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STRUCTURAL AND DYNAMIC STABILITY OF MODEL PREDATOR-PREY SYSTEMS

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PREFACE

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ABSTRACT

A modified set of Volterra's differential equations for dynamics of prey and predator populations is analysed. This modification takes three effects into consideration:

1) Satiation of predator resulting in the inability of either predation rate or predator reproduction rate to increase infinitely with growth of prey numbers;

2) Limited resources of prey, as a result of which prey populations cannot increase infinitely even in the absence of predators;

3) Limited external resources (unrelated to prey) of predators, as a result of which predator populations cannot grow infinitely even when there is an excess of prey; i.e.

$$\dot{x} = ax - \frac{bxy}{1+\alpha x} - \varepsilon x^2$$

$$\dot{y} = -cy + \frac{dxy}{1+\alpha x} - \mu y^2 .$$

Analysis of this set of equations gives many different behavioural regimes depending on the values of parameters.

This model as a whole can be used to demonstrate a number of situations: situations in which the behaviour of a predator-prey system is adequately described by Volterra's equations; situations in which these equations cannot describe the dynamics of prey-predator interactions; situations in which the system behaves similarly to Volterra's under certain initial conditions but not under other conditions.

1. Introduction

Growing environmental pollution caused by man's activity, rapid increase in population, and realization of the scarcity of natural resources raise enormous and pressing problems in ecology. Of primary importance is the problem of qualitative and quantitative prediction of the consequences of man's impact on natural communities. Particular problems involve determining the character and intensity of impacts which destroy stability of communities, elaborating optimum criteria and determining optimal modes of community exploitation and, finally, creating efficient methods for controlling community activity. It is obvious that observing natural phenomena alone is not enough to solve these problems and that it is necessary to build theoretical and experimental models of the processes operating in communities. These must be models on the basis of which one could frame, test, verify and refute hypotheses regarding functioning mechanisms of communities and the separate units within them.

Trophic interrelations do not encompass all the community processes but, according to present viewpoints, they are decisive factors in determining the structure and function of communities. It therefore seems expedient to make trophic interrelations the object of modelling in the first place. In the present case, the elementary modelling object must be the population pair "prey-predator" and the elementary behavioural phenomenom is the abundance dynamics (stable regimes in the first approximation) of such a system.

The first models of population dynamics in the prey-predator system were suggested by Volterra and Lotka [1-2]. Later, the ideas conveyed in these works were developed both in investigations on qualitative analysis of Volterra's generalized systems [3-6], and in studies where the main emphasis was placed on concrete biological mechanisms of population interrelations [7-9]. In the present paper a prey-predator model is developed in which central attention is focussed on studying two factors which seem to be of principal importance. First is presented the analysis of a concrete mechanism of prey and predator interrelations under which the predator is satiated (prey being available in abundance), and therefore neither the rate of prey consumption, nor that of predator reproduction increase infinitely with the growth of the prey number. Second, the analysis takes into account that the number of prey is not the only external factor which affects the dynamics of the predator number. The predator population, even if prey is abundant, can be limited by some other factors which are independent of prey resources, e.g., by scarcity of suitable habitat.

2. The Michaelis-Menton Equation and a Prey-Predator System

The classical Volterra model assumes that the rate of predator population growth increases, and that of prey decreases, linearly with the growth of both predator and prey:

$$\begin{aligned} \dot{x} &= ax - bxy \\ \dot{y} &= -cy + dxy \end{aligned} \qquad (1)$$

where x is the number of prey, y is the number of predators, and a, b, c, d are positive coefficients.

In such a system there are always fluctuations in the number of predators and prey around the values ($x_0 = \frac{c}{d}$, $y_0 = \frac{a}{b}$), with the amplitudes and period determined by the initial conditions (Fig. I).

This model has two major disadvantages, one of which is of a biological character and the other of a mathematical one. From the biological viewpoint, linear dependence of the rate of predation and predator reproduction on the number of prey is considered by many authors to be a very crude approximation of reality which is true only within some very narrow limits. From the mathematical viewpoint, the main drawback of the Volterra system is the fact that this system is not "robust." That is, the account of any factors or effects not taken into consideration when building the model, results in qualitative modifications of the system's behaviour. In particular, under such changes there are no longer oscillations of numbers with arbitrary, constant amplitudes and frequency depending only on the initial conditions. Thus, contrary to its widespread popularity, the Volterra model cannot explain the interrelated oscillations of the number of prey and predators with constant amplitudes and frequency which are sometimes present in natural and experimental communities. If the actual nature of prey and predator interrelations really corresponded to the Volterra model, then observed amplitudes and frequencies of oscillation should change within unbounded limits because of inevitable random external impacts. In order to explain oscillations of a stable character, one needs a model with a limit cycle, that is, a model describing the dynamics under which a system comes to the regime of stable oscillations with constant amplitudes and frequencies from any initial conditions.

The Volterra system is constructed similarly to the equations of chemical kinetics. The processes of prey reproduction and the natural mortality of predators are considered as monomolecular reactions or, in other words, as first order reactions the rate of which is proportional to a reagent concentration (in the given case, proportional to the prey or predator populations). Similarly, prey and predator interrelations are considered as second order reactions where prey are annihilated (and predators increase their number) at a rate proportional to the number of each of the interrelated populations.

Obviously, such an analogy between the processes of predation and bimolecular reactions is very crude. In fact, the kinetics of predation remind one not so much of bimolecular reactions proceeding according to the law of reacting masses, but rather of the mechanism of enzyme reactions. Let us consider the situation in more detail.

In such a scheme the predator performs the role of an enzyme which catalyses transformation of a substrate (prey) into a product (excrements of a predator). The analog of an enzyme is a hungry predator in this process, the analog of an enzyme-substrate complex is a predator hunting for a prey and a satiated predator, the analog of a dissociation reaction of an enzyme-substrate complex is a prey's escaping from a pursuing predator. On the whole, the process looks as follows in the suggested scheme: the predator finds randomly wandering prey and starts to pursue it (in chemical terms, it binds a substrate). The predator then either lets the prey escape or eats it, thus transforming the latter into a reaction product, and itself reverting into an initial state of hunger. At first sight, it does not seem right to consider a predator pursuing a prey and a satiated predator as being in the same state, but such an approach seems justified in the first approximation and as a very rough scheme (though still more subtle than that of Volterra).

According to this assumption a predation process is completely similar to the mechanism of enzyme reaction $S + E \leftarrow [ES] \rightarrow E + P$, where S is substrate, E the enzyme, ES the enzyme-substrate complex and P the reaction product. Kinetics of this reaction comply with the Michaelis-Menton equation, whose derivation can be found in any chemical kinetics text (for example [10]).

$$\dot{x} = -\frac{bN\,x\,y}{N + x} \qquad (2)$$

where in our case x means concentration of prey, y is the concentration of predators, N is the analog of the Michaelis constant (in this particular case a concentration of prey where half of the predators would be permanently hungry), bN is the maximum rate of predation per predator concentration unit, b is a constant relating to frequency of predator-prey collision, that is the same constant as in the classical Volterra equation (1)*.

Assuming that the prey population in the absence of predators increases exponentially, we obtain an equation

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* In chemical kinetics the Michaelis-Menton equation is based on the assumption that concentration of free substrate is always higher than concentration of bound substrate, or, equivalently, higher than the concentration of enzyme-substrate complex. In terms of ecology it means that at any given moment a relatively small proportion of a prey population is pursued by predators. This assumption seems to be justified.

for the dynamics of prey numbers in the prey-predator model:

$$\begin{aligned} \dot{x} &= ax - \frac{bN\,x\,y}{N + x} \quad \text{or} \\ \dot{x} &= ax - \frac{b\,x\,y}{1 + \alpha x}\,, \end{aligned} \tag{3}$$

where $\alpha = 1/N$.

