Towards a Predator-Prey Model Incorporating Age Structure: The Effects of Predator and Prey Size on the Predation of Daphnia magna by Ischnura elegans

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INTRODUCTION

The functional response of a predator relates the change in the number of prey consumed per predator to changes in prey density (Solomon 1949). Holling (1959a, 1961) has described three types of functional responses, all of which have now been observed experimentally. Not all results fit conveniently into this scheme (see Mori & Chant 1966; Sandness & McMurtry 1970). The most frequently described curve, particularly for invertebrate predators, is Holling's type 2 response, in which the curve rises at a decreasing rate to a plateau (for example, Burnett 1951, 1954; Morris 1963; Tostowaryk 1972; Fox 1973).

Holling (1959b) proposed an equation which incorporated what he considered to be the basic components of predation, namely the total time prey were exposed to predation, the rate of successful search (attack coefficient) and the handling time:

\[ N_a = \frac{T a N}{1 + a T_h N} \]  
(Holling 1959b, equation (4))

where \( N_a \) = number of prey eaten, \( T \) = total time prey are exposed to predation, \( N \) = prey density, \( a \) = attack coefficient and \( T_h \) = handling time.

In this form, the equation is commonly called the 'disc equation'; Holling, and many other workers, have applied it to type 2 functional response curves in a wide range of predators (e.g. Holling 1959b; Morris 1963; Hardman & Turnbull 1974). Equation (1) is an 'instantaneous equation' and as such makes no allowance for a reduction in prey numbers during the course of the experiment (exploitation). Consequently, it should only be used when an experiment is run for a very short time, or where predator search is systematic, so that exploited areas are not re-searched, or when a prey item is replaced as soon as one is eaten. A more robust equation for fitting a type 2 curve to experimental data, allowing for prey exploitation by randomly searching predator, has been proposed by Rogers (1972).

The two essential parameters of the disc equation and Rogers random predator equation, the attack coefficient, \( a \), and the handling time, \( T_h \), have been shown to vary with predator size (for one prey size) and with prey size (for one predator size) (Morris 1963; Tostowaryk 1972; Evans 1973; D. J. Thompson & J. H. Lawton, unpublished). However, there has been no systematic examination of the way in which \( a \) and \( T_h \) vary with both predator and prey size for one species of predator and its prey. This is a major gap in the development of general predator-prey models incorporating age structure (Hassell, Lawton & Beddington 1976).
MATERIALS AND METHODS

Predators, prey and experimental procedure

The predators used were nymphs of the damselfly *Ischnura elegans* (van der Lind.), collected from the Pocklington Canal near York (Nat. Grid ref. SE 786441) between April and June 1974 and from a pond at Brasside near Durham (Nat. Grid ref. NZ 291451) in May 1974.

The head widths, the greatest width across the eyes, and body lengths, the distance between the front edge of the head and the base of the caudal lamellae, of the nymphs were measured with a micrometer eyepiece, and the nymphs assigned to instars (Fig. 1). The last five instars were used in the experiments. Prior to the experiments, the nymphs were maintained in a constant temperature room at 8°C in 100-ml beakers containing dechlorinated tap water and a supply of food (*Daphnia magna* (Straus)).

The prey used during the experiments were also *D. magna*, which were maintained in culture in the laboratory, where they were fed on a suspension of baker's yeast. Five prey sizes were used in the experiments. The animals were separated into these five classes by passing them through a series of graded Endecotts Test Sieves. Care was taken during sieving to ensure that air did not become trapped under the carapaces of the *Daphnia*; when this happens, the *Daphnia* float and consequently become inaccessible to the predator. After the initial sieving, each size class was sorted twice more in order to minimize the variance.

Four replicates of between ten and twelve prey densities were used for each predator size with each prey size. Owing to the large numbers of *D. magna* required, the experiment had to be performed in several stages over a period of two months. The experimental procedure used throughout is described below.

