The Canadian Entomologist
Vol. XCI Ottawa, Canada, July 1959 No. 7

Some Characteristics of Simple Types of Predation and Parasitism
By C. S. Holling

Forest Insect Laboratory, Sault Ste. Marie, Ontario

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

\[ y = aT^n \]  

where \( y \) is the number of discs removed, \( x \) is the density of discs, \( T \) 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, \( T \), is allowed for

---

1 Contribution No. 556, Forest Biology Division, Research Branch, Department of Agriculture, Ottawa, Canada.
Effect of density upon the instantaneous rate of searching in experiment 1. Figures represent the measurements of the number of discs picked up per 9 square feet.

<table>
<thead>
<tr>
<th>No. of discs per 9 sq. ft.</th>
<th>Instantaneous rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>16</td>
<td>0</td>
</tr>
<tr>
<td>25</td>
<td>0</td>
</tr>
<tr>
<td>49</td>
<td>0</td>
</tr>
<tr>
<td>81</td>
<td>0</td>
</tr>
<tr>
<td>100</td>
<td>0</td>
</tr>
<tr>
<td>256</td>
<td>0</td>
</tr>
</tbody>
</table>

The curve is based on equation (4) above. It is obvious that the curve describes the data very well, the departure of the observed points from the calculated points is not significant (P>99%).

Although the validity of theory could not be tested, the sense of touch was used to measure the values of \( a \) and \( b \). It is apparent that \( b \) was again affected by the manner of handling the pencil, however, \( a \) was definitely affected by the density of discs. In the first experiment, the values of \( a \) (0.075 respectively) are quite different. This is to be expected for \( b \), although constant, were low.
of discs found, for the time taken. Thus, if \( b \) equals the time to pick out

given density, 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 re-
course 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 (\( P > 0.99 \)). 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, how-
ever, \( a \) 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 meas-
ured. 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.
would have a continually decreasing rate related to the distance
ed when $a$ and $b$ were constants with particular functions of $x$ that $a$ might take,
so that the proposed equation would be

$$ y = a' x + c $$.  

In order for $a$ to vary in this problem, equation (3) must remain unchanged,
into two constants, $a'$ and $c$, with $c$ is basically the same. Thus

$$ y = a' x + c $$

which simplifies to

$$ y = a' x $$

In words, this states that an additional prey reduces the time available for searching up. In the present experiment this difficulty the “predator” experience for
by the sound made when it was touched that when a disc was touched the subject tapped rapidly with the prey had indeed been located. Thus an $a'$ is added to the two basic ones of search.

From equation (6) it is now possible to have with $x$. The constant $b$ in the instantaneous rate of discovery, and can be

That is

$$ y = a' x $$

Substituting (8) in (6) we get

$$ y = T_b (a' x - a' x) $$

which simplifies to

$$ a' x $$

This is the specific relationship $a$ must have to the $x$ which accurately a set of data. The simple.

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

<table>
<thead>
<tr>
<th>No. discs per 9 sq. ft.</th>
<th>Inst. rate of discovery</th>
<th>Time to pick up 1 disc.</th>
</tr>
</thead>
<tbody>
<tr>
<td>$x$</td>
<td>$a$</td>
<td>$b$</td>
</tr>
<tr>
<td>4</td>
<td>0.387 ± 0.032</td>
<td>0.0496 ± 0.0012</td>
</tr>
<tr>
<td>9</td>
<td>0.370 ± 0.040</td>
<td>0.0518 ± 0.0013</td>
</tr>
<tr>
<td>16</td>
<td>0.284 ± 0.024</td>
<td>0.0496 ± 0.0012</td>
</tr>
<tr>
<td>25</td>
<td>0.343 ± 0.028</td>
<td>0.0476 ± 0.0011</td>
</tr>
<tr>
<td>49</td>
<td>0.254 ± 0.039</td>
<td>0.0504 ± 0.0009</td>
</tr>
<tr>
<td>81</td>
<td>0.201 ± 0.089</td>
<td>0.0180 ± 0.0010</td>
</tr>
<tr>
<td>100</td>
<td>0.176 ± 0.006</td>
<td>0.0182 ± 0.0007</td>
</tr>
<tr>
<td>160</td>
<td>0.144 ± 0.024</td>
<td>0.0495 ± 0.0010</td>
</tr>
<tr>
<td>256</td>
<td>0.100 ± 0.005</td>
<td>0.0508 ± 0.0011</td>
</tr>
</tbody>
</table>

and a plot of $1/a$ against $x$ should show the identification time factor. The determination response will be reflected by

