcing the regression through the origin requires the extension of the regression model beyond the range of the data. We discourage the adoption of this convention and 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 previously published data sets from a variety of sources (table 2; figure 3). In one case only the mean values of the number of prey killed were available, so we simulated the raw data by generating ten normally distributed values with a mean equivalent to the mean number of prey killed at each prey density and a coefficient of variation equal to 20% of that mean. Our literature review revealed coefficients of variation from 18% to 165%, with most data sets ranging from 30% to 90%. Our use of a 20% value is conservative. In two cases 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 samples sizes for each level were not given, so we used the largest sample sizes cited to simulate the raw data. In a third case the raw data were shared with us.

We used 2 types of models: 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 ecological interpretation. These functions are as follows:

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

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

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

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

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). 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, P_3 determines the rate of approach of the curves to the asymptote. The logistic curve, curve 6, is symmetric about 1/2 P_1, while the Gompertz is not necessarily symmetric.

The rationale for fitting these models was that at most two of these functions should fit any given data set. If two curves with different shapes fit a data set, the most parsimonious model may not be the correct one; in such a case the curve-fitting method is not statistically powerful enough to determine the correct shape of the functional response. 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, the unambiguous biological significance of the parameters of these models 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).

We employed an iterative method to estimate the parameters that gave the best fit for each model to each data set (BMDPAR; Dixon and Brown 1979). In two cases, we used the parameter values published in the original reports to fit our simulated versions of the original data and compute lack-of-fit statistics. This procedure allows us to have a crude calibration of our reconstruction of the original data.

The performance of the various models we fit to actual data sets is erratic (table 3). Although the data on Notonecta glauca can be adequately described by four models (F-values below 2), the data on Plea atomaria is not adequately fit by any model. The data on P. atomaria is not fit as well as the data on N. glauca (compare F-values). The Aphelinus 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.

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. This problem is illustrated by the fact that four models fit the N. glauca data adequately, while 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, 31% to 138% for the A. thomsoni variable-time experiment, but are only 20% of the mean in the P. atomaria data (as generated by a simulation).

For none of our data sets could we arrive at an unambiguous, objective choice of a model. The P. atomaria data have a high "signal-to-noise ratio," suggesting that, had the appropriate model been among those tested, we should have been able to recognize it. None of our six models appears to be the appropriate one. Each of the other three data sets, "noisier" than the P. atomaria data, were fit well by several models, precluding an objective choice.

Would better data, with less variation or with a simple pattern of variation, allow more accurate discrimination of functional responses, or is the protocol itself inadequate? The results from the P. atomaria data suggest the latter. Of course, the "true" functional response of data from nature can never be determined beyond doubt. We used simulated data from known functional responses to determine whether these analytical methods can discriminate accurately among response curves and predict correctly the positively density-dependent regions. We generated type-II and type-III curves, with equations 1 and 2, respectively. Constants for these models were taken from Hassell et al. (1977, their table 7) and kept as similar as possible for the two models to yield pairs of functional response curves as similar as possible. The simulated data sets were constructed by generating ten normally distributed values with a mean equal to the value of the true functional response at each of several levels of prey abundance. The coefficient of variation of the number of prey killed is approximately 20% at all levels of prey abundance (figure 4). Such a correlation of mean and variance is typical of data from nature (Williams and Juliano 1985).

We fit equations 3-6 to these simulated data sets using the iterative solution method. This procedure "replicates" our previous analyses of real data, except that in these cases we know the correct shape of the functional response. Thus we can evaluate the accuracy and precision of the iterative method _vis à 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 iterative curve-fitting method.

The curves numbered A, B, and C (see figure 4) generated by our simulations differ in the rate at which they approach the asymptote and in the height of that asymptote, whereas the "2" and "3" version of each curve are similar in these regards. Those curves identified as "2" are all decelerating curves (type-II), and "3" are sigmoid curves (type-III). Curves A2, A3, B2, and B3 are adequately described by both the Gompertz and logistic models (equations 5 and 6 respectively; table 4). Thus the type-II and type-III versions of these two curves are best fit by the same models: the F-values are very similar. The higher-order models, equations 5 and 6, have much lower F-values than the other models and thus give much better fits, irrespective of whether the real curves are type II or type III. None of the models yields a good fit to curve C2. Equations 3 and 6 fit curve C3; these equations describe type-I and type-III functional responses, respectively. This result illustrates the pitfalls of the curve-fitting approach: a "true" sigmoid curve (C3) is fit by one sigmoid-shaped model (equation 6), but not another (equation 5), and this same curve is fit equally well by two entirely distinct models (equations 3 and 6).

Only data set C2 is clearly fit better by the true functional response than by our ad hoc models (table 4). Interestingly, data sets A2, A3, B2, and B3 are fit by our ad hoc models as well as, if not better than, by those models originally used to generate them. Iterative solutions of the "true" model frequently improved its fit to the simulated data relative to the "fit" given by the "true" parameters. However, in each of these cases, at least one of the true parameter values fell outside the 95% confidence intervals for the parameters derived by iteration.

The equations that adequately fit our 6 artificial data sets do not necessarily predict correctly the range and location of the regions of prey density in which the predation rate is positively density-dependent (table 5). No equation predicted the narrow positive density-dependence manifested in the "observed data" in data set 1a. The Gompertz model universally came the closest to predicting correctly the density-dependent region and did so perfectly in one of the three cases, curve 2b (table 5). In the remaining two cases, however, it notably 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 5: curves A2, A3, B2).