On day one, the *Ischnura elegans* nymphs to be used were provided with an excess of food for 24 h. Only animals that had moulted between ten and two days previously were chosen. This was to ensure that the animals had recovered from moulting and settled down to a steady feeding rate. Following the 24 h of excess feeding, the nymphs were starved for 48 h. Throughout the whole of the experiment, they were maintained in 100-ml beakers at 8°C in the dark. It is known that *I. elegans* feeds equally well in the light and dark, the advantage of working in the dark being that it reduces the variance in numbers eaten which occurs when *Daphnia* are attracted to foci of light in the experimental beakers.

The *D. magna* for the experiment were counted into 100-ml beakers accurately using a Pasteur pipette. Densities ranging from five to 120 per beaker were employed. The level of water in the beakers was made up to 75 ml and a cocktail stick added as a 'fishing' site; *Ischnura* nymphs normally feed on prey items that swim or crawl past them. When the 48-h period of starvation was over, the nymphs were transferred to the beakers containing the *Daphnia* and allowed to feed for 24 h. They were then removed and the *Daphnia* recounted. Both the numbers of live and dead *Daphnia* were recorded. Dead *Daphnia* could have died 'naturally' or been killed by the damselfly nymphs and left since damselfly nymphs engage in 'wasteful killing' (see Johnson, Akre & Crowley 1975). A *Daphnia* that was more than half eaten was recorded as eaten whilst one that was less than half eaten was recorded as dead—a result of 'wasteful killing'. Fortunately, this somewhat arbitrary decision did not have to be made very frequently (less than 5% at
each density). The number of prey eaten by *Ischnura* of different sizes, over a range of prey densities and sizes therefore could be found.

*Estimation of attack coefficient, a and handling time, T_h*

With the procedure described, it was impracticable to replace prey that were eaten during the course of the experiment, so that the results are affected to some extent by prey exploitation. The equation which best describes the results is therefore the random predator equation of Rogers (1972), for one predator:

\[
N_a = N(1 - e^{-a(T - N_a T_h)})
\]  

(2)

where \(N_a, N, T, a\) and \(T_h\) are as defined for the disc equation (see Introduction).

![Figure 1](image)

**Fig. 1.** The relationship between head width and body length in nymphs of the damselfly *Ischnura elegans*. The ‘instar clouds’ of the last six instars are indicated by arrows.

The attack coefficient, \(a\), and the handling time, \(T_h\) can be estimated from eqn (2) by linear regression using the formula:

\[
\log \left( \frac{N - N_a}{N} \right) = a T_h N_a - a T \quad (T = 1)
\]  

(3)

There are two ways in which estimates of \(a\), particularly, and \(T_h\) may be unrealistic. First, in a normal, type 2, functional response which rises with a decreasing slope towards a plateau, there is a prey density beyond which the predator eats more or less a constant number of prey. In the regression of the logarithm of the number of survivors against the number of prey eaten, any points beyond this prey density merely provide more variance about the first point on the plateau, resulting in an increase in the slope of the line and a
Predation of *Daphnia magna*

lower intercept. This then leads to an increase in the estimate of $a$. Since the slope is $a$ times $T_h$ the estimate of the handling time will be reduced. This first type of discrepancy does not greatly alter the relative values of the $a$ and $T_h$ estimates providing that only a few points are on the plateau. The second type of discrepancy may be of greater importance; if the level of exploitation is too high at any prey density the logarithm of the number of survivors becomes very small indeed; at complete exploitation, it is, of course, the logarithm of zero. High exploitation has the effect, again, of increasing the estimate of $a$ and reducing that of $T_h$. It has been found by simulation that any exploitation greater than about 80% causes a significant bias in the estimates of $a$ and $T_h$. Consequently, any data points where the exploitation rose above this level were omitted from the regression. In actual fact, this involved only some penultimate and final instar nymphs, where two, sometimes three of the four replicates ate all the prey available. These two points will be more fully dealt with in a later publication.

