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Some Characteristics of Simple Types of Predation and Parasitism[1]

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In an earlier study (Holling, 1959) the basic and subsidiary components of predation were demonstrated in a predator-prey situation involving the predation of sawfly cocoons by small mammals. One of the basic components, termed the functional response, was a response of the consumption of prey by individual predators to changes of prey density, and it appeared to be at least theoretically important in population regulation. Because of this importance the functional response has been further examined in an attempt to explain its characteristics.

The analytical approach adopted required a predator-prey situation in which the functional response was basically simple and from which more complex types could be developed. An explanation of the basic response would then be the first step towards an explanation of more complex ones, such as those already demonstrated by the small mammals. Artificial predator-prey situations were devised which were found to meet these requirements, and the mathematical equation derived to explain the basic response also appeared to describe the published data concerning the effect of host density upon the number of hosts attacked by insect parasites.

Artificial Predator-Prey Situations

In the first artificial situation devised the "prey" were sandpaper discs four centimetres in diameter thumb-tacked to a three-foot square table. A blindfolded subject, the 'predator', stood in front of the table and searched for the discs for one minute by tapping with her finger. As each disc was found, it was removed, set to one side and searching continued. Each experiment was replicated eight times at densities of discs ranging from four to 256 per nine sq. ft.

The results of one such experiment are shown in Fig. 1, where it can be seen that the number of discs picked up increased at a progressively decreasing rate as the density of discs rose. At first thought one might expect a linear relationship, so that a doubling of the density of discs would result in a doubling of the number of discs picked up. The explanation for the departure from linearity might well involve the time that must be taken to pick up discs and dispose of them, in that at the higher densities, when large numbers of discs are located, a large proportion of the available time must be spent, not in searching, but in removing discs from the table. As a result, the apparent rate of discovery would be lower than at the lower densities where very few discs were found and most of the time available could be spent in actively searching for them.

Assuming this explanation to be correct, the simplest expression of the relationship is

$$y = aT_sx \tag{1}$$

where y is the number of discs removed, x is the density of discs, T_s is the time available for searching, and a is a constant equal to the rate of searching multiplied by the probability of finding a given disc. This constant will be termed the instantaneous rate of discovery. If a fixed interval of time, T_t, is allowed for
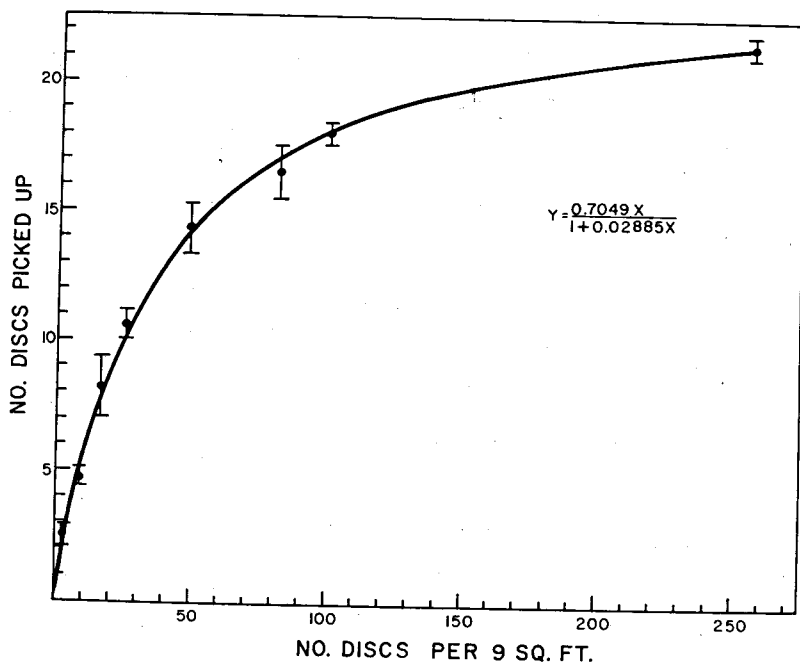
Fig. 1. Functional response of a subject searching for sandpaper discs by touch. (Averages ± 2 S.E. of 8 replicates.)

one experiment, T_s must vary with the number of discs found, for the time taken to remove discs decreases the searching time. Thus, if b equals the time to pick up one disc, then

$$T_s = T_t - by \qquad (2)$$

Substituting (2) in (1)

$$y = a(T_t - by)x \qquad (3)$$

which simplifies to

$$y = \frac{T_t ax}{1 + abx} \qquad (4)$$

When the constants a and b are not directly measured they can be calculated by transforming (4) into a straight-line equation:

$$\frac{y}{x} = -aby + T_t a \qquad (5)$$

When $\frac{y}{x}$ is plotted against y the slope of the line fitted by the least squares method is equal to $-ab$, and the intercept on the ordinate is equal to $T_t a$. The data illustrated in Fig. 1 were used to calculate a and b and the curve in the figure is based on equation (4) above. It is obvious that the curve describes the data very well; the departure of the observed from the calculated points is not significant (P>99%).

Even though the equation describes the data well, final proof that it is correct will only come when the assumptions upon which the equation is based are tested and proved. There are two such assumptions, i.e., that a, the instantaneous rate of

TABLE I.

