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AUTUMN COURSE ON MATHEMATICAL ECOLOGY

(16 November - 10 December 1982)

COMMUNITY DYNAMICS IN A SPATIALLY HOMOGENEOUS ENVIRONMENT

Part 1: Introduction to Communities

Part 2: Predation

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COMMUNITY DYNAMICS IN A SPATIALLY HOMOGENEOUS ENVIRONMENT

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COMMUNITY DYNAMICS IN A SPATIALLY
HOMOGENEOUS ENVIRONMENT

1. Introduction to Communities

Populations do not exist as isolated entities in a physical environment. They interact with other biological populations on a regular long term basis and, because of these interactions, often coevolve as an ecological unit. An assemblage of two or more biotic populations is called a community. The simplest structure, one composed of two species, and the possible interactions between these two components will be discussed first. There exist traditional classifications of two populations in terms of their interactions and this will be the point of departure for our notes. These distinctions, however, are certainly difficult to make since roles can depend upon life cycle stage, environment, and other circumstances.

1.1 Predation

The resource-consumer interaction described previously is an example of a more general two population interaction called predation. One population, called the predator population, utilizes the other population, called the prey, as a resource. The association is traditionally viewed as "beneficial" from the prey to the predator and as "negativistic" from predator to the prey. From an energy flow viewpoint, a diagram of this association is given in Figure 1.1.

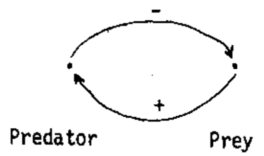


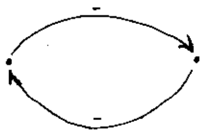
Fig. 1.1 The signs represent the energy flow in the predator-prey influence diagram.

From a modelling perspective, the predator-prey interaction can result in a negative per capita growth rate r in the prey population. If r remains negative then extinction of the population should result. This arrangement would not be beneficial to the predator population if it also went to extinction. What is the purpose of predator-prey associations? If there were not an advantage to the system, these interactions certainly would have gone to extinction by now. There are some obvious system benefits; predation usually is heaviest on the most susceptible individuals in the prey population such as the young, the old, and the weak. The removal of these individuals strengthens the prey population. There are some, perhaps not so obvious, advantages to predation. For example, Dyer (1980) has demonstrated that grazing can stimulate growth of the grazed plant species. Even more remarkable is the manner in which this astimulation occurs; the saliva of some herbivores can contain a hormone that initiates plant growth.

The way that a predator population reacts to a density of prey is the predator functional response. Examples of the typical types of functional responses that exist in the literature are those listed under resource-consumer interactions (Section 4 in the Population Ecology Notes): linear, sigmoid, and hyperbolic.

1.2 Competition

Section 2.1 describes the intraspecific competition between individuals of the same population for a set of resources. If two species must struggle for the same resources then interspecific competition results. Again, from an energy flow perspective, an influence diagram representing interspecific competition has each component having a negative influence upon the other. (Figure 1.2)



Competitor 1 Competitor 2

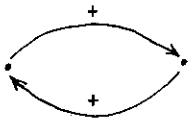
Fig. 1.2 An influence diagram for a community composed of two competitors.

As we argued in the predation case, competition must eventually confer some advantage to the system.

It is often convenient for modelling purposes to distinguish between two aspects of competition: exploitation and interference. Interference competition refers to a mechanism, usually behavioral, that keeps a competitor from using the available resources. Exploitation competition occurs when a competitor actually utilizes the available resource.

1.3 Cooperation

Another type of community which we shall consider is represented by the influence diagram in Figure 1.3.



Cooperator 1 Cooperator 2

Fig. 1.3 An influence diagram for energy flow in a cooperative community.

These cooperative communities exist for the mutual benefaction of each cooperator species.

1.4 Quantitive Predator-Prey Communities

Two of the figures in the Section 1.4 of the Population Dynamics Notes, namely Fig. 1.16 representing the dynamics of the lynx and snowshoe hare and Fig. 1.17 on the bean weavil and the wasp, should probably be viewed as communities not populations. There seems to be some question about the strength of the interaction between the lynx and the hare which prompted the word "probably" in the previous sentence. The lynx is a predator of the hare but it is doubtful that the predation pressure is of sufficient magnitude to cause the oscillations of the hare observed in Fig. 1.16 (e.g. Hutchinson, 1978).

Other classical laboratory predator-prey communities include the ciliates Paramecium and Didinium. D.nasutum is considerably larger than P.candatum and Didinium will in an unrestricted aquatic environment, consume all the Paramecium and then go to extinction (Luckinbill, 1973). ~~Holding~~ Adding methyl cellulose to the medium (which increases the viscosity of the liquid) and decreasing the food supply of the Paramecium will allow persistence of the community (Fig. 1.4; from Maynard Smith, 1974).

The oscillations present in each of these examples seems to be an important characteristic of many laboratory predator-prey communities (although see Section 2.4).

Competitive Communities

Figures 1.5 and 1.6 represent the dynamics of competitive communities.

Figure 1.5 gives the time evolution of a community composed of Paramecium aurelia and Glaucoma scintillans. The phase plane diagrams of several of these communities are indicated in Fig. 1.7. This system is discussed in more detail in Section 3.4.

