Sources of Variation in Predation Rates at High Prey Densities: an Analytic Model and a Mite Example

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ABSTRACT

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Some mathematical techniques for the analysis of satiation-based predation models previously developed by the first author are applied in the present paper to a model by the second author for predation by the predatory mite *Metaseiulus occidentalis* (Nesbitt). It turns out that for this predator the predation rate should keep increasing at high prey densities as the square root of the prey density, x. This particular shape of the functional response is shown to occur if and only if the upper satiation threshold for prey capture coincides with the maximum gut capacity. The functional response predicted by the model, moreover, is in fair quantitative agreement with predation rates observed by the third author in artificial arenas.

A further analysis of the model shows that the variance of the catch should also increase as the square root of x. This prediction is consistent in a qualitative manner with the continued increase in the variance of the catch. However, quantitatively, the observed variances are even too large to be compatible with any model in which the feeding rate is subject to regulation by a negative feedback. Therefore, the difference between predicted and observed variances is hypothesized to be due to nonhomogeneities in the experimental material. The inferred additional variance component proportional to x accords fairly well with the trend apparent in the data.

THE CASE FOR PHYSIOLOGICALLY STRUCTURED POPULATION MODELS

This paper deals with some mathematical principles explaining the peculiarities of the prey-catching behaviour of the predatory mite *Metaseiulus occidentalis* (Nesbitt) at high prey densities. However, before going into the specifics it seems expedient to remark on the larger context, as the methods

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used were developed as part of a larger research program dealing with the modelling of 'physiologically structured' populations (see Metz and Diekmann, 1986).

Temporal and spatial scales and the functional response

The old goal of population dynamics is dead. There just is not one, or even a few, mechanisms explaining all population behaviour. Rather, there is a great variety of possible mechanisms and a corresponding, though lesser, variety of population behaviours. This does not mean that population dynamics is dead as well — only that we should aim at the more modest goal of trying to understand the relation between particular biological mechanisms and their population-dynamical expression. This calls for a judicious interplay between experimentation and modelling. The ultimate aim is to arrive at a sufficiently well-organized collection of procedures and results so that we may, with some confidence, approach any practical situation that asks for our attention.

One possible organizing principle is the hierarchy of temporal and spatial scales. Some processes are fast and others are slow; some are very localized spatially, whereas others can only be studied over large spatial scales. The important point is that this difference in scales, if sufficient, allows us to study processes in partial isolation. We may, for example, study the local effects of predation within patches replete with prey without, for the time being, paying attention to the movement of a predator between such patches. On a large time-scale and a correspondingly larger spatial scale we may study predator movement among prey patches, assuming the outcome of the local, within-patch, processes as a given quantity. Whether the scales can indeed be separated in the indicated manner depends, of course, on the system under consideration. As a rule of thumb we may say that two characteristic times should differ at least by an order of magnitude (a factor of ten) to allow a separate treatment of the corresponding processes.

It is against this background that we should see the concept of functional response: it allows the separation of the relatively short behavioural time-scales from the longer population-dynamical ones. This does not mean that from the knowledge of the functional response we can go immediately to the full population dynamics. It may well be that the population dynamics itself also takes place on more than one scale, such as local predator-prey interactions, where the functional response plays its role, and a more global dynamics of patches in various stages of prey and predator occupation (cf. Diekmann et al., 1988, this volume).

The above considerations also imply that it does not suffice just to measure the functional response; its precise quantitative form may well depend on many local circumstances. Rather, we would like to model the predation process in such a way that we get some understanding of how the number of prey caught depends on the special features of the system. The functional response then is

one of a number of useful intermediaries in translating the effect of various modifications of the environment into their population-dynamical consequences. Its calculation from first principles, followed by a confrontation with the measurements, provides a test case for our understanding at the behavioural level. It also provides a stepping-stone towards the next level in the hierarchy of time and space-scales.

From individual processes to population equation

Mite predatory behaviour is made up of a large number of components (cf. Holling, 1966). The details of walking behaviour and sensory probing govern encounter rates; the reactions of predator and prey upon encounter determine whether that encounter turns out to be successful, whence a prey is caught it may be eaten in full or be partially discarded, etc. All this is covered in detail by Sabelis (1981, 1986). In the present paper we concentrate on just one aspect, the role of the state of the predator.

The mechanisms of population change lie in the reactions of individuals to their environments. However, these reactions may vastly differ between different individuals. For example, a per-capita feeding rate of a population usually is made up of feeding rates of individuals, some of which may be highly satiated while others may be very hungry. If we wish for a mechanistic understanding of feeding rates we cannot just lump all those individuals together. The only problem is how exactly we should make our distinctions. It is here that the concept of state comes to the fore.

Loosely speaking, the state of a system is a collection of variables such that the behaviour of the system at time t is fully determined (in a stochastic sense) by the state-cum-environment at time t, and that the state at time $t + \tau$ is fully determined by the state at time t plus the intervening environmental history. On a longer population-dynamic time-scale the behaviour of an individual may consist, for example, of giving birth or dying. In our present more modest context, behaviour will be considered to be the catching and eating of prey.

