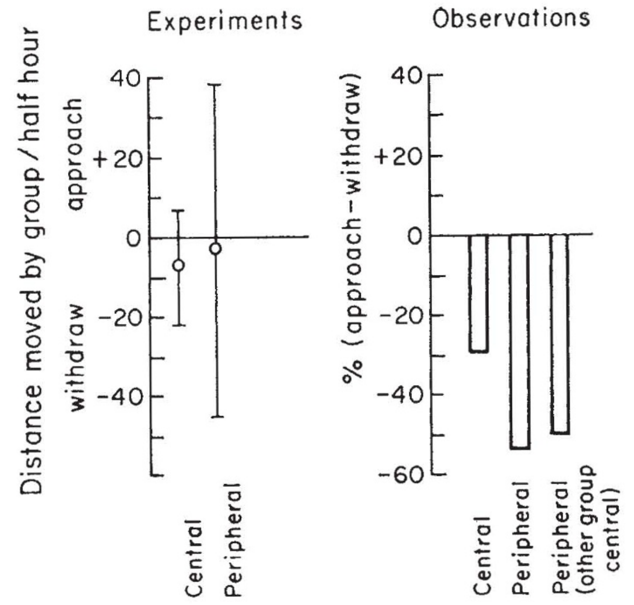


Fig. 3 Responses to whoopgobble calls when group is in the centre or periphery of its home range: comparison of experimental playbacks and naturally occurring calls. Conventions as in Fig. 2. Sample sizes: (experiments) 5, 10: (observations) 7, 30, 8.

of vocaliser, identity and size of vocalising groups, and level and location of resources can be investigated experimentally[6].

This work was supported by a grant from the National Institutes of Health. I thank M. S. Waser for assistance and T. Struhsaker and P. Marler for valuable discussion.

PETER M. WASER

Rockefeller University Field Research Center,
Millbrook, New York 12545

Received February 6; revised March 12, 1975.

[1] Chivers, D. J., *Folia primat.*, **10**, 48–102 (1969).
[2] Ripley, S., New York, in *Social communication among primates* (edit. by Altmann, S.), (University of Chicago, 1967). 237–254.
[3] Marler, P., *Science*, **163**, 93–95 (1969); *Behaviour*, **42**, 175–197 (1973).
[4] Gautier, J. P., *Biol. Gab.*, **5**, 117–145 (1969); *Biol. Gab*, **7**, 230–267 (1971).
[5] Ellefson, J. O., in *Primates: studies in adaptation and variability* (edit. by Jay, P., (Holt, Rinehart, and Winston, New York, 1968).
[6] Waser, P., thesis, Rockefeller Univ. New York, (1974).
[7] Waser, P., and Floody, O., *Z. Tierpsych.*, **35**, 85–101 (1974).
[8] Chalmers, N., *Folia primat.*, **9**, 258–280 (1968).

Dynamic complexity in predator-prey models framed in difference equations

THE complicated dynamics associated with simple first-order, nonlinear difference equations have received considerable attention (refs 1–4 and R. M. May and G. F. Oster, unpublished). In an ecological context, equations of this type provide a powerful and realistic means of modelling the behaviour of animal populations with non-overlapping generations, typified by many arthropods in temperate regions. May[4] has shown that such models, incorporating density dependence, have three regimes of dynamic solution in their parameter space, namely (1) a stable equilibrium point; (2) bifurcating cycles of period 2^n, $0 < n < \infty$, where n is a positive integer and (3) behaviour which has been termed chaotic, that is, cycles of any integral period or complete aperiodicity, depending on the initial conditions. May[4] has indicated that such complexity can also occur in the wider context of competition between two species, described by two first-order, nonlinear difference equations of similar form to those governing single-species growth.

In this paper, we illustrate the dynamics of a predator–prey model for populations with non-overlapping generations and show that the model yields patterns of behaviour closely analogous to those observed in the first-order (single-species) situation. These may be compared with results on the type of solution possible in predator–prey models framed as differential equations, which guarantee for a large class of models the existence of either stable equilibria or stable limit cycles[5].

