CHAOS AND PHASE-LOCKING IN PREDATOR-PREY MODELS IN RELATION TO THE FUNCTIONAL RESPONSE

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ABSTRACT

The dynamics of a simple predator-prey model:

$$\dot{x} = \phi x(1-x) - \gamma g(x)z \quad \text{(prey)}$$
$$\dot{y} = (x-y)/\tau \quad \text{(lagged prey)}$$
$$\dot{z} = \gamma g(y)z - \upsilon z \quad \text{(predator)}$$

with periodic forcing (ϕ) on the prey's reproductive rate and a functional response, g(x), is investigated in relation to parameters and the functional response. The system is sampled at the forcing period and plotted against a parameter for each of four functional responses: Linear, Type 1, Type 2 and Type 3. Sampling at the forcing period allows one to see when the system is phase-locked in some ratio with the forcing cycle. The analysis reveals very complicated and unexpected switching between different phase-locking ratios alternating with regions of quasiperiodic and chaotic behavior within each functional response as a parameter is varied. Of the four functional responses tested, the Type 2 response produces the most complex behavior.

RESUMEN

Se investigó la dinámica de un modelo simple de depredador/presa:

$$\dot{x} = \phi x(1-x) - \gamma g(x)z \quad \text{(presa)}$$
$$\dot{y} = (x-y)/\tau \quad \text{(presa rezagada)}$$
$$\dot{z} = \gamma g(y)z - \upsilon z \quad \text{(depredador)}$$

forzando periodicamente la tasa de reproducción de la presa y su respuesta funcional en relación a los parámetros y la reacción funcional. Se muestra el sistema durante el período forzado, y conjurado contra un parámetro para cada una de cuatro reacciones funcionales: Linear, Tipo 1, Tipo 2 y Tipo 3. Muestrear en el período forzado le permite a uno ver cuándo el sistema está en la fase cerrada en alguna proporción al ciclo forzado. El análisis revela unos cambios muy complicados e inesperados entre varios niveles de fase cerrada que alternan con regiones de comportamiento casi-periodos y caóticos dentro de cada respuesta funcional cuando un parámetro se varía. De las cuatro reacciones probradas, el Tipo 2 produjo el comportamiento más complejo.

The discovery of deterministic chaos in simple nonlinear models of weather (Lorenz 1963), ecological systems (May 1974, 1976) and chemical reactions (Rossler 1976) has added a new dimension to scientific inquiry. In ecology the possibility of such behavior in simple models raises the question of its existence in real highly complex natural systems and whether such a system could survive. It is quite a simple matter to write down predator-prey models which are chaotic (Gilpin 1979, Inoue & Kamifukumoto 1984, Allen 1989a). The primary ingredients for chaos in these models are the naturally arising nonlinear functions combined with time lags and periodic forcing from the environment (e.g., prey reproductive rate becoming a periodic function) (Allen in press).

At the heart of the nonlinear interaction between attacker and victim is the so called functional response of the predator to prey density. This function describes the per predator attack rate as a function of prey density (Holling 1959a,b, 1965).

Four types of functions have been commonly used for the functional response: 1) linear (an "insatiable" predator whose attack rate never saturates at any prey density), 2) a linear rise to a saturation plateau (Type 1), 3) a convex rise to a saturation plateau (Type 2) and 4) a sigmoid rise to a saturation plateau (Type 3). The form of the functional response is largely a reflection of the predator's behavior in response to the prey density and/or distribution in space. The Type 3 response is unique in its ability to produce attracting point ("stable") behavior in what would otherwise be an attracting cycle system, and this type of response has been generally associated with predators capable of learning (Holling 1959a,b, 1965, Murdoch & Oaten 1975). More recently, however, it has been shown that a Type 3 response can also result from more intense searching of high density prey patches (Murdoch & Oaten 1975, Oaten & Murdoch 1975, Van Lenteren & Bakker 1976, 1978, Hassell et al. 1977, Luck et al. 1979, Walde & Murdoch 1988). If the predator simply concentrates on patches without regard to density within the patch, however, then the interaction is not stabilizing (Allen 1989a).

While chaos has been shown to exist in simple predator-prey models, these have typically involved only a linear functional response (Gilpin 1979, Kot et al. 1988, Allen 1989a) or a Type 2 response (Inoue & Kamifukumoto 1984, Schaffer 1989). Little has been done on comparing the effect of the functional responses in a potentially chaotic system, and this is made a bit more interesting by the possibility of spatial density dependence producing a Type 3 response. In this paper I will examine the effect of the different types of functional responses on the dynamic behavior of a predator-prey model which is capable of chaotic dynamics.