If all individuals in a population experience, on the average, the same environment (this presupposes some sort of homogeneous mixing), and if we are interested in overall population properties such as total feeding rate, then the state of a population corresponds to a frequency distribution over the space of individual states. This frequency distribution moves due to the state changes of individuals, and it may also decrease due to deaths and increase due to births.

The tenet of the 'physiologically structured' population methodology is that we may write equations describing the changes of the population state on an infinitesimal basis, and subsequently extract from these equations information on population behaviour.

From this point of view the state concept forms a second organizing principle, next to that of the time-scales.

A SATIATION-BASED PREDATION MODEL

Biological ingredients

Sabelis (1981) and Fransz (1974) found that, in *M. occidentalis*, most char-
acteristics of predatory behaviour such as walking speed and pattern and prob-
ing behaviour are independent of feeding history. Only the rate at which prey
were actually taken once encountered, the so-called 'success ratio', and to a
lesser extent the handling time, did vary. Moreover, the whole feeding history
could be summarized in just one state variable, satiation, which can provision-
ally be equated to the amount of food in the gut, and which could be measured
by weighing the animals.

That indeed satiation is just a one-dimensional variable is not self-evident.
In fact, Johnson et al. (1975) describe what essentially is an example of a two-
dimensional satiation state in damselfly larvae, including as components the
contents of the fore and midgut, the former regulating the eating response,
while both together determine the capture rate. A non-physiological, input-
output based approach to the satiation concept can be found in Doucet and
van Straalen (1980), in which is also discussed the problem of testing whether
satiation really can be represented one-dimensionally.

There is also some very circumstantial evidence that *M. occidentalis* may
have a higher-dimensional satiation state. Overall, its success ratio is a de-
creasing function of gut content, except at very low gut contents where the
success ratio appears to drop again (cf. Fig. 1). Looked at from an adaptation-
ist point of view, this seems self-defeating. The explanation that by so doing
the animal conserves energy when energy sources are scarce cannot hold water
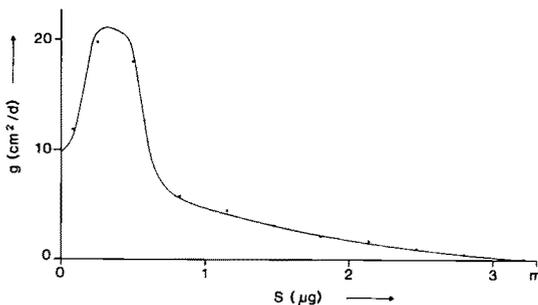as it does not appear to economize on moving; it only is more prone to overlook

Fig. 1. Rate constant of prey capture as a function of satiation for the predatory mite *Metaseiulus occidentalis* feeding on eggs of the spider mite *Tetranychus urticae* in an arena with a web (based on data in Sabelis, 1981). The continuous curve is given by the formula $g(s) = KR(s)$, with K, the rate constant of encounter, set equal to 21.05 cm^2/day, and with the success ratios $R(s) = 0.1(1-s/m) + 0.32(1-s/m)^2 + 0.65(1 + 10^6 (s/m - 0.11)^5)^{-1} + 1.16402564 * 10^{-6}$; $m = 3.3$ μg, the maxi-
mum gut capacity.

the prey it encounters. A possible mechanistic explanation is that very low gut contents occur only after periods of prolonged fasting, which also lead to a general energetic deficit. The low body energy levels alter the animal's behavioural mode. It may, for example, stop investing in eggs and start to search for richer pastures. If this explanation is correct one large meal would fill the gut but would not immediately cure the apparent lack of appetite. In that case, we would have to supplement our state description with some measure of the animal's overall energetic condition.

A second class of potential state variables derives from the handling of captured prey. If we wish to take account of handling times in a model which also includes satiation differences we cannot, as is often assumed, just diminish the rate of successful encounter by a Holling disk equation type correction factor. The correct mathematical representation of our mental image of the handling of prey is through the introduction of one or more state variables indicating the state of dispatch of the prey currently being handled. The end results are fairly complicated formulas, the details of which may be found in Metz and van Batenburg (1985a) and also in Metz and Diekmann (1986, part A, chapter III). However, in the case of the predatory mites considered by Sabelis (1981, 1986), handling times are sufficiently short that they can safely be neglected. This can easily be seen by the following argument. For *M. occidentalis* the highest experimentally observed capture rate of eggs of *Tetranychus urticae* is 18 per 24 h. The handling time at high satiation is 4 min. Therefore, even in the most extreme case the animal uses but 5% of its time budget in handling prey. At low satiation levels, handling times may be slightly longer, but this is more than offset by the lower prey-catching rates which lie at the root of these low satiation levels.

Summarizing, we may say that the state process underlying prey capture by *M. occidentalis* appears to be one-dimensional. The rate of successful encounter is a function of satiation and is proportional to prey density. Between captures, satiation decreases. Once a prey is caught, satiation makes an instantaneous upward jump. To complete the picture we note that satiation appears to decrease at a rate which is proportional to its current value, and that the jumps appear to depend only on the prey size, except when this would bring satiation above the maximum gut capacity, in which case the animal just fills its gut to the brim and then discards its prey.

