PERTURBED MODELS OF TWO OR THREE SPECIES, WITH HARVESTING OR STOCKING, CARRYING CAPACITY, AND LOWER CRITICAL DENSITY

by

Casey McConill

B.Sc.(Honours), Simon Fraser University, 1987

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
in the Department
of
Mathematics and Statistics

SIMON FRASER UNIVERSITY
May, 1992

APPROVAL

Name: Casey McConill

Degree: Doctor of Philosophy

Title of Thesis: Perturbed Models of Two or Three Species, with Harvesting or Stocking, Carrying Capacity, and Lower Critical Density

Examining Comittee:

Chair: Dr. A.H. Lachlan

Dr. G.N. Bojadziev
Senior Supervisor

Dr. M. Singh

Dr. G.A.C. Graham

Dr. E. Pechlaner

Dr. H.I. Freedman
External Examiner
Department of Mathematics
University of Alberta
Edmonton, Alberta

Date Approved: May 22, 1992

ABSTRACT

The behaviour of certain population models in $\Re^2$ and $\Re^3$ is investigated. Involved in the growth rate of the first species are both a carrying capacity and a lower critical density, and we allow for the inclusion of harvesting or stocking of one of the species. The three-species model represents a predator-predator-prey system, while the two-species model may, by suitable selection of the sign of certain terms, portray three types of interaction: predator-prey, competition, or cooperation. These features affect the nature and multiplicity of the models' equilibria, which are analyzed from the point of view of structural stability. The locations of the simple and multiple equilibria of the unperturbed systems are found, and the local natures and stability properties are determined. Of particular interest are nonhyperbolic simple equilibria, and multiple equilibria (also nonhyperbolic), which are structurally unstable and may change radically when perturbations are introduced. Under the influence of perturbations, such a simple equilibrium of the unperturbed system may change its nature and stability, while a multiple equilibrium of the unperturbed system may disappear or may split (bifurcate) into several equilibria. These drastic changes are studied; the new equilibria are located, and their nature and stability properties are found and compared with those same properties of the corresponding unperturbed equilibria.

ACKNOWLEDGEMENT

Special thanks to my parents Robert and Judy McConill for their support, to my supervisor Dr. George Bojadziev for all his help in the creation of this thesis, and to Dr. H.I. Freedman for his useful suggestions. Financial support, provided by the Natural Sciences and Engineering Research Council of Canada and Simon Fraser University, was greatly appreciated.

Table of Contents

List of Tables

List of Figures

Introduction

Population growth is a rich area of scientific interest. In viewing the world around us, it is apparent that a single specie's growth is not usually an isolated event; rather, there are other populations which affect this growth. Such population interactions may occur in a variety of ways, for example: they may compete with each other for needed resources, one species may prey upon another as its food source, or they might cooperate with each other improving their ability to survive. Mathematics is an important tool that can be employed in modelling these relationships; particularly, an autonomous system of ordinary differential equations might be used. Insight into the dynamics of the species' behaviour may then be gained by studying the mathematical model. Usually the differential equations are too complex to be solved analytically, and unless all constants and functions appearing in the equations are specified, neither can the system be solved numerically. It is possible though, to find and study the equilibria, at least numerically. The equilibria, which are steady-state solutions of the system of differential equations, can provide invaluable information regarding the behaviour of solutions near these equilibria.

In attempting to model a complex natural phenomenon (such as the interaction of populations) with a system of differential equations, it is necessary to make approximations and simplifications to the actual situation. Accordingly, the addition of perturbational terms characterised by a small positive parameter ε may provide for a more realistic model, as they can be thought of as representing uncertainties and unknown errors in the approximation. Freedman and Waltman [1, 2] and Freedman [3] have studied perturbed population models. In [1, 2], the model

$$\begin{aligned} u_1' &= \alpha u_1 - \beta u_1 u_2 - \varepsilon\, f_1(u_1, u_2), \\ u_2' &= -\gamma u_2 + \delta u_1 u_2 - \varepsilon\, f_2(u_1, u_2), \end{aligned}$$

was considered, which represents a two-species perturbed predator-prey system. Here and throughout this thesis, $()' = \frac{d()}{dt}$. In [3], the perturbed Kolmogorov model

$$\begin{aligned} u_1' &= u_1 F_1(u_1, u_2, \varepsilon\,), \\ u_2' &= u_2 F_2(u_1, u_2, \varepsilon\,), \end{aligned}$$

was investigated.

In addition to perturbations, harvesting or stocking of one or more of the species may be considered. For example, Yodzis [4] studied

$$\begin{aligned} x\prime &= X(x,y) - A, \\ y\prime &= Y(x,y) - B, \end{aligned}$$

where A, B represent the harvesting or stocking terms. Similarly, Brauer and Soudack [5, 6, 7, 8] considered

$$\begin{aligned} x\prime &= xf(x,y) - F, \\ y\prime &= yg(x,y) - G; \end{aligned}$$

F and G are the harvesting or stocking terms in this model. Harvesting of a population indicates that the members of a population are being removed at a constant rate. Stocking represents a constant rate of increase in a species. Harvesting or stocking can produce significant changes in a model, affecting the number, location, nature and stability of the equilibria; furthermore, multiple equilibria may appear or disappear.

Consider the perturbed two-species model with harvesting or stocking given by:

$$\begin{aligned} x\prime &= xF(x) - yg(x) + \varepsilon\phi(x,y), \\ y\prime &= -ay + byg(x) - R + \varepsilon\psi(x,y). \end{aligned} \tag{0.1}$$

By varying the sign of the function $g(x)$ and the constants a and b, a predator-prey (y "eats" x), cooperation, or competition relationship can be simulated. The function $F(x)$ tells us in what way the growth of x is proportional to its own size. How the two populations affect each other is controlled by $g(x)$. When $R \neq 0$, there is either harvesting ($R > 0$) or stocking ($R < 0$) of the second species y. This model, but with $R = 0$ (no harvesting or stocking) has been studied by Freedman [9], when he considered

$$\begin{aligned} x\prime &= xg(x) - y[p(x) + \varepsilon\ q(x)], \\ y\prime &= y[-s + cp(x) + \varepsilon\ cq(x)]. \end{aligned}$$

Note that the perturbational terms in (0.1) are of a more general nature than those considered in [9]. It should be mentioned that in [9], $g(x)$ (which corresponds to the $F(x)$

term in (0.1)) satisfies $g(0) = \alpha > 0$, $g_x(x) \le 0$ for $x \ge 0$, and $\exists K > 0$ such that $g(K) = 0$. Such a value K is called a carrying capacity. A carrying capacity is an upper limit on the size a population may grow to. A special case of model (0.1) was studied by Bojadziev, McConill and Yen [10]:

$$\begin{aligned} x\prime &= x[\alpha_1(L_2 - x)(x - L_1) + \beta_1 y] + \varepsilon\, f_1(x, y), \\ y\prime &= y(\alpha_2 + \beta_2 x) - R + \varepsilon f_2(x, y). \end{aligned}$$

In this model L_2 is a carrying capacity, and L_1 is something called a critical density. If the size of x falls below L_1 (in the absence of y at least), it will die out. Thus a critical density represents the minimum size necessary for a species to survive.

Bojadziev and Wong [11] analyzed a predator-predator-prey model with harvesting ($R = H > 0$) and perturbations of the form

$$\begin{aligned} x\prime &= xF(x) - yG(x) - R + \varepsilon\phi_1(x, y, z), \\ y\prime &= -ay + byG(x) - zK(y) + \varepsilon\phi_2(x, y, z), \\ z\prime &= -cz + rzK(y) + \varepsilon\phi_3(x, y, z). \end{aligned} \tag{0.2}$$

In Bojadziev and Wong's model, $F(x)$ satisfied $F(0) = \alpha > 0$, $F_x(x) \le 0$ for $x \ge 0$; thus, there is no critical density, and a carrying capacity is allowed for, but not explicitly assumed to exist. the same model as in [11] but with $\varepsilon = 0$ (no perturbations) has been studied by Bojadziev and Gerogiannakis [12] and by Freedman and Waltman (with $R = 0$) [13]. In these models as in (0.2), population z preys on y which is preying on x; this is called a food chain.

In this thesis I will study (0.1) and (0.2) under the assumption that $F(x)$ has both a carrying capacity and a critical density. As already mentioned, in [9] (see also [14]) and [11, 12, 13], $F(x)$ did not contain a lower critical density. A lower critical density is an important and interesting feature not often incorporated into population models; however, authors such as Bazikin [15] have discussed systems containing a critical density in addition to a carrying capacity. The harvesting or stocking term R will be allowed to take on any value here, but in [9, 11, 12] only certain values of R were considered. The cases of $\varepsilon = 0$ and $\varepsilon > 0$ will be analyzed. This thesis represents an extension of

[1, 3, 9, 10, 11, 12, 13], and will focus primarily on studying the equilibria of the perturbed and unperturbed models and comparing them.

An equilibrium of our systems of ordinary differential equations is a point satisfying $x' = y' = 0$ in the case of (0.1), or $x' = y' = z' = 0$ in the case of (0.2) (it is a steady-state solution). The nature and stability of an equilibrium may be determined by finding its eigenvalues. The eigenvalues are the roots of the characteristic equation

$$\det(J - \lambda I) = 0 ,$$

where J is the Jacobian of the system evaluated at the equilibrium, and I is the identity matrix. If all eigenvalues have negative real part, the equilibrium is asymptotically stable. Provided an orbit (solution) is sufficiently close to such an equilibrium, it will asymptotically approach the equilibrium as time tends to infinity. If one or more eigenvalues have positive real part and none have real part equal to zero, the equilibrium is unstable. Provided an orbit is near an unstable equilibrium, it will move away from the equilibrium as time tends to infinity. Thus we see that in the case of a hyperbolic equilibrium (no eigenvalue has real part equal to zero), its nature and stability predict the behaviour of solutions of the system near the equilibrium. This property does not hold for nonhyperbolic (at least one eigenvalue is zero or purely imaginary) equilibria.

In studying the effect of perturbations on the models' equilibria, we will see that hyperbolic equilibria retain their local stability properties while nonhyperbolic equilibria might not. In particular, multiple equilibria (which have one eigenvalue equal to zero and are thus nonhyperbolic) may disappear or bifurcate into several new simple hyperbolic equilibria. Hyperbolic equilibria are said to be structurally stable, while nonhyperbolic equilibria are not. Models with certain qualitative properties that remain unchanged when subjected to perturbations, such as the hyperbolic nature of an equilibrium, are seen as being more credible than highly sensitive ones which might undergo significant changes. It is therefore important to study such effects in a model.

The full conditions and assumptions imposed on the models (0.1) and (0.2) will be described in the next Chapter. The possible values of constants a, b, c, r and R will be given. We will specify the natures and biological interpretations of $F(x)$, $g(x)$, $G(x)$ and

$K(y)$, and the choices of a, b and $g(x) = \pm G(x)$ which lead to predator-prey, competitive, and cooperative interactions in (0.1) will be related. Furthermore, some research works that form the framework for this study will be surveyed; specifically, works that involve a carrying capacity or critical density, harvesting or stocking, and perturbations.

Chapter 2, "The Two-Species Model," will contain the analysis of (0.1). First the equilibria of the unperturbed model will be located. Equilibria will be classified as simple or multiple according to a derived condition. The local nature and stability properties of the simple equilibria shall then be determined. Perturbation's effects on the simple and multiple (double or triple) equilibria of the unperturbed system will be calculated. Bifurcations of the multiple equilibria will be observed: a double equilibrium will either split into two simple equilibria or disappear, a triple equilibrium will split into three simple equilibria or will shift to a simple equilibrium.

Following a similar pattern, system (0.2) will be examined in Chapter 3, "The Three-Species Model." In this chapter, as in Chapter 2, specific examples of the models will be presented. These examples are not derived from any real-world biological system, and in that sense are artificial. Regardless, we study them to give numerical confirmation to our analytic calculations, and because the phase diagrams produce visual descriptions of the models which are readily comprehensible. These numerical studies will illustrate, among other things, the perturbation of a simple equilibrium, and the bifurcation of a multiple equilibrium.

Chapter 1

PRELIMINARIES

Thorough descriptions of the models are given. Important results related to this study are presented.

1.1 The Models

In the introduction systems (0.1) and (0.2) were presented, but not all constraints were given. First take into consideration the functions $F(x)$, $g(x)$,$G(x)$, $K(y)$, $\phi(x,y)$, $\psi(x,y)$, $\phi_1(x,y,z)$, $\phi_2(x,y,z)$ and $\phi_3(x,y,z)$ which are assumed to be analytic in their arguments. Given the constants $a_0, L_1, L_2 > 0$ with $L_1 < a_0 < L_2$, we further assume that $F(x)$ and $g(x) = \pm G(x)$ satisfy the conditions

$$F(L_1) = F(L_2) = 0, \tag{1.1}$$

$$F_x(x) > 0 \quad \forall x \in [0, a_0), \tag{1.2}$$

$$F_x(x) < 0 \quad \forall x \in (a_0, \infty), \tag{1.3}$$

$$G(0) = 0, \tag{1.4}$$

$$G_x(x) > 0 \quad \forall x \geq 0. \tag{1.5}$$

Using $g(x) = \pm G(x)$ allows us to model different interactions with system (0.1). Similarly to $G(x)$, the function $K(y)$ is asummed to satisfy

$$K(0) = 0, \tag{1.6}$$

$$K_y(y) > 0 \quad \forall y \geq 0. \tag{1.7}$$

The terms a, b, c, r and R are constants. Depending on model (0.1)'s interaction, a and b may be positive or negative; in the case of model (0.2) however, a, b, c, and r are all assumed to be greater than zero. For both models constant R represents a harvesting or stocking term: $R = 0$ if there is no harvesting or stocking, $R = H > 0$ for harvesting, and $R = -S < 0$ for stocking. Harvesting or stocking in a system usually arises from the effort of an external agent or manager (an agent other than one of the species present in the system) to control either the system itself, or just the one species in that system. When a population is harvested, members of that population are removed (culled) at a constant rate; stocking represents an increase at a constant rate of a population. In models (0.1) and (0.2), we subject one species only to harvesting or stocking. It is possible to have harvesting or stocking of any one of the populations in these models, or to have harvesting or stocking of two or more of the species. These cases may be studied in a way similar to the study in this thesis, but we do not do this here.

Function $F(x)$ is the specific growth rate of the first species; it describes how the members of population x affect their own growth. This function is a kind of generalized quadratic function with roots at L_1 and L_2. For example, $F(x)$ might typically be $F(x) = (x - L_1)(L_2 - x)$. We show such a typical $F(x)$ in Fig.1.1, and in Fig.1.2 we show a typical $xF(x)$. Constants L_1 and L_2 that satisfy (1.1) respectively represent a lower critical density and an upper carrying capacity. In the absence of interspecies interactions, when the initial population of the first species is below L_1, that population will die out; while, if it is initially above L_1 it will asymptotically approach L_2. Functions $G(x)$ and $K(y)$ are the response functions for the second and third species respectively. Through $G(x)$, the interaction of x and y is achieved; while, $K(y)$ allows y and z to affect each other. Since $G(x)$ is an increasing function with $G(0) = 0$, we are indicating that the strength of interaction between x and y increases as x or y increases, and (obviously) that there is no interaction should either x or y die out. A similar relationship between the members y and z of (0.2) is expressed by $K(y)$.

System (0.2) describes a predator-predator-prey interaction. The lowest trophic level population, the prey, is represented by x. Population y is the second species (middle

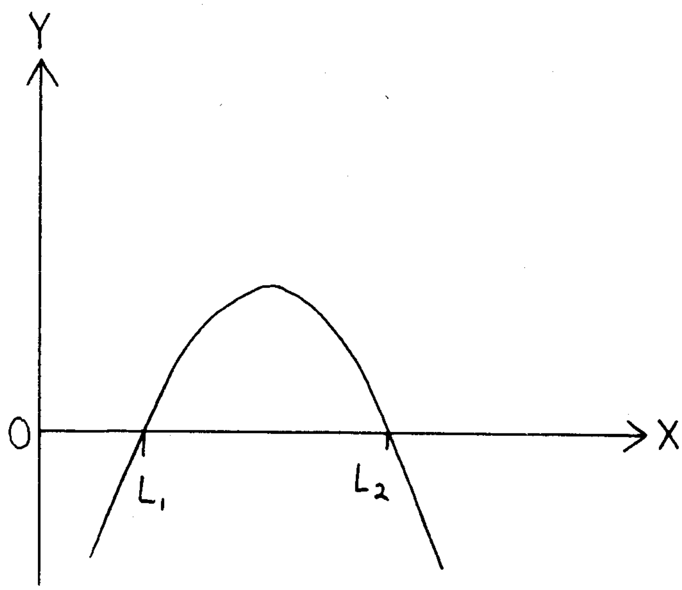

Figure 1.1: A typical $F(x)$

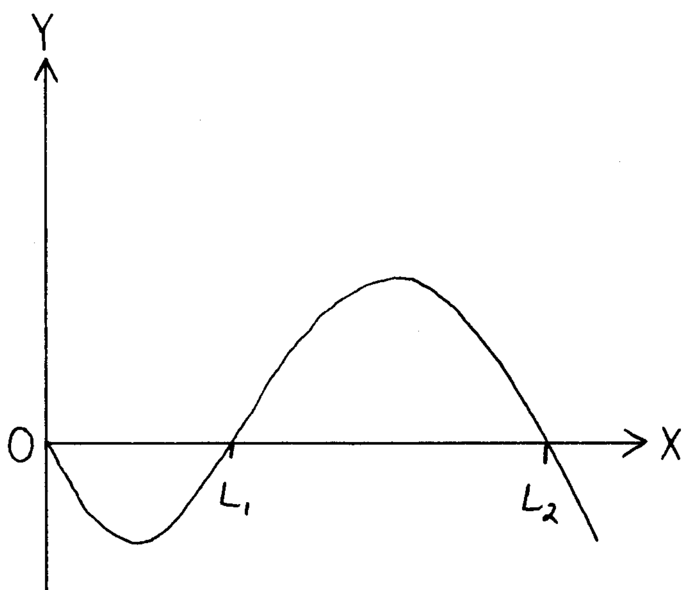

Figure 1.2: A typical $xF(x)$

trophic level) which preys upon x and is in turn preyed upon by z, the highest trophic level. The first and third populations do not directly interact with each other. In this system, as in [11, 12], R appears in the growth relationship of the first species x. With harvesting, we decrease the rate of growth of x. Since y feeds on x, this will tend to slow the growth of y; and as z in turn feeds on y, we expect the growth of z to also be slowed. Stocking has the opposite effect, tending to increase the growth of y and z in addition to directly speeding the growth of x. Thus harvesting or stocking of the first species x makes its effects felt up to the last species z of the food chain.

Three types of interaction are allowed in (0.1), these are achieved by suitable selection of the sign of a, b and $g(x)$:

(i) Predator-Prey

$$a > 0,\ b > 0,\ g(x) = G(x) \tag{1.8}$$

(ii) Competition

$$a < 0,\ b < 0,\ g(x) = G(x) \tag{1.9}$$

(iii) Cooperation

$$a < 0,\ b < 0,\ g(x) = -G(x) \tag{1.10}$$

In the case of predator-prey, y preys on x, and we have either harvesting or stocking of the predator y. Harvesting y should tend to increase the growth of x because y eats x; while, stocking y would slow the growth of x. When x and y are competing, harvesting y would again tend to increase x; stocking y would tend to decrease x. On the other hand, if x and y are cooperating, the growth rate of x should be increased when y is subjected to stocking, and the growth rate of x should be diminished when y is subjected to harvesting. Note that it is possible to study (0.1) with R on the first species. We are interested in multiple equilibria in the interior of the first quadrant though, and with R on the first species we only have the less interesting case of multiple equilibria on the boundary of the first quadrant (see Appendix B).

1.2 Models with Carrying Capacity, Critical Density

An upper carrying capacity represents the natural upper bound on the size of a population. This feature has appeared in many population models; for example, Freedman [9] (see also [14]) has studied the system

$$\begin{aligned} x' &= xg(x) - yp(x), \\ y' &= y[-s + cp(x)], \end{aligned} \tag{1.11}$$

where $g(x)$ satisfies $g(0) = \alpha > 0$, $g_x(x) \leq 0$ for $x \geq 0$ and $\exists K > 0$ such that $g(K) = 0$ (K is a simple root of $g(x) = 0$); thus, K is the carrying capacity of population x. Simple equilibria were found and studied. For the equilibrium in the interior of the first quadrant, Freedman determined that it was either asymptotically stable, or had a periodic solution (stable from the outside) surrounding it. Next, this model was considered subject to enrichment of the environment; i.e., $g(x)$ was replaced by $g(x, K)$ satisfying $g(0, K) = \alpha > 0$, $g(K, K) = 0$, $g_x(x, K) \leq 0$, $g_K(x, K) \geq 0$ and $g_{xK}(x, K) \geq 0$ for $x \geq 0$. It was assumed there was an equilibrium in the interior of the first quadrant that was a centre of the linearized system for some particular value K_0 of K. Utilizing the conditions on $g(x, K)$, a criterion for the existence of small amplitude periodic solutions about this equilibrium was derived.

In a series of papers, Brauer and Soudack [5, 6, 7, 8] studied predator-prey models of the form

$$\begin{aligned} x' &= xf(x, y) - F, \\ y' &= yg(x, y) - G. \end{aligned} \tag{1.12}$$

In these papers, the main interest was to investigate the role F and G played; however, it is important to note that a carrying capacity and critical density appeared in this system. The equation $f(x, y) = 0$ defined y as a single-valued function of x (under the given condition $f_y(x, y) \neq 0$), which was assumed non-negative in the interval $\alpha \leq x \leq K$, with $f(K, 0) = 0$; K is the carrying capacity of the first species. The possibility of $\alpha > 0$ with $f(\alpha, 0) = 0$ was allowed, in which case α is a lower critical density for population x.

The feature of both a carrying capacity and a critical density has been discussed by

Bazikin [15]. Indeed, Bazikin analyzed the model

$$\begin{aligned} x' &= x[\alpha_1(L_2 - x)(x - L_1) + \beta_1 y], \\ y' &= y(\alpha_2 + \beta_2 x). \end{aligned} \tag{1.13}$$

Other such models have been presented by Bazikin, some with critical density and saturation level (carrying capacity) for more than one species. In $\Re^3$, Bazikin looked at the system

$$\begin{aligned} x' &= ax(x - L_1)(L_2 - x) - b_1 xy, \\ y' &= -c_1 y + d_1 xy - b_2 yz, \\ z' &= -c_2 z + d_2 yz. \end{aligned} \tag{1.14}$$

Note that (1.13) is a special case of (0.1) with $R = \varepsilon = 0$, and (1.14) is a special case of (0.2) with $R = \varepsilon = 0$.

Bojadziev, McConill and Yen [10] have discussed (1.13) with harvesting or stocking and perturbations added, giving

$$\begin{aligned} x' &= x[\alpha_1(L_2 - x)(x - L_1) + \beta_1 y] + \varepsilon f_1(x, y), \\ y' &= y(\alpha_2 + \beta_2 x) - R + \varepsilon f_2(x, y). \end{aligned} \tag{1.15}$$

This too is a special case of (0.1) where in particular, $F(x) = \alpha_1(L_2 - x)(x - L_1)$.

1.3 Models with Harvesting or Stocking

Harvesting effects on competing species modelled by

$$\begin{aligned} x' &= X(x, y) - A, \\ y' &= Y(x, y) - B, \end{aligned}$$

were studied by Yodzis [4]. The harvesting terms A and B were not constants; rather, A was assumed to be a C^1 function (of x alone) such that $A(0) = 0$, A monotonically increasing on $0 < x < \varepsilon$ (ε a small parameter), and $A = a$ =constant for $x \geq \varepsilon$. There were analogous conditions imposed on B. The harvested and unharvested ($A = B = 0$) systems were compared. More precisely, for the unharvested system with at most one simple (not multiple) equilibrium in the interior of the population quadrant, Yodzis tried to determine whether or not harvesting would produce or destroy stable equilibrium points.

System (1.12) was probed by Brauer and Sanchez [16] as a predator-prey system with harvesting of the population x only ($G = 0$, $F > 0$). First the case $F = 0$ was considered: an equilibrium in the interior of the first quadrant was assumed to exist and a condition for the asymptotic stability of this point was given. Under the same assumptions for the case $F > 0$, the condition for the equilibrium to be asymptotically stable led to an upper bound on the harvesting rate, which the authors called a critical harvesting rate. Beyond this rate, the equilibrium would be unstable.

Brauer, Soudack and Jarosch [17], examined model (1.12) with harvesting of population y only ($F = 0$, $G > 0$). Conditions for which $\det J(G) = 0$ and $\mathrm{tr} J(G) = 0$ ($J(G)$ is the Jacobian of system (1.12) evaluated at an equilibrium satisfying $x > 0$, $y > 0$) were derived, which led to two "critical" harvesting rates. For a specific case of this model, computer simulations were run for various values of G (and for different values of K, a carrying capacity of the specified model).

In [5], Brauer and Soudack studied (1.12) with $F = 0$ and $G > 0$. This time they developed techniques for determining the regions of asymptotic stability (that portion of the x-y plane having the property that any orbit of the system with initial point in that region remains in that region for all time), and instability (that portion of the x-y plane such that for an orbit with initial point in that region, at least one of the species will die out). For a class of examples, by using computer simulations, they observed how these regions would change as G was varied. For the same model, but with $G = 0$ and $F > 0$ in [6], and with $F, G \leq 0$ in [7], a similar analysis was undertaken by Brauer and Soudack. Finally, in [8], these authors divided the F-G plane into different regions corresponding to different cases of behaviour of the model. Again using a numerical study of a specified system, they showed how to explicitly determine these regions in the F-G plane.

Freedman [9] (see also [14]) has added a source term (stocking) $r > 0$ to (1.11)

$$\begin{aligned} x' &= xg(x) - yp(x) + r, \\ y' &= y[-s + cp(x)]. \end{aligned}$$

He found that the equilibrium in the interior of the first quadrant would always be asymptotically stable for sufficiently large r. In that sense, stocking had a stabilizing effect on the model.

The predator-predator-prey model with harvesting

$$\begin{aligned} x' &= xf(x) - yg(x) - H, \\ y' &= -ay + byg(x) - zp(y), \\ z' &= -cz + rzp(y), \end{aligned} \tag{1.16}$$

has been investigated by Bojadziev and Gerogiannakis [12] (note that $f(x)$ had a carrying capacity, but no lower critical density). Harvesting effects on the location, nature and stability of the equilibria of the system were determined and a boundedness theorem was presented. The case $H = 0$ was earlier studied by Freedman [13].

As previously stated, Bojadziev, McConill and Yen [10] have examined the model (1.15). For $\varepsilon = 0$, the equilibria of the model were studied under either harvesting or stocking. Using graphical and analytical techniques, they showed what effect changing R had on the equilibria; they also showed how a double equilibrium could result for a certain critical harvesting or stocking value. Note that predator-prey, competition and cooperation interactions were allowed.

A qualitative discussion of the role harvesting or stocking can play in changing the structural stability of populations, illustrated by certain examples, was given by Bojadziev [18, 19].

1.4 Perturbed Models

Hausrath [20] proposed

$$\begin{aligned} E' &= gE - aHE + \varepsilon EF_1(E, H, P), \\ H' &= \gamma HE - \alpha H - fHP + \varepsilon HF_2(E, H, P), \\ P' &= bP - cP^2 + kHP + \varepsilon PF_3(E, H, P), \end{aligned}$$

as a model for the interaction between wolves (P), moose (H) and the food supply (E) of the moose in Isle Royale National Park (Isle Royale is an island in Lake Superior). For the case $P = 0$, the equilibrium in the interior of the first quadrant of the E-H plane was studied when $\varepsilon = 0$ and when $\varepsilon > 0$. This further was done for the case $P > 0$ with $\varepsilon = 0$ and $\varepsilon > 0$. Basically, for $\varepsilon = 0$ the equilibrium was asymptotically stable; the resulting perturbed equilibrium arising when $\varepsilon > 0$ remained asymptotically stable. Interestingly, the observed situation on Isle Royale compared favourably with the qualitative properties of this model.

Equilibrium $E(\frac{\gamma}{\delta}, \frac{\alpha}{\beta})$ was shown to be a centre (all solutions about the point are closed periodic orbits) for the unperturbed ($\varepsilon = 0$) version of the model

$$\begin{aligned} u_1' &= \alpha u_1 - \beta u_1 u_2 - \varepsilon f_1(u_1, u_2), \\ u_2' &= -\gamma u_2 + \delta u_1 u_2 - \varepsilon f_2(u_1, u_2), \end{aligned}$$

in Freedman and Waltman [1]. Then for $\varepsilon > 0$, under the assumption that the equilibrium changes position (either $f_1(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}) \neq 0$ or $f_2(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}) \neq 0$), Freedman and Waltman determined that the local nature of the perturbed equilibrium would be either a spiral or a centre (stable or unstable), and gave conditions for this. Further, conditions were derived under which there would be a stable limit cycle about this perturbed equilibrium. For the same system, the authors [2] considered the case $\varepsilon > 0$ such that $f_1(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}) = f_2(\frac{\gamma}{\delta}, \frac{\alpha}{\beta}) = 0$ (the equilibrium does not move when $\varepsilon > 0$). Using implicit function techniques, conditions for the existence of periodic solutions and the stability or instability of such solutions, were calculated.

The perturbed two-species Kolmogorov model

$$\begin{aligned} u_1' &= u_1 F_1(u_1, u_2, \varepsilon), \\ u_2' &= u_2 F_2(u_1, u_2, \varepsilon), \end{aligned}$$

was investigated in [3] by Freedman. He assumed there was an equilibrium $E(a_1, a_2)$ with $a_1, a_2 > 0$ when $\varepsilon = 0$. The associated perturbed equilibrium of the perturbed model was then located. These equilibria were studied as to their nature and stability and compared, for E a simple or a multiple equilibrium.

Perturbations to (1.11) were considered in Freedman [9], resulting in

$$\begin{aligned} x' &= xg(x) - y[p(x) + \varepsilon q(x)], \\ y' &= y[-s + cp(x) + \varepsilon cq(x)]. \end{aligned}$$

Here it was assumed that $p(x)$ was such that for $\varepsilon = 0$, there was an equilibrium in the interior of the first quadrant which was a centre (of the linearized system). The perturbed equilibrium was located (for $\varepsilon > 0$) and a theorem for the existence of stable small amplitude periodic solutions (or a limit cycle) surrounding this perturbed equilibrium was proved.

A Lotka-Volterra competition model with perturbations has been studied by Bojadziev and Kim [21]. They examined the equilibria for $\varepsilon = 0$ and $\varepsilon > 0$, determining the local nature and stability. A condition for the existence of a double equilibrium was given, and the splitting of this double equilibrium under the influence of perturbations was calculated. The system under scrutiny was

$$\begin{aligned} N_1' &= N_1(\alpha_1 - \tfrac{\alpha_1}{\theta_1}N_1 - \beta_1 N_2) - H + \varepsilon f_1(N_1, N_2), \\ N_2' &= N_2(\alpha_2 - \beta_2 N_1 - \tfrac{\alpha_2}{\theta_2}N_2) + \varepsilon f_2(N_1, N_2). \end{aligned}$$

Following Freedman and Waltman [3], Bojadziev and Sattar [22, 23] made an investigation of the perturbed three-species Kolmogorov model

$$N_i' = N_i F_i(N_1, N_2, N_3, \varepsilon); \ i = 1, 2, 3. \tag{1.17}$$

First for $\varepsilon = 0$ in [22, 23], it was assumed an equilibrium existed in the interior of the first octant. This equilibrium was assumed to be a simple equilibrium in [22], and a multiple equilibrium in [23]. For the simple equilibrium, the resulting perturbed equilibrium was located. A comparison of the possible nature and stability of the two equilibria was given. As to the multiple equilibrium, its possible bifurcation was investigated. In the case of the simple equilibrium, it was determined that the local stability of a hyperbolic equilibrium was unaffected by perturbations, while the stability of a nonhyperbolic equilibrium was affected. It is worth mentioning that system (1.17) has been studied from the point of view of persistence by Freedman and Waltman [24].

As discussed earlier, (1.15) was investigated by Bojadziev McConill and Yen [10]. The nature of this study for $\varepsilon = 0$ has been described in the previous section. When $\varepsilon > 0$, the authors calculated the bifurcation of a double equilibrium. A similar study of the model

(1.16) with perturbations,

$$
\begin{aligned}
x' &= xf(x) - yg(x) - H + \varepsilon\phi_1(x,y,z),\\
y' &= -ay + byg(x) - zp(y) + \varepsilon\phi_2(x,y,z),\\
z' &= -cz + rzp(y) + \varepsilon\phi_3(x,y,z),
\end{aligned}
$$

has been undertaken by Bojadziev and Wong [11], wherein they gave a condition for the existence of a multiple equilibrium then calculated its bifurcation (only for a double).

Bojadziev [25] has considered models of the form

$$x'' + f(x)x' + g(x) = \varepsilon\psi(x, x'),$$

which can be transformed to the differential system

$$
\begin{aligned}
x' &= y,\\
y' &= -g(x) - f(x)y + \varepsilon\psi(x,y).
\end{aligned}
$$

Of interest is that for $\varepsilon = 0$, this system has a triple equilibrium (under given assumptions on f and g). Bojadziev studied the bifurcation of this triple equilibrium.

Chapter 2

THE TWO-SPECIES MODEL

This chapter contains a study of system (0.1) under conditions (1.1)–(1.5), for the three cases of interaction determined by (1.8), (1.9) and (1.10). For the unperturbed model we locate and then determine the nature of the simple equilibria and the multiple equilibria. From these simple and multiple equilibria of the unperturbed system ($\varepsilon = 0$), new equilibria may arise as perturbations ($\varepsilon > 0$) are introduced. The location and nature of any such new equilibria are determined.

2.1 Simple Equilibria of the Unperturbed Model

When $\varepsilon = 0$ in model (0.1), we are left with the unperturbed model

$$\begin{aligned} x' &= xF(x) - yg(x), \\ y' &= -ay + byg(x) - R. \end{aligned} \tag{2.1}$$

An equilibrium point (sometimes called a critical point) of the system is one for which the right-hand-side of (2.1) is zero; consequently, we must look for solutions of the system of nonlinear equations

$$\begin{aligned} xF(x) - yg(x) &= 0, \\ -ay + byg(x) - R &= 0. \end{aligned} \tag{2.2}$$

Since we are modelling populations we only concern ourselves with the first quadrant $\Re^2_+$ (population quadrant $x, y \geq 0$). When $x > 0$, $g(x) > 0$ (see (1.4), (1.5)) and y can be eliminated from (2.2). The resulting equation is

$$p(x) = 0, \tag{2.3}$$

where

$$p(x) = xF(x)[bg(x) - a] - Rg(x). \tag{2.4}$$

If x is a root of (2.3), then we find the corresponding y-value from the first equation of (2.2):

$$y = \frac{xF(x)}{g(x)}. \tag{2.5}$$

When $x = 0$ (which satisfies the first equation of (2.2)) the corresponding y-value is

$$y = -\frac{R}{a}. \tag{2.6}$$

Since $x = 0$ is also a root of (2.3), we see that $E(x, y)$, with $x, y \geq 0$, is an equilibrium provided (x, y) satisfies either (2.3) and (2.5), or (2.3) and (2.6).