**RESULTS**

The mean head width of each predator instar and mean lengths of the prey in each size class used in the experiment are given in Tables 1 and 2 respectively.

**Table 1. Mean head widths at the largest five instars of *Ischnura elegans* nymphs**

<table>
<thead>
<tr>
<th>Predator instar</th>
<th>Mean head width (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>12</td>
<td>3.50</td>
</tr>
<tr>
<td>11</td>
<td>2.89</td>
</tr>
<tr>
<td>10</td>
<td>2.38</td>
</tr>
<tr>
<td>9</td>
<td>1.86</td>
</tr>
<tr>
<td>8</td>
<td>1.48</td>
</tr>
</tbody>
</table>

**Table 2. Mean length of the *Daphnia magna* size-classes used in the experiment**

<table>
<thead>
<tr>
<th>Prey size designation</th>
<th>Mean length (mm) ± 1 S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>2.93 ± 0.03</td>
</tr>
<tr>
<td>B</td>
<td>2.30 ± 0.04</td>
</tr>
<tr>
<td>C</td>
<td>1.70 ± 0.02</td>
</tr>
<tr>
<td>D</td>
<td>1.44 ± 0.02</td>
</tr>
<tr>
<td>E</td>
<td>1.10 ± 0.02</td>
</tr>
</tbody>
</table>

The functional response curves are shown in Fig. 2 (a)–(e). (Standard errors are fitted only to the top line of each instar for clarity.) $a$ and $T_h$ were estimated using eqn (3); in three cases, where the regression was not significant, ($P > 0.05$), $a$ and $T_h$ could not be calculated and no curve was fitted. The cases where this occurred refer to small nymphs (instars 8 and 9) feeding on very large prey, when they clearly had difficulty dealing with it and feeding rates were extremely low (see the lowest curve in Fig. 2(d) and the bottom two curves in 2(e)). In all other cases, functional responses were fitted to the data shown in Fig. 2 by means of an iterative Newton-Raphson technique (Sutton 1954) using eqn (2) with the appropriate estimates of $a$ and $T_h$ from eqn (3).

The fitted curves described the data well, though in some cases, for example the top
Fig. 2. The functional responses of five instars of *Ischnura elegans* to five arbitrary size-classes of *Daphnia magna*. Note that the vertical scales on (d) and (e) differ from those of (a), (b) and (c). Graph (a) is the responses of instar 12; (b) instar 11; (c) instar 10; (d) instar 9; (e) instar 8. Size A prey (●); B (○); C (■); D (□); E (▲). Standard errors (± 1 S.E.) are fitted to the top line for each instar.
Predation of Daphnia magna

curve of Fig. 2(a) there is a slight tendency to underestimate numbers eaten at low densities and overestimate at high densities.

From the calculations, the pattern of variation in \( a \) and \( T_h \) with prey and predator size was obtained; the results are plotted in Figs 3 and 4, which show the following important points (note that for ease of graphical representation, the scales on the axes in the two figures are reversed). It is clear from Fig. 3 that in general \( a \) decreases as prey size increases with predator size, whereas Fig. 4 shows that handling time increases with prey size and decreases as predator size increases. There are two further points of interest to note from Fig. 3. First, there is relatively little difference in the \( a \) values obtained for final instar nymphs feeding on prey of any size, and second, there is an indication that the levels of \( a \) for penultimate instars seem to be lower than might be expected for prey sizes B, C and D. These points will be returned to in the Discussion.

It should be noted that Figs 3 and 4 are ‘incomplete’, because the smaller predators experienced considerable difficulty when faced with only large prey. The fitted functional responses under these conditions were statistically non-significant because of the very low and rather variable feeding rates. Very low feeding rates, of course, may be caused either by very low \( a \) values and/or very high values for \( T_h \). It is clear from Figs 3 and 4 that both effects appear to be involved in the present case, with the ‘\( a \) surface’ declining effectively to zero in predator instars 8 and 9 feeding on prey in size-classes A and B, and the ‘\( T_h \) surface’ rising continually up, to a point when handling time becomes so large that it can no longer be estimated.