Below we shall concentrate on a female *M. occidentalis* preying on eggs of *T. urticae*. Figure 1 depicts its rate constant of successful encounter in the presence of a web, i.e. the area it searches per unit of time × its success ratio (Sabelis, 1981). This predator has the special property that its rate constant of successful encounter appears to stay non-zero for all admissable values of satiation, and to go smoothly to zero for satiation nearing the maximal value. As we shall show, it is precisely this property that is responsible for some curious aspects of its functional response.

The population equation

We start with introducing some notation. Satiation will be denoted as s, which ranges from 0 to m, the maximum gut capacity. The rate of decrease of satiation between catches will be denoted as f, where $f(s) = -as$ (a is the rate constant of digestion), and the size of a full upward jump of s by w. The rate constant of prey capture will be denoted as g, the smallest value of s for which $g(s) = 0$, the capture threshold as c, and prey density as x. Finally, we shall denote the population state as p, where $p(t,s)ds$ denotes the number of predators (per unit area, but we shall refrain from repeating this) having satiations between s and $s + ds$ at time t.

With this notation the population equation (see Metz and Diekmann, 1986, part A, chapter I for the details of derivation) becomes:

$$\frac{\partial p(t,s)}{\partial t} = -\frac{\partial f(s)p(t,s)}{\partial s} - x(t)g(s)p(t,s) + x(t)g(s-w)p(t,s-w) \tag{1a}$$

The easiest way to visualize what the components of this equation mean is to think of the population as a heap of sand on a conveyor belt (see Fig. 2). This conveyor belt moves to the left due to the decrease of satiation by digestion. This movement is represented by the first term on the right-hand side. To derive this term we just concentrate on a fixed length-element along the satiation axis and consider the changes in the number of predators in that length
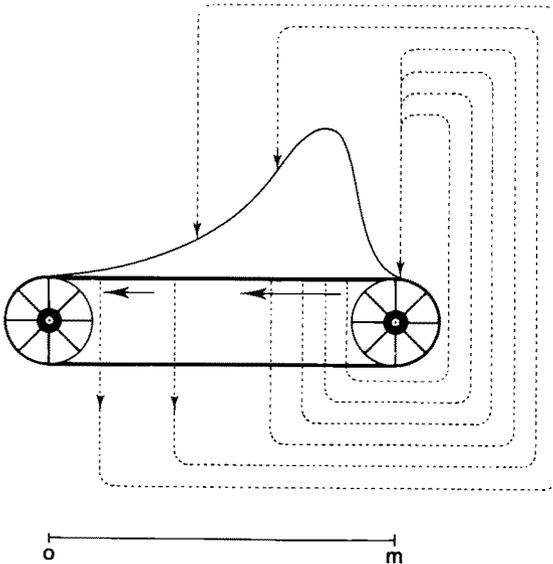

Fig. 2. Conveyor belt representation of a structured population model.

element due to outflow to the left and inflow from the right. The second term corresponds to removal of predators locally on the conveyor belt when they catch a prey, and the third term represents the local arrival of predators which have just eaten a prey item.

Equation (1a) still has to be completed with a side condition accounting for all the predators that do not complete the eating of their prey, due to their satiation reaching its maximum value. All these predators end their jump at position m on the conveyor belt. Equating $dt \times$ the arrival rate at m to the number of predators which are stacked on the length element of size $-f(m)dt$ which rolls past m during that time gives:

$$-f(m)p(t,m) = \int_{m-w} x(t)g(s)p(t,s)ds \qquad (1b)$$

Given the solution to (1) we can calculate the number of prey caught per unit of time as:

$$H(t) = \int_0^c x(t)g(s)p(t,s)ds \qquad (2)$$

If we wish to calculate the catch per predator we should divide through by the total number of predators. However, we specifically neglected any changes in predator number through births and deaths in phrasing our model. In other words, (1) conserves total predator number. Therefore we may just as well normalize right from the start and set

$$\int_0^m p(t,s)ds = 1 \qquad (3)$$

From now on we shall keep to this convention.

Formula (3) also points to another possible interpretation of our equations. If x would be a constant or, rather, a given function of time not influenced by the behaviour of a given predator, then convention (3) allows us to interpret $p(t,s)ds$ as the probability that that predator has satiation between s and $s+ds$, and H as the average rate at which it captures prey. We shall return to this interpretation (p. 198) when we calculate the variance of the catch.

THE FUNCTIONAL RESPONSE

Calculation procedure

As stated at the outset, the whole idea of a functional response is predicated upon a difference between the time-scales of behaviour and population dynam-

ics. As, generally, predators are much scarcer than their prey the capture of one prey item may mean much to a predator, but it corresponds to only a very slight relative decrease of the prey population. It is this difference in relative contributions which sets the differences in time-scales.