A Simple Predator-Prey Model

The model used here is a Lotka-Volterra type of system with the slight complication of periodic forcing of the prey reproductive rate and a one-stage lag in the predator's numerical response. These changes seem realistic and can greatly complicate the dynamic behavior even in the case of a linear functional response (Allen 1989a). The starting equations are

$$dx_o/dt_o = \phi r x_o(1-x_o/k) - ag(x_o)z_o \qquad \text{(prey)}$$
$$dy_o/dt_o = (x_o-y_o)/b \qquad \text{(lagged prey)}$$
$$dz_o/dt_o = \epsilon ag(y_o) - cz_o \qquad \text{(predator)}$$

where $\phi = (1+\delta\cos(2\pi t_o/T_o))$ is the periodic forcing with mean = 1, period T_o and amplitude δ ($0<\delta<1$). $g(\cdot)$ represents the functional response (note that the numerical response in the predator equation is a function of "lagged" prey). These equations can be simplified to dimensionless form by letting $x_o = xk$, $y_o = yk$, $z_o = z\epsilon k$, and $t_o = t/r$. We then have

$$\dot{x} = \phi x(1-x) - \gamma g(x)z \qquad \text{(1a)}$$
$$\dot{y} = (x-y)/\tau \qquad \text{(1b)}$$
$$\dot{z} = \gamma g(y)z - \upsilon z \qquad \text{(1c)}$$

where $\gamma = \epsilon a/r$, $\tau = br$ (mean time lag in the numerical response), $\upsilon = c/r$, $T = rT_o$ and $t = rt_o$. ($\dot{x} = dx/dt$).

The four functional responses, $g(x)$, are as follows:

$$g(x) = x \qquad \text{(Linear)}$$

$$g(x) = \begin{cases} x, & x < x_m \\ x_m, & x \geq x_m \end{cases} \qquad \text{(Type 1)}$$

$$g(x) = x_m \frac{x}{(x_m/2) + x} \qquad \text{(Type 2)}$$

$$g(x) = x_m \frac{x^2}{(x_m/2)^2 + x^2} \qquad \text{(Type 3)}$$

These are compared graphically in Figure 1. All of the saturation curves (Types 1, 2 and 3) share the same saturation prey density (x_m) and same midpoint ($x_m/2$) so as to keep them as similar as possible. These four attack functions give rise to four separate models whose dynamics we wish to investigate. From these models we first need to extract equilibria (fixed points) and determine conditions on the parameters for these points to be positive real numbers (since they represent population densities). This will help to limit the parameter space in which dynamic behavior is to be investigated.

In the absence of periodic forcing ($\delta = 0$), eqs. (1) have fixed points ($\overset{*}{x}, \overset{*}{y}, \overset{*}{z}$) for the different functional responses as follows:

$$\text{(Linear \& Type 1)} \quad \overset{*}{x} = \overset{*}{y} = \upsilon/\gamma, \quad \overset{*}{z} = (1-\overset{*}{x})/\gamma \qquad \text{(2a)}$$

$$\text{(Type 2)} \quad \overset{*}{x} = \overset{*}{y} = \frac{\upsilon x_m}{2(\gamma x_m - \upsilon)}, \quad \overset{*}{z} = \overset{*}{x}(1-\overset{*}{x})/\upsilon \qquad \text{(2b)}$$

$$\text{(Type 3)} \quad \overset{*}{x} = \overset{*}{y} = (x_m/2)\sqrt{\upsilon/(\gamma x_m - \upsilon)}, \quad \overset{*}{z} = \overset{*}{x}(1-\overset{*}{x})/\upsilon \qquad \text{(2c)}$$

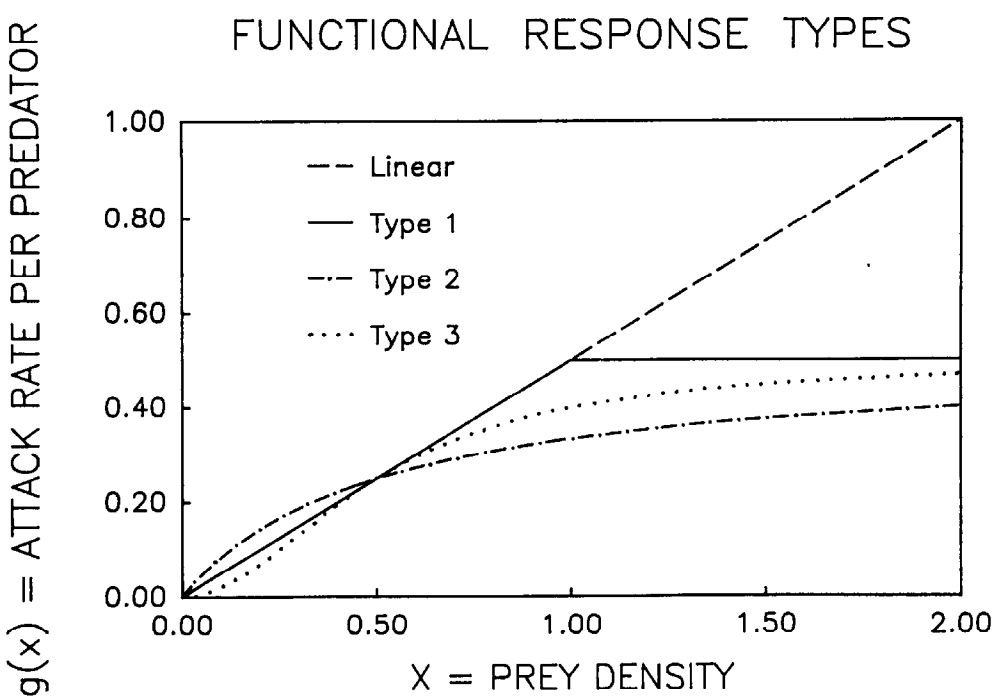

Fig. 1. The 4 most commonly used functional response curves, g(x), (See formulas following the model, eqs. (1)). All of the saturation curves have the same saturation attack rate: $g(x) = 0.5 = \gamma x_m$. γ (=0.5) is the slope of the linear response and x_m (=1.0 is the prey density which causes predator saturation. All curves share the same "half-saturation" prey density (= $x_m/2$ = 0.5).