For low concentrations of prey ($x \ll N$), this equation approximates the corresponding Volterra equation, whereas for higher values of x, it differs favourably from Volterra's in that it reflects the impossibility of infinite increase of the predation rate with growth of the prey population. In particular, equation (3) shows that at very high prey population densities the rate of predation is determined exclusively by the number of predators.

$$x \approx ax - bNy = ax - By \qquad (x \gg N). \tag{4}$$

Let us consider now the dynamics of the predator population. Based on Volterra's assumption that, first, predator populations in the absence of prey undergo exponential decay and, second, that a certain constant part of the consumed prey biomass is converted into predator biomass (it is not important whether it happens due to growth or reproduction), one obtains the following equation for dynamics of predator population size

$$\dot{y} = -cy + \frac{dxy}{1+\alpha x}. \tag{5}$$

Here, d/b is a ratio of conversion of prey biomass into predator biomass.

When a prey population is small, this equation corresponds to the Volterra equation. But when the value of x is higher, the equation differs favourably from Volterra's equation because it reflects the impossibility of unlimited increase of predator reproduction rate with the growth of prey population size. In particular, when the number of prey is big enough ($x >> N$), the rate of growth of the predator population will be determined exclusively by its own magnitude

$$\dot{y} \approx -cy + dNy = Dy \tag{6}$$

where D is a biotic potential of predator, i.e., a specific rate of growth of predator population, taking into account natural death rate when prey are in excess.

Thus we obtain a system of equations describing the dynamics of the interacting prey and predator populations which is free from one of the main faults of Volterra's system

$$\dot{x} = ax - \frac{bxy}{1+\alpha x} \tag{7}$$

$$\dot{y} = - cy + \frac{dxy}{1+\alpha x} . \qquad (7)$$

In the obtained model, contrary to Volterra's system, neither rate of predation nor growth rate of predator population increase infinitely with the growth of prey population, but rather are determined exclusively by the quantity of predators when the number of prey is large enough.*

It should be mentioned that the dependence of the predation rate on the number of prey, which is apparent from the proposed model, reminds one very much of the dependence determined empirically by Ivlev [13]:

$$r = R\,(1 - e^{-\xi P}) \qquad (8)$$

where r is the predator's ration, i.e. biomass of prey eaten by a predator per time unit; R is the limit ration, i.e. ration when prey are in excess, P is the prey population density. In both models the rate of predation

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* The existence of a similarity between the dependence of bacterial population growth rate on culture medium concentration and the dependence described by the Michaelis-Menten equation was mentioned by Monod [11], Noviek and Szilard [12], and others. This is important, because it suggests that in a phenomenological sense the process of predation and growth of "predator" population could be properly expressed also in those cases when the intimate mechanism of interaction essentially differs from the previously described one on which kinetics of enzyme reactions or its "ecological" variant is based.

when prey numbers are small is proportional to the product of number of prey and predators. But when prey numbers are larger, the predation rate is determined exclusively by the quantity of predators. This assumption allows us to assume that the properties of the system (7) considered below, and the results obtained relate in considerable part or even as a whole to the predator-prey system based on Ivlev's equation. The latter, however, requires special verification.

3. Study of the System

Let us study the system (7). We begin by finding the equilibrium points of the system, i.e. the values of predator and prey population which, in the absence of external effects, are constant. Then we determine the nature of stability of these equilibrium points.

Out of the algebraic system:

$$a\ (1+\alpha x)\ x - bxy = 0$$
$$-c\ (1+\alpha x)\ y - dxy = 0$$

one finds coordinates of two equilibrium points of the system: O and A, where

$$O\ \{x = 0,\ y = 0\};\quad A\{x = \frac{c}{d+c\alpha},\ y = \frac{a}{b}\cdot\frac{d}{d-c\alpha}\}.$$

Point O, similar to Volterra's system, is a saddle point (See Fig. II). This is apparent without any special verification, since it is clear that predators in the absence of prey are decreasing (i.e. the trajectory, coaxial with the ordinate axis, intersects the origin), and reproduction of prey in the absence of predators is unlimited (i.e. the trajectory, coaxial with the abscissa axis, starts at the origin). To discover the stability properties of point *A*, one linearises system (7) in the vicinity of point *A*. Let

$$x = x_0 + \zeta, \quad y = y_0 + \eta .$$

In that case:

$$\dot{\zeta} = \frac{\alpha b x_0 y_0}{(1+\alpha x_0)^2}\,\zeta - \frac{b x_0}{1+\alpha x_0}\,\eta$$

$$\eta = \frac{d y_0}{(1+\alpha x_0)^2} \cdot \zeta .$$

The characteristic equation of the system is:

$$\begin{vmatrix} \dfrac{\alpha b x_0 y_0}{(1+\alpha x_0)^2} - \lambda & \dfrac{-b x_0}{1+\alpha x_0} \\ \dfrac{d y_0}{(1+\alpha x_0)^2} & -\lambda \end{vmatrix} = \begin{vmatrix} \dfrac{\alpha a c}{d} - \lambda & \dfrac{-bc}{d} \\ \dfrac{a(d-\alpha c)}{b} & -\lambda \end{vmatrix} = 0$$

$$\text{or} \quad \lambda^2 - \alpha\frac{ac}{d}\lambda + \frac{ac(d-\alpha c)}{d} = 0.$$

The real part of the roots of the characteristic equation is always positive and, therefore, the point *A* is always unstable. It is not difficult to show that under $0 < \alpha < 2\frac{d}{a}\left(\sqrt{1+\frac{a}{c}} - 1\right)$, A is a focal point (Fig.II(i),II(ii)), but under $2\frac{d}{a}(\sqrt{1+\frac{a}{c}}-1) < \alpha < \frac{d}{c}$, A is a node point (Fig.II(iii)). Under $\alpha > \frac{d}{c}$, the coordinates of point A become negative having no ecological significance (Fig.II(iv)).*

Since under $\alpha \to 0$ the system (7) is transferred into the classic Volterra system (1) in which a corresponding singular point is a center, it could be said that satiation of predators in Volterra's system results in instability of the nontrivial equilibrium point. That means that if in Volterra's system oscillation in numbers of both predators and prey could take place in the absence of external effects for an indefinite period of time with an amplitude depending on initial conditions, then in the system considered numbers of both populations in the vicinity of the equilibrium point would fluctuate with ever growing amplitudes. To understand the outcome it is necessary to consider the behaviour of system (7) under large values of x.

Under $x \gg 1/\alpha$ system (7) has the following form:

$$\begin{aligned} \dot{x} &= ax - By \\ \dot{y} &= Dy \end{aligned} \tag{9}$$

where B is the maximum rate of predation per unit of

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* The latter inequality simply means that the maximum rate of predator reproduction, when prey are in excess (d/α), is less than its natural death rate. It is clear that under these conditions reproduction of prey is alway unlimited, but the predators die out.

predator or, in other words, the maximum ration of the predator; and D is the maximum net rate of predator population growth with natural death rate or biotic potential of the predator taken into account.

In order to determine the nature of the behaviour of system (9), one finds the sign of the trajectories' curvature on the phase plane, i.e. the sign of d^2y/dx^2. This allows us to predict whether trajectories always return to the region of low population numbers ($x<x_0$, $y<y_0$) passing the focal point repeatedly, or whether under certain initial conditions they go to infinity. We obtain:

$$d^2y/dx^2 = 0 \qquad y = \frac{a-D}{B} x.$$

It is not difficult to see that the latter equation means that a phase portrait of system (7) under $a < D$ has a shape seen in Figure II (i); and under $2\frac{d}{a}\ (1 + \frac{a}{c} -1) > \alpha$ and $a > D$ has a shape seen in Figure II (ii). The obtained result may be interpreted in the following way: if the biotic potential of a predator is less than the potential of prey (Fig.II(ii)) it appears that the prey population escapes from predator control, and the number of prey after several oscillations begins to increase unlimitedly and monotonically. The number of predators increases correspondingly in an unlimited and monotonic manner, but at a smaller rate. All phase trajectories go to infinity under the line $y = \frac{a - D}{B} x$. It is worth mentioning that a similar effect of escape of prey from predator (or parasite) control is well known [1]. If the biotic potential of the predator is greater than the potential of prey (Fig.II(i)), prey could not escape from the predator and, formally, in the model system there would be fluctuations of predators' and prey's numbers for a long period of time and with ever-growing amplitude. Actually that means that in some sequential cycle of the unwinding spiral the trajectory of the system will come so close to one of the coordinate axes that due to random stochastic fluctuation it will contact the axis and be absorbed by the latter. This outcome is inevitable because with each cycle of the spiral the trajectory will be more tightly pressed to the coordinate axes. In terms of ecology, that means that in a real situation corresponding to the proposed model, the amplitude of fluctuations of predator and prey numbers will increase so that with a minimum number of prey, either the predator eventually dies out due to scarcity of prey and the surviving part of the prey population reproduces itself unlimitedly (the trajectory contacts the abscissa axis), or the predator eliminates the entire prey population and then, naturally, dies out itself (trajectory contacts the ordinate axis).