Analysis of predation rate

Predation rate is the ratio of number of prey killed per unit time to number available. It can be thought of as the probability that a single prey individual will be killed at a given abundance of prey (Oaten and Murdoch 1975). To use the predation rate to discriminate among the three functional response models it is necessary to determine the slope of predation rate relative to prey abundance. A positive slope observed over any range of prey abundances is indicative of density-dependent prey killing, no slope indicates type-I responses, and a negative slope type-II (Figure 1b).

If one scans a plot of predation rate relative to prey availability, it is possible to pick places where the killing rate increases and to test for a significant increase in predation rate relative to the initial experimental prey density with a chi-square test (Collins et al. 1981). This technique creates a bias in the statistical test: the investigator chooses the prey densities to be tested for the desired result. This procedure heightens the chance of type-I statistical errors, that is, finding a significant difference when none exists. Data sets A2 and B2 provide examples of an increasing predation rate found by chance where the "true" functional response does not have one (table 5).

The predation rate (p) could 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 an effective one 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, while 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 have a transformation of the predation rate that is insensitive to the level 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. Thus, it is appropriate for all values of p and n. The statistical model employed by logit analysis is:

$$\ln\left(\frac{p}{1-p}\right) = \alpha + \beta N + \varepsilon$$

where p is the proportion of available prey killed. This model may be fitted to data with the use of a maximum likelihood estimator. The BMDPLR statistical routine (Dixon and Brown 1979) and SPSS X (Nie 1983) can conduct such analyses and are capable of including grouping variables in the analysis. In addition, valid lack-of-fit tests are available for logistic regression. An alternative method for the use of this model, called empirical logistic regression, is to use logit transformed values as the dependent variable. 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 jth level of prey available (N_j). This method requires the use of weighted least-squares regression on density, with the weights equal to:

$$\frac{N_j}{R_j(N_j - R_j)}$$

Empirical logistic regression requires that there be 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. Therefore, it is wise to use a maximum likelihood estimator in such instances, and it is necessary to do so when repeated observations at each y are not available.

We used the BMDPLR package to analyze our simulated data sets (curves A, B, and C) with the logit regression model. In this procedure, we used logit transformed predation rates as the dependent variable, and the log-transformed prey density as the independent variable. A type-I functional response should yield no significant regression. Type-II curves should have a linear model with negative slope as the best fit. A type-III curve should be fit best by a quadratic equation in the independent variable, with a positive slope over some region (see figure 1b). Thus we used a backward elimination technique to arrive at an appropriate statistical model, beginning with a cubic model. We sequentially removed the highest-order term, checking the lack-of-fit statistic at each step until it 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 analyses using the angular transformation and logit analysis gave similar predictions as to the best fit of our data (table 5). This result was to be expected for data sets A2 and A3 and C2 and C3 because the proportion of prey killed was generally btween 0.1 and 0.9 for these four data sets. For data sets B2 and B3, the logit analysis generates predictions closer to the observed values of p. More simulations would be necessary to determine whether this difference is meaningful, however, because the predicted values do not differ greatly between the techniques.

The predictions of models selected through logit analysis correspond much better to the "true" functional responses than the predictions derived from our curve fitting of deterministic models (table 5). In no instance did logit models predict the existence of a density-dependent region where no such region appeared in the observed data. In data set A3, the logit's prediction missed the "true" range by one level of the independent variable; however, the observed predation rate also declined at this point and the logit's prediction matches this change perfectly. In data sets B3 and C3, the logit's predictions also missed the "true" range by one level of the independent variable, but its incorrect predictions are only tenths of a percentage point in the wrong direction.

DISCUSSION

It is easy to see why the analysis of predation rate is a powerful technique for testing for density-dependent prey killing. Density-dependent prey killing is simply indicated by a positive slope of predation rate relative to prey availability. To detect a sigmoid relationship of number of prey killed to prey availability, it is necessary to detect a change in the slope from less than one to greater than one before the inflection point (Fig 1a and 1b). Hassell (1966) recommended that studies of the functional response focus on studies of predation rate. His recommendation was motivated by behavioral considerations; we are advocating a similar protocol from a strictly statistical view.

Although our results were equivocal concerning the superiority of logit analysis over least-squares with the angular transform, we suggest the use of logit analysis whenever possible. Our results indicate that this technique can discriminate type-II and type-III foraging modes and adequately predict density-dependent regions when they are present. 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 where incorrect results were obtained by use of the angular transformation, it is always possible that real data will have densities that are too low or predation rates that are too extreme for the angular transformation to be effective. In fact, functional response experiments frequently generate predation rates on the order of 10%

(Murdoch and Oaten 1975), especially experiments explicitly minimizing the level of prey exploitation (e.g. Akre and Johnson 1979). With logit analysis readily available and simple to apply, it seems pointless not to use it. Logit analysis has the additional advantage of ready availability of a lack- of-fit test, performed by BMDPLR, for unambiguous choice of appropriate models.