From eq. (2a) (Linear functional response) we must have ($\overset{*}{x} < 1$) for a positive predator fixed point ($\overset{*}{z}$) which implies

$$\gamma > \upsilon, \text{ or } \gamma/\upsilon > 1 \tag{3a}$$

i.e., the predator's attack rate (γ) must be greater than its mortality rate (υ) if it is to survive (which makes intuitive sense). From eq. (2b) (Type 2 functional response) we must also have a positive predator fixed point which leads in this case to

$$x_m > 1/((\gamma/\upsilon) - (1/2)) \tag{3b}$$

From eq. (2c) Type 3 functional response) similar argument leads to the relation

$$2(\gamma/\upsilon - \sqrt{(\gamma/\upsilon)^2 - 1}) < x_m < 2(\gamma/\upsilon + \sqrt{(\gamma/\upsilon)^2 - 1}) \tag{3c}$$

These requirements (eqs.(3)) are summarized graphically in Figure 2 where the γ/υ ratio is plotted against x_m showing the parameter region for positive, real fixed points. The simulations reported in this paper use parameter values from the lower righthand region of Fig. (2b), i.e., a predator with relatively high attack and low mortality rates which satiates (or saturates) quickly.

Model Simulation and Analysis of Dynamic Behavior

Solution of the differential equations (eqs. (1)) was carried out by 4th-order Runge-Kutta integration with a variable timestep using the programs from Press et al. (1986) written in Pascal. This software was run on an IBM-AT microcomputer, and when more computational speed was needed, a VAX-6320. Models like eqs. (1) have cycles within cycles: i.e. periodic cycles arise from the model itself and also from the independent forcing cycle. These cycles can interact in a very complex way to produce periodic, quasiperiodic or chaotic dynamics depending on parameters, initial conditions and (in our case) the functional response. One way of seeing the behavior of the model in response to changes is to simulate the system and use a plotting or sampling interval equal to the forcing period. This is a bit like flashing a strobe light on a rotating fan blade. When the fan (or model) appears to be standing still, it is "phase-locked" with the sampling interval, indicating a truly periodic oscillation. Otherwise the motion is quasiperiodic ("almost" periodic) or chaotic (having no repeating pattern). More detailed definitions of these dynamic behaviors can be found in Parker & Chua (1987) and Allen (1989a,b).

If the dynamics are such that one cycle of the model occurs during one forcing cycle, then sampling the system at the forcing period produces a single point, and we say that the model has 1:1 phase-locking with the forcing cycle. If the model completes its cycle on every other forcing cycle, then sampling at the forcing period produces two points, and we say that the model has 2:1 phase locking with the forcing cycle. If sampling at the forcing period produces no repeating points, then the model is either quasiperiodic or chaotic. These phenomena can be exploited graphically to map the model behavior as a function of the parameters.

Graphing the behavior as a functicn of a parameter is a rather simple but computationally intensive procedure. First, a parameter range is selected, and this range is evenly divided among the screen pixels along the horizontal axis on the computer screen. (That is, the x-axis represents the parameter.) Then the model is run for a long enough time for transient behavior to die down and attracting behavior to establish itself. (How long is long enough? In general, we don't know, but it can be very long indeed (Allen 1989a). When in doubt, it is best to be conservative. In the graphs to follow, 10000