The model we chose to investigate is an extension of the familiar Nicholson–Bailey host-parasite equations[6], which purport to describe the interactions between a population of herbivorous arthropods and their insect parasitoids. The original model is unstable for all parameter values[7]. Our extension, which eliminates this unrealistic behaviour, involves the inclusion of density-dependent self-regulation by the prey. The equations of the model are:

$$\begin{aligned} H_{t+1} &= H_t \exp[r(1 - H_t/K) - aP_t] \\ P_{t+1} &= \alpha H_t[1 - \exp(-aP_t)] \end{aligned} \qquad (1)$$

The self-regulation of the prey in the absence of predators has already been documented by May[4], with a stable equilibrium point for $0 < r < 2$, bifurcating cycles for $2 < r < 2.692$ and chaos for $2.692 < r$. The choice of an identical form of density dependence in a predator–prey model therefore enables us to compare the parameter values at which chaotic behaviour ensues, and hence indicate whether the introduction of a predator makes the onset of chaotic behaviour more or less likely.

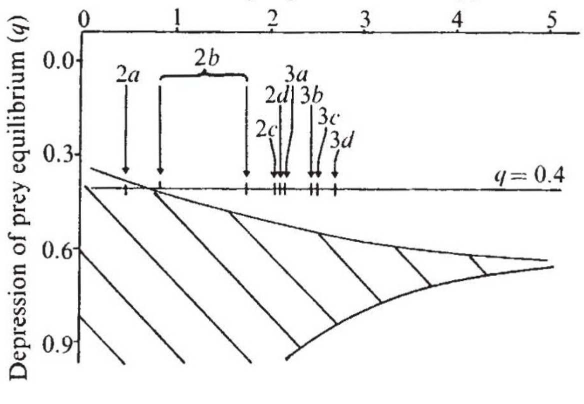
Analysis of the local stability properties of the model was performed using the method of Beddington[8]. The conditions for stability were found to depend on whether the roots of the equation

$$\begin{aligned} &\lambda^2 - \lambda(1 - r + \varphi) + (1 - rq)\varphi + r^2q(1 - q) = 0 \\ \text{where} \quad &\varphi = r(1 - q)/\{1 - \exp[-r(1 - q)]\} \end{aligned} \qquad (2)$$

lay within the unit circle. The parameter q is defined as the equilibrium prey population density, H^*, divided by the carrying capacity K; q is therefore a measure of the extent to which the predator can depress the prey below its carrying capacity. Application of the Schur-Cohn criteria[9] to equation (2) yields the demarcation of stable from unstable parameter space: this is illustrated in Fig. 1. Extensive numerical investigations within the domain of stable parameter space indicate that the equilibrium point is globally stable, although a Lyapunov function for the system has not been constructed.

Before considering the non-equilibrium behaviour of the model, we digress to point out the difficulties involved in recognising complicated dynamic behaviour in second-order models. *A priori*, we would expect limit cycles of integer period to be rare; it is more likely that the periods of any limit cycles that do exist will be predominantly non-integral, or indeed

Fig. 1 Stability boundaries for the predator–prey model, equation (1). The equilibrium point is stable inside the hatched area only. Simulations for the points marked on the transect $q = 0.4$ are illustrated in Figs 2 and 3.