4. Competition in Volterra's Model

The obvious weakness of the model considered is due to the fact that it contains regimes responding to unlimited reproduction of either prey alone or prey and predators. Thus, the behaviour of the system under great numbers of predators and, particularly, of prey is obviously not realistic because in fact neither predators nor prey can increase their numbers indefinitely. To improve the situation, in addition to the previously described interactions between predators and prey, it is necessary to take into account effects restricting the unlimited reproduction of populations, i.e. to put terms describing the effect of intraspecific competition among prey and among predators, respectively, into equations for the dynamics of numbers.

Competition here means decreasing reproduction or increasing death rate with growth of density of the corresponding population. Mechanisms of competition could be quite different and, respectively, terms describing effects of competition could have various forms. Let us confine ourselves to a simple assumption, often used in mathematical ecology, that with growth of population numbers, reproduction linearly decreases or, alternatively, death rate linearly increases. In other words, let us assume that competition among prey in system (7) brings us to the following system:

$$\dot{x} = ax - \frac{bxy}{1+\alpha x} - \varepsilon x^2 \qquad (10)$$

$$\dot{y} = -cy + \frac{dxy}{1+\alpha x}\ , \qquad (10)$$

and competition among predators gives the system:

$$\begin{aligned} \dot{x} &= ax - \frac{bxy}{1+\alpha x} \\ \dot{y} &= -cy + \frac{dxy}{1+\alpha x} - \mu y^2. \end{aligned} \qquad (11)$$

It is worth noting that competition, expressed by the term μy^2 in system (11), is competition among predators not for prey, because number of prey is not included in the term, but rather for any other resources unrelated to prey but required by the predator (i.e. simple competition for a territory).

Before considering systems (10) and (11), it is necessary to recall the result one obtains when the term of competition among prey is put into Volterra's model in the same way:

$$\begin{aligned} \dot{x} &= ax - bxy - \varepsilon x^2 \\ \dot{y} &= -cy + dxy\ , \end{aligned} \qquad (12)$$

and when the term of competition among predators is put into it:

$$\begin{aligned} \dot{x} &= ax - bxy \\ \dot{y} &= -cy + dxy - \mu y^2. \end{aligned} \qquad (13)$$

It is not difficult to show [15] that in the first case when ε is small, the "center" type singular point A in Volterra's system (1) is transformed into a stable focal point. Moreover, the "saddle" type $\{x = a/\varepsilon,\ y = 0\}$ singular point B, which expresses equilibrium number of prey in the absence of a predator, appears on the abscissa axis. Now the number of prey could not increase indefinitely (Fig. IV(i)). If ε grows, the stable focal point first is transformed into a stable node point (Fig. IV(ii)) and then, under $\varepsilon = ad/c$, it unites with the saddle point (Fig. IV(iii)). This latter combination of parameter values means that a stable coexistence of predators and prey is impossible because the number of prey, due to limitation by external resources, is so small that it can not support predators.

When competition between predators is taken into account (13), the center of Volterra's system is also transformed into a stable focal point and, for μ large enough, into a stable node point, but no new equilibrium points appear.

Competition between both predators and prey, taken into account simultaneously, gives the system:

$$\begin{aligned} \dot{x} &= ax - bxy - \varepsilon x^2 \\ \dot{y} &= -cy + dxy - \mu y^2. \end{aligned} \qquad (14)$$

The nature of behaviour of this system does not differ from the behaviour of system (12) in a qualitative way under various combinations of values of parameters ε and μ (Fig. III). Representative behaviours are shown in Fig. IV.

5. Summary Effect of Predator's Satiation and Competition among Prey

Let us now consider system (10)

$$\begin{aligned} \dot{x} &= ax - \frac{bxy}{1+\alpha x} - \varepsilon x^2 \\ \dot{y} &= -cy + \frac{dxy}{1+\alpha x} \end{aligned} \qquad (10)$$

in which effects of predators' satiation and competition among prey are taken into account. This system, similar to system (12), has two equilibrium points:

$$A \left\{x = \frac{c}{d-\alpha c}, \; y = \frac{d}{b} \cdot \frac{a(d-\alpha c) - \varepsilon C}{(d-\alpha c)^2}\right\}; \quad B \left\{x = \frac{a}{\varepsilon}, \; y = 0\right\}.$$

Let us consider the nature of the behaviour of the system in detail under various parameter values. First note that a point A has a biological meaning only if it lies in the region of positive values of variables,

$$\varepsilon < \frac{a(d - \alpha c)}{c} . \qquad (15)$$

Otherwise, point A departs from the first quadrant and changes from a saddle point to a stable node (Fig.VI(iii)). By studying inequality (15), we can see that point B is always a saddle and the condition necessary for stability of point A consists of satisfying the inequality

$$\varepsilon > \frac{b\alpha y_0}{(1+\alpha x_0)^2} \quad .$$

This could be easily shown by linearizing the system in the vicinity of this point. The stability condition of point *A* attains the most obvious and easily interpreted form in that interesting case when α is small (i.e. effects associated with satiation of the predator are weaker than effects of interaction of predators and prey, and terms of higher order than the first one can be ignored along α). Then the stability condition will be

$$\varepsilon > a\alpha .$$

Thus, if competition is intense enough, point *A* is stable (Fig.VI(i)) and the phase portrait of system (10) is in a qualitative way, similar to the portrait of system (12) (Fig.IV(i)). On the other hand, if competition is not intense enough, point *A* is not stable. Nevertheless, it is not difficult to see that trajectories could not go into infinity: neither prey nor predators could reproduce themselves unlimitedly because the number of prey is limited by external resources and the number of predators by the number of prey. Therefore, the existence of a limit cycle is inevitable. In particular, the separatrix line, which goes out from the saddle point *B* (Fig.VI(ii)), will spiral into the cycle from the outside.

Thus, with the fixed a,b,c,d, numerous possible values of parameters $\{\varepsilon,\alpha\}$ are separated into three regions (Fig.V), according to the three possible types of behaviour of system (10). Under values of α and ε associated with the region (iii) in system (10) a stable coexistence predator and prey is impossible. The predator always dies out and the number of prey is limited by the external resources.

In region (i) a situation arises where with any initial condition, the system undergoes damped oscillations and comes to a stable coexistence of predator and prey (Fig.VI(i)). In region (ii) there are no points of stable equilibrium at all, but there is a regime of stable oscillations with constant frequencies and amplitudes. The system also comes to this regime from any initial condition (Fig.VI(ii)).*

The possibility of existence of a limit cycle in such a simple and easily interpreted model is of great interest in itself. I would like to note that in Kilmer's work [7] an ecologically interpreted stable limit cycle was obtained

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* In order not to complicate the picture, we do not now make a distinction between a focal point and a node point and pay attention only to the fact of stability and instability of a point. Actually, behaviour of the system in the right lower angle of the region (i) and in the left upper angle of the region (ii) will somewhat differ from the ones shown (Fig.VI(i) and (ii), respectively). In the first case, a trajectory will meet not a focal point, but a stable node point. In the second case, an unstable node point (but not a focal point) will be inside the stable limit cycle.

only after introduction of many terms of high order into the model and before that, according to Kilmer, there were no concrete ecological models with meaningful stable limit cycles.

As was mentioned above, the occurrence in nature or in an experiment of stable interrelated oscillations of predators and prey numbers can be explained only if there is a limit cycle in a corresponding differential equation. Probably, some of the mutual oscillations of predator and prey numbers which are observed in nature could be interpreted with model (10).