Effect of density upon the instantaneous rate of discovery and the time to pick up each disc in experiment 1. Figures represent the averages ± 1 S. E. of eight replicates.

No. of discs per 9 sq. ft. x	Inst. rate of discovery a	Time to pick up 1 disc b
4	0.705 ± 0.060	0.0439 ± 0.0013
9	0.675 ± 0.075	0.0431 ± 0.0013
16	0.799 ± 0.081	0.0415 ± 0.0052
25	0.757 ± 0.030	0.0411 ± 0.0013
49	0.739 ± 0.049	0.0415 ± 0.0011
81	0.634 ± 0.032	0.0412 ± 0.0012
100	0.720 ± 0.079	0.0405 ± 0.0013
256	0.762 ± 0.105	0.0408 ± 0.0006

discovery, and b, the time taken to pick up one disc, are both constant at all prey densities. These two assumed constants were independently measured in an identical experiment and the results are presented in Table I. It requires no recourse to statistics to see that a and b are indeed constants, unaffected by changes of disc density. These measured values of a and b are almost identical to the values calculated from equation (5), i.e. 0.71 and 0.041 respectively. Hence it seems that this artificial situation demonstrates an extremely simple type of functional response where only two simply-operating, time-consuming behaviours — searching and handling of prey — are necessary to describe its characteristics. Moreover, it is a *basic* type, for it is difficult to imagine any predator-prey situation where at least these two behaviours are not involved.

With such a simple and easily measured functional response available it was then possible to manipulate the experiment in the hopes that some clues could be obtained to the explanation of more complicated functional responses. This was done by having the subject use a different and more ambiguous sense to locate the discs. In the experiment already described, the sense of touch was used — a very positive sense. In the next series of experiments the sense of hearing was used. These experiments were identical to the ones already described except that the subject, instead of searching for the discs with her finger, located them with the blunt end of a pencil during a two minute interval. Data from these experiments are presented in Fig. 2 and they closely resemble those already presented (Fig. 1). The curve is based on equation (4) and again the departure of the observed points from the calculated is not significant (P>99%). An additional set of data, obtained using a different subject as the "predator", was almost identical.

Although the validity of the equation had already been established when the sense of touch was used to locate discs, it again seemed worth while to measure the values of a and b. These measurements are presented in Table II and it is apparent that b was again constant, although slightly higher than before since handling the pencil made it harder to pick up the discs. Strangely, however, a was definitely affected by increase in prey density, decreasing in a regular manner from 0.387 to 0.100. Other anomalies are also apparent for, unlike the first experiment, the values of a and b calculated from equation (5) (0.37 and 0.075 respectively) are quite different from the values that were actually measured. This is to be expected for a because of its variability, but the measured values of b, although constant, were lower than the calculated value.
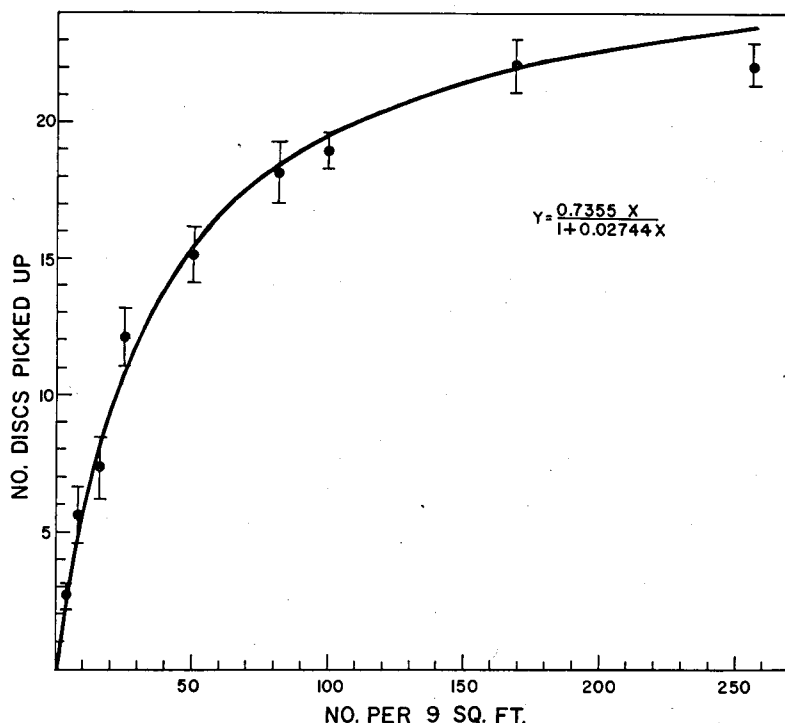
$$Y = \frac{0.7355\ X}{1 + 0.02744\ X}$$

Fig. 2. Functional response of a subject searching for sandpaper discs by sound. (Averages ± 2 S.E. of 8 replicates.)

The variability of a presents a paradox, for even though it does vary, equation (4), which was derived from the assumption that a was a constant, describes the data with satisfactory accuracy. The precise nature of this equation thus seems to be broader than it first appeared, and it is necessary now to explore its characteristics further. If b varied with changes of disc density the equation would not describe the data unless a varied in such a way as to mask the variability of b. On the other hand it is possible that a could vary in a very particular fashion so that the equation would still fit. Imagine a simple situation, for example, where b equals zero and a decreases with increasing disc density. The resulting curve

TABLE II.