In this section we are concerned with simple equilibria, which we label $E^0(x^0, y^0)$; an equilibrium $E^0(x^0, y^0)$ is called simple when x^0 is a simple (not multiple) root of (2.3), which occurs when

$$p_x(x^0) \neq 0. \tag{2.7}$$

Here the subscript x represents differentiation with respect to x.

We now study the different interactions case by case.

(i) **Predator-Prey** : Model (2.1) with condition (1.8).

(A) $R = 0$; *No harvesting or stocking.*

We must find the roots of (2.3) which reduces to $xF(x)[bg(x) - a] = 0$. Obviously $x^0 = 0$ is a solution and from (1.1), $x^0 = L_1, L_2$ are also solutions. The corresponding y-values from (2.6) and (2.5) are all $y^0 = 0$. Thus we always have the equilibria $E_0^0(0,0)$, $E_1^0(L_1, 0)$ and $E_2^0(L_2, 0)$. There is one more possibility: an equilibrium point in Int$\Re_+^2$ (interior of $\Re_+^2$). If $\frac{a}{b}$ $\in$Range$G(x)$, which guarantees there exists an $\check{x}$ such that

$$bg(\check{x}) - a = 0, \tag{2.8}$$

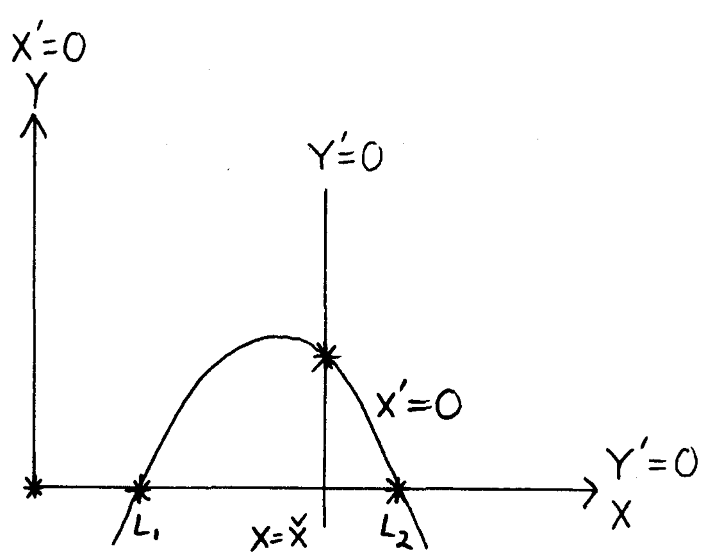

Figure 2.1: Predator-Prey or Competition with No Harvesting or Stocking

and if

$$L_1 < \check{x} < L_2, \tag{2.9}$$

which by (1.1)–(1.5) guarantees that the corresponding y-value defined by (2.5) satisfies $\check{y} > 0$; then, $E_3^0(\check{x}, \check{y})$ is an equilibrium point. The equilibria are shown by asterisks in Fig.2.1; the curve and the y-axis represent the first equation of system (2.2), while the x-axis and the line $x = \check{x}$ represent the second equation of this system.

(B) $R = H > 0$; *Harvesting.*

When $x^0 = 0$, (2.6) gives $y^0 = -\frac{H}{a} < 0$; this point is not in the population quadrant and is of no interest to us. The other possible simple equilibria, which we shall label $E^0(\hat{x}, \hat{y})$, are in Int$\Re_+^2$; $\hat{x}$ must satisfy (2.3) and (2.7) and $\hat{y}$ satisfies (2.5) with $x = \hat{x}$. There may be none, or there may be many such points; let us assume there is at least one. As in **(i)(A)** above, we must have $L_1 < \hat{x} < L_2$ so that $\hat{y} > 0$. From (2.3) with (2.4), $R = H > 0$, (1.1)–(1.5), (1.8) and $L_1 < \hat{x} < L_2$, we see that we must have $bg(\hat{x}) - a > 0$. Since (1.4) implies $bg(0) - a < 0$, there will be an $\check{x}$ satisfying (2.8) when $E^0(\hat{x}, \hat{y})$ exists. With (1.5) we can place a tighter bound on $\hat{x}$ and say

$$\max(L_1, \check{x}) < \hat{x} < L_2. \tag{2.10}$$

A necessary condition for the existence of $E^0(\hat{x}, \hat{y})$ in Int$\Re_+^2$ is that $\exists \check{x}$ satisfying (2.8) and

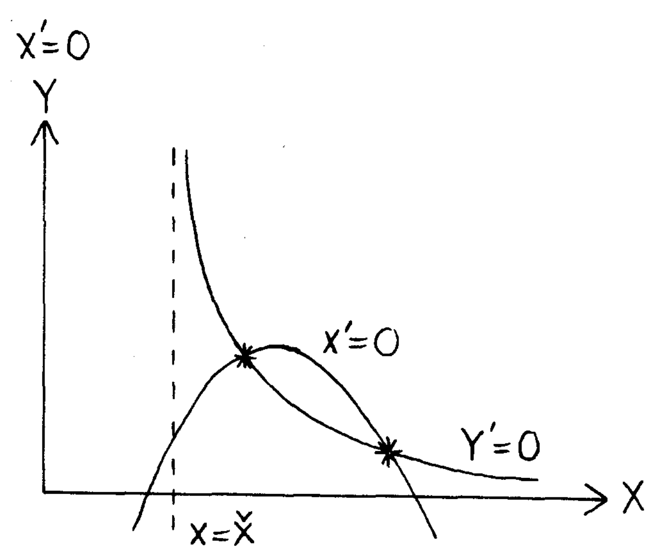

Figure 2.2: Predator-Prey with Harvesting or Competition with Stocking

that

$$\check{x} < L_2. \tag{2.11}$$

The equilibrium points are shown in Fig.2.2. The first equation of (2.2) is represented in the same manner as in 2.1; the second equation describes a decreasing curve with vertical asymptote at $x = \check{x}$ and horizontal asymptote along the x-axis. In Fig.2.2 we show the curves crossing twice, but of course there may be more than two equilibria (even numbers), or there may be none. In this figure one can see why (2.10) and (2.11) hold.

(C) $R = -S < 0$; *Stocking.*

We obtain an equilibrium $E_0^0(0, \frac{S}{a})$ from (2.6). If there exist $\hat{x}, \hat{y}$ satisfying (2.3)–(2.5) and (2.7), then $E^0(\hat{x}, \hat{y})$ is an equilibrium in $\text{Int}\Re^2_+$. An argument similar to that of **(i)(B)** above gives that if $\exists \check{x}$ satisfying (2.8), then a necessary condition for the existence of $E^0(\hat{x}, \hat{y})$ is

$$\check{x} > L_1. \tag{2.12}$$

When such an x exists,

$$L_1 < \hat{x} < \min(\check{x}, L_2)\,. \tag{2.13}$$

Note that if there is no $\check{x}$ satisfying (2.8), then $\hat{x}$ satisfies (2.9) with $\check{x}$ replaced by $\hat{x}$. The equilibria are shown in Fig.2.3 which is similar to Fig.2.2 with the difference being that the

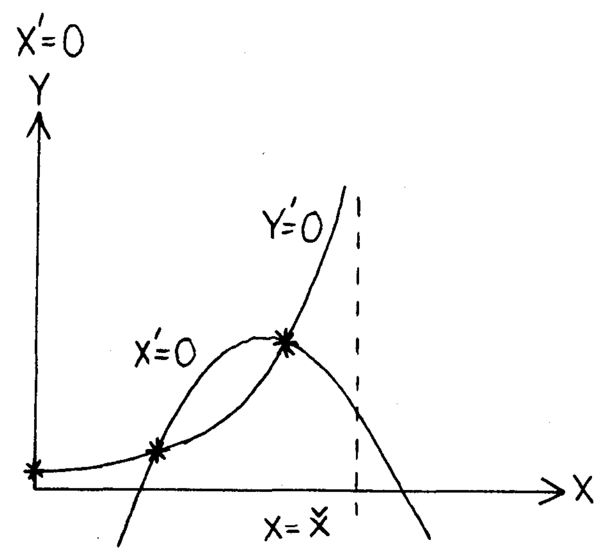

Figure 2.3: Predator-Prey with Stocking or Competition with Harvesting

second equation of (2.2) now represents an increasing curve (it has the same asymptotes as before).

(ii) Competition : System (2.1) with conditions (1.9).

(A) $R = 0$; *No harvesting or stocking.*

Similarly to **(i)(A)** we get three equilibria: $E_0^0(0,0)$, $E_1^0(L_1,0)$ and $E_2^0(L_2,0)$. Provided $\exists\check{x}$ satisfying (2.8) and (2.9), $E_3^0(\check{x},\check{y})$ is also an equilibrium with $\check{y}$ given by (2.5). The appropriate geometric interpretations are given by Fig.2.1.

(B) $R = H > 0$; *Harvesting.*

This is equivalent to case **(i)(C)** above. The only difference is that now we have $E_0^0(0,\frac{H}{a})$ instead of $E_0^0(0,\frac{S}{a})$. View Fig.2.3 to get a sense of the geometry.

(C) $R = -S < 0$; *Stocking.*

This case is equivalent to **(i)(B)**, hence Fig.2.2 applies.

(iii) Cooperation : Model (2.1) with (1.10).

(A) $R = 0$; *No harvesting or stocking.*

Like **(i)(A)** and **(ii)(A)** we again have $E_0^0(0,0)$, $E_1^0(L_1,0)$ and $E_2^0(L_2,0)$ as equilibria. This time $\Re_+^2$ contains no other equilibria. We show the equilibria in Fig.2.4. The first

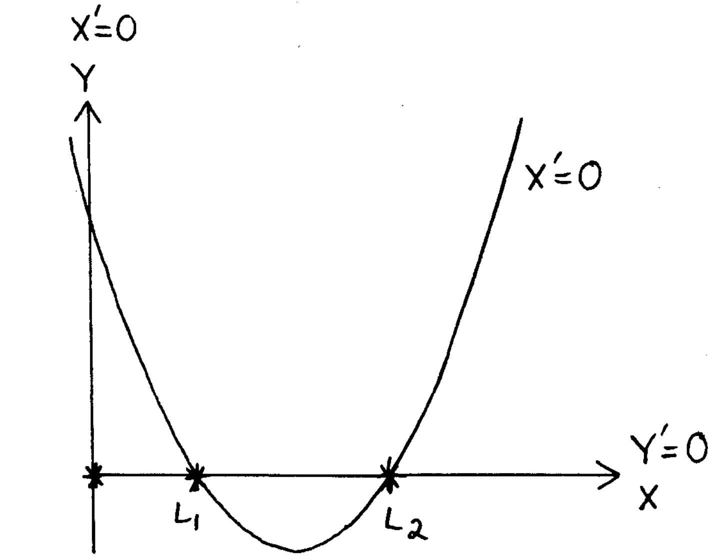

Figure 2.4: Cooperation with No Harvesting or Stocking

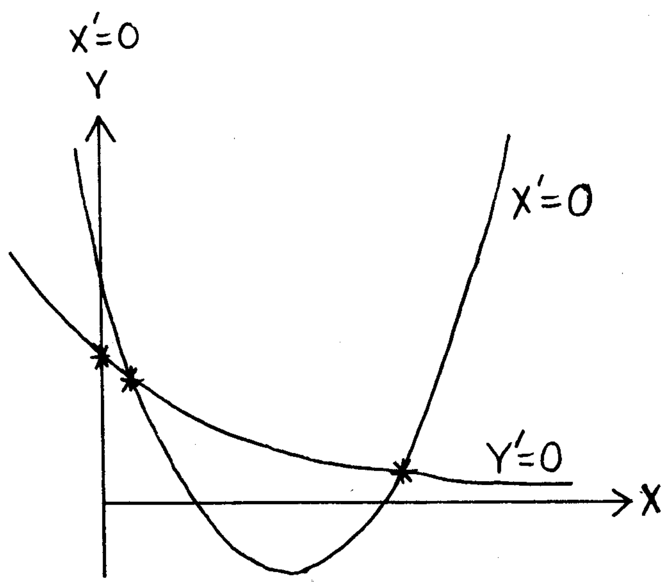

Figure 2.5: Cooperation with Harvesting

equation of (2.2) represents the y-axis and the curve, while the second equation represents only the x-axis (in $\Re^2_+$).

(B) $R = H > 0$; *Harvesting.*

$E_0^0(0, \frac{H}{a})$ is an equilibrium point, and if (2.3), (2.5) and (2.7) are satisfied, then $E^0(\hat{x}, \hat{y})$ is also an equilibrium. Since we must have $\hat{y} > 0$, (2.5), (1.1)–(1.5) and (1.10) reveal that

$$\hat{x} \in (0, L_1) \cup (L_2, \infty). \tag{2.14}$$

The equilibria are shown in Fig.2.5 where now the first equation of (2.2) is as in **(iii)(A)** above, but the decreasing curve represents the second equation of (2.2). As always there may be more or less equilibria in Int$\Re^2_+$ than the two shown.

(C) $R = -S < 0$; *Stocking.*

The left-hand-side of the second equation of (2.2) is $-ay - byG(x) + S > 0$ in $\Re^2_+$ (recall that $a, b < 0$); it represents a curve which is below the x-axis (for values of $x \geq 0$), thus there are no equilibria in $\Re^2_+$.

2.2 Stability Properties of the Simple Equilibria

We now look at the simple equilibria of (2.1), each of which we have denoted by $E^0(x^0, y^0)$. In order to determine their local nature and stability, we first find the Jacobian matrix $J(x, y)$ and evaluate it at $E^0(x^0, y^0)$. For system (2.1), this matrix is

$$J^0 = J(x^0, y^0) = \begin{pmatrix} \alpha_0 & \beta_0 \\ \gamma_0 & \delta_0 \end{pmatrix}, \tag{2.15}$$

where:

$$\begin{aligned} \alpha_0 &= F(x^0) + x^0 F_x(x^0) - y^0 g_x(x^0), \\ \beta_0 &= -g(x^0), \\ \gamma_0 &= b y^0 g_x(x^0), \\ \delta_0 &= b g(x^0) - a. \end{aligned} \tag{2.16}$$

The eigenvalues of (2.15), which are the roots of the characteristic equation

$$\det(J^0 - \lambda I) = \lambda^2 - q_1^0 \lambda + q_2^0 = 0, \tag{2.17}$$

are

$$\lambda^0_{1,2} = \frac{1}{2}(q^0_1 \pm \sqrt{(q^0_1)^2 - 4q^0_2}\ ), \tag{2.18}$$

where

$$\begin{aligned} q^0_1 &= \alpha_0 + \delta_0, \\ q^0_2 &= \det J^0 = \alpha_0\delta_0 - \beta_0\gamma_0. \end{aligned} \tag{2.19}$$

The eigenvalues determine the local nature and stability properties of the equilibria (see Appendix A for classification of equilibria via eigenvalues). It is known (see [26]) that for a simple equilibrium E^0,

$$\det J^0 = q^0_2 \neq 0. \tag{2.20}$$

Cases **(i)**, **(ii)** and **(iii)** (defined in the previous section) will be studied separately. First we derive some results involving $p(x)$ (as defined in (2.4)) that will help us investigate the equilibria.

<u>Lemma</u> The terms $p(x)$ and q^0_2 satisfy the relationship

$$q^0_2 = p_x(x^0). \tag{2.21}$$

<u>Proof</u> If we substitute the expressions (2.16) into q^0_2 given by (2.19) and use the fact that

$$ay^0 = by^0 g(x^0) - R = bx^0 F(x^0) - R$$

(from(2.2)), we get

$$\begin{aligned} q^0_2 &= [F(x^0) + x^0 F_x(x^0)][bg(x^0) - a] + bx^0 F(x^0) g_x(x^0) - Rg_x(x^0) \\ &= \tfrac{d}{dx}\{xF(x)[bg(x) - a] - Rg(x)\}|_{x=x^0} \\ &= p_x(x^0) \ \blacksquare \end{aligned}$$

Note that (2.21) implies that condition (2.20) for simple equilibria is equivalent to condition (2.7).

<u>Theorem 1</u> If $p_x(x^0) > 0$, then $E^0(x^0, y^0)$ is either a node, a focus, or a centre; being asymptotically stable if $q^0_1 < 0$, and unstable if $q^0_1 > 0$. If $p_x(x^0) < 0$, $E^0(x^0, y^0)$ is a

saddle point.

Proof By substituting the expression for q_2^0 as given in (2.21) into (2.18), the theorem follows immediately ∎

Theorem 2 Assume that the following two conditions hold:

1. $E_1^0(x_1^0, y_1^0)$ and $E_2^0(x_2^0, y_2^0)$ with $x_1^0 < x_2^0$ are simple equilibria of (2.1), and

2. $p(x) \neq 0 \quad \forall x \in (x_1^0, x_2^0)$.

Then either E_1^0 is a saddle point and E_2^0 is not a saddle point, or E_2^0 is a saddle point and E_1^0 is not a saddle point.

Proof Conditions 1 and 2 imply x_1^0 and x_2^0 are two simple roots of $p(x)$, and that there are no other roots of $p(x)$ between x_1^0 and x_2^0. Thus $p_x(x_1^0)p_x(x_2^0) < 0$. This, together with (2.21) and (2.18) prove the theorem ∎

Keeping these results in mind, we look at the individual cases.

(i) Predator-Prey

(A) $R = 0$; *No harvesting or stocking.*

We assume (2.8) and (2.9) hold. There are exactly four equilibria to study: $E_0^0(0,0)$, $E_1^0(L_1, 0)$, $E_2^0(L_2, 0)$ and $E_3^0(\check{x}, \check{y})$.

Equilibrium E_0^0. Using $(x^0, y^0) = (0,0)$ in (2.16) and (2.19), we see that the eigenvalues (2.18) are: $\lambda_1 = -a < 0$ and $\lambda_2 = F(0)$. From (1.1) and (1.2) $\lambda_2 < 0$. Thus E_0^0 *is an asymptotically stable node.*

Equilibrium E_1^0. This time the eigenvalues are $\lambda_1 = L_1 F_x(L_1)$ and $\lambda_2 = -a + bG(L_1)$. By (1.2), $\lambda_1 > 0$; by (2.8),(2.9) and (1.5) $\lambda_2 < 0$. This tells us that E_1^0 *is a saddle point.*

Equilibrium E_2^0. From the characteristic equation, we calculate that $\lambda_1 = L_2 F_x(L_2)$ and $\lambda_2 = -a + bG(L_2)$. From (1.3) $\lambda_1 < 0$; (2.8), (2.9) and (1.5) give $\lambda_2 > 0$. Like E_1^0, E_2^0 *is a saddle point.*

Equilibrium E_3^0. Now $q_1^0 = F(\check{x}) + \check{x}F_x(\check{x}) - \check{y}G_x(\check{x})$, and we don't know whether this is positive, negative or zero. Since $\check{x}$ satisfies (2.8), $\delta_0 = 0$, which leaves us with a simple expression for q_2^0 (see (2.19)): $q_2^0 = b\check{y}G(\check{x})G_x(\check{x}) > 0$ by (1.4) and (1.5). From (2.18) we see that if λ_1 and λ_2 are real, they have the same sign, hence E_3^0 *is not a saddle point.*

Now writing these points in the order E_0^0, E_1^0, E_3^0 and E_2^0, it is easily checked that the pairs E_0^0, E_1^0; E_1^0, E_3^0; and E_3^0, E_2^0 satisfy the conditions for **Theorem 2**. Corresponding to the above specified order, the nature of the equilibria goes: E_0^0—not a saddle, E_1^0—saddle, E_3^0—not a saddle and E_2^0— saddle. This result agrees completely with **Theorem 2**.

Note that E_0^0, E_1^0 and E_2^0 are *hyperbolic equilibria* (see [26]) since none of their eigenvalues have real part equal to zero; E_3^0 is nonhyperbolic if $q_1^0 = 0$, or hyperbolic if $q_1^0 \neq 0$.

(B) $R = H > 0$; *Harvesting.*

The only equilibria are of the type $E^0(\hat{x}, \hat{y})$ (see Section 2.1, case **(i)(B)**) which are in $\text{Int}\Re_+^2$. We cannot say anything about their stability other than what **Theorems 1** and **2** tell us.

(C) $R = -S < 0$; *Stocking.*

There is one equilibrium on the axis, $E_0^0(0, \frac{S}{a})$, whose eigenvalues (2.18) are $\lambda_1 = -a$, and $\lambda_2 = F(0) - \frac{S}{a}G_x(0)$. Now $\lambda_1 < 0$ and from (1.1), (1.2) and (1.5) we find $\lambda_2 < 0$. Thus E_0^0 *is an asymptotically stable node.* Any other equilibria that may exist are of the form $E^0(\hat{x}, \hat{y}) \in \text{Int}\Re_+^2$; again, we can only apply **Theorems 1** and **2** to these points.

(ii) Competition

The derivation of the eigenvalues and of the signs of the real part of those values is straightforward and similar to the case of **Predator-Prey** just discussed; therefore, we simply present the results without elaboration.

(A) $R = 0$; *No harvesting or stocking.*

We assume that (2.8) and (2.9) are satisfied so that $E_3^0(\check{x}, \check{y})$ is an equilibrium point.

$E_0^0(0,0)$ *is a saddle point;*

$E_1^0(L_1, 0)$ *is an unstable node;*

$E_2^0(L_2, 0)$ *is an asymptotically stable node;*

$E_3^0(\check{x}, \check{y})$ *is a saddle point.*

Writing these in the order E_0^0, E_1^0, E_3^0 and E_2^0, the nature of these points follows the pattern: E_0^0—saddle, E_1^0—not a saddle, E_3^0—saddle, and E_2^0—not a saddle. **Theorem 2** gives us precisely this result.

(B) $R = H > 0$; *Harvesting.*

$E_0^0(0, \frac{H}{a})$ *is a saddle point.*

$E^0(\hat{x}, \hat{y})$; here we resort to **Theorems 1** and **2**.

(C) $R = -S < 0$; *Stocking.*

$E^0(\hat{x}, \hat{y})$; similarly, we apply **Theorems 1** and **2**.

(iii) Cooperation

Once again we simply present the results.

(A) $R = 0$; *No harvesting or stocking.*

$E_0^0(0,0)$ *is a saddle point;*

$E_1^0(L_1, 0)$ *is an unstable node;*

$E_2^0(L_2, 0)$ *is a saddle point.*

Here also **Theorem 2** is in accordance with these results.

(B) $R = H > 0$; *Harvesting.*

$E_0^0(0, \frac{H}{a})$ *is an unstable node* if $F(0)+\frac{H}{a}G_x(0) > 0$, *or a saddle point* if $F(0)+\frac{H}{a}G_x(0) < 0$. For $E^0(\hat{x}, \hat{y})$ we refer to **Theorems 1** and **2**.

(C) $R = -S < 0$; *Stocking.*

There are no equilibria in $\Re_+^2$.

Now we present three examples in which the functions and constants in model (2.1) are specified; hence, we are able to locate equilibria of the type $E^0(\hat{x}, \hat{y})$ and determine their nature and stability properties. To obtain the figures, the system of differential equations has been solved numerically using a Runge-Kutta-Fehlberg method (see Danby [27]) starting from various initial points.

2.2.1 Example 1

Consider the predator-prey system without harvesting or stocking

$$\begin{aligned} x' &= x[1-(x-3)^4] - xy, \\ y' &= -5y + 2xy. \end{aligned}$$

We see from (2.1) that $F(x) = 1 - (x-3)^4$, $G(x) = x$, $a = 5$ and $b = 2$. Furthermore, it is easily checked that $L_1 = 2$, $a_0 = 3$ and $L_2 = 4$. Thus from **(i)(A)** of Section 2.1, we automatically know that $E_0^0(0,0)$, $E_1^0(2,0)$ and $E_2^0(4,0)$ are equilibria. Equation (2.8) for this model reads $2x - 5 = 0$, which is satisfied by $\check{x} = \frac{5}{2}$. Since $2 < \frac{5}{2} < 4$ (i.e.

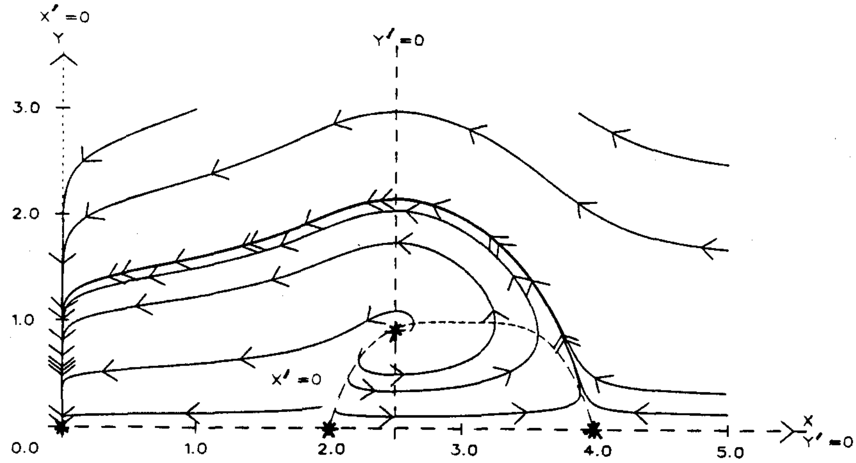

Figure 2.6: Example 1

(2.9) is satisfied), we find from (2.5) that $\check{y} = \frac{15}{16}$. Then $E_3^0(\frac{5}{2}, \frac{15}{16})$ is an equilibrium in Int$\Re_+^2$. From Section 2.2 we know that E_0^0 is an asymptotically stable node, E_1^0 is a saddle point, and E_2^0 is also a saddle point, but all we know about E_3^0 is that it is not a saddle point. Evaluating (2.16) and (2.19) at E_3^0, the eigenvalues (2.18) are $\lambda_{1,2} = \frac{5}{8}(1 \pm i\sqrt{11})$. Hence E_3^0 is an unstable focus. The phase portrait is shown on Fig.2.6. The orbits are the curves with arrows (which point in the direction of flow as time increases), the dashed lines indicate the curves where $x\prime = 0$ or $y\prime = 0$, and the equilibria are indicated by asterisks.

2.2.2 Example 2

Now we study a competition model with harvesting:

$$\begin{aligned} x\prime &= \tfrac{1}{3}x(x-2)(9-x) - xy, \\ y\prime &= 7y - xy - 8. \end{aligned}$$

We have from (2.1), $F(x) = \frac{1}{3}(x-2)(9-x)$, $G(x) = x$, $a = 7$, $b = 1$ and $R = H = 8$. In addition, $L_1 = 2$, $a_0 = \frac{11}{2}$ and $L_2 = 9$. From **(ii)(B)**, $E_0^0(0, \frac{8}{7})$ is a saddle point. Now we must see if there are any more equilibria. Equation (2.3) (with $x \neq 0$) can be

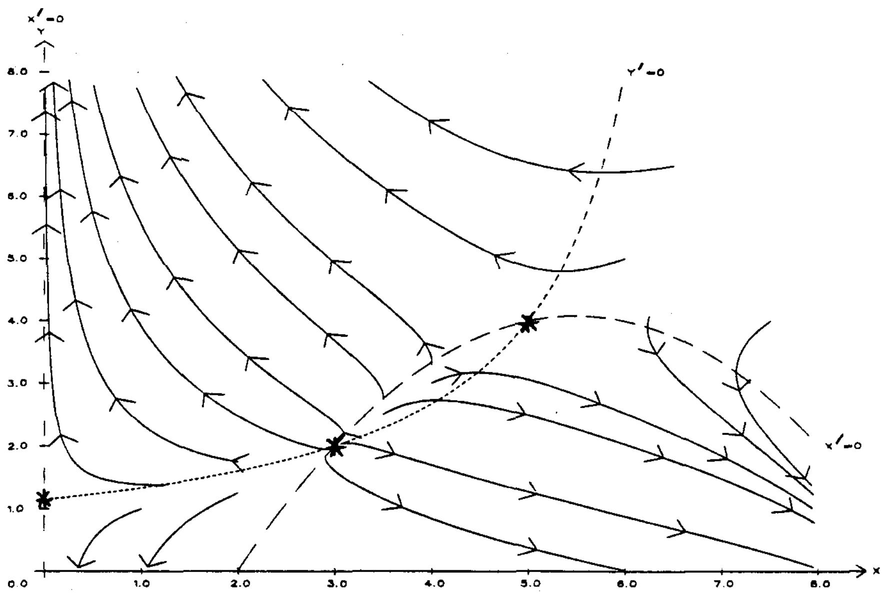

Figure 2.7: Example 2

written in the form $\frac{1}{3}x^3 - 6x^2 + \frac{95}{3}x - 50 = 0$; its roots are 3,5 and 10. Note that $\check{x} = 7$ satisfies (2.8), so according to (2.13) we must have $2 < \hat{x} < 7$. Thus only 3 and 5 give equilibria in $\Re^2_+$. From (2.5), we calculate the corresponding y-values, giving the equilibria $E_1^0(3,2)$ and $E_2^0(5,4)$. Further, we find $p_x(x) = \frac{4}{3}x^3 - 18x^2 + \frac{190}{3}x - 50$; $p_x(3) = 14 > 0$ and $p_x(5) = -\frac{50}{3} < 0$; hence, by **Theorem 1**, E_2^0 is a saddle point and E_1^0 is not a saddle point. We must calculate the eigenvalues for E_1^0 in order to completely detemine its stability; these are $\lambda_1 = 7$ and $\lambda_2 = 2$, indicating this equilibrium is an unstable node. The phase portrait for this example is shown on Fig.2.7.

2.2.3 Example 3

Finally we look at a model wherein the populations are cooperating:

$$
\begin{aligned}
x' &= \tfrac{1}{6}x(x-4)(7x-23) + xy, \\
y' &= 4y + xy - 18.
\end{aligned}
$$

Comparing this system with (2.1), we see that we have $R = H = 18 > 0$ (harvesting), $F(x) = \frac{1}{6}(x-4)(7x-23)$, $-g(x) = G(x) = x$, $a = 4$, $b = 1$, $a_0 = \frac{51}{14}$, $L_1 = \frac{23}{7}$, and

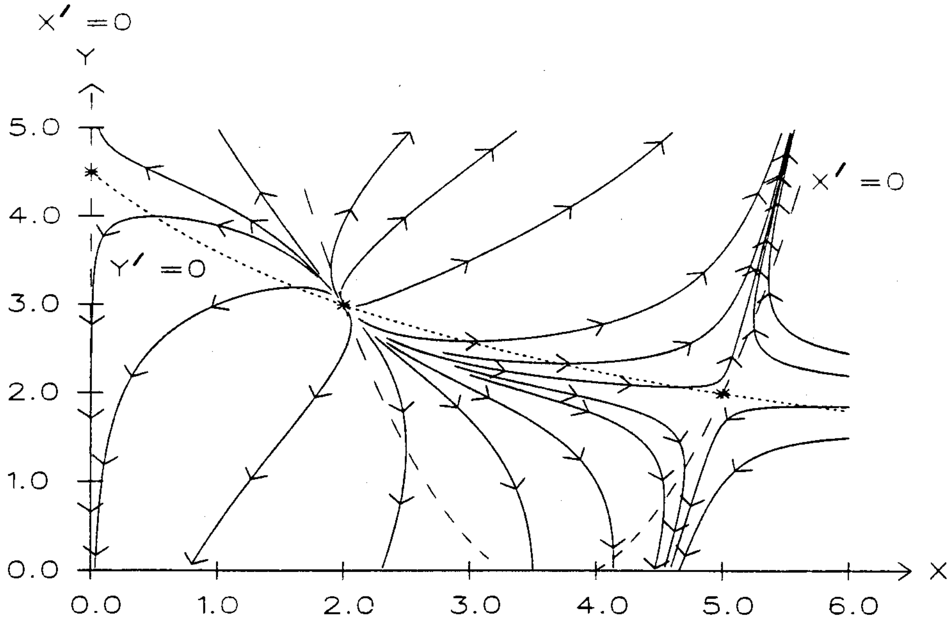

Figure 2.8: Example 3

$L_2 = 4$. According to **(iii)(B)** of Section 2.2, equilibrium $E_0^0(0, \frac{9}{2})$ is a saddle point since $F(0) + \frac{H}{a}G_x(0) = -\frac{65}{6} < 0$. For this model $p(x) = -\frac{7}{6}x^4 + \frac{23}{6}x^3 + \frac{56}{3}x^2 - \frac{130}{3}x$ (see (2.4)), which has non-zero roots at $-\frac{26}{7}$, 2 and 5. Only 2 and 5 give equilibria in the population quadrant: $E_1^0(2,3)$ and $E_2^0(5,2)$; which, according to **Theorems 1** and **2** must respectively be not a saddle and a saddle point. Since the eigenvalues of E_1^0 are $\lambda_{1,2} = \frac{1}{6}(41 \pm \sqrt{241}) > 0$, $E_1^0(2,3)$ is an unstable node. The phase portrait for this example is given on Fig.2.8.

2.3 Location and Nature of a Multiple Equilibrium of the Unperturbed System

In Sections 2.1 and 2.2 we only looked at simple equilibria of the unperturbed system (2.1). A multiple (critical) equilibrium of (2.1), which we label $E^c(x^c, y^c)$, occurs when condition (2.7) is not satisfied; that is, when

$$p_x^c = (F^c + x^c F_x^c)(-a + bg^c) + bx^c F^c g_x^c - R^c g_x^c = 0, \tag{2.22}$$

which is equivalent to $\det J^c = 0$, J^c is the Jacobian of (2.1) at $E^c(x^c, y^c)$. Here $p_x^c = p_x(x^c)$, $F_x^c = F_x(x^c)$, $g_x^c = g_x(x^c)$, $F^c = F(x^c)$ and $g^c = g(x^c)$. We call R^c the critical harvesting or stocking value. This number R^c is not necessarily unique as there may be more than one critical harvesting or stocking value. A further possibility is that for one value of R^c, there are several multiple equilibria.