On the other hand, it is necessary to make it clear that system (10) could not explain all the situations where correlated oscillations of predator and prey numbers are observed. For example, it is quite clear that the stable oscillations of *Paramecium* and *Didinium* laboratory populations observed in the experiments of Gause [16] (when artificial predation refuges and periodic reintroductions of prey were employed) were not stabilized by the factor of competition between prey for living space or other resources.

6. Effect of Predator Satiation and Intraspecific Competition among Predators

Let us now consider the situation when there is no competition in the prey population and when the size of the predator population, even with an excess of prey, is limited by a competition factor, such as living space.

Let us consider system (11)

$$\begin{aligned} \dot{x} &= ax - \frac{bxy}{1+\alpha x} \\ \dot{y} &= -cy + \frac{dxy}{1+\alpha x} - \mu y^2. \end{aligned} \tag{11}$$

By setting expressions for x and y to zero we find coordinates of specific points of the system:

$$\begin{aligned} x_1 &= \frac{b(d-\alpha c) - 2\,\mu a\alpha - Q}{2\,\mu a\alpha^2} \\ y_1 &= \frac{b(d-\alpha c) - Q}{2\,\mu ab} \\ x_2 &= \frac{b(d-\alpha c) - 2\,\mu ad + Q}{2\,\mu a\alpha^2} \\ y_2 &= \frac{b(d-\alpha c) + Q}{2\,\mu ab}, \end{aligned} \tag{16}$$

where

$$Q = \sqrt{b^2\,(d-\alpha c)^2 - 4abd\alpha\mu} \tag{17}$$

First of all, it is necessary to note that the necessary and sufficient condition for existence of two positive equilibrium points is the inequality:

$$\mu < \frac{b\,(d-\alpha c)^2}{4a\alpha d}. \tag{18}$$

Outside the regions determined by this inequality system (11) has no singular points at all, because the radicand in (16) and (17) is negative.

Consider system (11) under condition (18). With

$\alpha \to 0$, and then with $\mu \to 0$, it is not difficult to ascertain that the point $\{x_1,y_1\}$ in both cases corresponds to point *A* of the systems (13) and (7) respectively. Similarly, the point *C*: $\{x_2,y_2\}$ in both cases goes to infinity along both coordinates. The stability test shows that point *C* is always a saddle point and an arm of a separatrix line going to the right from the saddle point and asymptotically converging to $y = D/\mu$.

Proceeding from that, one imagines a phase portrait of the system with $\alpha >> \mu$ (Fig.VIII(i)) and $\mu >> \alpha$ (Fig.VIII(ii)). [The inequality (18) of course, is retained; this stipulation will no longer be repeated]. Consideration of these phase portraits makes it clear that they differ from one another in a qualitative way due to two peculiarities: First, by stability of point *A*, and, second, by behaviour of specific trajectories, passing from the saddle point *C*. For example, the trajectory going to the left from the saddle point passes to infinity (Fig.VIII(i)) or does not (Fig.VIII(iii)). It is clear that with a given α there must be some value of μ such that an arm of a separatrix line, going to the left from the saddle point, returns to the saddle point from underneath. In other words, in the space of the parameters $\{\alpha,\mu\}$ there must be two separatrix lines: while crossing one of them the stability of point *A* changes, while crossing the other there is a change in behaviour of the specific trajectories passing from the saddle point. To find the first separatrix line is not difficult. It is enough to linearise system (11) in the vicinity of point *A* and to obtain the expression of its stability:

$$\mu > \alpha b x_1/(1+\alpha x_1)^2.$$

In case where α and μ are small enough to permit terms of second and higher order to be ignored, stability of *A* is determined by a quite simple and easily interpreted inequality:

$$\mu > \alpha bc/d.$$

In other words, point *A* is a stable focal point when competition between predators is great enough in comparison with the effect of predators' satiation; and it is an unstable focal point when the relationship of these effects is reversed.

At the present time, an analytical expression for the second separatrix line has not been derived. The only thing that can be said proceeding from general considerations is that this line must pass through the origin of coordinates in $\{\alpha,\mu\}$ parameter space. It is even unknown whether it passes above or below the separatrix line dividing regions of stability from regions of instability for point *A*. Approximate numeral estimations suggest that both variants are possible (Fig.VII(i),(ii)). Phase portraits of the system for the region of parameter values lying between the two separatrix lines are given in both possible variants (Fig.VIII(iii),(iv)). One easily can see that in both cases there is necessarily a limit cycle in the system: stable (Fig.VIII(iii)) and unstable (Fig.VIII(iv)).

Let us now try to interpret the obtained regimes of behaviour of the system, in sequence, for all possible combinations of values of parameters α and μ.

In the absence of competition between predators, as we have already seen, the system has one equilibrium point - an unstable focal point or a node point (Fig. II). In this case the final result of interaction between predator and prey populations, regardless of initial conditions, is unlimited reproduction of both prey and predators with the prey escaping from predator control.*

With appearance of weak competition between predators, besides the unstable focal point, the saddle point *C* appears in the system (Fig.VIII(i)) and with that only the qualitative nature of dynamics of the processes remains unchanged. But the final result is the same - both predators and prey reproduce unlimitedly and prey escape from predator control.

With growing competition the system can behave in two ways depending on the values of other parameters. Let us consider both possible ways of evolution of the phase portrait of the system with μ increasing. In the first variant the focal point *A* is transformed from unstable to stable before the behaviour of the separatrix line changes in a

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* Here and below we ignore the fact that passage of the trajectory too close to one of the coordinate axes actually means that the corresponding population dies out.

qualitative way (Fig. VIII(iv)). An unstable limit cycle appears with the separatrix line coming to the saddle point C from below. That means that in the vicinity of point A some closed region of its stability appears. If the initial condition corresponds to the phase point inside the unstable limit cycle, there will be transient oscillations of numbers of predators and prey in the system, leading to a stable equilibrium. Otherwise, prey, as before, will escape the predator.

With a subsequent growth of μ the region encircled by the stable limit cycle grows and eventually the cycle becomes semistable, coinciding with a loop made by an arm of the separatrix line going out to the left from the saddle point C and coming into the saddle point from below. With a further increase of μ, this loop "breaks" (Fig. VIII(ii)). The region of stability of A is limited by a curve made of the arms of the separatrix line, coming into the saddle point. It is a curious thing that to the left of and below this curve there is some kind of "corridor" - a region of initial conditions for the system under which prey escape from the predators. It would be interesting to find out whether its width under plausible values of parameters is so insignificant that points inside the corridor correspond to the system with predator and prey essentially extinct.

The other possible mode of evolution of the phase portrait of the system is the following. With increase of μ

the equilibrium point remains an unstable focal point, while an arm of the separatrix line, going out to the left from the saddle point, eventually coincides with an arm coming into the saddle point from underneath. The resulting loop becomes a semistable cycle (stable inside and unstable outside). With further growth of μ, a stable limit cycle appears in the system (Fig. VIII(iii)). Trajectories going out from the unstable focal point *A* spiral out to the cycle from inside, and the separatrix line going out to the left from the saddle point spirals in from outside. The whole region inside the curve made by the arms of the separatrix line coming into the saddle point is a stability region for this limit cycle. In other words, under any initial conditions corresponding to a point inside this region, the system enters the regime of stable oscillations of predators and prey with constant frequency and amplitude.

With μ further increasing, the region inside the limit cycle diminishes and, correspondingly, the amplitude of the stable oscillations of population numbers also diminishes. And, at last, under $\mu \simeq \alpha bc/d$ the limit cycle becomes a stable focal point (Fig. VIII(ii)).*

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* Here as in the previous section, in order not to complicate the picture, we do not consider the behaviour of the system near point *A*, and limit ourselves to the fact of stability or instability. Actually, behaviour of the system in the right lower "angle" of region (i) and in the left upper "angle" of region (ii) (Fig. VII) differs somewhat from that shown in Figure VIII and VIII(ii). In the first case an unstable focal point is transformed into an unstable node point, and in the second case a stable focal point into a stable node point.

Thus, in system (12) the following regimes can be realized under various parameter value combinations:

(1) Under any initial conditions of population numbers the prey escape from predator control (Fig.VIII(i)).

