INTERNATIONAL ATOMIC ENERGY AGENCY
UNITED NATIONS EDUCATIONAL, SCIENTIFIC AND CULTURAL ORGANIZATION
INTERNATIONAL CENTRE FOR THEORETICAL PHYSICS
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SMR.780 - 13

FOURTH AUTUMN COURSE ON MATHEMATICAL ECOLOGY

(24 October - 11 November 1994)

"Community Dynamics in a Homogeneous Environment"

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These are preliminary lecture notes, intended only for distribution to participants.

Community Dynamics in a Homogeneous Environment

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Outline

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 of 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. These would not be considered communities in the classical ecological literature, but I will be consistent in using this term whenever species interactions are involved.

There exist traditional classifications of two-population systems in terms of the nature of the interactions, and these will provide the point of departure for these notes. Such distinctions, however, are often difficult to ascertain since roles can depend upon life cycle stage, environment, and many 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 "detrimental" from predator to the prey. Host-parasite interactions are often put into this category despite obvious differences in detail. From an energy flow viewpoint, a diagram of the predator-prey association is given in Fig. 1.1.

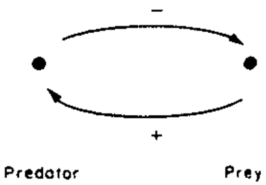

Fig. 1.1. The signs represent the energy flow in the predator-prey influence diagram

Predation can result in a negative per capita growth rate in the prey population; if it remains negative, then extinction of the population could result. Were the predator limited to that prey, the predator itself would go extinct. However, as prey become scarcer and harder to find, predators switch their diets to less expensive individuals. The same principle applies within a population: predators tend to take those that are the easiest to capture: the young, the old, and the weak. This has caused some to remark that stable predator-prey associations involve "prudent" predation.

Dyer (1980) has demonstrated that grazing can stimulate growth of the grazed plant species. Even more remarkable is the manner in which this stimulation occurs: the saliva of some herbivores can contain a hormone that initiates plant growth. There is a current debate on the beneficial aspects of grazing with the discussion focusing upon the idea that grasses and grazers have coevolved so that neither could coexist without the other. The references (Silvertown, 1982; Thompson and Uttley, 1982; Owen and Wiegert, 1983; Stenseth, 1983) make interesting reading.

The manner in which predation reacts to prey density is called the *predator functional response*. Examples of the typical types of functional responses that exist in the literature are those listed under resource-consumer interactions (Sect. 4 in the Population Ecology Chapter): 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 exhibiting a negative influence upon the other (Fig. 1.2).

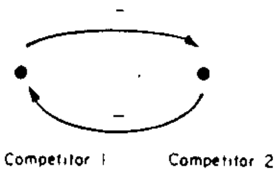

Fig. 1.2. An influence diagram for a community composed of two competitors

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 utilizing available resources. Exploitation competition occurs when a competitor actually utilizes the available resource.

There is much current argument about the role of competition in the determination of structure of an ecological community. Indeed, this discussion is rather spirited (Science, Vol. 221, 19 August 1983, p. 737), resulting in attacks on data, data interpretation, and even individuals.

1.3 Cooperation

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

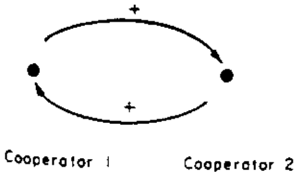

Fig. 1.3. An influence diagram for energy flow in a cooperative community

These *cooperative* communities are based on the mutual benefaction of the cooperator species. Although such effects may be indirect, the traditional classifications of cooperation generally refer only to the situation where both species growth rates are increased directly by the presence of the cooperating species. The past decade has seen a widening recognition of such interactions as fundamental components of many ecosystems.

1.4 Classical Examples of Two-Species "Communities"

In Sect. 1.4 of the Population Dynamics Chapter, Figs. 1.16 representing the dynamics of the lynx and snowshoe hare and 1.17, the bean weevil and the wasp, represent special cases of predator-prey "communities", although the strength of the interaction between the lynx and the hare is open to debate (e.g. Hutchinson, 1978).

A classical laboratory predator-prey community involves the ciliates *Paramecium* and *Didinium*. *D. nasutum* is considerably larger than *P. aurelia* and will, in an unrestricted aquatic environment, consume all the *Paramecium* and then go to extinction (Luckinbill, 1973). Adding methyl cellulose to the medium (which increases the viscosity of the liquid) and decreasing the food supply of the *Paramecium* will allow persistence (Fig. 1.4: from Maynard Smith, 1974). Oscillation, as in these examples, in an important characteristic of many predator-prey communities (although see Sect. 2.4).

The dynamics of competitive communities have been studied for many systems, and examples are given in Figs. 1.5–1.7.

This system is discussed in more detail in Sect. 3.4.

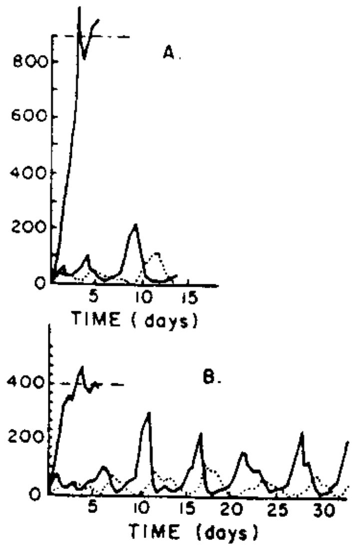

Fig. 1.4. Coexistence of *Paramecium aurelia* (solid curve) and *Didinium nasutum* (dashed curve), after Luckinbill (1973). A, medium with methyl cellulose; B, medium with methyl cellulose and reduced food for prey. In each graph, the upper solid curve is for *P. aurelia* grown by itself

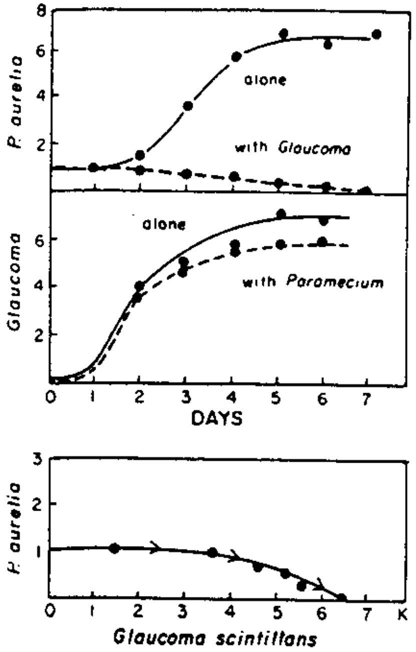

Fig. 1.5. Upper panel, *Paramecium aurelia* cultivated without (solid curve) and with (dashed curve) *Glaucoma scintilans*; middle panel. G. scintillans cultivated without (solid curve) and with (dashed curve) *P. aurelia*; bottom panel, phase plane trajectory (Gause modified) (by Hutchinson)

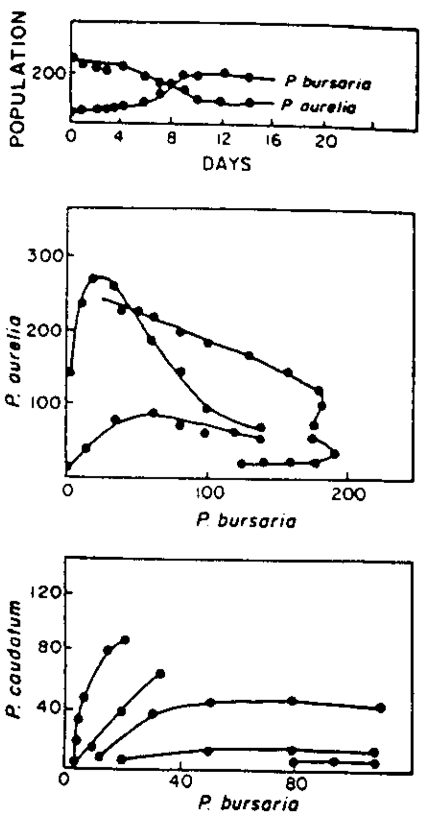

Fig. 1.6. Upper panel, Population of *Paramecium aurelia* and of *P. bursaria* introduced into the *P. aurelia* culture. Middle panel, *P. aurelia* and *P. bursaria*, are cultivated together. Bottom panel, trajectories when *P. caudatum*, is grown with *P. bursaria* (Gause, modified) (by Hutchinson)

When cooperative (mutualistic, symbiotic) communities are discussed, the most often cited (e.g., Boughey, 1973; DeAngelis et al., 1986) examples are lichens (fungus-algae) and the interactions between the clown fish-sea anemone, cleaner wrasse-large fish, ant-acacia, nitrogen fixing bacteria-legumes, mycorrhizal fungi-plants, and plant-pollinators. However, the average ecology textbook devotes much less space to such interaction than to predator-prey or competitive interactions. A possible reason for this is that the basic principles of cooperative communities do not seem to have been as developed as those of other types of interactions. Some theoretical aspects of cooperation are explored later.

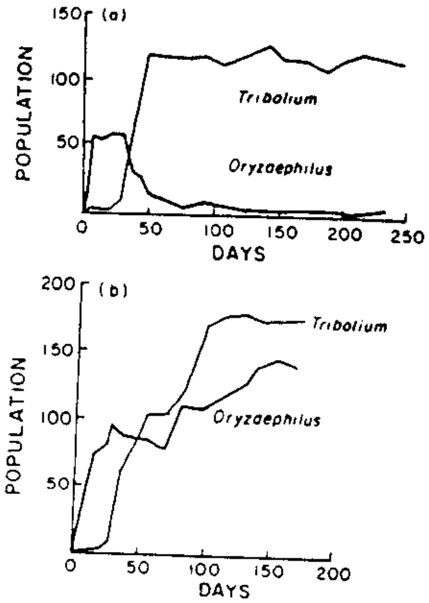

Fig. 1.7. (a) populations of the two grain beetles, *Tribolium confusum* and *Oryzaephilus surinamensis*, grown together in flour; (b) the same when refuges (short lengths of capillary tubing) are mixed with the flour (Crombie)

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; they might, for example, 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 i, are functions not only of x_i but also of the other interacting population.