We discourage behavioral studies that analyze the number of prey killed by fitting mechanistic foraging models and then ascribe biological significance to the parameters of the models. We have shown that many different mechanistic models can fit the same data. Very different biological interpretations could be ascribed to the parameters of these models at will, and only subjective criteria allow selection among the models (Smith 1952). Higher-order models usually give better fits than lower-order models, and this observation casts a shadow of uncertainty on the significance of parameter interpretations. We realize that we are advocating the abandonment of a popular analytical technique.

However, we concede that there may be other valid reasons for estimating the parameters of a mechanistic model that is chosen a priori (albeit subjectively). We suggest a new protocol for this purpose. The first step would be to determine whether the data display type-I, -II, -III foraging by logit analysis of predation rate. If the data display the type of foraging appropriate for the chosen mechanistic model, then the investigator may proceed to the second step. This second step entails estimating the parameters of the chosen, appropriate mechanistic model from a source independent of the data on which the fit (or the appropriateness) of that model was tested. For example, the original data set could be split; one-half of the data could be used to analyze the predation rate, and the other half could be used to estimate the parameters of the chosen mechanistic model (Selvin and Stuart 1966; James and McCulloch 1985). This procedure may be prohibitive because the size of the data set greatly affects the results of curve fitting. Some preliminary tests we conducted with simulated data sets having 5 instead of 10 observations per prey abundance, as reported here, indicated that more models give an adequate fit for the smaller data sets than for the larger. An alternative procedure would entail repeating the entire experiment to obtain independent data for parameter estimation. A variety of methods for parameter estimation were compared by Williams and Juliano (1985). Our suggested 2-step protocol corresponds to Box et al.'s (1978) "empirical" and "mechanistic" modelling; they provide extensive discussion of the rationale for such an approach.

Spitze (1985) suggested that the parameters of some mechanistic foraging models are instantaneous quantities, resulting from the combined effects of several behavioral acts, and therefore cannot be estimated independently of functional response data. We disagree. Based on results presented in this paper, we feel that a failure to estimate such parameters independently of functional response data precludes any critical hypothesis testing of the models in question or the parameters themselves. We agree with Royama (1971): curve fitting does not validate mechanistic models. We advocate testing the predictions of mechanistic models experimentally. For example, van Lenteren and Bakker (1976) compared the functional responses of parasitoids with a constant searching time in a prey patch to those allowed to vary the time spent in such a patch. Mechanistic models suggest that this difference could turn a type-II forager into a type-III forager (Hassell et al. 1977), and this was the case.

Our analyses also indicated that the lack-of-fit statistic was useful in determining viable models whereas the test for significant regression alone was a poor method. In fact, most models gave highly significant F statistics for regression. For example, data set B3, when fit by equation 3, had a high F value for lack-of-fit but an F for regression exceeding 283 and a coefficient of determination of 76%. Such models yielded high lack-of-fit values because of bias in the residuals that is not accounted for by the F for regression test (Draper and Smith 1981). Similar results were reported by Williams and Juliano (1985).

The question in our title, Can the functional response be determined, cannot be answered affirmatively in all cases. Our best analytical tools cannot cope with situations such as arose in data set B2, where the observed killing rate increased over a range of prey densities when the "true" rate did not. This artifact arose because the "true" killing rate was low. 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 variation alone yielded the appearance of a predation refuge at low prey abundance and density-dependent predation at slightly higher abundances. Many replicates may be necessary to estimate the predation rate correctly at low numbers of available prey. Instances where density--dependent predation occurs at such low prey availabilities have been reported (Collins _et_ _al_. 1981; van Lenteren and Bakker 1976), and we feel that such data might be re-examined in light of our results.

SUMMARY

We evaluated several methods for the analysis of functional response data by asking: Can a given method discriminate among functional responses, and can it accurately identify regions of positive density-dependent predation? The methods we evaluated were: curve fitting by eye, fitting of mechanistic foraging models, linear least-squares analysis using the angular transformation, and logit analysis. With the use of data from nature and simulations, we found only the analysis of predation rates with the angular transformation and logit analysis capable of determining the "true" functional response and accurately estimating regions of density-dependence. Of these two methods, functional response best fulfills 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. In most cases studied, several different deterministic foraging models adequately described the same data, indicating that these models cannot be used to determine which types of functional response a data set displays.

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Table 1. Results of curve fitting survey. Data sets A, B, C, and D correspond to figs. 1a, b, c, and d of Hassell _et_ _al_. 1977. Numbers are number of respondents choosing each functional response curve type as best describing each data set.

Data set	A			B			C			D		
Functional response type	I	II	III	I	II	III	I	II	III	I	II	III
	26	29	25	21	36	22	24	22	35	0	6	75
χ^2 statistic	0.33			5.34			3.63			128.7*		

* P < .001

Table 2. Sources of data sets analyzed.

Source	Predator	Prey	Comments
Hassell *et al*. 1977	*Notonecta glauca*	*Asellus aquaticus*	raw data shared by author
Hassell *et al*. 1977	*Plea atomaria*	*Aedes aegypti*	only mean number of prey killed published
Collins *et al*. 1981	*Aphelinus thomsoni*	*Drepanosiphum platanoidas*	mean and standard errors plotted

Table 3. Results from lack-of-fit analysis of models predicted by equations 1 through 6 to fit data sets taken from literature sources. Presence of a dash indicates that the iterative procedure failed to converge. F-literature are results of fitting parameter estimates from published sources, F-iteration are results from interative solutions.