(2) There is a comparatively small closed region such that under initial conditions corresponding to a phase point inside this region, attenuating oscillations take place which result in a stable equilibrium. Under initial conditions which are beyond the region, prey escape from the predator control (Fig.VIII(iv)).

(3) There is an open region of initial values such that under conditions corresponding to the phase points inside this region the system always comes to the regime of stable fluctuations of numbers with permanent frequency and amplitude (Fig.VIII(iii)).

(4) There is an open region of initial values from which the system, in a process of attenuating oscillations, comes to the stable equilibrium condition (Fig.VIII(ii)).

In summary, in the system where the effects of predator's satiation and of competition among predators for any resource unrelated to prey and available in fixed quantity are taken into consideration, there is always a region of initial values under which the prey population escapes from the predators and, moreover, under intense enough competition there could be a region of initial values from which the system comes either to a regime of stable oscillations or to a stable equilibrium state.

7. Effect of Predator Satiation, And Intraspecific Competition both among Predators and among Prey.

Now, in order to take into consideration the fact that even when prey escape from the predators the unlimited reproduction of prey is impossible, we consider competition among prey. The corresponding system of equations is as follows:

$$\begin{aligned} \dot{x} &= ax-\frac{bxy}{1+\alpha x} - \varepsilon x^2 \\ \dot{y} &= -cy + \frac{dxy}{1+\alpha x} - \mu y^2 \quad . \end{aligned} \qquad (19)$$

Setting $\dot{x}$ and $\dot{y}$ to zero, we obtain algebraic systems of equations that define the coordinates of the equilibrium points. This system leads to the cubic equation relative to x or y, but expressions for its solution are bulky. However, with known combinations of behaviour types of the predator-prey system, and taking into account any pair of the three effects [characterized by the parameters α (satiation of predator), μ (competition between predators), and ε (competition between prey)], one can qualitatively visualize the separation of the three-dimensional space of parameters $\{\alpha,\mu,\varepsilon\}$ into regions (Fig. IX), and the nature of behaviour of the system within each of these regions (Fig. X_i).

Separation of planes of coordinates $\{\alpha,\mu\}$, $\{\alpha,\varepsilon\}$, $\{\mu,\varepsilon\}$ into regions, of course, precisely corresponds with Figures III, V, and VII respectively. Referring to Fig. IX, the area intersecting the planes of the coordinates along <u>AB</u>, <u>AC</u>, and <u>BF</u> lines is the frontier of a region adjacent to the origin of the coordinates, beyond which the system has no entirely nontrivial equilibrium points and the point *B* is a stable node point (Fig. IV(iii)).

The region adjacent to the origin of the coordinates and confined by the planes of coordinates and by the area CABF, is separated, as shown in Figure IX, into six smaller regions. Let us consider the behaviour of the system in each of these regions. Here one should proceed from the known, using phase portraits of the system for the portions of planes of the coordinates confining these regions, as well as from the fact that the system always has either one or three nontrivial equilibrium points in region under consideration.

Behaviour of the system in the region (i) (Fig.IX) naturally coincides with its behaviour in the portions of the planes of coordinates OJB (Fig.VI(i)) and EOBF (Fig.IV (i),(ii)) confining this region. The system has one stable point A.*

In the same manner, behaviour of the system in the region AJKO does not differ from its behaviour on the frontier AJO of this region (see Fig.VI(ii)). There is a stable cycle and an unstable point inside this cycle. The separatrix line, coming out from the saddle point B spirals into the cycle from outside.

Unlike its behaviour in the regions (i) and (ii), behaviour

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* Here and below as well as above we ignore the difference between a focal point and a node point and consider only the fact of stability.

of the system inside the regions (iii), (iv) and (v) - (vi), separated by the coordinate plane $\{\alpha,\mu\}$, is not entirely the same as the behaviour of the system in the portions of the coordinate plane separating the corresponding regions. The fact is, that under any insignificant ε the saddle point B appears in the system and, simultaneously, the stable node point D appears. Behaviour of the system in the regions (iii) and (iv) could be seen in Figure X(iii), (iv). It is not difficult to see that the behaviour of the system in the regions of small number of prey (x) does not differ very much from behaviour of the system analysed without taking into consideration the competition among prey. But the principal difference is the following: if in the absence of competition among prey, escape of prey from predators means unlimited reproduction of prey, with such competition, escape means that the number of prey tends to be a value determined by the limit of external resources.

Behaviour of the system in the region $\underline{GHLKO}$ could be dual (the same as on the frontier of the region $\underline{OGH}$ - (see Fig.VIII(iii),(iv)) depending on relative position of the separatrix lines, one of which separates the stability region of point A and the other separates regions with different behaviour of the specific trajectories going through the saddle point C (Fig. VII).

Now it is clear that $\underline{OAKLDE}$ is a plane separating the region of the existence of the stable node point D and the saddle point *C*. With growth of ε, these points converge and, at last, disappear.

Knowing this, one can make some deliberations about the behaviour of the system in the region OGHLK - the only region which has no frontier with any coordinate planes. Behaviour of the system in this region could, naturally, be dual, because it depends on the relative position of the separatrix lines OJ and OG.

It is not difficult to see the following: if behaviour in the region OGHLK is characterised by the presence of the stable limit cycle, then with the disappearance of points *C* and *D* (when the frontier OKL is crossed), behaviour of the system in the region OJKL becomes qualitatively the same as in the region OAJK -- in the system there is a stable cycle with an unstable point *A* inside it.

It is quite another thing if behaviour of the system in the region OGHLK is characterised by the presence of an unstable limit cycle. In that case, with the disappearance of points *C* and *D*, the unstable cycle will continue to exist but necessarily becomes surrounded by a stable limit cycle to which the separatrix line, coming out of the saddle point *B*, spirals in from outside (Fig.X(vii)). Thus, one obtains an entirely new type of behaviour of the system. Moreover, under any initial conditions which are beyond the unstable limit cycle, the system enters a regime of stable oscillations, and under the initial conditions which correspond to the points inside the unstable cycle, the system comes to a state of stable equilibrium.

In summary, the provision of effects of satiation of predators and competition among both predators and prey in Volterra's system results in the following possible behavioural regimes:

(1) Predator dies out, number of prey is limited by external resources;

(2) Under any initial conditions the system comes to a state of stable equilibrium in which predator and prey determine each other's numbers;

(3) Under any initial conditions the system enters a state of stable oscillations;

(4) The system comes to a state of stable oscillations under any initial conditions except a small region around the state of equilibrium;

(5) The region of initial conditions is separated into two regions: out of the first one the system reaches a state of equilibrium in which number of prey is limited by external resources. Out of the other develops a state of stable equilibrium in which predator and prey limit each other's number, or a state of stable oscillations;

(6) Under any initial conditions the system reaches a state of stable equilibrium in which the number of prey is limited by external resources.

CONCLUSION

A model of the predator-prey system has been analysed. It is based on the following assumptions, some of which are derived from the classic Lotka-Volterra model:

(1) A population of prey in absence of predators and other factors limiting its number grows exponentially.

(2) The rate of decrease in number of prey due to predation is always proportional to the number of predators.

(3) The growth of the prey population, regardless of predators and particularly in their absence, is limited by the scarcity of some necessary resources in such a way that with increasing numbers the death rate increases (in a linear way) due to competition among prey for these resources. In the absence of predators, the dynamics of one prey population complies with a logistic equation.

(4) The rate of decrease in the number of prey due to predation is proportional to the number of prey when there are few prey, and does not depend on the number of prey when there is an excess of prey (effect of predators' satiation). This set of rules is analogous to the Michaelis-Menten equation:

$$\dot{x} \approx \frac{Bxy}{1+\alpha x} .$$

(5) In the absence of prey the number of predators decreases exponentially as predators die out.

(6) The increase in number of predators is proportional to the number of prey eaten. In other words, the ratio of conversion of prey biomass into predator biomass is constant.

(7) Even with an excess of prey, the increase in predators is limited by scarcity of resources unrelated to prey but necessary for the predator. Due to competition among predators for these resources, their death rate increases linearly with their growth in numbers. With an excess of prey, the dynamics of the predator population complies with a logistic equation.

