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HOLLING's "HUNGRY MANTID" MODEL FOR THE INVERTEBRATE
FUNCTIONAL RESPONSE CONSIDERED AS A MARKOV PROCESS.
PART 0: A SURVEY OF THE MAIN IDEAS AND RESULTS

Preprint

Holling's 'Hungry mantid' model for the invertebrate functional response considered as a Markov process. Part 0: A survey of the main ideas and results *)

by

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ABSTRACT

In this paper we present an analytical approach to Holling's simulation model for mantid predatory behaviour. Starting from a general representation as a Markov process, with a rather complicated state space, we introduce a series of approximations, suggested by the relative values of the various parameters. As an intermediate step we derive a set of coupled partial integro-differential equations from which we can calculate the functional response and the variance of the total catch. We end with simple explicit expressions for these same quantities.

KEY WORDS & PHRASES: *Functional response, foraging behaviour, continuous and jump Markov process, counting process, first order partial integro-differential equations*

1. Introduction

In his marvelous 1966 paper 'On the functional response of invertebrate predators to prey density' Holling describes the results of a beautiful set of experiments on the predatory behaviour of the mantid *Hierodula crassa* together with a rather complicated simulation model in which all the experimental detail is combined into one overall picture. He also makes a case for simulation as opposed to analytical methods. This now is a bit of a challenge, and in this paper we shall try to convince you that analytical methods are somewhat more powerful than Holling seemed to be aware of.

There was also a less frivolous reason for us to embark upon the research summarized here. Holling's (1959) secretary or disk model for predation has instigated a spate of applications, experimental as well as theoretical, which is still in full flow today. This is much less the case for his hungry mantid model, even if for predation (as opposed to insect parasitism) this model probably is much closer to biological reality. The reason, no doubt, is its complexity. By the judicious use of analytical methods we can break down this complexity step by step to arrive at various simple end results. At what place we end depends on the relative orders of magnitude of the various parameters. For the original parameter values of Holling's mantid the end result turns out to be very simple indeed.

2. The general invertebrate predator

Figure 1 shows a representation of the prey catching process broken down into its main components according to Holling. The rectangular boxes correspond to the various directly observable activities of a generalized invertebrate predator, with between parentheses a reference to the particular form this activity takes in a preying mantid. The duration and/or success of each of these activities may be influenced by the predator's satiation (or, equivalently, hunger as used in Holling's original model formulation). Satiation itself increases during eating and decreases otherwise.
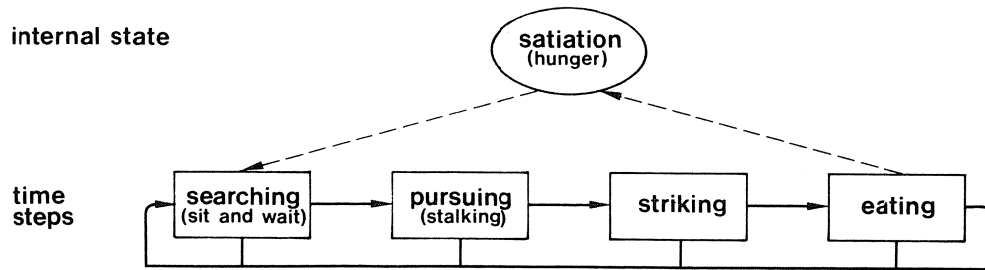
internal state

satiation
(hunger)

time
steps

searching
(sit and wait) → pursuing
(stalking) → striking → eating

Fig 1: Decomposition of the prey catching process according to Holling.

For his preying mantid Holling found that

(1) satiation decreases exponentially during periods of fasting (fig 2),

(2) the form of the search field remains constant, but

(3) the size decreases linearly with satiation, except that it can never become negative (fig 3),

(4) pursuit occurs at a constant speed, independent of satiation,

(5) the prey, flies in Holling's experiment, escaped during pursuit by flying away at a constant rate,

(6) strike success is constant, independent of satiation,

(7) speed of eating is constant independent of satiation, and so was the time needed to eat one fly, as fly size was kept rigorously constant.