The multiplicity of a multiple equilibrium may be of any order (see Andronov et al [28]). Later in this Section we will study a multiple equilibrium in more detail, concentrating on the cases of a double or triple equilibrium which occur respectively when

$$p^c = p_x^c = 0, \quad p_{xx}^c \neq 0, \tag{2.23}$$

or,

$$p^c = p_x^c = p_{xx}^c = 0, \quad p_{xxx}^c \neq 0. \tag{2.24}$$

We seek to determine the local nature of a multiple equilibrium $E^c(x^c, y^c)$ of the unperturbed model (2.1), which lies in $\Re_+^2$. First, we suppose that such a multiple equilibrium exists; i.e., we assume $\exists x^c, y^c \geq 0$ satisfying (2.3), either (2.5) or (2.6), and (2.23) or (2.24). Then following Andronov et al [28], and the papers [10, 21, 25], we shift $E^c(x^c, y^c)$ to the origin via the substitution $x = x^c + u$, $y = y^c + v$, after $F(x)$ and $g(x)$ have been expanded in Taylor series about x^c. The resulting differential system in (u, v) space is

$$\begin{aligned}
u\prime &= \alpha_c\ u + \beta_c\ v + \tfrac{1}{2}W_2^c\ u^2 - g_x^c uv + \tfrac{1}{6}W_3^c\ u^3 \\
&\quad - \tfrac{1}{2}g_{xx}^c u^2 v + O(u^4) + O(u^3 v), \\
v\prime &= \gamma_c\ u + \delta_c\ v + \tfrac{1}{2}by^c g_{xx}^c u^2 + bg_x^c uv + \tfrac{1}{6}by^c g_{xxx}^c u^3 \\
&\quad + \tfrac{1}{2}bg_{xx}^c u^2 v + O(u^4) + O(u^3 v); \\
W_2^c &= x^c F_{xx}^c + 2F_x^c - y^c g_{xx}^c, \\
W_3^c &= x^c F_{xxx}^c + 3F_{xx}^c - y^c g_{xxx}^c.
\end{aligned} \tag{2.25}$$

Here α_c , β_c , γ_c and δ_c are nothing but α_0, β_0, γ_0 and δ_0 (see (2.16)) with x^0 and y^0 replaced by x^c and y^c correspondingly. As usual, subscripts on F and g represent the order of differentiation with respect to x, and superscript c indicates evaluation of the function at (x^c, y^c).

We investigate two cases.

Case 1 $(x^c, y^c) \in \mathrm{Int}\Re^2_+$.

In (2.25) we make the substitution:

$$\xi = -\delta_c\, u + \beta_c\, v, \quad \eta = \alpha_c\, u + \beta_c\, v, \quad \tau = (\alpha_c + \delta_c)t, \tag{2.26}$$

where we must assume that $\alpha_c + \delta_c \neq 0$. This substitution produces the new system

$$\begin{aligned} \frac{d\xi}{d\tau} &= Q_1(\xi,\eta), \\ \frac{d\eta}{d\tau} &= \eta + Q_2(\xi,\eta); \end{aligned} \tag{2.27}$$

where:

$$\begin{aligned}
Q_1(\xi,\eta) = & -\frac{1}{\beta_c(\alpha_c+\delta_c)^3}\{[\tfrac{1}{2}\beta_c\,\delta_c\,W_2^c - \tfrac{1}{2}\beta_c^2\, by^c g_{xx}^c - \delta_c\,(b\beta_c + \delta_c)g_x^c]\eta^2 \\
& + [-\beta_c\,\delta_c\,W_2^c + \beta_c^2\, by^c g_{xx}^c - (\alpha_c - \delta_c)(b\beta_c + \delta_c)g_x^c]\eta\xi \\
& + [\tfrac{1}{2}\beta_c\,\delta_c\,W_2^c - \tfrac{1}{2}\beta_c^2\, by^c g_{xx}^c + \alpha_c\,(b\beta_c + \delta_c)g_x^c]\xi^2\} \\
& - \frac{1}{\beta_c(\alpha_c+\delta_c)^4}\{[\tfrac{1}{6}\beta_c\,\delta_c\,W_3^c - \tfrac{1}{6}\beta_c^2\, by^c g_{xxx}^c - \tfrac{1}{2}\delta_c\,(b\beta_c + \delta_c)g_{xx}^c]\eta^3 \\
& + [-\tfrac{1}{2}\beta_c\,\delta_c\,W_3^c + \tfrac{1}{2}\beta_c^2\, by^c g_{xxx}^c - \tfrac{1}{2}(\alpha_c - 2\delta_c)(b\beta_c + \delta_c)g_{xx}^c]\eta^2\xi \\
& + [\tfrac{1}{2}\beta_c\,\delta_c\,W_3^c - \tfrac{1}{2}\beta_c^2\, by^c g_{xxx}^c - \tfrac{1}{2}(\delta_c - 2\alpha_c)(b\beta_c + \delta_c)g_{xx}^c]\eta\xi^2 \\
& + [-\tfrac{1}{6}\beta_c\,\delta_c\,W_3^c + \tfrac{1}{6}\beta_c^2\, by^c g_{xxx}^c - \tfrac{1}{2}\alpha_c\,(b\beta_c + \delta_c)g_{xx}^c]\xi^3\} \\
& + O(\eta^4) + O(\eta^3\xi) + O(\eta^2\xi^2) + O(\eta\xi^3) + O(\xi^4), \\
Q_2(\xi,\eta) = & -\frac{1}{\beta_c(\alpha_c+\delta_c)^3}\{[-\tfrac{1}{2}\alpha_c\,\beta_c\,W_2^c - \tfrac{1}{2}\beta_c^2\, by^c g_{xx}^c + \delta_c\,(\alpha_c - b\beta_c)g_x^c]\eta^2 \\
& + [\alpha_c\,\beta_c\,W_2^c + \beta_c^2\, by^c g_{xx}^c + (\alpha_c - \delta_c)(\alpha_c - b\beta_c)g_x^c]\eta\xi \\
& + [-\tfrac{1}{2}\alpha_c\,\beta_c\,W_2^c - \tfrac{1}{2}\beta_c^2\, by^c g_{xx}^c - \alpha_c\,(\alpha_c - b\beta_c)g_x^c]\xi^2\} \\
& - \frac{1}{\beta_c(\alpha_c+\delta_c)^4}\{[-\tfrac{1}{6}\alpha_c\,\beta_c\,W_3^c - \tfrac{1}{6}\beta_c^2\, by^c g_{xxx}^c + \tfrac{1}{2}\delta_c\,(\alpha_c - b\beta_c)g_{xx}^c]\eta^3 \\
& + [\tfrac{1}{2}\alpha_c\,\beta_c\,W_3^c + \tfrac{1}{2}\beta_c^2\, by^c g_{xxx}^c + \tfrac{1}{2}(\alpha_c - 2\delta_c)(\alpha_c - b\beta_c)g_{xx}^c]\eta^2\xi \\
& + [-\tfrac{1}{2}\alpha_c\,\beta_c\,W_3^c - \tfrac{1}{2}\beta_c^2\, by^c g_{xxx}^c + \tfrac{1}{2}(\delta_c - 2\alpha_c)(\alpha_c - b\beta_c)g_{xx}^c]\eta\xi^2 \\
& + [\tfrac{1}{6}\alpha_c\,\beta_c\,W_3^c + \tfrac{1}{6}\beta_c^2\, by^c g_{xxx}^c + \tfrac{1}{2}\alpha_c\,(\alpha_c - b\beta_c)g_{xx}^c]\xi^3\} \\
& + O(\eta^4) + O(\eta^3\xi) + O(\eta^2\xi^2) + O(\eta\xi^3) + O(\xi^4).
\end{aligned} \tag{2.28}$$

We seek a solution to

$$\eta + Q_2(\xi,\eta) = 0, \tag{2.29}$$

in the vicinity of $(0,0)$, of the form

$$\eta(\xi) = M\xi + N\xi^2 + O(\xi^3). \tag{2.30}$$

Substitution of (2.30) in (2.29) and solving for M, N gives

$$\begin{aligned} M &= 0, \\ N &= \frac{1}{\beta_c\,(\alpha_c+\delta_c)^3}[-\tfrac{1}{2}\alpha_c\,\beta_c\,W_2^c-\tfrac{1}{2}\beta_c^2\,by^c g_{xx}^c-\alpha_c\,(\alpha_c-b\beta_c)g_x^c]. \end{aligned} \tag{2.31}$$

Now we use (2.30) in $Q_1(\xi,\eta)$ given by (2.28) and find that in the vicinity of $(0,0)$

$$Q_1(\xi,\eta(\xi)) = A_1\xi^2 + A_2\xi^3 + O(\xi^4), \tag{2.32}$$

with

$$\begin{aligned} A_1 &= -\frac{1}{\beta_c\,(\alpha_c+\delta_c)^3}[\tfrac{1}{2}\beta_c\,\delta_c\,W_2^c-\tfrac{1}{2}\beta_c^2\,by^c g_{xx}^c+\alpha_c\,(b\beta_c+\delta_c)g_x^c], \\ A_2 &= B_1+B_2N; \\ B_1 &= -\frac{1}{\beta_c\,(\alpha_c+\delta_c)^4}[-\tfrac{1}{6}\beta_c\,\delta_c\,W_3^c+\tfrac{1}{6}\beta_c^2\,by^c g_{xxx}^c-\tfrac{1}{2}\alpha_c\,(b\beta_c+\delta_c)g_{xx}^c], \\ B_2 &= -\frac{1}{\beta_c\,(\alpha_c+\delta_c)^3}[-\beta_c\,\delta_c\,W_2^c+\beta_c^2\,by^c g_{xx}^c-(\alpha_c-\delta_c)(b\beta_c+\delta_c)g_x^c]; \end{aligned} \tag{2.33}$$

N is given in (2.31).

We have calculated, using formulas (2.3), (2.2), (2.16), (2.22) and (2.33) that

$$A_1 = -\frac{1}{2(\alpha_c+\delta_c)^3}p_{xx}^c, \tag{2.34}$$

and if $p_{xx}^c = 0$, then

$$A_2 = \frac{1}{6(\alpha_c+\delta_c)^4}p_{xxx}^c. \tag{2.35}$$

Making use of (2.34) and (2.35), we conclude that:

(a) If (2.23) is satisfied so that E^c is a double equilibrium, then $A_1 \neq 0$; and according to [28], since the lowest power of ξ in $Q_1(\xi,\eta(\xi))$ is 2, an even number, E^c is a saddle-node which bifurcates into a saddle point and a node.

(b) If (2.24) is satisfied so that E^c is a triple equilibrium and $A_1 = 0$ while $A_2 \neq 0$; then according to [28], since the lowest power of ξ in $Q_1(\xi,\eta(\xi))$ is 3, an odd number, E^c is a topological node when $A_2 > 0$ ($p_{xxx}^c > 0$), or a topological saddle point when $A_2 < 0$ ($p_{xxx}^c < 0$).

Case 2 $(x^c, y^c) \in$ the boundary of $\Re_+^2$.

Here we are able to find the coordinates of the possible multiple equilibria.

If $(x^c, y^c) \in x$-axis and $x^c > 0$, which is only possible for the case of predator-prey and competition with $R = 0$, then the analysis in **Case 1** above holds. Using formulas (2.8), (2.5), (2.22) and (1.1), we find that such a multiple equilibrium must be located at either the point $(L_1, 0)$ or $(L_2, 0)$ and that it will always be a double equilibrium.

If $(x^c, y^c) \in y$-axis, which is only possible in the case of cooperation with $R = H > 0$, then the one possible multiple equilibrium is located at the point $(0, \frac{H}{a})$. This critical equilibrium may be a double or triple (or greater) equilibrium. Since in this case $\alpha_c = \beta_c = 0$, we cannot use substitution (2.26). If we instead use $\xi = \gamma_c\, u$, $\eta = \gamma_c\, u + \delta_c\, v$, $\tau = \delta_c\, t$, we obtain for ξ and η a system of the form (2.27). Following the same procedure, we get for Q_1 expression (2.32), but now we calculate that

$$A_1 = \frac{1}{2\delta_c^2\, \gamma_c} p_{xx}^c, \tag{2.36}$$

and when $p_{xx}^c = 0$, then

$$A_2 = \frac{1}{6\gamma_c^2\, \delta_c^2} p_{xxx}^c. \tag{2.37}$$

The conclusions drawn in **Case 1 (a)** and **(b)** remain valid.

We investigate two examples.

2.3.1 Example 4

Let us look at the predator-prey model with harvesting

$$\begin{aligned} x' &= x(x-2)(7-x) - xy, \\ y' &= -14y + 3xy - 16. \end{aligned}$$

Equation (2.3) for this model reduces to $p(x) = -3x^4 + 41x^3 - 168x^2 + 180x = 0$. The roots are $x = 0, \frac{5}{3}, 6$. It is easily checked that only $x = 6$ satisfies (2.10); thus, by **(i)(B)** of Section 2.1, $E(6,4)$ is the only equilibrium in $\Re^2_+$. As $p_x(6) = 0$, and $p_{xx}(6) = -156 \neq 0$, $E(6,4)$ is a double equilibrium; a saddle-node. The phase portrait is presented on Fig.2.9.

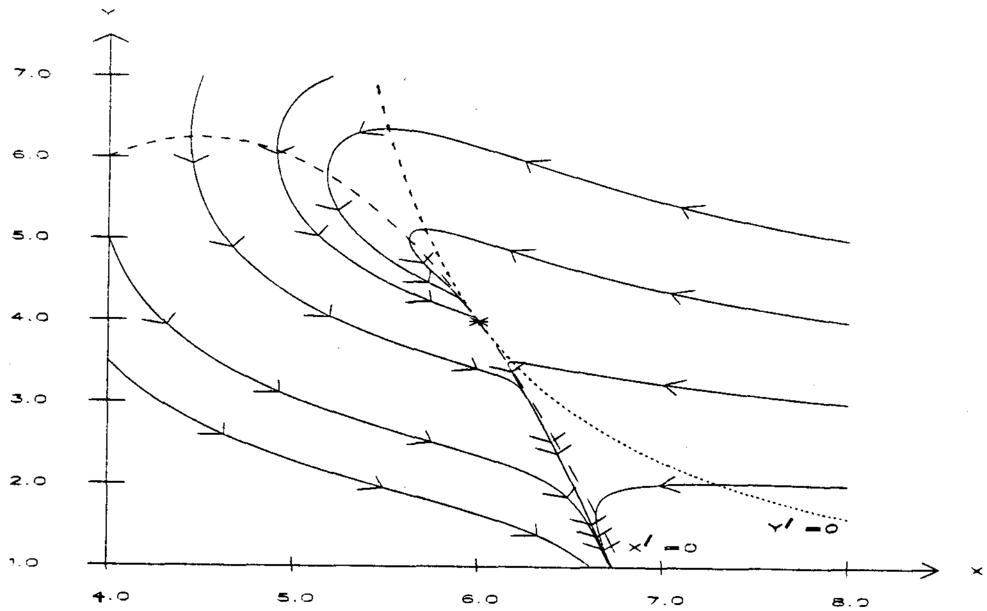

Figure 2.9: Example 4

2.3.2 Example 5

Consider the model

$$\begin{aligned} x\prime &= x(-x^4 + 22x^3 - \frac{4031}{24}x^2 + \frac{2935}{6}x - \frac{8105}{24}) - xy, \\ y\prime &= -y + xy - 9. \end{aligned}$$

This is again a predator-prey model with harvesting. Equation (2.3) reads $-x^6 + 23x^5 - \frac{4559}{24}x^4 + \frac{15771}{24}x^3 - \frac{19845}{24}x^2 + \frac{7889}{24}x = 0$, which has solutions $x = 0, 7, 1 + \frac{\sqrt{6}}{12}, 1 - \frac{\sqrt{6}}{12}$. Only $x = 7$ and $x = 1 + \frac{\sqrt{6}}{12}$ satisfy (2.10) (recall that $x = 0$ does not give an equilibrium in $\Re^2_+$ for a predator-prey system with harvesting). Now $p_x(7) = p_{xx}(7) = 0$, but $p_{xxx}(7) = -\frac{6041}{4} \neq 0$, and $p_x(1 + \frac{\sqrt{6}}{12}) \approx 95.7$. Thus $E^0(1 + \frac{\sqrt{6}}{12}, 18\sqrt{6})$ is a simple equilibrium, while $E^c(7, \frac{3}{2})$ is a triple equilibrium. Moreover, according to (2.35) and **Case 1 (b)**, $E^c(7, \frac{3}{2})$ is a topological saddle point since $p_{xxx}(7) < 0$. We show the phase portrait in Fig.2.10 for a neighbourhood of the triple equilibrium; observe how it resembles a saddle point.

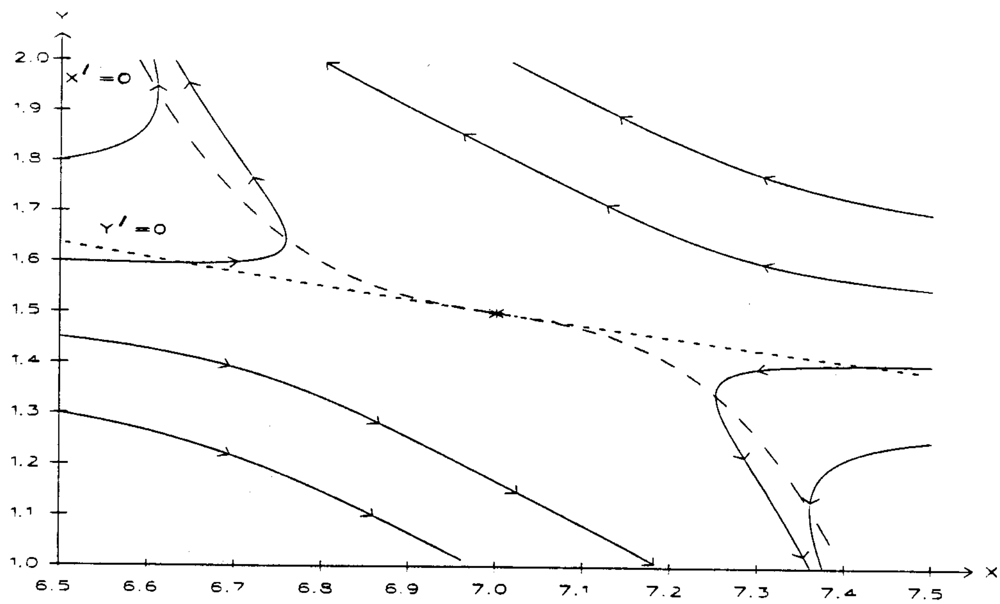

Figure 2.10: Example 5

2.4 Perturbations of a Simple Equilibrium

Suppose $E^0(x^0, y^0)$ is a simple equilibrium in $\Re^2_+$ of (2.1) (recall: x^0 satisfies (2.3) and (2.7)). We seek the associated perturbed equilibrium $E^p(x^p, y^p)$ of system (0.1) in the form of an asymptotic expansion (see Kevorkian and Cole [29]):

$$\begin{aligned} x^p &= x^0 + \varepsilon\, m_1 + O(\varepsilon^{\,2}), \\ y^p &= y^0 + \varepsilon\, n_1 + O(\varepsilon^{\,2}). \end{aligned} \tag{2.38}$$

For $\varepsilon\, = 0$, model (0.1) reduces to model (2.1) and E^p to E^0.

The expressions for x^p and y^p given in (2.38) must satisfy the equations

$$\begin{aligned} xF(x) - yg(x) + \varepsilon\, \phi(x,y) &= 0, \\ -\,ay + byg(x) - R + \varepsilon\, \psi(x,y) &= 0. \end{aligned} \tag{2.39}$$

In (2.39) we expand $F(x)$, $g(x)$, $\phi(x,y)$ and $\psi(x,y)$ in Taylor series about (x^0, y^0) and obtain the system

$$
\begin{aligned}
x[F^0 + F_x^0(x-x^0) + O((x-x^0)^2)] - y[g^0 + g_x^0(x-x^0) + O((x-x^0)^2)] & \\
+ \varepsilon\, [\phi^0 + O((x-x^0)) + O((y-y^0))] &= 0, \\
-ay + by[g^0 + g_x^0(x-x^0) + O((x-x^0)^2)] - R & \\
+ \varepsilon\, [\psi^0 + O((x-x^0)) + O((y-y^0))] &= 0.
\end{aligned}
\tag{2.40}
$$

We substitute (2.38) into (2.40), noting that (x^0, y^0) satisfies (2.2), and divide the result by ε , giving

$$
\begin{aligned}
\alpha_0\, m_1 + \beta_0\, n_1 + \phi^0 + O(\varepsilon) &= 0, \\
\gamma_0\, m_1 + \delta_0\, n_1 + \psi^0 + O(\varepsilon) &= 0,
\end{aligned}
\tag{2.41}
$$

where α_0 , β_0 , γ_0 and δ_0 are given in (2.16). In (2.40), subscript x indicates differentiation with respect to x. Superscript 0 in (2.40) and (2.41) indicates evaluation of the functions at (x^0, y^0). We assume here that we do not have $\phi^0 = \psi^0 = 0$; otherwise, $(x^p, y^p) = (x^0, y^0)$, and the unperturbed equilibrium is not shifted by the addition of perturbational terms. This is a special case not considered here.

Since $E^0(x^0, y^0)$ is a simple equilibrium, $q_2^0 = \alpha_0\, \delta_0 - \beta_0\, \gamma_0 \neq 0$ according to (2.20) with (2.19). Neglecting the terms of order $O(\varepsilon)$ in (2.41) produces

$$
\begin{aligned}
m_1 &= \tfrac{1}{q_2^0}(\beta_0\, \psi^0 - \delta_0\, \phi^0), \\
n_1 &= \tfrac{1}{q_2^0}(\gamma_0\, \phi^0 - \alpha_0\, \psi^0).
\end{aligned}
\tag{2.42}
$$

Thus (2.38) with (2.42) represents the approximate location of the perturbed equilibrium $E^p(x^p, y^p)$.

To study the local nature and stability of E^p, first we find the Jacobian matrix for system (0.1) and evaluate it at E^p:

$$
J^p = J^0 + \varepsilon \begin{pmatrix} \theta_0 & \rho_0 \\ \sigma_0 & \tau_0 \end{pmatrix} + O(\varepsilon^2), \tag{2.43}
$$

where J^0 is given in (2.15),

$$
\begin{aligned}
\theta_0 &= m_1 W_2^0 - n_1 g_x^0 + \phi_x^0, & \rho_0 &= -m_1 g_x^0 + \phi_y^0, \\
\sigma_0 &= m_1 b y^0 g_{xx}^0 + n_1 b g_x^0 + \psi_x^0, & \tau_0 &= m_1 b g_x^0 + \psi_y^0,
\end{aligned}
\tag{2.44}
$$

and W_2^0 is W_2^c given in (2.25) with superscript c replaced by superscript 0.

The characteristic equation, $\det(J^p - \lambda I) = 0$ (I is the 2×2 identity matrix), reduces to

$$\lambda^2 - q_1^0 \lambda + q_2^0 + \varepsilon \left[-(\theta_0 + \tau_0)\lambda + \Omega_0 \right] + O(\varepsilon^2) = 0, \qquad (2.45)$$

where q_1^0 and q_2^0 are to be found in (2.19) and

$$\Omega_0 = \alpha_0 \tau_0 + \delta_0 \theta_0 - \beta_0 \sigma_0 - \gamma_0 \rho_0 . \qquad (2.46)$$

Suppose that $\lambda_{1,2}^0$ are the eigenvalues of $E^0(x^0, y^0)$; then, we search for the perturbed eigenvalues in the form

$$\lambda_s^p = \lambda_s^0 + \varepsilon\, l_s + O(\varepsilon^2), \quad s = 1, 2, \qquad (2.47)$$

with λ_s^0 as given in (2.18). Substituting (2.47) into (2.45), then setting the coefficient of ε to zero (the term without ε , that is ε^0, is already zero since $(\lambda_s^0)^2 - q_1^0\lambda_s^0 + q_2^0 = 0$) allows us to solve for l_s:

$$l_s = (-1)^s \frac{\lambda_s^0(\theta_0 + \tau_0) - \Omega_0}{\sqrt{(q_1^0)^2 - 4q_2^0}}, \quad s = 1, 2. \qquad (2.48)$$

Equation (2.48) is only valid provided

$$(q_1^0)^2 - 4q_2^0 \neq 0. \qquad (2.49)$$

Now we study the eigenvalues (2.47) using (2.18) and (2.48).

(i) Suppose $E^0(x^0, y^0)$ has eigenvalues (2.18) that have non-zero real part and are not repeated (in such a case E^0 is a hyperbolic equilibrium). Then E^0 is a saddle if the eigenvalues λ_1^0, λ_2^0 are real and of opposite sign; a proper node if λ_1^0, λ_2^0 are real, distinct and of the same sign; or a focus if λ_1^0, λ_2^0 are complex (with nonzero real part). Since ε is sufficiently small, from (2.47) with (2.18) and (2.48) we see that λ_1^p, λ_2^p are close to λ_1^0, λ_2^0. This implies $E^p(x^p, y^p)$ has the same local nature and stability as $E^0(x^0, y^0)$.

(ii) Suppose $E^0(x^0, y^0)$ is a centre of the *linearized* model (2.1) (it may be a centre or a weak focus for the nonlinearized model (2.1)); it is nonhyperbolic. In this case $q_1^0 = 0$ and $q_2^0 > 0$. Using (2.18) and (2.48) we observe that (2.47) becomes

$$\lambda_s^p = (-1)^s i\sqrt{q_2^0} + \frac{1}{2}\varepsilon\ [\theta_0\ + \tau_0\ + (-1)^s i\frac{\Omega_0}{\sqrt{q_2^0}}] + O(\varepsilon^{\ 2}), \quad s = 1,2. \tag{2.50}$$

So if $\theta_0\ + \tau_0\ \neq 0$, then $\lambda_{1,2}^p$ are complex with non-zero real part; $E^p(x^p, y^p)$ is a focus and it may be asymptotically stable if $\theta_0\ + \tau_0\ < 0$, or unstable if $\theta_0\ + \tau_0\ > 0$. We do not consider the case where $\theta_0\ + \tau_0\ = 0$; it requires investigation to $O(\varepsilon^{\ 2})$. Under the influence of perturbations, we observe that the nonhyperbolic equilibrium E^0 may change its nature and stability.

(iii) Suppose $E^0(x^0, y^0)$ is a node-star; $\lambda_{1,2}^0 = \frac{1}{2}q_1^0$, $(q_1^0)^2 - 4q_2^0 = 0$; condition (2.49) is not satisfied. In this case (2.47) is not appropriate; instead we try to find $\lambda_{1,2}^p$ in the form

$$\lambda_s^p = \frac{1}{2}q_1^0 + \varepsilon^{\ 1/2} l_s^1 + \varepsilon\ l_s^2 + O(\varepsilon^{\ 3/2}), \quad s = 1,2.$$

Substituting this last expression into (2.45), we determine that the coefficients of $\varepsilon^{\ 0}$ and $\varepsilon^{\ 1/2}$ are identically zero. Setting the coefficient of ε to zero allows us to solve for l_s^1. The result is:

$$l_s^1 = (-1)^s\sqrt{\frac{1}{2}q_1^0(\theta_0\ + \tau_0\ ) - \Omega_0\ }, \quad s = 1,2. \tag{2.51}$$

So l_s^1 may be real or complex. Assuming $l_s^1 \neq 0$ we have that λ_s^p may be real and distinct but of the same sign, or complex with nonzero real part. Equilibrium $E^p(x^p, y^p)$ may thus be a proper node or a focus; in either case though, it has the same stability property as $E^0(x^0, y^0)$, since for sufficiently small ε the real part of λ_s^p is of the same sign as as the term q_1^0. In this case, the stability of the hyperbolic equilibrium $E^0(x^0, y^0)$ does not change when perturbations are introduced even though its nature may change.

Two examples are now investigated.

2.4.1 Example 6

For this example, we look at the perturbed predator-prey model without harvesting or stocking:

$$
\begin{aligned}
x\prime &= x(x-1)(9-x)-xy, \\
y\prime &= -3y+xy+\varepsilon\,(-1)^n y, \quad n=1,2.
\end{aligned}
$$

So we see that $F(x)=(x-1)(9-x)$, $G(x)=x$, $a=3$, $b=1$, $L_1=1$, $L_2=9$, $a_0=5$, $\phi(x,y)\equiv 0$ and $\psi(x,y)=-y$ for $n=1$, $\psi(x,y)=y$ for $n=2$. When $\varepsilon\ =0$ the system has equilibria: $E_0^0(0,0)$ an asymptotically stable node, $E_1^0(1,0)$ a saddle point, $E_2^0(9,0)$ a saddle point, and $E_3^0(3,12)$ an unstable node-star as $(q_1^0)^2-4q_2^0=(12)^2-(4)(36)=0$. In Fig.2.11 we show the phase portrait of the unperturbed system. In Fig.2.12 we show an expanded view of E_3^0.

From the discussion in this Section, under the influence of perturbations ($\varepsilon\ >0$) E_0^p will be an asymptotically stable node, E_1^p will be a saddle point, and E_2^p will be a saddle point. Equilibrium E_3^p may be either a proper node or a focus, but will remain unstable. We now determine what E_3^p is.

Equation (2.16) gives $\alpha_0\ =12$, $\beta_0\ =-3$, $\gamma_0\ =12$ and $\delta_0\ =0$; furthermore, $\phi^0\ =0$ and $\psi^0\ =(-1)^n 12$. Thus (2.42) gives $m_1=(-1)^{n+1}$, $n_1=(-1)^{n+1}4$. From (2.44) we obtain: $\theta_0\ =(-1)^n 2$, $\rho_0\ =(-1)^n$, $\sigma_0\ =(-1)^{n+1}4$ and $\tau_0\ =0$. Then (2.51) takes the form $l_s^1=(-1)^s 6\sqrt{(-1)^n}$. Thus E_3^p which is given approximately by $E_3^p(3+(-1)^{n+1}\varepsilon\ ,12+(-1)^{n+1}4\varepsilon\ )$ has eigenvalues given by $\lambda_{1,2}^p=6\pm 6\sqrt{(-1)^n}\varepsilon\ ^{1/2}+O(\varepsilon\ )$. For $n=1$, $E_3^p(3+\varepsilon\ ,12+4\varepsilon\ )$ has eigenvalues $\lambda_{1,2}^p=6\pm 6i\varepsilon\ ^{1/2}+O(\varepsilon\ )$. This means that E_3^p is an unstable focus for $n=1$. The case $n=1$, $\varepsilon\ =\frac{1}{2}$ is drawn on Fig.2.13, and on Fig.2.14 where we show a close up view of E_3^p. On the other hand, when $n=2$, $E_3^p(3-\varepsilon\ ,12-4\varepsilon\ )$ has eigenvalues $\lambda_{1,2}^p=6\pm 6\varepsilon\ ^{1/2}+O(\varepsilon\ )$, making it an unstable proper node. This case is shown on Fig.2.15 and on Fig.2.16 (neighbourhood of E_3^p), where again we use the value $\varepsilon\ =\frac{1}{2}$.