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

The per capita growth rate is the difference between the birth rate and the death rate, and 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

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

$$\frac{dx_2}{dt} = x_2 f_2(x_1, x_2). \qquad (1.1)$$

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

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

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 *Kolmogorov type*.

The partial derivatives of f_i determine the classification of the community (see also Ginzburg, 1983). These are given in Table 1.4. The partial derivatives $\partial f_i / \partial x_i$ represent intraspecific competition effects or density dependent interactions.

The Kolmogorov 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 emanating 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, as there can be 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 is built on 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. Lotka-Volterra models have been much studied and much criticized in the ecological literature for many reasons. They are difficult to apply in particular situations because the interaction coefficients cannot be computed. However, though these models may not mimic data sets exactly, they are useful in building hypotheses. While these types of models remain prevalent in the literature, current efforts to model communities are becoming much more sophisticated (see Turelli, these notes).

2. Predation

2.1 Volterra's Principle

V. Volterra, in analyzing a problem posed by his son-in-law U. D'Ancona, concluded that a moderate amount of harvesting of a prey population can, increase the average number of prey while, decreasing the average 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

$$\begin{aligned}\frac{dx_1}{dt} &= x_1(a_1 - b_1 x_2)\\ \frac{dx_2}{dt} &= x_2(-a_2 + b_2 x_1).\end{aligned} \tag{2.1}$$

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 equation (by eliminating t) and then solved in a closed form by separating variables. This leads to the solutions

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

where c is constant. It can be shown that for each c this relation defines a closed curve in $x_1 - x_2$ space and, as such, represents a periodic solution of (2.1) 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 indiscriminate and results in a fixed proportion (hx_i) of both predator and prey being removed. The model (2.1) with harvesting is

$$\begin{aligned}\frac{dx_1}{dt} &= x_1(a_1 - h - b_1 x_2)\\ \frac{dx_2}{dt} &= x_2(-a_2 - h + b_2 x_1).\end{aligned} \tag{2.2}$$

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 and a decrease in predators.

If the prey species is a desired species, as it was in Volterra's situation of edible fish (prey) and selachians (predators), 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 the ladybird beetle *(Novius cardinalis)*, harvesting is not beneficial. This latter predator-prey system was causing only minor difficulty for the California citrus growers until indiscriminate "harvesting" by the insecticide (DDT) was initiated. As predicted, the prey population exploded and trouble ensued (Braun, 1975).

An excellent discussion of Volterra's Principle may be found in Braun (1975). Harvesting in more general predator-prey models is treated in the papers by Brauer and Soudak (1979a, b), and Brauer et al. (1976), and Brauer (1984).

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 at least one strictly decreasing, then the equilibrium (x_1^*, x_2^*) is asymptotically stable.*

If, in addition to all previous hypotheses,

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

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

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

$$\begin{aligned}\frac{dx_1}{dt} &= x_1(a_1 - b_{11}x_1 - b_{12}x_2)\\ \frac{dx_2}{dt} &= x_2(-a_2 + b_{21}x_1)\end{aligned}$$

satisfies the conditions of the theorem, so the equilibrium $\left(\frac{a_2}{b_{21}}, \frac{a_1 b_{21} - b_{11} a_2}{b_{21} b_{12}}\right)$ is globally asymptotically stable. The difference between this model and Volterra's is the inclusion of a carrying capacity for the prey species. The global asymptotic stability should be contrasted with the neutrally stable (cycles of the) Volterra model.

Indication of Proof of Theorem.

The function

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

is a Liapunov function for (2.3). Since $\dot{V}$ can only be zero at x_1^* or x_2^*, LaSalle's theorem (LaSalle and Lefschetz, 1961) on the extent of asymptotic stability implies that all solutions approach (x_1^*, x_2^*) as t approaches infinity.

2.3 Generation of Cycles in Predator-Prey Models

Cyclic variation in communities is a documented phenomenon (Figs. 1.14–1.18). Many of these variations do not correlate with known periodic exogenous forces such as diel or seasonal cycles. Some occur in predator-prey relationships; for example, see Figs. 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. I will not belabor these points, it is my purpose to demonstrate the existence of a reasonable community model that exhibits cyclic behavior. To this end, I consider the Kolmogorov model (1.1). 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 (e.g., Coleman, 1976).

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

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 per capita growth rate of the prey.

(H2) $\frac{\partial f_2}{\partial x_1} > 0$.

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

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

Density dependent effects are imposed independent of population densities.

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

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

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

The predator population also is limited by effects of crowding.

(H5) $f_1(0, x_2^T) = 0$ for some $x_2^T > 0$.

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.

(H6) $f_1(x_1^c, 0) = 0$ for some $x_1^c > 0$.

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).

(H7) $f_2(x_1^T, 0) = 0$ for some $x_1^T > 0$.

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 $h \in C^1[0, x_1^c]$, $h' < 0$, $h(0) = x_2^T$, $h(x_1^c) = 0$.

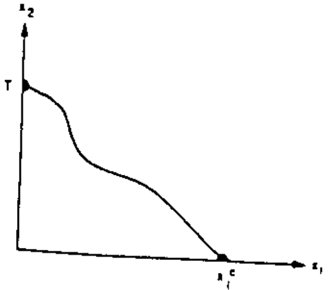

Fig. 2.1. The prey isocline defined by $x_2 = h(x_1)$

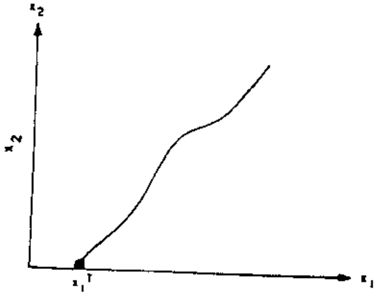

Fig. 2.2. The predator isocline defined by $x_1 = q(x_2)$

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.

(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 $g(0) = x_1^T$.

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

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

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

(H13) The prey isocline has a hump, Fig. 2.3 (Rosenzweig, 1969).

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 the 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 Fig. 2.4.*

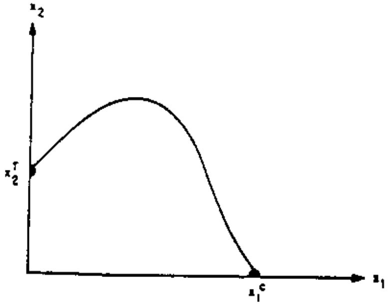

Fig. 2.3. The prey isocline has a hump

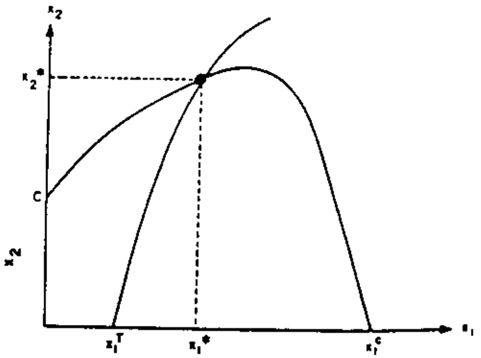

Fig. 2.4. An assumed structure for the predator prey isoclines

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 (1.1) has a limit cycle in $\mathbb{R}_+^2$.

Indication of Proof. Consider the rectangle formed by the coordinate axes and the lines $x_1 = x_1^c$ and $x_2 = x_2^c$ where x_2^c is given by $f_2(x_1^c, x_2^c) = 0$. The ω-limit set of any trajectory, $\omega(\Gamma^+)$, in this rectangle 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), (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* (1.1) *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 (H11), (H14), and (H15) imply the existence of a prey isocline, $x_2 = h(x_1)$, like that described in (H9) but $0 \leqq g' \leqq g(x_2)/x_2$; similarly, the existence of a predator isocline $x_1 = g(x_2)$ with properties similar to those indicated in (H10) but $h' \leqq h(x_1)/x_1$ 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 Kolmogorov 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 Freedman, 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

$$\frac{dx_1}{dt} = a_1 x_1 - b_1 x_1^2 - b_{12} x_1 x_2 ,$$

$$\frac{dx_2}{dt} = a_2 x_2 - b_2 x_2^2 / x_1 .$$

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 exceeds a_2/b_2 (that is, there are few prey per predator), then the predator population decreases.

The Liapunov function of Hsu-Harrison can be used to show that Leslie's model is globally asymptotically 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 (May, 1976).

Table 2.1. Life history data for 8 natural prey-predator systems (after Tanner, 1975)

Prey-predator	Geographical location	Apparent dynamical behavior
Sparrow – hawk	Europe	Equilibrium
Muskrat – mink	Central North America	Equilibrium
Hare – lynx	Boreal North America	Cyclic
Mule deer – mountain lion	Rocky Mountains	Equilibrium
White-tailed deer – wolf	Ontario	Equilibrium
Moose – wolf	Isle Royale	Equilibrium
Caribou – wolf	Alaska	Equilibrium
White sheep – wolf	Alaska	Equilibrium

2.5 Simple Food Chains

A simple food chain is a chain of predation where the dynamics of each population is determined by those species occupying the preceding and succeeding trophic levels. For example, the chain composed of 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

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

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* $a_{11} > 0$.

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

The function u is defined by

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

and satisfies

$$\frac{du}{dt}(x(t)) \leqq -mu(x(t)) + b ,$$

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

Solving this inequality leads to

$$u(t) \leqq u(0)\exp(-mt) + b/m .$$

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: $\limsup_{t\to\infty} x_n(t) > 0$. The system level parameter is defined by

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

where

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

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 $\mu < 0$.*

Indication of the Proof. 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, $j = 1, 2, \ldots, n$. Then, again applying the comparison principle to (5.1) it follows that

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

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 $r_i > 0$, $i = 1, 2, \ldots, n$ and $x > 0$; define

$$\varrho(x) = \prod_{i=1}^{n} x_i^{r_i}$$

on the set $S = \{x \in R^n : 0 < x_n \leqq \lambda\}$. By differentiating ϱ along trajectories on (5.1) and by proper choice of the r_i, some cancellations occur. This results in

$$\frac{d\varrho}{dt} = \varrho[r_1\mu - r_{n-1}a_{n-1,n}x_n] . \tag{5.2}$$

On S, if λ is sufficiently small, the quantity in the brackets is positive; hence $d\varrho/dt > 0$. This implies that along trajectories $\varrho(t)$ is increasing; however, when $x_n \to 0$ so does ϱ. This contradiction shows that persistence is valid for (5.1).