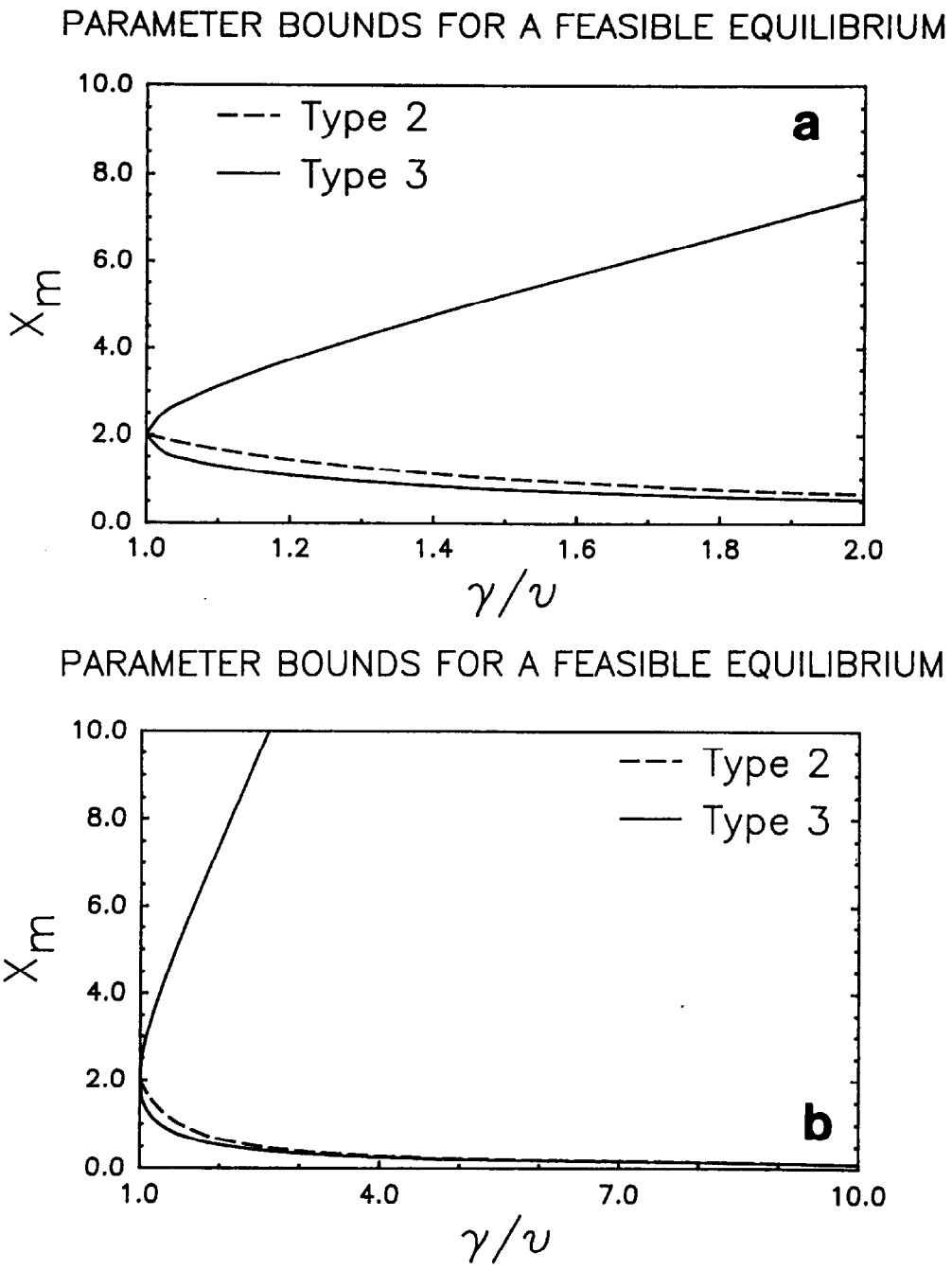

Fig. 2. Relationship between x_m and the γ/υ ratio for the existence of a positive, real predator and prey fixed point in the absence of periodic environmental forcing. γ/υ must always be > 1. In addition, parameters must lie above the dashed line for a Type 2 response and between the solid lines for a Type 3 response.

transient points were discarded before the graph was started.) After transient behavior has been discarded, many points are plotted at intervals of the forcing period at the parameter value on the x-axis. If all the points fall in the same place, then the system is phase-locked 1:1 with the forcing cycle for this parameter value. If (say) five points

appear, then the system is phase-locked 5:1 with the forcing cycle. The result of doing this over a range of parameter values is a flowing pattern of lines whose number represents the phase-locking ratio which can be seen to change in response to the changing parameter.

What if the system does not phase-lock, i.e., lines fail to appear, and one sees only a smear of points over some bounded vertical range? This indicates either quasiperiodic or chaotic dynamics at the parameter value being observed. Distinguishing further between quasiperiodicity and chaos is not as simple as the phase-locking case. One tell-tale sign of chaos is the well-known "period-doubling" route to chaos. Thus if one sees phase-locking lines each of which divides again and again (period-doubling) to give rise to a vertical smear of points as a parameter changes, it is likely that the smear of points represents a chaotic region for the parameter. Abrupt changes from phase-locking lines to irregular points may represent either quasiperiodic or chaotic dynamics.

Results and Discussion

The predator's mortality rate (υ), the attack rate (γ) and the satiation level (x_m) were varied at each of the four functional responses to illustrate the dynamical behavior typical of this model and how it is influenced by the functional response. In all simulations, the forcing cycle was held at $\delta = 0.5$ and $T = 10$ and mean lag in the numerical response was $\tau = 4$. These choices are somewhat arbitrary, and no attempt has been made to cover the whole parameter space. The effect of varying the predator's mortality rate (υ) from 0.05 to 0.1 is shown in Figure 3. At the start of each graph, initial (x,y,z) conditions were (0.5,0.5,0.5) and 10000 initial time periods were discarded before any plotting began. At each parameter increment along the x-axis, 300 initial forcing periods (3000 time points) were discarded and the next 50 were plotted. The mortality rate was

