

STATISTICAL DIFFICULTIES IN THE ANALYSIS OF PREDATOR FUNCTIONAL RESPONSE DATA

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Abstract

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The utility of the 'random predator equation' of Royama (1971) and Rogers (1972) as a summary of the functional response relationship between predatory feeding behavior and prey density is questioned on the grounds that statistical assumptions in the regression analysis are not met by the linearized form of the equation. The absence of an alternative linearization that does not violate these assumptions necessitates the use of Holling's (1959) disc equation for the description of experimentally derived functional response relationships, when the comparison of parameters of different populations of predator or prey is a more important objective than a precise estimation.

The statistical validity of the traditional linearization of the disc equation is questioned. An alternative transformation is proposed, which removes the statistical problems associated with the former transformation, and which permits a higher degree of explanation of variance in the independent variable by the regression.

Résumé

L'utilité de l'équation du "random predator" (prédateur recherchant sa proie au hasard) de Royama (1971) et Rogers (1972), pour représenter la relation entre la réponse fonctionnelle caractérisant le comportement alimentaire d'un prédateur et la densité de sa proie est remise en question parce que les prémisses statistiques de l'analyse de régression ne sont pas satisfaites par la forme linéarisée de l'équation. L'absence d'une forme de linéarisation qui ne viole pas ces conditions oblige à l'emploi de l'équation ("disc equation") de Holling (1959) pour décrire les réponses fonctionnelles obtenues expérimentalement lorsque la comparaison des paramètres entre populations différentes est plus importante que leur estimation précise.

La validité de la méthode habituelle de linéarisation de l'équation "disc" est remise en question. Une autre transformation est proposée laquelle ne présente pas les problèmes statistiques de la première, et qui permet d'expliquer une part plus grande de la variance de la variable indépendante par la régression.

Many of the critical aspects of predator and prey interactions can be discerned by examining the relationship between predator feeding behavior and the density of prey. If the components of this relationship can be estimated, the parameters of the resulting equation should provide a succinct summary of the mutual adaptations of predators and their prey and should be useful tools for comparative studies of coevolution (Livdahl 1979), in addition to their more common application in the prediction of the dynamics of predator and prey population densities. The comparative use of functional response relationships would benefit from an inspection of the statistical methods used to estimate the parameters of certain descriptive equations, and that is our aim in this paper.

The most widely used description of the functional response of invertebrate predators to changes in prey density is the disc equation of Holling (1959):

$$\frac{N_a}{P} = \frac{aNT}{1 + aT_h N} \quad [1]$$

in which N_a/P denotes the number of successful attacks (N_a) per predator (P) during the time of exposure of prey to the predator (T); N denotes the initial density of prey; and a and T_h represent the rate of successful attack and the time required to handle the prey, respectively.

The biological assumptions of the disc equation are discussed elsewhere (Hassell *et al.* 1976; Royama 1971). Although the assumptions appear stringent, the disc equation describes laboratory data remarkably well in many cases. Conformity of experimental results with the equation indicates either that the assumptions are not frequently violated, that their violation does little to alter the basic form of the relationship, or that the estimated parameters serve in an adequate predictive capacity even if they do not in fact estimate precisely the quantities that they claim to stand for. For example, Fox and Murdoch (1978) observed reasonable compliance of their data with the disc equation, although they were able to observe through direct observation that handling time and attack rates were not constants through time or across prey densities. Nonetheless, the asymptote of the functional response relationship must still be fixed largely by the capacity of the predator to ingest prey, and the rate at which the curve approaches the asymptote must still result largely from the ability of the predator to find and capture prey.

Royama (1971) and Rogers (1972) noted that the disc equation is an instantaneous equation and is unsatisfactory for experimental data when an appreciable amount of time is involved in the experiments. Integrating over the rate of change of prey density, they adapt the disc equation for the description of experimental data:

$$N_s = N \{1 - \exp[-a(PT - N_s T_h)]\} \quad [2]$$

A linearized form of this equation is:

$$\log_e \left[1 - \frac{N_s}{N} \right] = aT_h N_s - aTP \quad [3]$$

This equation has been used by Rogers (1972) and by Hassell *et al.* (1976) in regression analyses. There are several disadvantages to the use of this equation, despite its underlying biological and mathematical logic.