Conversely if $\mu < 0$, then ϱ satisfies (5.2) and

$$\frac{d\varrho}{dt} \leqq r_1\mu\varrho .$$

Thus, $\varrho \to 0$ and an extinction must occur. □

What is the situation when there is an apparently unlimited supply of a resource? (i.e., $a_{11} = 0$). There are lots of problems associated with dimensionality in Lotka-Volterra models and here we find some additional ones. The persistence-extinction parameter, μ_0, of a food chain of length $n = 2m + 1$ is

$$\mu_0 = a_{10} - \sum_{j=1}^{m} a_{2j+1,0}\prod_{i=1}^{j}\frac{a_{2i-1,2i}}{a_{2i+1,2i}} .$$

Theorem 5.3. *Let $a_{11} = 0$. The food chain modelled by* (5.1) *is persistent provided $\mu_0 > 0$; it is not persistent if $\mu_0 < 0$.*

Indication of the Proof. In the previous result with carrying capacity, 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 Volterra auxiliary function:

$$V(x_1, x_2, \ldots, x_n) = \sum_{i=1}^{n} \alpha_i(x_i - \beta_i - \beta_i \log x_i/\beta_i) .$$

A 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. □

As demonstrated in the next theorem, persistence in simple food chains with carrying capacity is related to the stability of an equilibrium. 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.

Theorem 5.4. *Let the system* (5.1) *with $a_{11} > 0$ 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.*

Indication of the Proof. 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

$$\frac{dx_i}{dt} = x_i(b_i + a_{i,i-1}x_{i-1} - a_{ii}x_i - a_{i,i+1}x_{i+1})$$
$$a_{ij} > 0,\ i \neq j,\ a_{11} > 0 .$$

This is rewritten using the equilibrium x^* as

$$\begin{aligned}\frac{dx_i}{dt} &= a_{i,i-1}[x_{i-1} - (x_{i-1}^*)]\\ &\quad - a_{ii}[x_i - (x_i^*)]\\ &\quad - a_{i,i+1}[x_{i+1} - x_{i+1}^*]x_i .\end{aligned}$$

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 $C_i a_i = C_{i+1}a_{i+1,i}$, has

$$\frac{dV}{dt} = -\sum_{i=1}^{n} C_i a_{ii}[x_i - x_i^*]^2 \leqq 0 .$$

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 proved by an inductive argument on n. □

2.6 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

$$\begin{aligned}\frac{dx_1}{dt} &= x_1\left[a_{10}(t,x) - \sum_{i=1}^{n} a_{1i}(t,x)x_i\right]\\ \frac{dx_2}{dt} &= x_j\left[-a_{j0}(t,x) + \sum_{i=1}^{j-1} a_{ji}(t,x)x_j - \sum_{i=j+1}^{n} a_{ji}(t,x)x_i\right] \quad 1 \leqq j \leqq n-1 \qquad (5.2)\\ \frac{dx_n}{dt} &= x_n\left[-a_{n0}(t,x) + \sum_{i=1}^{n-1} a_{ni}(t,x)x_i\right].\end{aligned}$$

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

$$0 < m_{ij} \leqq a_{ij}(t,x) \leqq M_{ij} \qquad t \in R_+, x \in R_+^n . \qquad (5.3)$$

For $j \neq 0$, the symmetry condition means that $a_{ij} = 0$ if and only if $a_{ji} = 0$. 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 6.1. *Assume that (5.3) holds. If there is an $n-1$ column vector $r = (r_2, \ldots, r_n)^T$ with $r_i > 0, 2 \leqq i \leqq n$, satisfying the vector matrix inequality $Ar \geqq b$ and such that $\mu(r) = m_{10} - \sum_{i=2}^{n} r_i M_{i0} > 0$, then $\limsup_{t\to\infty} x_n(t) > 0$ for any solution $x(t)$ of (5.2) with $x(0) > 0$; 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, an example is presented. In general, 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 if $a_{13} = a_{31} = 0$. 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 6.1, r_2 and r_3 must be chosen so that

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

A possible choice here is

$$r_3 = \frac{a_{12}}{a_{32}}, \qquad r_2 = \frac{\left(a_{11} - \dfrac{a_{12}}{a_{32}} a_{31}\right)}{a_{21}} .$$

If r_2 is positive, the resulting persistence criterion is

$$\mu_0 = a_{10} - \left[\frac{a_{11} - \dfrac{a_{12}}{a_{32}} a_{31}}{a_{21}} \right] a_{20} - \frac{a_{12}}{a_{32}} a_{30} > 0 .$$

It is possible for μ_0 to be positive and μ_r to be negative; hence, persistence of the top predator is enhanced by omnivory.

It is interesting that when omnivory is present, $\mu_0 > 0$ is not sufficient for the persistence of the food chain. In particular, if

$$\nu = a_{10} + \frac{a_{13}}{a_{23}} a_{20} - \frac{a_{11} + \dfrac{a_{13}}{a_{23}} a_{21}}{a_{31}} a_{30} > 0 ,$$

there are solutions close to the equilibrium

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

that approach this equilibrium. An argument similar to those above, using the function $\varrho = x_1^{-1} x_2^{r_2} x_3^{-r_3}$, may be employed to show that $\nu < 0$ is a persistence criterion for the intermediate level predator. The full food chain persistence criteria are $\mu_0 > 0$ and $\nu < 0$. 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 (1984) has employed the persistence function technique to arrive at a linear programming problem. He concludes that omnivory enhances trophic structure persistence.

2.7 Other Simple Food Chains

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

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 g(x_1) - x_2 p(x_1) , \\ \frac{dx_2}{dt} &= x_2[-r + cp(x_1)] - x_3 q(x_2) , \\ \frac{dx_3}{dt} &= x_3[-s + dq(y)] , \end{aligned} \tag{7.1}$$

where r, s, c, and d are positive constants. They proved the persistence of (7.1) under fairly general conditions on the functions g and q. The interested reader can refer to the original paper or Freedman (1980). Freedman and Waltman (1984) have extended these food chain results to a Kolmogorov model and strengthened the results by establishing that components have a positive limit inferior as t approaches infinity.

The definition of persistence as $\limsup_{t \to \infty} x(t) > 0$ or $\liminf_{t \to \infty} x(t) > 0$ is for mathematical convenience rather than ecological reality. A more appropriate definition of persistence would involve a threshold for all components, but few results exist for such systems.

3. Competition

3.1 Lotka-Volterra-Gause Models

Gause (1934) developed a theory of competition based upon experimental work and theoretical studies grounded on the Lotka-Volterra type model,

$$\begin{aligned} \frac{dx_1}{dt} &= x_1(a_1 - b_1 x_1 - b_{12} x_2) , \\ \frac{dx_2}{dt} &= x_2(a_2 - b_2 x_2 - b_{21} x_1) . \end{aligned} \tag{3.1}$$

It can be demonstrated that there are four ecologically feasible outcomes to the competition modelled by (3.1) (Fig. 3.1).

The two populations can coexist. In this case, the system has a unique positive equilibrium that is globally asymptotically stable. For later usage it is convenient to denote this coexistence by the symbol $x_1 \leftrightarrow x_2$ (Fig. 3.1a).

The positive equilibrium can also be a hyperbolic (saddle) point: The winner of the competition depends upon the initial population sizes. The function that governs the interaction is defined by the separatrices of the hyperbolic point. Notation for this outcome is $x_1 \overset{\downarrow}{\underset{\uparrow}{\leftrightarrow}} x_2$ (Fig. 3.1b).

The remaining outcomes are for the cases that one population dominates the other, so that independent of initial population size, the dominant population survives while the second goes to extinction. This is denoted by $x_1 \gg x_2$ or $x_2 \gg x_1$ according to whether x_1 or x_2 wins the competition (Figs. 3.1c and d). There is another type of system that is excluded from the above classification. This is the case where the parameters of one population, x_1, are a constant multiple, k, of the other population, x_2. This leads to an infinite number of equilibria and the relationship $x_1 = (\text{constant})(x_2)^k$ must hold between the two populations. This situation is related to the concept of competitive exclusion discussed later in Sect. 3.5.

The available resources can have an effect upon the competition between two species. While this topic is not developed here, the reader is referred to Leon and Tumpson (1975) and Hsu and Hubbell (1979).

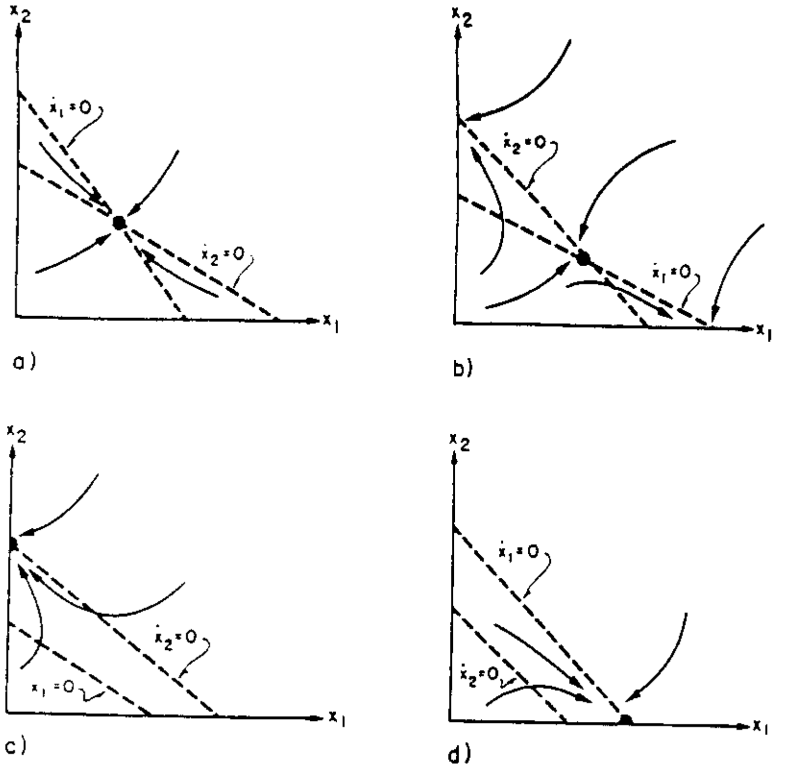

Fig. 3.1a–d. Outcomes of competition as determined by a Lotka-Volterra model. a $x_1 \leftrightarrow x_2$. b $x_1 \not\leftrightarrow x_2$. c $x_2 \gg x_1$. d $x_1 \gg x_2$. See text for details

3.2 Competition Models of Kolmogorov Type

The Kolmogorov model

$$\frac{dx_1}{dt} = x_1 f_1(x_1, x_2),$$
$$\frac{dx_2}{dt} = x_2 f_2(x_1, x_2), \tag{3.2}$$

with competitive interactions has a relatively restricted asymptotic behavior in that no limit cycles can arise. The hypotheses required to achieve this result include

(C1) $\frac{\partial f_1}{\partial x_2}(x_1, x_2) < 0; \quad \frac{\partial f_2}{\partial x_1}(x_1, x_2) < 0.$

Hence, if either population in the competition increas
other species decreases.