Effect of density upon the instantaneous rate of discovery and the time to pick up each disc in experiment 2. Figures represent the averages ± 1 S. E. of eight replicates.

No. discs per 9 sq. ft. x	Inst. rate of discovery a	Time to pick up 1 disc. b
4	0.387 ± 0.032	0.0496 ± 0.0012
9	0.3.0 ± 0.040	0.0518 ± 0.0013
16	0.284 ± 0.024	0.0496 ± 0.0012
25	0.345 ± 0.028	0.0476 ± 0.0011
49	0.254 ± 0.039	0.0504 ± 0.0009
81	0.201 ± 0.089	0.0480 ± 0.0010
100	0.176 ± 0.006	0.0482 ± 0.0007
169	0.144 ± 0.024	0.0495 ± 0.0010
256	0.100 ± 0.005	0.0503 ± 0.0011

would have a continually decreasing slope and would resemble the curves obtained when a and b were constants with b greater than zero. Furthermore, particular functions of x that a might take would render the two curves indistinguishable, so that the proposed equation would apply to both.

In order for a to vary in this particular fashion, the basic characteristics of equation (3) must remain unchanged. This can be achieved by separating a into two constants, a' and c, with c affecting the variable y so that equation (3) is basically the same. Thus

$$y = a' (T_t - (b + c) y) x \tag{6}$$

which simplifies to

$$y = \frac{T_t a x}{1 + (b + c) x} \tag{7}$$

In words, this states that an additional time-consuming behaviour is operating that reduces the time available for searching by a fixed amount, c, for each disc picked up. In the present experiment this new behaviour appeared to arise from the difficulty the "predator" experienced in making a positive identification of a disc by the sound made when it was touched by the pencil. Close observation showed that when a disc was touched there was a distinct hesitation during which the subject tapped rapidly with the pencil in order to confirm the fact that a disc had indeed been located. Thus an additional component — identification time — is added to the two basic ones of searching and handling of prey.

From equation (6) it is now possible to derive the precise relationship a must have with x. The constant b in this equation is not involved in a, the instantaneous rate of discovery, and can be expressed in terms of a, y, and x, from (3). That is

$$b = \frac{T_t a x - y}{a y x} \tag{8}$$

Substituting (8) in (6) we get

$$y = T_t a' x - a' yx \left(\frac{T_t ax - y}{a y x} \right) - a' cy$$

which simplifies to

$$a = \frac{a'}{1 + a'cx} \tag{9}$$

This is the specific relationship a must have with x if equation (4) is to describe accurately a set of data. The simplest condition prevails when the identification of prey is virtually instantaneous, as was the case in the experiment where the discs were located by touch, for then $c = 0$ and $a = a'$, a constant. Unless a is actually measured, however, there is no way to determine whether it is a constant. If equation (4) is found to describe accurately an observed set of data, this indicates that a is either a constant or varies in the way expressed by (9).

If a is actually measured, however, equation (9) can be transformed into

$$\frac{1}{a} = cx + \frac{1}{a'} \tag{10}$$

and a plot of $1/a$ against x should yield a straight line whose slope equals c, the identification time factor. The degree to which equation (4) describes a functional response will be reflected by the closeness of fit of the observed points to
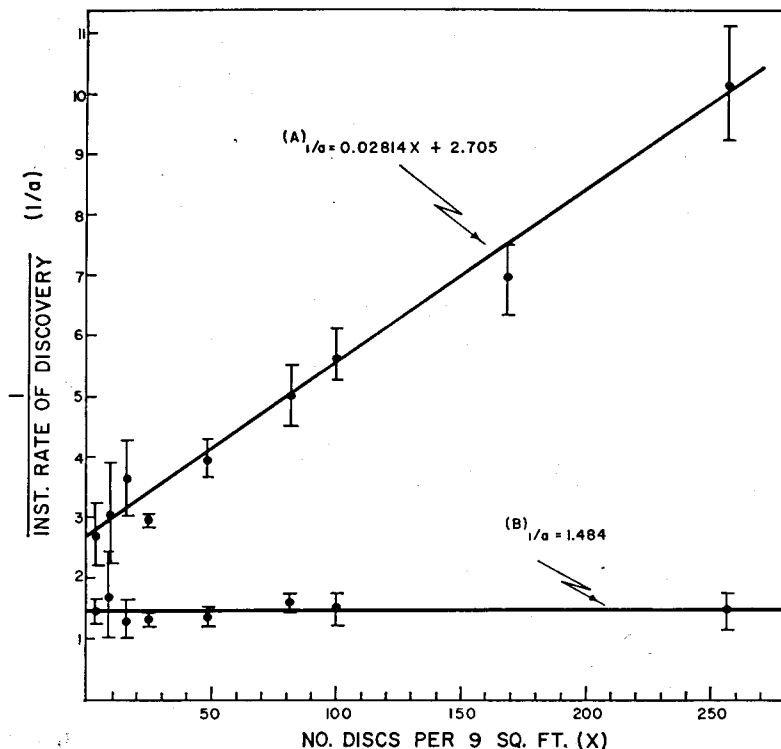
Fig. 3. Effect of disc density upon the instantaneous rate of discovery. (Averages ± 2 S.E. of 8 replicates.)