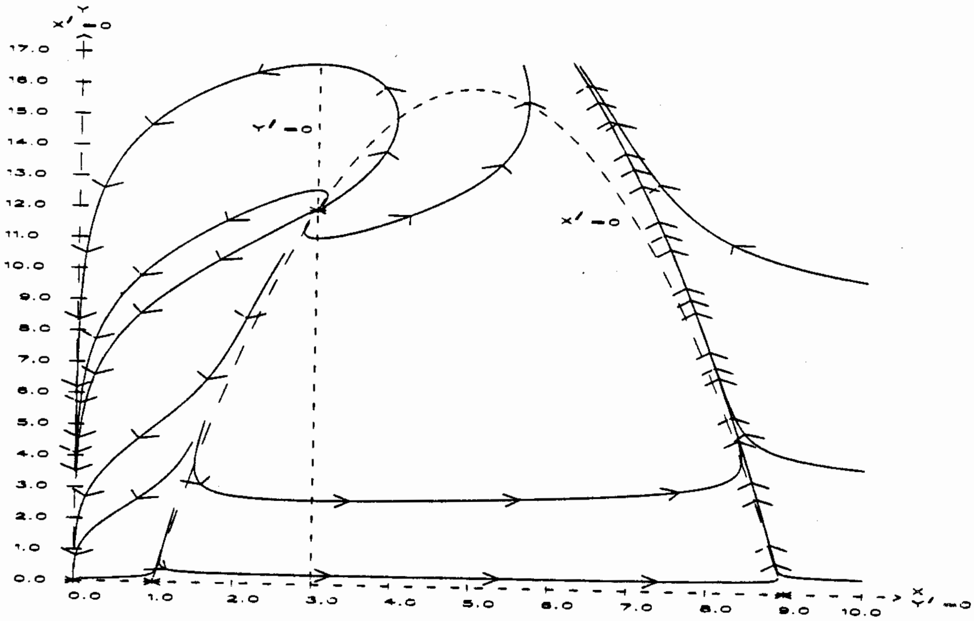

Figure 2.11: Example 6 with $\varepsilon = 0$

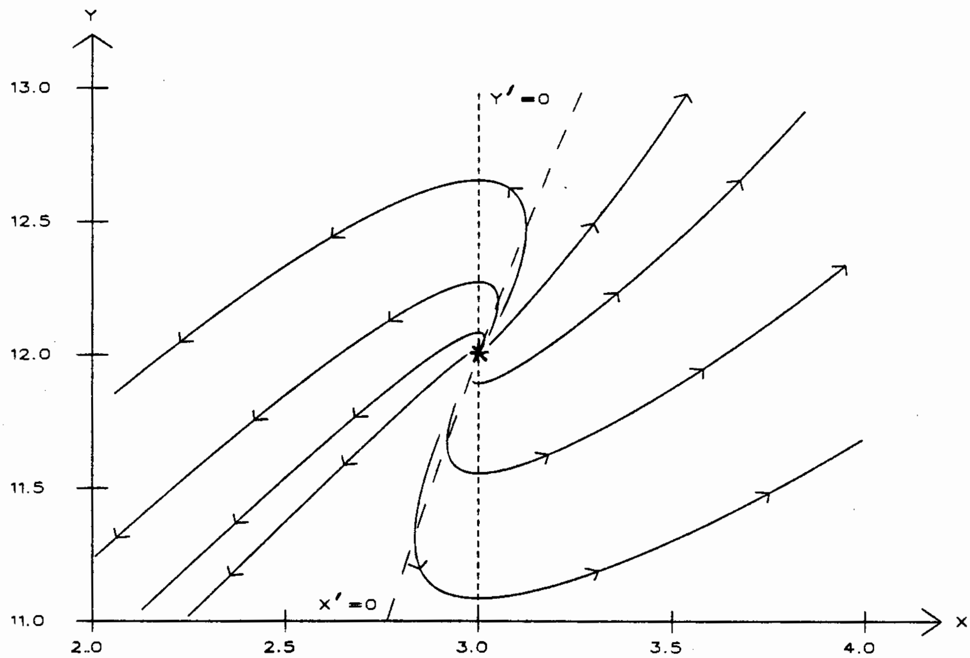

Figure 2.12: Example 6 with $\varepsilon = 0$, expanded view

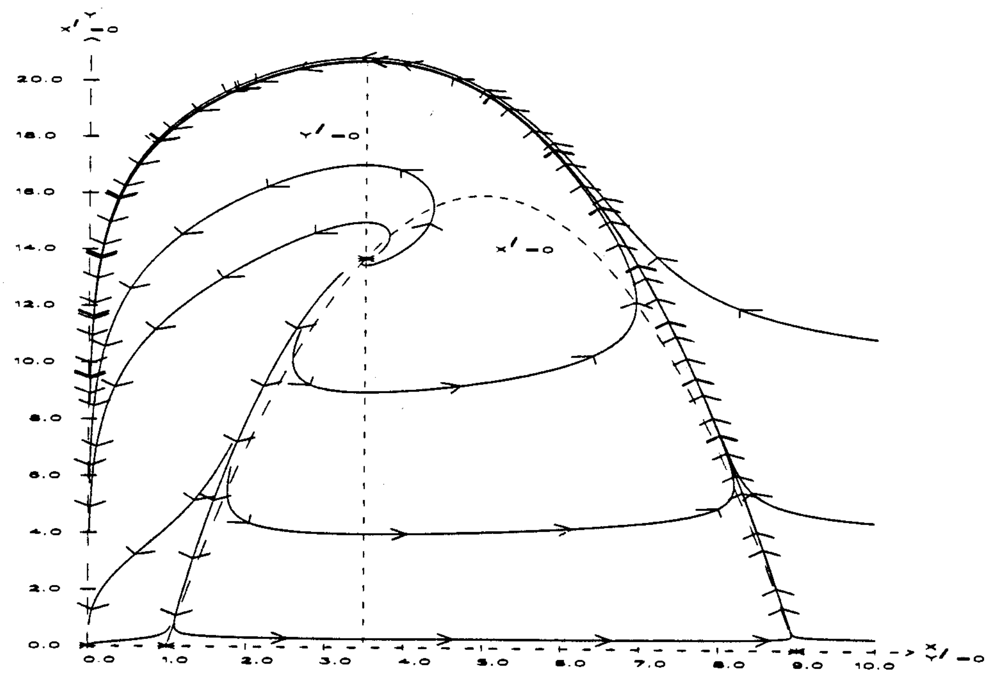

Figure 2.13: Example 6 with $n = 1$ and $\varepsilon\ = 0.5$

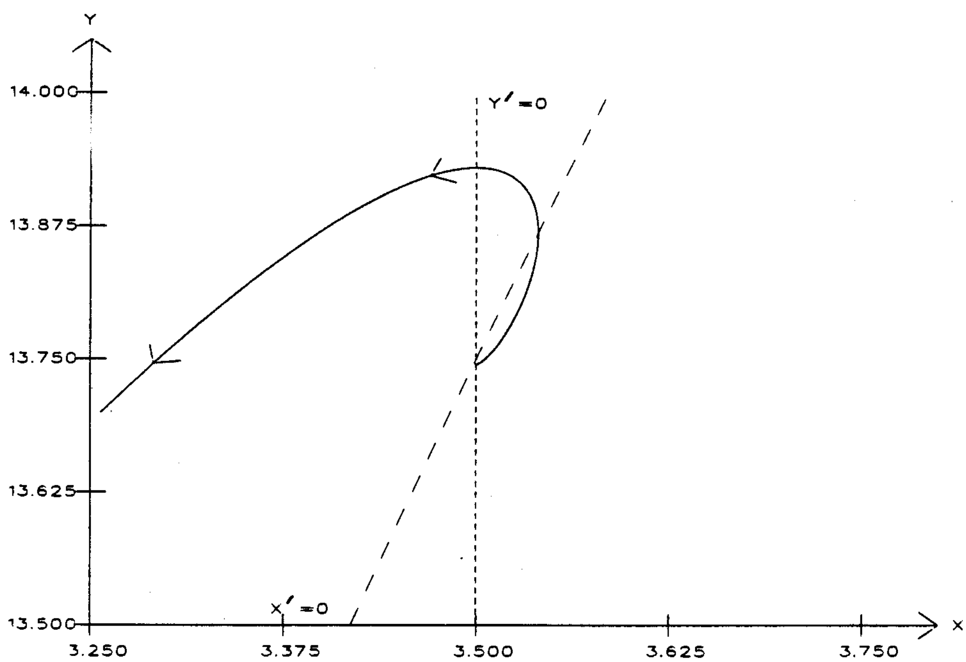

Figure 2.14: Example 6 with $n = 1$ and $\varepsilon = 0.5$, expanded view

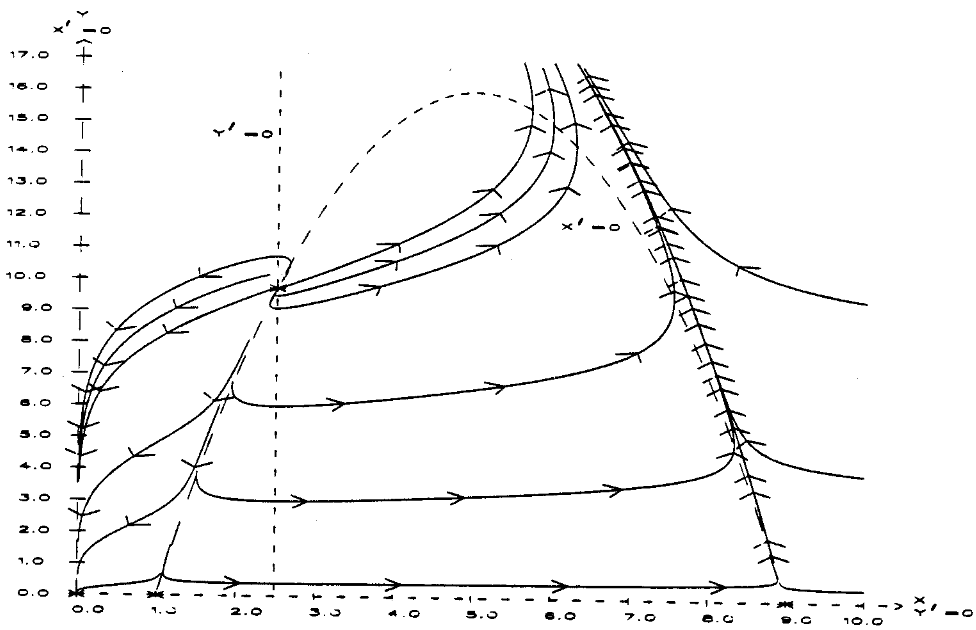

Figure 2.15: Example 6 with $n = 2$ and $\varepsilon\ = 0.5$

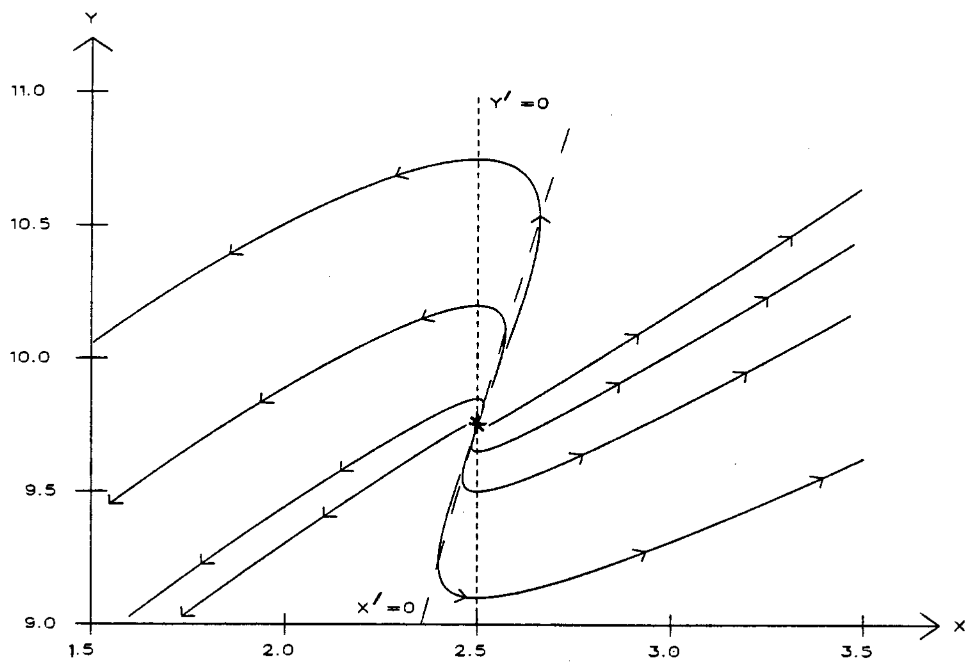

Figure 2.16: Example 6 with $n = 2$ and $\varepsilon\ = 0.5$, expanded view

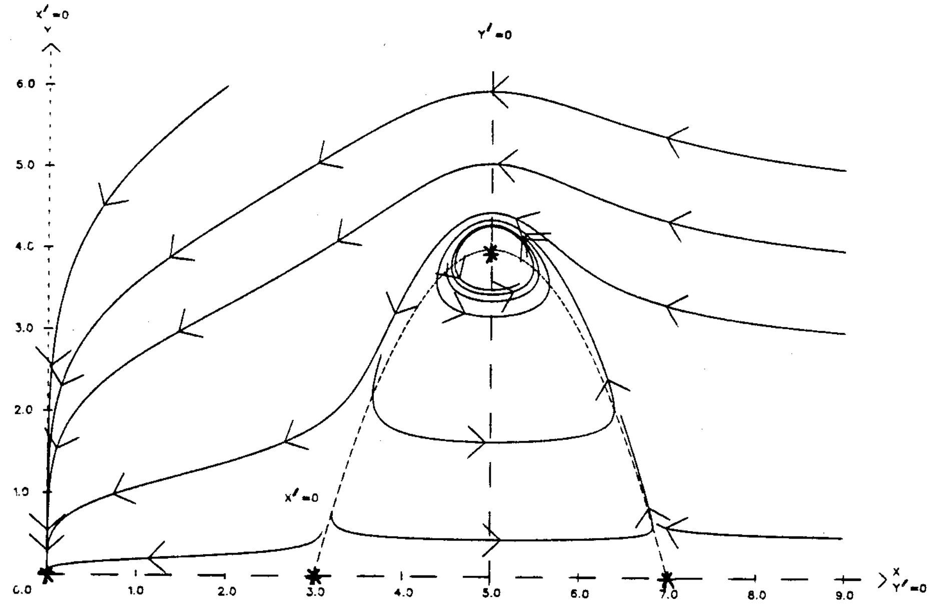

Figure 2.17: Example 7 with $\varepsilon\ = 0$

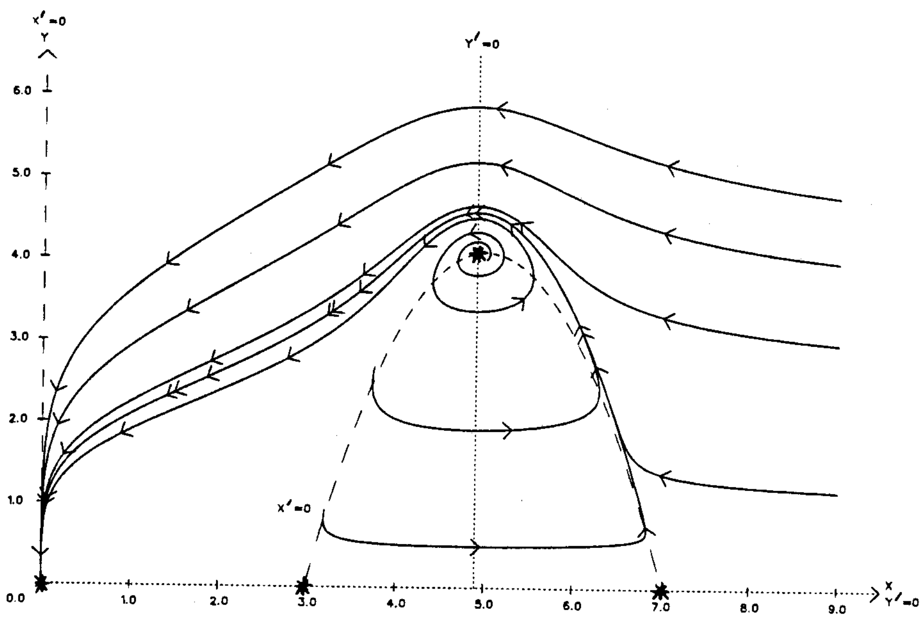

Figure 2.18: Example 7 with $\varepsilon\ = 0.1$

2.4.2 Example 7

The model

$$
\begin{aligned}
x\prime &= x(x-3)(7-x) - xy + \varepsilon\ x, \\
y\prime &= -5y + xy + \varepsilon\ y,
\end{aligned}
$$

is an example of a perturbed predator-prey system without harvesting or stocking. When $\varepsilon = 0$, the equilibria are: $E_0^0(0,0)$ an asymptotically stable proper node, $E_1^0(3,0)$ a saddle point, $E_2^0(7,0)$ a saddle point, and $E_3^0(5,4)$ a centre of the *linearized* unperturbed model (the eigenvalues at this point are $\lambda_{1,2}^0 = \pm 2i\sqrt{5}$). In fact, from Fig.2.17, wich shows the phase portrait of the system with $\varepsilon = 0$, we see that E_3^0 appears to be an asymptotically stable (weak) focus for the unperturbed model.

If we now consider the model with $\varepsilon > 0$, we know that E_0^p will be an asymptotically stable node, and E_1^p and E_2^p will be saddle points. Calculations give that to $O(\varepsilon)$, E_3^p is $E_3^p(5-\varepsilon, 4+\varepsilon)$, and at this point the Jacobian (2.43) is

$$
J^p = \begin{pmatrix} 10\varepsilon & -5+\varepsilon \\ 4+\varepsilon & 0 \end{pmatrix}.
$$

Thus, we find that to order $O(\varepsilon)$ the eigenvalues (2.50) are $\lambda_{1,2}^p = \pm 2i\sqrt{5} + \varepsilon\ (5 \pm i\frac{\sqrt{5}}{20})$. Equilibrium E_3^p is an unstable focus. The results for the perturbed model are displayed in Fig.2.18 were we have used the value $\varepsilon = 0.1$. Under the influence of perturbations, the nonhyperbolic equilibrium E_3^0 has gone from being asymptotically stable, to unstable.

2.5 Bifurcation of a Multiple Equilibrium

In this Section we examine the effect of perturbations on a multiple equilibrium $E^c(x^c, y^c)$ of the unperturbed system, determining the conditions under which E^c splits (bifurcates) into several new equilibria.

We assume that either a double or triple equilibrium exists in $\Re_+^2$; hence, we assume there is an $E^c(x^c, y^c)$ with $x^c, y^c \geq 0$ satisfying (2.3)–(2.5) and either (2.23) (double) or (2.24) (triple). Following the method of [25], which is a slight generalization of the method used in [10], [11] and [21] (see also [29] for a detailed look at perturbation methods), we seek a perturbed equilibrium $E^*(x^*, y^*)$ in the form

$$\begin{aligned} x^* &= x^c + \varepsilon^{\mu} m_1 + \varepsilon^{2\mu} m_2 + \varepsilon^{3\mu} m_3 + O(\varepsilon^{4\mu}), \\ y^* &= y^c + \varepsilon^{\mu} n_1 + \varepsilon^{2\mu} n_2 + \varepsilon^{3\mu} n_3 + O(\varepsilon^{4\mu}). \end{aligned} \tag{2.52}$$

The pair (x^*, y^*) must satisfy the perturbed system (2.39); therefore, we substitute (2.52) into (2.40) with superscript 0 replaced by c in (2.40). The coefficient of ε^0 is zero since $E^c(x^c, y^c)$ satisfies (2.2) (which is just (2.39) with $\varepsilon = 0$), so we may divide the resulting expression by ε^{μ} which leaves us with:

$$\begin{aligned} &\alpha_c\, m_1 + \beta_c\, n_1 + \varepsilon^{\mu}(\alpha_c\, m_2 + \beta_c\, n_2 + \tfrac{1}{2} W_2^c\, m_1^2 - g_x^c m_1 n_1) + \varepsilon^{2\mu}(\alpha_c\, m_3 \\ &\quad + \beta_c\, n_3 + \tfrac{1}{6} W_3^c\, m_1^3 + W_2^c\, m_1 m_2 - g_x^c m_2 n_1 - g_x^c m_1 n_2 - \tfrac{1}{2} g_{xx}^c m_1^2 n_1) \\ &\quad + O(\varepsilon^{3\mu}) + \varepsilon^{1-\mu}\phi^c + \varepsilon\,(\phi_x^c\, m_1 + \phi_y^c\, n_1) + \varepsilon^{1+\mu}(\phi_x^c\, m_2 + \phi_y^c\, n_2 \\ &\quad + \tfrac{1}{2}\phi_{xx}^c\, m_1^2 + \phi_{xy}^c\, m_1 n_1 + \tfrac{1}{2}\phi_{yy}^c\, n_1^2) + O(\varepsilon^{1+2\mu}) = 0, \\ &\gamma_c\, m_1 + \delta_c\, n_1 + \varepsilon^{\mu}(\gamma_c\, m_2 + \delta_c\, n_2 + \tfrac{1}{2} b y^c g_{xx}^c m_1^2 + b g_x^c m_1 n_1) + \varepsilon^{2\mu}(\gamma_c\, m_3 \\ &\quad + \delta_c\, n_3 + \tfrac{1}{6} b y^c g_{xxx}^c m_1^3 + b y^c g_{xx}^c m_1 m_2 + b g_x^c m_2 n_1 + b g_x^c m_1 n_2 + \tfrac{1}{2} b g_{xx}^c m_1^2 n_1) \\ &\quad + O(\varepsilon^{3\mu}) + \varepsilon^{1-\mu}\psi^c + \varepsilon\,(\psi_x^c\, m_1 + \psi_y^c\, n_1) + \varepsilon^{1+\mu}(\psi_x^c\, m_2 + \psi_y^c\, n_2 \\ &\quad + \tfrac{1}{2}\psi_{xx}^c\, m_1^2 + \psi_{xy}^c\, m_1 n_1 + \tfrac{1}{2}\psi_{yy}^c\, n_1^2) + O(\varepsilon^{1+2\mu}) = 0. \end{aligned} \tag{2.53}$$

Note that it is necessary to go to higher order in the Taylor expansions than is shown in (2.40) to get (2.53). Also, we assume that we don't have $\phi^c = \psi^c = 0$ (otherwise $E^*(x^*, y^*) = E^c(x^c, y^c)$), and that $q_1^c = \alpha_c + \delta_c \neq 0$. As usual, W_2^c and W_3^c appearing in the above formula are to be found in (2.25).

To solve (2.53) we set coefficients of successive powers of ε equal to zero. Since at least one of ψ^c or ϕ^c is not zero, for some $l = 1, 2, 3, \ldots$ we must have $1 - \mu = l\mu$. Therefore, only $\mu = 1, \frac{1}{2}, \frac{1}{3}, \ldots$ are possible values.

We investigate two cases.

Case 1 $(x^c, y^c) \in \mathrm{Int}\Re_+^2$.

Since $x^c, y^c > 0$, it turns out that $\alpha_c, \beta_c, \gamma_c, \delta_c \neq 0$ (see (2.16) with (1.4) and (1.5) and use the fact that $p_x^c = \alpha_c\,\delta_c - \beta_c\,\gamma_c = 0$). We have evaluated five subcases, making use of A_1, A_2 (given by (2.34), (2.35)) and the expressions:

$$\begin{aligned} D_1 &= \alpha_c \psi^c - \gamma_c \phi^c , \\ D_2 &= \gamma_c \phi^c_y - \alpha_c \psi^c_y - \delta_c \phi^c_x + \beta_c \psi^c_x - b g^c_x \phi^c - g^c_x \psi^c . \end{aligned} \tag{2.54}$$

(i) $A_1 \neq 0$, $D_1 = 0$. Since $A_1 \neq 0$ implies $p^c_{xx} \neq 0$, we know that $E^c(x^c, y^c)$ is a double equilibrium. In this case $\mu = 1$ should be used in (2.52).

Setting successive powers of ε equal to zero in (2.53) gives us a series of systems of equations, of which only the fist two are needed in order to solve for m_1 and n_1. These two systems are:

$$\alpha_c m_1 + \beta_c n_1 + \phi^c = 0, \quad \gamma_c m_1 + \delta_c n_1 + \psi^c = 0; \tag{2.55}$$

$$\begin{aligned} \alpha_c m_2 + \beta_c n_2 + \tfrac{1}{2} W^c_2 m_1^2 - g^c_x m_1 n_1 + \phi^c_x m_1 + \phi^c_y n_1 &= 0, \\ \gamma_c m_2 + \delta_c n_2 + \tfrac{1}{2} b y^c g^c_{xx} m_1^2 + b g^c_x m_1 n_1 + \psi^c_x m_1 + \psi^c_y n_1 &= 0. \end{aligned} \tag{2.56}$$

The condition $D_1 = 0$ guarantees that (2.55) has a solution (recall that $\alpha_c \delta_c - \beta_c \gamma_c = 0$). Eliminating m_1, m_2 and n_2 from (2.55) and (2.56), we obtain the quadratic equation

$$c_1 n_1^2 + c_2 n_1 + c_3 = 0, \tag{2.57}$$

where:

$$\begin{aligned} c_1 &= \frac{\beta_c}{\alpha_c} (\alpha_c + \delta_c)^3 A_1, \\ c_2 &= b y^c g^c_{xx} \phi^c \frac{\beta_c}{\alpha_c} - b g^c_x \phi^c - \psi^c_x \beta_c + \psi^c_y \alpha_c - W^c_2 \psi^c \frac{\delta_c}{\gamma_c} \\ &\quad - g^c_x \psi^c + \phi^c_x \delta_c - \phi^c_y \gamma_c , \\ c_3 &= \frac{1}{2\alpha_c} b y^c g^c_{xx} (\phi^c)^2 - \phi^c \psi^c_x - \frac{1}{2\alpha_c} W^c_2 \psi^c \phi^c + \psi^c \phi^c_x . \end{aligned} \tag{2.58}$$

If $c_2^2 - 4c_1c_3 > 0$, then there are two real solutions of (2.57). This, together with (2.55) gives two new equilibria, which are approximately $E^*_s(x^c + \varepsilon m_{1s}, y^c + \varepsilon n_{1s})$, $s = 1, 2$, where

$$m_{1s} = -\frac{\beta_c}{2c_1\alpha_c}[-c_2 + (-1)^s\sqrt{c_2^2 - 4c_1c_3}] - \frac{\phi^c}{\alpha_c}, \quad n_{1s} = \frac{1}{2c_1}[-c_2 + (-1)^s\sqrt{c_2^2 - 4c_1c_3}].$$

If $c_2^2 - 4c_1c_3 < 0$, the double equilibrium disappears under the influence of perturbations. If $c_2^2 - 4c_1c_3 = 0$, higher order terms m_2 and n_2 should be calculated.

(ii) $A_1 \neq 0$, $D_1 \neq 0$. Again $E^c(x^c, y^c)$ is a double equilibrium, but this time we use in (2.52) $\mu = \frac{1}{2}$. Proceeding as before, the two systems of equations that we must solve are:

$$\alpha_c m_1 + \beta_c n_1 = 0, \quad \gamma_c m_1 + \delta_c n_1 = 0; \tag{2.59}$$

$$\begin{aligned} \alpha_c\, m_2 + \beta_c\, n_2 + \tfrac{1}{2} W_2^c\, m_1^2 - g_x^c m_1 n_1 + \phi^c &= 0, \\ \gamma_c\, m_2 + \delta_c\, n_2 + \tfrac{1}{2} b y^c g_{xx}^c m_1^2 + b g_x^c m_1 n_1 + \psi^c &= 0. \end{aligned} \tag{2.60}$$

From these systems we derive the quadratic equation

$$c_1 n_1^2 + D_1 = 0, \tag{2.61}$$

where c_1 is found in (2.58) and D_1 in (2.54). Provided $c_1 D_1 < 0$ we again see that the double equilibrium $E^c(x^c, y^c)$ produces two perturbed equilibria given to $O(\varepsilon^{\,1/2})$ by $E_s^*(x^c + \varepsilon^{\,1/2} m_{1s}, y^c + \varepsilon^{\,1/2} n_{1s})$, $s = 1, 2$, where

$$m_{1s} = (-1)^{s+1} \frac{\beta_c}{\alpha_c} \sqrt{\frac{-D_1}{c_1}}, \quad n_{1s} = (-1)^s \sqrt{\frac{-D_1}{c_1}}.$$

When $c_1 D_1 > 0$ the double equilibrium disappears under the influence of perturbations. When $c_1 D_1 = 0$ further study is required.

(iii) $A_1 = 0$, $A_2 \neq 0$, $D_1 \neq 0$. Looking at (2.34) and (2.35), $A_1 = 0$, $A_2 \neq 0$ implies $E^c(x^c, y^c)$ is a triple equilibrium. The choice for μ in this case is $\mu = \frac{1}{3}$. Here we must use the first three systems of equations that result from (2.53): (2.59) together with

$$\begin{aligned} \alpha_c\, m_2 + \beta_c\, n_2 + \tfrac{1}{2} W_2^c\, m_1^2 - g_x^c m_1 n_1 &= 0, \\ \gamma_c\, m_2 + \delta_c\, n_2 + \tfrac{1}{2} b y^c g_{xx}^c m_1^2 + b g_x^c m_1 n_1 &= 0; \end{aligned} \tag{2.62}$$

$$\begin{aligned} \alpha_c\, m_3 + \beta_c\, n_3 + \tfrac{1}{6} W_3^c\, m_1^3 + W_2^c\, m_1 m_2 - g_x^c m_2 n_1 & \\ - g_x^c m_1 n_2 - \tfrac{1}{2} g_{xx}^c m_1^2 n_1 + \phi^c &= 0, \\ \gamma_c\, m_3 + \delta_c\, n_3 + \tfrac{1}{6} b y^c g_{xxx}^c m_1^3 + b y^c g_{xx}^c m_1 m_2 + b g_x^c m_2 n_1 & \\ + b g_x^c m_1 n_2 + \tfrac{1}{2} b g_{xx}^c m_1^2 n_1 + \psi^c &= 0. \end{aligned} \tag{2.63}$$

We eliminate m_3 and n_3 from (2.63), then use (2.62) to remove m_2 from the resulting equation; the term n_2 also disappears due to $A_1 = 0$. Finally, using (2.59), we arrive at the cubic equation

$$M m_1^3 - D_1 = 0, \tag{2.64}$$

where

$$M = \frac{\alpha_c}{\beta_c} (\alpha_c + \delta_c)^4 A_2. \tag{2.65}$$

Since $M \neq 0$ (because $A_2 \neq 0$) and $D_1 \neq 0$, (2.64) has one real and two imaginary solutions. This case always results in one simple perturbed equilibrium which is approximately represented by $E^*(x^c + \varepsilon^{1/3} m_1, y^c + \varepsilon^{1/3} n_1)$, with

$$m_1 = \sqrt[3]{\frac{D_1}{M}}, \quad n_1 = -\frac{\alpha_c}{\beta_c}\sqrt[3]{\frac{D_1}{M}}.$$

(iv) $A_1 = 0$, $A_2 \neq 0$, $D_1 = 0$, $D_2 = 0$. Again E^c is a triple equilibrium and we should use $\mu = \frac{1}{3}$ as in subcase **(iii)**; thus, equation (2.64) will again result. Since $D_1 = 0$ and $M \neq 0$, we find that $m_1 = n_1 = 0$. After substituting these values into (2.53) we make use of the first five systems of equations that result:

$$\alpha_c\, m_2 + \beta_c\, n_2 = 0, \quad \gamma_c\, m_2 + \delta_c\, n_2 = 0; \tag{2.66}$$

$$\alpha_c\, m_3 + \beta_c\, n_3 + \phi^c = 0, \quad \gamma_c\, m_3 + \delta_c\, n_3 + \psi^c = 0; \tag{2.67}$$

$$\begin{aligned} \alpha_c\, m_4 + \beta_c\, n_4 + \tfrac{1}{2}W_2^c\, m_2^2 - g_x^c m_2 n_2 &= 0, \\ \gamma_c\, m_4 + \delta_c\, n_4 + \tfrac{1}{2}by^c g_{xx}^c m_2^2 + bg_x^c m_2 n_2 &= 0; \end{aligned} \tag{2.68}$$

$$\begin{aligned} \alpha_c\, m_5 + \beta_c\, n_5 + W_2^c\, m_2 m_3 - g_x^c m_2 n_3 - g_x^c m_3 n_2 + \phi_x^c\, m_2 + \phi_y^c\, n_2 &= 0, \\ \gamma_c\, m_5 + \delta_c\, n_5 + by^c g_{xx}^c m_2 m_3 + bg_x^c m_2 n_3 + bg_x^c m_3 n_2 + \psi_x^c\, m_2 + \psi_y^c\, n_2 &= 0; \end{aligned} \tag{2.69}$$

$$\begin{aligned} \alpha_c\, m_6 + \beta_c\, n_6 + \tfrac{1}{2}W_2^c\, m_3^2 + W_2^c\, m_2 m_4 + \tfrac{1}{6}W_3^c\, m_2^3 - \tfrac{1}{2}g_{xx}^c m_2^2 n_2 & \\ - g_x^c m_3 n_3 - g_x^c m_2 n_4 - g_x^c m_4 n_2 + \phi_x^c\, m_3 + \phi_y^c\, n_3 &= 0, \\ \gamma_c\, m_6 + \delta_c\, n_6 + \tfrac{1}{2}by^c g_{xx}^c m_3^2 + by^c g_{xx}^c m_2 m_4 + \tfrac{1}{6}by^c g_{xxx}^c m_2^3 + \tfrac{1}{2}bg_{xx}^c m_2^2 n_2 & \\ + bg_x^c m_3 n_3 + bg_x^c m_2 n_4 + bg_x^c m_4 n_2 + \psi_x^c\, m_3 + \psi_y^c\, n_3 &= 0. \end{aligned} \tag{2.70}$$

Using elimination, the equation

$$M m_2^3 - c_3 = 0, \tag{2.71}$$

may be derived from (2.66)–(2.70). This is the same M as in (2.65) and the same c_3 as in (2.58). With $D_1 = D_2 = A_1 = 0$, c_3 simplifies to $c_3 = \frac{\phi^c}{\beta_c}(\gamma_c\, \phi_y^c - \alpha_c\, \psi_y^c)$. As in **(iii)** $M \neq 0$; provided $c_3 \neq 0$ we have one perturbed simple equilibrium given to $O(\varepsilon^{2/3})$ by $E^*(x^c + \varepsilon^{2/3} m_2, y^c + \varepsilon^{2/3} n_2)$ with

$$m_2 = \sqrt[3]{\frac{c_3}{M}}, \quad n_2 = -\frac{\alpha_c}{\beta_c}\sqrt[3]{\frac{c_3}{M}}.$$

If $c_3 = 0$, then $m_2 = n_2 = 0$ and it is necessary to calculate higher order terms m_3, n_3.

(v) $A_1 = 0,\ A_2 \neq 0,\ D_1 = 0,\ D_2 \neq 0.$ Here E^c is still a triple equilibrium, but now we use $\mu = \frac{1}{2}$; consequently, (2.59) and (2.60) are still valid. One more system:

$$\begin{aligned}\alpha_c\ m_3 + \beta_c\ n_3 + \tfrac{1}{6}W_3^c\ m_1^3 + W_2^c\ m_1 m_2 - g_x^c m_2 n_1 & \\ - g_x^c m_1 n_2 - \tfrac{1}{2}g_{xx}^c m_1^2 n_1 + \phi_x^c\ m_1 + \phi_y^c\ n_1 &= 0, \\ \gamma_c\ m_3 + \delta_c\ n_3 + \tfrac{1}{6}by^c g_{xxx}^c m_1^3 + by^c g_{xx}^c m_1 m_2 + bg_x^c m_2 n_1 & \\ + bg_x^c m_1 n_2 + \tfrac{1}{2}bg_{xx}^c m_1^2 n_1 + \psi_x^c\ m_1 + \psi_y^c\ n_1 &= 0,\end{aligned} \tag{2.72}$$

is required. From (2.59), (2.60) and (2.72) we may derive the following cubic equation:

$$m_1(Mm_1^2 - \frac{\alpha_c}{\beta_c}D_2) = 0. \tag{2.73}$$

This equation always has $m_1 = 0$ as a solution. When $m_1 = 0$, $n_1 = 0$ also, so we go to the next higher order terms m_2 and n_2. It is not very difficult to find that provided $c_2 c_3 \neq 0$:

$$m_2 = \frac{\beta_c\ c_3}{\alpha_c\ c_2} - \frac{\phi^c}{\alpha_c}, \quad n_2 = -\frac{c_3}{c_2}.$$

If $c_2 c_3 = 0$, further study is required. If $\alpha_c\ \beta_c\ MD_2 > 0$, there are two additional real solutions of (2.73):

$$m_{1s} = (-1)^s\sqrt{\frac{\alpha_c\ D_2}{\beta_c\ M}}, \quad n_{1s} = (-1)^{s+1}\frac{\alpha_c}{\beta_c}\sqrt{\frac{\alpha_c\ D_2}{\beta_c\ M}}, \quad s = 2, 3.$$

Thus, if $c_2 c_3 \neq 0$ and $\alpha_c\ \beta_c\ MD_2 > 0$, the triple equilibrium $E^c(x^c, y^c)$ of the unperturbed system bifurcates into three perturbed simple equilibria $E_s^*(x_s^*, y_s^*)$, $s = 1, 2, 3$, where:

$$x_1^* = x^c + \varepsilon\ m_2 + O(\varepsilon^{\ 3/2}), \quad y_1^* = y^c + \varepsilon\ n_2 + O(\varepsilon^{\ 3/2});$$

and

$$x_s^* = x^c + \varepsilon^{\ 1/2} m_{1s} + O(\varepsilon\ ), \quad y_s^* = y^c + \varepsilon^{\ 1/2} n_{1s} + O(\varepsilon\ ), \quad s = 2, 3.$$

If $c_2 c_3 \neq 0$ and $\alpha_c\ \beta_c\ MD_2 < 0$, then E_1^* is the only perturbed equilibrium.

Case 2 (x^c, y^c) is on the boundary of $\Re_+^2$.

First we consider multiple equilibria on the x-axis. In Section 2.3, **Case 2**, we saw that the only such possibility is for a double equilibrium at either $E^c(L_1, 0)$ or $E^c(L_2, 0)$.

There are just two subcases to consider here which depend on whether or not $D_1 = 0$, where $D_1 = \alpha_c\ \psi^c$ (this is the same D_1 as given by (2.54) because here $\alpha_c\ ,\beta_c\ \neq 0$ and $\gamma_c\ = \delta_c\ = 0$).

(i) $D_1 = 0$. The results are exactly as in **Case 1(i)** above, but now

$$\begin{aligned} c_1 &= -\,b\beta_c\ g_x^c, \\ c_2 &= -\,bg_x^c\phi^c\ -\beta_c\ \psi_x^c\ +\alpha_c\ \psi_y^c\ , \\ c_3 &= -\,\phi^c\ \psi_x^c\ , \end{aligned} \tag{2.74}$$

instead of those values given in (2.58).

(ii) $D_1 \neq 0$. The results are as in **Case 1(ii)** above, but with c_1 as in (2.74). Note that here $E_1^*(x^c + m_{11}\varepsilon^{\ 1/2}, n_{11}\varepsilon^{\ 1/2})$ is not in $\Re_+^2$ as $n_{11} = -\sqrt{\frac{-D_1}{c_1}} < 0$.