(C2) There exists a $K > 0$ such that for $x_i \geq K$, $i = 1$ or 2, $f_i(x_1, x_2)$ are nonpositive.

When either population is sufficiently large, neither of them can grow.

(C3) There exist carrying capacities x_1^c, x_2^c where $f_1(x_1, 0) > 0$ for $x_1 < x_1^c$ and $f_1(x_1, 0) < 0$ for $x_1 > x_1^c$; $f_2(0, x_2) > 0$ for $x_2 < x_2^c$ and $f_2(0, x_2) < 0$ for $x_2 > x_2^c$.

Theorem 3.1. *The limit of any solution of* (3.2) *exists and is an equilibrium, and hence populations tend to one of a finite number of limiting populations, provided* (C1), (C2), *and* (C3) *are satisfied.*

Indication of Proof. The complete details of the proof may be found in Hirsch and Smale (1974). The basic analysis employs the decomposition of the population quadrant into regions determined by flows across isoclines. Then each type of region is analyzed to determine the characteristics of the feasible ω-limit sets. As indicated in the theorem statement, all ω-limit points are equilibria (and in particular, there are no limit cycle behaviors associated with competitive systems of Kolmogorov type). The stability of these equilibria is relatively easy to determine and it is shown that there exists at least one asymptotically stable equilibrium.

3.3 Competition in Laboratory and Natural Communities: Some Classical Examples

Gause, stimulated by the theoretical work of Volterra, undertook some laboratory experiments that led to outcomes much like the theoretical work predicted (Sect. 3.1). His work on two yeast populations was not definitive because of the production of ethyl alcohol (yeast are fine for making wine but not for interacting) which, in turn, shut down reproduction.

Apparently not discouraged, Gause continued his work in aquatic systems, this time using ciliates. Using *Glaucoma scintillans* and *Paramecium aurelia*, he found that the smaller organism, *Glaucoma*, was not inhibited by the *Paramecium* while the growth of the *Paramecium* population was hindered by the presence of *Glaucoma*.

Gause also employed three species of paramecium in some experiments: *P. aurelia*, *P. caudatum*, and *P. bursaria*. The outcomes of competition between these species were:

1. *P. caudatum* ≫ *P. aurelia* if metabolic products was completely removed.
2. *P. aurelia* ≫ *P. caudatum* in most other instances; hence the winner of the competition could be changed by a perturbation in environment.
3. *P. aurelia* ↔ *P. bursaria*. (This might not be direct competition for a resource since *P. bursaria* tended to feed on the sediments.) The data indicates that multiple equilibria might result.

P. caudatum and *P. bursaria* mixtures led to inconclusive results. Stable equilibrium coexistence did occur in certain instances, and *P. caudatum* $\ll$ *P. bursaria*, occured if *P. bursaria* was initially present in sufficiently high densities.

Another classical competition experiment was that of Park (1954, 1962) using metazoa. *Tribolium confusum* and *T. castaneum* were used in a homogeneous environment, with different temperature and humidity ranges.

T. confusum, grown by itself in a hot, wet environment, reached peak densities. However, when it was grown with *T. castaneum* (which did moderately well in a hot wet environment), *T. castaneum* won the competition. In a cool dry environment, neither species did well. In this setting, *T. confusum* dominated the competition. Two aspects of classical ecological dogma are illustrated by these experiments. Environmental conditions are important factors in competition and extraction of information from population to community levels is not, in general, a feasible objective.

Many factors can provide a basis for changing the outcome of competition. These include refuge, predation, and genetic effects. Crombie (1945, 1946) utilized flour beetles and, by adding a refuge, changed the outcome of competition from one of competitive dominance to stable coexistence. Pimentel et al. (1965), using houseflies and blowflies, were able to change the dominance in this system through selection for superior competitors.

As indicated in Fig. 1.8, Connell (1961) studied the competition between two barnacle populations in an intertidal community. The barnacles of the genera *Balanus* and *Chthamalus* competed interspecifically for space on the rocks in the intertidal. The *Balanus* were vigorous and tended to dominate *Chthamalus* in the lower zones, while the situation was reversed in the upper regions.

3.4 Competition for a Single Nutrient in Continuous Cultures of Microorganisms

Hsu et al. (1977), (see also Novick and Szilard, 1950; Herbert et al., 1956) developed a theory of competition between microorganisms, such as phytoplankton, for a single limiting nutrient. Their modelling efforts were motivated by chemostat experiments in which the initial input, S^0, and dilution rate, D, of the nutrient were known constants and the environmental medium was homogeneous.

Let $x_i(t)$ denote the concentration of the ith population at time t; $S(t)$ denote the concentration of substrate at time t; m_i is the maximum growth rate of the ith population; y_i is the growth yield for the ith population and a_i is the Michaelis-Menten half saturation constant. The model is

$$\frac{dS(t)}{dt} = (S^0 - S(t))D - \sum_{i=1}^{n} \frac{m_i}{y_i}\frac{x_i(t)S(t)}{a_i + S(t)}$$

$$\frac{dx_i(t)}{dt} = \frac{m_i x_i(t)S(t)}{a_i + S(t)} - Dx_i(t)\,,$$

$$S(0) = S^0\,,$$

$$x_i(0) = x_{i0} > 0\,.$$

Theorem 3.2 (Extinction). *Let* $b_i = m_i/D$. *If either* $b_i \leqq 1$ *or* $\frac{a_i}{b_i - 1} > S^0$ *(when* $b_i > 1$*) then* $\lim_{t\to\infty} x_i(t) = 0$.

Extinction results if the maximum growth rate m_i of the ith population is less than the dilution rate or if the metabolic needs of the population, $a_i/(b_i - 1)$ exceeds the initial amount of nutrient present in the system.

Theorem 3.3 (Persistence of one Population). *Let* i *be an integer,* $1 \leqq i \leqq n$, *and suppose* $0 < a_i/(b_i - 1) < a_j/(b_j - 1)$ *for all* $j \neq i$, $j = 1, 2, \ldots, n$. *Let* $S^0 > a_i/(b_i - 1)$ *and* $b_i > 1$. *Then*

$$\lim_{t\to\infty} S(t) = \frac{a_i}{b_i - 1}\,,$$

$$\lim_{t\to\infty} x_i(t) = y_i\left(S^0 - \frac{a_i}{b_i - 1}\right),$$

$$\lim_{t\to\infty} x_j(t) = 0 \qquad j \neq i\,.$$

The proof of this last theorem is long and involved, although not difficult to understand; the interested reader is referred to the original article for details.

This competition model has again led to a globally asymptotically stable equilibrium. Survival of a population is determined by the smallest of the ratios: $a_i/(b_i - 1)$. This indicates that when a single resource is limiting for a community, only one population can survive. The validity of this statement and the presence of cycles in competitive systems is explored in the next section.

3.5 The Proposition of Competitive Exclusion

Gause's experiments with *Paramecium caudatum* and *P. aurelia* resulted in *P. aurelia* dominating in the competition for a single limiting resource in most cases. From these experiments and from the mathematical theory developed by Volterra arose the proposition that an ecological community in which there are n species cannot persist on less than n limiting resources. (A resource is limiting if it is necessary for maintenance and development of the community and its supply is exhaustable by sufficient utilization.)

While Gause's research was in the laboratory, there also exist classical studies of competition with exclusion in natural ecosystems. R. MacArthur (1958) studied five species of warblers that appeared to be so similar in ecological preferences that competitive exclusion was violated. He found that they feed and occupy different levels in their forested environment and that competitive exclusion held for this community.

Theoretical aspects of competitive exclusion have been well developed in recent years. The work of Hsu et al. (1977) mentioned previously in Sect. 3.4 supported the concept of competitive exclusion if the ratio of the Michaelis-Menten parameters of each population was distinct from the others. They also demonstrated that whenever two species have equal Michaelis-Menten ratios, it is possible for both species to survive.

Related to competitive exclusion is the "paradox of the plankton" (Hutchinson, 1978). The coexistence of many species of phytoplankton in a well mixed body of water with only a few limiting nutrients (usually one) seems to violate competitive exclusion. The analysis of Hsu, Hubbell, and Waltman suggested that, for the species to survive, the Michaelis-Menten parameter ratios should be very similar. Theoretically, this allows exclusion to proceed very slowly.

Levin (1970) also provided a theoretical basis for a higher dimensional competition exclusion. He considered the model:

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 f_1(x_1, \dots, x_n; y_1, \dots, y_m) \\ &\vdots \\ \frac{dx_n}{dt} &= x_n f_n(x_1, \dots, x_n; y_1, \dots, y_m), \end{aligned} \tag{3.3}$$

where x_i are state variables representing species in the community and y_j represent environmental parameters. Any quantity that influences f_i is called a limiting factor. He also allowed combination of influences; for example, if a species requires and utilizes two resources R_1, R_2 with utilization efficiencies α_1, α_2 then $\alpha_1 R_1 + \alpha_2 R_2$ is a single limiting factor. Suppose that there exists a minimal independent set of limiting factors $\{z_1(x_1, \dots, x_n; y_1, \dots, y_m), \dots, z_p(x_1, \dots, x_n; y_1, \dots, y_m)\}$ where $p \leqq m+n$, and that the growth rates f_i are linear functions

(i) $f_i = \alpha_{i2} z_i + \alpha_{i2} z_2 + \dots + \alpha_{ip} z_p + \gamma_i$.