![Fig. 3. The effect of prey and predator size on the 'attack coefficient'.](image-url)
DISCUSSION

Although, at first sight, the overall shape of the 'a surface' obtained in the present study is relatively simple, varying nearly monotonically with both predator and prey size, it is possible that in other predators, more complex surfaces with 'turn-over points' could occur. Indeed, a closer examination of Fig. 3 provides some hint that there may also be a tendency for this to happen with the present Ischnura–Daphnia system. In general, it is not unreasonable to suggest that there will be a prey size for each instar at which the attack coefficient is at its maximum; prey may either be too large or too small to be dealt with effectively. The preferred prey size for each instar would then appear as peaks on the surface of Fig. 3. For instars 8 and 9, these peaks, if they exist, occur at smaller prey sizes than those presented in the experiment, since $a$ is still rising at prey size E. In instar 10, there is some evidence that the optimum prey size is around size D, since $a$ for size E

![Figure 4](image-url)
Predation of Daphnia magna is lower than for D. In penultimate instars, the peak is again in the region of sizes D and E. Final instars show no discernible peak. Further work is required on other predators before it is possible to say whether the relatively simple *Ischnura–Daphnia* attack coefficient surface is, or is not, typical of other invertebrate predators.

The sub-components of $a$ and $T_h$ have been listed by Holling (1963). The sub-components of $a$ can be considered to include (1) the reactive distance of the predator for prey, i.e. the maximum distance at which a predator will react by attacking prey, (2) the speed of movement of the predator, (3) the speed of movement of the prey and (4) the capture success, which is defined as the proportion of prey coming close enough to be attacked that are successfully captured. The sub-components of $T_h$ can be considered to include (1) time spent orientating to, pursuing and subduing prey, (2) time spent eating prey and (3) time spent in a ‘digestive pause’ during which the predator is not hungry enough to eat further prey. Whilst it is possible to argue about the detailed interpretation of each of these sub-components, they obviously provide a reasonably realistic breakdown of the factors which must influence $a$ and $T_h$.

The overall values of $a$ and $T_h$ are a composite picture of the behaviour of these individual sub-components. Viewed in terms of these sub-components, it is much easier to make *a priori* predictions of the likely changes in $T_h$ with prey and predator size than it is for $a$, because all the sub-components of $T_h$ vary in the same direction; this is certainly not true for $a$. Thus, whereas prey that are large relative to the predator will require longer to subdue, eat and digest (all causing an increase in $T_h$), these same prey may be spotted further away (giving rise to an increase in $a$), move faster (again increasing $a$) but escape more easily (leading to a decrease in $a$). Nymphs of *Ischnura elegans* hunt by remaining stationary on ‘fishing sites’ so the ‘speed of movement of predator’ sub-component can be ignored. The effects of prey speed of movement are difficult to assess, as the relative activities of the various *Daphnia* size-classes have not yet been measured, but the constant value of $a$ obtained for final instar nymphs suggests that it is evenly balanced with the increase in reactive distance and reduction in capture success which occurs with increased prey size. In instars 8, 9 and 10, $a$ is more variable; it has a high value with small prey and declines as prey size increases. The probable explanation is that the decline in capture success with increased prey size is not matched by an increase in the reactive distance. The possible ‘preference peaks’ discussed above would correspond, in Holling’s terms, to the prey size for each instar where $a$ is optimized, i.e. where the predator can capture the prey successfully and where it responds to them from a comparatively long distance.

Very few data are available for comparison with the above results, and none of them are ‘complete’ in the sense that they are slices across the surface in the predator or prey planes, dealing with one predator instar on prey of various sizes, or vice-versa.