Fig 1.6 represents another classical example of competition - Parks b~~i~~eetles

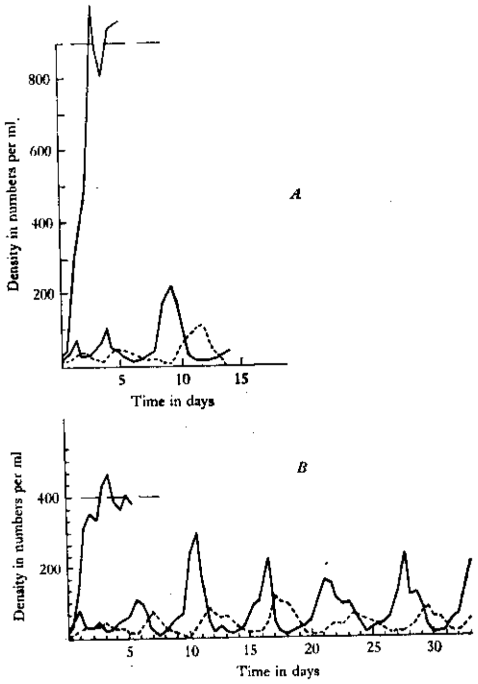


Figure 1.4. Coexistence of Paramecium aurelia (full line) and Didinium nasutum (broken line), after Luckinbill (1973). A, medium with methyl cellulose; B,medium with methyl cellulose and reduced food for prey. In each graph, the upper full line is for P.aurelia on its own.

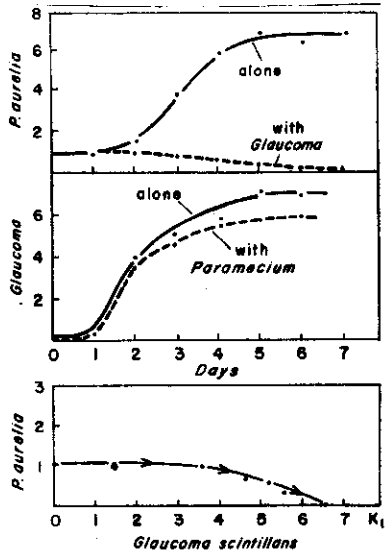


Figure 1.5. Upper panel, Paramecium aurelia cultivated without (solid line) and with (Broken line) Claucoma scintillans; middle panel. G.scintillans cultivated without (solid line) and with (broken line) P.aurelia; bottom panel, phase plane trajectory. (Gause modified).

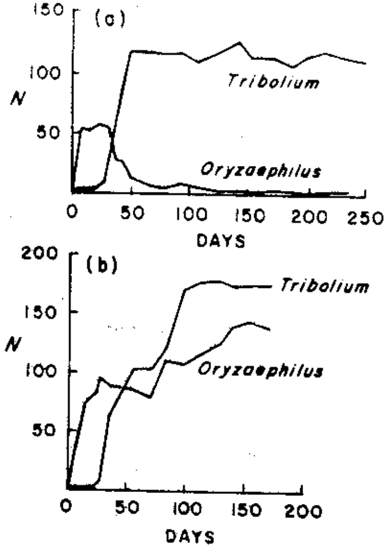


Figure 1.6. (a) Populations of the two grain beetles, Tribolium confusum and Oryzaephilus surinamensis, cultivated together in flour; (b) the same when short lengths of capillary tubing are mixed with the flour (Crombie).

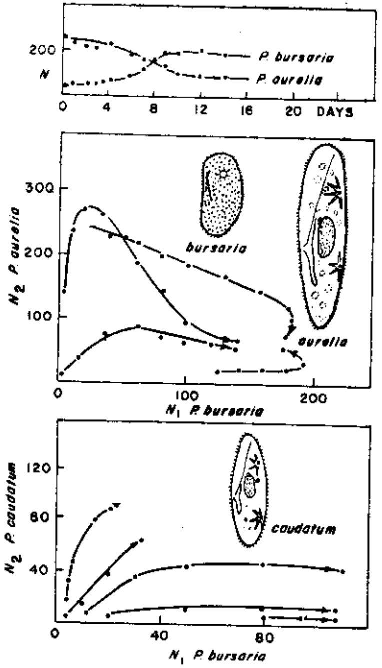


Figure 1.7. Upper panel, population of Paramecium aurelia and of P.bursaria introduced into the P.aurelia culture. Middle panel, trajectories converging on a stable point when P.aurelia and P.bursaria are cultivated together. Bottom panel, trajectories when P.caudatum, much more sensitive to metabolic products, is cultivated with P.bursaria (Gause, modified).

Figure 1.8 demonstrates the dynamic behaviour of a community of barnacles of the genera Balanus and Chthamalus who are competing for space in an interidal community. This community, studied by Connell (1961), is an excellent representative of competition in nature.

Cooperative Communities

The dynamics of completely cooperative communities are scarce in the literature. When cooperative communities are discussed many are mentioned: lichen (fungus-algae), clown fish - sea anemone, cleaner wrasse - large fish, ant-Acacia, nitrogen fixing bacteria-legumes, mycorr hizal fungi-plants, and others. However, in none of the standard tests I investigated is there any graphic illustration of the dynamics of a cooperative community. Some theoretical aspects will be developed later.

1.5 Two Species Community Models

Let $x_1 = x_1(t)$ and $x_2 = x_2(t)$ be measurements of two populations at time t; for example, they might denote population numbers, biomass, or densities. It is reasonable to assume that the birth rate, B_i, and the death rate, D_i, of population x_i, are functions not only of x_i but also the other population as well:

$$B_i = B_i(x_1,x_2), \quad D_i = D_i(x_1,x_2), \quad i = 1,2.$$

As another initial hypothesis, it is assumed that the per capita growth rate is the difference between birth rate and death rate. The resulting model is

$$\frac{1}{x_1}\frac{dx_1}{dt} = B_1(x_1,x_2) - D_1(x_1,x_2) \equiv f_1(x_1,x_2)$$

$$\frac{1}{x_2}\frac{dx_2}{dt} = B_2(x_1,x_2) - D_2(x_1,x_2) \equiv f_2(x_1,x_2)$$

or

$$(1.1) \qquad \begin{aligned} \frac{dx_1}{dt} &= x_1f_1(x_1,x_2) \\ \frac{dx_2}{dt} &= x_2f_2(x_1,x_2) \end{aligned}$$

For convenience, it is assumed that the functions f_i have continuous partial derivatives in the two dimensional nonnegative cone $\mathbb{R}_+ \times \mathbb{R}_+$. This particular form of a community model is called a model of Kolmogovov type.

