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## THE FUNCTIONAL RESPONSE OF PREDATORS

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The use of natural enemies to control pest populations has almost always been an empirical business. Enemies have been chosen on the basis of what has been known about their general life

history, propensity to attack the pest, synchrony with the pest, physiological adaptation to the pest's climate, and so on. Little research has been done to explain the way that predation operates in some enemies that have been successful and in others that have not. There have been good reasons for this state of affairs. Given the state of the art, and the financial support, the trial-and-error approach was a wise one.

In the past decade the situation has changed. Ecology and biological control have started to produce new techniques that may be useful, such as the modelling of entire pest situations (Conway, this Congress). We now understand a good deal about how predators work, at least in the laboratory, and we have recognized a variety of ways in which they can respond to changes in prey density so as to control the prey. These include the numerical response discussed by Readshaw (this Symposium) and the functional response which I will discuss below. The major question for pest control now is whether or not these kinds of techniques and analyses (which are of great interest to theoretical and 'pure ecology') can be used for screening potential enemy species, for deciding the best time at which to release millions of parasitoids, and so on.

#### THE FUNCTIONAL RESPONSE

We are interested in making the pest population both sparse and consistently sparse through time. The ability of a predator population to make a prey population sparse depends on the *average* values of the crucial parameters such as the predator's density, searching efficiency, the number of refuges for prey, etc. The degree of constancy of the lowered prey density, by contrast, is determined more by how the parameters of the predator population *vary* in response to changes in prey density. In particular, they must vary so as to lead to density-dependent prey mortality. It is this latter aspect that I will discuss.

The functional response (Solomon 1949) is defined by a function ( $N = f(D)$ ) that relates the number of prey eaten per predator per unit time ( $N$ ) to the density of the prey ( $D$ ). It describes how the attack rate of an individual predator varies with prey density. Three main types have been recognized (Fig. 1) (Holling 1959), though some results do not fit nicely into this scheme (Mori & Chant 1966; Sandness & McMurty 1970). Only the S-shaped curve (type 3) produces density dependent mortality (in the interval a-b in Fig. 1). The experiments that yield results like those in Fig. 1 have lasted a short time relative to the life span of the predator; generally they last a few hours. So the term functional response in general usage describes a *short-term behavioral* phenomenon.

Notice that the criterion for type of response is the form of the curve, i.e. the result of predation, rather than the mechanism. This reflects the differing consequences that the three prey curves have for prey stability. This criterion is preferable to defining response types according to the mechanism involved (e.g. presence or absence of learning) because, as we shall see, there is no one-to-one relationship between mechanism and the form of the response.

I want to make two major points about the functional response. First, it has become the convention to divide the responses made by predators to changes in prey density into two categories: the numerical response (changes in predator density), and the functional response. But since the functional response has come to mean a short-term behavioral phenomenon it excludes several other ways in which predators can respond to variation in the density of their prey. I will show that a number of other responses must be considered that have not received much attention until now. The second point is that the effect upon prey density of a predator with a particular kind of functional response depends on environmental factors in addition to the basic form of the response itself, and may sometimes be density dependent even when the underlying functional response itself is *not* density dependent. In particular I will discuss the effect of the predator's having more than one prey species.

Before elaborating these two points, we need to review current information on the functional response. There have been two main approaches to the problem. One is the 'component-analysis' approach in which the details of the behaviour of an individual predator (and its prey) are studied and then integrated in a computer model that predicts predation rate as a function of, say, prey density. The other approach is more immediately interested in populational consequences, has been more frankly empirical, or curve-fitting, and tries to determine the form of the functional response for some interesting conditions. (These and other modeling approaches are reviewed by Royama (1971).)

The great bulk of both sorts of information comes from laboratory studies, the few data from

the field that are available being difficult to evaluate. Thus all of the statements made in this section about predators refer only to laboratory situations.