this straight line. The values of $1/a$ for the two experiments already described are plotted against x in Fig. 3. When the sense of touch was used to locate the discs the line (B) runs parallel to the axis of abscissa so that the slope, or c, equals 0. That is, no measurable time was taken to identify discs. When the sense of hearing was used to locate discs, the points lie along a sloping straight line (A) in the manner predicted by equation (9). The slope of this line, 0.028, is the number of minutes taken in hesitating over each disc. This provides the explanation for the high value of b as calculated from equation (5), since the identification time factor, c (0.028), was incorporated with the actual value of b (0.049). These two measured values of b and c add to give 0.077, very similar to the value 0.075 calculated from equation (5).

Before proceeding to natural predator-prey situations, it is worth while to recapitulate the conclusions arising from the artificial situations. In the first of these only two time-consuming behaviours — searching and handling of prey — determined the form of the functional response, and neither of these behaviours acted concurrently. That is, while the prey were being handled, searching stopped. Moreover, these two activities acted in the simplest possible fashion so that both the rate of searching and the time spent in handling prey was a constant at all "prey" densities. Since all predator-prey situations must involve at least these two behaviours, this functional response represents a *basic* type from which more complex ones can be derived, and equation (4) is hence the *basic functional response equation*.

One of these more complex types was demonstrated in the second artificial situation in which the discs were located by the sense of hearing. In this case a third time-consuming component, identification time, was added to the two basic activities. This component acted in a very simple fashion, by decreasing the time available for searching by a certain fixed amount for each disc discovered. As a result of this experiment, it became clear that the basic equation (4) would hold not only when a and b were constant, but also when a varied in the very precise fashion described in equation (9) and b was again a constant.

The effects of three time-consuming behaviours have thus far been described, but other components might also affect the functional response in natural situations. The ones that first come to mind concern satiation in the case of predators, and egg complement in the case of parasites. Both these factors will place an ultimate upper limit on the functional response and will affect the rising phase as well. Their effect might well be expressed in the time taken in resting — an additional time-consuming behaviour. Thus as the predator becomes more satiated and as the parasite runs out of eggs more and more time would be spent in resting. If the amount of this time was directly proportional to the number of prey or hosts attacked, then the basic equation (4) could be simply rewritten as

$$y = \frac{T_t\, a\, x}{1 + (b + d)\, x}$$

where d is the time spent resting on each prey or host. This is of course basically the same as equation (4) and (7). Other possibilities also exist, however, and the true explanation must await further experiments which independently measure the effects of separate components.

Natural Predator-Prey Situations

In order to apply the basic functional response equation to natural situations, the density of predators or parasites must be constant, the density of hosts or prey must be measured, and the number of hosts or prey attacked in a given period of time must be known. The only true predator-prey information of this sort available in the published literature is for small mammals preying upon sawfly cocoons (Holling, 1959).

Each of the functional responses demonstrated by small mammals under these conditions shows an S-shaped rise up to a maximum consumption. Hence it is pointless to apply equation (4) since this equation predicts a continually decreasing slope. Apparently an additional component is affecting the response by causing the searching rate to be stimulated by each prey found. Experiments are now being conducted to investigate this possibility. There is, however, a considerable body of parasite-host information available in the literature, and inspection of this shows functional responses at least visually similar to those demonstrated in the disc experiments.