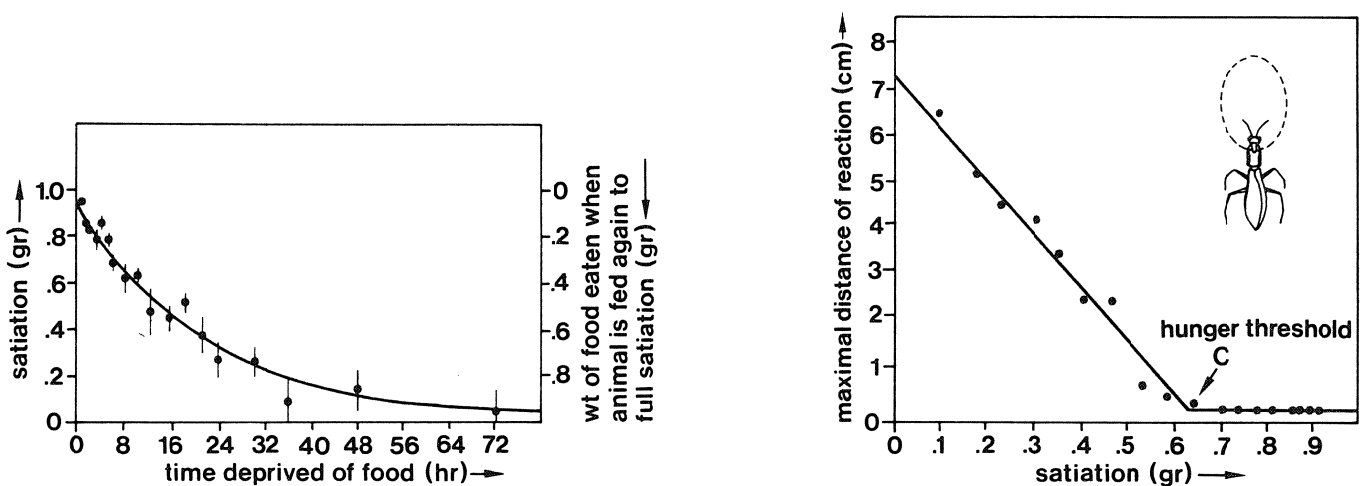

Fig 2: The decrease of satiation (≡ gut content) during a period of fasting in the mantid *Hierodula crassa*. Adapted from Holling (1966).

Fig 3: The size of the mantid's search field as a function of satiation. Adapted from Holling (1966).

To this list the following additional remarks have to be made:

(a) The fact that the search field is not circular was corrected for by Holling by the introduction of an equivalent circular field, based on the assumption that prey arrived from random directions. This is alright for the calculation of prey arrival rates, but not for the calculation of the probability of prey escaping during pursuit. For the sake of the exposition we shall not go into such minor refinements of Holling's original calculations, however.

(b) Exponential decrease of satiation by now seems to be an almost universal law for invertebrate predators (and many vertebrates as well). See e.g. Sabelis (1981) for a recent reference. In the following we shall therefore often make this special assumption as it considerably simplifies many of the calculations.

(c) In Holling's experiments prey speed depended on prey density. This will be accounted for here by referring to effective prey density, i.e. prey density multiplied by the speed reduction relative to the speed at zero density.

On the basis of those observations Holling devised a simulation model which successively generated the time intervals spent in the various activities. This simulation model was completely deterministic: Holling did not take into account the inherent random nature of the search process but immediately replaced any random quantity by its expectation, even if he had to deal with some nonlinear function of that same quantity later in his calculations. Still, the result of a fully stochastic simulation by the second author turned out to match pretty well that of Holling's deterministic one. The reason for this later proved to be that both the full stochastic process and Holling's deterministic version are very near to still another deterministic approximation to be derived below by analytic means. The quality of Holling's predictions therefore hinges on the special values of the parameters leading to the latter approximation. In the general case one will need a fully stochastic model formulation.