Two problems arise from the use of the logarithm of the proportion $[1 - (N_s/N)]$ as the dependent variable. First, the variance of proportionate data depends upon the mean. Ordinarily, an angular transformation could be used to remove this dependence. In this case, a transformation of this sort would drastically alter the original model which the analysis is intended to examine. An additional difficulty arises when all of the prey are consumed by the predator. In such instances, the observation cannot be used in the analysis because the predicted value is $\log_e(0)$. The remedy of adding 1 to all observations alters the form of the model to be inspected.

A further objection concerns the use of N_s , which clearly depends on N , as the independent variable. Attempts to provide an alternative linear transformation, in which all terms of N_s are incorporated in the dependent variable, have failed because the parameters to be estimated by the regression, a and T_h , cannot both be kept on the right side of the equation. Because of these difficulties, the "random predator equation" of Royama (1971) and Rogers (1972) is not as useful as it first appears.

The problem of nonlinearity can be side-stepped by applying standard nonlinear least squares techniques to the untransformed data. However, a curvilinear model in the form of [2] still relies on the use of the dependent variable N_s in the construction of an independent predictor (note the presence of N_s on the right side of the equation). Polynomial fits of the form

$$N_s = A + BN + CN^2 + DN^3 \dots \quad [4]$$

will frequently provide potent descriptions of the data, but the biological significance of the coefficients is not clear, and the meaningful parameters a and T_h will only emerge as combinations of the coefficients. Because each coefficient is an estimate, the construction of confidence intervals about the estimated a and T_h values would be an awkward and cumbersome task, if it is possible at all. It is revealing to note the absence of confidence intervals for a and T_h in the functional response literature when nonlinear regression is

used (Hassell 1978). However, the utility of comparisons of functional response parameters depends critically on the ability to construct confidence intervals. Consequently, a linear relationship is desirable when relative estimates of attack rate and handling time are sought. Linearity is also a necessary condition for various powerful statistical techniques, including multiple regression and analysis of covariance.

A simple linear relationship can be obtained from [1] without the overt violation of statistical assumptions. Confidence intervals for a and T_h emerge directly from the regression analysis. For these reasons, we suggest the use of the transformation presented below when two or more functional response relationships are to be compared.

Analysis of Data Using the Disc Equation

Holling (1959) suggested the following linear transformation of [1] for use in regression analysis:

$$\frac{N_s}{N} = -aT_h N_s + TaP \quad [5]$$

This transformation has been adopted in subsequent studies in which regressions have been performed (Holling 1965; Clarke 1963; Messenger 1968; Griffiths 1969; Rogers 1972).

This equation violates assumptions required by regression analysis in a manner similar to [3]: the independent variable is not independent, and the variance in the dependent variable should depend on its mean.

We suggest the use of a different linear transformation as a remedy to these problems. A linearization is obtained easily by reciprocating both sides of [1], to yield:

$$\frac{P}{N_s} = \frac{1}{aTN} + \frac{T_h}{T} \quad [6]$$

Here, data are simply plotted as reciprocals. The slope of the line fitted by least squares is the reciprocal of the attack rate, and the intercept multiplied by the time of exposure produces the handling time.