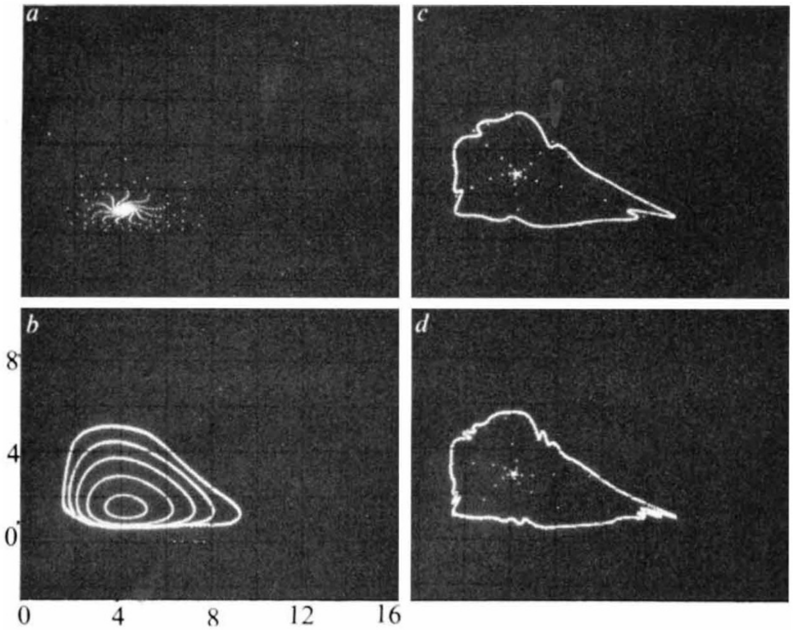


Fig. 2*a*, The realised trajectory for the model in the domain of oscillatorily stable parameter space $r = 0.5$, initial densities $H_0 = 8.6$, $P_0 = 1.1$. The plot indicates the time path followed to the equilibrium point. $q = 0.4$, $\alpha = 1$, $K = 10$ throughout Figs 2 and 3. All plots are shown to the same scale. *b*, A succession of closed trajectories, realised after varying time periods from the initial point $H_0 = 3$, $P_0 = 3$. The parameter values, moving outward from the smallest curve, are (1) $r = 0.75$, (2) $r = 0.9$, (3) $r = 1.1$, (4) $r = 1.35$, (5) $r = 1.8$. Simulations indicated that the populations homed in on the closed curve trajectories from all regions of phase space. *c*, The realised trajectory of the model with $r = 2.1$ and initial densities close to equilibrium. The final closed curve is substantially different from the family of curves illustrated in *b*. *d*, as *c* with $r = 2.15$. The closed curve has now developed five kinked areas where the population points occur more frequently. Ordinates and abscissae are H_t and P_t respectively.

irrational. Correspondingly, limit cycles will be extremely difficult to detect simply by viewing the trajectory of one or both populations as a function of time. At most, this will permit a distinction only between integer cycles and other behaviour. In general, we would expect the existence of limit cycles in second-order models to be characterised by the populations following closed trajectories in phase space. We have performed our numerical simulations with this in mind: the non-equilibrium behaviour of the model was investigated by plotting the realised trajectory in phase space, using a storage oscilloscope on line to a computer.

The results of the simulations are presented in the context of a transect in parameter space (Fig. 1). The various types of behaviour of the model, corresponding to points on the transect, are illustrated in Figs 2 and 3. An initially stable point is succeeded by a hierarchy of stable limit cycles of increasing, non-integral period and increasing complexity, ultimately breaking down to cycles of integral period k (where $k = 5$), which then bifurcate to cycles of period $2k, 4k, \ldots, 2^n k$. These are followed by a regime of complex, but bounded, behaviour consisting either of limit cycles of high integral period ($2^n k > 10{,}000$) or of aperiodic chaos. The implications of the model in other zones of parameter space will be discussed elsewhere. The most important difference in these regions hinges on the basic period, k, of the integer cycles. Clearly, when compared with May's[4] results for a single-species model, the introduction of a predator has produced qualitatively new behaviour.

In the particular example illustrated predation has resulted in chaotic or high period limit cyclic behaviour for values of the prey growth rate parameter r only slightly below that in the single-species case. For other values of the parameter q however, we find that the onset of chaos occurs at values of r both significantly below (for example, $q = 0.30$, $r \approx 2.1$) and significantly above (for example, $q = 0.50$, $r \approx 3.3$) that of the single-species case ($r = 2.692$). A rough characterisation of what is obviously a somewhat complicated relationship is that the further the predator depresses the prey below its carrying capacity, the lower is the growth rate required for chaos. As a caveat, we note that the introduction of thresholds into population models (for example, an Allee[10] effect) will necessarily exclude the high amplitude limit cycles and larger chaotic domains. Nevertheless, our preliminary studies suggest that models incorporating such thresholds display effectively similar patterns of behaviour.

