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The nature of predation: prey dependent, ratio dependent or neither?

Peter A. Abrams and Lev R. Ginzburg

To describe a predator–prey relationship, it is necessary to specify the rate of prey consumption by an average predator. This functional response largely determines dynamic stability, responses to environmental influences and the nature of indirect effects in the food web containing the predator–prey pair. Nevertheless, measurements of functional responses in nature are quite rare. Recently, much work has been devoted to comparing two idealized forms of the functional response: prey dependent and ratio dependent. Although we agree that predator abundance often affects the consumption rate of individual predators, this phenomenon requires more attention. Disagreement remains over which of the two idealized responses serves as a better starting point in building models when data on predator dependence are absent.

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The rate of prey consumption by an average predator is known as the functional response; this can be classified as: (1) prey dependent, when prey density alone determines the response; (2) predator dependent, when both predator and prey populations affect the response; and (3) multispecies dependent, when species other than the focal predator and its prey species influence the functional response. Until recently, predation theory was dominated by prey-dependent models and by Holling's[1] three-type classification of these responses. Arditi and Ginzburg[2] stimulated recent interest in alternative forms for functional responses with their suggestion that a ratio-dependent functional response was a better starting point for modeling predation. Ratio dependence is a particular type of predator dependence in which the response only depends on the ratio of prey population size to predator population size, not on the absolute numbers of either species. Figure 1 illustrates a prey-dependent response and a comparable ratio-dependent response.

The publication of Arditi and Ginzburg's suggestion received both support and criticism[3–7]. The question underlying the debate is: how does predator population density influence the average predator's consumption rate? The answer to this question has an important influence on when and why predator–prey systems fluctuate, how they are likely to evolve and how they respond to environmental changes. The debate has persisted for more than a decade, in part, because ecologists know pitifully little about the nature of functional responses. Following prey-dependent theory, early empirical work typically measured the number of prey eaten by single predators in small cages[8]. This design eliminates the possibility of seeing anything other than prey dependence. Observations of
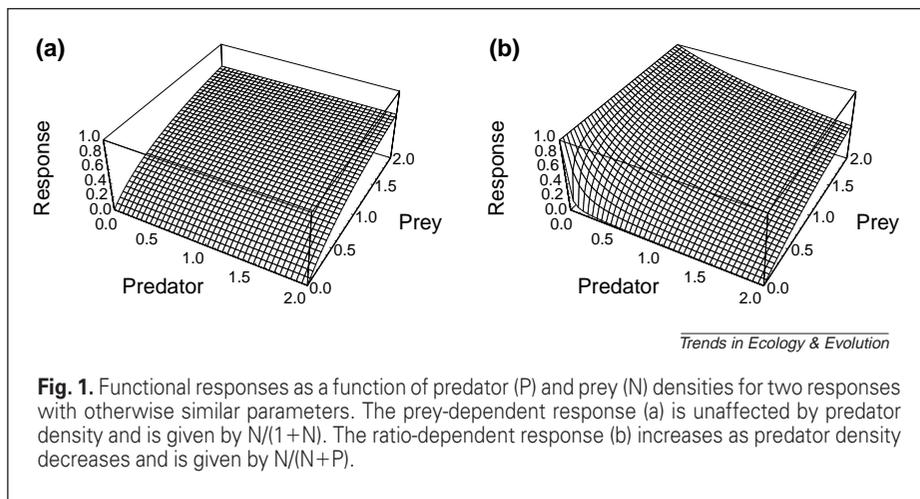
Fig. 1. Functional responses as a function of predator (P) and prey (N) densities for two responses with otherwise similar parameters. The prey-dependent response (a) is unaffected by predator density and is given by N/(1+N). The ratio-dependent response (b) increases as predator density decreases and is given by N/(N+P).

predator interference behavior led to some population-cage experiments in which predator, as well as prey, density was varied (see meta-analyses[9,10]). However, few such studies were carried out, and most of these were performed in artificial environments that excluded the potential influences of species other than predator and prey, and that might have distorted the effects of predator density.