Theorem 3.4. *No asymptotically stable equilibrium or periodic solution can be attained in a community modelled by* (3.3) *in which some r components are limited by less than r limiting factors.*

Indication of the Proof. If the first r components are limited by less than r factors, because of the linearity of the f_i, there exist β_i, δ not all zero such that

$$\beta_1 f_1 + \dots + \beta_r f_r = \delta .$$

Employing the Eqs. (3.3), we obtain the expression

$$\beta_1 \frac{\dot{x}_1}{x_1} + \beta_2 \frac{\dot{x}_2}{x_2} + \dots + \beta_r \frac{\dot{x}_r}{x_r} = \delta .$$

Integration leads to

$$x_1^{\beta_1}(t) \dots x_r^{\beta_r}(t) = K e^{\delta t} .$$

Using the equilibrium condition, we obtain that δ must be zero, and that each solution lies on the surface

$$x_1^{\beta_1} \dots x_r^{\beta_r} = K ,$$

for some K. Any small perturbation will more the system to a different surface, indicating the impossibility of asymptotic stability. ☐

While the above mentioned works support the proposition of competitive exclusion, not all theoretical research does.

McGehee and Armstrong (1977) showed, for certain standard models where competitive exclusion occurs, that, topologically, the result is not robust. They, modify a model by several small nonlinear perturbations, and end up with a persistent system (in fact, one with a cyclic behavior).

Kaplan and Yorke (1977) demonstrate that Levin's work is not robust in that there exists a nonlinear n-dimensional system

$$\frac{dx_i}{dt} = x_i f_i(r_1(x), \dots, r_k(x)), \quad k < n$$

which has an asymptotically stable periodic solution. Related competitive exclusion ideas will be discussed in the next section.

The concepts of competitive exclusion and niche theory have been interrelated in the literature. The reader is referred to Hutchinson (1978) and Whittaker and Levin (1975) for discussions on the theory of the niche.

3.6 Stability in Higher Dimensional Competitive Communities

The analytical theory of higher dimensional communities of competitors is only beginning to develop. To give an indication of some of the types of available results, I discuss persistence in a three dimensional Lotka-Volterra model. For other recent results the monograph of Waltman (1983) is a good reference.

Three Dimensional Lotka-Volterra Models of Competition

Persistence-Extinction Phenomena. While the case has been adequately made to not place too much biological faith in the interpretation and output of Lotka-Volterra type models, there are some mathematically interesting aspects that will be mentioned here.

The Lotka-Volterra type model for a competitive community consisting of three populations is

$$\frac{dx_i}{dt} = x_i\left(a_{i0} - \sum_{j=1}^{3} a_{ij} x_j\right) i = 1, 2, 3 . \tag{3.4}$$

The system (3.4) has a solution $x = (x_1, x_2, x_3)$ that goes to extinction if there exists a positive initial condition such that the solution through this initial value satisfies $\lim_{t \to \tau} x_i(t) = 0$ for some i, $i = 1, 2, 3$, and some $\tau \in (0, \infty]$. For (3.4) and, in fact, for all models of Kolmogorov-type with sufficient continuity requirements, finite time extinction is not possible provided initial value problems have unique solutions. The extinction planes $(x_i = 0)$ are invariant for such models and uniqueness of initial value problems guarantees that no trajectory that is ever in an extinction plane at a finite time can emanate from the population octant. If the system (3.4) has no solution that goes to extinction, it is called *persistent*.

To determine persistence of the community model (3.4), I first classify the types of extinction that can occur (Hallam et al., 1979). A comparison of components of solutions of (3.4) with appropriate logistic equations coupled with a differential inequality argument establishes all solutions of (3.4) are bounded. It is evident that complete extinction cannot result since for small x_i, all species have positive growth rates.

Two Population Extinction. Necessary conditions for the existence of a trajectory satisfying $\lim_{t\to\infty} x_k(t) > 0$ and $\lim_{t\to\infty} x_j(t) = 0$, $j \neq k$, are

$$a_{jk}a_{k0} \geqq a_{j0}a_{kk} \qquad j \neq k\,. \tag{3.5}$$

If the weak inequality in (3.5) is replaced with strict inequality then the inequality is also sufficient for the existence of a trajectory that has the two population extinction behavior described above.

Proof. Any extinction trajectory of this type must approach the equilibrium $x_k^* = a_{k0}/a_{kk}$; $x_j^* = 0$, $j \neq k$. This equilibrium can be attracting only if it is not situated in either of the regions where $dx_j/dt > 0, j \neq k$. This implies that inequality (3.5) must be satisfied.

Conversely, a linearization implies that the above equilibrium has a nontrivial stable manifold that intersects the positive population octant; and, hence, there exist solutions with the desired asymptotic behavior. ☐

Single Population Extinction. Define the system parameters

$$b_{ij} = a_{i0}a_{jj} - a_{j0}a_{ij}$$

$$C_{ij} = a_{ii}a_{jj} - a_{ij}a_{ji}$$

$$d_k = a_{k0} - a_{ki}\left[\frac{b_{ij}}{C_{ij}}\right] - a_{kj}\left[\frac{b_{ji}}{C_{ij}}\right], \qquad k \neq i, j, i \neq j\,.$$

A necessary condition for the existence of a trajectory satisfying $\lim_{t\to\infty} x_k(t) = 0$ and $\lim_{t\to\infty} x_j(t) > 0$, $j \neq k$, are

$$b_{ij}b_{ji} \geqq 0 \qquad i \neq j; i, j \neq k\,, \tag{3.6}$$

$$d_k \leqq 0\,. \tag{3.7}$$

Indication of the Proof. The ω-limit set of any such extinction trajectory is the equilibrium $x_k^* = 0$, $x_i^* = \dfrac{b_{ji}}{C_{ij}}$, $x_j^* = \dfrac{b_{ji}}{C_{ij}}$. Thus, b_{ij} and b_{ji} must be of the same sign; hence, (3.6) is valid. The equilibrium cannot be located in the region where $dx_k/dt > 0$; geometrically, this requires that the equilibrium cannot be below the line which is the intersection of S_k and the $x_k = 0$ plane. This is inequality (3.7).

The converse of this extinction result is also valid. There are two cases. If both b_{ij} and b_{ji} are positive, there is a positive equilibrium in the $x_i x_j$-plane with a stable manifold that intersects the positive octant. When $b_{ij} < 0$, $b_{ji} < 0$, and $d_k < 0$, the equilibrium is a saddle point with only a single trajectory of single population extinction type. ☐

Persistence Results. Since the extinction results are almost necessary and sufficient, persistence can be determined when some of the extinction criteria are violated. The approach taken here is to assume that interactions between each of the two population community, as are known, then determine what conditions, are required for the system to be persistent.

In terms of the system parameters, the two species interactions can be described by

$$x_i \gg x_j \Leftrightarrow b_{ij} > 0,\ b_{ji} < 0\,;$$

$$x_i \leftrightarrow x_j \Leftrightarrow b_{ij} > 0,\ b_{ji} > 0\,;$$

$$x_i \nleftrightarrow x_j \Leftrightarrow b_{ij} < 0,\ b_{ji} < 0\,.$$

Persistence can occur in the following cases:

A.1 $\quad x_i \gg x_j, \quad x_j \gg x_k, \quad x_k \gg x_i\,;$

A.2 $\quad x_i \leftrightarrow x_j, \quad x_i \gg x_k, \quad x_k \gg x_j\,;$

A.3 $\quad x_i \leftrightarrow x_j, \quad x_i \leftrightarrow x_k, \quad x_j \gg x_k\,;$

A.4 $\quad x_i \leftrightarrow x_j, \quad x_j \leftrightarrow x_k, \quad x_k \leftrightarrow x_i\,.$

Case A.1 has been studied extensively (e.g. May and Leonard, 1975; Gilpin, 1975; Grossberg, 1978). Grossberg demonstrated that the attractor is a cycle graph connecting the carrying capacities of the individual populations. This arrangement of two population interactions is rather unusual in that persistence is known automatically from the interactions.

For the arrangements A.2, A.3, and A.4, at least one additional relationship between the population parameters must be prescribed. These relationships require that a systems level parameter, d_k be positive. The biological interpretation of the d_k is that of an invasibility parameter indicating the ability of a population represented by x_k to invade a community at equilibrium: $x_i \leftrightarrow x_j$.

The persistence criteria are A.2, $d_k \geqq 0$; A.3, $d_j \geqq 0$ and $d_k \geqq 0$; A.4, $d_i \geqq 0$, $d_j \geqq 0$, and $d_k \geqq 0$. If, in any of the above arrangements, $d_k < 0$ then extinction of a population occurs. With the exception of A.1 just knowing all two population interactions is not sufficient to determine persistence. Any arrangement other than the forms above lead to extinction. In particular, any arrangement that contains an unstable competitive pair ($x_i \nleftrightarrow x_j$) cannot be persistent. This is not a robust property and is a consequence of the Lotka-Volterra model.

Stability and Persistence. This model has some interesting dynamical features. The intransitive arrangement, A.1, has already been mentioned, with the ω-limit set being a cycle graph. It is interesting that the arrangement A.1 is persistent without auxiliary conditions satisfied, and has an asymptotic behavior where $\limsup_{t\to\infty} x_i(t) > 0$ for each $i = 1, 2, 3$, but it is not the case that $\liminf_{t\to\infty} x_i(t) > 0$ for an $i = 1, 2, 3$.

Goh (1977) has demonstrated that (3.4) with coefficients given by

$$a_{1j}=2, 0.8, 0.5, 0.7;$$

$$a_{2j}=1.5, 1, 0.2, 0.3; \; j=0, 1, 2, 3,$$

$$a_{3j}=2.1, 0.2, 1, 0.9$$

has an asymptotically stable equilibrium (1, 1, 1) and a trajectory with components x_1 and x_3 that go to extinction. The underlying arrangement is of the extinction form $x_i \leftrightarrow x_k$, $x_j \gg x_k$, $x_i \not\leftrightarrow x_j$. Hence, it is possible for a competitive system to have an asymptotically stable interior equilibrium although the system is not persistent.