3. The behaviour of a predator represented as a Markov process

The main difference between Holling's secretary model and his mantid model is that in the former we have a unique Markovian searching state, during which the predator searches at a constant rate, whereas in the latter model, we have to deal with a continuum of searching states characterized by different values of the satiation. The Markov property of the searching activity in the secretary model leads us automatically to renewal theory as the source of appropriate tools (For a description of that tool box see Cox (1962). A discussion of the fundamental role played by the Markov property in the analysis of behaviour sequences can be found in Metz (1974) and Metz et al. (1983).). In the mantid's case we have no way to turn but to the general theory of Markov processes.

To represent our hungry mantid as a Markov process we have to specify a state space, i.e. we have to look for a set of characteristics the value of which at any one time contains all information about past events relevant to the prediction of the animal's future behaviour (A more detailed account of the construction of state spaces for animal behaviour can be found in Metz (1977, 1981)). One possible such state space is depicted in figure 4 together with some segments of possible trajectories representing various behaviour sequences that may occur after a prey has entered the predator's visual field.

Having arrived at a Markovian description we can write down a complicated set of partial integrodifferential equations for the probability distribution of the predator's state. These equations can not be solved explicitly, however, and for
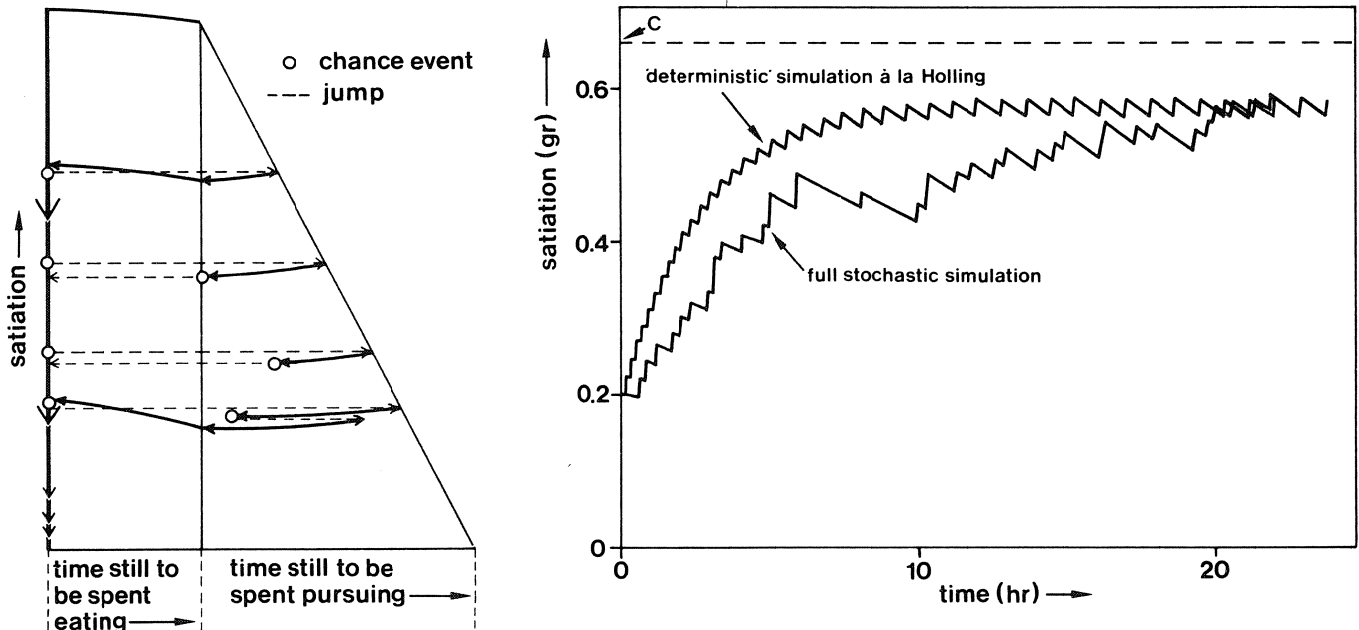