Burnett's series of experiments (Burnett, 1951, 1954, 1958), in which fixed numbers of *Dahlbominus fuliginosus* (Nees) [under the name *fuscipennis* (Zett.)] searched for sawfly cocoons at various densities, are particularly appropriate to test the validity of a mathematical model, for they range from laboratory conditions, through semi-natural conditions when the parasite searched on a lawn, to natural conditions when the parasites searched in a mixed woodlot. The results of his laboratory experiments (Burnett, 1951) are shown in Fig. 4, where each of the four graphs represents the functional response obtained under different experimental conditions. The lines drawn through the points are based upon the
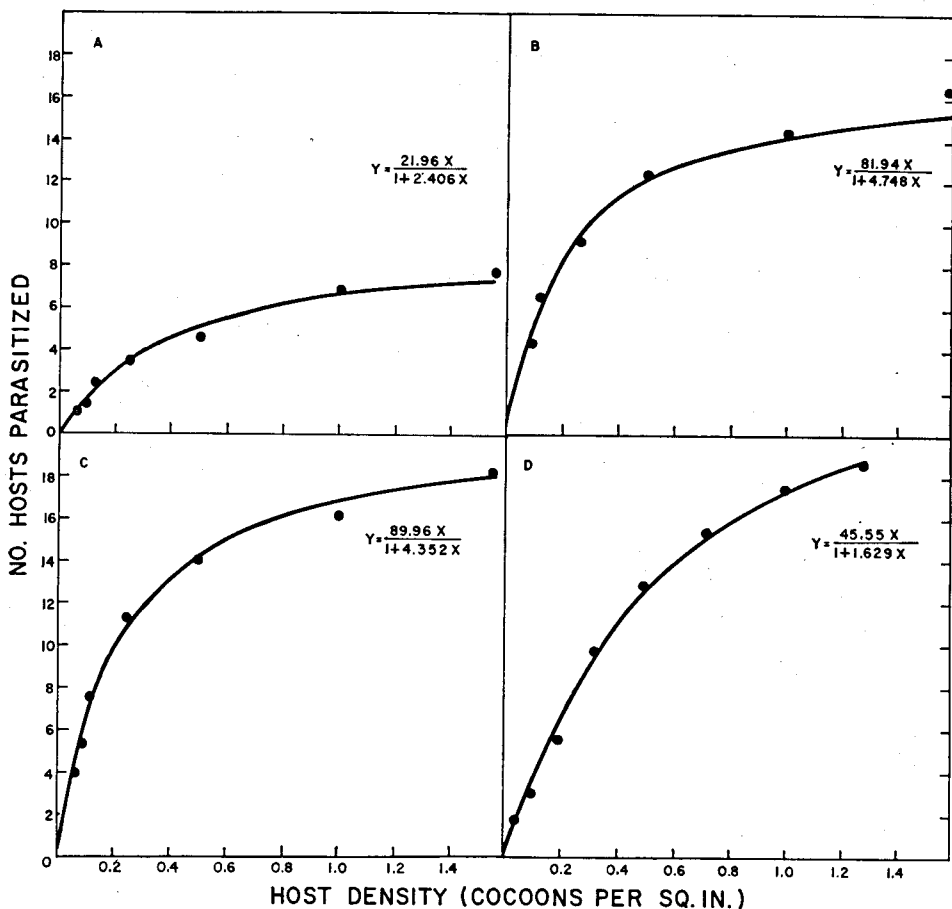
Fig. 4. Functional responses of *Dahlbominus fuliginosus* (Nees) searching for *Neodiprion sertifer* (Geoff.) cocoons in the laboratory. (Burnett, 1951).

A, B, and C: Experiments conducted at 16, 20 and 24°C respectively with different host densities achieved by changing the cage size.

D: Experiment conducted at 24°C with cage size constant.

basic equation (4) and it can be seen that it closely describes the data (P>99%). The data appearing in graphs A, B, and C represent different temperature conditions. The effect of these different temperatures was exerted through the constants a, the instantaneous rate of discovery, and b, the time spent in handling the hosts. Thus a increased from 0.9 to 3.4 to 3.7 as the temperature increased and b decreased from 2.6 to 1.4 to 1.2. Changing the area of search (Fig. 4D) modified the response mainly by decreasing a from 3.7 to 1.9. The value of b was only slightly changed, i.e. from 1.2 to 0.9.

The experiments conducted when the parasites searched for *Neodiprion sertifer* (Geoff.) cocoons distributed on a lawn (Burnett, 1954) are shown in Fig. 5, and again equation (4) can be seen to closely describe the observed points (P>99%). This equation fitted equally well when *Dahlbominus* was searching for *Neodiprion lecontei* (Fitch) cocoons distributed in a woodlot (Fig. 6A, P>99%) (Burnett, 1958). Thus it seems that the basic functional response equation describes with satisfactory accuracy the functional responses of *D. fuliginosus* searching for sawfly cocoons under a wide variety of conditions. The
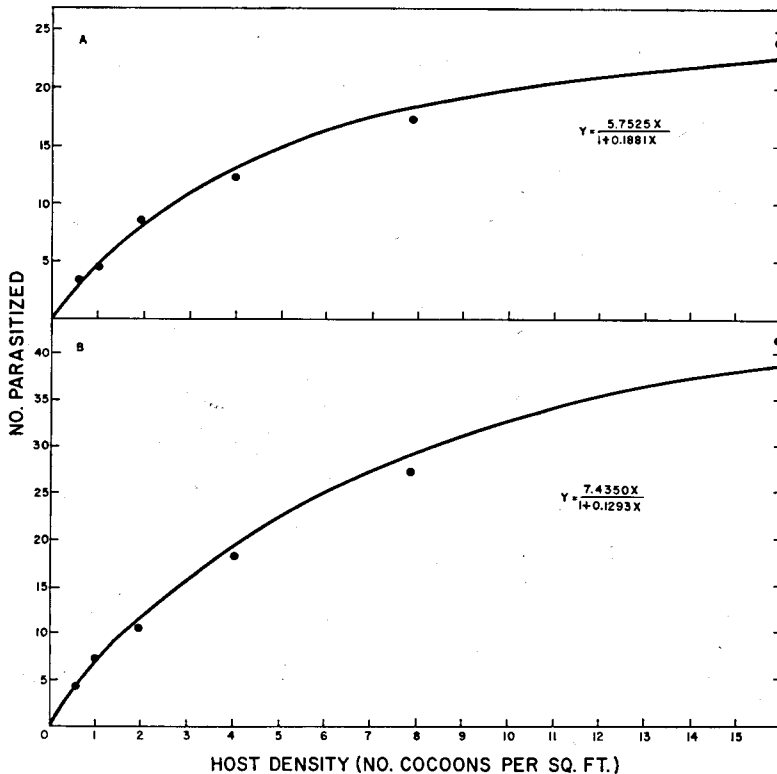
Fig. 5. Functional responses of *Dahlbominus fuliginosus* (Nees) searching for *Neodiprion sertifer* (Geoff.) cocoons on a lawn. (Burnett, 1954).
A: Temperature below 17.5°C.
B: Temperature 17.5°C to 24°C.

only differences in the responses under these different conditions are in the values of the instantaneous rates of discovery and in the time spent in non-searching activities.