Strobeck (1973) gave necessary and sufficient conditions for local stability by employing the Routh-Hurwitz criteria. He also presented the two examples. The first has coefficients

$$a_{1j}=\tfrac{12}{3}, 1/3, 2/3, 4/3;$$

$$a_{2j}=3/2, 1/18, 1/6, 1/3; \; j=0, 1, 2, 3;$$

$$a_{3j}=4, 1/3, 1/3, 1.$$

This system has the two species arrangement $x_1 \leftrightarrow x_2$, $x_2 \leftrightarrow x_3$, $x_1 \leftrightarrow x_3$, and $d_1>0$, $d_3>0$. It is persistent and the equilibrium is asymptotically stable.

The second example multiplies the first and third components above by 3 to give coefficients $3a_{1j}$; a_{2j}; and $3a_{3j}$. This does not change the equilibrium or the species arrangement, but it does modify its stability to that of instability.

4. Models of Cooperation

Perhaps the most interesting and beneficial association between two species is the act of cooperation. This interaction has been suggested as an evolutionary objective of selection by Odum (1974) and others. The interaction can be classified as *obligatory* in the sense that survival of each population depends upon the presence of the other, or it can be *facultative* in that the association is not obligatory.

Classical examples of cooperation [which to various degrees have also been referred to as mutualism, symbiosis, commensalism, or amensalism (Odum, 1974)] include the algal and fungal components of lichens, the clown fish *(Amphirion percula)* and sea anemones, the ant-*Acacia* system (Janzen, 1966) and plant-pollinator systems.

4.1 Lotka-Volterra Models with Facultative Associations

In the absence of interspecific effects, the individual populations are assumed to be governed by logistic equations; hence the model with mass action interaction terms is

$$\frac{dx_1}{dt}=x_1(a_1-b_1x_1+c_{12}x_2),$$

$$\frac{dx_2}{dt}=x_2(a_2-b_2x_2+c_{21}x_1),$$

where

a_i, b_i, c_{ij} are positive constants.

This model has two possible types of asymptotic behavior. There can exist a positive equilibrium that is globally asymptotically stable (in the case when $b_1b_2-c_{12}c_{21}>0$). The second type of behavior occurs if $b_1b_2-c_{12}c_{21}\leqq 0$; the result is, as aptly described by May, "an orgy of mutual benefaction", specifically, there is unbounded growth for each component.

4.2 Obligatory Interactions as Modelled by Lotka-Volterra Kinetics

For obligatory interactions it is assumed that each population, in the absence of the interacting species, will decay exponentially and that interactions are represented by mass action formulations. Hence, the resulting model is

$$\frac{dx_1}{dt}=x_1(-a_1+b_1x_2),$$

$$\frac{dx_2}{dt}=x_2(-a_2+b_2x_1). \tag{4.1}$$

Models such as (4.1) can exhibit a stupendus orgy of mutuality since it can be demonstrated that they have solutions with a finite escape time [that is, there exists a $T<\infty$ such that $\lim_{t\to T} x_1(t)=\infty$ or $\lim_{t\to T} x_2(t)=\infty$]. For example, with $a_1=a_2=b_1=b_2=1$ the substitution $v=x_1-x_2$ leads to the temporal representation $V(t)=V(0)e^{-t}$. To demonstrate a finite escape, we can use the transformation $w=x_2^{-1}$ to show that

$$dw/dt+(-1+V(0)e^{-t})w=-1.$$

The classification of those solutions w that vanish at finite time can be obtained, and these solutions correspond to those solutions of (4.1) with finite escape time. There is also a threshold below which initial populations of each component population tend to extinction.

A graphical solution of (4.1) is presented in Fig. 4.1. The equilibrium is a saddle point with regions of growth and extinction determined by the separatrices of the saddle point.

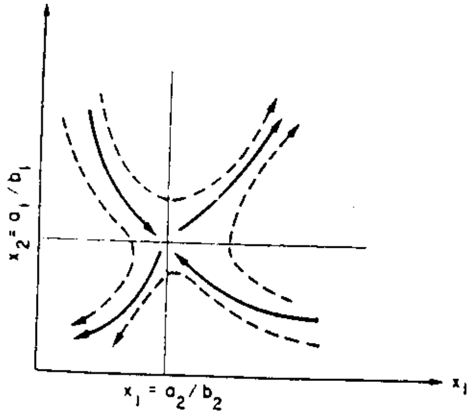

Fig. 4.1. Phase plane diagram of a Lotka-Volterra model of obligatory cooperation

4.3 Other Models of Cooperation

While the preceding model contains some desirable properties, such as an extinction threshold, the unbounded growth of solutions is certainly undesirable from a modeling perspective. Vandermeer and Boucher (1978) address the question "How should the isoclines be constructed for cooperative systems?" If interspecific interactions become weaker as population densities become large, then this might have the effect of curving the isoclines towards each other so that they again intersect. At this second intersection will be a stable equilibrium, and the unpleasant unboundedness of solutions present in the original model (4.1) does not occur here (Fig. 4.2).

The model might now have the form

$$\frac{dx_1}{dt} = x_1(-a_1 + b_1(x_1, x_2)x_2),$$

$$\frac{dx_2}{dt} = x_2(-a_2 + b_2(x_1, x_2)x_1),$$

where b_1, b_2 are decreasing functions of both x_1, x_2.

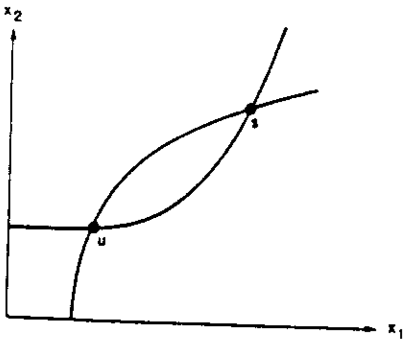

Fig. 4.2. Feasible isoclines for a cooperative system. *u* and *s* indicate an unstable and a stable equilibrium respectively

An example of a community where this situation might exist is the legume and bacteria *(Rhizobium)* system (Vandermeer and Boucher, 1978). Properties of this interaction include:

i) There is a minimal population of bacteria necessary for successful plant establishment. The few bacteria generally present are insufficient for crop growth and inoculation is often required to achieve an establishable community.

ii) Additional bacteria inoculum have little effect on nodulation and thus, presumably, on plant growth and reproduction). This occurs above a certain threshold level; for example, on red clover seedlings grown in culture, additions above $10^4\,(\mathrm{ml})^1$ of rhizosphere produce no discernible changes in growth.

iii) The number of bacteria present in the soil when symbiotic with legumes are usually substantially greater then the number needed for nodulation.

In another attempt to formulate a realistic model, May (1976) proposed modifying the carrying capacity of the logistic equation to reflect dependence upon the density of the complementary population. The system is written here in a slightly different form to be consistent with earlier discussions:

$$\frac{dx_1}{dt} = x_1\left[r_1 - \frac{C_1 x_1}{B_1 + \alpha_1 x_2}\right],$$

$$\frac{dx_2}{dt} = x_2\left[r_2 - \frac{C_2 x_2}{B_2 + \alpha_2 x_1}\right].$$

This formulation has the effect of increasing the equilibrium values of each of the components over the individual population carrying capacities.

Kolmogorov-Type Models

The general model of a cooperative two dimensional community of Kolmogorov-type is

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

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

where for $x_1 \geqq 0$, $x_2 \geqq 0$, the following requirements are imposed:

(M1) $\frac{\partial f_1}{\partial x_2} > 0, \quad \frac{\partial f_2}{\partial x_1} > 0$ (the interaction is cooperative)

(M2) $x_1 \frac{\partial f_i}{\partial x_1} + x_2 \frac{\partial f_i}{\partial x_2} \leqq -\alpha < 0, \quad i = 1, 2$

(changes in f_i along outward vector from origin is negative)

(M3) $f_i(0,0) > 0, \quad i = 1, 2$ (small populations grow)

(M4) $f_1(K_1, 0) = f_2(0, K_2) = 0$
(there is a carrying capacity for each population).

The reader is referred to Albrecht et al. (1974) who demonstrated that there is a feasible equilibrium which is globally asymptotically stable.

4.4 Stability in Higher Dimensional Cooperative Communities

An equilibrium, x^*, of the Kolmogorov system

$$\frac{dx_i}{dt} = x_i g_i(x), \qquad i = 1, 2, \ldots, n, \quad x = (x_1, x_2, \ldots, x_n)^T \tag{4.2}$$

is asymptotically stable if and only if the eigenvalues of the community matrix $S = (s_{ij})$,

$$s_{ij} = \frac{\partial}{\partial x_j}(x_i g_i(x))|_{x = x^*}$$

have negative real parts. Since $s_{ij} = x_i^* \dfrac{\partial g_i}{\partial x_j}(x^*)$, x^* is asymptotically stable if and only if all of the eigenvalues of DA gave negative real parts where $D = \text{diag}(x_1^*, x_2^*, \ldots, x_n^*)$ and A is the *interaction matrix*, $A = \dfrac{(\partial g_i(x^*))}{\partial x_j}$.

For competitive and predator-prey systems, equilibrium stability is independent of the stability of the interaction matrix. That is, there exist competitive and predator-prey communities for which the *community matrix* DA is unstable even though the interaction matrix A has eigenvalues with negative real parts; conversely, there exist communities for which the community matrix DA is asymptotically stable even though the interaction matrix is unstable (e.g. Strobeck, 1973).

A pleasant property of cooperative systems is that the above difficulties are simplified in that stability of an equilibrium is determined solely by the interaction matrix. Assuming that (4.2) is completely cooperative, that is,

$$\frac{\partial g_i}{\partial x_j}(x) \geqq 0, \; x \in R_n^+, \qquad i \neq j,$$

we obtain the following classification of stability.

Theorem 4.1. *A cooperative community modelled by* (4.1) *has an (asymptotically) stable, feasible equilibrium* x^* $(x^* > 0)$ *if and only if the interaction matrix* A *is asymptotically stable.*

Indication of the Proof. The concept of an M-matrix is useful in the subsequent arguments. The following criteria are equivalent

1. A is an M-matrix

2. All eigenvalues of A have positive real parts
3. A is nonsingular and $A^{-1} \geqq 0$
4. There exists a $z > 0$ such that $Az > 0$
5. There exists a $y > 0$ such that $A^T y > 0$
6. The principal minors of A are positive.