The growth rate of a predator population depends not only on what individuals eat, but also on how they convert consumed prey into new predators. The numerical response describes the per capita population growth rate as a function of all variables that influence it. Together, the functional and numerical responses provide a complete description of predator population dynamics. Knowledge of both is required to understand fully how predators and prey interact. The most common assumption is that the numerical response is a linearly increasing function of the functional response. The classification of the numerical response as prey, predator or multi-species dependent is then identical to the classification of the functional response. However, predator density and the densities of other species can influence the numerical response independently of their effect on the functional response. Box 1 shows how functional and numerical responses are typically incorporated into models of population dynamics.

The recent controversy over ratio dependence has generated many articles but almost no renewed study of functional responses in natural settings. A search of articles citing Arditi and Ginzburg[2] uncovered 63 articles published during the past five years. Most of these were reviews or were theoretical. Only 17 articles drew conclusions about functional responses based on empirical data and, of these, there was only a single direct measurement of a functional response[11]; one other study measured a numerical response[12]. The remaining 15 empirical works made inferences about functional responses based on other observations, such as changes in the biomass of food-web components with fertilization[13–15]. Indirect inferences have the disadvantage of being subject to alternative interpretations[6,7,16–18]. Currently, we are far from knowing the form of functional responses for a representative sample of species in natural habitats. Because most species are predators or prey (or both), this ignorance impairs the ability to make informed decisions about the management of exploited populations and the conservation of endangered species. Therefore, we would like to see future efforts devoted to measuring both functional and numerical responses in natural environments. The following are four features that we expect to be found when these measurements are made.

Box 1. Common differential equation models of predator–prey systems

The dynamics of predator–prey systems are often described by differential equations, which represent time continuously. A common framework for such a model is:

$$\frac{dP}{dt} = Pf\big[g(N,P),P\big]$$

$$\frac{dN}{dt} = Nr(N) - Pg(N,P)$$

where P and N are the predator and prey density, respectively; g is the functional response; and f is the numerical response of the predator. The function r represents prey per capita growth rate, which decreases with N in most models. The predator's numerical response, f, increases with consumption rate per individual, g, and might be affected positively or negatively by predator density. The functional response g is usually assumed to increase with prey density, N, and decrease (or not change) with predator density, P. However, exceptions exist to both of these rules.

In prey-dependent models, g is independent of P; in ratio-dependent models, g depends on N and P only via their ratio, N/P. The two most commonly used forms for prey-dependent functional responses are: (1) linear (CN); and (2) a nonlinear form, known as the disk equation[7]:

$$\frac{CN}{1+ChN}$$

where C is the encounter rate with prey by a searching predator, and h is the handling time of one prey item (during which other prey cannot be caught). An analogous ratio-dependent formula for g is:

$$\frac{C(N/P)}{1+Ch(N/P)} = \frac{CN}{P+ChN}$$

where C and h have the same interpretation as before. The linear form, CN/P for ratio-dependent responses is seldom used; it predicts that total prey consumption is independent of predator numbers. A predator-dependent formula suggested independently by Beddington[21] and DeAngelis *et al.*[22] is:

$$\frac{CN}{1+ChN+\gamma P}$$

where γ is a measure of predator interference during foraging. Hassell and Varley[41] presented another flexible predator-dependent response, in which the parameter C in a prey-dependent response is replaced by C/P^m; this reduces to prey dependence when $m = 0$ and ratio dependence when $m = 1$.

The most common formula for the numerical response is a linear one, $f = bg(N,P)-d$, where b is a conversion efficiency of food into offspring and d is a per capita death rate. When the numerical response is directly affected by predator density, the most common formula[42] is also linear, $f = bg(N,P)-d-aP$, where a is a measure of the per capita effect of direct predator density dependence (e.g. aggression). The Leslie model[31] assumes that the numerical response is independent of the functional response, which is prey dependent. At the same time the numerical response has the logistic form $f = r[1-a(P/N)]$.