The partial derivatives of f_i determine the classification of the community. These are given in Table 1.4.

	$\frac{\partial f_1}{\partial x_2}$	$\frac{\partial f_2}{\partial x_1}$
Predation	$-$	$+$
Competition	$-$	$-$
Cooperation	$+$	$+$

Table 1.4 The signs of the partial derivatives determine the category of the two species interaction.

The partial derivatives $\partial f_i/\partial x_i$ represent intraspecific competition effects and represent density dependent interactions.

The Kolmogovov model has numerous properties that are useful in analyzing behavior of the community. From the theory of ordinary differential equations, we know that through each point in $\mathbb{R}_+^2 = \mathbb{R}_+ \times \mathbb{R}_+$ there exists a unique trajectory of (1.1). The space $\mathbb{R}_+^2$ is invariant for (1.1); indeed, by the uniqueness of solutions to initial value problems, any trajectory eminating from the first quadrant in x_1-x_2 space, $\{\mathbb{R}_+ - \{0\}\} \times \{\mathbb{R}_+ - \{0\}\}$, remains there for all time. This has implications when extinction is the objective of a study; there is no finite time extinction for populations modelled by (1.1).

1.6 Lotka-Volterra Systems

A simple form of f_i is a linear function: $f_i(x_1,x_2) = a_i + b_{1i}x_1 + b_{2i}x_2$. This traditional hypothesis results in logistic dynamics in the absence of the interacting species and a mass action interaction term. With a linear per capita growth rate, this model is often called a Lotka-Volterra model in reference to the men who first used it to study two dimensional communities.

2. Predation

2.1 Volterra's Principle

V. Volterra, in analyzing a problem posed by D'Ancona, his future son-in-law, concluded that a moderate amount of harvesting of a prey population can, on the average, increase the number of prey and, at the same time, decrease the number of predators in the system. If the level of harvesting is reduced the predator population will increase and the prey population will decrease.

This result was obtained by using the model

$$\begin{aligned} \frac{dx_1}{dt} &= x_1(a_1 - b_1x_2) \\ \frac{dx_2}{dt} &= x_2(-a_2 + b_2x_1) \end{aligned} \tag{2.1}$$

This system has two equilibria: I: $(0,0)$, II: $\left(\frac{a_2}{b_2}, \frac{a_1}{b_1}\right)$. Linearization shows that I is unstable; but that no conclusion can be drawn about II. Hence, we must work harder to analyze II. Fortunately, (2.1) can be written as a first order system and then solved in a closed form by using the variables separable method. This leads to the solution

$$\frac{x_1^{a_2}}{e^{b_2 x_1}} \; \frac{x_2^{a_1}}{e^{b_1 x_2}} = c$$

where: c is a constant. It can be shown that this relation defines a closed curve in $x_1 - x_2$ space and, as such, represent periodic solutions of (2.1) each of which contains II in its interior. The equilibrium II is the time average of each periodic trajectory: e.g. $a_2/b_2 = \frac{1}{p} \int_0^p x_1(s)ds$ where p is the period of the trajectory.

To obtain Volterra's Principle, suppose that harvesting is indiscriminant and results in a fixed proportion (hx_i) of both predator and prey being removed. The model (2.1) with harvesting is

$$\begin{aligned} \frac{dx_1}{dt} &= x_1(a_1 - h - b_1x_2) \\ \frac{dx_2}{dt} &= x_2(-a_2 - h + b_2x_1). \end{aligned} \tag{2.2}$$

The interior equilibrium of (2.2) is $\left(\frac{a_2 + h}{b_2}, \frac{a_1 - h}{b_1}\right)$ so, on the average, indiscriminate harvesting results in an increase in prey species and a decrease in predators.

If the prey species is desirable, as it was in Volterra's situation of edible fish (prey) and selachians (predator), harvesting is desirable. On the other hand, if the prey species is undesirable, as occurred with the prey population of Cottony Cushion scale insects (Icerya purchasi) and the predator populations of a ladybird beetles (Novius cardinalis), harvesting is not beneficial. This predator-prey system was causing little difficulty for the California citrus growers until indiscriminate harvesting by insecticide (DDT) was initiated. As predicted, the prey population exploded and troubles ensued.

2.2 Asymptotic Stability in Predator - Prey Models

Harrison (1979), expanding on a technique of Hsu (1978), has discussed the global asymptotic stability of an equilibrium of a general predator-prey model. The model is

$$\begin{aligned} \frac{dx_1}{dt} &= a(x_1) - f(x_1)b(x_2) \\ \frac{dx_2}{dt} &= n(x_1)g(x_2) + c(x_2) \end{aligned} \tag{2.3}$$

where f and g are positive on $\mathbb{R}_+$; $a(x_1)$ represents the growth rate due to all factors except predation; $c(x_2)$ represents the rate of increase or decrease of the predator: $n(x_1)$ and $b(x_2)$ are assumed to be nondecreasing functions; $f(x_1)\, b(x_2)$ is the functional response of the predator and $n(x_1)\, g(x_2)$ is the numerical response of the predator.

Let (x_1^*, x_2^*) be a positive equilibrium for the system (2.3) and assume that

$$\begin{aligned} &[n(x_1) - n(x_1^*)]\,[x_1 - x_1^*] > 0, \quad x_1 \neq x_1^*; \\ &[b(x_2) - b(x_2^*)]\,[x_2 - x_2^*] > 0, \quad x_2 \neq x_2^*. \end{aligned}$$

Theorem 2.1 If in a neighborhood of (x_1^*, x_2^*), $a(x_1)/f(x_1)$ and $c(x_2)/g(x_2)$ are both nonincreasing with one strictly decreasing, then the equilibrium (x_1^*, x_2^*) is asymptotically stable.