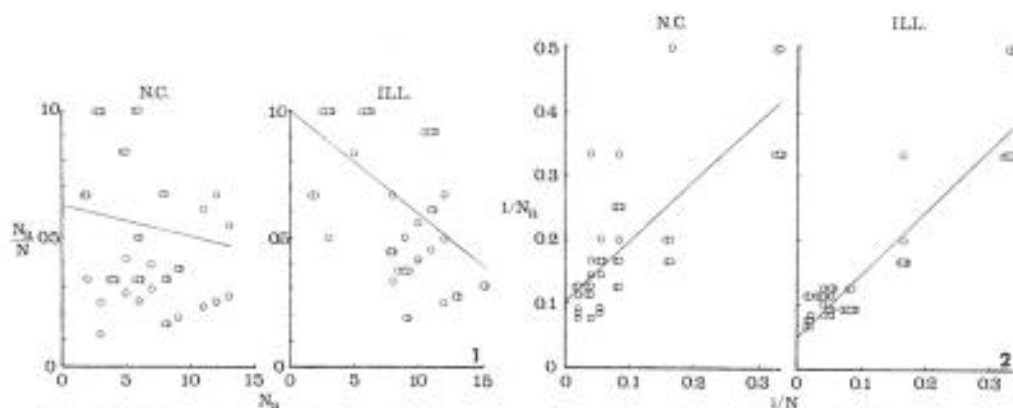
This transformation is a standard analytical tool in biochemistry for the description of enzyme-substrate kinetics (the Lineweaver-Burk plot) based on the Henri-Michaelis-Menton model. Interestingly, that model is mathematically identical to the disc equation, and it also describes the behavior of an instantaneous property (reaction velocity). In practice, the velocity is measured by the accumulation of a product over a finite time interval, but the analysis is performed as if the velocity is an instantaneous quantity.

A Comparison of the Two Types of Transformations

The remainder of this paper compares estimates of the functional response parameters, a and T_h , as well as the amount of variation explained by the regressions, when the proportional transformation [5] and the reciprocal transformation [6] are used.

To compare the transformations, we have used the mean value of data presented by Burnett (1951) for parasitism of *Neodiprion sertifer* (Geoff.) cocoons by *Dahlbominus fuscipennis* (Zett.). The same data were used by Holling (1959) and Rogers (1972) in their analyses. Additionally, we have used functional response data for predation by the treehole mosquito *Toxorhynchites rutilus septentrionalis* (Dyar and Knab) on two geographic strains (North Carolina and Illinois) of *Aedes triseriatus* (Say) (Livdahl 1979).

Linear regressions using the proportional transformation (Fig. 1) and the reciprocal transformation (Fig. 2) are presented for the data of Livdahl (1979). The predicted relationships between N_s and N for the proportional (dashed line) and reciprocal (solid line) transformations appear in Fig. 3. These analyses, as well as analyses based on the data of Burnett (1951), are summarized in Table 1.



FIGS. 1-2. Linear regressions based on (1) the proportional transformation (eq. [5]) and on (2) the reciprocal transformation (eq. [6]) for the functional response of *Toxorhynchites rufilar* to variation in the density of two geographic strains of its prey, *Aedes triseriatus*. Strains of prey were obtained from northern Illinois (ILL.) and North Carolina (N.C.); the predator is from North Carolina, and is not found in northern Illinois. See text for explanation of symbols. Data are from Livdahl (1979).

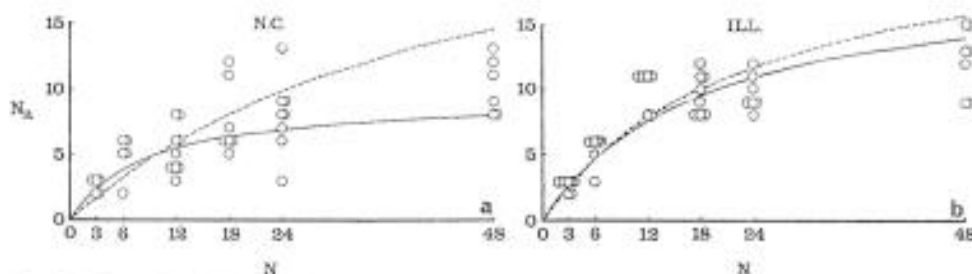


FIG. 3. The predicted relationships between the number attacked and initial prey density. Solid lines: reciprocal transformation; dashed lines: proportional transformation. Data are the same as in Figs. 1 and 2.