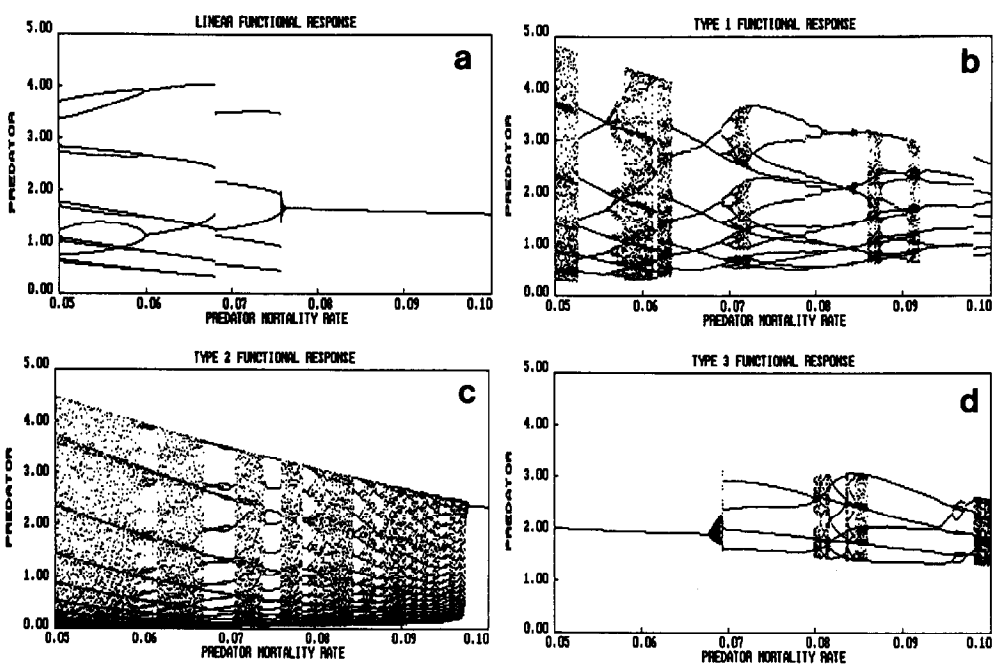

Fig. 3. The effect of varying the predator's mortality rate (υ) on the model dynamics (the predator) for each of the four functional responses. The other parameters are $\delta = 0.5$, $T = 10$, $\tau = 4$, $x_m = 0.25$, $\gamma = 0.5$.

then incremented, and the procedure was repeated using the final (x,y,z) values of the previous increment as starting values. Since we are solving differential equations, this procedure requires considerable computational effort, and the calculations were done on a VAX-6320 where typical run times were on the order of one hour per graph.

The effect of varying the predator's attack rate (γ on the model dynamics is shown in Figure 4, and the effect of the satiation level of prey (x_m) is shown in Figure 5. In all of the simulations, Figures 3-5, one is struck with the intricate switching of phase-locking from one ratio to another in a complex, seemingly arbitrary manner often alternating with bands of quasiperiodicity and chaos (indicated by period-doubling cascades). This degree of dynamical complexity is a bit surprising and would bewilder an observer using only standard simulation techniques. In fact the complex dynamical changes are confusing enough even when they are exposed in these graphs.

Some overall messages are apparent from the graphs. First, the Type 2 functional response is much less apt to phase-lock with the forcing cycle, being more prone to quasiperiodicity and chaotic dynamics and exhibits an extremely complicated sequence of switching between phase-locking and chaos. Both linear and Type 3 functional responses appear to phase-lock a bit more than Type 1 and certainly more than Type 2. The idea that the Type 3 response is more stabilizing than the Type 2 seems to be true here, although the Type 3 response does go through some complicated changes. In addition, the effect of changing the forcing cycle (δ and T) and the lag in the numerical response (τ) have not been studied here.

As a quick check on the credibility of the graphs we can examine a test case to see if the actual dynamics agrees with that predicted by the diagrams. Consider the expanded version of the interesting section of Figure 5b between x_m = 0.30 to 0.34 in Figure 6. For this range of saturation prey densities, there are alternating intervals of phase-locking, period-doubling cascades and apparently chaotic bands. Choosing x_m =