If, in addition to all previous hypotheses,

$$\begin{cases} a(x_1) \geq b(x_2^*)f(x_1) & 0 < x_1 < x_1^* \\ a(x_1) \leq b(x_2^*)f(x_1) & x_2^* < x_1 < \infty , \end{cases}$$

$$\begin{cases} c(x_2) \geq -n(x_1^*)g(x_2) & 0 < x_2 < x_2^* \\ c(x_2) \leq -n(x_1^*)g(x_2) & x_2^* < x_2 < \infty , \end{cases}$$

with the inequalities strict according to whether $a(x_1)/f(x_1)$ or $c(x_2)/g(x_2)$ is strictly decreasing, then (x_1^*, x_2^*) is globally asymptotically stable.

Example: The Lotka-Volterra predator-prey system

$$\frac{dx_1}{dt} = x_1(a_1 - b_{11}x_1 - b_{12}x_2)$$

$$\frac{dx_2}{dt} = x_2(-a_2 + b_{21}x_1)$$

satisfies the conditions of the Theorem so the equilibrium $\left(\frac{a_2}{b_{21}} = \frac{a_1b_{21} - b_{11}a_2}{b_{21}b_{12}}\right)$ is globally asymptotically stable. The difference between this model and Volterra's model is inclusion of a carrying capacity for the prey species. The behavior of global asymptotic stability is contrasted with the neutrally stable (periodic) Volterra model.

Indication of Proof of Theorem.

The function

$$V(x_1,x_2) = \int_{x_1^*}^{x_1} \frac{n(s) - n(x_1^*)}{f(s)}\, ds + \int_{x_2^*}^{x} \frac{b(s) - b(x_2^*)}{g(s)}\, ds$$

is a Liapunov function for (13-1). Since $\dot{V}$ can only be zero at x_1^* or x_2^*, LaSalle's Theorem on the extent of asymptotic stability implies all solutions approach (x_1^*, x_2^*) as t approaches infinity.

2.3 Ecological Cycles in Predator-Prey Models

Periodic variation in communities is a documented phenomenon (Figures 1.14 - 1.18). Many of these variations do not correlate with known periodic exogeneous forces such as diel cycles or seasonal cycles. Some of these cycles occur in predator-prey relationships; for example, see Figures 1.16 (lynx-hare system) and 1.17 (wasp-bean weevil system). Many explanations of cyclic behavior have been suggested ranging from poor data to the hypothesis that the predator cycle has nothing to do with the prey cycle. These points will not be belabored as it is my purpose to demonstrate the existence of a reasonable community model that exhibits cyclic behavior. To this end, the Kolmogovov model (1.1) is considered. The Lotka-Volterra model, with its simple nonlinearities, cannot have a limit cycle.

A subset of the following hypotheses can lead to cyclic system behavior.

$$\text{(H1)} \qquad \frac{\partial f_1}{\partial x_2} < 0.$$

This is a portion of the assumption that the system is of predator-prey type; (H1) implies that an increase in the predator population decreases the percapita growth rate of the prey.

$$\text{(H2)} \qquad \frac{\partial f_2}{\partial x_1} < 0.$$

This completes classification as a predator-prey system and states that an increase in the prey population benefits the predator population.

$$\text{(H3)} \qquad \frac{\partial f_1}{\partial x_1} < 0$$

Density dependent effects are imposed independent of population densities.

$$\text{(H3a)} \qquad \left.\frac{\partial f_1}{\partial x_1}\right|_{x_2=0} < 0.$$

An increase in the prey population has an adverse effect upon the prey growth rate when there are no predators around.

$$\text{(H4)} \qquad \frac{\partial f_2}{\partial x_2} < 0$$

The predator population also is limited by effects of crowding.

$$\text{(H5)} \qquad f_1(0,x_2^T) = 0 \quad \text{for some} \quad x_2^T > 0.$$

There is a size of the predator population, x_2^T, beyond which the prey population is decreasing even when the prey population is small.

$$\text{(H6)} \qquad f_1(x_1^c,0) = 0 \quad \text{for some} \quad x_1^c > 0.$$

There exists a carrying capacity, x_1^c, for the prey population in the absence of the predator population. For $x_1 > x_1^c$, the growth rate of the prey is decreasing by (H3)

$$\text{(H7)} \qquad f_2(x_1^T,0) = 0 \quad \text{for some} \quad x_1^T > 0.$$

There exists a threshold prey level necessary to support the predator population.

(H8) $x_1^c > x_1^T$

If this inequality is not satisfied, extinction of the prey population will occur.

(H9) The equation $f_1(x_1,x_2) = 0$ can be solved uniquely, via the Implicit Function Theorem, for $x_2 = h(x_1)$ where $h \in C^1[0,x_1^c]$, $h' < 0$, $h(0) = x_2^T$, $h(x_1^c) = 0$.

This hypothesis is, of course, related to (H3), but it is given to specify the prey isocline. The curve $x_2 = h(x_1)$ can be interpreted as the carrying capacity of the predator population at density x_1 of the prey population.

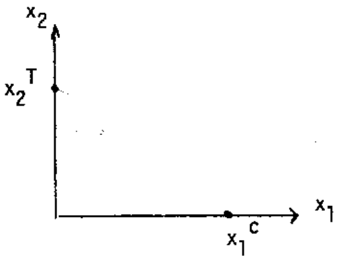


Fig. 2.1 The prey isocline defined by $x_2 = h(x_1)$.