Now consider a multiple equilibrium on the y-axis; which, according to **Case 2** of Section 2.3, is located at $E^c(0, \frac{H}{a})$ and may be a double or triple (or more) equilibrium. We study five subcases which depend on A_1 and A_2 specified by (2.36) and (2.37), and on $D_1 = -\gamma_c\ \phi^c$ and $D_2 = \gamma_c\ \phi_y^c\ - \delta_c\ \phi_x^c\ - g_x^c\psi^c$ (note that $\alpha_c\ = \beta_c\ = 0$ and $\gamma_c\ ,\delta_c\ \neq 0$ here). The results in subcases **(i)–(v)** below, are the same as in subcases **(i)–(v), Case 1** above, with the following exceptions:

(i) $A_1 \neq 0$, $D_1 = 0$. Here we have that

$$\begin{aligned} c_1 &= -\,\delta_c^3 A_1, \\ c_2 &= -\,\frac{\delta_c}{\gamma_c}(2F_x^c - y^c g_{xx}^c)\psi^c\ - g_x^c\psi^c\ + \delta_c\ \phi_x^c\ - \gamma_c\ \phi_y^c\ , \\ c_3 &= -\,\frac{(\psi^c\ )^2}{\gamma_c}(F_x^c - \tfrac{1}{2}y^c g_{xx}^c) + \phi_x^c\ \psi^c\ . \end{aligned} \tag{2.75}$$

Also $m_{1s} = -\frac{\delta_c}{2c_1\gamma_c}[-c_2 + (-1)^s\sqrt{c_2^2 - 4c_1c_3}\,] - \frac{\psi^c}{\gamma_c}$.

(ii) $A_1 \neq 0$, $D_1 \neq 0$. Now we should use c_1 given by (2.75) rather than (2.58) and in the expression for m_{1s} we must replace $\frac{\beta_c}{\alpha_c}$ by $\frac{\delta_c}{\gamma_c}$. In addition, $E_2^*(m_{12}\varepsilon^{\ 1/2}, \frac{H}{a} + n_{12}\varepsilon^{\ 1/2})$ is not in $\Re_+^2$ since $m_{12} = -\frac{\delta_c}{\gamma_c}\sqrt{\frac{-D_1}{c_1}} < 0$.

(iii) $A_1 = 0$, $A_2 \neq 0$, $D_1 \neq 0$. Instead of (2.65), M is found to be

$$M = \gamma_c^3\delta_c\ A_2. \tag{2.76}$$

Use $\frac{\gamma_c}{\delta_c}$ rather than $\frac{\alpha_c}{\beta_c}$ in n_1. If $D_1 M < 0$, then $m_1 = \sqrt[3]{\frac{D_1}{M}} < 0$ and $E^*(m_1\varepsilon^{\ 1/3}, \frac{H}{a} + n_1\varepsilon^{\ 1/3})$ is no longer in $\Re_+^2$.

(iv) $A_1 = 0$, $A_2 \neq 0$, $D_1 = 0$, $D_2 = 0$. The quantity c_3 is found in (2.75), M in (2.76), and now $n_2 = -\frac{\gamma_c}{\delta_c}\sqrt[3]{\frac{c_3}{M}}$. If $Mc_3 < 0$, then it is easily seen that $E^*(m_2\varepsilon^{\ 2/3}, \frac{H}{a} + n_2\varepsilon^{\ 2/3})$ is not in $\Re^2_+$.

(v) $A_1 = 0$, $A_2 \neq 0$, $D_1 = 0$, $D_2 \neq 0$. Observe that equation (2.73) now reads $m_1(Mm_1^2 - \frac{\gamma_c}{\delta_c}D_2) = 0$, with M as in (2.76). With these changes, we calculate that $m_2 = \frac{\delta_c}{\gamma_c}\frac{c_3}{c_2} - \frac{\psi^c}{\gamma_c}$ and $n_2 = -\frac{c_3}{c_2}$; where of course, c_2 and c_3 are found in (2.75). Finally, $m_{1s} = (-1)^s\sqrt{\frac{\gamma_c}{\delta_c}\frac{D_2}{M}}$, $n_{1s} = (-1)^{s+1}\frac{\gamma_c}{\delta_c}\sqrt{\frac{\gamma_c}{\delta_c}\frac{D_2}{M}}$, $s = 2, 3$; E_3^* is no longer in $\Re^2_+$ as $m_{13} < 0$.

2.6 Nature of the Perturbed Multiple Equilibria

The equilibria bifurcating, under the influence of perturbations, from a double or triple equilibrium of the unperturbed system have been located. We now determine the nature of these perturbed equilibria. Looking at the cases considered in Section 2.5, only values of $\mu = 1, \frac{1}{2}$, and $\frac{1}{3}$ were needed for (2.52); thus, we study here these three cases.

(i) $\mu = 1$. Perturbed equilibria given to $O(\varepsilon\ )$ by $E^*(x^c + m_1\varepsilon\ , y^c + n_1\varepsilon\ )$ arose from a double equilibrium in **Case 1(i)** and **Case 2(i)** of Section 2.5. The Jacobian J^* at such a point is similar to (2.43):

$$J^* = J^c + \varepsilon\begin{pmatrix}\theta_c & \rho_c\\ \sigma_c & \tau_c\end{pmatrix} + O(\varepsilon^{\ 2}),\quad J^c = \begin{pmatrix}\alpha_c & \beta_c\\ \gamma_c & \delta_c\end{pmatrix}, \tag{2.77}$$

where α_c , β_c , γ_c , δ_c , θ_c , ρ_c , σ_c and τ_c are respectively α_0 , β_0 , γ_0 , δ_0 , θ_0 , ρ_0 , σ_0 and τ_0 with superscript 0 repaced by superscript c in (2.16) and (2.44). Taking into consideration that $\det J^c = \alpha_c\,\delta_c\ - \beta_c\,\gamma_c\ = 0$, the eigenvalues for $E^c(x^c, y^c)$ are $\lambda_1^c = 0$ $\lambda_2^c = q_1^c = \alpha_c\ + \delta_c$; therefore, the eigenvalues for E^* are

$$\lambda_1^* = \frac{\Omega_c}{q_1^c}\varepsilon\ + O(\varepsilon^{\ 2}),\quad \lambda_2^* = q_1^c + O(\varepsilon\ );\quad \Omega_c\ = \alpha_c\,\tau_c\ + \delta_c\,\theta_c\ - \beta_c\,\sigma_c\ - \gamma_c\,\rho_c$$

(Ω_c is Ω_0 (2.46) evaluated at (x^c, y^c) instead of (x^0, y^0)). Recall that we assumed $q_1^c \neq 0$ for a multiple equilibrium, so λ_1^* is well defined. Provided that $\Omega_c\ \neq 0$, E^* must be a saddle or a node. If $\Omega_c\ = 0$, λ_1^* must be calculated to higher order. When E^c is a double equilibrium, it was found (Section 2.3) to be a saddle-node, which under the influence of perturbations splits into a saddle and a node according to [28].

(ii) $\mu = \frac{1}{2}$. Subcase (ii) of **Cases 1** and **2** in the preceding section saw equilibria of the form $E^*(x^c + m_1\varepsilon^{1/2}, y^c + n_1\varepsilon^{1/2})$ arise from the double equilibrium $E^c(x^c, y^c)$ when perturbations were introduced. At E^* the Jacobian is

$$J^* = J^c + \varepsilon^{1/2} J^d + O(\varepsilon), \quad J^d = \begin{pmatrix} \theta_d & \rho_d \\ \sigma_d & \tau_d \end{pmatrix}. \tag{2.78}$$

Matrix J^c is given in (2.77) and

$$\begin{aligned} \theta_d &= m_1 W_2^c - n_1 g_x^c, & \rho_d &= -m_1 g_x^c, \\ \sigma_d &= m_1 b y^c g_{xx}^c + n_1 b g_x^c, & \tau_d &= m_1 b g_x^c. \end{aligned} \tag{2.79}$$

To $O(\varepsilon^{1/2})$ the characteristic equation is

$$\lambda^2 - q_1^c\lambda + \varepsilon^{1/2}[-(\theta_d + \tau_d)\lambda + \Omega_d] = 0; \quad \Omega_d = \alpha_c\,\tau_d + \delta_c\,\theta_d - \beta_c\,\sigma_d - \gamma_c\,\rho_d\,.$$

We seek $\lambda_{1,2}^*$ in the form

$$\lambda_s^* = \lambda_s^c + \varepsilon^{1/2} l_s^1 + O(\varepsilon); \quad s = 1, 2.$$

Substitiuting λ_s^* into the characteristic equation and setting the coefficient of $\varepsilon^{1/2}$ to zero, we solve for l_s^1. With this we find

$$\lambda_1^* = \frac{\Omega_d}{q_1^c}\varepsilon^{1/2} + O(\varepsilon), \quad \lambda_2^* = q_1^c + O(\varepsilon^{1/2}).$$

Utilizing the fact that m_1, n_1 satisfy (2.59) and (2.60), we have established that $\Omega_d = m_1 p_{xx}^c$. Thus, for the double equilibrium $\Omega_d \neq 0$ and E^* is a saddle or a node. In fact, we know fom Section 2.3 that the double equilibrium, when it does not disappear under the influence of perturbations, produces two equilibria: one saddle and one node.

When $E^c(x^c, y^c)$ is a triple equilibrium as in subcase (v) of **Cases 1** and **2** of the previous Section, we now see that $\Omega_d = 0$ since $p_{xx}^c = 0$. It will be necessary to go to higher order in the evaluation of λ_1^*, and to do this requires knowing E^* to order $O(\varepsilon)$.

Let us assume we have $E^*(x^c + m_1\varepsilon^{1/2} + m_2\varepsilon, y^c + n_1\varepsilon^{1/2} + n_2\varepsilon)$ with m_2 and n_2 explicitly calculated. The Jacobian at E^* is

$$J^* = J^c + \varepsilon^{1/2} J^d + \varepsilon J^e + O(\varepsilon^{3/2}), \quad J^e = \begin{pmatrix} \theta_e & \rho_e \\ \sigma_e & \tau_e \end{pmatrix},$$

where:

$$\begin{aligned}
\theta_e &= m_2 W_2^c - n_2 g_x^c + \tfrac{1}{2} m_1^2 W_3^c - m_1 n_1 g_{xx}^c + \phi_x^c, \\
\rho_e &= -m_2 g_x^c - \tfrac{1}{2} m_1^2 g_{xx}^c + \phi_y^c, \\
\sigma_e &= m_2 b y^c g_{xx}^c + n_2 b g_x^c + \tfrac{1}{2} m_1^2 b y^c g_{xxx}^c + m_1 n_1 b g_{xx}^c + \psi_x^c, \\
\tau_e &= m_2 b g_x^c + \tfrac{1}{2} m_1^2 b g_{xx}^c + \psi_y^c.
\end{aligned}$$

Reminder: W_2^c and W_3^c are given in (2.25). The characteristic equation to $O(\varepsilon)$ is

$$\lambda^2 - q_1^c\lambda - \varepsilon^{1/2}(\theta_d + \tau_d)\lambda + \varepsilon\,[-(\theta_e + \tau_e)\lambda + \Omega_e + \det J^d] = 0,$$

where $\Omega_e = \alpha_c\,\tau_e + \delta_c\,\theta_e - \beta_c\,\sigma_e - \gamma_c\,\rho_e$, and $\det J^d = \theta_d\,\tau_d - \sigma_d\,\rho_d$. The eigenvalues are therefore

$$\lambda_1^* = \frac{1}{q_1^c}(\Omega_e + \det J^d)\varepsilon + O(\varepsilon^{3/2}), \quad \lambda_2^* = q_1^c + O(\varepsilon^{1/2}).$$

Assuming $\Omega_e + \det J^d \neq 0$, E^* must be a saddle or a node. If this term is zero, it is necessary to calculate to higher order; we do not consider this here.

(iii) $\mu = \frac{1}{3}$. This value for μ was used in **Case 1(iii)** and **Case 2(iii)** of Section 2.5, where E^* was calculated to $O(\varepsilon^{1/3})$. As E^c is a triple equilibrium, it is necessary to know E^* to $O(\varepsilon^{2/3})$ in order to determine its stability. We assume we have $E^*(x^c + m_1\varepsilon^{1/3} + m_2\varepsilon^{2/3}, y^c + n_1\varepsilon^{1/3} + n_2\varepsilon^{2/3})$ with m_2 and n_2 known. Such a point has Jacobian

$$J^* = J^c + \varepsilon^{1/3} J^d + \varepsilon^{2/3} \begin{pmatrix} \theta_f & \rho_f \\ \sigma_f & \tau_f \end{pmatrix} + O(\varepsilon).$$

Expressions J^c and J^d are found in (2.77) and (2.78) respectively. In addition:

$$\begin{aligned}
\theta_f &= m_2 W_2^c - n_2 g_x^c + \tfrac{1}{2} m_1^2 W_3^c - m_1 n_1 g_{xx}^c, & \rho_f &= -m_2 g_x^c - \tfrac{1}{2} m_1^2 g_{xx}^c, \\
\sigma_f &= m_2 b y^c g_{xx}^c + n_2 b g_x^c + \tfrac{1}{2} m_1^2 b y^c g_{xxx}^c + m_1 n_1 b g_{xx}^c, & \tau_f &= m_2 b g_x^c + \tfrac{1}{2} m_1^2 b g_{xx}^c.
\end{aligned}$$

Calculations give the eigenvalues:

$$\lambda_1^* = \frac{1}{q_1^c}(\Omega_f + \det J^d)\varepsilon^{2/3} + O(\varepsilon), \quad \lambda_2^* = q_1^c + O(\varepsilon^{1/3}),$$

where $\Omega_f = \alpha_c \tau_f + \delta_c \theta_f - \beta_c \sigma_f - \gamma_c \rho_f$. As usual, E^* is a saddle or a node provided $\Omega_f + \det J^d \neq 0$.

Finally, $E^*(x^c + m_2\varepsilon^{2/3} + m_3\varepsilon, y^c + n_2\varepsilon^{2/3} + n_3\varepsilon)$ is the type of perturbed equilibrium that appeared in **Case 1(iv)** and **Case 2(iv)** of Section 2.5. Coefficients m_2 and n_2 have been explicitly calculated, and now we assume that m_3 and n_3 are known. We find the eigenvalues to be:

$$\lambda_1^* = \frac{\Omega_g}{q_1^c}\varepsilon + O(\varepsilon^{4/3}), \quad \lambda_2^* = q_1^c + O(\varepsilon^{2/3});$$

$$\Omega_g = \alpha_c \tau_g + \delta_c \theta_g - \beta_c \sigma_g - \gamma_c \rho_g,$$

$$\theta_g = m_3 W_2^c - n_3 g_x^c + \phi_x^c, \qquad \rho_g = -m_3 g_x^c + \phi_y^c$$

$$\sigma_g = m_3 b y^c g_{xx}^c + n_3 b g_x^c + \psi_x^c, \qquad \tau_g = m_3 b g_x^c + \psi_y^c.$$

Once again E^* is a saddle or node when $\Omega_g \neq 0$.

Next we will study an example of a double equilibrium, and one of a triple equilibrium.

2.6.1 Example 8

Let's look at the system studied in Example 4, but we add the perturbational terms $\phi(x,y) = x$, $\psi(x,y) = y$ to the model:

$$\begin{aligned} x\prime &= x(x-2)(7-x) - xy + \varepsilon x, \\ y\prime &= -14y + 3xy - 16 + \varepsilon y. \end{aligned}$$

We already know that $E^c(6,4)$ is a double equilibrium (a saddle node) of the unperturbed ($\varepsilon = 0$) model, now we study the bifurcation of E^c under the influence of perturbations. From (2.16) $\alpha_c = -18, \beta_c = -6, \gamma_c = 12$, and $\delta_c = 4$. From (2.54) we calculate that $D_1 = -144 \neq 0$; thus, we are dealing with **Case 1(ii)** of Section 2.5. Next, from (2.58), $c_1 = 26$. Therefore, $m_{1s} = (-1)^{s+1} 2\sqrt{\frac{2}{13}}$ and $n_{1s} = (-1)^s 6\sqrt{\frac{2}{13}}$, $s = 1, 2$. To $O(\varepsilon^{1/2})$ the perturbed equilibria are $E_1^*(6 + 2\sqrt{\frac{2}{13}}\varepsilon^{1/2}, 4 - 6\sqrt{\frac{2}{13}}\varepsilon^{1/2})$ and $E_2^*(6 - 2\sqrt{\frac{2}{13}}\varepsilon^{1/2}, 4 + 6\sqrt{\frac{2}{13}}\varepsilon^{1/2})$.

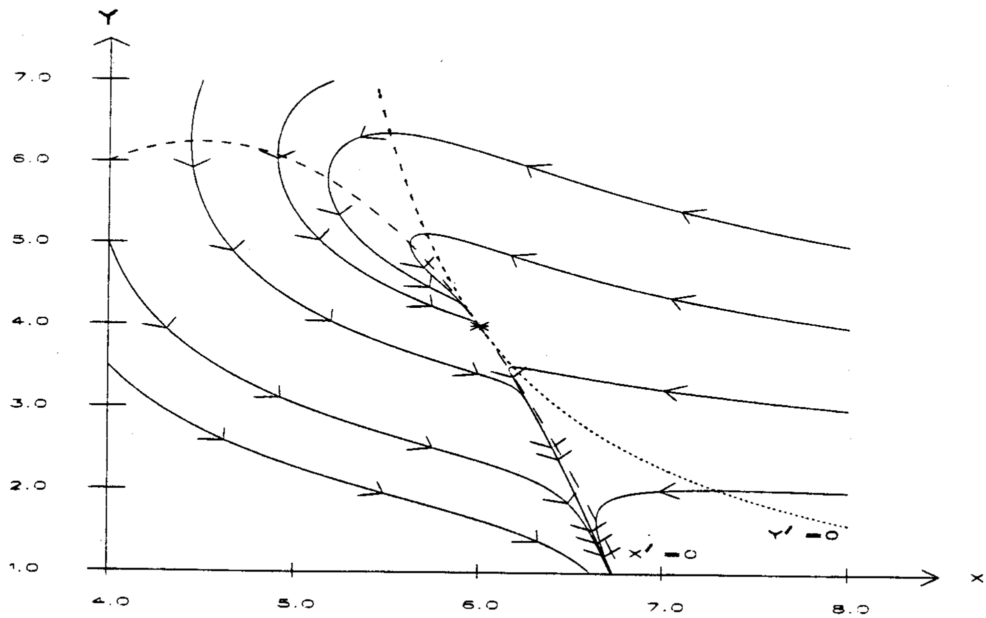

Figure 2.19: Example 8 with $\varepsilon\ = 0$

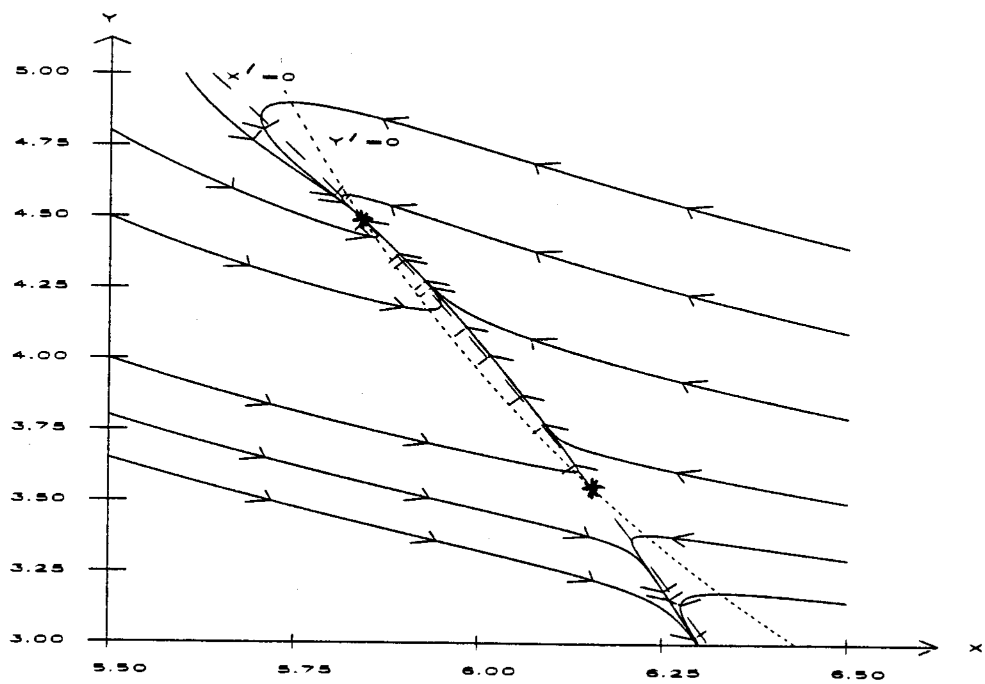

Figure 2.20: Example 8 with $\varepsilon\ = 0.04$

To find the nature of these equilibria, we go to case **(ii)** of Section 2.6 (double equilibrium with $\mu = \frac{1}{2}$). After some elaborations we find the eigenvalues for E_1^* are

$$\lambda_1^* = \frac{156}{7}\sqrt{\frac{2}{13}}\varepsilon^{1/2} + O(\varepsilon), \quad \lambda_2^* = -14 + O(\varepsilon^{1/2}),$$

and for E_2^* are

$$\lambda_1^* = -\frac{156}{7}\sqrt{\frac{2}{13}}\varepsilon^{1/2} + O(\varepsilon), \quad \lambda_2^* = -14 + O(\varepsilon^{1/2}).$$

Just as expected, one (E_1^*) is a saddle and the other (E_2^*) is a node. For $\varepsilon = 0$, we show a neighbourhood of the double equilibrium in Fig.2.19 (this is the same as Fig.2.9). In Fig.2.20, we show the two perturbed equilibria E_1^* and E_2^*, where we have chosen the value $\varepsilon = 0.04$ with which to carry out the calculations.

2.6.2 Example 9

Now we consider the model

$$\begin{aligned} x' &= x(-x^4 + 22x^3 - \tfrac{4031}{24}x^2 + \tfrac{2935}{6}x - \tfrac{8105}{24}) - xy - \varepsilon\,\tfrac{1}{6}x, \\ y' &= -y + xy - 9 + \varepsilon\,(10x - 69). \end{aligned}$$

This model has perturbational terms $\phi(x,y) = -\frac{1}{6}x$ and $\psi(x,y) = 10x - 69$. With $\varepsilon = 0$ the system reduces to the model of Example 5; therefore, for convenience, we present Fig.2.10 again in Fig.2.21, which shows the triple equilibrium $E^c(7, \frac{3}{2})$. Since $D_1 = 0$ and $D_2 = -\frac{413}{6}$ (see (2.54)), we are in **Case 1(v)** of Section 2.5. As $\alpha_c\ \beta_c\ MD_2 = (-\frac{7}{4})(-7)(-\frac{6041}{96})(-\frac{413}{6}) > 0$, we should look to case **(ii)** of Section 2.6. Because E^c is a triple equilibrium, we need E_s^*, $s = 1,2,3$, to order $O(\varepsilon)$ to determine the stability of the perturbed equilibria. Note that E_1^* is already known to the required order from **Case 1(v)** of Section 2.5, while a little extra work is required to find E_2^* and E_3^* to $O(\varepsilon)$. The result is

$$E_1^*(7, \frac{3}{2} - \frac{1}{6}\varepsilon), \quad E_s^*(7 + (-1)^s 2\sqrt{\frac{59}{863}}\varepsilon^{1/2}, \frac{3}{2} - (-1)^s\frac{1}{2}\sqrt{\frac{59}{863}}\varepsilon^{1/2} - \frac{134}{863}\varepsilon), \quad s = 2,3.$$

The eigenvalues for E_1^* according to case **(ii)** of Section 2.6 are:

$$\lambda_1^* = \frac{826}{51}\varepsilon + O(\varepsilon^{3/2}), \quad \lambda_2^* = \frac{17}{4} + O(\varepsilon^{1/2});$$

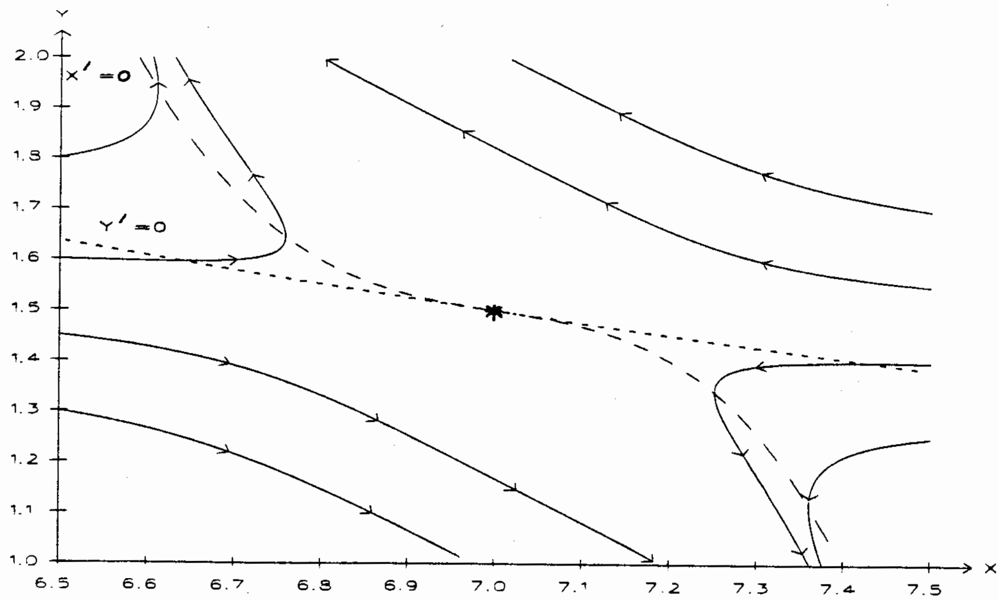

Figure 2.21: Example 9 with $\varepsilon = 0$

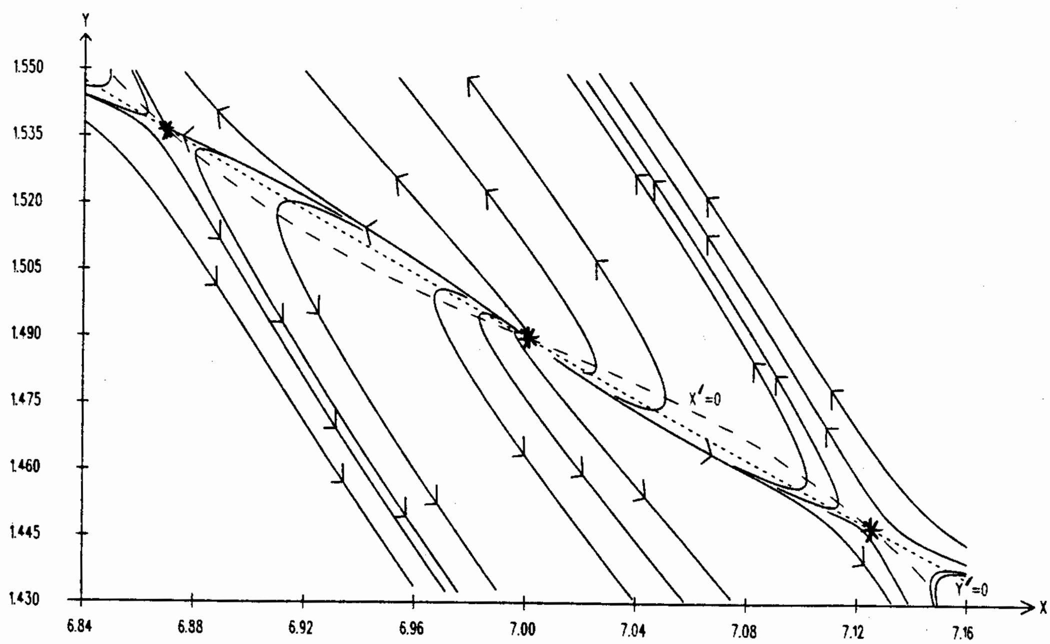

Figure 2.22: Example 9 with $\varepsilon = 0.06$

and, for E_s^*, $s = 2, 3$, are

$$\lambda_1^* = -\frac{4810418}{88026}\varepsilon + O(\varepsilon^{3/2}), \quad \lambda_2^* = \frac{17}{4} + O(\varepsilon^{1/2}).$$

Thus E_1^* is an unstable node, while E_2^* and E_3^* are saddle points (recall: E^c is a topological saddle point). We show these three equilibria in Fig.2.22 in which we have used the value $\varepsilon = 0.06$.

2.7 Tables

We present two tables that summarize the effect of perturbations on simple and multiple equilibria of the unperturbed system. A simple equilibrium that is of the type proper node, focus or node-star is hyperbolic. A simple equilibrium of the type centre or a multiple equilibrium is nonhyperbolic. Note how the local stability properties of hyperbolic equilibria are not affected by perturbations.

$E^0(x^0, y^0)$	$E^p(x^p, y^p)$	Changes in Nature, Stability
Proper Node	Proper Node	No Changes
Focus	Focus	No Changes
Node-Star	Focus or Proper Node	Only Nature Changes
Centre of Linearized System	Focus	Nature and Stability May Change

Table 2.1: Perturbations of a Simple Equilibrium

Multiplicity of $E^c(x^c, y^c)$	μ	Number of Perturbed Equilibria	Nature of $E^*(x^*, y^*)$
Double	1	0	
		2	One Saddle, One Node
	$\frac{1}{2}$	0	
		2	One Saddle, One Node
Triple	$\frac{1}{2}$	1	May be a Saddle or a Node
		3	
	$\frac{1}{3}$	1	

Table 2.2: Bifurcations of a Multiple Equilibrium

Chapter 3

THE THREE-SPECIES MODEL

We analyze the three-species food chain model (0.2) under the assumptions (1.1)–(1.7). The pattern of Chapter 2 will be followed here: First we study the simple equilibria, then the multiple equilibria, of the unperturbed system. We end by investigating the effect of perturbations on these simple and multiple equilibria. As much of the results and their derivation are similar to those of the two-species model, we will be concise.

3.1 Simple Equilibria of the Unperturbed Model

The unperturbed case of model (0.2) results when we set $\varepsilon = 0$:

$$\begin{aligned} x' &= xF(x) - yG(x) - R, \\ y' &= -ay + byG(x) - zK(y), \\ z' &= -cz + rzK(y). \end{aligned} \tag{3.1}$$

We seek the simple (not multiple) equilibria $E^0(x^0, y^0, z^0)$ in $\Re^3_+$ ($x, y, z \geq 0$, the population octant); (x^0, y^0, z^0) must satisfy

$$xF(x) - yG(x) - R = 0, \tag{3.2}$$

$$-ay + byG(x) - zK(y) = 0, \tag{3.3}$$

$$-cz + rzK(y) = 0. \tag{3.4}$$

Three different types of simple equilibria are considered: $E_1^0(\bar{x},0,0)$,$E_2^0(\check{x},\check{y},0)$, and $E_3^0(\tilde{x},\tilde{y},\tilde{z})$.

For $E_1^0(\bar{x},0,0)$, (3.3) and (3.4) are automatically satisfied, while $\bar{x}$ must satisy the equation $xF(x) - R = 0$. There may be more than one such equilibrium; each is simple provided $F(\bar{x}) + \bar{x}F_x(\bar{x}) \neq 0$.

Now, $E_2^0(\check{x},\check{y},0)$ is an equilibrium when $\check{x}$ satisfies $bG(\check{x}) - a = 0$ (in which case $\check{x} > 0$) and $\check{x}F(\check{x}) - R > 0$; $\check{y}$ is given by $\check{y} = \frac{\check{x}F(\check{x})-R}{G(\check{x})}$ (so $y > 0$). Since $bG(\check{x}) - a = 0$ can have at most one solution, and since corresponding to each $\check{x}$ there is only one $\check{y}$, E_2^0 is simple.

Finally, $E_3^0(\tilde{x},\tilde{y},\tilde{z})$ is found in the following way: first we find $\tilde{y}$ satisfying the equation $-c+rK(\tilde{y}) = 0$ ((3.4) with $z \neq 0$); there is at most one such solution and it satisfies $\tilde{y} > 0$ by (1.6), (1.7). With $\tilde{y}$ known, we find $\tilde{x}$ from (3.2). We introduce the notation

$$Q(x,y) = xF(x) - yG(x) - R; \tag{3.5}$$

$\tilde{x}$ satisfies $\tilde{Q} = 0$, where $\tilde{Q} \equiv Q(\tilde{x},\tilde{y})$. For a given $\tilde{y}$, there may be more than one $\tilde{x}$ satisfying $\tilde{Q} = 0$, and thus more than one such equilibrium of the form $E_3^0(\tilde{x},\tilde{y},\tilde{z})$ (but each has the same $\tilde{y}$-value). Equilibrium $E_3^0(\tilde{x},\tilde{y},\tilde{z})$ is simple when

$$\tilde{Q}_x \equiv Q_x(\tilde{x},\tilde{y}) = F(\tilde{x}) + \tilde{x}F_x(\tilde{x}) - \tilde{y}G_x(\tilde{x}) \neq 0. \tag{3.6}$$

With $\tilde{x}$ and $\tilde{y}$ known, $\tilde{z}$ is found from (3.3): $\tilde{z} = \frac{-a\tilde{y}+b\tilde{y}G(\tilde{x})}{K(\tilde{y})}$. Of course, we must have $-a + bG(\tilde{x}) > 0$ so that $\tilde{z} > 0$.

We investigate the following cases which depend on R.

(A) $R = 0$; *No harvesting or stocking.*

We can explicitly say that $E_{1_1}^0(0,0,0)$, $E_{1_2}^0(L_1,0,0)$ and $E_{1_3}^0(L_2,0,0)$ are equilibria by (1.1). In addition, for $E_2^0(\check{x},\check{y},0)$ we know that $\check{x}$ satisfies (2.9); otherwise, $\check{y} \leq 0$. If E_2^0 and E_3^0 both exist as equilibria in $\Re_+^3$, then $\tilde{x} > \check{x}$.

(B) $R = H > 0$; *Harvesting.*

We must have $L_1 < \bar{x} < L_2$, $L_1 < \check{x} < L_2$ and $L_1 < \tilde{x} < L_2$. If E_2^0 and E_3^0 are both equilibria in $\Re_+^3$, $\check{x} < \tilde{x}$.

(C) $R = -S < 0$; *Stocking.*

Now we require $0 < \bar{x} < L_1$ or $L_2 < \bar{x}$, and it is no longer necessary that $L_1 < \check{x} < L_2$ and $L_1 < \tilde{x} < L_2$.