Guided by the difference in time-scales we set the prey density to a constant value and consider the steady population state $\hat{p}(.)$, which can be calculated from

$$0 = -\frac{df(s)\hat{p}(s)}{ds} - xg(s)\hat{p}(s) + xg(s-w)\hat{p}(s-w) \tag{4a}$$

together with the normalization condition

$$1 = \int_0^m \hat{p}(s)ds \tag{4b}$$

(In Metz and van Batenburg (1985b) it is shown that $\hat{p}$ defined this way automatically satisfies (2b); the exponential convergence of $p(t,.)$ to $\hat{p}$ for constant x was proven by Heijmans (1984)). Given the solution to (4) the functional response can be calculated from

$$F(x) = \int_0^c xg(s)\hat{p}(s)ds \tag{5}$$

(Note that $\hat{p}$ also depends on x.)

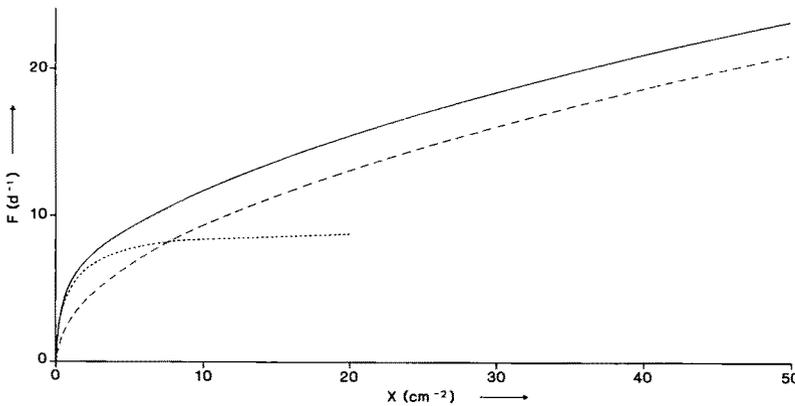The best way to integrate (4a) numerically is to use so-called 'upwind dif-

Fig. 3. The functional response calculated from Formulas (4) and (5) for $f(s) = -as$, $a = 2.93$ day^{-1}, $w = 1\ \mu g$, and g as in Fig. 1 except that K was set equal to 46.55 cm^2/day to make the change from a webbed to an unwebbed arena, (———), together with the results from approximation Formulas (8) (.......), and (10) (- - - -).

ferencing' on a fixed grid of width $\Delta = w/k$, k some integer, replacing $-\mathrm{d}f(s)\hat{p}(s)/\mathrm{d}s = \mathrm{d}(as\hat{p}(s)/\mathrm{d}s$ by $(-as_i\hat{p}(s_i) + as_{i+1}\hat{p}(s_{i+1}))/\Delta$, for $s_i = i\Delta$, and using some arbitrary value of $\hat{p}(\Delta)$ to start the integration. (It may be necessary to renormalize a few times during the integration to prevent overflow.) After the integration is performed the result is normalized to conform to (4b). Finally, F is calculated by the numerical equivalent of (5). (This procedure is, barring some minor details, equivalent to the procedure for calculating F based on the queueing model expounded in Sabelis (1981, 1986).)

The result of calculating F in such a manner for *M. occidentalis* feeding on eggs of *T. urticae* in an unwebbed arena is displayed in Fig. 3, together with the results from some approximations to be discussed in the following subsections.

Approximation formulas

At very low prey densities satiation hovers, most of the time, very near to zero; therefore, for very small x

$$F(x) = g(0)x \tag{6}$$

Figure 3 shows that F is too curved over the range of x values of practical interest for (6) to be of any use. Clearly, the functional response can only be understood by paying careful attention to the changes in satiation.

Below we shall argue that in *M. occidentalis* the shape of the functional response is dominated by the, to a large extent, wasteful killing at high satiation levels. As part of that argument we shall first consider yet another poor approximation: the fact that this approximation does poorly, and that the final approximation which we shall consider does so well — contrary to our experience for some other animals for which such wasteful killing does not occur or occurs only rarely — precisely makes our point.

When x is constant, a predator eating numerous small prey experiences only relatively minor satiation fluctuations due to the operation of the law of large numbers. Taking this line of argument to its extreme we may consider a predator whose satiation process satisfies

$$\frac{\mathrm{d}s}{\mathrm{d}t} = -f(s) + xwg(s) \tag{7}$$

The functional response is just the prey capture rate for s at its steady-state value:

$$F(x) = xg(\hat{s}) \tag{8a}$$

with $\hat{s}$ defined by

$$xwg(\hat{s}) = f(\hat{s}) \tag{8b}$$

The result of this calculation for the *Metaseiulus–Tetranychus* system is also

indicated in Fig. 3. (Note that Fig. 4 in Metz and van Batenburg (1985b) which purports to show the good quality of approximation (8), refers to a thought experiment in which there was assumed to be no restriction on the gut capacity.)

Metz and van Batenburg (1985b) also consider a correction term to (8) taking account of the curvature of g. To that end they fitted the *Metaseiulus* success-ratio data with a much smoother curve than the one shown in Fig. 1. For such smooth g curves their approximation performs almost unbelievably well. For the g curve used in the present paper the correction term gives next to no improvement compared to (8).