Data	Equation	F-literature	F-iteration	df
A. thomsoni	1	0.6	0.5	5,133
(constant-time expt.)	2	0.8	0.3	4,133
	3		4.4	6,133
	4		1.2	6,133
	5		0.14	4,133
	6		0.08	4,133
A. thomsoni	1		0.9	5,133
(variable-time expt.)	2		0.8	4,133
	3		7.3	6,133
	4		1.2	6,133
	5		0.7	4,133
	6		0.7	4,133
P. atomaria	1	5.9	4.5	7,81
	2	18.7	---	6,81
	3		37.4	8,81
	4		5.8	8,81
	5		3.3	6,81
	6		2.3	6,81

Table 3 (continued).

Data	Equation	F-literature	F-iteration	df
N. glauca	1		1.3	9,78
	2		1.0	8,78
	3		5.3	10,78
	4		6.2	10,78
	5		1.9	8,78
	6		1.1	8,78

Table 4. 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

Table 4 (continued).

Data	Equation	F-true	F-iteration	df
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

Table 5. 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. Brackets enclose density-dependent portions of curves.

			Models			
Number available	"True"	Observed	Logistic	Gompertz	Logit analysis	Angular transform
			CURVE A2			
5	.340	.260	.402	.369	.392	.334
7	.321	.329	.323	.311	.343	.301
10	.297	.320	.270	.270	.295	.270
15	.262	.260	.231	.238	.245	.234
20	.234	.200	.214	.220	.214	.210
25	.211	.196	.203	.206	.191	.192
30	.192	.197	.193	.193	.174	.177
45	.150	.151	.160	.157	.141	.148
60	.123	.135	.129	.127	.121	.127
80	.099	.099	.099	.099	.103	.108
100	.083	.079	.080	.080	.091	.095

Table 5 (continued).

			Models			
Number available	"True"	Observed	Logistic	Gompertz	Logit analysis	Angular transform
CURVE A3						
5	.298	.300	.428	.377	.349	.316
7	.345	.329	.387	.375	.374	.351
10	.381	.430	.371	.382	.381	.367
15	.385	.387	.371	.381	.367	.364
20	.358	.380	.361	.359	.341	.347
25	.322	.324	.334	.327	.314	.326
30	.287	.267	.299	.293	.288	.301
45	.209	.200	.212	.212	.222	.237
60	.161	.163	.160	.161	.172	.181
80	.123	.134	.120	.121	.126	.123
100	.099	.097	.096	.097	.094	.080

Table 5 (continued).

			Models			
Number available	"True"	Observed	Logistic	Gompertz	Logit analysis	Angular transform
			CURVE B2			
5	.045	.000	.005	.001	.004	.000
7	.044	.000	.008	.006	.011	.002
10	.043	.020	.020	.024	.021	.013
15	.040	.053	.051	.048	.035	.028
20	.038	.050	.054	.051	.042	.035
25	.036	.040	.045	.045	.043	.038
30	.034	.033	.038	.039	.042	.039
45	.030	.024	.025	.026	.031	.031
60	.026	.025	.019	.020	.020	.022

Table 5 (continued).

			Models			
Number available	"True"	Observed	Logistic	Gompertz	Logit analysis	Angular transform
CURVE B3						
5	.044	.000	.065	.040	.016	.000
7	.058	.014	.061	.049	.032	.012
10	.072	.090	.064	.063	.055	.044
15	.084	.087	.075	.081	.081	.079
20	.086	.095	.085	.089	.091	.093
25	.084	.080	.089	.089	.092	.096
30	.079	.080	.086	.084	.088	.092
45	.063	.071	.065	.065	.067	.068
60	.050	.048	.049	.050	.048	.042

Table 5 (continued).

			Models			
Number available	"True"	Observed	$N-Ne^{-p}$	Gompertz	Logit analysis	Angular transform
CURVE C3						
5	.313	.260	.638	.721	.243	.243
7	.381	.343	.638	.615	.343	.349
10	.455	.460	.638	.551	.447	.453
15	.535	.533	.638	.528	.543	.547
20	.586	.575	.638	.541	.595	.597
25	.620	.612	.638	.566	.624	.628
30	.643	.637	.638	.594	.642	.646
45	.678	.680	.638	.661	.662	.668
60	.683	.693	.638	.686	.661	.669
80	.665	.606	.638	.665	.647	.658
100	.630	.639	.638	.611	.627	.641

Figure Legends

Figure 1. Plots of the functional response. a. Three functional response types plotted as the number of prey killed relative to the number of prey available. b. The same three functional responses plotted as predation rate or proportion of available prey killed relative to number available. After Ricklefs, 1979.

Figure 2a. Demonstration of data where best fit by linear least-squares yields estimates outside the possible range of predation rate. b. The potential impact of the choice of x values is shown in this figure. The data differ from those in figure 2 by the addition of observations at several high prey abundances. Note that the fitted line differs greatly from that in figure 2a.

Figure 3. 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 1 point. Open circles indicate 2 overlapping points, open triangles 3, and open squares 4, and numbers are plotted for respectively higher numbers of overlapping points.

Figure 4. 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 1 point. Open circles indicate 2 overlapping

points, open triangles 3, and open squares 4, and numbers are plotted for respectively higher numbers of overlapping points.