3.2 Stability Properties of the Simple Equilibria

Similarly to the two-species case, we have found the eigenvalues from the Jacobian of (3.1) for each equilibrium; these determine an equilibrium's stability properties. See Appendix A for classification of an equilibrium according to its eigenvalues. Keeping in mind that $a, b, c, r > 0$, the results are as follows:

(A) $R = 0$; *No harvesting or stocking.*

We assume all five equilibria exist.

Equilibrium $E^0_{1_1}(0,0,0)$. The eigenvalues are $\lambda^0_1 = F(0) < 0$, $\lambda^0_2 = -a < 0$ and $\lambda^0_3 = -c < 0$. Equilibrium $E^0_{1_1}(0,0,0)$ *is an asymptotically stable node.*

Equilibrium $E^0_{1_2}(L_1,0,0)$; $\lambda^0_1 = L_1F_x(L_1) > 0$, $\lambda^0_2 = -a+bG(L_1) < 0$, and $\lambda^0_3 = -c < 0$; $E^0_{1_2}$ *is a saddle node* (do not confuse this type of saddle node with that type corresponding to a double equilibrium of the two dimensional model).

Equilibrium $E^0_{1_3}(L_2,0,0)$; $\lambda^0_1 = L_2F_x(L_2) < 0$, $\lambda^0_2 = -a+bG(L_2) > 0$, and $\lambda^0_3 = -c < 0$; $E^0_{1_3}(L_2,0,0)$ *is a saddle node.*

Equilibrium $E^0_2(\check{x},\check{y},0)$; $\lambda^0_1 = -c+rK(\check{y})$, $\lambda^0_s = \frac{1}{2}[\check{Q}_x + (-1)^s\sqrt{\check{Q}^2_x - 4a\check{y}G_x(\check{x})}\,]$, $s = 2,3$; $\check{Q}_x = F(\check{x}) + \check{x}F_x(\check{x}) - \check{y}G_x(\check{x})$. If $-c + rK(\check{y}) < 0$ and $\check{Q}_x < 0$ then E^0_2 is asymptotically stable. If in addition $\check{Q}^2_x - 4a\check{y}G_x(\check{x}) < 0$, $E^0_2$is an asymptotically stable node focus; or if $\check{Q}^2_x - 4a\check{y}G_x(\check{x}) > 0$, E^0_2 is an asymptotically stable node; while if $\check{Q}^2_x - 4a\check{y}G_x(\check{x}) = 0$, $\lambda^0_2 = \lambda^0_3$ and the equilibrium is an asymptotically stable node star. If none of the above holds, $E^0_2(\check{x},\check{y},0)$ is unstable.

Equilibrium $E^0_3(\tilde{x},\tilde{y},\tilde{z})$; the characteristic equation is

$$\lambda^3 + p_1\lambda^2 + p_2\lambda + p_3 = 0, \tag{3.7}$$

where,

$$\begin{aligned} p_1 &= H_1 - \tilde{Q}_x\ , \quad p_2 = H_2 - H_1\tilde{Q}_x\ , \quad p_3 = -c\tilde{z}K_y(\tilde{y})\tilde{Q}_x\ , \\ H_1 &= a - bG(\tilde{x}) + \tilde{z}K_y(\tilde{y}), \quad H_2 = b\tilde{y}G(\tilde{x})G_x(\tilde{x}) + c\tilde{z}K_y(\tilde{y}). \end{aligned} \tag{3.8}$$

Of course, $\tilde{Q}_x$ is found in (3.6). According to the Routh-Hurwitz criteria, E^0_3 is asymptotically stable provided

$$p_1 > 0, \quad p_3 > 0, \quad p_1p_2 > p_3.$$

Note that $p_3 > 0$ when $\tilde{Q}_x < 0$. According to a theorem by Bojadziev and Gerogiannakis [12], the Routh-Hurwitz criteria are satisfied when

$$\tilde{y}K_y(\tilde{y}) \geq \frac{c}{r}, \quad \tilde{Q}_x < 0.$$

If there are several different equilibria of this type, since $\tilde{Q}_x$ alternates in sign among these points, so will p_3; therefore, not all of these equilibria can satisfy the Routh-Hurwitz criteria.

(B) $R = H > 0$; *Harvesting.*

Equilibrium $E_1^0(\bar{x}, 0, 0)$; $\lambda_1^0 = \bar{Q}_x$ $(\bar{Q}_x \equiv Q_x(\bar{x}, 0))$, $\lambda_2^0 = -a + bG(\bar{x})$ and $\lambda_3^0 = -c < 0$. If $\bar{Q}_x < 0$ and $-a + bG(\bar{x}) < 0$ then E_1^0 is asymptotically stable; otherwise it is unstable. Note that if $\bar{x} < a_0$ (see (1.2), (1.3)) then $\bar{Q}_x > 0$; and we must have $\bar{x} < \check{x}$ to make $-a + bG(\bar{x}) < 0$. If there are several equilibria of this type, $\bar{Q}_x$ alternates sign among them; not all can be asymptotically stable.

Equilibrium $E_2^0(\check{x}, \check{y}, 0)$. The eigenvalues are the same as for E_2^0 of case **(A)** above. The same comments apply.

Equilibrium $E_3^0(\tilde{x}, \tilde{y}, \tilde{z})$. The situation is equivalent to that of E_3^0 in **(A)** above.

(C) $R = -S < 0$; *Stocking.*

Equilibrium $E_1^0(\bar{x}, 0, 0)$. The eigenvalues have the same form as in the case of equilibrium E_1^0 of **(B)**, so this equilibrium is asymptotically stable if $\bar{Q}_x < 0$ and $-a + bG(\bar{x}) < 0$. We know that either $0 < \bar{x} < L_1$, or $L_2 < \bar{x}$; $\bar{Q}_x < 0$ when $L_2 < \bar{x}$, and $-a + bG(\bar{x}) < 0$ only if $\bar{x} < \check{x}$.

Equilibrium $E_2^0(\check{x}, \check{y}, 0)$. The results are the same as in **(A)**, equilibrium E_2^0, but we add that it is now possible to have $L_2 < \check{x}$, guaranteeing that $\check{Q}_x < 0$.

Equilibrium $E_3^0(\tilde{x}, \tilde{y}, \tilde{z})$. We obtain the same results as for E_3^0 of **(A)**. Furthermore, it may be that $L_2 < \tilde{x}$, in which case $\tilde{Q}_x < 0$.

Now we look at two case studies.

3.2.1 Example 10

The model without harvesting or stocking

$$
\begin{aligned}
x' &= \frac{8}{5}x(x-1)(7-x) - 2xy, \\
y' &= -3y + 2xy - yz, \\
z' &= -4z + yz,
\end{aligned}
$$

has $F(x) = \frac{8}{5}(x-1)(7-x)$, $G(x) = 2x$, $K(y) = y$, $a = 3$, $b = 1$, $c = 4$, $r = 1$, $L_1 = 1$ and $L_2 = 7$. According to Section 3.1, case **(A)**, the equilibria are $E^0_{1_1}(0,0,0)$, $E^0_{1_2}(1,0,0)$, $E^0_{1_3}(7,0,0)$, $E^0_2(\frac{3}{2},\frac{11}{5},0)$, $E^0_{3_1}(2,4,1)$ and $E^0_{3_2}(6,4,9)$. From Section 3.2, **(A)**, we find that $E^0_{1_1}$ is an asymptotically stable node, $E^0_{1_2}$ is a saddle node, and $E^0_{1_3}$ is also a saddle node. The eigenvalues for E^0_2 are $\lambda^0_1 = -\frac{9}{5}$, $\lambda^0_s = \frac{117}{40} + (-1)^s\frac{1}{40}i\sqrt{7431}$, $s = 2,3$; this equilibrium is a saddle focus. The characteristic equation for $E^0_{3_1}$ is $\lambda^3 - \frac{64}{5}\lambda^2 + 36\lambda - \frac{256}{5} = 0$, so the eigenvalues are $\lambda^0_1 \approx 9.61$, and $\lambda^0_s \approx \frac{1}{2}[3.19 + (-1)^s i\sqrt{11.13}]$, $s = 2,3$; making $E^0_{3_1}$ an unstable node focus. Equilibrium $E^0_{3_2}$ has eigenvalues aproximately given by: $\lambda^0_1 = -35.79$, and $\lambda^0_s = \frac{1}{2}[-2.61 + (-1)^s i\sqrt{147.69}]$, $s = 2,3$; therefore, $E^0_{3_2}$ is an asymptotically stable node focus. We show the phase plot in Fig.3.1. The positive z-axis is into the paper in this perspective projection, as it is for all other plots in this chapter. The lines with arrows are selected orbits and the equilibria are marked by asterisks. Note that in all plots in this chapter, the arrow heads reside in a plane perpendicular to the x-z plane.

3.2.2 Example 11

Consider the system

$$
\begin{aligned}
x' &= x(x-\frac{3}{2})(\frac{13}{2}-x) - 5xy - 20, \\
y' &= -\frac{7}{2}y + xy - yz, \\
z' &= -z + 4yz.
\end{aligned}
$$

The equilibria for this model are $E^0_{1_s}(-\frac{\sqrt{139}}{3}\cos[\frac{2\pi}{3} + (-1)^s\theta] + \frac{8}{3},0,0)$, $s = 1,2$, $\theta = \frac{1}{3}\arccos(\frac{872\sqrt{139}}{19321})$; $E^0_2(\frac{7}{2},\frac{2}{35},0)$, $E^0_{3_1}(4,\frac{1}{4},\frac{1}{2})$ and $E^0_{3_2}(5,\frac{1}{4},\frac{3}{2})$. Approximately, the first two equilibria are: $E^0_{1_1}(3.3974,0,0)$ and $E^0_{1_2}(5.6454,0,0)$. Calculations give the eigenvalues

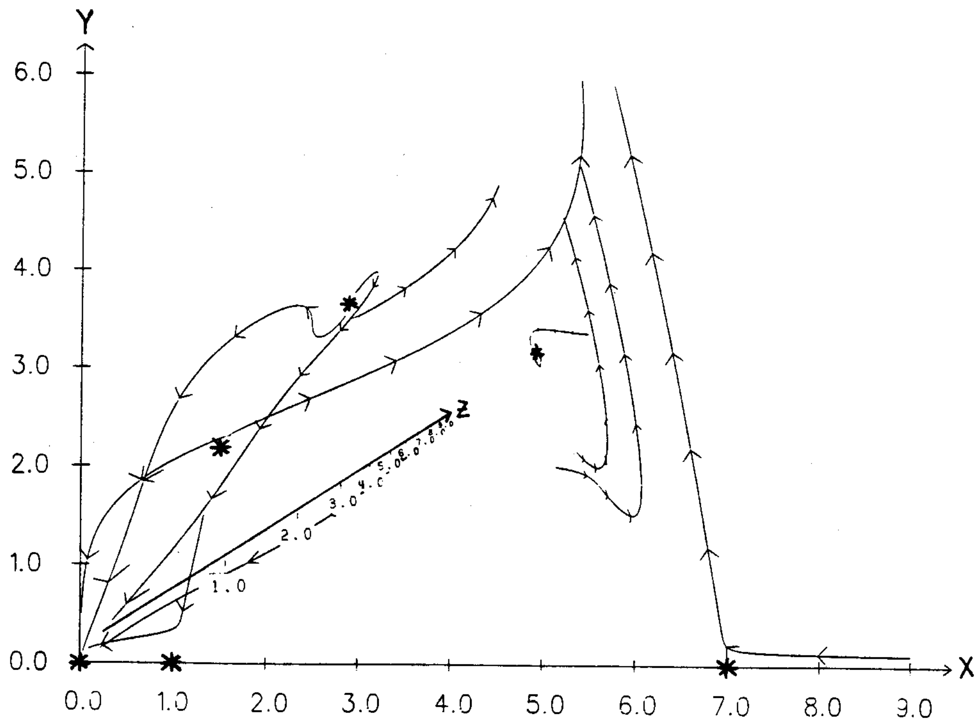

Figure 3.1: Example 10

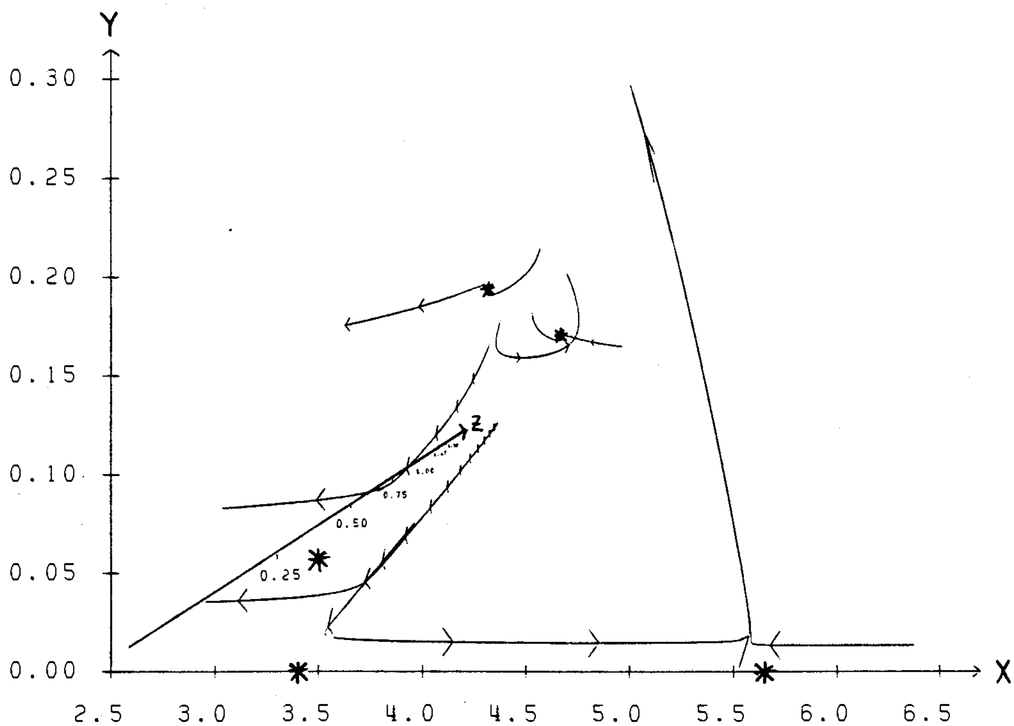

Figure 3.2: Example 11

$\lambda_1^0 \approx 9.98$, $\lambda_2^0 \approx -0.10$ and $\lambda_3^0 = -1$ for $E_{1_1}^0$; thus, this point is an unstable saddle node. Equilibrium $E_{1_2}^0$ is a saddle node because $\lambda_1^0 \approx -15.03$, $\lambda_2^0 \approx 2.15$ and $\lambda_3^0 = -1$. We find $\lambda_1^0 \approx -0.77$, $\lambda_2^0 \approx 9.10$ and $\lambda_3^0 \approx 0.11$ are the eigenvalues corresponding to the equilibrium E_2^0; hence, this is also a saddle node. The equilibrium $E_{3_1}^0$ is an unstable node focus since $\lambda_1^0 \approx 3.694$, and $\lambda_s^0 \approx \frac{1}{2}[1.306 + (-1)^s i\sqrt{0.997}]$, $s = 2, 3$. Lastly, $E_{3_2}^0$ has eigenvalues $\lambda_1^0 \approx -4.771$, $\lambda_s^0 \approx \frac{1}{2}[-1.229 + (-1)^s i\sqrt{6.035}]$, $s = 2, 3$; making it an asymptotically stable node focus. In Fig.3.2 we show the phase diagram.

3.3 Existence of a Multiple Equilibrium of the Unperturbed System

We are interested in discovering a multiple equilibrium $E^c(x^c, y^c, z^c)$ of the unperturbed model (3.1) in Int$\Re_+^3$. Multiple equilibria on the boundary of $\Re_+^3$ may exist, but they are of less interest and we do not study them here. This point may be located in the same way we found equilibria of the type $E_3^0(\tilde{x}, \tilde{y}, \tilde{z})$ in Section 3.1. The (unique) y-value, y^c, is determined by solving (3.4) with $z > 0$. The term x^c is then a root of the equation

$$Q(x, y^c) = 0, \tag{3.9}$$

where $Q(x, y)$ is given in (3.5). Since (3.3) then gives z^c when x^c, y^c are known, and since it gives a unique z for each pair x, y, it is equation (3.9) which controls the multiplicity of the equilibrium. Here, we assume $Q_x^c \equiv Q_x(x^c, y^c) = 0$ in order to have a multiple equilibrium. Two types of multiple equilibria will be studied in more detail in later sections: a double equilibrium, which occurs when

$$Q^c = 0, \quad Q_x^c = 0, \quad Q_{xx}^c \neq 0, \tag{3.10}$$

and a triple equilibrium, which occurs when

$$Q^c = 0, \quad Q_x^c = 0, \quad Q_{xx}^c = 0, \quad Q_{xxx}^c \neq 0. \tag{3.11}$$

As usual, superscript c indicates evaluation of the function at x^c, y^c and subscript x represents the order of differentiation with respect to x. Again we call R^c the critical harvesting

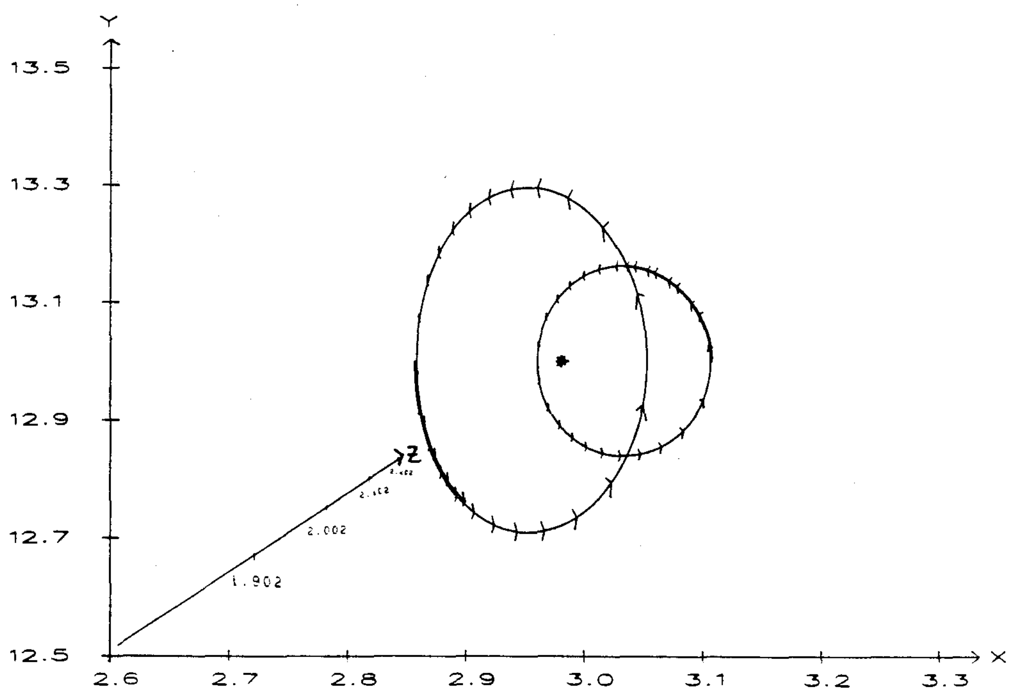

Figure 3.3: Example 12

or stocking value; unlike the two-species case, a multiple equilibrium may occur in $\mathrm{Int}\Re^3_+$ when there is no harvesting or stocking ($R^c = 0$). The characteristic equation (3.7) is still valid, but now all function evaluations are at (x^c, y^c, z^c) rather than $(\tilde{x}, \tilde{y}, \tilde{z})$ in (3.8), and we replace $\tilde{Q}_x$ by $Q^c_x \equiv 0$. Thus, (3.7) reduces to $\lambda(\lambda^2 + H^c_1\lambda + H^c_2) = 0$. The terms H^c_1 and H^c_2 are H_1 and H_2 respectively, given in (3.8), but evaluated at x^c, y^c, z^c. Note that $H^c_2 > 0$, so there is only one eigenvalue equal to zero.

Below, we examine two models; one with a double equilibrium, and the other with a triple equilibrium.

3.3.1 Example 12

The model

$$
\begin{aligned}
x' &= x(x-2)(7-x) - xy + 27, \\
y' &= -y + xy - yz, \\
z' &= -13z + yz,
\end{aligned}
$$

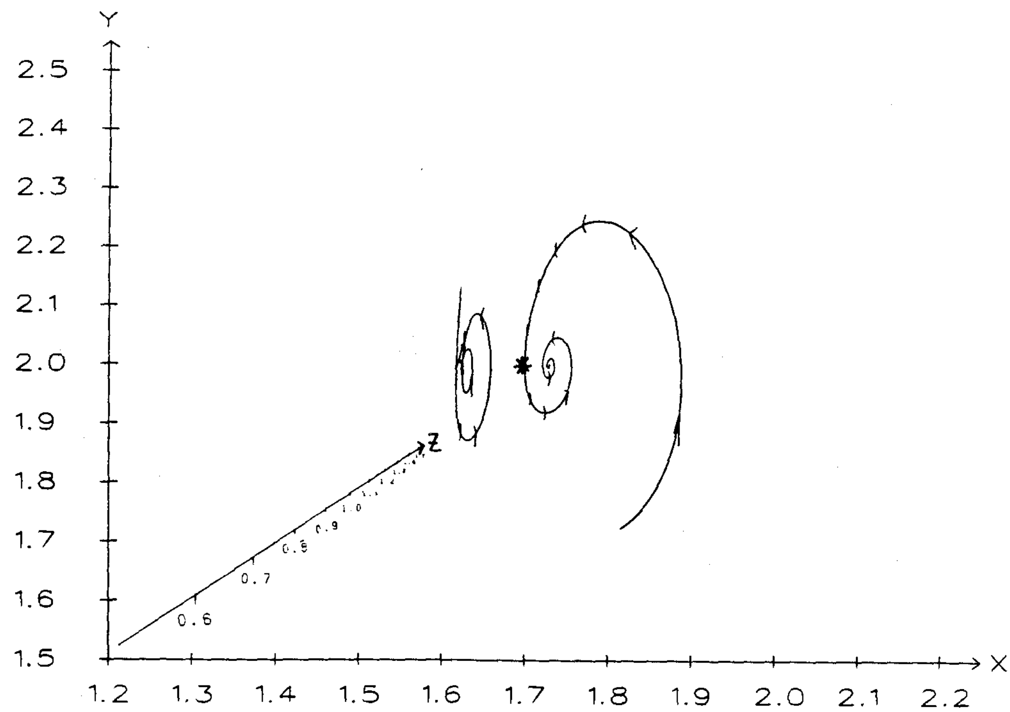

Figure 3.4: Example 13

has only one equilibrium in Int$\Re^3_+$ located at $(3, 13, 2)$. From (3.9), $Q(x, 13) = -x^3 + 9x^2 - 27x + 27$; thus, $Q_x(3, 13) = 0$, $Q_{xx}(3, 13) = 0$ and $Q_{xxx}(3, 13) = -6 \neq 0$. We have a triple equilibrium at $E^c(3, 13, 2)$ and $R^c = -27$ is the critical stocking value. In Fig.3.3 we show a neighbourhood of E^c. We have calculated a number of different orbits starting "near" the equilibrium, and they were all qualitatively similar to the two orbits shown. These orbits (numerically at least) are very nearly (but not) closed. The smaller orbit starts at (3.25,13,2) and the larger at (2.75,13,2). Although it is not readily apparent from the figure, these orbits do pass through a range of z values.

3.3.2 Example 13

For this example we look at the system

$$\begin{aligned} x\prime &= x(x-1)(3-x) - xy + \frac{50}{7}, \\ y\prime &= -3y + 3xy - y^2 z, \\ z\prime &= -4z + y^2 z. \end{aligned}$$

Utilising the results of Section 3.1, the only equilibrium in the population octant's interior is at the point $(\frac{5}{3}, 2, 1)$. We calculate $Q(x, 2) = -x^3 + 4x^2 - 5x + \frac{50}{27}$, $Q_x(\frac{5}{3}, 2) = 0$, and $Q_{xx}(\frac{5}{3}, 2) = -2 \neq 0$. Equilibrium $E^c(\frac{5}{3}, 2, 1)$ is a double equilibrium, which is shown on Fig.3.4. The orbit to the right of the equilibrium begins at (1.889,1.501,0.8187) and stops at approximately (1.742,2.002,1.102). The orther orbit starts at (1.5,2.3,1.0) and ends at a point near (1.537,1.989,0.8011).

3.4 Perturbations of a Simple Equilibrium

We assume $E^0(x^0, y^0, z^0)$ is a simple equilibrium of system (3.1) in $\mathrm{Int}\Re^3_+$. Simple equilibria on the boundary of $\Re^3_+$ can be handled in a way analogous to that described below; we do not do this here. The corresponding perturbed equilibrium $E^p(x^p, y^p, z^p)$ of system (0.2) must satisfy the equations

$$\begin{aligned} xF(x) - yG(x) - R + \varepsilon\ \phi_1(x, y, z) &= 0, \\ -\ ay + byG(x) - zK(y) + \varepsilon\ \phi_2(x, y, z) &= 0, \\ -\ cz + rzK(y) + \varepsilon\ \phi_3(x, y, z) &= 0. \end{aligned} \tag{3.12}$$

Similarly to (2.38) we seek the solution in the form

$$\begin{aligned} x^p &= x^0 + \varepsilon\ m_1 + O(\varepsilon^{\ 2}), \\ y^p &= y^0 + \varepsilon\ n_1 + O(\varepsilon^{\ 2}), \\ z^p &= z^0 + \varepsilon\ s_1 + O(\varepsilon^{\ 2}). \end{aligned} \tag{3.13}$$

Proceeding in the usual fashion, we may solve for m_1, n_1, s_1 by substituting (3.13) into (3.12). This produces the following:

$$\begin{aligned} m_1 &= -\frac{rz^0K_y^0\phi_1^0 + G^0\phi_3^0}{rz^0K_y^0Q_x^0}, \\ n_1 &= -\frac{\phi_3^0}{rz^0K_y^0}, \\ s_1 &= \frac{-by^0G_x^0(rz^0K_y^0\phi_1^0 + G^0\phi_3^0) - (-a + bG^0 - z^0K_y^0)Q_x^0\ \phi_3^0 + rz^0K_y^0Q_x^0\ \phi_2^0}{rz^0K_y^0Q_x^0\ K^0}. \end{aligned} \tag{3.14}$$

The notation is as usual and of course, $Q_x^0 \equiv Q_x(x^0, y^0)$ (see (3.5)). Note that (1.6) and (1.7) imply $K^0, K_y^0 \neq 0$ since $y^0 > 0$. Also, $Q_x^0 \neq 0$ because we assumed $E^0(x^0, y^0, z^0)$

is a simple equilibrium; therefore, m_1, n_1 and s_1 are well defined. A further assumption we make is that at least one of ϕ_1^0, ϕ_2^0, ϕ_3^0 is non-zero. If this does not hold, $E^p = E^0$ and there is no need to use (3.13) to solve (3.12).

With the equilibrium E^p located up to the order of ε , we find the characteristic equation at this point to be

$$\lambda^3 + p_1^0\lambda^2 + p_2^0\lambda + p_3^0 + \varepsilon\ (b_1^0\ \lambda^2 + b_2^0\ \lambda + b_3^0\ ) + O(\varepsilon\ ^2) = 0, \tag{3.15}$$

where:

$$\begin{aligned} b_1^0 &= -B_{11}^0 - B_{22}^0 - B_{33}^0, \\ b_2^0 &= Q_x^0\ (B_{22}^0 + B_{33}^0) + G^0 B_{21}^0 - by^0 G_x^0 B_{12}^0 - H_1^0(B_{11}^0 + B_{33}^0) \\ &\quad + K^0 B_{32}^0 - rz^0 K_y^0 B_{23}^0, \\ b_3^0 &= Q_x^0\ (H_1^0 B_{33}^0 - K^0 B_{32}^0 + rz^0 K_y^0 B_{23}^0) - G^0(by^0 G_x^0 B_{33}^0 + K^0 B_{31}^0) \\ &\quad - rz^0 K_y^0(by^0 G_x^0 B_{13}^0 + K^0 B_{11}^0), \end{aligned} \tag{3.16}$$

with

$$\begin{aligned} &B_{11}^0 = Q_{xx}^0 m_1 - G_x^0 n_1 + \phi_{1x}^0, && B_{12}^0 = -G_x^0 m_1 + \phi_{1y}^0, \\ &B_{13}^0 = \phi_{1z}^0, && B_{21}^0 = by^0 G_{xx}^0 m_1 + bG_x^0 n_1 + \phi_{2x}^0, \\ &B_{22}^0 = bG_x^0 m_1 - z^0 K_{yy}^0 n_1 - K_y^0 s_1 + \phi_{2y}^0, && B_{23}^0 = -K_y^0 n_1 + \phi_{2z}^0, \\ &B_{31}^0 = \phi_{3x}^0, && B_{32}^0 = rz^0 K_{yy}^0 n_1 + rK_y^0 s_1 + \phi_{3y}^0, \\ &B_{33}^0 = rK_y^0 n_1 + \phi_{3z}^0. \end{aligned} \tag{3.17}$$

The terms p_1^0, p_2^0, p_3^0 and H_1^0 are p_1, p_2, p_3 and H_1, (see (3.8)) calculated at x^0, y^0, z^0 rather than $\tilde{x}$, $\tilde{y}$, $\tilde{z}$; m_1, n_1, s_1 are specified by (3.14).

Suppose we have distinct eigenvalues λ_j^0 , $j = 1,2,3$, for the unperturbed simple equilibrium E^0. Then $3(\lambda_j^0\ )^2 + 2p_1^0\lambda_j^0\ + p_2^0 \neq 0$ for $j = 1,2,3$. The eigenvalues for the associated perturbed equilibrium E^p are

$$\lambda_j^p\ = \lambda_j^0\ - \frac{b_1^0\ (\lambda_j^0\ )^2 + b_2^0\ \lambda_j^0\ + b_3^0}{3(\lambda_j^0\ )^2 + 2p_1^0\lambda_j^0\ + p_2^0}\varepsilon\ + O(\varepsilon\ ^2),\quad j = 1,2,3. \tag{3.18}$$

Immediately we observe that if λ_j^0 , $j = 1,2,3$, are real and distinct, or if λ_1^0 is real and λ_j^0, $j = 2,3$ are complex with nonzero real part, then so are λ_j^p , $j = 1,2,3$. Additionally, since ε is sufficiently small, the real part of λ_j^p is of the same sign as the real part of λ_j^0, $j = 1,2,3$. In these cases, $E^0(x^0, y^0, z^0)$ and $E^p(x^p, y^p, z^p)$ are of the same (local) nature and stability. However, if λ_1^0 is real and λ_j^0, $j = 2,3$ are purely imaginary; then, λ_1^p is real and of the same sign as λ_1^0, but λ_j^p, $j = 2,3$, are in general complex with nonzero real part. In this case, the nature and stability of E^0 and E^p are not the same.

What if we have repeated eigenvalues of the form $\lambda_1^0 \neq \lambda_2^0 = \lambda_3^0$? The eigenvalues of E^0 satisfy $3(\lambda_j^0)^2 + 2p_1^0\lambda_j^0 + p_2^0 = 0$, $j = 2,3$, but $3(\lambda_1^0)^2 + 2p_1^0\lambda_1^0 + p_2^0 \neq 0$. Equation (3.18) holds for λ_1^p, but for λ_j^p, $j = 2,3$, we get a new expression:

$$\lambda_j^p = \lambda_2^0 + (-1)^j\sqrt{-\frac{b_1^0\,(\lambda_2^0)^2 + b_2^0\,\lambda_2^0 + b_3^0}{3\lambda_2^0 + p_1^0}}\,\varepsilon^{1/2} + O(\varepsilon), \quad j = 2,3. \tag{3.19}$$

Since $\lambda_2^0 = \lambda_3^0$ is a double root of the characteristic equation, $3\lambda_2^0 + p_1^0 \neq 0$, and λ_j^p, $j = 2,3$, are well defined. Clearly λ_j^p, $j = 2,3$, may be real or complex, but will have real part of the same sign as λ_2^0. Since λ_1^p is of the same sign as λ_1^0, E^p and E^0 have the same stability, but not necessarily the same nature.

Finally we look at the case when $\lambda_1^0 = \lambda_2^0 = \lambda_3^0$. Since $(\lambda_1^0)^3 + p_1^0(\lambda_1^0)^2 + p_2^0\lambda_1^0 + p_3^0 = 3(\lambda_1^0)^2 + 2p_1^0\lambda_1^0 + p_2^0 = 3\lambda_1^0 + p_1^0 = 0$, we find

$$\begin{aligned} \lambda_1^p &= \lambda_1^0 + \sqrt[3]{-b_1^0\,(\lambda_1^0)^2 - b_2^0\,\lambda_1^0 - b_3^0}\,\varepsilon^{1/3} + O(\varepsilon^{2/3}), \\ \lambda_j^p &= \lambda_1^0 + [\tfrac{1}{2}\sqrt[3]{b_1^0\,(\lambda_1^0)^2 + b_2^0\,\lambda_1^0 + b_3^0} \\ &\quad + (-1)^j\tfrac{\sqrt{3}}{2}i\sqrt[3]{b_1^0\,(\lambda_1^0)^2 + b_2^0\,\lambda_1^0 + b_3^0}\,]\varepsilon^{1/3} + O(\varepsilon^{2/3}), \quad j = 2,3. \end{aligned} \tag{3.20}$$

The real part of λ_j^p, $j = 1,2,3$, is of the same sign as λ_1^0; however, we get one real and two complex eigenvalues. The nature of E^p and of E^0 are different, but the stability is the same.

The above results are based on the assumption that $b_1^0\,(\lambda_j^0)^2 + b_2^0\,\lambda_j^0 + b_3^0 \neq 0$ for the appropriate values of j in (3.18), (3.19) and (3.20). When this last quantity is zero, higher order calculations must be carried out; we do not consider this here.

Let us consider a couple of examples.

3.4.1 Example 14

When $\varepsilon = 0$ in the perturbed system

$$\begin{aligned} x' &= x(x-2)(8-x) - xy + 6 + \varepsilon\, 7z, \\ y' &= -y + xy - y^2 z + \varepsilon\, x, \\ z' &= -z + \frac{1}{49} y^2 z + \varepsilon\, y, \end{aligned}$$

there are two equilibria in $\text{Int}\Re^3_+$: $E_1^0(\frac{7}{2}+\frac{\sqrt{41}}{2}, 7, \frac{5}{14}+\frac{\sqrt{41}}{14})$ and $E_2^0(3,7,\frac{2}{7})$. For E_1^0 the eigenvalues are $\lambda_1^0 \approx -1.92$, $\lambda_2^0 \approx -6.80$ and $\lambda_3^0 \approx -20.68$. Equilibrium E_1^0 is an asymptotically stable node. For E_2^0, the eigenvalues are $\lambda_1^0 = 8$ and $\lambda_j^0 = (-1)^j i\sqrt{5}$, $j = 2,3$. We know that E_1^p will be an asymptotically stable node, like E_1^0; but we expect E_2^p to have different stability properties than E_2^0. To order $O(\varepsilon)$, we discover $E_2^p(3-\frac{1037}{40}\varepsilon, 7-\frac{343}{4}\varepsilon, \frac{2}{7}-\frac{279}{1960}\varepsilon)$. The eigenvalues are then $\lambda_1^p = 8+\frac{66638}{805}\varepsilon + O(\varepsilon^2)$, and $\lambda_j^p = (-1)^j i\sqrt{5} + [-\frac{311131}{12880} + (-1)^{j+1} i \frac{3136431}{193200}\sqrt{5}]\varepsilon + O(\varepsilon^2)$, $j = 2,3$. For sufficiently small ε, E_2^p is a saddle focus. We show the phase portrait (when $\varepsilon = 0$) for a neighbourhood of E_2^0 in Fig.3.5, and in Fig.3.6 we show the phase portrait (when $\varepsilon = 0.01$) in a neighbourhood of E_2^p.