The final approximation which we shall consider assumes x to be sufficiently large to make it unlikely that the satiation ever comes more than w below the maximum gut capacity m. In that case every capture results in satiation being set equal to m, making it relatively easy to calculate the mean time between captures. In the stationary state the average capture rate just equals (mean time between captures)$^{-1}$. If we also make some further approximations along the lines laid out in Metz and van Batenburg (1985a) appendix 3, and set

$$b = -g'(c)$$

for convenience of notation, we obtain

$$F(x) = a\left[\ln(m/c) + \sqrt{\frac{a\pi}{2bcx}} \right] \tag{9}$$

Equation (9) implies that usually the functional response goes to an asymptote which equals $a/\ln(m/c)$. Only when, as appears to be the case in *M. occidentalis*, the capture threshold and the maximum gut capacity coincide $(c=m)$, the functional response keeps increasing as

$$F(x) = \sqrt{\frac{2abcx}{\pi}} \tag{10}$$

Approximation (10) is also depicted in Fig. 3; it can be seen that it performs not too badly.

As (10) is essentially based on the reset of s to m upon a prey capture, which corresponds to a killing that is at least partially wasteful, the good performance of (10) implies that this wasteful killing dominates the shape of the functional response.

Confrontation with the data

Figure 4 shows a set of measurements by Kuchlein (unpublished data) of predation rates by *M. occidentalis* females preying on eggs of *T. urticae* placed

on a fresh leaf disc (see the Appendix for the details of the experimental pro-
cedure), together with the functional response already depicted in Fig. 3. The
fit, at least for high prey densities, is surprisingly good, taking into account
that all parameters were estimated in separate experiments. The direct mea-
surements of the capture rate therefore confirm the coincidence of the capture
threshold and the maximum gut capacity suggested by the data points in Fig.
1.

We should make one cautionary remark, however. As is shown by Formula
(10), the catching rate at high prey density is rather sensitive to b, the slope
of g at m. It is particularly difficult to estimate b with some precision. Three
curves fitting the data points in Fig. 1 about equally well in an overall sense
turned out to have b values which differed by as much as 30%. The curve which
appears in Fig. 1 was derived as a sort of middle-of-the-road compromise be-
tween a number of least-squares fits with formulas of the form
$u(m-s)+v(m-s)^2$ to the last 3, 4, etc. data points in combination with an
ad-hoc formula to take care of the hump at low satiations. This way we tried
to do as much right as possible to the importance of the behaviour of g near m.

A final point worth noticing is the relatively poor fit of the calculated func-
tional response at low values of x. The data points lie consistently under the
predicted curve. (n.b. The dip in g at low satiations also leads to an S-shaped
appearance of the calculated functional response, but this effect is only notice-
able for extremely low values of x, and cannot even be seen on the scale of Figs.
3 and 4.) The data on the success ratio underlying the function g which we
used in our calculations were all collected in the presence of a web. The absence
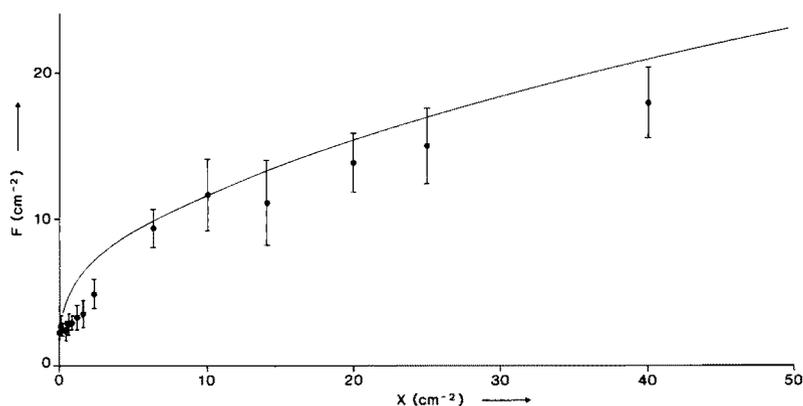

Fig. 4. Experimentally determined prey capture rates for female *M. occidentalis* feeding on *T.
urticae* eggs in an unwebbed arena. Data from Kuchlein (unpublished). The error bars correspond
to two standard deviations. The continuous line is the theoretical functional response from Fig.
3.

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of a web in Kuchlein's experiment (data not presented) was only accounted for by changing the encounter rate to a new value, estimated from observations of the walking behaviour on clean leaf discs. Apparently, being on an otherwise clean leaf disc does not disturb the predator when the going is sufficiently good. But the discrepancy between observed and predicted capture rates at low prey density points to some behavioural change. Our guess is that the predators were trying to leave the experimental arena. Having a really low satiation is indicative of being in a prey patch of poor quality. Combined with the absence of any indirect indicators of prey presence, this should make any right-minded predator decide to try its luck elsewhere.

THE VARIANCE OF THE CATCH

Calculation procedure

As indicated earlier (p. 193), the assumption of constant x allows us to interpret our model as a stochastic process pertaining to one individual. The phrasing in the previous section also often alluded to this fact. Yet all the results discussed in that section are meaningful and can be derived in the context of a purely deterministic model dealing with an (infinitely) large population of predators.