Three other bodies of host-parasite data are available, and the next three figures represent the functional responses demonstrated by *Chelonus texanus* Cress. searching for eggs of *Anagasta kühniella* (Zell.) (Fig. 6B) (Ullyett, 1949a); by *Cryptus inornatus* Pratt searching for cocoons of the beet webworm *Loxostege sticticalis* (L.) (Fig. 6C) (Ullyett, 1949b); and by *Nasonia vitripennis* (Walker) searching for puparia of *Musca domestica* L. (Fig. 6D) (De Bach and Smith, 1941). Again equation (4) is seen to describe the data very well and even the poorest fit (Fig. 6D) is highly significant (P>95%).

Although the basic functional response equation is seen to describe with satisfactory accuracy a wide variety of responses obtained under a variety of conditions, it is still dangerous to suppose that it completely *explains* the responses of these parasites. In order to completely verify the equation the assumptions upon which it is based must be tested in each case just as they were tested for the disc experiments. If this were done it might well be found that additional assumptions need to be added in order to completely describe these responses. But even if this is true, the two time-consuming behaviours, searching and handling of prey, are involved just as they were in the basic functional response revealed in the first disc experiment.
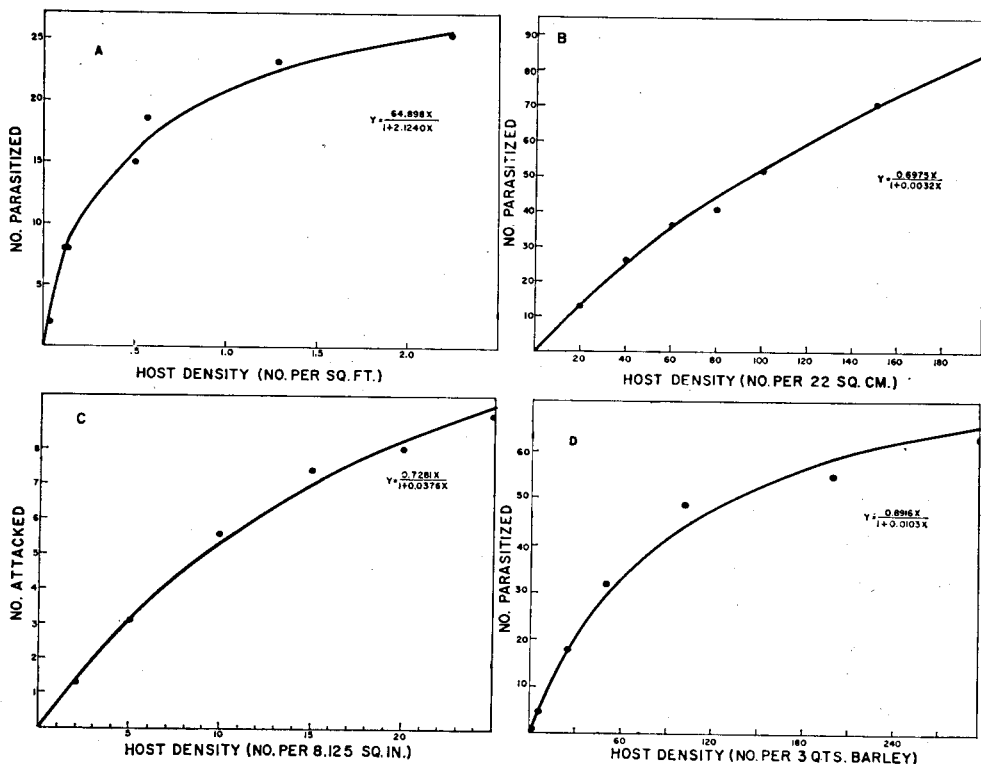
Fig. 6. A: Functional responses of *Dahlbominus fuliginosus* (Nees) searching for *Neodiprion lecontei* (Fitch) cocoons in a plantation. (Burnett, 1958).

B: Functional response of *Chelonus texanus* Cress. searching for eggs of *Anagasta kühniella* (Zell.) in the laboratory. (Ullyett, 1949a).

C: Functional response of *Cryptus inornatus* Pratt searching for cocoons of *Loxostege sticticalis* (L.) in the laboratory. (Ullyett, 1949b).

D: Functional response of *Nasonia vitripennis* (Walker) searching for puparia of *Musca domestica* L. (De Bach and Smith, 1941).

Other Mathematical Models

A number of equations have been proposed in the past to describe the effects of prey density upon the number of prey attacked. Many of these have been derived by transformation techniques and regression analyses, but since they provide no insight into mechanisms their value is limited. Moreover, a change of experimental conditions often requires a major change in the equation. Thus Burnett (1951) found that the functional responses of *D. fuliginosus* observed under laboratory conditions (see Fig. 4), could be described by a natural logarithm function of host density, whereas under semi-natural conditions (Burnett, 1954) (see Fig. 5) a square-root function had to be adopted. It has already been shown that equation (4) can apply in a wide variety of conditions simply by calculating the new values of the parameters.

