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Computation of the Fitness and Functional Response of Holling's "Hungry Mantid" by the WKB Method

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Abstract. We derive a differential-difference equation for the fitness of a predatory insect such as a mantid. If the gut capacity of the mantid is large compared to individual prey items, the equation for fitness can be solved by the WKB method. We also compute the prey attack rate as a function of prey density.

Holling [1] describes the predatory behavior of the mantid Hierodula crassa. The prey catching process of the hungry mantid is assumed to be driven by satiation (gut content) of the mantid and involves four distinct phases. These are searching, pursuing, striking and eating. Searching is a random process in which prey encounters are a function of prey density and the width of the search field of the mantid. Thus success in search increases with the product of prey density and the width of the search field of the mantid. Pursuing occurs at a constant rate and with a fixed probability of success; both are independent of satiation. If pursuit fails, i.e. the prey escapes, the the mantid goes back to searching. If pursuit succeeds then the mantid immediately strikes its prey. Striking has a fixed probability of success that is independent of satiation. If the mantid is successful in striking its prey then it immediately eats the prey at a constant rate independent of satiation. Holling found that satiation decreased exponentially during periods when the mantid was not eating.

Holling developed a deterministic simulation of the satiation process. Metz and van Batenburg [2 – 4] developed a full stochastic simulation; they discuss Holling's model and also lay the groundwork for treating the process analytically. The most important simplification is the use of negligible handling time, for which a prey capture results in the instantaneous increase in satiation equal to the effective prey weight. Further simplifications involve combining searching, pursuing and striking by assuming that prey are captured at a rate $xg(S)$, where x is the prey density, $g(S)$ is the satiation dependent rate prey capture and $S(t)$ is the satiation of the mantid at time t. These simplifications together are called the "gobbler model". The salient feature of this model is that the state space of the mantid reduces to one dimension, that of satiation S. The stochastic process $S(t)$ as described by the gobbler model has the following forward equation for its probability density

$$\frac{\partial p(s,t)}{\partial t} = \frac{\partial(asp(s,t))}{\partial s} - xg(s)p(s,t) + xg(s-w)p(s-w,t) \tag{1.1}$$

In this equation $p(s,t)ds = Pr\{s \le S(t) \le s + ds\}$, w denotes prey weight, and between captures

$$\frac{dS}{dt} = -aS \tag{1.2}$$

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Equation (1.1) has the boundary condition $p(s,t) = 0$ for $s \geq c + w$, where c is a satiation threshold defined by $g(s) = 0$ for $s \geq c$, and the initial condition $p(s,0) = p_0(s)$. Metz and van Batenburg [3] derive Equation (1.1) and model $g(s)$ as a non-linear function of s. Heijmans [5] shows that solutions of the adjoint of equation (1.1) converge to a stationary distribution. The adjoint equation is

$$\frac{\partial n(s,t)}{\partial t} = -as\frac{\partial n(s,t)}{\partial s} - xg(s)n(s,t) + xg(s)n(s+w,t) \tag{1.3}$$

The adjoint equation is called a backward equation. If $n(s,0) = \eta(s)$ then the solution of the forward and backward equations are related by

$$\int_0^{c+w} p(s,t)\eta(s)ds = \int_0^{c+w} p_0(s)n(s,t)ds \tag{1.4}$$

Despite formulating and proving the existence of solutions to equation (1.1) and (1.3) neither Metz and van Batenburg nor Heijmans attempt to solve them. Here we formulate a backward equation for the fitness of the mantid and solve it approximately by the WKB method [6].

2. FORMULATION

Let $S^*(t^*)$ denote the gut content of a mantid at time t^*. We assume that the prey weight, w, is small compared to the gut capacity of a mantid which is denoted by $\sum$. The dynamics of S^* are written

$$dS^*(t^*) = -\alpha S^* dt^* + w d\pi^* \tag{2.1}$$

where $d\pi^* = 1$ with probability $\lambda^*(S^*)dt^* + o(dt)$ and 0 otherwise. Prey captures are a Poisson jump process [7].