Though all assumptions on which the model is based are very crude approximations of reality (particularly for small numbers of prey and predators), they allow us to describe and interpret the following situations from a single point of view:

(1) There is one state of stable equilibrium *D*, in which

the numbers of predators and prey are different from zero and the number of prey is limited by a scarcity of some resources, but not by a "pressure" from predators (Fig.X(iii)).

(2) There are two states of stable equilibrium. One of them is the same as in the above point *D*. In the other state, the numbers of predators and prey limit each other. The region of stability of the second state could be both closed and open (Fig.X(iv)). Numbers of predators and prey approach this state in a form of attenuating oscillations.

(3) There is the state of stable equilibirum *D* and the state of stable oscillations of numbers near state *A* (Fig.X(v)).

(4) Near state *A* there is only the state of stable oscillations. The nature of oscillation stimulation could be both smooth (when stable oscillations with certain amplitudes of oscillation in the number of predators and prey as well as with a certain period could be arrived at under any initial conditions (Fig.X(ii)) and drastic (Fig.X(vii)).

(5) There is only one state of stable equilibrium *A*, when the predator and prey populations limit each other (Fig.X(i)).

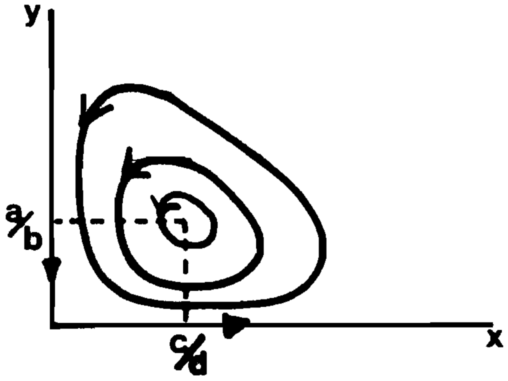

Figure I. Dynamics of population size of predator (Y) and prey (X) according to Volterra's classical model: phase portrait of a system.

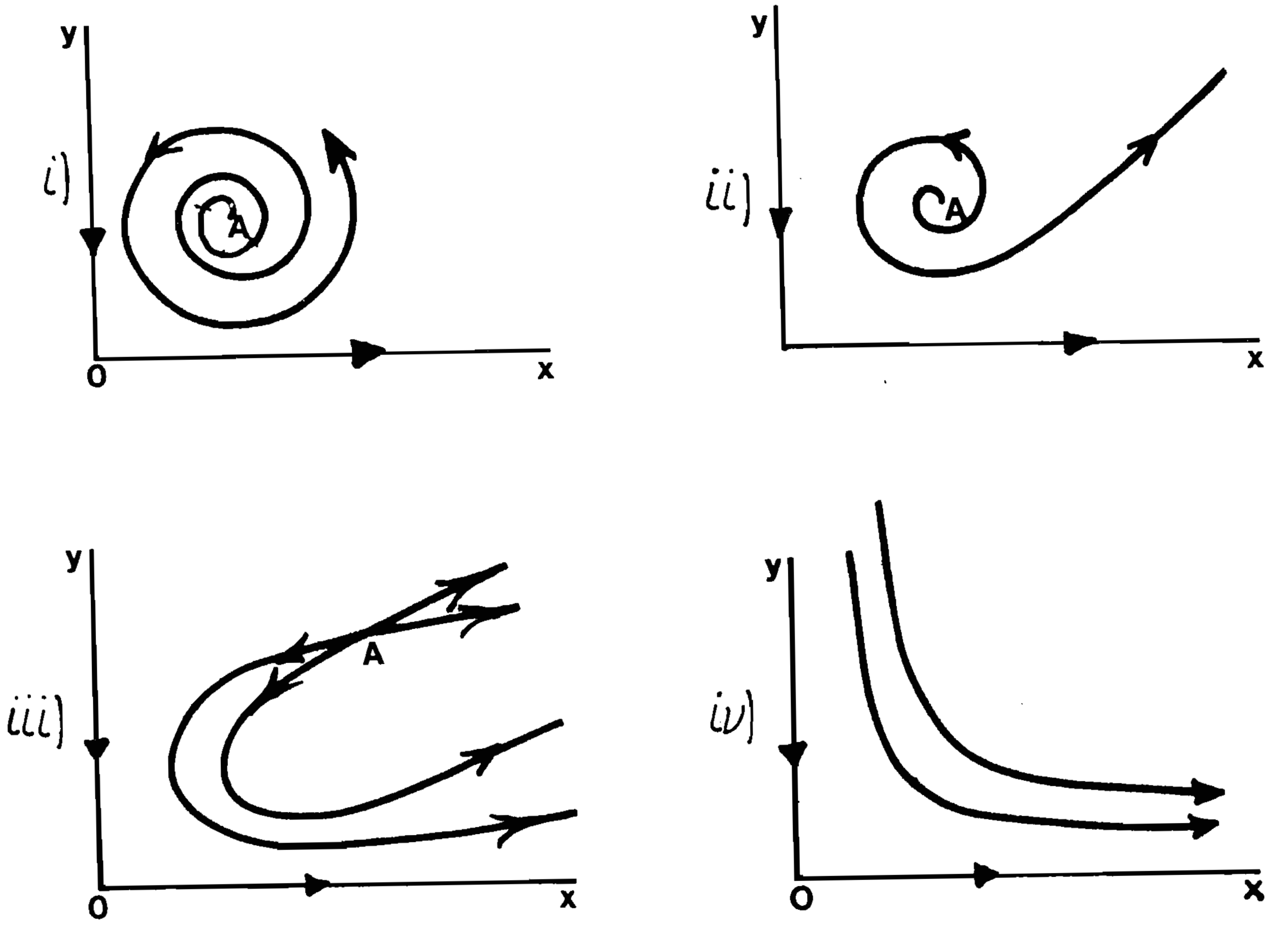

Figure II. Phase portraits of system (7) with

(i) $\alpha < D$

(ii) $D < a, \quad \alpha < 2\frac{d}{a}\left(\sqrt{1 + \frac{a}{c}} - 1\right)$

(iii) $2\frac{d}{a}\left(\sqrt{1 + \frac{a}{c}} - 1\right) < \alpha < \frac{d}{c}$

(iv) $\alpha > \frac{d}{c}$

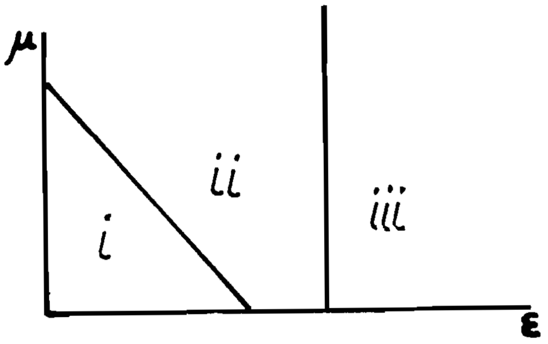

Figure III. Separation of the space of parameters $\{\varepsilon, \mu\}$ of the system (14).