Table I. Comparisons between the proportional (P) and reciprocal (R) transformations ([5] and [6], respectively)

Source	Transformation	a	T_k	r^2	
Burnett (1951)	16°C	P	0.043	47.817	0.83
		R	0.040	39.504	0.99
	20°C	P	0.123	22.798	0.72
		R	0.089	14.016	0.88
24°C	P	0.185	22.983	0.98	
	R	0.177	21.679	0.99	
Livdahl (1979) Illinois	P	0.040	1.013	0.27	
	R	0.043	1.234	0.85	
North Carolina	P	0.026	0.848	0.06	
	R	0.047	2.557	0.58	

The most noteworthy aspect of Table I is the consistent difference in the coefficient of determination (r^2) of the two transformations, indicating that the reciprocal transformation provides a more thorough description of the relationship. T_k and a values are also

Table II. The sensitivity of the proportional transformation to variation about the mean N_p . Data are from Livdahl (1979)

Source	Data set	a	T_h	r^2
Illinois	All data	0.040	1.013	0.27
	Means only	0.048	1.275	0.59
North Carolina	All data	0.026	0.848	0.06
	Means only	0.045	2.056	0.82

sensitive to which type of transformation is used, but not in any apparent systematic fashion. The coefficients derived from Burnett's data are not as drastically affected by the type of transformation as are those from Livdahl. The difference arises from the use of means for Burnett's data, in which variation about those means is ignored. The sensitivity of the proportional transformation to such variation is illustrated in Table II. The coefficients of determination for Burnett's data are probably greatly exaggerated because of this sensitivity.

In the light of the violation of statistical assumptions by [4] and the higher degree of precision in the estimation of regression coefficients by [5], there appears to be no reason for the continued use of [4] in the analysis of functional response data.

Discussion

A thoughtful look at the analytical methods used for functional response experiments reveals a dilemma for the investigator. The appropriately transformed disc equation is more amenable to linear regression techniques, because it is less likely to violate assumptions than the random predator equation. However, the parameters obtained may be somewhat less informative in biological terms, because an instantaneous equation is used to describe the results of a finite period of exposure of predators to prey. Unfortunately, the biologically reasonable random predator equation requires the use of nonlinear techniques in which statistical comparisons of fitted parameters among predator or prey populations are not easy to perform.

In addition, it appears that the parameters obtained in either approach are not, in fact, what they claim to be because the attack rate and handling time are subject to variation in the course of the experiment, and to variation among different prey densities (Fox and Murdoch 1978; Eveleigh and Chant 1981*a,b*).

This problem is circumscribed by recent evidence that invertebrate predators can apparently respond to prey density in a sigmoid manner, although we are aware of no studies in which this departure from the type II functional response has actually been tested statistically. In fact, examples of sigmoid functional responses involving invertebrate predators have relied heavily on visual inspection (Takahashi 1968; McQueen 1969; Murdoch and Oaten 1975; Hassell *et al.* 1977). In one paper (Hassell *et al.* 1977), an attempt was made to demonstrate the inadequacy of the 'type II' relationship simply by showing a nonsignificant regression relationship using the 'random predator' equation of Royama (1971) and Rogers (1972). This dependence upon a negative result to reject what should be treated as a null hypothesis is vulnerable to the variability of the experimental system. In fact, a nonsignificant relationship can nearly always be obtained in variable systems if few observations are available. Hassell *et al.* (1977) do not describe their precise analytical methods for the rejection of the type II relationship, but an unsuccessful attempt to fit the type II curve is not surprising if they relied on the linearized version of the 'random predator equation', for reasons that we have set forth above. A more satisfactory approach to the refutation of the 'type II' functional response would be a test for nonlinearity using the reciprocally transformed disc equation as the null model.

We advocate the use of the reciprocal transformation of the disc equation particularly for instances in which the important result is not the precise meanings of the parameters, but the presence or absence of differences among them when comparisons are drawn among two or more populations of predators or prey. For other purposes, this transformation will not be satisfactory, particularly when the attack rate and handling time are to be used for modelling purposes (e.g. Hassell *et al.* 1977; Hassell 1978), or when the principal aim is a very detailed examination of a particular interaction between predator and prey populations (e.g. Eveleigh and Chant 1981a,b,c). In such cases, confidence intervals about the estimated parameters may not be essential, and the parameters should be obtained through iterative nonlinear least squares techniques.

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