Precise prey dependence and ratio dependence will both be rare
Prey dependence must break down at sufficiently high predator densities. Even if there is normally no interference among predators, at high enough densities predators will be unable to avoid

interfering with each other's search or food capture. Similarly, ratio dependence must break down at sufficiently low predator densities; interference cannot occur if predator individuals are separated by sufficiently great distances. Rarity of the predators cannot allow them to capture large numbers of prey when prey density is extremely small; nevertheless, this is predicted by ratio-dependent models[3,6]. Although departures from the ideal are most evident for these limiting cases, some degree of departure from the pure models probably occurs over a wide range of densities in any system.

Predator dependence will be common

Ratio dependence is only one of many conceivable functional responses that depend on predator density (predator dependent). Many biological processes can produce predator dependence: (1) group hunting by the predator[19]; (2) facultative and costly antipredator defense by the prey[20]; (3) density dependent and time-consuming social interactions among the predators; (4) aggressive interactions between searching predators that encounter each other[21,22]; and (5) a limited number of high-quality sites where predators capture prey rapidly. This incomplete list probably contains at least one factor that applies to most randomly chosen predator–prey pairs in nature. In addition to being common, predator dependence might be positive rather than negative (e.g. group hunting) and might decline with predator density more rapidly than in ratio-dependent responses. The latter is true of some models with adaptive antipredator behavior[20]. Although they might represent a biased sample[10], most laboratory measurements of the effect of predator density on functional responses have found significant predator dependence[9,10].

Predator dependence can also arise in a model when a system, with two or more categories of prey differing in their trophic characteristics, is described using total prey density as the single variable describing the prey population. Analyses of systems in which prey can move into and out of a refuge from predation[23–25] are a case in point. When predator numbers are high enough that they catch most of the prey emerging from the refuge, they effectively divide the total number of emerging prey among themselves. If the number emerging is proportional to the number in the refuge, the functional response can be expressed as a ratio of total prey to total predator numbers[24]. It is also possible to express the functional response as a prey-dependent function of the number

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When reproduction is not continuous, the dynamics of predator–prey systems are often better described by difference equations than differential equations. In these models, prey density (N) decreases between reproductive events owing to predation. In the simplest case, predator and prey have the same reproductive interval, and predator density (P) remains approximately constant within that interval. Then, the change in prey numbers within an interval is given by:

$$\frac{dN}{dt} = -g(N,P)P - DN$$

where D is a per capita death rate owing to causes other than predation, and g is the predator's functional response. This equation can often be integrated to yield a formula for final prey numbers at the end of an interval, given initial numbers N_0. For example, when there is a linear, prey-dependent (instantaneous) functional response ($g = CN$, where C is a capture rate constant), the number of surviving prey declines exponentially, so that, at time t within an interval, the number of surviving prey is $N_0\exp[(-CP-D)t]$. The number of prey eaten per predator (i.e. the averaged functional response) is C multiplied by this quantity integrated over a single time interval:

$$\frac{CN_0[1 - \exp(-CP - D)]}{CP + D}$$

Note that when CP is large, both absolutely and relative to D, this average functional response is approximately equal to CN_0/P, but this ratio-dependent approximation breaks down when P is small. If the predator's numerical response is directly proportional to this averaged functional response, then it too will be predator dependent as in the above formula.

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of prey outside the refuge at any given moment in time. Reeve's[11] empirical study provides an empirical example of the ratio-dependent formulation. Other types of spatial heterogeneity can also lead to predator dependence[19,23–25].

A final mechanism generating predator dependence is the averaging of the functional response over the predator's or prey's reproductive period. Time-averaged functional responses that are expressed as a function of initial prey numbers probably exhibit more predator dependence than responses measured over short timescales. This occurs because depletion of prey over time will reduce the number consumed per predator and depletion is greater with more predators[2]. Box 2 shows how this occurs in a model where predators and prey have synchronized generations.