Cockrell (1974), working on the predation of four arbitrary prey sizes of *Asellus aquaticus* L. by adult *Notonecta glauca* L., showed that $a$ declined approximately linearly and $T_h$ increased exponentially as prey size increased. This result is very similar to those described above for the last three instars of *Ischnura*, where in all cases, the handling time for the largest prey category was considerably longer than for the next largest.

Rather more information is available on the effect of predation of one predator on a range of prey sizes. D. J. Thompson & J. H. Lawton (unpublished), working on predation of *Daphnia magna* (using prey size-class C, as in the present study), by the last six nympha1 instars of a second species of damselfly, *Lestes sponsa* Hans., showed that $a$ increases and $T_h$ decreases with increased predator size exactly as in the present study.
Further data of this nature may be obtained by recalculating information on predation of *Podisus modestus* Dallas (a pentatomid bug) on larvae of the sawfly *Neodiprion swainei* Middleton given by Tostowaryk (1972, p. 63) and information on a spider, *Linyphia triangularis* Clerck, feeding on *Drosophila melanogaster* Meig. given by Turnbull (1962, Table 1). In the case of Turnbull’s data, it is possible to calculate $a$ and $T_h$ directly from the information given in his Table 1 for all instars of the predator. In the case of Tostowaryk’s data, a mixture of prey of different species, activities and sizes was employed and the only information of use in the present context is that for second instar larvae being preyed upon by three different predator instars (second, third and fourth). When the appropriate calculations are made for both these studies, the results are again similar with $a$ increasing and $T_h$ decreasing with increased predator size, although the exact shapes of the curves differ. A more detailed review of the shapes of $a$ and $T_h$ plots is given by Hassell *et al.* (1976).

It is important to realise that the values of $a$ and $T_h$ calculated from the functional response curves of Fig. 2 represent average values of the parameters over the 24-h period. Because the predators were starved beforehand, it is probable that hunger levels decreased throughout the experiment, but at different rates for different prey densities. If the experiment had been started with satiated predators, the hunger level may have changed not only at different rates, but even in different directions at each of the prey densities employed. These changes in hunger level during the experiment are known to affect certain of the sub-components of $a$ and $T_h$ in *Ischnura*, exactly as in Holling’s mantids (Holling 1966). Thus it is known, for example, that the reactive distance of *Ischnura* at high hunger levels increases, because starved animals are prepared to leave their fishing sites and actually stalk prey. It is also known that the ‘digestive pause’ (per prey item) following each successful attack is certainly not constant but increases supraproportionally as the number of prey consumed gets higher.

The fact that the values calculated for $a$ and $T_h$ are therefore ‘average’ values probably explains why the random predator equation predicts, in some instances, slightly lower numbers eaten than observed at low densities and a higher number at high densities.

Further work is in progress to explore more fully the effects of hunger, prey encounter-rates and so on, on the detailed changes in the functional response of *Ischnura* during the course of one 24-h period. However, the data obtained in the present paper suggest that much progress can be made in this field by considering the average values of $a$ and $T_h$ with particular predator and prey size-classes.

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SUMMARY

(1) The functional responses of five instars of *Ischnura elegans* feeding on five arbitrary size-classes of *Daphnia magna* were obtained.

(2) The two basic components of predator–prey models, the attack coefficient, $a$, and
the handling time, $T_h$, were estimated from the data using the random predator equation of Rogers (1972).

(3) Two ways in which the parameter estimates from the random predator equation may be unrealistic are discussed; they are the use of too many points on the plateau of a type 2 functional response curve in estimating $a$ and $T_h$ and the use of data points in which over-exploitation had occurred.

(4) The variation of $a$ and $T_h$ with prey and predator size is described. Both increase nearly monotonically, $a$ with increased predator size and decreased prey size, $T_h$ with decreased predator size and increased prey size. The possible effects of prey and predator size on the sub-components of $a$ and $T_h$ are discussed.

(5) The consequences of the fact that the $a$ and $T_h$ values used are averages over the time the experiment was run are considered.

REFERENCES


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