Other equations have been proposed, however, by adopting certain simple and apparently reasonable assumptions. Lotka (1923) and Volterra (1926), for example, developed similar mathematical models to describe the change of prey or host density with time, and assumed, for this purpose, that the number attacked per predator was directly proportional to prey density. Nicholson and Bailey (1935) made the same assumption under the conditions of a constant predator

density. Such functional responses should appear as straight lines, rising in-
definitely as prey density increases. The only functional responses that have been
demonstrated with real animals however, are the S-shaped responses of small
mammals and the responses of parasites which have continually decreasing slopes.
Neither response is linear. Moreover it is difficult to imagine a situation where a
predator's or parasite's attacks could increase indefinitely with increase of prey
or host density; satiation or egg complement must impose an upper level for most
predators and parasites, and even those predators that continue to kill after being
satiated must reach an upper limit determined by the time required to kill. Thus
the equations of Lotka, Volterra, and Nicholson and Bailey do not describe the
facts.

Recently Watt (1959) has presented a more realistic equation to describe
the effects of both prey and predator density upon the number of prey attacked.
His equation is as follows:

$$N_A = PK \left(1 - e^{-aN_oP^{1-b}}\right) \tag{11}$$

where N_A represent the number attacked, N_o the initial density of prey, P the
number of predators searching, K the maximum number of attacks that can be
made per predator and a a positive constant. This equation applies to a broader
variety of conditions than the disc equation since the effects of predator density
are included. When future experiments are conducted, the equations proposed
here will be broadened to cover the same range of conditions. Now, however,
equation (11) must be rewritten to permit comparison with the disc equation.
This can be done by considering P as a constant so that PK, the maximum
number of attacks that can be made by P predators, becomes a constant-K'.
Similarly aP^{1-b} becomes a constant — a'. Equation (11), when predator density
is constant, thus becomes

$$N_A = K' \left(1 - e^{-a'N_o}\right)$$

or, by replacing N_A and N_o for the symbols employed in this paper, i.e. y and
x respectively,

$$y = K' \left(1 - e^{-a'x}\right) \tag{12}$$

In this form Watt's equation is identical to the one proposed by Gause (1934)
and can be directly compared to those presented in this paper.

The basic assumption from which it is derived is that a given number of
predators can generate a certain maximum number of attacks, K', and that the
rate of attack is proportional "to still unutilized opportunity" (Gause 1934,
P. 55) for attack. That is

$$\frac{dy}{dx} = a' (K' - y)$$

Watt applied his equation to the same parasite-host data that have been
discussed in this paper, as well as to others in which the density of parasites varied,
and found that his equation described the results with satisfactory accuracy.
The basic functional response equation also provides an accurate description, even
though it was derived from different assumptions. It is necessary, therefore, to
examine the equations in detail to determine, if possible, which is the more ac-
ceptable.

In order to apply Watt's equation a value for K' must be calculated using the
data available. When, as in the case of the parasite data, only y and x are measur-
ed, equation (12) is transformed to

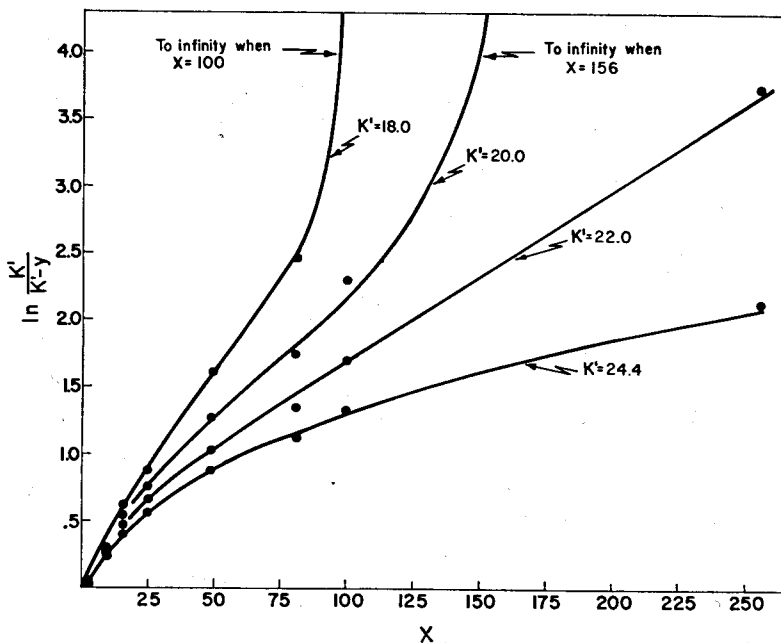$$\ln \frac{K'}{K' - y} = a'x \tag{13}$$

Fig. 7. Test of the fit of the equation $y = K'$ $(1-e^{-a'x})$ to data obtained in the first disc experiment.

and values for K' are chosen by trial and error until a plot of $\ln\dfrac{K'}{K'-y}$ against x yields a straight line. This value is then chosen as the correct one, and the slope of the line provides the value for a'.