(H10) $f_2(x_1,x_2) = 0$ can be solved uniquely for $x_1 = g(x_2)$ where $g \in C^1[0,\infty)$, $g' > 0$, and $g(0) = x_1^T$

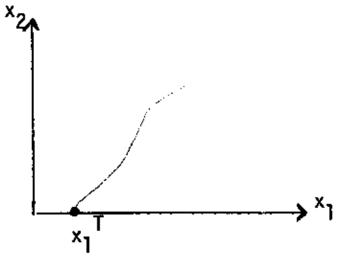


Fig. 2.2 The predator isocline defined by $x_1 = g(x_2)$

(H11) $x_1 \frac{\partial f_1}{\partial x_1}(x_1,x_2) + x_2 \frac{\partial f_1}{\partial x_2}(x_1,x_2) < 0$

Mathematically, this condition states that the change in f_1 along the outward normal vector eminating from the origin is negative.

(H12) $x_1 \frac{\partial f_2}{\partial x_1}(x_1,x_2) + x_2 \frac{\partial f_2}{\partial x_2}(x_1,x_2) > 0$

(H13) The prey isocline curve has a hump, Figure 2.3, (Rosenzweig, 1969)

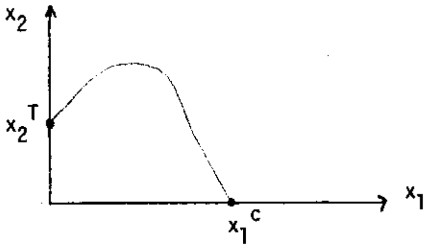


Fig. 2.3 The prey isocline has a hump.

This is an analogue of (H9) by replacing (H3) by (H3a).

(H14) $(x_1 - x_1^c)\, f_1\, (x_1,0) < 0$

(H15) $(x_2 - x_2^T)\, f_1\, (0,x_2) < 0$

(H16) $(x_2 - x_2^c)\, f_2\, (x_1,0) > 0$

These last three conditions guarantee that equilibria on extinction axes are unique.

Theorem 2.2 (Limit Cycles). Let f_1, f_2 satisfy (H1), (H2), (H3a), (H4) - (H8), and (H13). In addition, suppose that the prey-predator isoclines have the configuration in Figure 2.4.

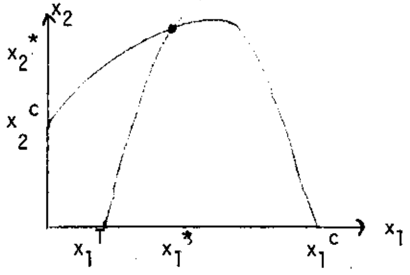


Figure 2.4

and that $a + d > 0$, $ad - bc > 0$ where

$$a = x_1^* \frac{\partial f_1}{\partial x_1} (x_1^*, x_2^*)$$

$$b = x_1^* \frac{\partial f_1}{\partial x_2} (x_1^*, x_2^*)$$

$$c = x_2^* \frac{\partial f_2}{\partial x_1} (x_1^*, x_2^*)$$

$$d = x_2^* \frac{\partial f_2}{\partial x_2} (x_1^*, x_2^*)$$

Then, system (8-1) has a limit cycle in $\mathbb{R}_+^2$.

Indication of Proof

The retangle formed by the coordinate axes and the lines $x_1 = x_1^c$ and $x_2 = x_2^i$ where x_2^i is given by $f_2(x_1^c, x_2^i) = 0$. The ω-limit set of any trajectory, $\omega(\Gamma^+)$, in this retangle is a limit cycle. This may be demonstrated by showing that $\omega(\Gamma^+)$ contains no critical point. The equilibrium (x_1^*, x_2^*) is repellent; all extinction type equilibria are hyperbolic. To eliminate the possibility of a cycle graph, note that (x_1^*, x_2^*) cannot be in a cycle graph and if the extinction equilibria are in the cycle graph, $\omega(\Gamma^+)$ is unbounded. Hence, $\omega(\Gamma^+)$ is a limit cycle.

Another closely related result is

Theorem 2.3 Let hypotheses (H1), (H4), (H5), (H6), (H7), (H8), (H11), (H12), (H14), (H15), and (H16) be satisfied. In addition, suppose $f_1(0,0) > 0$ [that is, for small populations of predator and prey, the prey population increases]. Then, the predator-prey model (8-1) has a unique equilibrium with positive components. If this equilibrium is not asymptotically stable there is a limit cycle in $\mathbb{R}_+^2$ which is asymptotically stable from the outside.

Indication of Proof

For complete details see Albrecht et al. (1974). The hypotheses (H1), (H5), (H6), (H14) and (H15) imply the existence of a prey isocline,

$x_2 = h(x_1)$, as described in (H9); similarly, the existence of a predator isocline $x_1 = g(x_2)$ with the properties as indicated in (H10) follows. Since $x_1^c > x_1^T$, a single positive equilibrium exists. It can be shown that any trajectory must cycle about the equilibrium. The limit set could be the equilibrium or a limit cycle which is stable from the outside.

Remark. Another mathematical technique that is employed to generate cycles is a Hopf bifurcation. Waltman (1964) used this method to find periodic solutions to the Kolmogovov predator-prey system

$$\frac{dx_1}{dt} = \alpha x_1 \; f_1(x_1,x_2)$$

$$\frac{dx_2}{dt} = x_2 \; f_2(x_1,x_2)$$

There are many recent results that generate cyclic behavior by applying a bifurcation theorem (see Freidman, 1980).