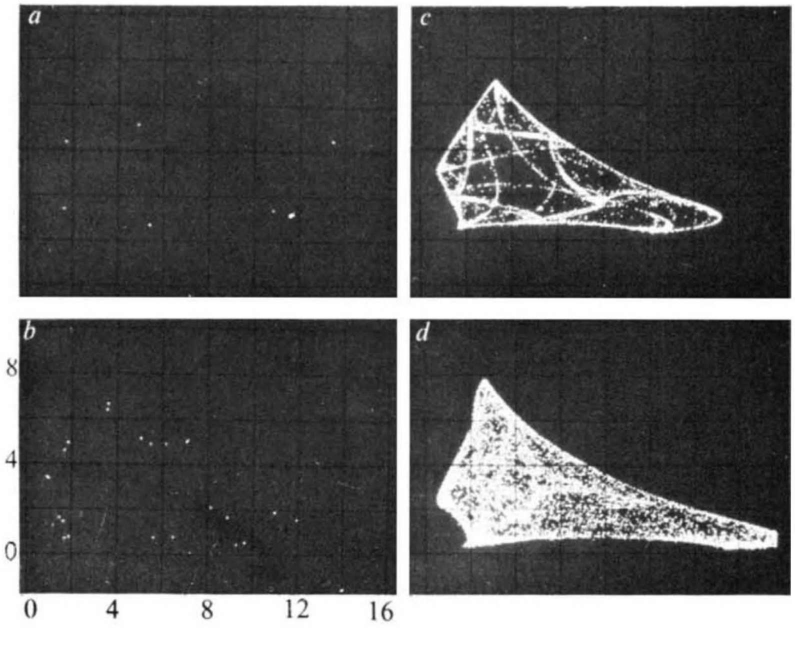


Fig. 3 *a* and *b*, Point limit cycles of period 5 and 20 realised after 100 iterations of the model from an initial point. Parameter values: (*a*) $r = 2.2$; (*b*) $r = 2.488$. Between these two points in parameter space lies a domain of stable ten-point cycles and for $r > 2.488$ cycles of period 40, 80 . . . have been found. *c* and *d*, Realisation of 10,000 points from the population trajectory started at initial densities $H_0 = 3$, $P_0 = 3$. *c*, $r = 2.55$. The structured, bounded figure shown possesses well defined areas where no points appear for iterations > 100,000. *d*, $r = 2.75$. Increased numbers of iterations yield a dense cover over the whole figure, within the limits of the oscilloscope resolution. Ordinates and abscissae are H_t and P_t respectively.

The existence of high period cycles or chaotic behaviour in predator-prey models (the distinction is unimportant for practical purposes) may be of considerable importance in interpreting the patterns of fluctuation shown by many arthropod populations in the field, as this implies the possibility of long term coexistence between predator and prey within well defined limits, but of a seemingly random nature. The temptation to ascribe such behaviour to 'environmental fluctuation' is obvious. Thus a recognition that such behaviour may occur in an extremely simple, entirely deterministic predator-prey model is of considerable importance.

We thank Professor Robert May for discussions.

J. R. BEDDINGTON
C. A. FREE
J. H. LAWTON

Department of Biology,
University of York,
Heslington,
York YO1 5DD, UK

Received March 3; accepted March 16, 1975.

[1] Li, T.-Y., and Yorke, J. A., *SIAM J. math. Anal.*, (in the press).
[2] Lorenz, E. N., *J. atmos. Sci.*, **20**, 448–64 (1963).
[3] Lorenz, E. N., *Tellus*, **16**, 1–11 (1964).
[4] May, R. M., *Science*, **186**, 645–7 (1974).
[5] May, R. M., *Science*, **177**, 900–2 (1972).
[6] Nicholson, A. J., and Bailey, V. A., *Proc. zool. Soc. Lond.*, 551–98 (1935).
[7] Hassell, M. P., and May, R. M., *J. anim. Ecol.*, **42**, 693–726 (1973).
[8] Beddington J. R., *J. theor. Biol.*, **47**, 65–74 (1974).
[9] Marden, M., *The Geometry of the Zeros of a Polynomial in a Complex Variable* (American Mathematical Society, New York, 1949).
[10] Allee, W. C., *Social Life of Animals* (Heinemann, London, 1939).

Prey death rates and rate of increase of arthropod predator populations

CENTRAL to our understanding of predator–prey dynamics is the relationship between the death rate imposed on the prey by the predators and the rate of increase, or numerical response, of the predator population. Most of the familiar mathematical models of predator–prey systems involve the assumption that there is a simple linear relationship between the number of prey killed and predator reproduction[1–4]. Although this assumption is valid for most insect host–parasitoid systems[2], the rate of increase of other predatory arthropods is a more complex function of the prey consumed. For successful reproduction, each instar must find and eat several prey to complete development. Thus the predator rate of increase will depend on the duration of, and the survival rate within each instar and the fecundity of the adults. Where models for the predator rate of increase have incorporated more complex nonlinear relationships[5,6], these relationships are of too abstract a character to allow simple experimental corroboration or refutation. In this paper we propose models that characterise the effect of prey consumption on the components of the predator rate of increase that are specifically designed to relate our hypotheses to field or laboratory data.