Since the first disc experiment provides a basic functional response from which all others are derived it was chosen as the first test of the validity of Watt's equation. More than y and x were measured in this experiment so that the true value of K' could be calculated without resorting to the indirect trial and error method. Since only two time-consuming behaviours were involved the maximum number of discs would be picked up (K') when all the available time was spent in picking up discs i.e. when

$$bK' = T_t$$

from which

$$K' = \frac{T_t}{b}$$

Thus in the first disc experiment K' should equal 1/0.0409 or 24.4. It can be seen from Fig. 7, however, that this value for K' yields a line with a decreasing slope. This is sufficient disproof of Watt's equation in this instance, but if the value for K' was not actually known, as in the case of the parasite data, lower values would have been assigned in an attempt to straighten the line. The effect of such lower values are also shown in Fig. 7. Dropping the value to 22.0 still does not straighten the line, and when it is lowered to 20.0 or less, the line bends towards infinity when $K'-y = 0$. All the data from the disc experiments and from five of the 10 sets of parasite data suggested this sort of relationship. In order to fit Watt's equation in these cases, K' was arbitrarily assigned the lowest value possible before the line began bending to infinity. In the disc experiments,

TABLE III.

Comparison of the Descriptive Value of the Disc and Watt's Equation.

Source of data		Sums of squares of deviations of observed from calculated values.	
		$Y = \dfrac{Ttax}{1 + abx}$	$Y = K'(1 - e^{-a'x})$
Disc experiment No. 1 (touch)		*0.9*	24.4
Disc experiment No. 2 (auditory)	(a)	*4.5*	23.1
	(b)	*3.5*	10.4
Dahlbominus fuliginosus (Nees) vs.	(a)	*0.6*	0.9
Neodiprion sertifer (Geoff.) in the lab.	(b)	*4.1*	7.8
(Burnett, 1951)	(c)	*0.7*	15.0
	(d)	1.1	*0.4*
D. fuliginosus vs. *N. sertifer over a lawn.*	(a)	*2.6*	5.7
(Burnett, 1954)	(b)	*6.5*	10.5
D. fuliginosus vs. *Neodiprion lecontei* (Fitch) in a plantation. (Burnett, 1958)		4.6	*3.1*
Chelonus texanus Cress. vs. *Anagasta kühniella* (Zell.) in the lab. (Ullyett, 1949b)		*14.0*	23.0
Cryptus inornatus Pratt vs. *Loxostege sticticalis* (L.) in the lab. (Ullyett, 1949b)		0.6	*0.3*
Nasonia vitripennis (Walker) vs. *Musca domestica* L. in the lab. (De Bach and Smith, 1941)		49.5	*26.5*

where the true value of K′ was known, this is of course inaccurate, but some arbitrary criterion had to be adopted in order to compare the two equations.

Table III compares the sums of the squares of the deviations of the observed number of attacks from the number calculated from each equation. The lower of each pair of values are underlined to indicate which equation best describes the data. Four of the 13 functional responses are better described by Watt's equation and nine by the disc equation. The mere fact, however, that the disc equation is more accurate in a wider variety of situations than Watt's equation is insufficient evidence, by itself, to discard the latter. Complete proof or disproof will only come when his basic assumptions are tested. Unfortunately such a test cannot be made with the parasite data since the true values of K′ are not known. In the disc experiments, where the true values are known, Watt's equation is inaccurate. Since the functional responses demonstrated in these experiments are basic ones, it follows that Watt's equation is either inaccurate or at least incomplete in all situations.

Since the conflict between these two equations has arisen largely because of the different approaches adopted, it is appropriate, in closing, to contrast the two. Watt approached the problem by developing a number of sets of assumptions, that seemed reasonable on the basis of an intimate knowledge of the available literature. The equations derived from each set of assumptions were then tested against existing data and the one that described the greatest array was selected

as the proper one.   Such an approach holds the promise of providing at least partial answers quickly, and this has considerable merit when so much biological information requires an analysis that will yield the insight into mechanisms that is necessary to suggest further work or practical control measures.   There is, however, the danger that the selected equation will not provide an accurate *explanation* of the data in appropriate biological terms, even though it provides an adequate *description* of the data.   Moreover, the approach tends to produce a restricted model, for there is no indication how models for more or less complex types of responses can be derived, nor indeed that other types exist.

The approach adopted in the present paper was different in that it began with the discovery of a *basic* functional response.   That is, the only components operating were the ones that *had* to be present in all situations.   All other components, that may be present in some situations and not in others, can be considered as subsidiary ones that can be analysed and incorporated after the basic response is fully explained.   Thus the mathematical equation which incorporates the explanation of the basic response will evolve in logical steps along causal pathways that become progressively more complex.   At any point along these pathways natural responses may be discovered, the explanation and description of which may be embodied by appropriate modifications of the basic equation.   The approach also requires a proof that the equation accurately describes and explains the basic response, a proof that relies not only on the fitting of the equation to the data, but also on the testing of the basic assumptions by independently measuring the assumed constants.   Hence the resulting mathematical models are accurate and are not restrictive.

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