Example. Another two dimensional model that uses logistic dynamics and mass action interactions for the prey population while the carrying capacity of the predator is a function of prey density is due to Leslie (1948). His model is

$$\frac{dx_1}{dt} = a_1x_1 - b_1x_1^2 - b_{12}x_1x_2$$

$$\frac{dx_2}{dt} = a_2x_2 - b_2x_2^2/x_1$$

This density dependence is probably best understood by considering the ratio of the number of prey per predator. If x_2/x_1 is small (so that there are many prey per predator) then the predators grow exponentially. If x_2/x_1 is large (that is, there are few prey per predator), in particular, above a_2/b_2, then the predator population decreases.

The Liapunov function of Hsu-Harrison can be used to show that Leslie's model is globally symptotically stable.

2.4 Do Predator - Prey Systems Approach Equilibria or Cycle?

Tanner (1975) studied numerous predator-prey communities and found evidence of stable equilibrium communities and cyclic behavior. While the majority of the systems he reviewed exhibited a dynamic behavior that approached an equilibrium, there was some evidence for factors that determine cycles. A propensity for a stable limit cycle seems to exist when the intrinsic growth rate of the prey population exceeds that of its predators. A prey population with a relatively high growth rate in an environment with a relatively large carrying capacity is needed for cyclic behavior.

Table 2.1. Impressionistic summary of life history data for 8 natural prey-predator systems. (After Tanner, 1975).

Prey-predator	Geographical location	Apparent dynamical behavior
sparrow - hawk	Europe	equilibrium point
muskrat - mink	central North America	equilibrium point
hare - lynx	boreal North America	cycles
mule deer - mountain lion	Rocky Mountains	equilibrium point
white-tailed deer - wolf	Ontario	equilibrium point
moose - wolf	Isle Royale	equilibrium point
caribou - wolf	Alaska	equilibrium point
white sheep - wolf	Alaska	equilibrium point

2.5 Simple Food Chains

A simple food chain is a chain of predator-prey communities where the dynamics of a population is determined by those species occupying the preceding and succeeding trophic levels. For example, the chain composed of a nutrient, a plant population, a herbivore population, and a carnivore population form a simple food chain.

A Lotka-Volterra model of a simple food chain of length n is

$$
\begin{aligned}
\frac{dx_1}{dt} &= x_1(a_{10} - a_{11}x_1 - a_{12}x_2) \\
\frac{dx_2}{dt} &= x_2(-a_{20} + a_{21}x_1 - a_{23}x_3) \\
&\;\;\vdots \qquad\qquad\qquad \vdots \\
\frac{dx_{n-1}}{dt} &= X_{n-1}(-a_{n-1,0} + a_{n-1,n-2}X_{n-2} - a_{n-1,n}X_n) \quad . \qquad l\;c \\
\frac{dx_n}{dt} &= X_n(-a_{n0} + a_{n,n-1}X_{n-1}) \qquad l.c
\end{aligned}
\tag{5.1}
$$

In the preceding model, all parameters are positive with the exception of a_{11} which is nonnegative.

If the resource (lowest) level of the simple food chain has a carrying capacity then solutions of (5.1) with positive initial conditions are bounded. If $a_{11}=0$, then the unbounded growth of the resource is propagated throughout the system. First, the case $a_{11} > 0$ is developed; this model might be applicable in a situation where a resource is limited in supply and all other trophic levels are limited only by the available resource on the preceding trophic level.

Theorem 5.1. All solutions of (5.1) with positive initial conditions are bounded provided $a_{11} > 0$.

<u>Indication of the Proof.</u> The boundedness of the resource level component is readily established by using the comparison principle.

The function $\overset{u}{\checkmark}$ is defined by

$$\overset{u}{\cancel{\mu}}(x) = \sum_{j=1}^{n} \left(\sum_{i=1}^{j-1} a_{i,i+1} \prod_{k=j}^{n-1} a_{k+1,k} \right) x_j$$

satisfies

$$\frac{d\overset{u}{\cancel{\mu}}}{dt}\left(x(t)\right) \leq - m\, u(x(t)) + b$$

where $m = \min_{1 \leq j \leq n} a_{j0}$, $b = \max_{x_1} \left(x,(2a_{10} - a_{11}x_1)/ \prod_{k=1}^{n-1} a_{k+1,k}\right)$

Solving this inequality leads to

$$u(t) \leq u(0) \exp(-mt) + b/\cancel{\mu}m$$

Since u is a linear function of x_i, each component x_i is bounded. The details of this argument as well as those of the next theorem can be found in Gard and Hallam (1979).

Persistence of the simple food chain is determined by a single system level parameter. Here persistence is defined in terms of the survival of the top predator: $\overset{\text{lim}}{\cancel{\ln}} \sup_{t \to \infty} \overset{\text{l.c.}}{\textcircled{X}}_n(t) > 0$. The system level parameter is defined by

✓

$$\overset{\mu}{\cancel{\mu}} = a_{10} - \frac{a_{11}}{a_{21}} \left[a_{20} + \sum_{j=2}^{\overset{k}{\cancel{\ell}}} \left(\prod_{i=2}^{j} \frac{a_{2i-2,2i-1}}{a_{2i,2i-1}} \right) a_{2j,0} \right]$$

✓

$$- \sum_{j=1}^{\ell} \left(\prod_{i=1}^{j} \frac{a_{2i-1,2i}}{a_{2i+1,2i}} \right) a_{2j+1,0}$$

where

✓

$$k = \begin{cases} n/2 & \text{if } n \text{ is even} \\ \frac{n-1}{2} & \text{if } n \text{ is odd} \end{cases} \qquad \ell = \begin{cases} (n/2)-1 & \text{if } n \text{ is even} \\ \frac{n-1}{2} & \text{if } n \text{ is odd} \end{cases}$$

Theorem 5.2. Let $a_{11} > 0$. The simple food chain modelled by (5.1) is persistent if $\mu > 0$; it is not persistent if $\mu < 0$.