3.4.2 Example 15

Consider this system:

$$\begin{aligned} x' &= x(x-2)(10-x) - xy + 45 + \varepsilon\, 768z, \\ y' &= -\frac{1}{96}y + \frac{3}{1280}xy - yz + \varepsilon\, \frac{151}{160}y, \\ z' &= -24z + yz - \varepsilon\, \frac{1}{768}x. \end{aligned}$$

There is an equilibrium $E^0(5, 24, \frac{1}{768})$ with eigenvalues $\lambda_1^0 = \frac{1}{2}$, and $\lambda_j^0 = \frac{1}{4}$, $j = 2,3$, when $\varepsilon = 0$. This equilibrium is an unstable node star, and we show a neighbourhood of this point in Fig.3.7. With $\varepsilon > 0$, since we have repeated eigenvalues for E^0, we expect that while E^p will be unstable, it will not be a node star. Indeed this is what we find: $E^p(5+24\varepsilon, 24+5\varepsilon, \frac{1}{768}+\varepsilon)$ has eigenvalues $\lambda_1^p = \frac{1}{2} - \frac{29329}{60}\varepsilon + O(\varepsilon^2)$, $\lambda_j^p = \frac{1}{4} + (-1)^j i \frac{5}{8}\sqrt{\frac{83}{6}}\varepsilon^{1/2} + O(\varepsilon)$, $j = 2,3$; hence, E^p is an unstable node focus. With the value $\varepsilon = 0.001$, we show a neighbourhood of E^p in Fig.3.8.

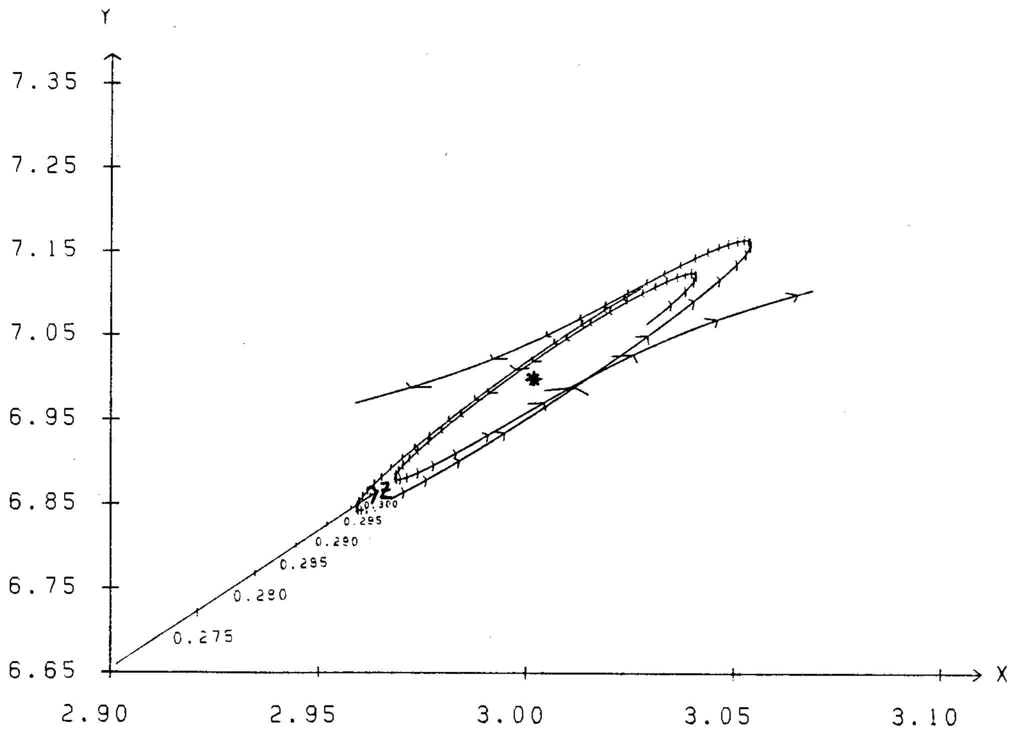

Figure 3.5: Example 14 with $\varepsilon = 0$

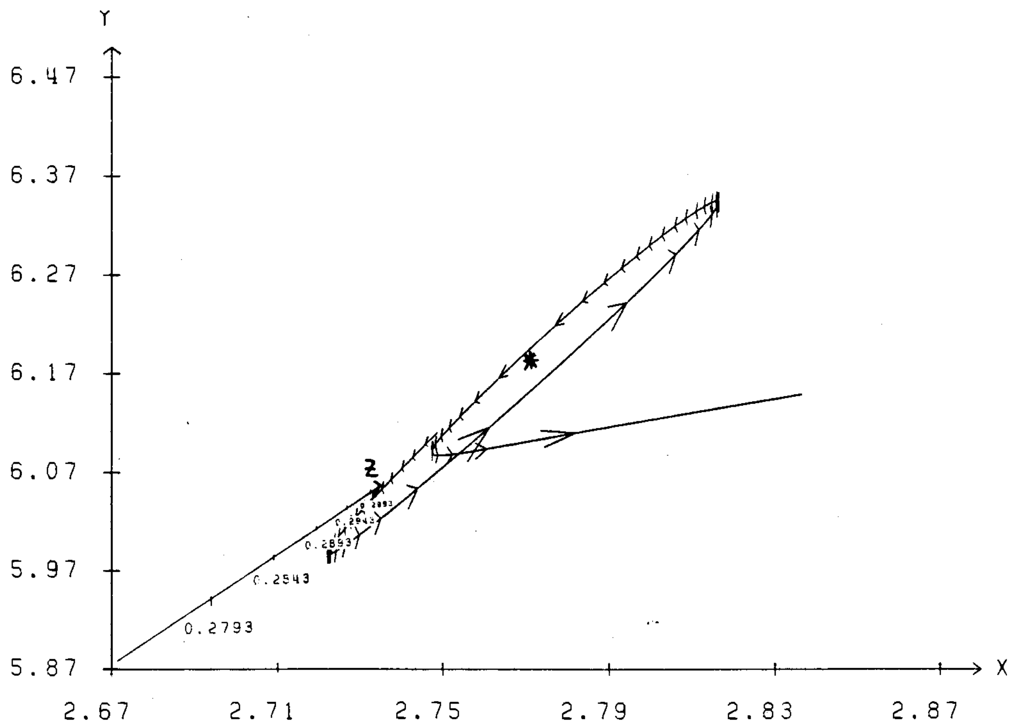

Figure 3.6: Example 14 with $\varepsilon = 0.01$

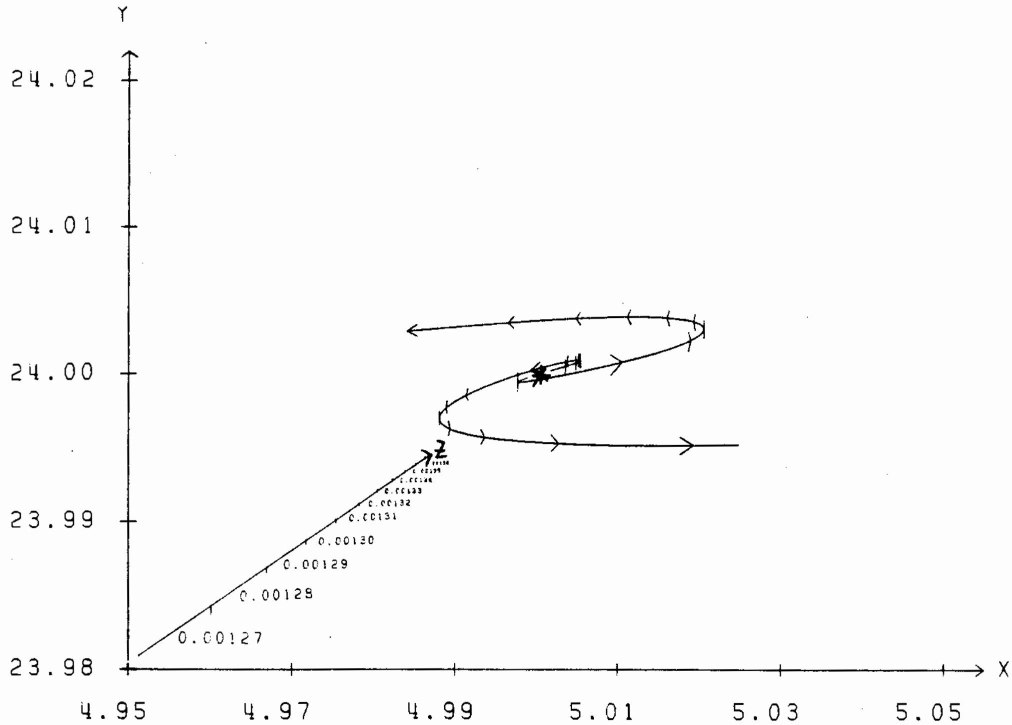

Figure 3.7: Example 15 with ε $= 0$

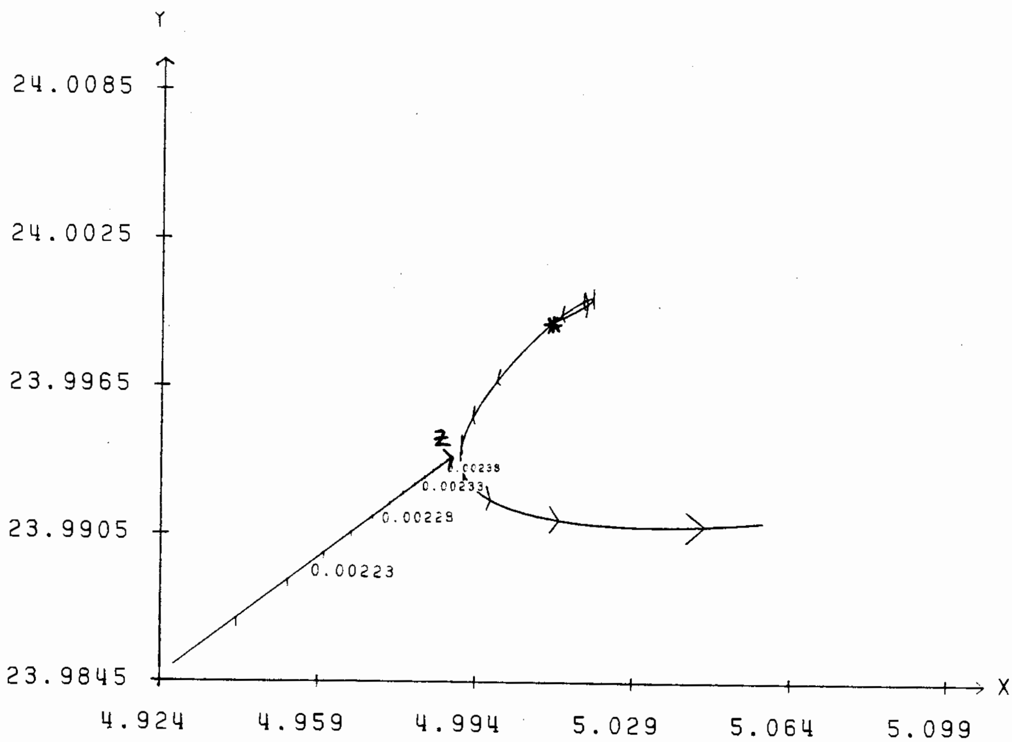

Figure 3.8: Example 15 with ε $= 0.001$

3.5 Bifurcation of a Multiple Equilibrium

We assume $E^c(x^c, y^c, z^c) \in \text{Int}\Re^3_+$ is a double or triple equilibrium of the unperturbed system (3.1). Proceeding as in Section 2.5 by searching for perturbed equilibria $E^*(x^*, y^*, z^*)$ that may be generated by $E^c(x^c, y^c, z^c)$ under the influence of perturbations, we assume x^*, y^*, and z^* are in the form

$$\begin{aligned} x^* &= x^c + \varepsilon^{\mu} m_1 + \varepsilon^{2\mu} m_2 + \varepsilon^{3\mu} m_3 + O(\varepsilon^{4\mu}), \\ y^* &= y^c + \varepsilon^{\mu} n_1 + \varepsilon^{2\mu} n_2 + \varepsilon^{3\mu} n_3 + O(\varepsilon^{4\mu}), \\ z^* &= z^c + \varepsilon^{\mu} s_1 + \varepsilon^{2\mu} s_2 + \varepsilon^{3\mu} s_3 + O(\varepsilon^{4\mu}). \end{aligned} \tag{3.21}$$

Substitution of (3.21) into (3.12) gives us three equations:

$$\begin{aligned} &- n_1 G^c + \varepsilon^{\mu}(-n_2 G^c - m_1 n_1 G^c_x + \tfrac{1}{2} m_1^2 Q^c_{xx}) + \varepsilon^{2\mu}(-n_3 G^c \\ &\quad + m_1 m_2 Q^c_{xx} - n_1 m_2 G^c_x - m_1 n_2 G^c_x + \tfrac{1}{6} m_1^3 Q^c_{xxx} \\ &\quad - \tfrac{1}{2} n_1 m_1^2 G^c_{xx}) + O(\varepsilon^{3\mu}) + \varepsilon^{1-\mu}\phi^c_1 + \varepsilon(m_1 \phi^c_{1x} \\ &\quad + n_1 \phi^c_{1y} + s_1 \phi^c_{1z}) + O(\varepsilon^{1+\mu}) = 0, \\ &by^c G^c_x m_1 + (-a + bG^c - z^c K^c_y) n_1 - K^c s_1 + \varepsilon^{\mu}[by^c G^c_{xx} m_2 \\ &\quad + (-a + bG^c - z^c K^c_y) n_2 - K^c s_2 + bG^c_x m_1 n_1 - K^c_y n_1 s_1 \\ &\quad + \tfrac{1}{2} by^c G^c_{xx} m_1^2 - \tfrac{1}{2} z^c K^c_{yy} n_1^2] + \varepsilon^{2\mu}[by^c G^c_x m_3 + (-a + bG^c \\ &\quad - z^c K^c_y) n_3 - K^c s_3 + by^c G^c_{xx} m_1 m_2 + bG^c_x n_1 m_2 \\ &\quad + bG^c_x m_1 n_2 - z^c K^c_{yy} n_1 n_2 - K^c_y n_2 s_1 - K^c_y n_1 s_2 \\ &\quad + \tfrac{1}{2} bG^c_{xx} n_1 m_1^2 - \tfrac{1}{2} K^c_{yy} s_1 n_1^2 + \tfrac{1}{6} by^c G^c_{xxx} m_1^3 \\ &\quad - \tfrac{1}{6} z^c K^c_{yyy} n_1^3] + O(\varepsilon^{3\mu}) + \varepsilon^{1-\mu}\phi^c_2 + \varepsilon(m_1 \phi^c_{2x} \\ &\quad + n_1 \phi^c_{2y} + s_1 \phi^c_{2z}) + O(\varepsilon^{1+\mu}) = 0, \\ &rz^c K^c_y n_1 + \varepsilon^{\mu}(rz^c K^c_y n_2 + rK^c_y n_1 s_1 + \tfrac{1}{2} rz^c K^c_{yy} n_1^2) \\ &\quad + \varepsilon^{2\mu}(rz^c K^c_y n_3 + rz^c K^c_{yy} n_1 n_2 + rK^c_y n_2 s_1 \\ &\quad + rK^c_y n_1 s_2 + \tfrac{1}{2} rK^c_{yy} s_1 n_1^2 + \tfrac{1}{6} rz^c K^c_{yyy} n_1^3) \\ &\quad + O(\varepsilon^{3\mu}) + \varepsilon^{1-\mu}\phi^c_3 + \varepsilon(m_1 \phi^c_{3x} \\ &\quad + n_1 \phi^c_{3y} + s_1 \phi^c_{3z}) + O(\varepsilon^{1+\mu}) = 0. \end{aligned} \tag{3.22}$$

With μ known, we set successive coefficients of powers of ε to zero, producing a series of systems of equations which we use to solve for m_1, n_1, s_1. Using the terms

$$\begin{aligned} D_1 &= rz^c K_y^c \phi_1^c + G^c \phi_3^c, \\ D_2 &= K^c (G_x^c \phi_3^c + G^c \phi_{3x}^c + rz^c K_y^c \phi_{1x}^c) \\ &\quad + by^c G_x^c (rK_y^c \phi_1^c + G^c \phi_{3z}^c + rz^c K_y^c \phi_{1z}^c), \\ Q_{xx}^c &= x^c F_{xx}^c + 2F_x^c - y^c G_{xx}^c, \\ Q_{xxx}^c &= x^c F_{xxx}^c + 3F_{xx}^c - y^c G_{xxx}^c, \end{aligned} \tag{3.23}$$

we have evaluated five cases.

(i) $Q_{xx}^c \neq 0$, $D_1 = 0$. Equilibrium E^c is a double equilibrium since $Q_{xx}^c \neq 0$ (see (3.10)). We use $\mu = 1$ in (3.21). From the equations resulting from (3.22), we derive

$$c_1 m_1^2 + c_2 m_1 + c_3 = 0, \tag{3.24}$$

where

$$\begin{aligned} c_1 &= \tfrac{1}{2} rz^c K_y^c Q_{xx}^c, \\ c_2 &= G_x^c \phi_3^c + rz^c K_y^c \phi_{1x}^c + G^c \phi_{3x}^c + \frac{by^c G_x^c}{K^c}(rK_y^c \phi_1^c \\ &\quad + rz^c K_y^c \phi_{1z}^c + G^c \phi_{3z}^c), \\ c_3 &= \phi_1^c \phi_{3y}^c - \phi_3^c \phi_{1y}^c + \frac{rz^c K_{yy}^c (\phi_1^c)^2}{2G^c} + \frac{1}{K^c}(rK_y^c \phi_1^c + rz^c K_y^c \phi_{1z}^c \\ &\quad + G^c \phi_{3z}^c)[\frac{\phi_1^c}{G^c}(-a + bG^c - z^c K_y^c) + \phi_2^c]. \end{aligned} \tag{3.25}$$

If $c_2^2 - 4c_1c_3 > 0$, there are two perturbed equilibria given to $O(\varepsilon)$ by $E_j^*(x^c + \varepsilon m_{1j}, y^c + \varepsilon n_1, z^c + \varepsilon s_{1j})$, $j = 1, 2$, where

$$m_{1j} = \frac{1}{2c_1}[-c_2 + (-1)^j \sqrt{c_2^2 - 4c_1c_3}], \quad n_1 = \frac{\phi_1^c}{G^c},$$
$$s_{1j} = \frac{1}{K^c}\{\phi_2^c + \frac{\phi_1^c}{G^c}(-a + bG^c - z^c K_y^c) + \frac{by^c G_x^c}{2c_1}[-c_2 + (-1)^j \sqrt{c_2^2 - 4c_1c_3}]\}.$$

If $c_2^2 - 4c_1c_3 < 0$, the double equilibrium vanishes under the influence of perturbations. For $c_2^2 - 4c_1c_3 = 0$, it is necessary to go to higher order terms.

(ii) $Q_{xx}^c \neq 0$, $D_1 \neq 0$. As in (i) above, E^c is a double equilibrium, but now we should use $\mu = \frac{1}{2}$; with this we obtain the equation

$$c_1 m_1^2 + D_1 = 0.$$

Constant c_1 is given in (3.25) and D_1 is defined in (3.23). Two equilibria result when $c_1 D_1 < 0$: $E_j^*(x^c + m_{1j}\,\varepsilon^{1/2}, y^c, z^c + s_{1j}\,\varepsilon^{1/2})$, $j = 1, 2$;

$$m_{1j} = (-1)^j \sqrt{-\frac{D_1}{c_1}}, \quad s_{1j} = (-1)^j \frac{by^c\, G_x^c}{K^c} \sqrt{-\frac{D_1}{c_1}}.$$

Note that we have only given E_j^* to $O(\varepsilon^{1/2})$ and $n_1 = 0$. When $c_1 D_1 > 0$, the double equilibrium disappears. The conditions for this case guarantee that $c_1 D_1 \neq 0$.

(iii) $Q_{xx}^c = 0$, $Q_{xxx}^c \neq 0$, $D_1 \neq 0$. Now we must use $\mu = \frac{1}{3}$ for the triple equilibrium E^c. The equation which determines m_1 is found to be

$$M m_1^3 + D_1 = 0. \tag{3.26}$$

Of course, D_1 is as usual, and M is

$$M = \frac{1}{6} r z^c\, K_y^c\, Q_{xxx}^c\,. \tag{3.27}$$

Only one equilibrium results in this case, which to $O(\varepsilon^{1/3})$ is $E^*(x^c + m_1\,\varepsilon^{1/3}, y^c, z^c + s_1\,\varepsilon^{1/3})$, with

$$m_1 = \sqrt[3]{-\frac{D_1}{M}}, \quad s_1 = \frac{by^c\, G_x^c}{K^c} \sqrt[3]{-\frac{D_1}{M}}.$$

(iv) $Q_{xx}^c = 0$, $Q_{xxx}^c \neq 0$, $D_1 = 0$, $D_2 = 0$. We again use $\mu = \frac{1}{3}$, so (3.26) holds; but, since $M \neq 0$ and $D_1 = 0$, $m_1 = 0$. We also find $n_1 = s_1 = 0$. The equation for m_2 is

$$M m_2^3 + c_3 = 0,$$

with M and c_3 respectively found in (3.27) and (3.25). Thus similarly to case **(iii)** above, there is one and only one perturbed equilibrium resulting from E^c. To $O(\varepsilon^{2/3})$, this equilibrium is $E^*(x^c + m_2\,\varepsilon^{2/3}, y^c, z^c + s_2\,\varepsilon^{2/3})$, where

$$m_2 = \sqrt[3]{-\frac{c_3}{M}}, \quad s_2 = \frac{by^c\, G_x^c}{K^c} \sqrt[3]{-\frac{c_3}{M}}.$$

(v) $Q^c_{xx} = 0$, $Q^c_{xxx} \neq 0$, $D_1 = 0$, $D_2 \neq 0$. Once again we are dealing with a triple equilibrium, but now we use $\mu = \frac{1}{2}$. This value of μ yields the equation

$$m_1 \left(K^c M m_1^2 + D_2\right) = 0, \tag{3.28}$$

where M is specified by (3.27), and D_2 is defined in (3.23). Note that $K^c M \neq 0$ and $D_2 \neq 0$. The value $m_1 = 0$ is always one real root of (3.28). With $m_1 = 0$, we find that $n_1 = s_1 = 0$, so we try to find the next higher order terms. Calculations give us equation (3.24) with m_2 in place of m_1. Since $c_1 = 0$ due to the assumption $Q^c_{xx} = 0$, we have

$$c_2 m_2 + c_3 = 0.$$

Provided we do not have $c_2 = 0$, $c_3 \neq 0$, this case always gives rise to at least one perturbed equilibrium: $E_1^*(x^c + m_2\,\varepsilon, y^c + n_2\,\varepsilon, z^c + s_2\,\varepsilon)$, with

$$m_2 = -\frac{c_3}{c_2}, \quad n_2 = \frac{\phi_1^c}{G^c}, \quad s_2 = \frac{1}{K^c}[-by^c\, G_x^c\, \frac{c_3}{c_2} + (-a + bG^c - z^c\, K_y^c)\frac{\phi_1^c}{G^c} + \phi_2^c\,].$$

Reexamining (3.28), two more perturbed equilibria arise when $K^c M D_2 < 0$: to $O(\varepsilon^{1/2})$ these are $E_j^*(x^c + m_{1j}\,\varepsilon^{1/2}, y^c, z^c + s_{1j}\,\varepsilon^{1/2})$, $j = 2, 3$, where

$$m_{1j} = (-1)^j\sqrt{-\frac{D_2}{K^c M}}, \quad s_{1j} = (-1)^j\frac{by^c\, G_x^c}{K^c}\sqrt{-\frac{D_2}{K^c M}}.$$

These two equilibria disappear if $K^c M D_2 > 0$, leaving only E_1^*. Further study is required if $c_2 c_3 = 0$.

3.6 Nature of the Perturbed Multiple Equilibria

In Section 3.5, we only needed the values $\mu = 1$, $\mu = \frac{1}{2}$ and $\mu = \frac{1}{3}$ for (3.21). In this section, we consider only these three cases.

(i) $\mu = 1$. In case (i) of the previous Section, we found perturbed equilibria given to order $O(\varepsilon)$ by $E^*(x^c + m_1\,\varepsilon, y^c + n_1\,\varepsilon, z^c + s_1\,\varepsilon)$. Such an equilibrium has characteristic equation

$$\lambda^3 + H_1^c\lambda^2 + H_2^c\lambda + \varepsilon\,(b_1^c\lambda^2 + b_2^c\lambda + b_3^c) = 0,$$

where b_1^c, b_2^c and b_3^c are b_1^0, b_2^0 and b_3^0 (see (3.16) and (3.17)) with superscript 0 replaced by superscript c, and H_1^c and H_2^c are H_1 and H_2 (see (3.8)) evaluated at (x^c, y^c, z^c) rather than at $(\tilde{x}, \tilde{y}, \tilde{z})$. Note that the term Q_x^c appearing in b_2^c and b_3^c is identically zero.

Suppose the eigenvalues for E^c are $\lambda_1^c = 0$ and λ_2^c, λ_3^c. If $\lambda_2^c \neq \lambda_3^c$, the eigenvalues for E^* are

$$\lambda_1^* = -\frac{b_3^c}{H_2^c}\varepsilon + O(\varepsilon^2), \quad \lambda_j^* = \lambda_j^c - \frac{b_1^c(\lambda_j^c)^2 + b_2^c\lambda_j^c + b_3^c}{3(\lambda_j^c)^2 + 2H_1^c\lambda_j^c + H_2^c}\varepsilon + O(\varepsilon^2), \quad j = 2,3;$$

while, if $\lambda_2^c = \lambda_3^c$, they are

$$\lambda_1^* = -\frac{b_3^c}{H_2^c}\varepsilon + O(\varepsilon^2), \quad \lambda_j^* = \lambda_2^c + (-1)^j\sqrt{-\frac{b_1^c(\lambda_2^c)^2 + b_2^c\lambda_2^c + b_3^c}{3\lambda_2^c + H_1^c}}\,\varepsilon^{1/2} + O(\varepsilon), \quad j = 2,3.$$

Of course, if $b_3^c = 0$ or $b_1^c(\lambda_2^c)^2 + b_2^c\lambda_2^c + b_3^c = 0$ it is necessary to study higher order terms; we do not do this here.

(ii) $\mu = \frac{1}{2}$. Perturbed equilibria to $O(\varepsilon^{1/2})$ of the type $E^*(x^c + m_1\varepsilon^{1/2}, y^c, z^c + s_1\varepsilon^{1/2})$ arose from a double equilibrium in case **(ii)** of Section 3.5. We calculate the characteristic equation at such a point to be

$$\lambda^3 + H_1^c\lambda^2 + H_2^c\lambda + \varepsilon^{1/2}(b_1^d\lambda^2 + b_2^d\lambda + b_3^d) + O(\varepsilon) = 0.$$

Expressions b_j^d, $j = 1,2,3$ are:

$$\begin{aligned}
&b_1^d = -B_{11}^d - B_{22}^d, && b_2^d = -H_1^c B_{11}^d - by^c G_x^c B_{12}^d + G^c B_{21}^d + K^c B_{32}^d,\\
&b_3^d = -rz^c K^c K_y^c B_{11}^d; && B_{11}^d = Q_{xx}^c m_1,\\
&B_{12}^d = -G_x^c m_1, && B_{21}^d = by^c G_{xx}^c m_1,\\
&B_{22}^d = bG_x^c m_1 - K_y^c s_1, && B_{32}^d = rK_y^c s_1.
\end{aligned} \tag{3.29}$$

Similarly to the discussion in case **(i)** above, there are two possibilities for the characteristic values:

$$\lambda_1^* = -\frac{b_3^d}{H_2^c}\varepsilon^{1/2} + O(\varepsilon), \quad \lambda_j^* = \lambda_j^c - \frac{b_1^d(\lambda_j^c)^2 + b_2^d\lambda_j^c + b_3^d}{3(\lambda_j^c)^2 + 2H_1^c\lambda_j^c + H_2^c}\varepsilon^{1/2} + O(\varepsilon), \quad \text{or}$$

$$\lambda_1^* = -\frac{b_3^d}{H_2^c}\varepsilon^{1/2} + O(\varepsilon), \quad \lambda_j^* = \lambda_2^c + (-1)^j\sqrt{-\frac{b_1^d(\lambda_2^c)^2 + b_2^d\lambda_2^c + b_3^d}{3\lambda_2^c + H_1^c}}\,\varepsilon^{1/4} + O(\varepsilon^{1/2}),$$

where $j = 2,3$. The first are for when $\lambda_2^c \neq \lambda_3^c$, the second for when $\lambda_2^c = \lambda_3^c$. Since we are dealing with a double equilibrium, $Q_{xx}^c \neq 0$ and thus $b_3^d \neq 0$.

When we have a triple equilibrium (case **(v)** of Section 3.6) we do have $b_3^d = 0$ because $Q_{xx}^c = 0$. It is therefore necessary to know E^* to $O(\varepsilon)$: $E^*(x^c + m_1 \varepsilon^{1/2} + m_2 \varepsilon, y^c + n_2 \varepsilon, z^c + s_1 \varepsilon^{1/2} + s_2 \varepsilon)$. In case **(v)** of Section 3.6, we have done this explicitly for E_1^*; for E_2^* and E_3^* we now assume that m_2, n_2, and s_2 have been calculated. The characteristic equation to $O(\varepsilon)$ is then

$$\lambda^3 + H_1^c\lambda^2 + H_2^c\lambda + \varepsilon^{1/2}(b_1^d\lambda^2 + b_2^d\lambda) + \varepsilon(b_1^e\lambda^2 + b_2^e\lambda + b_3^e) = 0.$$

The terms b_1^d and b_2^d are given in (3.29), but now $Q_{xx}^c = 0$, so $B_{11}^d = 0$ also. We give b_j^e, $j = 1,2,3$ below:

$$\begin{aligned} b_1^e &= -B_{11}^e - B_{22}^e - B_{33}^e, \\ b_2^e &= -H_1^c(B_{11}^e + B_{33}^e) - by^c G_x^c B_{12}^e + G^c B_{21}^e - rz^c K_y^c B_{23}^e + K^c B_{32}^e - B_{12}^d B_{21}^d, \\ b_3^e &= -rz^c K^c K_y^c B_{11}^e - bry^c z^c G_x^c K_y^c B_{13}^e - G^c K^c B_{31}^e - by^c G^c G_x^c B_{33}^e; \end{aligned}$$

$$B_{11}^e = \tfrac{1}{2}Q_{xxx}^c m_1^2 - G_x^c n_2 + \phi_{1x}^c, \quad B_{12}^e = -\tfrac{1}{2}G_{xx}^c m_1^2 - G_x^c m_2 + \phi_{1y}^c,$$
$$B_{13}^e = \phi_{1z}^c, \quad B_{21}^e = \tfrac{1}{2}by^c G_{xxx}^c m_1^2 + by^c G_{xx}^c m_2 + bG_x^c n_2 + \phi_{2x}^c,$$
$$B_{22}^e = \tfrac{1}{2}bG_{xx}^c m_1^2 + bG_x^c m_2 - z^c K_{yy}^c n_2 - K_y^c s_2 + \phi_{2y}^c, \quad B_{23}^e = -K_y^c n_2 + \phi_{2z}^c,$$
$$B_{31}^e = \phi_{3x}^c, \quad B_{32}^e = rz^c K_{yy}^c n_2 + rK_y^c s_2 + \phi_{3y}^c, \quad B_{33}^e = rK_y^c n_2 + \phi_{3z}^c.$$

Note that B_{12}^d and B_{21}^d are found in (3.29).

If $\lambda_2^c \neq \lambda_3^c$, the eigenvalues for E^* are

$$\lambda_1^* = -\frac{b_3^e}{H_2^c}\varepsilon + O(\varepsilon^{3/2}), \quad \lambda_j^* = \lambda_j^c - \frac{b_1^d(\lambda_j^c)^2 + b_2^d\lambda_j^c}{3(\lambda_j^c)^2 + 2H_1^c\lambda_j^c + H_2^c}\varepsilon^{1/2} + O(\varepsilon), \quad j = 2,3.$$

On the other hand, if $\lambda_2^c = \lambda_3^c$, the eigenvalues are

$$\lambda_1^* = -\frac{b_3^e}{H_2^c}\varepsilon + O(\varepsilon^{3/2}), \quad \lambda_j^* = \lambda_2^c + (-1)^j\sqrt{-\frac{b_1^d(\lambda_2^c)^2 + b_2^d\lambda_2^c}{3\lambda_2^c + H_1^c}}\,\varepsilon^{1/4} + O(\varepsilon^{1/2}), \quad j = 2,3.$$

(iii) $\mu = \frac{1}{3}$. Suppose $E^*(x^c + m_1 \varepsilon^{1/3} + m_2 \varepsilon^{2/3}, y^c, z^c + s_1 \varepsilon^{1/3} + s_2 \varepsilon^{2/3})$ is the perturbed equilibrium we are studying. Coefficients m_1 and s_1 have been calculated for this point in case **(iii)** of Section3.5. Assuming we know m_2 and s_2,

$$\lambda^3 + H_1^c\lambda^2 + H_2^c\lambda + \varepsilon^{1/3}(b_1^d\lambda^2 + b_2^d\lambda) + \varepsilon^{2/3}(b_1^f\lambda^2 + b_2^f\lambda + b_3^f) + O(\varepsilon) = 0$$

is the characteristic equation with terms b_1^d and b_2^d given in (3.29) (of course, $Q_{xx}^c = B_{11}^d = 0$ here), and:

$$b_1^f = -B_{11}^f - B_{22}^f, \quad b_2^f = -H_1^c B_{11}^f - by^c\, G_x^c\, B_{12}^f + G^c\, B_{21}^f + K^c\, B_{32}^f - B_{12}^d B_{21}^d,$$
$$b_3^f = -rz^c\, K^c\, K_y^c\, B_{11}^f; \quad B_{11}^f = \tfrac{1}{2} Q_{xxx}^c\, m_1^2\,,$$
$$B_{12}^f = -G_x^c\, m_2 - \tfrac{1}{2} G_{xx}^c\, m_1^2\,, \quad B_{21}^f = by^c\, G_{xx}^c\, m_2 + \tfrac{1}{2} by^c\, G_{xxx}^c\, m_1^2\,,$$
$$B_{22}^f = bG_x^c\, m_2 - K_y^c\, s_2 + \tfrac{1}{2} bG_{xx}^c\, m_1^2\,, \quad B_{32}^f = rK_y^c\, s_2\,.$$

The eigenvalues may be given by one of two expressions:

$$\lambda_1^* = -\frac{b_3^f}{H_2^c}\varepsilon^{2/3} + O(\varepsilon), \quad \lambda_j^* = \lambda_j^c - \frac{b_1^d(\lambda_j^c)^2 + b_2^d\lambda_j^c}{3(\lambda_j^c)^2 + 2H_1^c\lambda_j^c + H_2^c}\varepsilon^{1/3} + O(\varepsilon^{2/3}), \quad \text{or}$$
$$\lambda_1^* = -\frac{b_3^f}{H_2^c}\varepsilon^{2/3} + O(\varepsilon), \quad \lambda_j^* = \lambda_2^c + (-1)^j\sqrt{-\frac{b_1^d(\lambda_2^c)^2 + b_2^d\lambda_2^c}{3\lambda_2^c + H_1^c}}\,\varepsilon^{1/6} + O(\varepsilon^{1/3}),$$

where $j = 2, 3$. The first set of eigenvalues is for the case $\lambda_2^c \neq \lambda_3^c$, the second for the case $\lambda_2^c = \lambda_3^c$.