Fig 4: A Markovian state space for Holling's mantid. In the state space some segments of trajectories are depicted showing the various possible events that may happen after the sighting of a prey. The upper segment corresponds to a successful prey capturing sequence. In the second segment the strike is unsuccessful. In the third segment the prey escapes during pursuit, and the fourth segment corresponds to the very rare event that during a unsuccessful pursuit a new prey has entered the visual field.

Fig 5: A simulated sample path of the satiation process together with the result of a deterministic simulation according to Holling's rules. The chosen sample path is not very representative as most sample paths kept much nearer to the path of the deterministic simulation.

reasons of costs a Monte Carlo solution, i.e. a stochastic simulation, may well be preferrable to a full blown numerical one. However, the parameter values of Holling's mantid, and probably of many other predators as well, are such that all movements off the satiation axis are much more rapid than the downward movement of satiation due to digestion. Since moreover the jumps from the satiation axis are relatively infrequent compared to the return rate to the satiation axis, the main probability mass will be concentrated on the satiation axis itself. This effect is also demonstrated in figure 5, which shows a sample path of the satiation process, together with a deterministic simulation following Holling's rules. Here it can be seen that on catching a prey the satiation jumps almost instantaneously to its new level. Therefore we can turn to a simple approximating process in which all the horizontal movements in figure 4 are assumed to be instantaneous.

4. Negligable handling time

From now on we shall assume that 'handling time' is negligable. i.e. if a denotes the rate constant of digestion and $\&_s\tau$ denotes the expected time needed to return to the satiation axis after leaving this axis at s, we assume $a\&_s\tau \ll 1$. Under this assumption our predator can be modelled in terms of one state variable, satiation, denoted as S, the density p of which satisfies the forward equation

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

with

$$f(s) = -as \tag{2}$$

the digestion rate, w the prey weight, and xg(s) the catching rate where x is the effective prey density. To make (1) well-defined we introduce the convention that gp equals zero for s negative. Moreover we have to add the (boundary) condition

$$p(s,t) = 0 \quad \text{for} \quad s \geqslant s_{max} \geqslant c+w$$

where c is the satiation threshold, i.e. the value of s for which g first becomes zero.

For Holling's mantid the catching rate can be expressed as

$$xg(s) = xb(1-s/c)^+q(s), \quad q(s) = \exp[-d(1-s/c')^+]. \tag{3}$$

The first term of g equals the width of the search field times the (maximal) prey velocity times the strike success, and q is the probability that the prey does not escape during pursuit. To calculate q we observe that the probability of a fly staying put during the 'pursuit' equals the exponential of minus the escape rate times the pursuit time. The pursuit time equals the pursuit distance divided by the pursuit velocity. Finally the pursuit distance equals the observation distance

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minus the strike distance. It is the introduction of this latter term which makes
$c' < c$.

As an exercize we may integrate the left and right hand sides of (1) over s,
and use $\lim_{s \downarrow 0} fp = \lim_{s \uparrow \infty} fp = 0$ to arrive at $\frac{d}{dt} \int_0^\infty p(s,t)ds = 0$, and, since the total
probability mass at time zero equals zero,

$$\int_0^\infty p(s,t)ds = 1 \tag{4}$$

in conformity to our expectations. (The main reason for introducing this seemingly
trivial calculation here is that below analogous calculations will be made without
going into the specifics.)