For the quantity which we shall discuss in this section, the variance of the total catch, the stochastic interpretation is indispensable. This also means that we have to introduce some new notation. We shall use N to denote the total catch by a single predator and S will denote its satiation. Both S and N are random functions of time. E will denote the expectation operator (i.e. taking averages) and VAR and COV will, as usual, refer to variances and covariances. Below we shall quote only the results, and refrain from giving even an heuristic derivation, as this would take us too far afield (see Metz and van Batenburg (1985b) for the technical details).

After a short initial phase, the precise nature of which depends on the way the experiment was started, the variance of the catch starts to grow linearly with time at a rate v which can be calculated from

$$v(x) = x(2\text{cov}(N,g(S)) + \text{E}g(S))$$ (11)

In this expression

$$x\text{E}g(S) = F(x)$$ (12)

And $\text{cov}(N,g(S))$ can be calculated from

$$\text{cov}(N,g(S)) = \int_0^{\zeta} g(s)\hat{z}(s)\,\mathrm{d}s$$ (13)
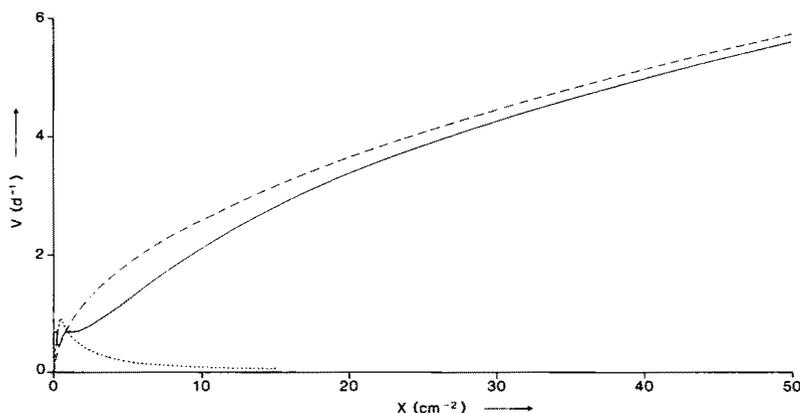
where $\hat{z}$ satisfies

Fig. 5. The variance of one day's catch calculated from Formulas (11) to (14), for the same parameter values as in Fig. 3 (————), together with the results from approximation Formulas (16) (.......), and (18) (- - - -).

$$0 = -\frac{\mathrm{d}f(s)\hat{z}(s)}{\mathrm{d}s} - xg(s)\hat{z}(s) + xg(s-w)\hat{z}(s-w)$$
$$+ xg(s-w)\hat{p}(s-w) - F(x)\hat{p}(s)$$

$$0 = \int_0^m \hat{z}(s)\,\mathrm{d}s \tag{14}$$

Equation (14) can be solved numerically in exactly the same manner as (4), the only difference being that instead of normalizing we have to add a multiple of $\hat{p}$ in order to satisfy the integral condition.

The result of calculating v for the *Metaseiulus* example is displayed in Fig. 5 together with the result of some approximation formulas to be discussed below. Comparison with Fig. 3 shows that the variance is always well below the mean, as is to be expected for a point process in which the occurrence of a point event lowers the rate at which subsequent point events occur.

Approximation formulas

This subsection follows exactly the same pattern as its earlier-given counterpart (p. 195). To avoid needless repetition we only give the details of an argument where it differs from the corresponding argument in that subsection.

The argument from p. 195 can be extended to show that, at very low prey densities, the catch follows approximately a Poisson process, implying that for sufficiently small x

$$v(x) = F(x) = g(0)x \tag{15}$$

When taking the limit for infinitely many, infinitely small prey which gave us Formula (8), we lose any information about the variance. To recover this information we can consider a so-called diffusion approximation around the deterministic limit. The resulting approximation for v is

$$v(x) = xg(\hat{s}) \left(\frac{f'(\hat{s})}{f'(\hat{s}) + xwg(\hat{s})} \right)^2 \tag{16}$$

The approximation for large x corresponding to Formula (9) can be found by using the fact that the forced passing through m makes the catch process into a so-called renewal process. Using the formulas in Cox (1962, p. 40) together with some further approximations we find

$$v(x) = \frac{2(1 - \pi/4)a^2}{bcx \left(\ln(m/c) + \sqrt{\dfrac{a\pi}{2bcx}} \right)^3} \tag{17}$$

(n.b. The factor $(1 - \pi/4)$ is erroneously wanting in Formulas (3.5), (6.4), and (A3.2) of Metz and van Batenburg (1985b)). Our Formula (17) implies that, for large prey densities, the variance off the catch decreases to zero, except when the capture threshold and the maximum gut capacity coincide. In that case v keeps increasing, as

$$v(x) = \frac{4(1 - \pi/4)}{\pi} \left(\frac{2abcx}{\pi} \right)^{\frac{1}{2}} \tag{18}$$

Both Approximations (16) and (18) are displayed in Fig. 5, showing that, according to our model for *M. occidentalis*, also the variance of the catch is dominated by the wasteful killing resulting from the coincidence of capture threshold and maximum gut capacity.