In most studies it has been shown that a predator, given varying densities of a *single prey species*, eats more prey at higher prey densities, but does so at a decelerating rate, so that the response causes prey mortality that is inversely density dependent (type 2 in Fig. 1). This deceleration may occur because, as more prey become available and get eaten, the predator spends more time dealing with, and therefore less time hunting for, prey. Alternatively, or additionally, when the prey are common the predator eats more and, getting closer to satiation, hunts either more slowly or less of the time.

Where an attempt has been made to fit the type 2 data to a model they have provided reasonable fits either to a model suggested by Holling (1959) and Rashevsky (1959) (see below) or to a model proposed by Watt (Watt 1959; Glass 1970). This type of response has been found in a wide variety of predators including predatory insects (Holling 1966; Morris 1963; Clark 1963; Fox 1970; Fox & Murdoch, unpublished), insect parasitoids (Burnett 1954; Griffiths 1969; Messenger 1968), mites (Chant 1961), seashore snails (Murdoch 1969), starfish (Landenberger

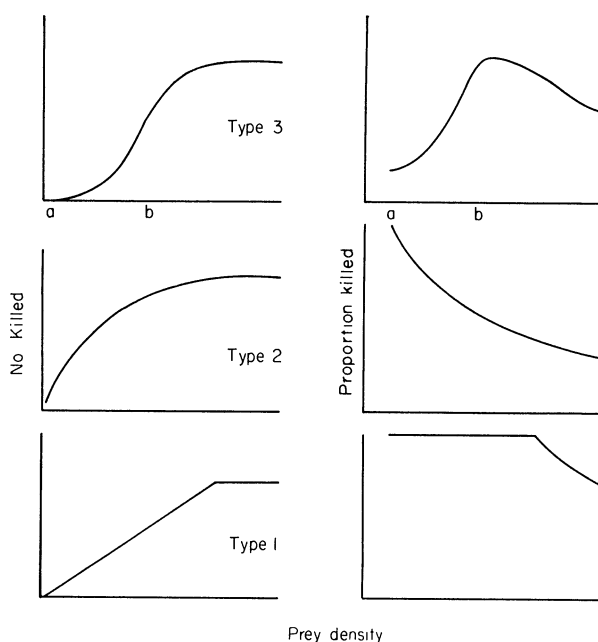


Fig. 1. Three types of relationships between prey density and the attack rate of a single predator (the functional response). Only type 3 yields density dependent mortality, in the interval a-b.

1968) and fish (Ivlev 1961). Most experiments of this type have been done with invertebrate predators.

However, in a few experiments predators have actually shown a density dependent (type 3 in Fig. 1) response when only *one prey species* was available. Thus, when the predator is 'naive' to the prey or the situation, those individuals given low prey densities meet few prey and take a long time to realize that they are prey, while those given high densities learn quickly and attack the prey at a high rate. Reed (1969) showed that this caused a sigmoid response by bluegill fish to mosquito larvae. Since such naivety is short-lived, this mechanism is likely to be unimportant in the field. However a type 3 response has also been found for some parasitoids given only one prey species (e.g. Burnett 1964; Takahashi 1968). In these parasitoids it seems that the S-shaped response might actually operate in nature over the entire life of the adult parasitoid since the low attack rates at low prey density seem to be caused by the predator not receiving enough stimulus from the prey to make it hunt intensively.

One can imagine other mechanisms that would produce a sigmoid curve. For example, in the field it is quite possible that there would be a small number of secure refuges for the prey so that as prey density increased a greater proportion would be vulnerable to attack. For our purposes, however, it is probably a safe bet that most predators and parasitoids that are given only one prey species will have a type-2 response, at least in the laboratory. So we need to look to other aspects of predation for stabilizing mechanisms.

#### OTHER RESPONSES BY PREDATORS

I now elaborate the first point foreshadowed above, which is that one must consider responses by the predator that are not numerical but which nonetheless operate on a time scale longer than the functional response. One such response follows from the fact that true predators grow. Their growth rate depends partly upon their feeding rate (the functional response), and their feeding rate in turn depends upon their size (Fig. 2). Integrating these processes yields a 'developmental' response to prey density (Murdoch 1971). In that paper I modelled a predatory snail that has a type 2 (inversely density dependent) functional response over the short run and showed that the effect of feeding upon growth and then the feedback of growth upon feeding can change this response towards a type 3. The hypothetical relationships in this earlier paper have now been confirmed and amplified, using notonectids preying upon mosquito larvae (Fox & Murdoch, unpublished).