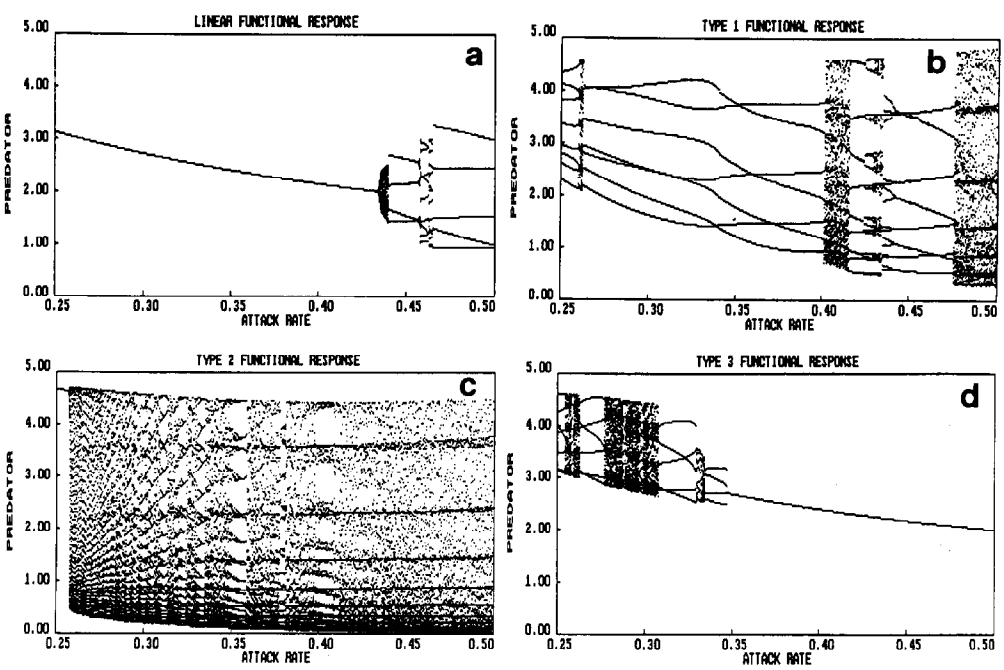

Fig. 4. The effect of varying the predator's attack rate (γ) on the model dynamics (the predator) for each of the four functional responses. The other parameters are: δ = 0.5, T = 10, τ = 4, x_m = 0.25, υ = 0.05.

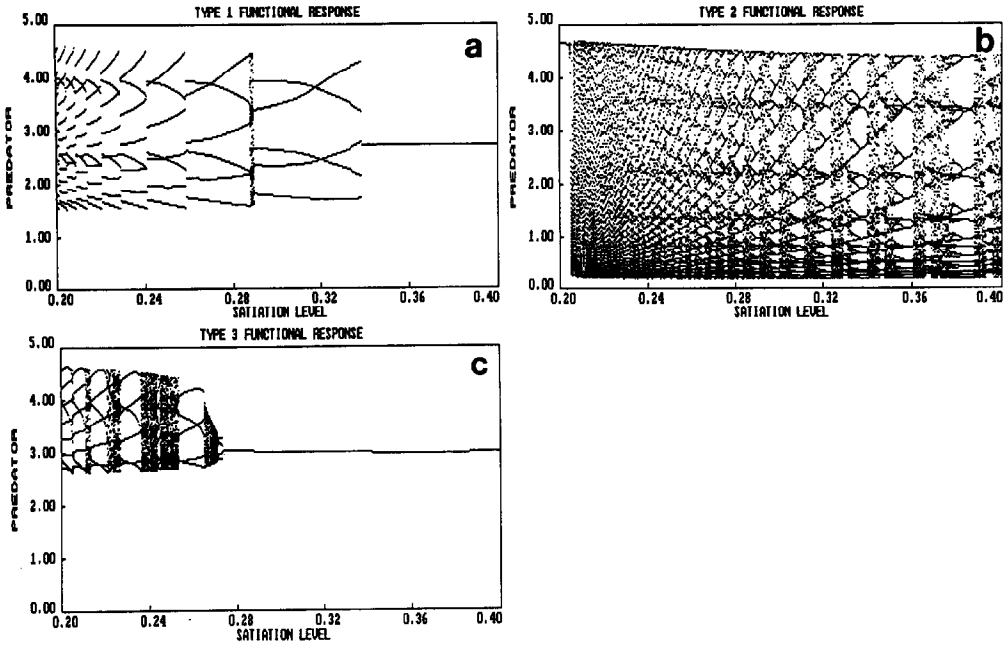

Fig. 5. The effect of the satiation level of prey density on the model dynamics (the predator) for the three "saturating" types of functional response. (Linear does not saturate.) The other parameters are: $\delta = 0.5$, $T = 10$, $\tau = 4$, $\upsilon = 0.1$, $\gamma = 0.5$. Note the period-doubling cascades suggesting chaotic dynamics in (b). (An expanded part of (5b) is shown in Fig. 6.)

