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Hopf Bifurcation in Host-Parasitoid Models

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For a wide class of host-parasitoid models a reduction to Arnold's normal form can be carried out in an explicit way. In the case of Hopf bifurcation the shape and size of the elliptic limit curve can be derived in terms of the parameters of the model. Some models have a rich bifurcation behaviour with both forward and backward Hopf bifurcation, and with a transition zone in the parameter plane for which there exists a pair of limit curves, one stable and one unstable. The theory is confirmed and illustrated by numerical experiments.

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1. Introduction

Some time ago J.A.J. Metz showed me a number of intriguing computer experiments in connection with host-parasitoid models of the kind

$$\begin{cases} x_{n+1} = x_n \phi(y_n), \\ y_{n+1} = a x_n - x_{n+1} \ , \ a > 1, \end{cases} \tag{1.1}$$

where x_n , y_n are the numbers of hosts and parasitoids of generation n. The function $\phi(y)$ is assumed to be differentiable with $\phi'(y) < 0$, $\phi(0) = a$ and $\phi(\infty) < 1$. The function $\phi(y)$ contains a second parameter $b > 0$, which enables us to study bifurcation phenomena with respect to the non-trivial equilibrium for various combinations of a,b in the parameter plane. It is perhaps of interest to note that the iterative process (1.1) is invertible with

$$\begin{cases} x_n = (x_{n+1} + y_{n+1})/a, \\ y_n = \phi^{-1}(a x_{n+1}/(x_{n+1} + y_{n+1})). \end{cases} \tag{1.1a}$$

Metz and his coworkers [2,4,6] considered in particular the so-called Hassell-Varley (HV) model and a new model in which interaction between parasitoids was taken into account, the so-called parasitoid-parasitoid interaction (PP) model. The HV-model showed the usual characteristics of Hopf bifurcation

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in the unstable part of the parameter plane. However, the bifurcation behaviour of the PP-model appeared to be much more complicated. Instead of a single invariant curve — the Hopf circle — two such curves could be present, one attracting and the other repelling. For some parameter values there was none such curve. Metz succeeded in giving a qualitative explanation of his findings based upon the theory of normal forms. In this paper his ideas are worked out in a quantitative way. Our results can also be applied to a recent model proposed by HASSELL [5]. This model appears to have the same complicated bifurcation behaviour as the PP-model.

Leaving aside the trivial equilibrium $x=y=0$ there exists a single non-trivial equilibrium

$$x = \frac{c}{a-1}, \; y = c, \tag{1.2}$$

with c as the unique root of

$$\phi\,(c) = 1. \tag{1.3}$$

For a certain line in the parameter plane the eigenvalues $\lambda,\bar{\lambda}$ are complex and of modulus one. Across this line, the so-called Hopf line, we may expect Hopf bifurcation. Close to the Hopf line we may write

$$\lambda = (1+\mu)e^{i\alpha} \quad , \; 0 < \alpha < \pi, \tag{1.4}$$

where μ is a small quantity, the bifurcation parameter. In the special cases considered in this paper the parameters μ,α are in a 1, 1-correspondence with the model parameters a,b. Thus the Hopf line corresponds to a part of the unit circle in the complex λ-plane. The eigenvalue equation of the non-trivial equilibrium is of the form

$$\lambda^2 - \lambda\,(1+L\,/\,a) + L = 0, \tag{1.5}$$

where

$$L = -\frac{ac\phi'(c)}{a-1}. \tag{1.6}$$

At the Hopf line we have $L=1$ so that $\lambda + \bar{\lambda} = 1+1/a$. This gives

$$\cos\alpha = \frac{1}{2}(1+\frac{1}{a}). \tag{1.7}$$

Since $1 < a < \infty$, the value of α is restricted to the interval $0 < \alpha < \pi\,/\,3$. Thus a periodic solution of (1.1) would imply a period of 7 or more. Stated as a theorem

THEOREM
For any periodic solution of a model of the class (1.1) the period is seven or more.