FIG 1

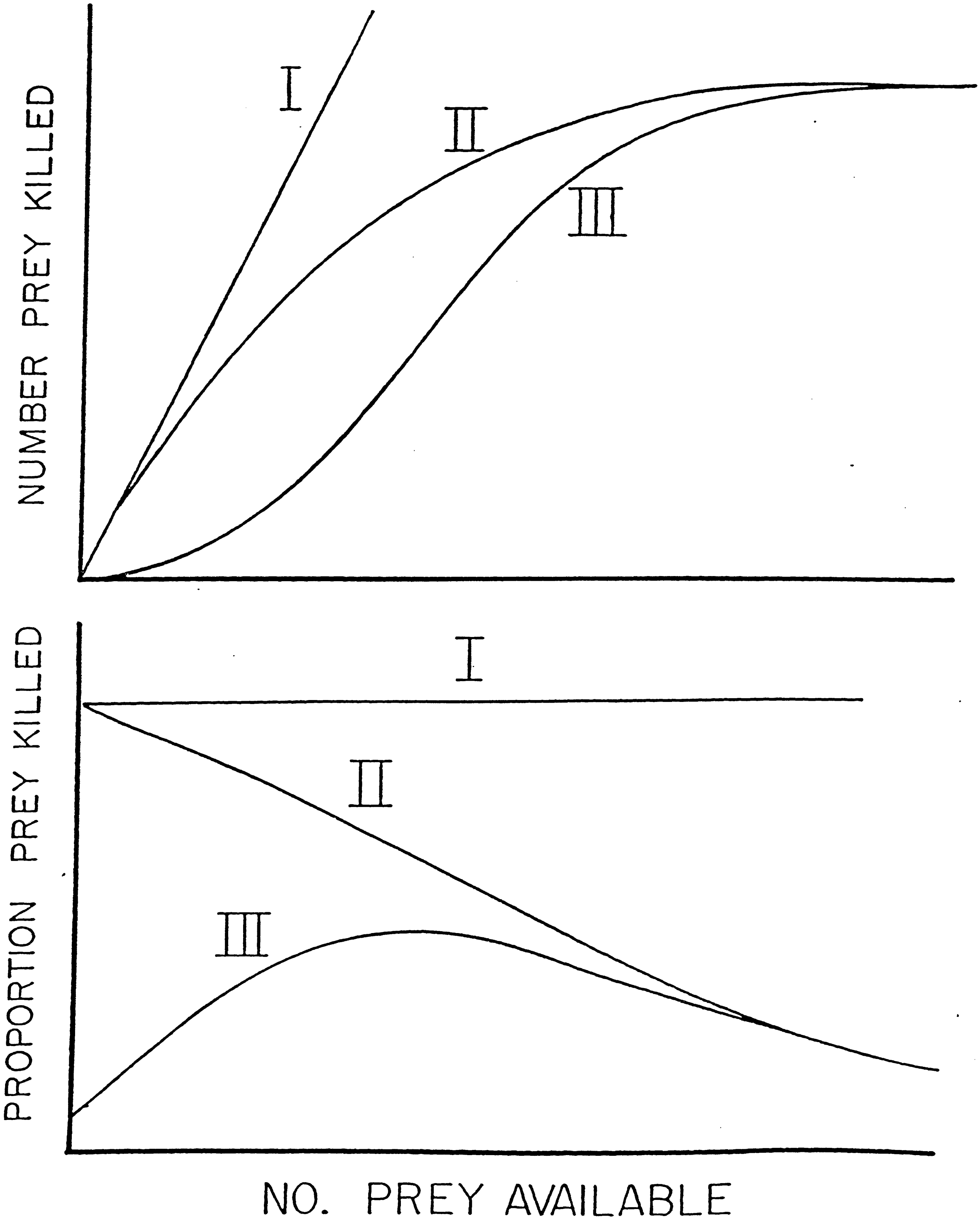
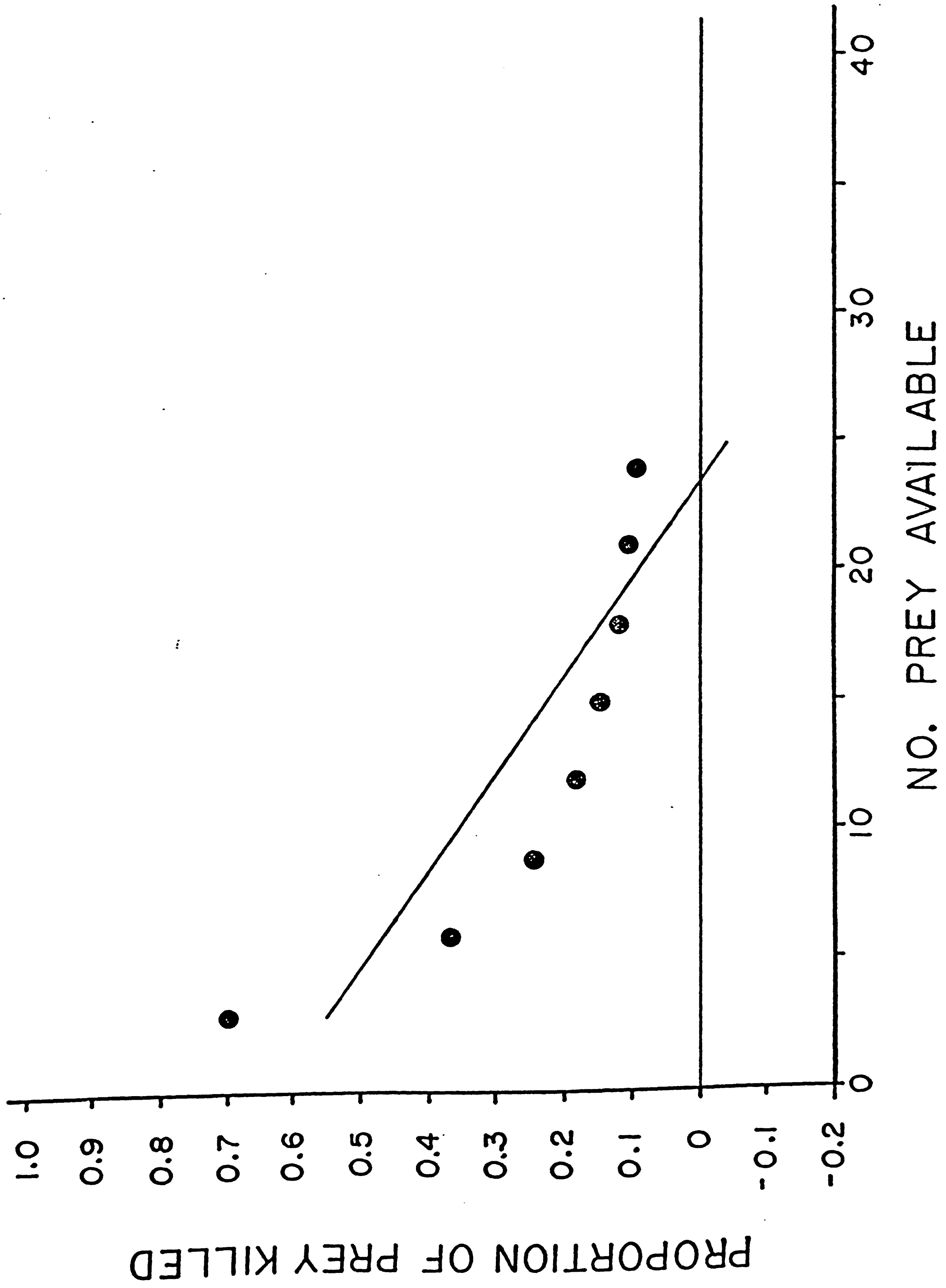