It is clear that our main interest is not in the distribution of S, but in
the number of prey caught, N. Intuitively we write down immediately from 'law of
mass action' considerations

$$\frac{d\&N}{dt} = x \int_0^\infty g(s)p(s,t)ds = x\&g(S). \tag{5}$$

A more formal derivation can be given by using the 'generation expansion',

$$\frac{\partial p_n}{\partial t} = - \frac{\partial f p_n}{\partial s} - xg p_n + xg(s-w)p_{n-1}(s-w), \tag{6}$$

where

$$p_n(s,t)ds \stackrel{\text{def}}{=\!=} P \{s < S(t) \leqslant s+ds, N(t)=n\},$$

and $p_{-1}=0$ by convention. Multiplying the left and right hand sides of (6) with n,
n^2, summing over n, and collecting terms gives us (5) again, but also

$$\frac{d \, var(N)}{dt} = x\{2 \, cov[N,g(S)] +\&g(S)\}, \tag{7}$$

where $cov[N,g(S)]$ can be calculated from

$$cov[N,g(S)] = \int_0^\infty g(s) \, z(s,t) \, ds \tag{8}$$

and

$$\frac{\partial z}{\partial t} = - \frac{\partial f z}{\partial s} - xgz + xg(s-w) \, z(s-w) + xg(s-w) \, p(s-w) - xp\&g(S). \tag{9}$$

By the same methods as before we find moreover that

$$\int_0^\infty z(s,t) \, ds = 0. \tag{10}$$

H. Heymans of the Mathematical Centre at Amsterdam has proven existence
and uniqueness of the solutions to the equations for p and z, as well as

the exponential convergence of those solutions to the stationary solutions defined by

$$0 = - \frac{df\hat{p}}{ds} - xg\hat{p} + xg(s-w)\hat{p}(s-w) \tag{11a}$$

$$1 = \int_0^\infty \hat{p}(s)ds \tag{11b}$$

$$0 = - \frac{df\hat{z}}{ds} - xg\hat{z} + xg(s-w)\hat{z}(s-w) + xg(s-w)\hat{p}(s-w) - x\hat{p}\int_0^\infty g(\sigma)\hat{p}(\sigma)d\sigma \tag{12a}$$

$$0 = \int_0^\infty \hat{z}(s)ds. \tag{12b}$$

Moreover, probabilistic considerations tell us that

$$(N - \mathcal{E}N)/(\text{var } N)^{\frac{1}{2}} \overset{\frown}{\longrightarrow} \text{Gaussian}(0,1). \tag{13}$$

To calculate $\hat{p}$ numerically we make use of the fact that (11a) reduces on $(0,w]$ to an ordinary differential equation. So we can choose a starting value $\hat{p}(w) = \hat{p}_w > 0$ and integrate backwards from w to zero. Next we integrate from w to $2w$, using the known values of $\hat{p}$ on $(0,w]$, and so on. It can be shown that $\hat{p}$ stays positive on $(0,c+w)$ and becomes exactly zero at $c+w$. Due to the linearity of (9a) we can normalize afterwards to conform to (11b). The only troublesome aspect may be the singular nature of (11a) at $s=0$, due to the fact that $f(0)=0$. As a result $\hat{p}$ may diverge for $s \downarrow 0$. However, near to $s=0$ we can easily derive an analytical approximation to $\hat{p}$ to replace the numerical one. The result of such a numerical calculation for Holling's mantid parameters and the lowest, highest and middle prey density used by Holling in his final experiments is shown in figure 6.

The calculation of $\hat{z}$ proceeds in exactly the same manner as that of $\hat{p}$ except that instead of normalizing we add some multiple of $\hat{p}$ to satisfy (12b).