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

\[
y = a'(T_x - (b + c)y)x
\]

which simplifies to

\[
y = \frac{T_x ax}{1 + (b + c)x}
\]

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

\[
b = \frac{T_x ax - y}{ayx}
\]

Substituting (8) in (6) we get

\[
y = T_x a'x - ayx - a'cy
\]

which simplifies to

\[
a = \frac{a'}{1 + cx}
\]

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

\[
\frac{1}{a} = cx + \frac{1}{a'}
\]

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
One of these more complex types of situation in which the discs were located is a third time-consuming component, identity of activities. This component acted in a time available for searching by a certain number of predators. As a result of this experiment, it became evident that the number of predators did not hold only when the values of a and b were calculated in a precise fashion described in equation (9).

The effects of three-time-consuming activities but other components might also be the same as equation (4) and (7). The true explanation might be found in the effects of separate components. The true explanation must await further investigation. The effects of separate components.

Natural Predator-Prey Situations

In order to apply the basic function, the density of predators or parasitic infections must be measured, and the number of time must be known. The only available in the published literature are parasitic infections (Holling, 1959).

Each of the functional responses under different conditions shows an S-shaped rise up to a point where the effect of equation (4) since it involves the searching slope. Apparently an additional factor being taken into account is the possibility of parasite-host information available. This shows functional responses at least in the range of disc experiments.

Burnett's series of experiments with numbers of Daphnia pulex, searched for sawfly cocoons at various temperature conditions, through semi-natural conditions when the parasite-host information available shows functional responses at least in the range of disc experiments.
two experiments already described use of tach was used to locate the abscissa so that the slope, or e, equals 0 to identify discs. When the sense plane along a sloping straight line (A) the slope of this line, 0.028, is the time for each disc. This provides the completed from equation (5), since the distributed with the actual value of b we add to 0.077, very similar to 6.

In many situations, it is worth while to artificial situations. In the first of the searching and handling of prey the same, and neither of these behaviours were being handled, searching in the simplest possible fashion so that in handling prey was a constant situation. Situations must involve at least represents a basic type from which (4) is hence the basic functional

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 saturation in the case of predators, and egg complement in the case of parasites. Both these factors will place an 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

$$y = \frac{T_1 a x}{1 + (b + d) x}$$

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 Dambelominus fuliginosus (Nees) [under the name fuscipennis (Zeit.)] 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.

The 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 sertifer* (Geoff.) cocoons on a lawn. (Burnett, 1951).
A: Temperature below 17.5°C.
B: Temperature 17.5°C to 24°C.

only differences in the responses under each of the instantaneous rates of discovery activities.

Three other bodies of host-parasite research for eggs of *Anagasta kuehniella* Zeller, *Cryptus morratus* Pratt searching for *Trichogramma ostrinieae* (L.) (Fig. 6C) (Ullyett, 1941) searching for puparia of *Musca domestica* (L., 1841). Again equation (4) is seen to be a good fit (Fig. 6D), although the least satisfactory accuracy is a wide variety of conditions, it is still dangerous to supposed these parasites. In order to complete the study which it is based must be tested in the future. If this were done in experiments, the number of parasitoids need to be added in order to see if it is true, the two time periods of prey, are involved just as they were in the first disc experiment.
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 Cebelus texanus Cress. searching for eggs of Anagasta kuehiella (Zell.) (Fig. 6B) (Ulyett, 1949a); by Cryptus inornatus Pratt searching for cocoons of the beet webworm Loxostege sticticalis (L.) (Fig. 6C) (Ulyett, 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.
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 were definitely as prey density increases. It was demonstrated with real animals how the efficiency of mammals and the responses of parasites and predators is linear. Moreover, the results of predation or parasitism are affected by factors such as host density, satiation of predators, and parasites, and even the number of satiated must reach an upper limit (e.g. in the equations of Lotka, Volterra, and others).

Recently Watt (1959) has proposed the effects of both prey and predator densities. His equation is as follows:

$$ N_A = \frac{K}{N_P + a} $$

where $N_A$ represent the number of prey attacked, $N_P$ the number of predators searching, $K$ the number of attacks made per predator and $a$ a positive constant, for a variety of conditions than the discus here are included. When future experiments are broadened to cover the cases here, equation (11) must be rewritten (12) and (12) can be reduced by considering the number of attacks that can be made in the limits of a predator's field of vision. Similarly $aP^b$ becomes a constant $a$ and $b$ is constant, thus becomes

$$ N_A = \frac{K}{N_P + a} $$

or, by replacing $N_A$ and $N_P$ for $x$ and $y$ respectively,

$$ y' = \frac{x}{y + a} $$

In this form Watt's equation is identical to (4) and can be directly compared to it.