NUMBER PREY KILLED
I
II
III
PROPORTION PREY KILLED
I
II
III
NO. PREY AVAILABLE

Fig 2a



PROPORTION OF PREY KILLED
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
NO. PREY AVAILABLE
0
10
20
30
40

FIG 2b

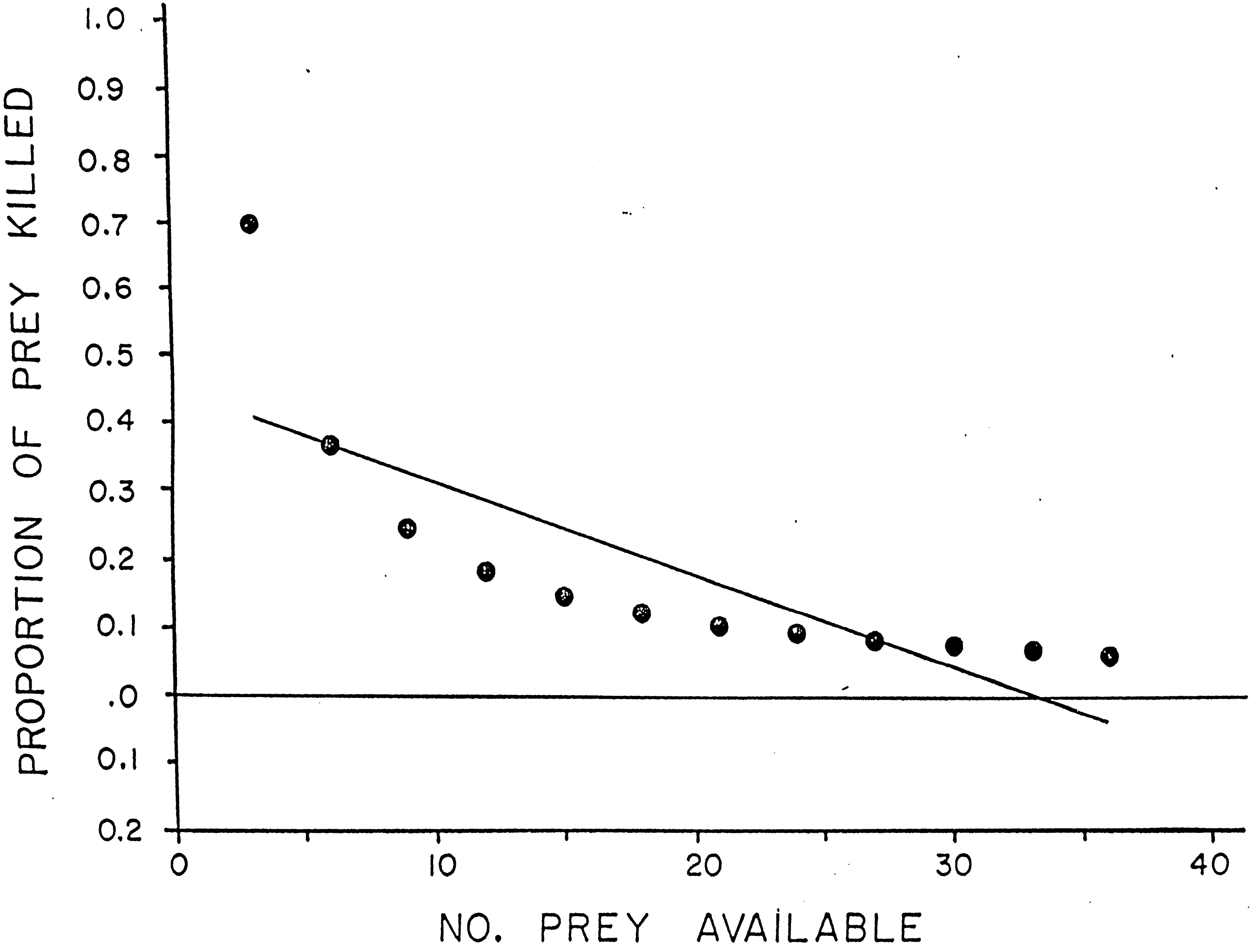
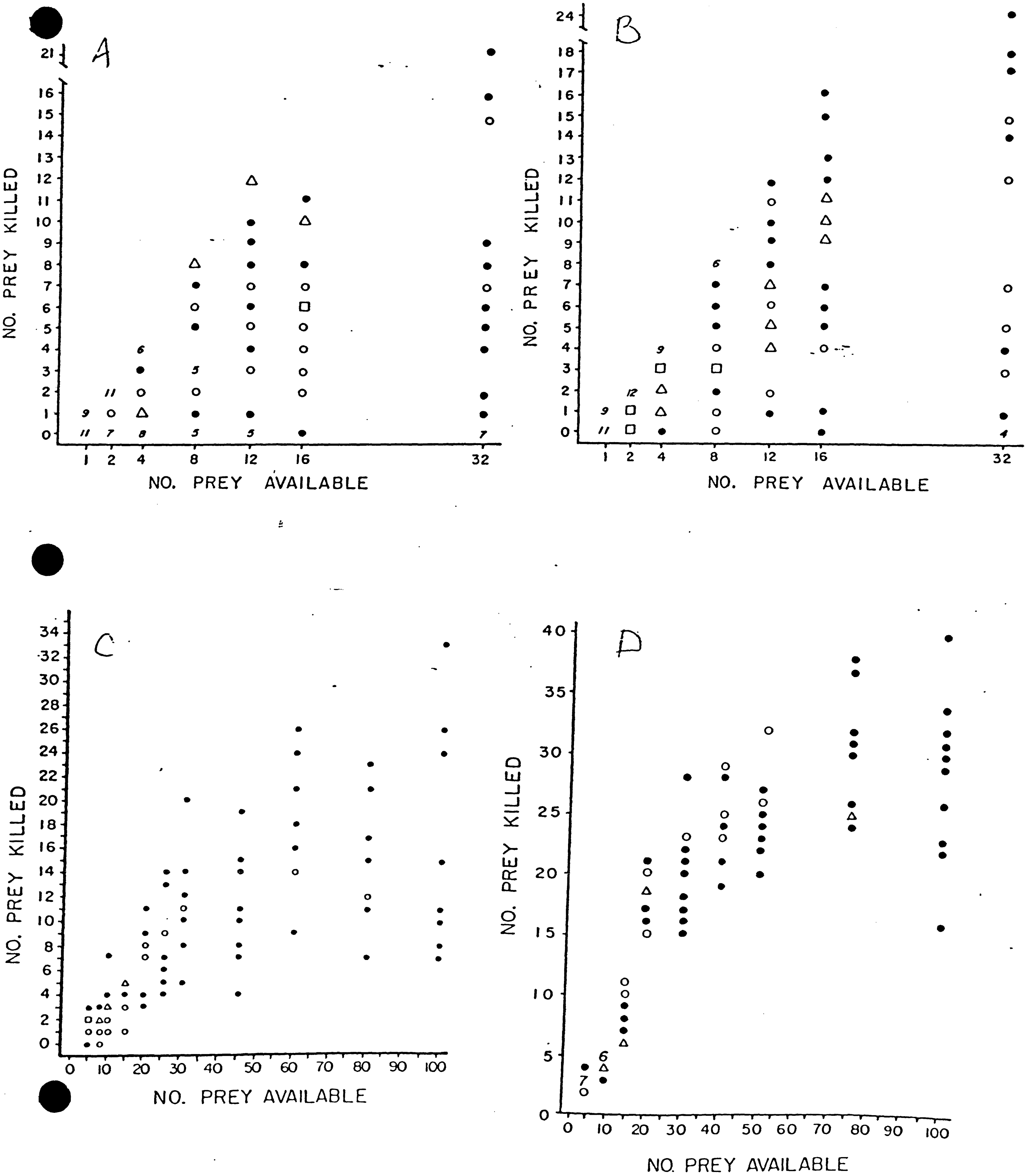