Finally if we know $\hat{p}$ we can calculate the functional response F as

$$F(x) = x \int_0^\infty g(s) \, \hat{p}_x(s) \, ds \tag{14}$$

where the subscript x refers to the fact that $\hat{p}$ is dependent on the parameter s. For Holling's mantid the functional response is numerically found to be increasing and concave, but we do not yet have any proof of such properties. Direct probabilistic considerations tell us that

$$\frac{dF}{dx}(0) = g(0) \tag{15}$$

$$\lim_{x \to \infty} F(x) = \left(- \int_0^{c+w} f(s)ds\right)^{-1}. \tag{16}$$

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P

5

0

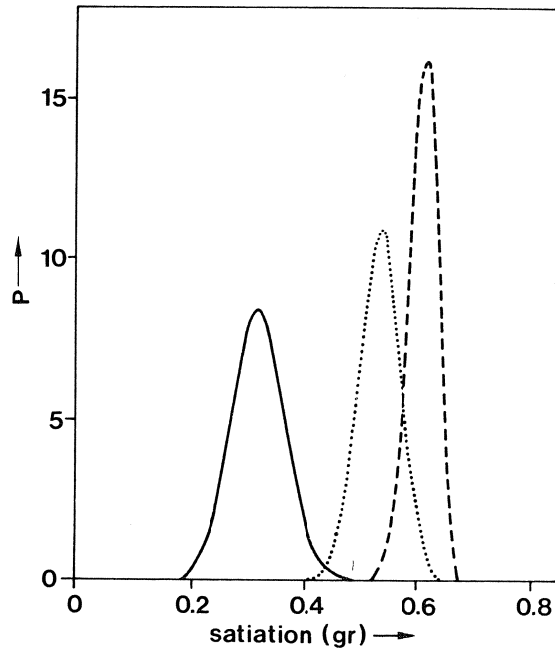0   0.2   0.4   0.6   0.8

satiation (gr) ⟶

Fig 6: Calculated stationary distribution of the satiation for Holling's mantid for three values of the effective prey density, corresponding to the lowest, the highest and one middle prey density used by Holling in his final experiments.

To arrive at more managable results we have to go on to the next approximation stage.

5. Small prey weights

If we look at figure 5 again we see that the prey weight is very small relative to the satiation threshold c, but the accumulated prey weight during a few hours of eating still leads to a considerable upwards shift of S despite the continuous digestion. Therefore we introduce the new parameter $\xi \overset{\text{def}}{=\!=} x.w$, and look what happens to (1) if w becomes small, ξ remaining constant:

$$\frac{\partial p}{\partial t} = - \frac{\partial fp}{\partial s} - xgp + xg(s-w)p(s-w) \approx - \frac{\partial fp}{\partial s} - xgp + [xg(s)p(s) - xw \frac{\partial gp}{\partial s}(s)] .$$

In the limit when w↓0 we get

$$\frac{\partial p}{\partial t} = - \frac{\partial (f+\xi g)p}{\partial s} ,$$

i.e. the 'jumpterms' have disappeared. So the prey catching process has become completely deterministic: the predator is slurping prey soup.

[Remark: The fact that we can make our approximation in two steps is based on the fact that $\dot{a}_s \tau \ll w/c \ll 1$ for all s.]
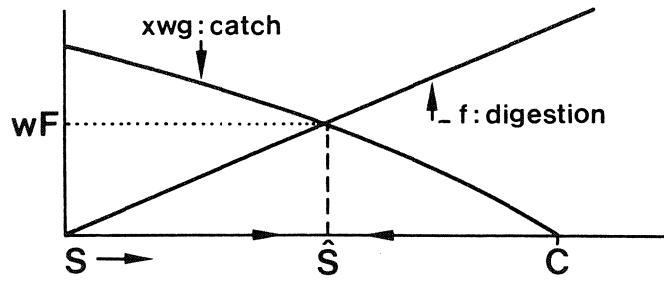
Fig 7: The processes contributing to the satiation in the deterministic limit model for one particular value of the effective prey density. Also indicated are the equilibrium level of the satiation, $\hat{s}$, and the corresponding value of the functional response F.