Responses will often be affected by species other than predator and prey

Prey- and predator-dependent responses do not exhaust the range of possible functional response dependencies. Prey commonly forage less when in the neighborhood of predators that they are able to detect[26]. This creates an effect of the predator density on the functional response of their prey to the prey's food[27]. Similarly, food density changes the optimal risk-taking of foragers; normally, this affects the functional response of the predators to those foragers[27]. These effects can only be observed when the functional response is measured in the presence of the higher and lower trophic level species; there have still not been any studies that have systematically varied the densities of

these other species to measure their impacts on the functional response. Mutual adaptations of two or more behaviorally flexible species can result in functional responses that depend on species farther removed than one trophic level above the predator or below the prey[28]. Aggression and social interactions usually change depending on the outcome of previous interactions, thus implying that recent past predator density often affects the functional response. Risk-taking behavior is also highly dependent on previous food intake[26,29], thus making predator responses dependent on the previous density of their prey's food. All of these points argue for multispecies dependence.

Predator dependence of the numerical response will be common

Many of the arguments already made here apply to numerical, as well as functional, responses. The numerical response determines how a predator's per capita growth rate changes with population densities. Most models assume that the per capita population growth rate increases monotonically with the amount eaten. Thus, a predator-dependent functional response will often produce a numerical response with similar predator dependence (Box 1). This 'conversion rule'[30] is a reasonable assumption for many predator–prey models. However, the numerical response cannot always be expressed in terms of the functional response alone. Other variables might affect the numerical response when predators interact cooperatively or competitively over some resource other than their prey, or when the timescale of predator and prey reproduction is significantly

longer than that over which the functional response is measured. In the second case, the conversion rule applies if the short-term functional response is integrated over the time between reproductive bouts before entering into the numerical response (Box 2). In either case, the numerical response is still predator dependent.

One frequently reappearing predator–prey model, originated by Leslie[31], assumes that the predator's functional response is prey dependent; however, the numerical response is both ratio dependent and independent of the functional response (Box 1). In this model, the predator's growth rate is logistic, with a carrying capacity proportional to current prey abundance. When the functional response approaches an asymptote at high prey densities, as in a recent model of vole cycles[32], this model has several biologically undesirable features. It implies that when predators are consuming as much as they are capable of, increasing prey density will still significantly increase predator growth rate, although the predator's consumption is not increased significantly. It indirectly implies that a predator genotype with a higher prey encounter rate will not have a selective advantage, because the rate of catching prey has no direct effect on fitness. It also implies that when prey density is so low that predators capture vanishingly few prey, the predator will still achieve rapid growth if its own density is low enough. Functional and numerical responses need to be more closely related than in Leslie's[31] model.

What empirical work should be done?

There seems to be a widespread opinion that functional responses are an old topic that was thoroughly studied decades ago. However, this is certainly not the case for field measurements. Reeve's recent study[11] of predation by clerid beetles (Cleridae) on the bark beetle, *Dendroctonus frontalis*, is a rare example where predator and prey densities were both varied in field enclosures.

Two approaches to measuring functional response are possible. The first is to directly measure the number of prey killed in an environment, with known or estimated population densities of all of the species that might affect the response. The second is to estimate the number of prey killed from measurements of prey population sizes at the beginning and end of a short time interval. The first approach can only be applied when predation events can be observed. The second approach is usually less precise because both the initial and final prey population

estimates are affected by measurement errors. Both approaches require the ability to control or to accurately measure the densities of all of the relevant species. The number of possible combinations of densities increases rapidly with the number of other relevant species. Although there are often logistical problems associated with these measurements, similar problems must be confronted in most experimental field studies of interacting populations. There are examples of successful field measurements of functional responses (e.g. wolf[33] and moose[34]), although these have usually only quantified the consequences of variation in prey population density.

In the absence of direct measurements, some types of indirect evidence might allow deductions about the form of functional responses. To date, these approaches have been controversial because of the large number of alternative explanations for the observations. Changes in the biomasses of trophic levels, in response to nutrient enrichment, have been used to argue for particular functional responses of the predators in these systems[4]. The most commonly observed change is an increase in all trophic levels, which is predicted by models of food chains in homogeneous environments where predators have ratio- or strongly predator-dependent responses[2,4]. This pattern is not predicted by comparable models of food chains with prey-dependent functional and numerical responses[2,4]. However, the pattern can also be predicted by models with prey-dependent functional responses if there are two or more species on each trophic level, if there are predator-dependent numerical responses, if the system undergoes population fluctuations and under several other sets of conditions[6].