According to the theory of normal forms, the two-dimensional map (1.1) can be written in the following form

$$z_{n+1} = \lambda z_n + A_{21}\, z_n^2 \bar{z}_n + h.o.t.\,, \tag{1.8}$$

where $z,\bar{z}$ are local complex coordinates at the equilibrium. The constant A_{21}, taken at $\mu=0$, is an essential parameter of the model. In the plane determined by the conjugate complex variables $z,\bar{z}$ we have an invariant circle, the Hopf circle, with its radius R given by

$$\frac{\mu}{R^2} = \mathrm{Re}(-e^{-i\alpha}A_{21}). \tag{1.9}$$

For the original variables x,y this corresponds to an invariant curve of elliptical shape surrounding the equilibrium point. If $\mu/R^2 > 0$ we have forward Hopf bifurcation, with an attracting invariant curve around an unstable equilibrium ($\mu>0$). If $\mu\,/\,R^2<0$ we have backward Hopf bifurcation, with a repelling invariant curve around a stable equilibrium ($\mu < 0$). In some models there exists a critical value α_0 for which $\mathrm{Re}(e^{-i\alpha_0}A_{21}) = 0$. Close to this critical value there is a bifurcation of a more complicated kind, called "crater bifurcation" by J.A.J Metz. It is characterized by the simultaneous occurrence of a stable and of an unstable invariant curve. A sketch of the mathematical theory will be given in the Appendix.

In this paper the reduction of (1.1) to its normal form (1.5) is carried out in an explicit way. If $\phi(y)$ has the following Taylor expansion at the equilibrium value

$$\phi(c(1+t)) = 1 - At + ABt^2 - ACt^3 + \dots, \tag{1.10}$$

with (at the Hopf line)

$$A = 1 - 1/a, \tag{1.11}$$

then the following results have been obtained. The radius R of the Hopf circle in the $z,\bar{z}$-plane is given by

$$\frac{2\mu}{R^2} = A - (A+1)B + 4B^2 - 3C. \tag{1.12}$$

The corresponding ellipse in the original x,y-plane is given by

$$a(a-1)dx^2 - (a-1)dxdy + dy^2 = \frac{(3a+1)c^2R^2}{a}, \tag{1.13}$$

where dx,dy are local coordinates at the equilibrium $x = c/\,(a-1)\,, y = c$. This theory will be applied to the following few special cases:

$$\phi(y) = \frac{a}{1+y^b}, \quad (S), \tag{1.14}$$

$$\phi(y) = a\exp(-y^b), \quad (HV), \tag{1.15}$$

(HASSELL and VARLEY [1]),

$$\phi(y) = a\exp\left(-\frac{\sqrt{1+y}-1}{b}\right), \quad (PP), \tag{1.16}$$

(METZ, VAZ NUNEZ [2]),

$$\phi(y) = a(\theta e^{-y} + (1-\theta)e^{-by}), \quad (H), \tag{1.17}$$

(HASSELL [5]),

The main results are as follows.

S-model. Unstable for $b > 1$. Hamiltonian for $b=1$ on a logarithmic scale. No Hopf bifurcation. Formally $R=\infty$ for all values of a.

HV-model. Forward Hopf bifurcation for all a.

PP-model. Forward Hopf bifurcation for $a > 3.85$ and backward Hopf bifurcation for $a < 3.85$.

H-model. As in the previous model. If $\theta = ½$ there is forward Hopf bifurcation for $a > 2.29$ and backward Hopf bifurcation for $a < 2.29$.

2. REDUCTION TO THE NORMAL FORM

In this section the reduction of (1.1) to the normal form (1.8) will be carried out explicitly. The first step is the use of a new variable

$$w = x\phi(y). \tag{2.1}$$

Then (1.1) can be replaced by

$$\begin{cases} x_{n+1} = w_n, \\ w_{n+1} = w_n\phi(ax_n - w_n). \end{cases} \tag{2.2}$$