The off diagonal elements of the matrix DA are nonnegative. The matrix DA is asymptotically stable if and only if $-DA$ is an M-Matrix. Property 5 yields that $-DA$ is an M-matrix is equivalent to the existence of a vector x, $x > 0$, such that $-(DA)^T x = -A^T Dx > 0$. Hence, this is equivalent to the existence of a $y > 0$ such that $-A^T y > 0$. Since $a_{ij} \geqq 0$ for $i \neq j$, this is equivalent to the statement that $-A$ is an M-matrix. This results in the conclusion of the theorem. □

There are several interesting consequences of Theorem 4.1. Since $-A$ is an M-Matrix, the stability of an equilibrium, x^*, is equivalent to the existence of a vector $d > 0$ such that $Ad < 0$. Writing this statement in terms of the components, we obtain the inequality

$$d_i |a_{ii}| > \sum_{\substack{j=1 \\ j \neq i}}^{n} d_j a_{ij}, \qquad i = 1, 2, \ldots, n. \tag{4.3}$$

When (4.3) holds, A is called quasi-diagonally dominant. An interpretation of (4.3) is that for stability of x^*, the intraspecific competition must dominate the interspecific interaction terms. In an analogous manner, a column diagonal dominance property can be found.

Employing property 6 of M-matrices, a simple algebraic relationship may be obtained for the stability of an equilibrium;

$$(-1)^K \begin{vmatrix} a_{11} & a_{12} & \cdots & a_{1K} \\ a_{21} & a_{22} & \cdots & a_{2K} \\ \vdots & & & \vdots \\ a_{K1} & a_{K2} & \cdots & a_{KK} \end{vmatrix} > 0, \qquad K = 1, 2, \ldots, n$$

(is equivalent to $-A$ has positive principal minors).

The above consideration has focused upon local stability properties. There are global stability results that can be obtained in a similar fashion.

Theorem 4.2. *For the Lotka-Volterra system of cooperation,*

$$\frac{dx_i}{dt} = x_i\left(r_{i0} + \sum_{j=1}^{n} a_{ij} x_j\right), \qquad a_{ij} > 0 \tag{4.4}$$

a feasible equilibrium, x^*, *is globally asymptotically stable if and only if all the principal minors of* $-A$ *are positive.*

Indication of the Proof. It has been previously demonstrated that x^* is locally stable with this set of hypotheses. To establish global stability, a Liapunov function of Volterra type is useful. The function

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

has derivatives along trajectories of (4.4) expressed in terms of a quadratic form with matrix $CA+A^TC$ where $C=\operatorname{diag}(C_1,C_2,\ldots,C_n)$ (see Goh, 1977). If $CA+A^TC$ is negative definite, global asymptotic stability results. When the negative of an M-matrix is stable there exists a matrix $C=\operatorname{diag}(C_1,C_2,\ldots,C_n)$, $C_i>0$ such that $CA+A^TC$ is negative definite. Thus, global stability of x^* follows. □

This material is related to that found in Siljak (1975), Goh (1979), and Travis and Post (1979).

5. Communities Composed of Populations with Different or Mixed Functional Roles

Models of communities of two and three dimension are explored in this section. First, the stability of a community in which the functional role of a population changes with the density is considered. Next, we turn to some three dimensional communities of Lotka-Volterra type with determinate roles for populations, but the coupling in the food web will be different than discussed previously. The community matrix role in three dimensional systems is investigated.

5.1 A Two Species Model with Density Dependent Functional Roles

Hastings (1978) has proved a general stability theorem for Kolmogorov type models.

Theorem 5.1. *Sufficient conditions for the global stability of an equilibrium* (x_1^*,x_2^*) *of*

$$\frac{dx_1}{dt}=x_1f_1(x_1,x_2),$$
$$\frac{dx_2}{dt}=x_2f_2(x_1,x_2),\tag{5.1}$$

are

i) (x_1^*,x_2^*) *exists and is an unique equilibrium that is locally asymptotically stable.*

ii) *Both species sustain density dependent mortalities at all densities:*

$$\frac{\partial f_1}{\partial x_1}<0,\quad \frac{\partial f_2}{\partial x_2}<0.$$

iii) *There exist constants* $A>0$, $B>0$ *such that*

a) *for any* $x_2>B$, *there is a* $C>0$ *such that* $f_1(C,x_2)<0$.

b) *For any* $x_1>A$, *there is a* $D>0$ *such that* $f_2(x_1,D)<0$.

Indication of the Proof. Let (x_1^0,x_2^0) be any initial position. The rectangle bounded by the x_1,x_2 axes and the lines $x_1=\bar{x}_1=\max(x_1^*,A,C,x_1^0)$, $x_2=\bar{x}_2=\max(x_2^*,B,D,x_2^0)$ is invariant under the flow defined by (5.1). Transform the system by using the Volterra transformation $u_1=\ln x_1$, $u_1=\ln x_2$. This leads to

$$\frac{du_1}{dt}=f_1(e^{u_1},e^{u_2}),$$
$$\frac{du_2}{dt}=f_2(e^{u_1},e^{u_2}).$$

Since

$$\frac{\partial f_1}{\partial u_1}+\frac{\partial f_2}{\partial u_2}=\frac{\partial f_1}{\partial x_1}e^{u_1}+\frac{\partial f_2}{\partial x_2}e^{u_2}<0,$$

the Bendixson nonexistence criterion implies that (5.1) does not have a limit cycle. Hence, global asymptotic stability results for (5.1). □

A Functional Role Determined by Density Dependence

It is not a trivial task to determine the functional role of a population in a community; indeed, it is often the case that a species will assume many different roles depending upon average age of the population, the density of the population, and other factors. The snail *(Thais)* is both a competitor and a prey for the starfish *(Pisaster)* (see Paine, 1966). Bluegill-bass interactions are also indeterminate in their interaction relationships: both predation and competition can occur between both species.

A system that models two populations where predation is the dominant interaction at high densities of the prey population and where competition dominates at low population levels is

$$\frac{dx_1}{dt}=x_1(1-d_1x_1-d_2x_2-d_3x_1x_2),$$
$$\frac{dy_1}{dt}=x_2(1-d_4x_2-d_5x_1+d_6x_1^2).$$

Hastings (1978) has found sufficient conditions for a globally asymptotically stable equilibrium to be $4d_6>d_5^2$, $d_4>d_2$, and $d_2d_6>d_3d_5$.

5.2 The Community Matrix

We have observed that the community matrix has an important role in discussions of stability. This role is now explored in more detail. The principal model with an essence of lower order nonlinearity is the classical Lotka-Volterra model

$$\frac{dx_i}{dt} = x_i\left(r_i - \sum_{j=1}^{n} b_{ij}x_j\right), \qquad i = 1, 2, \ldots, n.$$

These equations may be written in matrix form as

$$\frac{dx}{dt} = (\operatorname{diag}(x_i))(r - Bx), \tag{5.2}$$

where $x = (x_1, x_2, \ldots, x_n)^T$, $r = (r_1, r_2, \ldots, r_n)^T$, and $B = (b_{ij})$. A nontrivial equilibrium x^* of (5.2) is (locally) asymptotically stable if and only if the eigenvalues of the matrix $-(\operatorname{diag}(x^*))B$ all have negative real parts. This matrix, more commonly written as $-(\operatorname{diag}(x_i^* b_{ii}))(I + A)$ where $A = (a_{ij})$, $a_{ij} = b_{ij}/b_{ii}$ if $i \neq j$ and $a_{ii} = 0$, will be called the *community matrix* of (5.2). There have been numerous attempts to derive methods of estimating a_{ij} from field and laboratory data, especially in the case of competitive communities (e.g., Gause, 1934; MacArthur and Levins, 1967; Vandermeer, 1969; Schoener, 1974; Hallett and Pimm, 1979). Because of the appeal of the community matrix and the fact that the parameters a_{ij} seem to have offered the best possibility for estimation in the past, it would be desirable to extract as much information as possible from the system (5.2) using only the matrix $I + A$. This approach can be developed without quantitative knowledge of r_i and b_{ii}.

As indicated in Sect. 4.4, the properties of $I + A$ are sufficient to determine the stability of n dimensional cooperative communities and also some communities of mixed mutualism and competition (Travis and Post, 1979). However, the examples of Strobeck (1973) in Sect. 3.6 show that the properties of $I + A$ are not sufficient to determine stability since both systems have the same community matrix.

The following result is valid only for dimension 3. Extensions to dimension 4 and higher are, at best, difficult (Clark and Hallam, 1982). Assumptions include that r is a 3-vector with positive entries and B is a 3×3 matrix with positive diagonal elements. To indicate parameter dependence, the system (2) will be denoted by $LV(r, B)$: the diagonal matrix $\operatorname{diag}(x_i^* b_{ii})$, (when $B^{-1}r = x^* > 0$), by $D(r, B)$; and the community matrix $I + A = \operatorname{diag}(b_{ii}^{-1})B$ by $CM(B)$. The second order principal minors of $I + A$ will be denoted by

$$M_1 = 1 - a_{23}a_{32}, \qquad M_2 = 1 - a_{13}a_{31}, \qquad M_3 = 1 - a_{12}a_{21}.$$

The next theorem gives conditions which are sufficient to ensure that the stability of a positive equilibrium of $LV(r, B)$ depends only on the community matrix. The conditions are also necessary in the sense that if they are not satisfied then either no positive equilibrium can exist for any choice of r and B or it is always possible to find examples, such as those of Strobeck, of distinct systems with the same community matrix but with different stability properties.