Figure 7 depicts what happens to our soup eating predator. Its satiation will quickly stabilize at some value $\hat{s}$, defined by

$$-f(\hat{s}) = xwg(\hat{s}) \tag{17}$$

and

$$F(x) \approx xg(\hat{s}) \tag{18}$$

Both $\hat{s}$ and F can be read off immediately in the figure. Changing x corresponds to multiplying the wg curve by different constants. From the construction we can easily prove that for f linear and g decreasing F will always increase. When g is moreover concave F will be concave too.

When pursuit is always successful, i.e. if g is equal to $b(1-s/c)$, and if $f(s) = -as$ as usual, the model formulation derived here corresponds exactly to that of Rashevsky (1959).

6. (Local) linearization

During the limiting process described in the previous section we have lost all information concerning the variance of the catch. To retrieve this information we may consider a diffusion approximation locally around the deterministic trajectory. It is easier, however, to derive the results we need by more direct means. To this end we consider a 'linearized' version of the satiation process, which results from replacing g with a straight line. For the sake of the exposition we shall do this here by setting q equal to 1 in (3). For a local linearization we should replace g with its tangent line at $\hat{s}$. Moreover it is essential for the following calculations that $f(s) = -as$.

As a first step we observe that, on neglecting the probability mass situated between c and c+w,

$$\&g(S) \approx b(1-\&S/c).\tag{19}$$

To calculate $\&S$ we multiply both sides of (1) with s and integrate over s to obtain

$$\frac{d\&S}{dt} = -a\&S + xw\&g(S) \approx -(a + xwb/c)\&S + xwb.\tag{20}$$

Proceeding in this manner we can also derive approximate differential equations for variances, covariances and so on. We shall not bother you here with the detailed calculations, but confine ourselves to giving the two most important final results:

$$\frac{d\&N}{dt}(\infty) = \frac{bx}{1+xwb/(ac)},\tag{21}$$

which corresponds to the deterministic result (18) under the same assumptions on f and g, and

$$\frac{d \text{ var } N}{dt}(\infty) = \frac{bx}{(1+xwb/(ac))^3}.\tag{22}$$

As a 'worst case' check of the accuracy of (21) we can let $x \to \infty$, giving

$$\frac{d\&N}{dt}(\infty) = ac/w,$$

which should be compared to an exact value, calculated from (16), of

$$a/\ln(1+w/c) = (ac/w)(1+\tfrac{1}{2}w/c+o(w/c)).$$

So (21) is correct to first order in w/c even for p concentrated near the satiation threshold. For Holling's mantid w/c = 0.0372.

The limiting value of $\frac{d \text{ var }(N)}{dt}(\infty)$ for $x \to \infty$ calculated from (22) even is exact (i.e. zero).

7. Concluding remarks

The main conclusion that emerges from our analysis is that a clear specification of Holling's 'hungry mantid' model as a stochastic process leads to a great number of additional insights. First of all we found that Holling's deterministic simulation method was not as general as he thought. It only works under specific conditions on the parameters; conditions which also make it possible to derive a much simpler deterministic model of the type discussed in section 5. These conditions are short handling time, $a\&_s\tau \ll 1$ for all s, and small prey weight, $w/c \ll 1$. For Holling's mantid even the stronger assumption $a\&_s\tau \ll w/c \ll 1$ holds, which made it possible to derive a very simple approximate expression for the asymptotic variance of the total catch. If the handling time is small but the prey weight not it is still possible to derive more complicated equations from which we can calculate numerically the functional response as well as the asymptotic

the various approximations seem to be pretty robust.

Various extensions of the previous calculations are possible. One important possibility is to consider variable prey size. In that case we are not only interested in the variance of the number of prey caught but also in the variance of the accumulated prey weight, as this effectively determines the probability of a predator dying due to random starvation. We may also consider different regions of the parameter space. For example, when $a\&_s\tau$ and w/c are both small but of the same order of magnitude, we get a different deterministic limit in which Holling's secretary model becomes merged into a Rashevsky type hunger model as deduced in section 5. These topics as well as a more detailed exposition of the preceding calculations will be the subject of forthcoming papers.

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