Let $\varepsilon = \frac{w}{\sum}$ be a small parameter that measures the relative increase in gut contents due to prey captures. The satiation dependent rate of prey capture is explicitly assumed to depend inversely on the small parameter ε: as the effective weight of a single prey decreases relative to the demands of metabolism, the rate at which the mantid captures these small prey must increase. Recall that in the formulation of Metz and van Batenburg the satiation dependent rate of prey capture was $xg(S)$. Let T_c denote a characteristic time such as the lifetime of a mantid and introduce the scaling $t = \frac{t^*}{T_c}$, $S = \frac{S^*}{\sum}$, $\lambda^*(S^*) = \frac{\lambda(S)}{\varepsilon}$. and $d\pi = 1$ with probability $\frac{\lambda(S)dt}{\varepsilon} + o(dt)$ and 0 otherwise. Setting $c = \alpha T_c$, equation (2.1) now becomes

$$dS = -cSdt + \varepsilon d\pi. \tag{2.2}$$

Consider an interval of time $0 \leq t \leq T$ and define

$$\omega(s,t,T) = E_{S(T)}\left[F(S(T)) \mid S(t) = s\right]. \tag{2.3}$$

The function $F(s)$ is called a terminal fitness function and provides a measure of "reward" at time T [8].

The law of total probability implies that

$$\omega(s,t,T) = E_{dS}\left[E_{S(T)}\left[F(S(T)) \mid S(t+dt) = s + dS\right]\right]. \tag{2.4}$$

We use (2.2) in (2.4), Taylor expand in powers of dt and let $dt \to 0$ to obtain [10]

$$0 = -cs\omega_s(s,t,T) + \omega_t(s,t,T) + \frac{\lambda(s)}{\varepsilon}\left[\omega(s+\varepsilon,t,T) - \omega(s,t,T)\right]. \tag{2.5}$$

This is a partial differential-difference equation with the end condition $\omega(s,T,T) = F(s)$. Notice that up to differences in notation (2.5) is precisely (1.3), the backward equation and adjoint of equation (1.1).

3. Fitness Computed by the WKB-method

We now assume that the terminal fitness function $F(s)$ takes the form

$$F(s) = 1 - e^{-\frac{\phi(s)}{\varepsilon}} \tag{3.1}$$

where $\phi(s)$ is a specified function. We then seek a solution in the form

$$\omega(s,t,T) \sim 1 - k(s,t,T)e^{-\frac{\Psi(s,t,T)}{\varepsilon}} \tag{3.2}$$

where $k(s,t,T) = \sum k_i(s,t,T)\varepsilon^i$ and the $\{k_i(s,t,T)\}$ and $\Psi(s,t,T)$ are to be determined. Inserting (3.2) into equation (2.5) and dividing by $e^{-\frac{\Psi(s,t,T)}{\varepsilon}}$ we obtain

$$0 = -c\left[-k_s + \frac{k\Psi_s}{\varepsilon}\right] + \left[-k_t + \frac{k\Psi_t}{\varepsilon}\right] +$$

$$+\frac{\lambda(s)}{\varepsilon}\left[-k(s+\varepsilon,t,T)e^{-\frac{\Psi(s,t,T)-\Psi(s+\varepsilon,t,T)}{\varepsilon}} + k(s,t,T)\right] \tag{3.3}$$

Taylor expanding $k(s+\varepsilon,t,T)$ and $\Psi(s+\varepsilon,t,T)$ about (s,t,T), collecting terms of like powers of ε and successively setting their coefficients equal to zero gives

$$\Psi_t - c\Psi_s + \lambda(s)\left[1 - e^{-\Psi_s}\right] = 0 \tag{3.4}$$

$$k_{0_t} + k_{0_t}\left[-c + \lambda(s)e^{-\Psi_s}\right] - k_0\left[\lambda(s)e^{-\Psi_s}\frac{\Psi_{ss}}{2}\right] = 0 \tag{3.5}$$

We solve equation (3.4) by the method of characteristics [10]. Along the characteristics of Eqn(3.4), we find that Eqn(3.5) may be written

$$\frac{dk_0}{dt} - k_0\left[\lambda(s)e^{-\Psi_s}\frac{\Psi_{ss}}{2}\right] = 0 \tag{3.6}$$

The solution to (3.6) involves one arbitrary constant. We obtain initial conditions for the characteristic equations and the arbitrary constant from (3.6) by comparing the ansatz (3.2) with the final data (3.1).

4. Computation of Functional Response by WKB

The stationary functional response FR is defined by

$$FR = x\int g(s)v(s)ds \tag{4.1}$$

where, as before x = prey density, $g(s) = \text{Prob}\{\text{successful strike given that } S = s\}$ and $v(s)$ is the stationary probability density for S; that is $v(s)ds + o(ds) = \text{Prob}\{s \le S \le s + ds\}$. This stationary density satisfies the differential-difference equation

$$0 = \frac{\partial}{\partial s}\left[\varepsilon asv(s)\right] - xg(s)v(s) + xg(s-\varepsilon w)v(s-\varepsilon w) \tag{4.2}$$