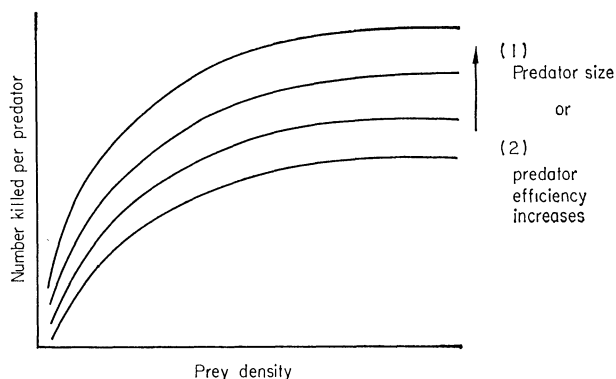


FIG. 2. Hypothetical functional response curves for a predator that is growing or whose efficiency is increasing with time.

A different sort of response, namely an increase in predator efficiency with experience, can have an effect similar to the growth effect. To simplify matters, ignore the developmental response by assuming that the predator does not grow. We can imagine that through the season, or at least for a part of the season, a predator might learn to find or handle its prey better and better as it eats more and more until a maximum degree of efficiency is reached. Looking again at Fig. 2, one can see that a predator that has a type 2 response at each point in time could again climb up these response curves as its efficiency increased with time.

To explore the consequences of this I assumed that a predator has a type-2 response as shown in Fig. 2 and then I defined the parameters of the model so that efficiency increases to a maximum as a function of feeding experience. The actual model used in the Holling equation (mentioned earlier) which states that the number of prey eaten,  $N$ , is the product of the density available  $D$ , the attack rate (or the probability of capture for each prey while the predator is searching)  $a$ , and the time spent searching at that rate. The time spent searching is the total time of the experiment,  $T$ , less the time spent dealing with the prey,  $bN$ . So we have;

$$N = (T - bN)aD,$$

which is rearranged to give

$$N = \frac{aDT}{1 + abD}. \quad (1)$$

Either or both of the parameters  $a$  and  $b$  could change with experience. I have done some computations to illustrate the possible effects of increasing efficiency. In the example shown in Fig. 3, only hunting efficiency,  $a$ , changed, handling time being kept constant. Efficiency increased with each meal but the amount of efficiency gained with each meal declined as the number of meals increased. It was also assumed that the density of prey available each day increased over the entire period, as might happen at the start of the season. The number killed per day as a function of prey density (and therefore of time) is shown in Fig. 3. Comparing Fig. 3 with Fig. 2 it can be seen that in this case we have changed a type-2 (inversely density dependent) response to a type-3 (density-dependent) response. This process of increasing efficiency with experience is known to occur in some predators, such as birds (Salt and Willard 1971; Orians 1969; Recher & Recher 1969). I do not know if insect predators can become more efficient with experience.

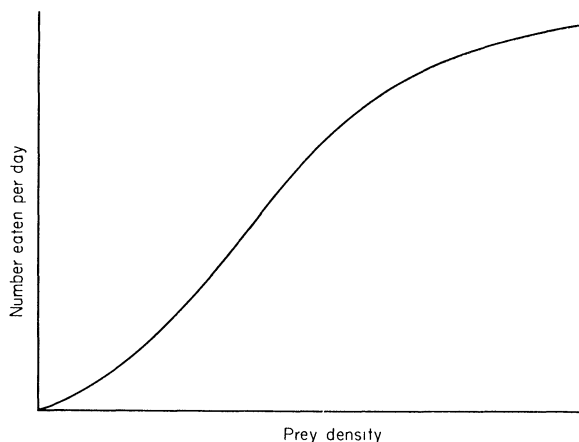


FIG. 3. Changes in number eaten per predator as the prey density increases through time and the predator becomes more efficient with experience.