Confrontation with the data

Figure 6 shows the variances of catches in Kuchlein's data which also formed the basis of Fig. 4. Clearly, the observed variances are far above the calculated ones. In fact they are well above the Poisson variances, showing that no process in which there is a negative feedback from the capturing of a prey to the capture rate can explain the observations. The only possible explanation seems to be some sort of nonhomogeneity among the many replicates. Such nonhomogeneities only slightly affect the means, whereas the effect on the variance is considerable.
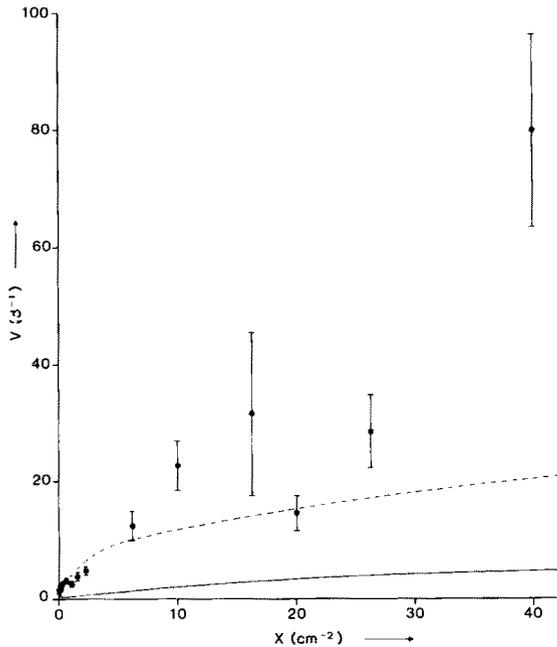
Fig. 6. Observed daily variances of the catch, from the same data set as in Figure 4. The error bars correspond to one standard deviation. The continuous line is the theoretical daily variance from Fig. 5, the broken line corresponds to the daily variance of a Poisson process with the same mean.

Interestingly enough, it is not necessary to leave it at this seemingly defeatist statement, thanks to the simple form of Formula (10). Let

$$Q := \left(\frac{2abc}{\pi} \right)^{\frac{1}{2}} \tag{19}$$

Nonhomogeneity among the replicates would mean that Q is a random variable. Let, as before, the catch be denoted as N; then, for sufficiently large x, the conditional mean and variance of the catch given Q are

$$\mathrm{E}N \mid Q = Q\, x^{\frac{1}{2}} \quad \text{and} \quad \mathrm{VAR}(N \mid Q) = \frac{4(1-\pi/4)}{\pi}\, Q\, x^{\frac{1}{2}} \tag{20}$$

Taking the expectation over Q we get

$$\mathrm{E}N = \mathrm{E}\, \mathrm{E}N \mid Q = \mathrm{E}Q\, x^{\frac{1}{2}} \tag{21}$$

which is the same formula as (10), provided we substitute an appropriate estimate for $\mathrm{E}Q$. However, for the variance we find

$$\text{VAR}(N) = \text{E VAR}(N \,|\, Q) + \text{VAR}(EN \,|\, Q) \tag{22}$$
$$= \frac{4(1-\pi/4)}{\pi} \, EQ \, x^{\frac{1}{2}} + \text{VAR}(Q)x$$

i.e. in addition to the term corresponding to (18) there has appeared a linear term $\text{VAR}(Q)\,x$. (This feature is again directly due to the coincidence of capture threshold and maximum gut capacity. If m is larger than c then the variance component due to the stochastic nature of the catch process goes to zero and any variance component due to nonhomogeneities in the experimental material becomes constant for large x.)

Judging from the fit of F we had apparently hit upon a fairly good estimate of EQ. Therefore we can test whether relation (22) indeed holds good by plotting the difference of the observed and predicted variances for the larger x values against x. Figure 7 shows the result. It is not particularly good, but neither is it particularly bad, taking into account the rather crude assumption that the replicates for all series of experiments were nonhomogeneous in exactly the same manner.

As final check we estimated $\text{VAR}(Q)$ by a weighted least-square procedure,
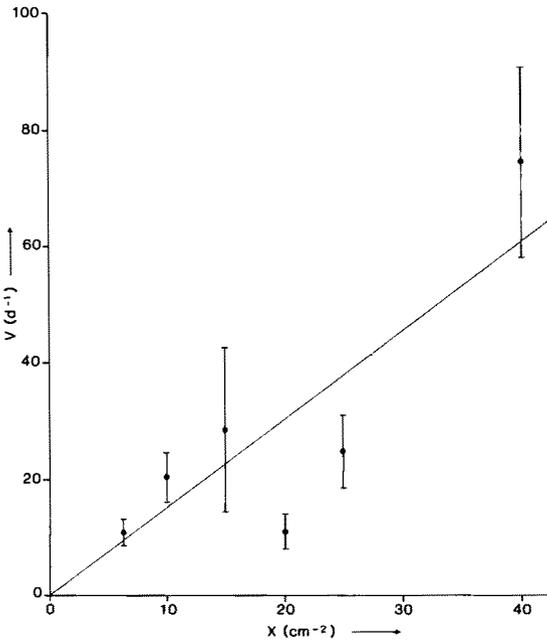

Fig. 7. The observed daily variance for the six highest prey densities from Fig. 6 after subtraction of the variance component inherent to the predation process itself.

taking account of the pattern in the estimated error bars. The result is that, to explain the data, we have to assume a coefficient of variation of Q of ca 40%.