Theorem 5.2. *Let A denote a 3×3 matrix whose diagonal elements are zero.*
A. *If $I + A$ satisfies either*
(i) $\det(I + A) \leqq 0$, *or*

(ii) $\det(I + A) > 0$ *and* $M_i \leqq 0$, $i = 1, 2, 3$; *then for any choice of* r *and* B *where* $CM(B) = I + A$, $LV(r, B)$ *cannot have a positive stable equilibrium.*
B. *If $I + A$ satisfies*
(iii) $\det(I + A) > 0$, $M_i \geqq 0$, $i = 1, 2, 3$, $\sum_{i=1}^{3} M_i > 0$, *and*
$\sqrt{\det(I + A)} \leqq \sqrt{M_1} + \sqrt{M_2} + \sqrt{M_3}$,

where equality can hold only if $M_1 M_2 M_3 = 0$, then for any choice of r *and* B *where* $CM(B) = I + A$, *a positive equilibrium of $LV(r, B)$ is stable.*

C. *Suppose that $I + A$ satisfies none of the conditions,* (i), (ii), *or* (iii). *If* (iv): *there is no positive vector x such that $(I + A)x > 0$, then for any choice of* r *and* B *where* $CM(B) = I + A$, *$LV(r, B)$ can have no positive equilibrium. If* (v): *there exists* $x > 0$ *such that $(I + A)x > 0$, then there exist matrices r, B, $\tilde{r}$, $\tilde{B}$ with the properties* $CM(B)$ $= CM(\tilde{B}) = I + A$, $B^{-1}r = x^* > 0$, $\tilde{B}^{-1}\tilde{r} = \tilde{x}^* > 0$, *$x^*$ is a stable equilibrium of* *$LV(r, B)$, aNd $\tilde{x}^*$ is an unstable equilibrium of $LV(\tilde{r}, \tilde{B})$.*

Two observations are relevant to part C of Theorem 5.2. If $C(v)$ holds it is always possible to choose $x^* = \tilde{x}^*$. If $a_{ij} > 0$ so that the system represents competition, then $C(iv)$ cannot hold and x^* and $\tilde{x}^*$ in $C(v)$ may be chosen arbitrarily.

Quasi Weak Diagonal Dominance.

A matrix $C = (c_{ij})_{n \times n}$ is *weakly diagonally dominant* if $|c_{ii}| > |c_{ij}|$ for $i = 1, \ldots, n$. and $j \neq i$. The matrix C is *quasi weakly diagonally dominant* if there exists a diagonal matrix D with positive diagonal elements such that $D^{1}CD$ is weakly diagonally dominant. Quasi weak diagonal dominance might hold for many ecological systems as it relates interspecific and intraspecific interactions. The following theorem due to Fiedler and Ptak (1967) illustrates this and leads to some interesting observations.

Theorem 5.3. *If $n \geqq 2$ and C is any matrix, then C is quasi weakly diagonally dominant if and only if, for any set of distinct indices,* $1 \leqq i_1, i_2, \ldots, i_k \leqq n$,

$$|c_{i_1 i_2} c_{i_2 i_3} \cdots c_{i_{k-1} i_k} c_{i_k i_1}| \leqq |c_{i_1 i_1} c_{i_2 i_2} \cdots c_{i_k i_k}| \tag{5.3}$$

Applied to the matrix B of the system $LV(r, B)$, the condition (5.3) is a direct generalization of the well known condition which is necessary and sufficient for the stability of a positive equilibrium of a competitive system when $n = 2$: $|b_{12}b_{21}|$ $|b_{11}b_{22}|$. This condition is usually translated as "intraspecific interactions are stronger than interspecific interactions", and this interpretation also seems appropriate when $n > 2$. Note that (5.3) holds for B if and only if it holds for $CM(B)$ $= I + A$, and, in this case, takes the form:

$$|a_{i_1 i_2} a_{i_2 i_3} \cdots a_{i_k i_1}| \leqq 1. \tag{5.4}$$

It is well known that $\det(I + A) > 0$ is a necessary condition for stability and also that it is not, in general, sufficient if $n > 2$. However, in the three species case, condition (5.4) simplifies matters considerably and leads to a nice classification of stable equilibria.

Theorem 5.4. *Let $n=3$; $r>0$; and B be a matrix with positive diagonal elements such that B (or $I+A$) is quasi weakly diagonally dominant. Then, a positive equilibrium of $LV(r, B)$ is stable if and only if* $\det(I+A)>0$.

As remarked previously, quasi weak diagonal dominance might be valid for many community models. For a competitive community, it is a consequence of some of the formulations of the competition coefficients a_{ij}. As an illustration it is noted that one of the more familiar formulations first suggested by Gause for $n=2$ and generalized by Levins (1968) and MacArthur (1968), can be extended to include the case of a continuous resource spectrum as follows:

$$a_{ij}=\frac{\int_S p_i(x)\,p_j(x)\,dx}{\int_S p_i^2(x)\,dx}, \tag{5.5}$$

where $p_i(x)\,dx$ denotes the probability that species i will utilize the portion $(x, x+dx)$ of the resource spectrum in a unit of time, and S denotes the resource continuum. If "$\|\ \|$" denotes the inner product and norm in the appropriate inner product space, it follows, for distinct indices $i_1, i_2, \ldots, i_k$

$$\begin{aligned} a_{i_1i_2}a_{i_2i_3}\ldots a_{i_ki_1} &= \frac{(p_{i_1}\cdot p_{i_2})(p_{i_2}\cdot p_{i_3})\ldots(p_{i_k}\cdot p_{i_1})}{\|p_{i_1}\|^2\,\|p_{i_2}\|^2\ldots\|p_{i_k}\|^2} \\ &\leqq \frac{(\|p_{i_1}\|\,\|p_{i_2}\|)(\|p_{i_2}\|\,\|p_{i_3}\|)\ldots(\|p_{i_k}\|\,\|p_{i_1}\|)}{\|p_{i_1}\|^2\,\|p_{i_2}\|^2\ldots\|p_{i_k}\|^2}=1\,. \end{aligned}$$

Therefore $I+A$ is quasi weakly diagonally dominant.

There are extensions of these results to the Kolmogorov-type system

$$\frac{dx_i}{dt}=x_if_i(x), \qquad i=1,2,\ldots,n$$

where

$$\partial f_i/\partial x_i<0\,.$$

The proof of Theorems 5.2 and 5.3 are not given here; they may be found in Clark and Hallam (1982).

5.3 A Two Dimensional Competitive Subcommunity and Another Population

The effects of introducing a population into a competitive subcommunity is now explored. We have previously studied the case where the added population was a competitor with each of the other two populations. In this section some consequences of introducing a cooperative population or a predator population are described. The mathematical details are similar to those for the Lotka-Volterra competitive model.

The Third Population is a Cooperator (Hallam, 1980)

For a Lotka-Volterra model of a competitive subcommunity and an added cooperator, certain hypotheses about the coefficients are required to eliminate the "orgy" effect. With these imposed, extinction of the populations can be classified. Employing two-population interactions, there are some interesting outcomes. The introduction of cooperator can destroy the stable competitive subcommunity by driving one of the competitors to extinction. This can be accomplished by the symbiotic population helping one of the competitors too much.

The Third Population is a Predator

Models of a community containing a predator and two prey populations are numerous in the recent literature (e.g., Cramer and May, 1972; Vance, 1978; Gilpin, 1978; Freedman and Waltman, 1984). Most analyses have focused upon the processes of predation and competition as mechanisms that can generate diversity in communities. Two of these mechanisms that can be identified by model analysis are predator-mediated coexistence and competition-induced coexistence.

Predator-mediated coexistence is concerned with regulation of a dominant competitor by predation in order that the complete community might persist. Instances of predator mediated coexistence are well documented in the ecological literature. Classical experiments relating to predator mediated coexistence include those of Utida (1953) where the presence of a parasitic wasp, *Neocatolaccus mamezophagus*, could lead to coexistence of two bean weevil populations and Slobodkin (1961, 1964) where effects of predation on competing hydra populations were investigated. Paine (1966) performed a classic experiment where a top predator in a marine system was removed, and a collapse of the lower trophic system occurred. See Connell (1975) and Caswell (1978) for additional instances of occurrence or nonoccurrence of predator mediated coexistence.

Other references, related at least peripherally to the model studied here, in which a predator is introduced into a competitive subcommunity include Neill (1975) and Addicott (1974). Yodzis (1976) discussed effects of constant rate predation on competitive systems.

Employing a Lotka-Volterra model, an analysis of persistence and extinction (Hallam, 1981), shows that there can be two forms of predator mediated coexistence; these are given by the arrangements

$$v_1 \gg v_2; \quad v_1 \leftrightarrow p; \quad v_2 \leftrightarrow p;$$

and

$$v_1 \gg v_2; \quad v_1 \leftrightarrow p; \quad p \downarrow v_2\,.$$

In these arrangements, the competition notation is as in Sect. 3.6 for the prey populations v_1, v_2. The interactions between predator and prey indicated by $v_i \leftrightarrow p$ and $p \downarrow v_i$ represent an asymptotic stability coexistence for both predator and prey and the survival of the prey population only respectively. Both arrangements above require invasion capability of complementary species at equilibrium subcommunities if persistence is to occur.

Gilpin (1978), using a model employed by Vance (1978), numerically demonstrated that chaotic behavior can arise in a three dimensional system composed of two prey and a predator. While the parameter set utilized to find chaotic behavior is a limiting case of an arrangement whose persistence development is indicated in Hallam (1981), it can be shown there are parameter sets in the persistent arrangement that lead to chaotic motion. Not only is the phenomena of predator-mediated coexistence of ecological interest, the mathematical description of the dynamics can be very complicated as well.

The persistence analysis also leads to another possible mechanism of coexistence, namely, "competition induced coexistence". An analysis of the Lotka-Volterra model shows that this can occur in two ways:

$$v_1 \leftrightarrow v_2; \quad v_1 \leftrightarrow p; \quad p \downarrow v_2$$

and

$$v_1 \leftrightarrow v_2; \quad p \downarrow v_1; \quad p \downarrow v_2.$$

Two arrangements of subcommunities were classified in this category. The largest increase in diversity occurs in an arrangement where a predator cannot survive on either of the prey species but it can persist if it is able to invade the stable competitive subcommunity at its equilibrium density. Certain herbivore plant systems could theoretically fit into this category.

The terms "predator mediated coexistence" and "competition induced coexistence" refer to persistence in a community attained by effects of species upon subcommunities. Analysis indicates that determination of coexistence can depend up on all subcommunities as well as upon species interactive capabilities. In the case of predator mediated coexistence, a persistent community can be achieved theoretically by introduction of a prey competitor into a predator-prey subsystem in which the predator need not even be able to survive. The phenomenon of predator mediated coexistence might be masked in such a situation. Persistence, since it is dependent upon subsystems composition and interrelationships, is a community property and phrases as simple as "predator mediated coexistence" are probably not totally adequate descriptions.

As a concluding comment, I recommend the books of Cohen (1978) and Pimm (1982), which contain many documented food webs. It is clear from examining the diagrammed webs that structure can be very complex and that the analysis presented here is only an embarkation into a study of food webs.

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