No doubt these two examples do not exhaust the kinds of additional responses we might examine. There may also be an interaction between the functional and the numerical responses, since the functional response of the individual predator may be a function of predator density. Hassell & Rogers (1972) have found strong interference between individual parasitoids (*Nemeritis canescens*) attacking flour moth larvae in the laboratory, though there has been some argument over the relevance of these conditions to field situations (Griffiths & Holling 1969). The effect of such interference will not invariably be the same, but in some models and under some circumstances it will tend to stabilize prey populations by reducing 'overkill' at high parasitoid densities.

#### FUNCTIONAL RESPONSE WITH TWO OR MORE PREY SPECIES

To expand upon my second major point we turn to ways in which the functional response itself may produce stability in one or other prey population where two (or more) prey species are present. The simplest situation would be that the predator preys upon the two prey species simply as an extension of the way it attacks one species. We can model this very simply as follows. Assume that when one prey species is present, the predator's attack rate is defined by eqn (1). To get the two-prey species system we simply let  $a_1$  and  $a_2$  be the attack rates and  $b_1$  and  $b_2$  be the handling times for prey species 1 and 2, respectively:

$$\begin{aligned} N_1 &= (T - b_1 N_1 - b_2 N_2) a_1 D_1; \\ N_1 &= (T - b_1 N_1 - b_2 N_2) a_2 D_2. \end{aligned} \quad (2)$$

Notice that it immediately follows that

$$\begin{aligned} N_1 &= a_1 D_1; \\ N_2 &= a_2 D_2; \end{aligned} \quad (3)$$

and if we think of the ratio  $a_1:a_2$  as a measure of the predator's preference for species 1, then we are saying that the relative frequency of prey eaten is simply their relative frequency in the environment, modified by a preference *which is constant* (Murdoch 1969).

Solving the simultaneous equations in (2) we get:

$$N_1 = \frac{a_1 D_1 T}{1 + a_1 b_1 D_1 + a_2 b_2 D_2}; \quad (4)$$

$$N_2 = \frac{a_2 D_2 T}{1 + a_1 b_1 D_1 + a_2 b_2 D_2};$$

and in general for  $k$  prey species

$$N_i = \frac{a_i D_i T}{1 + \sum_{i=1}^k a_i b_i D_i}. \quad (5)$$

Remembering that we are interested in the absolute predation rate upon one prey species, say species 1, we can see from eqn (4) that this depends upon the way species 2 changes in density ( $D_2$ ) as well as upon the way species 1 changes ( $D_1$ ). The analysis becomes complex at this point because there are so many possibilities, and there is no space here to present details. The main point is that, although the model assumes that the predator has a type-2 response to each prey species when that species is alone, a great range of responses to each species occurs when two prey species are present together.

For simplicity let the handling times be the same ( $b_1 = b_2$ ), then the relative values of  $a_1$  and  $a_2$  indicate preference. It can then be shown that usually the response to the preferred prey is type 2, sometimes it is type 3 to the less preferred prey, in other circumstances the number eaten actually decreases with prey density, and sometimes the response is undefined. Of particular interest, stabilizing mortality on the less-preferred species occurs when the preferred prey is decreasing at the same time that the alternative prey is increasing, a situation that must occur fairly commonly in the field.

This model makes the simplest possible assumptions. For example, it assumes that a predator has the same degree of 'preference' for one of the species regardless of the relative abundance of the two prey. But there is some evidence that predators sometimes come to concentrate upon the more abundant prey, so that the rarer species is mainly ignored. That is, preference is variable and tends to become stronger or weaker for a prey species as that species forms a larger or smaller proportion of the food available. In eqn (3) this would be modelled by letting the ratio  $a_1:a_2$  increase as the ratio  $D_1:D_2$  increased. This idea of changing preference is what I have called 'switching' (Murdoch 1969), what the population geneticists call 'frequently dependent predation' (Clarke 1962; Manly, Miller & Cook 1972), and, if we make some assumptions, what Tinbergen (1960) called 'search image'. Note that this relates the *ratio* eaten ( $N_1:N_2$ ) to the *ratio* available ( $D_1:D_2$ ), but makes no statements about the functional response itself. To find out how this process might affect the functional response we must incorporate the changing preference into eqn (4). When eqn (4) is thus modified it is difficult to get general analytic solutions and many outcomes are possible. In summary, under many circumstances switching produces a type-3 response. However, it is frequently *not* stabilizing for the less preferred species, and yields a type-2 response to the preferred prey when that species is increasing faster than the non-preferred prey! So we must be careful in inferring population consequences from behavioral mechanisms.