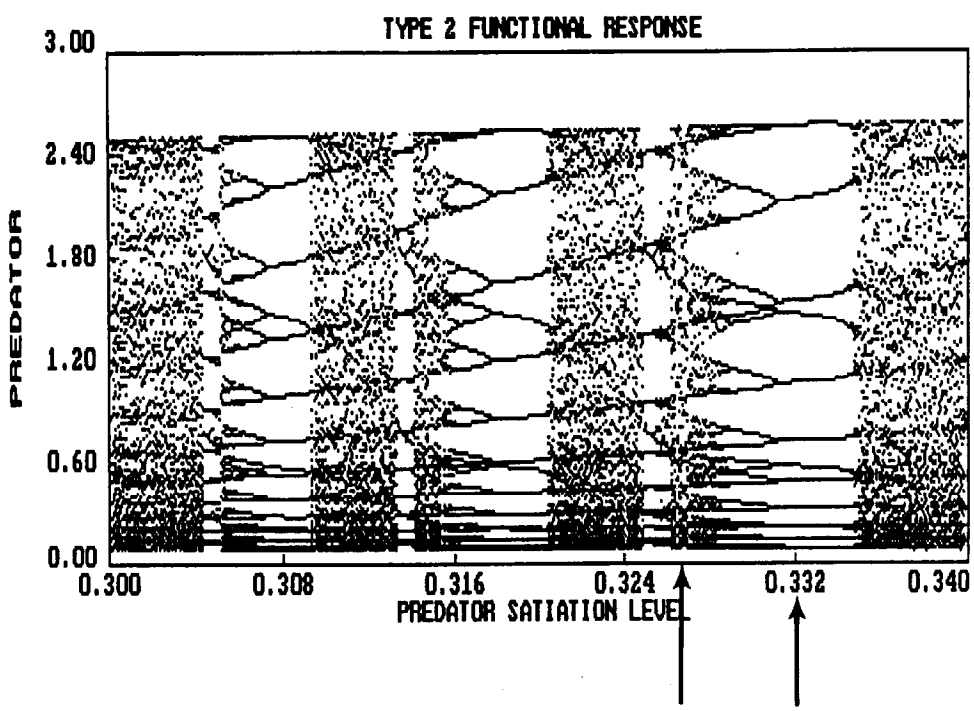

Fig. 6. An expanded part of Fig. 5b. from $x_m = 0.30$ to 0.34. The period-doubling is more apparent. Simulation for $x_m = 0.332$ (periodic) and $x_m = 0.327$ (probably chaotic) are shown in Fig. 7.

0.332 in a phase-locked region, we simulate the system (eqs.(1)) with all other parameters as in Figure 5. The first 10000 transient time intervals are discarded and the next 10000 are plotted (with lines between points) in (x,y,z) phase space in Figure 7a, and we see a periodic cycle as expected. We now choose $x_m = 0.327$ in an apparently chaotic region nearby and repeat the procedure above, plotting the result in Figure 7b. As predicted, we now see a swirling mass of flow lines which is either quasiperiodic or more likely chaotic. Another phase-space view is shown in Figure 7c and a time plot in Figure 7d. The small change of 0.05 in x_m has produced a dramatic change in the kind of dynamics that we see.

Summary, Conclusions and a Disclaimer

It has been shown that a simple type of periodically forced predator-prey model can have very complicated and unexpected transitions in dynamic behavior as parameters vary and that these transitions are greatly influenced by the type of functional response exhibited by the predator. The Type 3 functional response appears to be somewhat more likely to phase-lock with the forcing cycle than the Type 2 response although there is complicated behavior from all responses. These results do not change the basic notion that the Type 3 response is somewhat more stabilizing than the Type 2, but they do add another dimension to the problem. If the behavior of the predator determines the

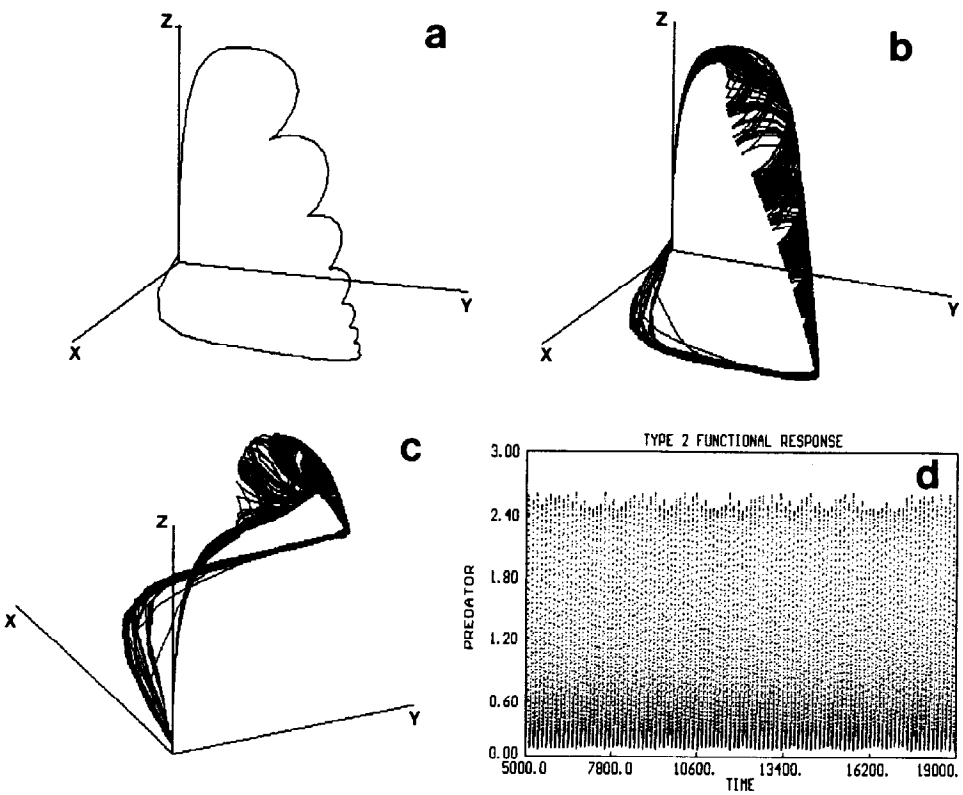

Fig. 7. (a). Simulation of the point $x_m = 0.332$ from Fig. 6. Periodic, phase-locked dynamics. (b). Simulation of the point $x_m = 0.327$ from Fig. 6. Probably chaotic dynamics. (In all plots the other parameters are as in Fig. 5.) (c). Another view of (b). (d). Time plot of (b) and (c)—5000 points discarded 14000 plotted. No repeating pattern develops.