Time series of population densities provide another avenue for deducing the form of functional responses. This requires that the demography and numerical responses of both predator and prey be well known. If the functional response is the only important unknown relationship, the response that best reproduces the dynamics is most likely to approximate the actual response. This approach is most likely to succeed in laboratory systems with a single species of predator and a single species of prey, and it has been applied to some laboratory systems with protozoan predators and prey[35,36]. In theory, the most decisive indirect tests of functional response form could come from cases where the qualitative nature of population dynamics is determined by functional response form. One example is the potential for both

predator and prey to become deterministically extinct in simple models with ratio-dependent responses, but not in comparable systems with prey-dependent, or moderately predator-dependent, responses[37,38]. Unfortunately, the same possibility exists when functional responses are not ratio dependent, but there is a time lag in the predator's numerical response to food intake. Ratio-dependent functional responses and time lags with nonratio-dependent responses are both potential explanations for Gause's[39] classic observation of mutual extinction in the protozoans, *Paramecium* and *Didinium*.

Even when it is not conclusive, indirect evidence can help to eliminate some possible forms of models of predation. However, given our present lack of knowledge of most component relationships of predator–prey systems, single indirect methods are unlikely to be decisive in identifying functional response form. As our general knowledge of predation increases, indirect evidence will become more informative. For now, applied biologists who need to predict population densities are well advised to try to determine the real form of the functional and numerical responses of the predators in their system. If that cannot be done, models should have a flexible form of the functional response that can incorporate predator or other-species dependence.

What is the controversy about?

If we both agree that functional responses in nature are unlikely to be either purely prey or purely ratio dependent, why is there a controversy? There are two topics about which we disagree. The first is the appropriate mathematical representation when reproduction is not continuous and when significant prey depletion can occur between reproductive events. Abrams feels that this calls for the use of methods that represent the functional response on a continuous basis and reproduction on a discrete basis; for example, as is done in the Nicholson–Bailey host–parasitoid model. Ginzburg thinks that the predator reproductive period is the minimal indivisible unit of time over which both functional and numerical responses should be measured, because capturing interaction is the goal of the model. Ginzburg believes that differential equation models simply approximate this unit as an instant relative to the longer timescale of population dynamics. Because these two different methods predict significantly different dynamics, more is involved in this disagreement than simply a philosophy of modeling.

The second disagreement is over criteria for judging idealized models of predation. These are simple models that are used for theoretical studies of food webs or when no knowledge of the functional response form is available. Abrams feels that idealized models are primarily conceptual, rather than predictive, tools. He favors prey-dependent models as the basic building blocks for theory because they are based on a single, well defined set of assumptions; this makes it clear how to modify them when the assumptions are known to be deficient. Approximate ratio dependence can arise in so many ways that extending and modifying such responses is more problematic[40]. It is also conceptually easier to add, than to remove, a process (predator dependence) that might or might not be present and that, if present, might have a variety of forms.

However, Ginzburg thinks that there is a legitimate predictive use for idealized models as simple as the ratio-dependent example in Box 1. The limited evidence available suggests that even when functional responses are measured on the short term they are closer to ratio dependent than prey dependent[9]. Averaging of functional responses over reproductive intervals will shift trophic functions further towards ratio dependence. Ginzburg feels that such averaged responses should be the basis of both differential and difference equation models because these averages determine long-term population dynamics. Based on the preponderance of evidence, ratio dependence serves well as a starting point in theoretical and applied models.

We are hopeful that future theoretical and empirical work will enable us to resolve these differences.

Conclusions

In nature, most predator functional responses probably depend on population densities of species other than prey, and measuring these other dependencies has been unjustly ignored. More empirical work can establish what these dependencies are. At present, the most pressing task is to use both empirical measurements and theory to learn more about functional responses in the field, and about the ecological processes underlying them.

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