Much of the data available for testing these models comes from experiments in which a number of predators are exposed to a variety of prey densities. Thus it is necessary to utilise an expression for the number of prey attacked in terms of prey density N and predator density P. Indeed this is ultimately the form in which population models are likely to be framed. An instantaneous form for the number of prey attacked per predator, N_a, in time T assuming random search and random distribution of prey is, with unit area

$$N_a = aNT/[1+aT_hN+bT_w(P-1)] \qquad (1)$$

where a defines the rate of encounters between predators and prey, T_h is the handling time, b the encounter rate between predators and T_w the time wasted on an encounter between predators[7]. In many cases the assumptions of random search and random prey distribution are invalid[2,8] and in these situations a and b will be functions of the relative distribution of predator and prey.

For simplicity, and because this is the most usual type of experimental design, we explore the relationship between the prey death rate defined by equation (1) and the predator rate of increase for a single predator confronting a variety of prey densities. This simplifies equation (1) to

$$N_a = aNT/(1+aT_hN) \qquad (2)$$

the well known 'disc equation' of Holling[9,10].

Energetic considerations demand that a predator must allocate at least some food for maintenance. Accordingly this determines a threshold below which growth will not take place and eggs will not be produced. The growth rate of a predator g and the fecundity F will therefore be related to the energy intake I from food consumption by essentially similar models; thus

$$g = \delta(I-c) \qquad (3)$$

$$F = \lambda(I-c) \qquad (4)$$

where c is a constant determined by the maintenance energy

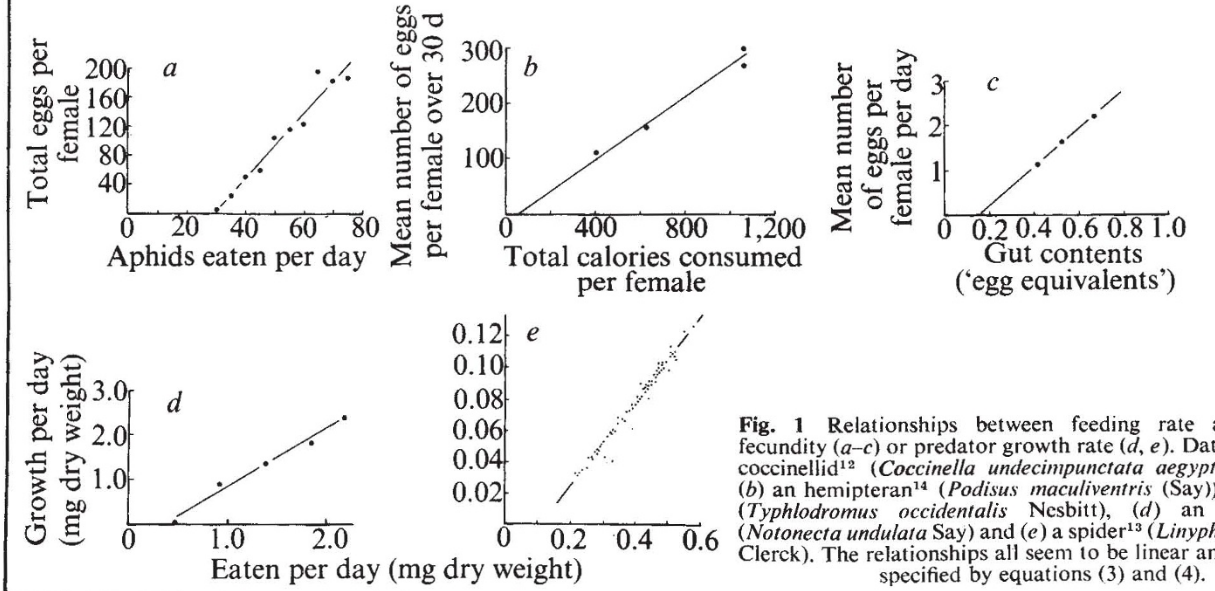


Fig. 1 Relationships between feeding rate and predator fecundity (*a–c*) or predator growth rate (*d*, *e*). Data are for (*a*) a coccinellid[12] (*Coccinella undecimpunctata aegyptiaca* Reiche), (*b*) an hemipteran[14] (*Podisus maculiventris* (Say)), (*c*) a mite[16] (*Typhlodromus occidentalis* Nesbitt), (*d*) an hemipteran[17] (*Notonecta undulata* Say) and (*e*) a spider[13] (*Linyphia triangularis* Clerck). The relationships all seem to be linear and of the form specified by equations (3) and (4).