Finally, case **(iv)** of Section 3.5 gave rise to a perturbed equilibrium to $O(\varepsilon)$ given by $E^*(x^c + m_2\,\varepsilon^{2/3} + m_3\,\varepsilon, y^c + n_3\,\varepsilon, z^c + s_2\,\varepsilon^{2/3} + s_3\,\varepsilon)$. With the expressions:

$$b_1^g = -B_{22}^g, \quad b_2^g = -by^c\, G_x^c\, B_{12}^g + G^c\, B_{21}^g + K^c\, B_{32}^g;$$
$$B_{12}^g = -G_x^c\, m_2\,, \quad B_{21}^g = by^c\, G_{xx}^c\, m_2\,, \quad B_{22}^g = bG_x^c\, m_2 - K_y^c\, s_2\,, \quad B_{32}^g = rK_y^c\, s_2\,;$$
$$b_3^h = -rz^c\, K^c\, K_y^c\, B_{11}^h - bry^c\, z^c\, G_x^c\, K_y^c\, B_{13}^h - G^c\, K^c\, B_{31}^h - by^c\, G^c\, G_x^c\, B_{33}^h;$$
$$B_{11}^h = -G_x^c\, n_3 + \phi_{1x}^c\,, \quad B_{13}^h = \phi_{1z}^c\,, \quad B_{31}^h = \phi_{3x}^c\,, \quad B_{33}^h = rK_y^c\, n_3 + \phi_{3z}^c\,;$$

we find that either the eigenvalue are

$$\lambda_1^* = -\frac{b_3^h}{H_2^c}\varepsilon + O(\varepsilon^{5/3}), \quad \lambda_j^* = \lambda_j^c - \frac{b_1^g(\lambda_j^c)^2 + b_2^g\lambda_j^c}{3(\lambda_j^c)^2 + 2H_1^c\lambda_j^c + H_2^c}\varepsilon^{2/3} + O(\varepsilon), \quad j = 2, 3,$$

when $\lambda_2^c \neq \lambda_3^c$, or

$$\lambda_1^* = -\frac{b_3^h}{H_2^c}\varepsilon + O(\varepsilon^{5/3}), \quad \lambda_j^c = \lambda_2^c + (-1)^j\sqrt{-\frac{b_1^g(\lambda_2^c)^2 + b_2^g\lambda_2^c}{3\lambda_2^c + H_1^c}}\,\varepsilon^{1/3} + O(\varepsilon^{2/3}), \quad j = 2, 3,$$

when $\lambda_2^c = \lambda_3^c$.

We will now illustrate some of the results of the last two sections with a couple of examples.

3.6.1 Example 16

To the model given in Example 12, let us add the perturbational terms $\phi_1(x,y,z) = \frac{1}{3}x^2$, $\phi_2(x,y,z) = 1$ and $\phi_3(x,y,z) = -z$, which gives us the system

$$\begin{aligned} x\prime &= x(x-2)(7-x) - xy + 27 + \varepsilon\, \frac{1}{3}x^2, \\ y\prime &= -y + xy - yz + \varepsilon\,, \\ z\prime &= -13z + yz - \varepsilon\, z. \end{aligned}$$

For $\varepsilon = 0$ there is a triple equilibrium $E^c(3,13,2)$. For convenience, we show a neighbourhood of this triple equilibrium in Fig.3.9, which is the same as Fig.3.3. Considering now $\varepsilon > 0$, we calculate that $D_1 = 0$, $D_2 = 26$ and $K^c\, MD_2 = -676$; thus we are in case (v) of Section 3.5 and we expect to get three perturbed equilibria since $K^c\, MD_2 < 0$. Giving the calculations only to $O(\varepsilon)$, we find: The equilibria are $E_1^*(3, 13+\varepsilon, 2+\frac{1}{13}\varepsilon)$, $E_2^*(3+\varepsilon^{1/2}+\frac{1}{6}\varepsilon, 13+\varepsilon, 2+\varepsilon^{1/2}+\frac{19}{78}\varepsilon)$ and $E_3^*(3-\varepsilon^{1/2}+\frac{1}{6}\varepsilon, 13+\varepsilon, 2-\varepsilon^{1/2}+\frac{19}{78}\varepsilon)$. For E_1^*, the characteristic equation is $\lambda^3 + 65\lambda + \varepsilon(-\frac{12}{13}\lambda^2 + 6\lambda - 26) = 0$, which has eigenvalues $\lambda_1^* = \frac{2}{5}\varepsilon$, $\lambda_j^* = (-1)^j i\sqrt{65} + \varepsilon\,[\frac{17}{65} + (-1)^j i\frac{3}{65}\sqrt{65}]$, $j = 2,3$. Equilibrium E_1^* is an unstable node focus. For E_s^*, $s = 2,3$, the characteristic equation is $\lambda^3 + 65\lambda + (-1)^s\varepsilon^{1/2}26\lambda + \varepsilon(\frac{27}{13}\lambda^2 + \frac{31}{3}\lambda + 52) = 0$; thus, E_2^* has eigenvalues $\lambda_1^* = -\frac{4}{5}\varepsilon$, $\lambda_j^* = (-1)^j i\sqrt{65} + (-1)^j i\frac{1}{5}\sqrt{65}\varepsilon^{1/2} + [-\frac{83}{130} + (-1)^j i\frac{58}{975}\sqrt{65}]\varepsilon$, $j = 2,3$, and E_3^* has eigenvalues $\lambda_1^* = -\frac{4}{5}\varepsilon$, $\lambda_j^* = (-1)^j i\sqrt{65} + (-1)^{j+1} i\frac{1}{5}\sqrt{65}\varepsilon^{1/2} + [-\frac{83}{130} + (-1)^j i\frac{58}{975}\sqrt{65}]\varepsilon$, $j = 2,3$. We conclude that E_2^* and E_3^* are asymptotically stable node foci. In Fig.3.10 we show the phase portrait about the three perturbed equilibria resulting when we use the value $\varepsilon = 0.1$

3.6.2 Example 17

Consider the system

$$\begin{aligned} x\prime &= x(x-1)(3-x) - xy + \frac{50}{27} + \varepsilon\, 2y, \\ y\prime &= -3y + 3xy - y^2z + \varepsilon\, x, \\ z\prime &= -4z + y^2z + \varepsilon\, 12z. \end{aligned}$$

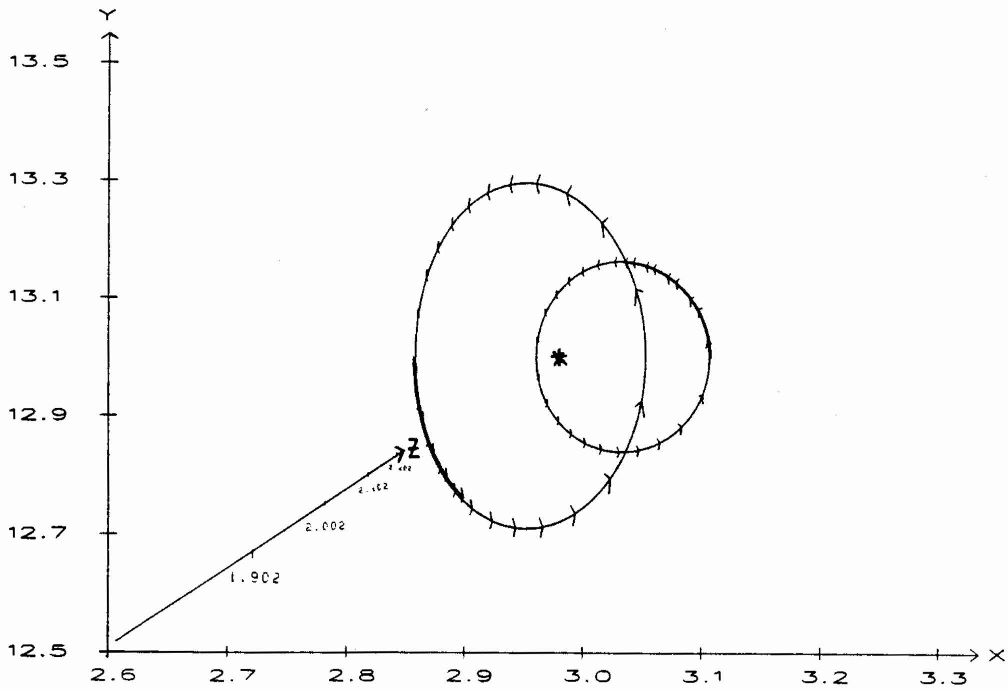

Figure 3.9: Example 16 with $\varepsilon = 0$

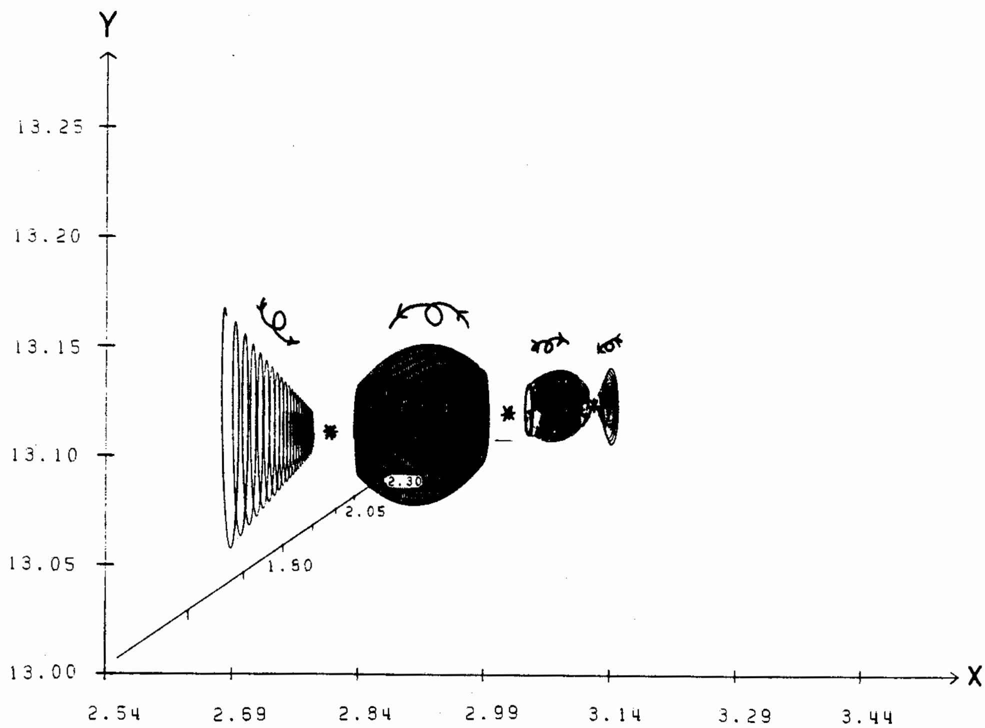

Figure 3.10: Example 16 with $\varepsilon = 0.1$

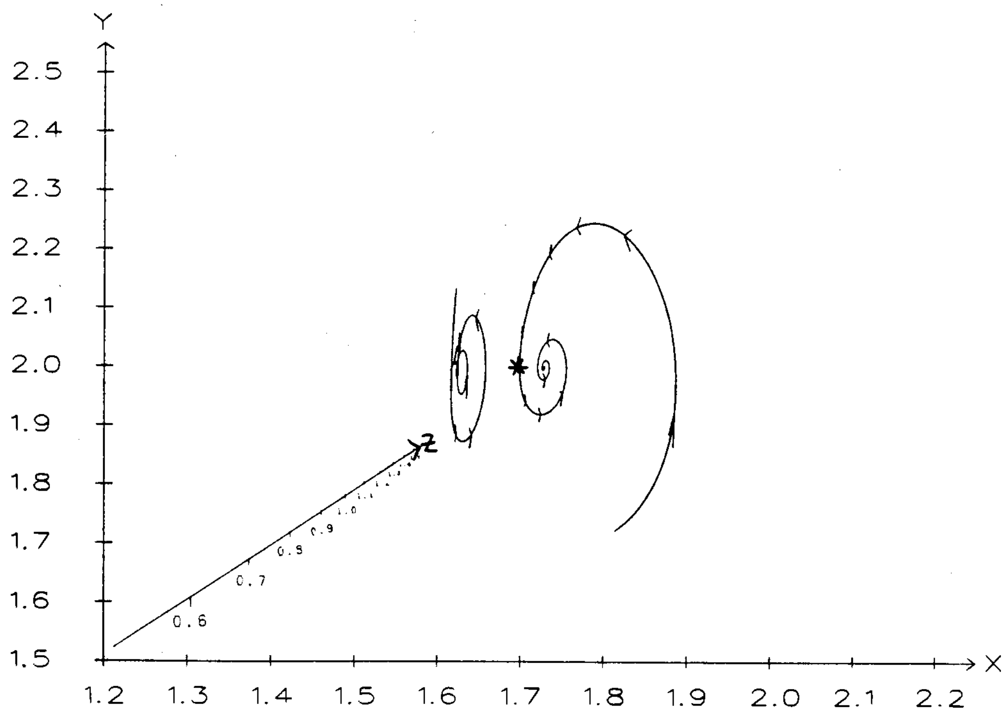

Figure 3.11: Example 17 with $\varepsilon\ = 0$

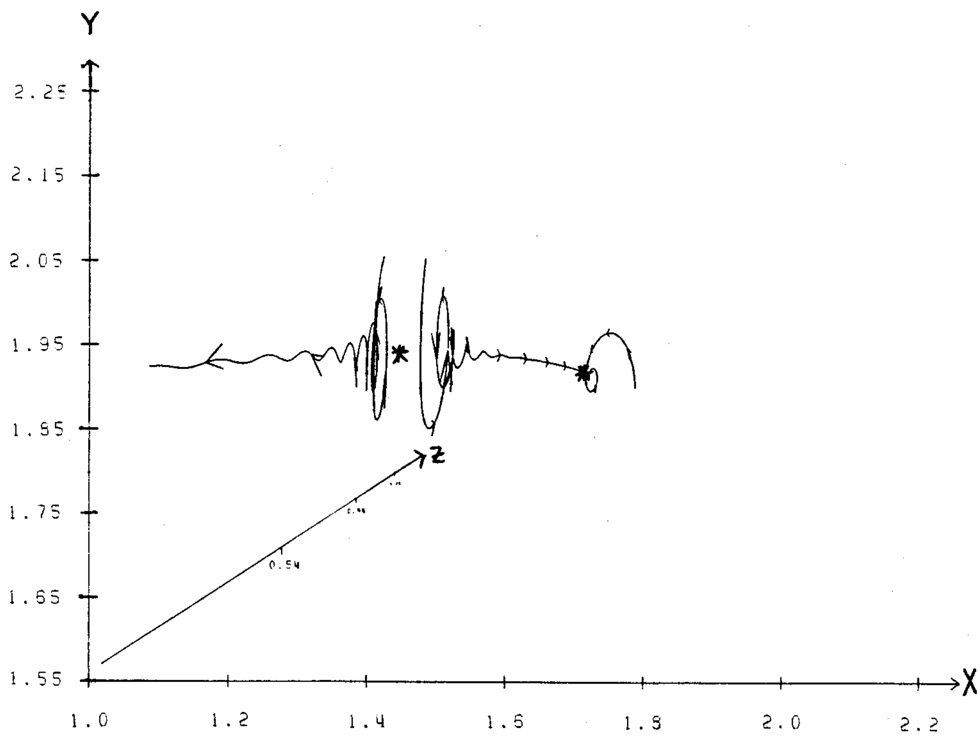

Figure 3.12: Example 17 with $\varepsilon\ = 0.01$

This is just the system given in Example 13 with additional perturbed terms $\phi_1(x,y,z) = 2y$, $\phi_2(x,y,z) = x$ and $\phi_3(x,y,z) = 12z$. When $\varepsilon = 0$, we know from Example 13 that there is a double equilibrium at $E^c(\frac{5}{3}, 2, 1)$; this is shown in Fig.3.11, which is the same as Fig.3.4. Since this is a double equilibrium, and since $D_1 = 36$, we are in case **(ii)** of Section 3.5. We calculate that E^c bifurcates into the perturbed equilibria $E_1^*(\frac{5}{3} - 3\varepsilon^{1/2}, 2, 1 - \frac{9}{2}\varepsilon^{1/2})$ and $E_2^*(\frac{5}{3} + 3\varepsilon^{1/2}, 2, 1 + \frac{9}{2}\varepsilon^{1/2})$, which have characteristic equation $\lambda^3 + 2\lambda^2 + 26\lambda + (-1)^s\varepsilon^{1/2}(15\lambda^2 + 102\lambda + 96) = 0$, $s = 1, 2$. The eigenvalues of this equation, for E_1^*, are $\lambda_1^* = \frac{48}{13}\varepsilon^{1/2}$, $\lambda_j^* = -1 + (-1)^j 5i + [\frac{147}{26} + (-1)^{j+1}\frac{1083}{130}i]\varepsilon^{1/2}$, $j = 2, 3$. The eigenvalues for E_2^* are in turn $\lambda_1^* = -\frac{48}{13}\varepsilon^{1/2}$, $\lambda_j^* = -1 + (-1)^j 5i + [-\frac{147}{26} + (-1)^j \frac{1083}{130}i]\varepsilon^{1/2}$, $j = 2, 3$. Equilibrium E_1^* is a saddle focus while E_2^* is an asymptotically stable node focus. We show a neighbourhood of these two perturbed equilibria in Fig.3.12, the calculations for which have been carried out using the value $\varepsilon = 0.01$.

3.7 Tables

We present two tables that summarize the effect of perturbations on simple and multiple equilibria of the unperturbed system. As for the two-species model, the local stability properties of hyperbolic equilibria (nodes, saddle nodes, node foci, saddle foci, node stars, saddle stars, and stars) are unaffected by perturbations. Nonhyperbolic equilibria (vortex foci, double and triple equilibria) may experience a change in stability properties when subjected to perturbations.

$E^0(x^0, y^0, z^0)$	$E^p(x^p, y^p, z^p)$	Changes in Nature, Stability
Node	Node	No Changes
Saddle Node	Saddle Node	No Changes
Node Focus	Node Focus	No Changes
Saddle Focus	Saddle Focus	No Changes
Node Star	Node or Node Focus	Only Nature Changes
Saddle Star	Saddle Node or Saddle Focus	Only Nature Changes
Star	Node Focus	Only Nature Changes
Vortex Focus of Linearized System	Node Focus or Saddle Focus	Nature and Stability May Change

Table 3.1: Perturbations of a Simple Equilibrium

Multiplicity of $E^c(x^c, y^c, z^c)$	μ	Number of Perturbed Equilibria	Nature of $E^*(x^*, y^*, z^*)$
Double	1	0	May be a Node, a Saddle Node, a Node Focus, or a Saddle Focus
		2	
	$\frac{1}{2}$	0	
		2	
Triple	$\frac{1}{2}$	1	
		3	
	$\frac{1}{3}$	1	

Table 3.2: Bifurcations of a Multiple Equilibrium

Conclusion

We have studied the two perturbed population models (0.1) and (0.2). In each model, one species' growth rate was subject to an upper carrying capacity L_2 and a lower critical density L_1. There was also a term R representing harvesting, stocking, or no harvesting or stocking of one of the populations. With regard to the three dimensional model (0.2), a predator-predator-prey interaction was simulated; while, the two dimensional model (0.1) accommodated predator-prey, competition or cooperation between the species. Perturbations were investigated by studying their effect on the equilibria of the unperturbed models. To this end we located the equilibria of the unperturbed models, making a distinction between simple and multiple equilibria; then, we considered the perturbation of a simple equilibrium, and the bifurcation of a multiple equilibrium.

In seeking the equilibria of the unperturbed two dimensional model, we introduced $p(x)$. Expression $p(x)$ played an important role throughout our investigation of (0.1). An equilibrium $E^0(x^0, y^0)$ was simple when $p(x^0) = 0$ and $p_x(x^0) \neq 0$. An equilibrium $E^c(x^c, y^c)$ was multiple provided $p(x^c) = p_x(x^c) = 0$: being double if $p_{xx}(x^c) \neq 0$, or triple if $p_{xx}(x^c) = 0$ and $p_{xxx}(x^c) \neq 0$.

Once the simple equilibria were located, we examined their local natures and stability properties. Here $p(x)$ appeared. In **Theorem 1**, we proved that if $p_x(x^0) > 0$, then E^0 was not a saddle point; while if $p_x(x^0) < 0$, then E^0 was a saddle point. **Theorem 2** showed how "successive" equilibria must alternate in nature between that of a saddle point and that of a non-saddle point.

Using the theory of Andronov et al [28], we were able to determine the local natures of double and triple equilibria of the unperturbed model. A double equilibrium was a saddle node, and a triple equilibrium was a topological node when $p_{xxx}(x^c) > 0$, or a topological saddle point when $p_{xxx}(x^c) < 0$.

Starting with a simple equilibrium E^0 of the unperturbed model and allowing perturbations to be introduced, we located the associated perturbed equilibrium $E^p(x^p, y^p)$. We compared the possible local stability properties of the two, the results of which are given in Table 2.1. We found that hyperbolic equilibria (nodes, foci and saddle points) retain their local stability properties (but not necessarily their local natures in the case of node stars), while nonhyperbolic equilibria (centres) might experience changes in stability properties.

For E^c a double or triple equilibrium, we evaluated five cases in studying its bifurcation. The number and location of perturbed simple equilibria $E^*(x^*, y^*)$ arising from E^c were found. Zero or two simple equilibria were produced by a double equilibrium. A triple equilibrium gave one or three simple equilibria. From [28] we knew that of the two simple equilibria coming from a double equilibrium, one must be a saddle and the other a node. In the case of a triple equilibrium, we were only able to say that the perturbed simple equilibria could be saddle points or nodes. We presented these results in Table 2.2.

Our investigation of the three species model followed a similar pattern to that of the two species model. We found the expression $Q(x, y)$ which occupied a position like that of $p(x)$. An equilibrium $E^0(x^0, y^0, z^0)$ was simple provided $Q(x^0, y^0) = 0$ and $Q_x(x^0, y^0) \neq 0$; $E^c(x^c, y^c, z^c)$ was a double if $Q(x^c, y^c) = Q_x(x^c, y^c) = 0$, $Q_{xx}(x^c, y^c) \neq 0$, or a triple if $Q(x^c, y^c) = Q_x(x^c, y^c) = Q_{xx}(x^c, y^c) = 0$, $Q_{xxx}(x^c, y^c) \neq 0$.

We determined the locations and natures of the simple equilibria of the unperturbed model and found that part of the Routh-Hurwitz criteria for asymptotic stability was $Q_x(x^0, y^0) < 0$. The associated perturbed equilibrium $E^p(x^p, y^p, z^p)$ of the perturbed system was found. In Table 3.1 we gave the results of the comparison between the stability properties of E^0 and E^p. Once again it was determined that hyperbolic equilibria would not lose their local stability properties, but that nonhyperbolic equilibria might do so.

Finally, we studied the bifurcation of E^c into perturbed simple equilibria $E^*(x^*, y^*, z^*)$. As shown in Table 3.2, a double equilibrium could give rise to two or zero simple equilibria, and a triple to one or three simple equilibria.

These theoretical results have been illustrated for both the two and three dimensional models with specific examples. We have numerically solved the systems of ordinary differential equations and plotted the resulting orbits. It was hoped that this would give greater insight into the changes induced by perturbations.

Appendix A

CLASSIFICATION OF EQUILIBRIA VIA EIGENVALUES

For the two dimensional model, the nature and stability of a simple equilibrium $E^0(x^0, y^0)$ of the unperturbed system is classified (see [26]) according to its eigenvalues λ_1^0 , and λ_2^0 :

A Real and Distinct Eigenvalues

1. If $\lambda_s^0 < 0$, $s = 1, 2$, E^0 is an asymptotically stable node

2. If $\lambda_1^0 < 0$, $\lambda_2^0 > 0$, E^0 is a saddle point

3. If $\lambda_s^0 > 0$, $s = 1, 2$, E^0 is an unstable node

B Repeated Eigenvalues

4. If $\lambda_1^0 = \lambda_2^0 < 0$, E^0 is an asymptotically stable node-star

5. If $\lambda_1^0 = \lambda_2^0 > 0$, E^0 is an unstable node-star

C Complex Eigenvalues with Nonzero Real Part

6. If $\mathrm{Re}\lambda_s^0 < 0$, $s = 1, 2$, E^0 is an asymptotically stable focus

7. If $\mathrm{Re}\lambda_s^0 > 0$, $s = 1, 2$, E^0 is an unstable focus

D Purely Imaginary Eigenvalues

8. E^0 is a centre of the *linearized* system; it may be a centre or a focus of the nonlinearized system

For a simple equilibrium $E^0(x^0, y^0, z^0)$ of the unperturbed three species model, with eigenvalues λ_1^0 , λ_2^0 , λ_3^0 , we use the system of classification found in [22]:

A Real and Distinct Eigenvalues

1. If $\lambda_s^0 < 0$, $s = 1, 2, 3$, E^0 is an asymptotically stable node

2. If $\lambda_1^0 < 0$, $\lambda_s^0 > 0$, $s = 2, 3$, or if $\lambda_1^0 > 0$, $\lambda_s^0 < 0$, $s = 2, 3$, E^0 is a saddle node

3. If $\lambda_s^0 > 0$, $s = 1, 2, 3$, E^0 is an unstable node

B Double Eigenvalues

4. If $\lambda_1^0 < 0$, $\lambda_2^0 = \lambda_3^0 < 0$, E^0 is an asymptoically stable node star

5. If $\lambda_1^0 < 0$, $\lambda_2^0 = \lambda_3^0 > 0$, or if $\lambda_1^0 > 0$, $\lambda_2^0 = \lambda_3^0 < 0$, E^0 is a saddle star

6. If $\lambda_1^0 > 0$, $\lambda_2^0 = \lambda_3^0 > 0$, E^0 is an unstable node star

C Triple Eigenvalues

7. If $\lambda_1^0 = \lambda_2^0 = \lambda_3^0 < 0$, E^0 is an asymptotically stable star

8. If $\lambda_1^0 = \lambda_2^0 = \lambda_3^0 > 0$, E^0 is an unstable star

D One Real and Two Complex Eigenvalues with Nonzero Real Part

9. If $\lambda_1^0 < 0$, $\mathrm{Re}\lambda_s^0 < 0$, $s = 2, 3$, E^0 is an asymptotically stable node focus

10. If $\lambda_1^0 < 0$, $\mathrm{Re}\lambda_s^0 > 0$, $s = 2, 3$, or if $\lambda_1^0 > 0$, $\mathrm{Re}\lambda_s^0 < 0$, $s = 2, 3$, E^0 is a saddle focus

11. If $\lambda_1^0 > 0$, $\mathrm{Re}\lambda_s^0 > 0$, $s = 2, 3$, E^0 is an unstable node focus

E One Real and Two Purely Imaginary Eigenvalues

12. If $\lambda_1^0 < 0$, E^0 is a convergent vortex focus of the *linearized* system; it may be a convergent vortex focus, a saddle focus, or an asymptotically stable node focus of the nonlinearized system

13. If $\lambda_1^0 > 0$, E^0 is a divergent vortex focus of the *linearized* system; it may be a divergent vortex focus, a saddle focus, or an unstable node focus of the nonlinearized system

Appendix B

AN ALTERNATIVE TWO-SPECIES MODEL

We take a brief look at model (2.1) with harvesting or stocking of the first species x rather than y:

$$\begin{aligned} x' &= xF(x) - yg(x) - R, \\ y' &= -ay + byg(x). \end{aligned}$$

Equilibria of this model must satisfy

$$\begin{aligned} xF(x) - yg(x) - R &= 0, \\ -ay + byg(x) &= 0. \end{aligned}$$

Here, if $y \neq 0$, x must be a root of $-a + bg(x) = 0$; if such an x exists, it is unique. Provided $xF(x) - R > 0$, y is given by $y = \frac{xF(x)-R}{g(x)}$. We get only one y-value for a given x-value. For $y = 0$, we find x from the equation $xF(x) - R = 0$; there may be more than one solution of this equation, or there may be multiple solutions. We are thus led to the conclusion that if a multiple equilibrium exists, it must be on the x-axis.

Bibliography

[1] H.I. Freedman and P. Waltman. Perturbations of two dimensional predator-prey equations. SIAM J. App. Math., Vol. 28, pp. 1–10 (1975).

[2] H.I. Freedman and P. Waltman. Perturbations of two dimensional predator-prey equations with an unperturbed critical point. SIAM J. Appl. Math., Vol. 29, pp. 719–733 (1975).

[3] H.I. Freedman. A perturbed Kolmogorov-type model for the growth problem. Math. Biosci., Vol. 23, pp. 127–149 (1975).

[4] P. Yodzis. The effects of harvesting on competitive systems. Bull. Math. Biol., Vol. 38, pp. 97–109 (1976).

[5] F. Brauer and A.C. Soudack. Stability regions and transition phenomena for harvested predator-prey systems. J. Math. Biol., Vol. 7, pp. 319–337 (1979).

[6] F. Brauer and A.C. Soudack. Stability regions in predator-prey systems with constant rate prey harvesting. J. Math. Biol., Vol. 8, pp. 55–71 (1979).

[7] F. Brauer and A.C. Soudack. Constant-rate stocking of predator-prey systems. J. Math. Biol., Vol. 11, pp. 1–14 (1981).

[8] F. Brauer and A.C. Soudack. Coexistence properties of some predator-prey systems under constant rate harvesting and stocking. J. Math. Biol., Vol. 12, pp. 101–114 (1981).

[9] H.I. Freedman. Graphical stability, enrichment and pest control by a natural enemy. Math. Biosci., Vol. 31, pp. 207–225 (1976).

[10] G. Bojadziev, C. McConill and L. Yen. Certain perturbed models of two interacting populations with harvesting or stocking. Proceedings Int. AMSE Conf. "Modelling and Simulation", Karlsruhe (Germany), July 20–22, Vol. 1A, pp. 47–62 (1987).

[11] G. Bojadziev and L. Wong. Bifurcations of a predator-predator-prey model with harvesting. Proceedings Int. AMSE Conf. "Modelling and Simulation", Karlsruhe (Germany), July 1987, Vol. 4, pp. 3–11.

[12] G. Bojadziev and A. Gerogiannakis. A predator-predator-prey system with constant rate prey harvesting. "Qualitative Properties of Differential Equations"—Proceedings of the 1984 Edmonton Conference, pp. 59–68 (1987).

[13] H.I. Freedman and P. Waltman. Mathematical analysis of some three-species food chain models. Math. Biosc., Vol. 33, pp. 257–276 (1977).

[14] H.I. Freedman. Deterministic Mathematical Models in Population Ecology. Marcel Dekker, New York 1980.

[15] A.D. Bazikin. Mathematical Biophysics of Interacting Populations. Moscow Izdat. Nauka, 1985.

[16] F. Brauer and D.A. Sanchez. Constant rate population harvesting: Equilibrium and stability. Theor. Pop. Biol., Vol. 8, pp. 12–30 (1975).

[17] F. Brauer, A.C. Soudack and A.C. Jarosch. Stabilization and destabilization of predator-prey systems under harvesting and nutrient enrichment. Int. J. Control, Vol. 23, pp. 553–573 (1976).

[18] G. Bojadziev. Harvesting or stocking can be a structurally stabilizing factor in species interactions. Proc. Int. AMSE Conf. "Modelling and Simulation," Pomona (USA), Dec. 16–18, Vol. 4, pp. 19–28 (1987).

[19] G. Bojadziev. Structural instability in population dynamics due to harvesting. Proc. Int. AMSE Conf. "Modelling and Simulation," Istanbul (Turkey), June 1988, Vol. 4A, pp. 35–44.

[20] A.R. Hausrath. Stability properties of a class of differential equations modelling predator-prey relationships. Math. Biosci., Vol. 26, pp. 267–281 (1975).

[21] G. Bojadziev and H. Kim. Perturbed Lotka-Volterra competition model with harvesting. Proc. Int. AMSE Conf. "Modelling and Simulation," Williamsburg (USA), Sept. 2, pp. 2–13 (1986).

[22] G. Bojadziev and M.A. Sattar. Perturbations in the three dimensional Kolmogorov model. Math. Biosci., Vol. 78, pp. 293–305 (1986).

[23] G. Bojadziev and M.A. Sattar. Bifurcations in the three dimensional Kolmogorov model. Math. Biosci., Vol. 86, pp. 51–66 (1987).

[24] H.I. Freedman and P. Waltman. Persistence in models of three interacting predator-prey populations. Math. Biosci., Vol. 68, pp. 213–231 (1984).

[25] G. Bojadziev. Perturbed higher order population models. Math. Modelling, Vol. 8, pp. 772–777 (1987).

[26] M.W. Hirsch and S. Smale. Differential Equations, Dynamical Systems, and Linear Algebra. Academic Press, New York, 1974.

[27] J.M.A. Danby. Computing Applications to Differential Equations: Modelling in the Physical and Social Sciences. Reston Publishing Co. , Reston, Va. , 1985.

[28] A.A. Andronov, E.A. Leontovich, I.I. Gordon and A.G. Maier. Theory of Bifurcations of Dynamic Systems on a Plane. Moscow Izdat. Nauka, 1967 (English translation John Wiley and Sons, New York, 1973).

[29] J. Kevorkian and J.D. Cole. Perturbation Methods in Applied Mathematics. Springer-Verlag, New York, 1981.