The basic assumption from which Watt's equation is derived is that the rate of attack is proportional to the product of the numbers of the two species (e.g. P. 55) for attack. That is

$$ \frac{dN_A}{dt} = aN_PN_A $$

Watt applied his equation to the data available. When, as in the case of the milkweed bug, equation (12) is transformed to

$$ y' = \frac{x}{y + a} $$

such functions have been used in the study of the movement of a fluid.
density. Such functional responses should appear as straight lines, rising indefinitely 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:

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

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

$$N_A = K'(1 - e^{-aN_o})$$

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

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

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 acceptable.

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 measured, equation (12) is transformed to

$$\ln \frac{K'}{K' - y} = a'x \quad (13)$$
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 $\ln(K'/y)$ 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

$$bK' = T_i$$

from which

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

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 $K'\cdot y = 0$. 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,

where the true value of $K'$ was known an arbitrary criterion had to be adopted.

Table III compares the sums of the number of attacks from the number of each pair of values are underlying the data. Four of the 13 functional equation and nine by the disc equation and the equation is more accurate in a wide of evidence, by itself, to conclude that only when his basic assumption test cannot be made with the partial known. In the disc experiment, the equation is inaccurate. Since the experiments are basic ones, it follows or at least incomplete in all situations.

Since the conflict between the different approaches adopted, Watt approached the problem by that seemed reasonable on the basis literature. The equations derived against existing data and the one
TABLE III.
Comparison of the Descriptive Value of the Disc and Watt's Equation.

<table>
<thead>
<tr>
<th>Source of data</th>
<th>Sums of squares of deviations of observed from calculated values.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Disc experiment No. 1 (touch)</td>
<td>( Y = \frac{T_{\text{tax}}}{1 + abx} )</td>
</tr>
<tr>
<td>Disc experiment No. 2 (auditory)</td>
<td>( Y = K' (1 - e^{-ax}) )</td>
</tr>
<tr>
<td>(a)</td>
<td>0.9</td>
</tr>
<tr>
<td>(b)</td>
<td>24.4</td>
</tr>
<tr>
<td>Daklbomius fuliginosus (Nees) vs.</td>
<td>( a_x^x )</td>
</tr>
<tr>
<td>Neodiprion sertifer (Geoff.) in the lab. (Burnett, 1951)</td>
<td>23.1</td>
</tr>
<tr>
<td>(a)</td>
<td>0.6</td>
</tr>
<tr>
<td>(b)</td>
<td>10.4</td>
</tr>
<tr>
<td>(c)</td>
<td>0.9</td>
</tr>
<tr>
<td>(d)</td>
<td>7.8</td>
</tr>
<tr>
<td>(e)</td>
<td>15.0</td>
</tr>
<tr>
<td>(f)</td>
<td>0.4</td>
</tr>
<tr>
<td>D. fuliginosus vs. N. sertifer over a lawn. (Burnett, 1984)</td>
<td>5.7</td>
</tr>
<tr>
<td>(a)</td>
<td>5.5</td>
</tr>
<tr>
<td>(b)</td>
<td>10.5</td>
</tr>
<tr>
<td>D. fuliginosus vs. Neodiprion lecontei</td>
<td>( a_3 )</td>
</tr>
<tr>
<td>(Fitch) in a plantation. (Burnett, 1958)</td>
<td>5.1</td>
</tr>
<tr>
<td>Odonus lecanus Cress. vs. Anagasta kuhniella (Zell) in the lab. (Ullyett, 1949b)</td>
<td>23.0</td>
</tr>
<tr>
<td>Cryptus inornatus Pratt vs. Loxostegia</td>
<td>0.6</td>
</tr>
<tr>
<td>stactalina (L.) in the lab. (Ullyett, 1949b)</td>
<td>0.3</td>
</tr>
<tr>
<td>Nasus vitripennis (Walker) vs. Musca domestica L. in the lab. (De Bach and Smith, 1941)</td>
<td>26.5</td>
</tr>
</tbody>
</table>

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 is 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.

Acknowledgments

I wish to acknowledge the considerable assistance rendered by Dr. R. M. Belyea and Mr. A. W. Ghent through discussion and criticism of the manuscript. I must also thank Miss Patricia Baie, whose ‘predatory’ behaviour provided data for the major portion of this paper.

References


(Received May 7, 1959)