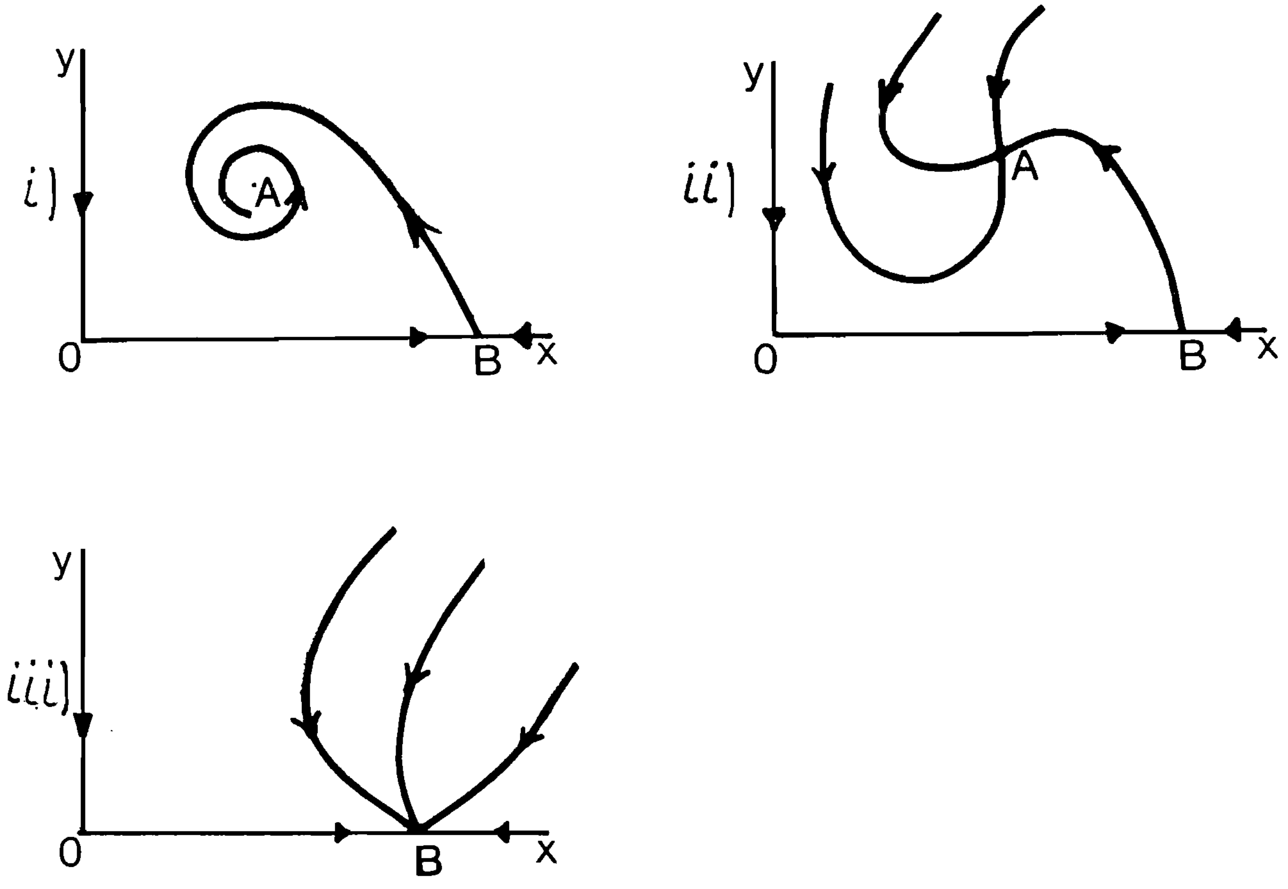

Figure IV. Phase portraits of the system (14) for corresponding regions of the space of parameters {ε. μ} (see Fig. III).

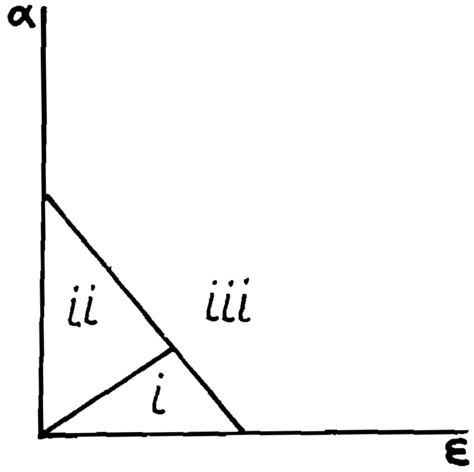

Figure V. Separation of the space of parameters $\{\alpha, \varepsilon\}$ of the system (10).

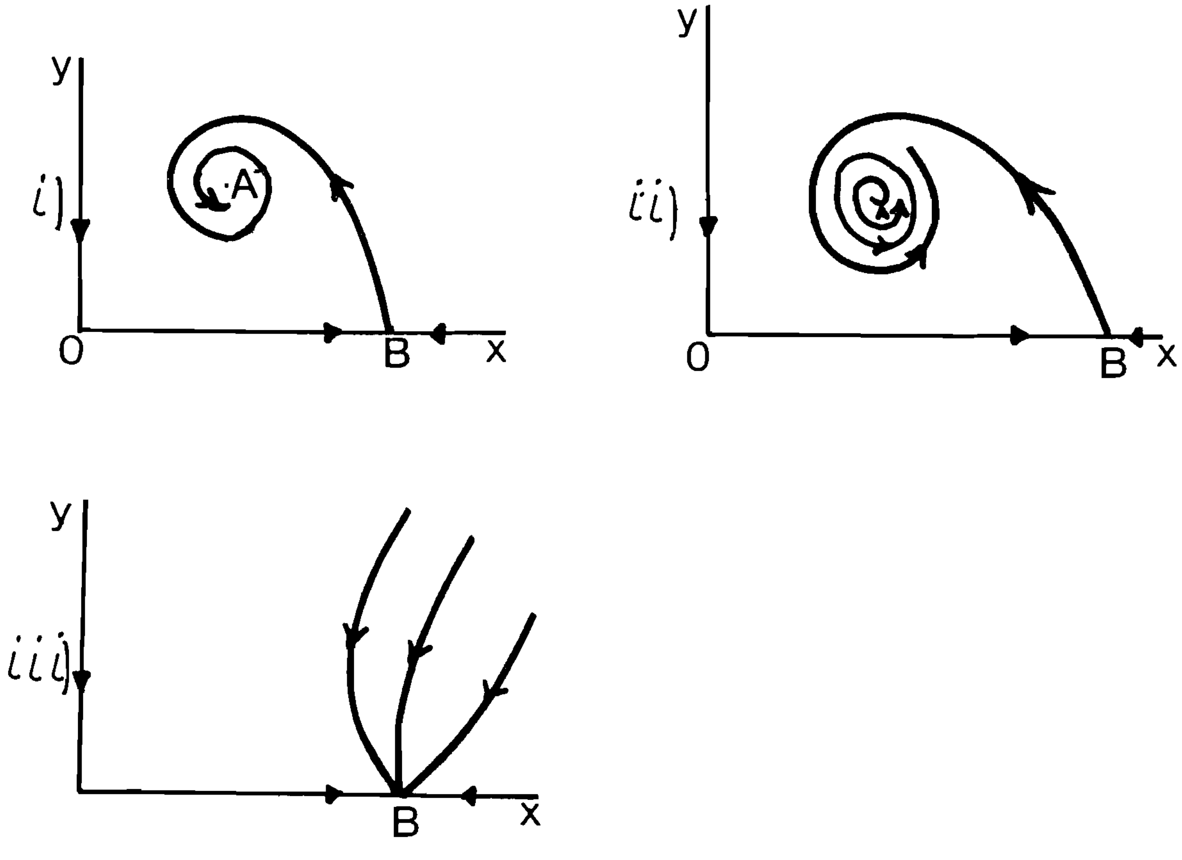

Figure VI. Phase portraits of the system (10) for corresponding regions of the space of parameters $\{\alpha,\varepsilon\}$ (see Figure V).

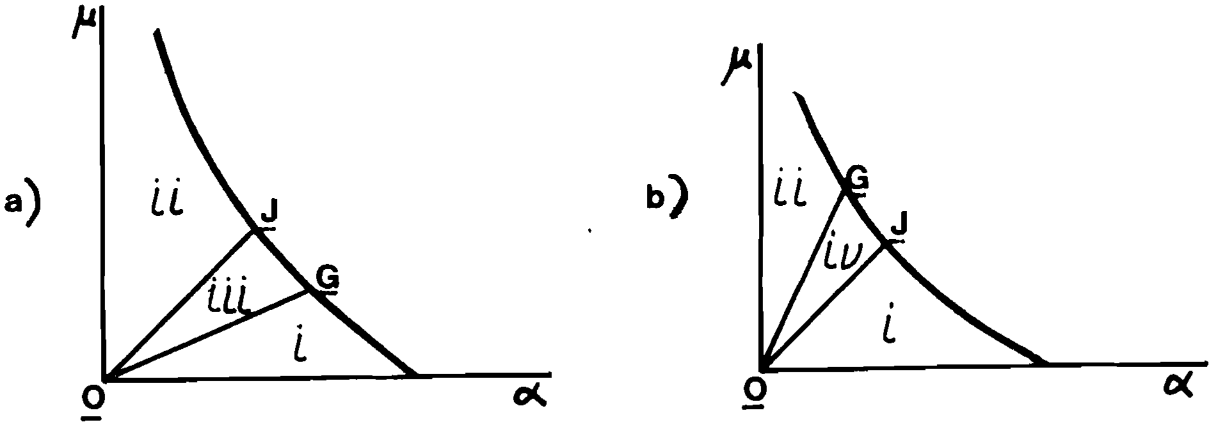

Figure VII. Two possible variants of separation of the parameter space of the system (11). OJ - separatrix line between stability and instability regions of point A; OG - separatrix line between regions with qualitative different behaviour of special trajectories passing through the saddle point B.