It would be useful to know when we can expect stabilizing predation caused by switching to occur. Recent work on sea-shore snails (Murdoch 1969), coccinellids preying upon aphids (Murdoch & Marks 1972), birds feeding on artificial bait (Manly *et al.* 1972), and fish feeding on mosquito larvae (Smyth & Murdoch, unpublished) supports the notion that it will most likely occur when preference between prey is weak and the two prey are distributed differently. Two possible mechanisms are: (1) that the predator tends to remain in those areas where prey are abundant; and (2) that the predator becomes conditioned to attacking the more abundant prey.

Most of this discussion has been based on predation models rather than upon experimental data or field observations. There is a need now for more information about predators in situations where more than one prey species is available, and especially from field situations.

## ANALYSIS OF PREDATION AND INTEGRATED CONTROL

The theoretical laboratory analysis of predation processes, such as those discussed above, is only beginning, and it is no wonder that this approach has not been incorporated so far into the evaluation of natural enemies. The main question is: is it worthwhile to try to develop these techniques so that they can be used in a control programme to help decide which enemies to use and how and when to use them? At present we cannot tell until we try. Against the idea of using this approach must be ranked the facts that a good deal of fundamental research is necessary, and evaluating the whole process is complex and time-consuming. Integrating the responses in a useful way is a challenge not yet successfully met. The problem is simplest in the host-specific parasite, which is biological control's favourite weapon. But can we really be so certain that this kind of enemy is always or generally the best? Huffaker & Kennett (1969) have claimed that 'Vast experience indicates that *just about any old mediocre parasite or predator can reduce high densities, but only very good ones can prevent high densities from developing in the first place*'. From theoretical considerations a good enemy for the second purpose might be a general predator that 'switches' to the pest from some alternative prey. It might even be worth building up the density of a polyphagous non-switching predator on an alternative prey population that has a seasonal decline as the pest species is starting to increase.

The functional and numerical responses of predators clearly are important processes to study. But I have tried to show that other aspects of predation may be equally important—the developmental response, long-term learning, the presence of other prey species and how they change in density, the predator's response to the several prey species, whether there is interference among individual predators and at what densities it is important. Integrating these processes in a useful way presents a problem. However, predators do have these features and if we are to use enemies efficiently we should understand them.

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## THE NUMERICAL RESPONSE OF PREDATORS TO PREY DENSITY

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One of the most fundamental and difficult problems in ecology concerns the influence of natural enemies on the abundance of animal populations. We know from experience (e.g. from successful biological control) and intuitive reasoning that many species of insects and mites are kept at extremely low levels of abundance by parasites or predators or both, but we are unable in most instances to prove conclusively that this is so, or to explain the complex predation processes involved. For convenience, the terms prey and predator will be used to cover all types of natural enemy situations.

From theoretical considerations based on the classical works of Lotka (1925) and Volterra (1926), and later Nicholson (1933), it is clear that in order to control its prey population the predator has to exert an increasing percentage effect as the prey density rises. Milne (1957) went so far as to insist that this increasing percentage effect had to be 'unfailingly exact' and, indeed, related only to the numbers of prey present.

One of the ways by which a predator can conceivably vary its effect on the prey population is by change in numbers—the numerical response (Solomon 1949), and it is this aspect of predation that concerns us here. My intention is to illustrate the numerical responses and the effects of two very different kinds of predator in order to see whether or not it might be possible to generalize about the mechanism and function of the numerical response in ecology.