Sabelis (1981, pp. 154–156, tables 58 and 59) reports variance mean ratios of the catch in the presence of a web of ca. 0.5. These values are about twice as large as those predicted by the model, which suggests that in Sabelis' experiments there also was some parameter variation. Yet these values are considerably lower than the values of up to 3 seen in Kuchlein's (unpublished) data. Possible explanations for this differences are:

(i) the leaf discs in Kuchlein's experiments lacked the usual arrestment stimuli produced by the prey, such as a web, faeces, etc. We have already argued that this may induce the predator to try leaving the experimental arena. Any variance in this escape reaction adds to the variance in Q;

(ii) the experiments were carried out by a number of different persons;

(iii) the replicates were obtained over a $1\frac{1}{2}$-year period, which corresponds to about 40 generations of both predator and prey, so that there may be well have been genetic changes in the stock cultures.

Considering these possible additional sources of variation we do not feel a variability of 40% in Q to be unexpectedly large.

CONCLUDING REMARKS

Our modelling of the predation behaviour of *M. occidentalis* has led to a number of insights. First, there is a relatively poor prediction of the functional response at low prey densities. This points to the presence of some behavioural components which we have not taken into consideration, such as the possible tendency to start emigrating when the going is poor. Secondly, we have found an interesting explicit formula which should approximate the functional response when prey densities are not too low. This formula may also be used direct for the fitting of experimental prey capture data. Finally, we have given an explanation for the curious behaviour of both the functional response and the variance of the catch at high prey densities in terms of the particular form of wasteful killing exercised by this predator. Those phenomena are by their very nature mathematical, but they are also intrinsic properties of the animal. The fact that at high prey densities the functional response keeps increasing as the square root of x makes it a new type, viz. without an upper limit, to be included in the commonly recognized range of types first introduced by Holling (1959).

comments on an earlier draft, and the participants of the symposium of the Population Dynamics of Spider Mites and Predatory Mites, Amsterdam, 5–11 July 1987, for sharpening our thinking about the usefulness of what at first was just an intellectually pleasing exercise.

APPENDIX: THE PREDATION EXPERIMENT

The following features of the experimental procedure are relevant here:

(1) The experimental arena consisted of a disc punched out of a leaf of a Lima bean, floating upside down on water-soaked cotton wool in a Petri dish; the water barrier surrounding the disc prevented the mites from escaping. The area of the leaf disc was equal to 5 cm^2 except at the two lowest prey densities in which areas of 20 cm^2 and 50 cm^2 were used.

(2) Eggs of *T. urticae* were sampled from infested bean leaves and transferred with the aid of a fine brush to the leaf disc. In this way, prey densities of 1 egg per 50 cm^2, 1 egg per 20 cm^2, and 1, 2, 3, 4, 6, 8, 12, 32, 50, 75, 100, 125, and 200 eggs per 5 cm^2 were obtained. To facilitate counting the prey, eggs were positioned on the leaf disc in groups of 5 when their total number was equal to or exceeded 50.

(3) Young adult females of *M. occidentalis* (2–5 days old since the final moult) were placed on the disc at 16:00 h on the day before the actual predation experiment.

(4) Prey eggs that died due to predation or other causes were replaced the next morning at 08:30 h, and then at half-hour intervals until 17:30 h. Only the last 6 h of the 9-h experiment were used, to ensure steady-state conditions.

(5) To check whether prey mortality was due to predation or to other causes (such as the manipulation during egg transfer to the leaf disc) some control experiments without predators were carried out in a series parallel to the predation experiment.

(6) The total egg mortality over the last 6 h of the predation experiment was corrected for the mortality measured in the control experiments. To reduce the fluctuations in the measured mortality in the control experiments a weighted mean with weights 1/8, 1/4, 1/4, 1/4, 1/8 over the nearest density classes was used. For the next-to-highest and highest densities we used the weights 1/7, 2/7, 2/7, 2/7, and 1/3, 1/3, 1/3. For the two lowest densities, comparable weights were used.

(7) The numbers of replicates of the experiments at each prey-egg density level were, in order of increasing prey density: 240, 70, 200, 100, 103, 200, 75, 75, 75, 150, 60, 60, 60, 60, 203.

(8) The experiments were done at a temperature of 25–26°C and a relative humidity of 60–80%.

(9) The experiments were carried out between June 1977 and December

1978 by a changing combination of three, out of four, technical assistants, with delays between subsequent experiments of up to 7 months.

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