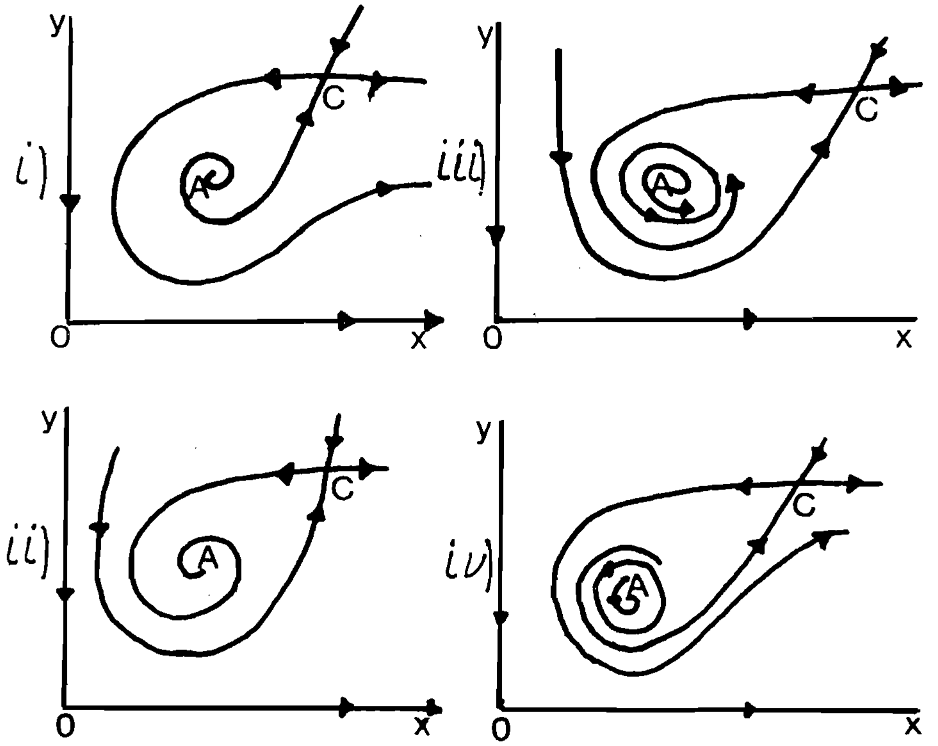

Figure VIII. Phase portraits of the system (11) for corresponding regions of the space of parameters $\{\alpha,\mu\}$ (see Figure VII).

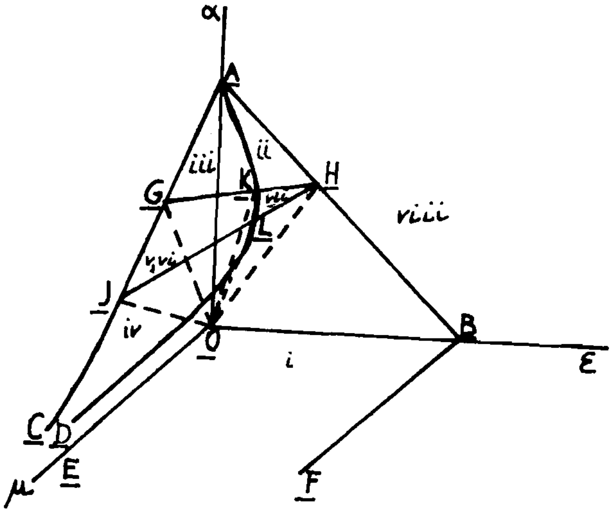

Figure IX. Separation of the space of parameters $\{\alpha, \varepsilon, \mu\}$ of the system (19).

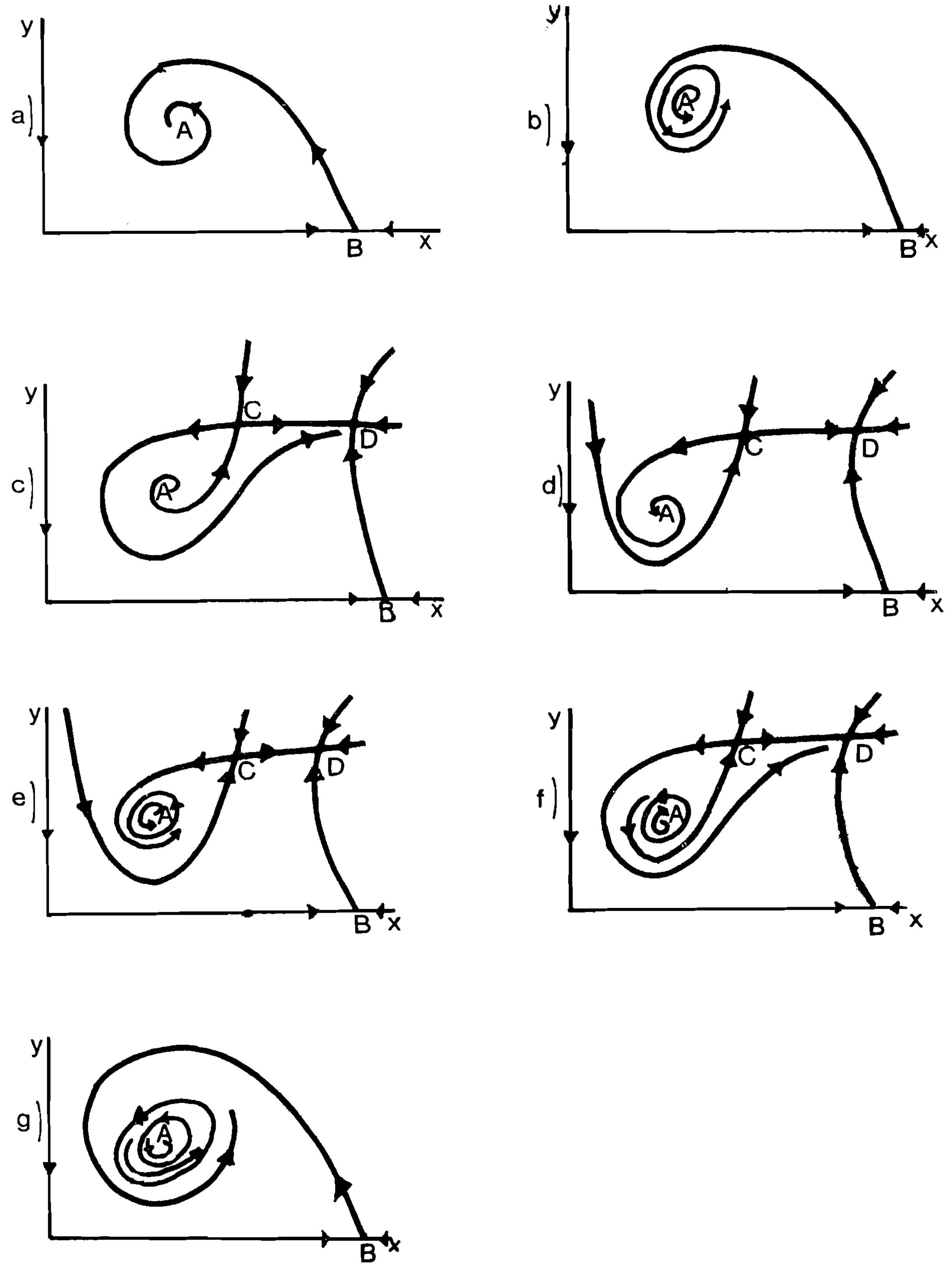

Figure X: Phase portraits of the system (19) for corresponding regions of the space of parameters (see Figure IX).

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