<u>Indication of the Proof.</u> Assume for purpose of contradiction that the food chain has a trajectory that satisfies $\lim_{t\to\infty} x_j(t)=0$ for some j, j=1,2,...,n. Then, again applying the comparison principle to (5.1) it follows that

$$\frac{dx_{j+1}}{dt} \leq - \frac{a_{j+1,0}}{2} x_{j+1}$$

and that $\lim_{t\to\infty} x_{j+1}(t) = 0$. In particular, if there is extinction the top predator must go to extinction.

Now, it will be shown, by using a persistence function, that the existence of a trajectory going to extinction leads to a contradiction.

Let $r_i > 0$, i=1,2,...,n and $x > 0$; define

$$\overset{\rho}{\cancel{p}}(x) = \prod_{i=1}^{n} \overset{\text{l.c.}}{\textcircled{X}}_i^{\,r_i}$$

on the set $S = \{x \in R_+^n : 0 < x_n \leq \lambda\}$. By differentiating $\overset{\rho}{p}$ along trajectories on (5.1) and by proper choice of the r_i some cancellations occur. This results in

$$(5.2) \qquad \frac{\overset{d\rho}{dp}}{dt} = \overset{\rho}{p}\left[r_1\mu - r_{n-1}\, a_{n-1,n}\, x_n\right]$$

On S, if λ is sufficiently small, the quantity in the brackets is positive; hence $d\overset{\rho}{p}/dt > o$. This implies that along trajectories $\overset{\rho}{p}(t)$ is increasing; however, when $x_n \to o$ so does $\overset{\rho}{p}$. This contradiction shows that persistence is valid for (5.1).

Conversely if $\mu < o$, then p satisfies (5.2) and

$$\frac{d\rho}{dt} \leq r_1 \mu \overset{\rho}{p}.$$

Thus, $\overset{\rho}{p} \to o$ and an extinction must occur.

What is the situation when there is an apparently unlimited supply of a resource? (i.e. $a_{11} = o$). There are lots of problems with dimensionality in Lotka-Volterra models and here we find some additional ones. The persistence-extinction parameter, μo, of a food chain of length n is

$$\mu o = a_{10} - \sum_{j=1}^{m} a_{2j+1,0} \prod_{i=1}^{j} \frac{a_{2i-1,2i}}{a_{2i+1,2i}}$$

Theorem 5.2. Let $a_{11}=0$. The food chain modelled by (5.1) is persistent provided $\mu o > 0$; it is not persistent if $\mu o < 0$.

Indication of the Proof. In the previous result, the boundedness of solutions was required. ~~As remarked above,~~ it is not possible to demonstrate boundedness of solutions ~~here; however,~~ any solution that goes to extinction, is bounded. This may be proved by using the classical VoHerra au$\overset{x}{s}$iliary function.

$$V(X_1, X_2, \ldots, X_n) = \sum_{i=1}^{n} {}_i(X_i - \beta_i - \beta_i \log X_i/\beta_i)$$

As proper choice of α_i and β_i (see Gard and Hallam (1979) leads to $\dot{V}(t) < 0$ if t is sufficiently large. This shows the boundedness of solutions that go to extinction

The remainder of the argument is much like that of Theorem 5.2 and will be omitted.

An interesting situation results for odd dimensional models without carrying capacity in that persistence can result even though there is no positive equilibrium. In this case, for dimension three it can be shown that the trajectories are unbounded. The final result relates persistence and stability of simple food chains.

Theorem 5.4. Let the system (5.1) with $a_{11} \neq 0$ have a positive equilibrium. Then, this equilibrium is asymptotically stable and the entire positive orthant is the domain of attraction. If the system (5.1) is persistent, it has a positive equilibrium which is globally asymptotically stable.

<u>Indication of the Proof.</u> The first part of the proof is due to Harrison who uses La Salle's Theorem on the extent of asymptotic stability. The proof allows for carrying capacities on each trophic level of the food chain. The system is assumed to be of the form

$$\frac{dx_i}{dt} = X_i\,(b_i + a_{i,i-1} X_{i-1} - a_{ii} X_i - a_{i,i+1} X_{i+1})$$

$$a_{ij} > 0,\ i \neq j,\ a_{11} > 0,\ a_{11} \geq 0.$$

This is rewritten using the equilibrium x^* as

$$\begin{aligned}\frac{dx_i}{dt} &= a_{i,i-1}\left[X_{i-1} - (X_{i-1}^*)\right] \\ &- a_{ii}\left[X_i - (X_i^*)\right] \\ &- a_{i,i+1}\left[X_{i+1} - X_{i+1}^*\right] X_i\end{aligned}$$

The Volterra Liapunov function

$$V(x) = \sum_{i=1}^{n} C_i\left[X_i - X_i^* - X_i^* \ln \frac{X_i}{X_i^*}\right]$$

with C_i chosen as $C_i a_{i,i+1} = C_{i+1} a_{i+1,i}$, has

$$\frac{dV}{dt} = - \sum_{i=1}^{n} C_i a_{ii} \left[X_i - X_i^*\right]^2 \leq 0$$

Since $a_{11} > 0$, the set of points where $\frac{dV}{dt} = 0$ consists of only X^*. By La Salle's Theorem, all solutions approach X^* as $t \to \infty$.

The last statement of the Theorem may be provided by an inductive argument on n.