We now use the WKB ansatz

$$v(s) \sim k(s)e^{-\frac{\Psi(s)}{\varepsilon}} \tag{4.3}$$

and substitute this into Eqn(4.2). To leading order in the small parameter, we obtain

$$as\Psi_s = xg(s)\left[e^{\Psi_s w} - 1\right] \tag{4.4}$$

We choose the solution of (4.4) that insures integrability of $v(s)$ and assume that Ψ has a minimum at s_{eq} defined by

$$as_{eq} = wxg(s_{eq}) \tag{4.5}$$

This choice of s_{eq} corresponds to the rest point of the equation obtained by averaging the analogue of Eqn(2.1). The next order in ε gives the equation

$$\frac{k_s}{k} = \frac{e^{\Psi_s w}x\left[wg_s + \frac{1}{2}w^2 g\Psi_{ss}\right] - a}{as - gxwe^{\Psi_s w}} \equiv \rho(s) \tag{4.6}$$

We solve this to obtain

$$k = ce^{\left[\int^s \rho(s')ds'\right]} \tag{4.7}$$

We now compute the functional response by evaluating the integral in Eqn(4.1) by Laplace's method. The result is

$$FR = xg(s_{eq})k(s_{eq})e^{-\frac{\Psi(s_{eq})}{\varepsilon}}\sqrt{2\pi}\left[\frac{\varepsilon}{\Psi_{ss}(s_{eq})}\right]^{\frac{1}{2}} \tag{4.8}$$

5. COMMENTS

1. In part II of their work, Metz and van Batenburg [4] use diffusion approximations; this is equivalent to assuming that Ψ_s is small.

2. Also in [4], Metz and van Batenburg describe a multi-dimensional extension in which the two state variables are satiation $S(t)$ and accumulated number of encounters $N(t)$. The density $v_n(s,t)$ is defined by

$$v_n(s,t)ds = Pr\{S(t) \in (s, s+ds),\ N(t) = n\} \tag{5.1}$$

and satisfies the forward equation

$$\frac{\partial v_n}{\partial t} = \frac{\partial}{\partial s}\left[\varepsilon asv_n\right] - xg(s)v_n(s,t) + xg(s-\varepsilon w)v_{n-1}(s-\varepsilon w, t) \tag{5.2}$$

This can be solved by assuming an anstaz of the form

$$v_n(s,t) = k_n(s,t)e^{-\frac{\Psi(s,t)}{\varepsilon}} \tag{5.3}$$

The equation for Ψ is obtained as a solvability condition for the linear equations characterizing the k_n[10].

3. In the general problem, there are actually two small parameters. The first, used here, is $\varepsilon = \frac{w}{\sum}$. The second is $\eta = \tau_h a$ where τ_h is the handling time. We have implicitly assumed that $\eta = 0$, but considerable work could be done on the asymptotics of the two parameter problem.

REFERENCES

1. C.S. Holling, *The Functional Response of Invertebrate Predator to Prey Density*, Mem. of the Ent. Soc. of Can. **48** (1966), 1–86.
2. J.A.J. Metz and F.H.D. van Batenburg, *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, Lect. Notes in Biomath. **54** (1985), 29–41.
3. J.A.J. Metz and F.H.D. van Batenburg, *Holling's "hungry mantid" Model for the Invertebrate Functional Response Considered as a Markov Process.*
   Part I: The Full Model and Some of its Limits, J. of Math. Bio **22** (1985), 209–239.
4. J.A.J. Metz and F.H.D. van Batenburg, *Holling's "hungry mantid" Model for the Invertebrate Functional Response Considered as a Markov Process.*
   Part II: Negligible Handling Time, J. of Math. Bio **22** (1985), 239–257.
5. H.J.A.M. Heijmans, *Holling's "hungry mantid" Model for the Invertebrate Functional Response Considered as a Markov Process.*
   Part III: Stable Satiation Distribution, J. of Math. Bio **22** (1984), 115–143.
6. C.M. Bender and S.A. Orszag, "Advanced Mathematical Methods for Scientists and Engineers," McGraw-Hill, New York, 1978.
7. S. Karlin and H.M. Taylor, "A First Course in Stochastic Processes," Academic Press, New York, 1975.
8. M. Mangel and C.W. Clark, "Dynamic Modeling in Behavioral Ecology," Princeton Univ. Press, Princeton, N.J., 1988.
9. F. Johns, "Partial Differential Equations," Springer-Verlag, New York, 1978.
10. C.S. Peters, *Applications of the WKB Method to Stochastic Problems in Operations Research and Biology Ph.D. Dissertation, Graduate Group in Applied Mathematics, University of California, Davis.*

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