functional response, then within that behavior there also exists the possibility of sudden and unexpected shifts in the attracting dynamics due to small and seemingly inconsequential changes in behavior or environment.

While these results are interesting and important, it should be noted that there are several things "wrong" with the model (eqs. (1)) as given. Among the most glaring of these is that there is no genetics, there is no explicit spatial component and the predator's mortality is not effected by a scarcity of prey. Inclusion of any of these factors will certainly have a profound effect on the dynamics. It is not immediately obvious whether the inclusion of such factors would greatly simplify the dynamics, but we would hope that the main results are fairly robust to such changes. That is, that there is a surprising degree of complexity both within and between the functional responses in such models and that without detailed analyses such as this we can never hope to understand them.

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References Cited

Allen, J. C. 1989a. Are natural enemy populations chaotic?, *in* L. L. MacDonald, J. A. Lockwood and J. A. Logan (eds.), Estimation and analysis of insect populations. Springer, New York.

Allen, J. C. 1989b. Patch-efficient parasitoids, chaos and natural selection. Florida Entomol. 72: 52-64.

Allen, J. C. Factors contributing to chaos in population feedback systems. Ecol. Modelling (in press).

Gilpin, M. E. 1979. Spiral chaos in a predator-prey model. American Nat. 113: 306-308.

Hassell, M. P., J. H. Lawton, and J. R. Beddington. 1977. Sigmoid functional responses by invertebrate predators and parasitoids. J. Anim. Ecol. 46: 249-262.

Holling, C. S. 1959a. Some characteristics of simple types of predation and parasitism. Canadian Entomol. 91: 385-398.

Holling, C. S. 1959b. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Canadian Entomol. 91: 293-320.

Holling, C. S. 1965. The functional response of invertebrate predators to prey density. Mem. Entomol. Soc. Canada 48: 1-86.

Inoue, M., and H. Kamifukumoto. 1984. Scenarios leading to chaos in a forced Lotka-Volterra model. Prog. Theor. Phys. 71: 168-181.

Kot, M., W. M. Schaffer, G. L. Truty, D. J. Graser, and L. F. Olsen. 1988. Changing criteria for imposing order. Ecol. Modelling 43: 75-110.

Lorenz, E. N. 1963. Deterministic nonperiodic flow. J. Atmos. Sci. 20: 130-141.

Luck, R. F., J. C. Van Lenteren, P. H. Twine, and L. Kuenen. 1979. Prey or host searching behavior that leads to a sigmoid functional response in invertebrate predators and parasitoids. Res. Popul. Ecol. 20: 257-264.

May, R. M. 1974. Biological populations with nonoverlapping generations: Stable points, stable cycles and chaos. Science 186: 645-647.

May, R. M. 1976. Simple mathematical models with very complicated dynamics. Nature 261: 459-467.

MURDOCH, W. W., AND A. OATEN. 1975. Predation and population stability. Adv. Ecol. Res. 9: 1-131.

OATEN, A., AND W. W. MURDOCH. 1975. Functional response and stability in predator-prey systems. American Nat. 109: 289-298.

PARKER, T. S., AND L. O. CHUA. 1987. Chaos: A tutorial for engineers. Proc. I.E.E.E. 75: 982-1008.

PRESS, W. H., B. P. FLANNERY, S. A. TEUKOLSKY, AND W. T. VETTERLING. 1986. Numerical recipes: The art of scientific computing. Cambridge Univ. Press, Cambridge England. pp. 550-560.

ROSSLER, O. E. 1976. Chaotic behavior in a simple reaction system. Zeit. für Naturforschung 31a: 259-264.

SCHAFFER, W. M. 1989. Perceiving order in the chaos of nature, *in* M. Boyce (ed.), Evolution of life histories: Theory and pattern from mammals. Yale University Press, New Haven, Conn.

VAN LENTEREN, J. C., AND K. BAKKER. 1976. Functional responses in invertebrates. Netherlands J. Zool. 26: 567-572.

VAN LENTEREN, J. C., AND K. BAKKER. 1978. Behavioral aspects of the functional responses of a parasite (*Pseudeucoila bochei* Weld) to its host (*Drosophila melanogaster*). Netherlands J. Zool. 28: 213-233.

WALDE, S. J., AND W. W. MURDOCH. 1988. Spatial density-dependence in parasitoids. Ann. Rev. Entomology 33: 441-466.