Effects of Omnivory in Food Chains

To indicate some extensions of the classical models to which the persistence function techniques are applicable, Gard (1982) has considered the system

$$\frac{dX_1}{dt} = X_1 \left[a_{10}(t,x) - \sum_{i=1}^{n} a_{1i}(t,x) X_i\right]$$

$$(5.2) \qquad \frac{dX_i}{dt} = X_j \left[-a_{jo}(t,x) + \sum_{i=1}^{j-1} a_{ji}(t,x) X_j - \sum_{ji=j+1}^{n} a_{ji}(t,x) X_i\right]$$

$$z \leq j \leq n-1$$

$$\frac{dX_n}{dt} = X_n \left[- a_{no}(t,x) + \sum_{i=1}^{n-1} a_{ni}(t,x) X_i\right]$$

The a_{ij} continuous functions of t and x that either vanish identically or satisfy, for some constants m_{ij} and M_{ij},

$$(5.3) \qquad o < m_{ij} \leq a_{ij}(t,x) \leq M_{ij} \qquad t \in R_+,\ x \in R_+^n$$

For $j \neq o$, the symmetry condition $a_{ij} \equiv o$ if and only if $a_{ji} \equiv o$. Multiple level feeding can occur in these models.

Define the matrices A and b by

$$A = \begin{bmatrix} m_{21} & m_{31} & m_{41} & \cdots & m_{n1} \\ 0 & m_{32} & m_{42} & \cdots & m_{n2} \\ -M_{23} & 0 & m_{43} & \cdots & m_{n3} \\ \vdots & & & & \\ -M_{2,n-1} & \cdots & M_{n-2,n-1} & 0 & M_{n,n-1} \end{bmatrix}$$

$$b = \begin{pmatrix} M_{11} \\ M_{12} \\ \vdots \\ M_{1,n-1} \end{pmatrix}$$

Theorem 5.5. Assume that (5.3) holds if there is an n-1 column vector $r = (r_2, \ldots r_n)^T$ with $r_i > o$, $2 \leq i \leq n$, satisfying the vector matrix inequality $Ar \geq b$ and such that $\mu(r) = m_{10} - \sum_{i=2}^{n} r_i M_{io} > o$ then $\limsup_{t \to \infty} X_n(t) > o$ for any solution x(t) of (5.2) with $X(0) > o$; i.e. the top predator persists.

As an illustration of the criteria required for persistence in the case of omnivory and in the case of a simple food chain. In general, we find that omnivory enhances top predator persistence from the perspective that the persistence criterion is more readily satisfied when omnivory is present.

Example: The Lotka-Volterra system

$$\frac{dx_1}{dt} = X_1\,(a_{10} - a_{11}X_1 - a_{12}X_2 - a_{13}X_3)$$

$$\frac{dx_2}{dt} = X_2\,(-a_{20} + a_{21}X_1 - a_{23}X_3)$$

$$\frac{dx_3}{dt} = X_3\,(-a_{30} + a_{31}X_1 + a_{32}X_2)$$

is a simple food chain of $a_{13} = a_{31} = 0$. It is a food chain with omnivory provided a_{13} and a_{31} are nonzero. The parameter that determines persistence for the simple food chain is

$$\mu_s = a_{10} - \frac{a_{11}}{a_{21}}\,a_{20} - \frac{a_{12}}{a_{32}}\,a_{30}$$

To apply Theorem 5.5. to the case of r_2 and r_3 must be chosen so that

$$\begin{pmatrix} a_{21} & a_{31} \\ 0 & a_{32} \end{pmatrix} \begin{pmatrix} r_2 \\ r_3 \end{pmatrix} \geq \begin{pmatrix} a_{11} \\ a_{12} \end{pmatrix}.$$

A possible choice here is

$$r_3 = \frac{a_{12}}{a_{32}}, \quad r_2 = \frac{a_{11} - \frac{a_{12}}{a_{32}}\,a_{31}}{a_{21}}$$

Assuming r_2 is positive, the resulting persistence criterion is

$$\mu_o = a_{10} - \left[\frac{a_{11} - \frac{a_{12}}{a_{32}}\,a_{31}}{a_{21}}\right] a_{20} - \frac{a_{12}}{a_{32}}\,a_{30} > 0.$$

It is possible for μ_o to be positive and μ_s to be negative; hence, persistence of the top predator is enhanced by omnivory.

It is interesting tht when omnivory is present, $\mu_o > 0$ is not sufficient for the persistence of the food chain. In particular, if

$$\overset{\Upsilon}{V} = a_{10} + \frac{a_{13}}{a_{23}}\,a_{20} - \left[\frac{a_{11} + \frac{a_{13}}{a_{23}}\,a_{21}}{a_{31}}\right] a_{30} > 0$$

there are solutions close to the equilibrium

$$\left(\frac{a_{30}}{a_{31}} \; , \; 0 \; , \; \frac{a_{10} - a_{11}\frac{a_{30}}{a_{31}}}{a_{13}} \right)$$

that approach this equilibrium. An argument, using the function $\overset{\rho}{p} = X_1^{-1}\,X_2^{r_2}\,X_3^{-r_3}$, similar to those above may be employed to show that $\overset{\Upsilon}{V} < 0$ is a persistence criterion for the intermediate level predator. The full food chain persistence criteria are $\mu_o > 0$ and $\overset{\Upsilon}{V} < 0$. An interpretation of these inequalities is that the intrinsic growth rate of the resource, a_{10}, must be large enough to support both predators.

For a general food web, Gard (1983) has employed the persistence function technique to arrive at a linear programming problem. He concludes that omnivory enhances trophic structure persistence.

Other Simple Food Chains

Freedman and Waltman (1977) have studied a general three dimensional model of a food chain:

$$\frac{dx_1}{dt} = x_1 g(x_1) - X_2 p(x_1) \tag{5.4}$$

$$\frac{dx_2}{dt} = x_2\left[-r + cp(x_1)\right] - X_3\overset{q}{\cancel{g}}(X_2)$$

$$\frac{dx_3}{dt} = x_3\left[-s + d\,\overset{q}{\cancel{g}}(y)\right]$$

where r,s,c, and d are positive constants. They proved the persistence of (5.4) under fairly general conditions on the functions g and $\overset{q}{\cancel{g}}$. The interested reader can refer to the original paper or Freedman (1980).