PROPORTION OF PREY KILLED
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
.0
0.1
0.2
0
10
20
30
40
NO. PREY AVAILABLE

Fig 3


A
NO. PREY KILLED
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 21
NO. PREY AVAILABLE
1 2 4 8 12 16 32
9 11 11 7 6 8 5 5 5 7
B
NO. PREY KILLED
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 24
NO. PREY AVAILABLE
1 2 4 8 12 16 32
9 11 12 9 6 4
C
NO. PREY KILLED
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34
NO. PREY AVAILABLE
0 10 20 30 40 50 60 70 80 90 100
D
NO. PREY KILLED
0 5 10 15 20 25 30 35 40
NO. PREY AVAILABLE
0 10 20 30 40 50 60 70 80 90 100
7 6

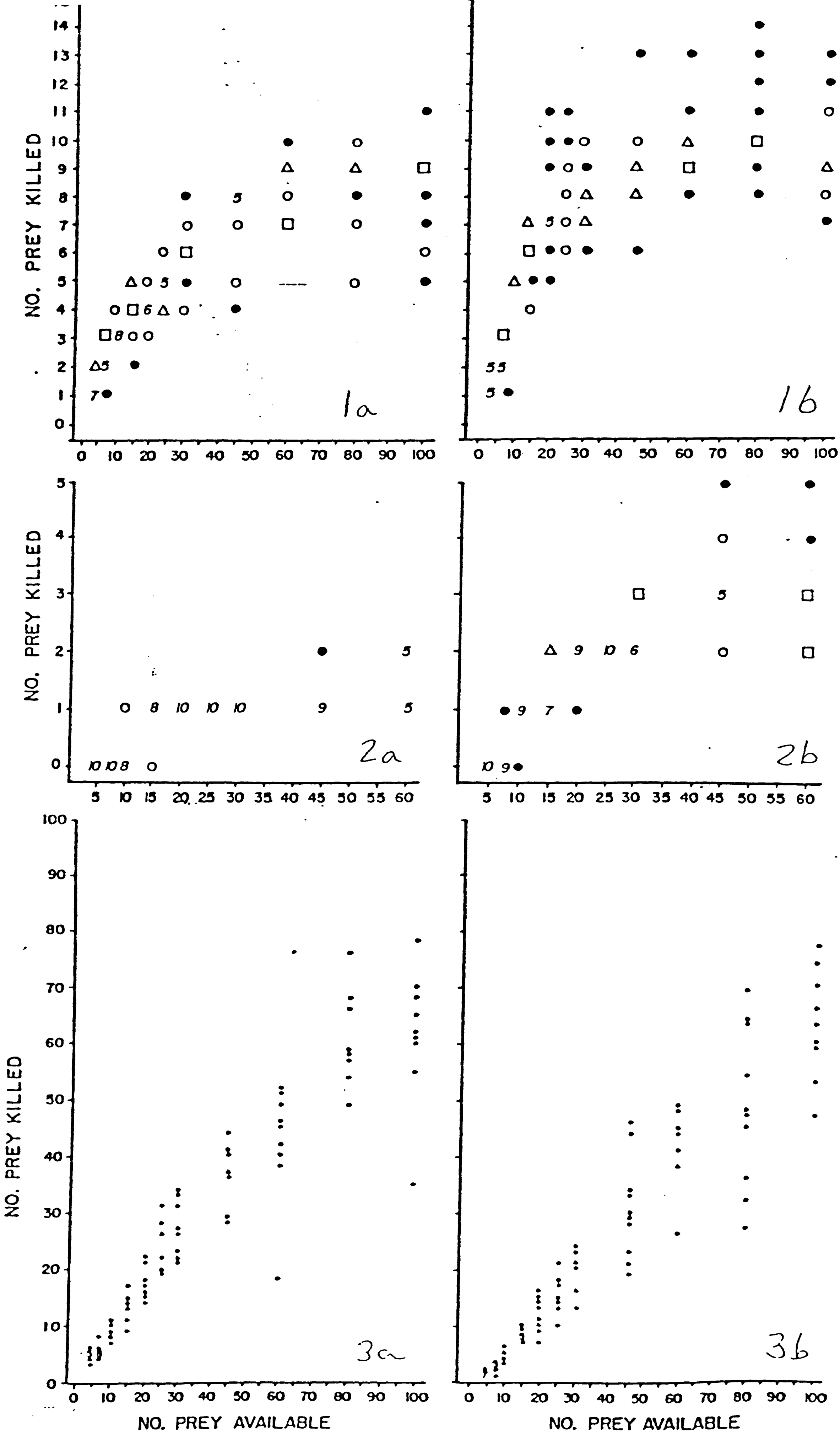

NO. PREY KILLED
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14
0 10 20 30 40 50 60 70 80 90 100
7 Δ5 □8 5 6 5
1a
55 5 5
1b
NO. PREY KILLED
0 1 2 3 4 5
5 10 15 20 25 30 35 40 45 50 55 60
10 10 8 8 10 10 10 9 5 5
2a
10 9 9 7 9 10 6 5
2b
NO. PREY KILLED
0 10 20 30 40 50 60 70 80 90 100
0 10 20 30 40 50 60 70 80 90 100
NO. PREY AVAILABLE
3a
3b
NO. PREY AVAILABLE

FIG 4