Let $\lambda,\bar{\lambda}$ be the eigenvalues of the equilibrium as determined by (1.5). Then by a linear transformation, x,w can be replaced by complex coordinates $z,\bar{z}$ where z is an eigenvector associated to λ. Explicitly

$$\begin{cases} cz = a\sigma\,(\bar{\lambda}x - w) - c_0, \\ c\bar{z} = a\bar{\sigma}\,(\lambda x - w) - \bar{c}_0, \end{cases} \tag{2.3}$$

where σ is a scaling factor and where c_0 is determined by the condition

$$z = 0 \quad \text{for} \quad x = w = c/(a-1).$$

The factor σ is chosen in such a way that

$$ax - w = c(1+z+\bar{z}). \tag{2.4}$$

In the eigenvector coordinates $z,\bar{z}$ the map (2.2) takes the form

$$z_{n+1} = \lambda z_n + a_{20}z_n^2 + a_{11}z_n\bar{z}_n + a_{02}\,\bar{z}_n^2 + h.o.t.\,, \tag{2.5}$$

and a similar relation with conjugate complex quantities. From (2.3) we obtain

$$\begin{aligned} cz_{n+1} &= a\sigma(\bar{\lambda}x_{n+1} - w_{n+1}) - c_0 = \\ &= a\sigma w_n(\bar{\lambda} - \phi(ax_n - w_n)) - c_0, \end{aligned}$$

so that in view of (2.4)

$$cz_{n+1} = a\sigma w_n(\bar{\lambda} - \phi(c(1+z_n + \bar{z}_n))) - c_0. \tag{2.6}$$

From (2.3) we obtain by inversion a relation of the kind

$$w = \frac{c}{a-1}\,(1 + c_1 z + c_2\bar{z}). \tag{2.7}$$

Using also the expansion (1.10), we obtain

$$\begin{aligned} z_{n+1} = \frac{a\sigma}{a-1}\{&(1+c_1z_n+c_2\bar{z}_n)\,[\bar{\lambda}-1 + A(z_n+\bar{z}_n) - AB(z_n+\bar{z}_n)^2 + \\ &+AC\,(z_n + \bar{z}_n)^3 \cdots] - (\bar{\lambda}-1)\}, \end{aligned} \tag{2.8}$$

which is identical with (2.5). Although

$$\lambda = (1+\mu)e^{i\alpha} \tag{2.9}$$

we need the coefficients a_{20},a_{11},a_{02} etcetera only at the Hopf line where $\mu = 0$. Then the calculation may be simplified somewhat. We have

$$\begin{cases} A = 1 - 1/a = 2(1-\cos\alpha)\,, \\ c_1 = 1-\bar{\lambda}\,, c_2 = 1-\lambda, \end{cases} \tag{2.10}$$

and

$$\sigma = \frac{\lambda^2}{1+\lambda} = \frac{1}{2\cos\frac{1}{2}\alpha}\exp\left(\tfrac{3}{2}i\alpha\right). \tag{2.11}$$

Thus the nonlinear terms of (2.5) can be derived from

$$z_{n+1} = \sigma[1 + (1-\bar{\lambda})z_n + (1-\lambda)\bar{z}_n)]\,[z_n + \bar{z}_n - \tag{2.12}$$

$$- B(z_n + \bar{z}_n)^2 + C(z_n + \bar{z}_n)^3 \cdots] + \text{ linear terms.}$$

Without difficulty we read off the following expressions

$$a_{20} = \sigma\,(1-\bar{\lambda}-B),$$
$$a_{11} = \sigma\,(2-\lambda-\bar{\lambda}-2B),$$
$$a_{02} = \sigma\,(1-\lambda-B),$$

and also

$$a_{21} = \sigma\,(\lambda + 2\bar{\lambda}-3)B + 3\sigma\,C.$$

From the theory of normal forms the following formula can be derived

$$\frac{\mu}{R^2} = \frac{1}{2}|\,a_{11}|^2 + |a_{02}|^2 - \mathrm{Re}\frac{(2-\bar{\lambda})a_{11}a_{20}}{\lambda(1-\lambda)} - \mathrm{Re}\,\bar{\lambda}a_{21}. \tag{2.13}$$

Substitution of the expressions for the coefficients obtained above gives the surprisingly simple result

$$\frac{2\mu}{R^2} = A - (A+1)B + 4B^2 - 3C, \tag{2.14}$$

where R is the radius of the Hopf circle in the coordinates $z,\bar{z}$ of (2.3) and (2.5). However, in the original x,y coordinates the Hopf circle is transformed into an invariant curve of elliptical shape. From (2.1) and (2.3) we obtain the local linear transformation

$$cdz = \sigma\,(a(\bar{\lambda}-1)dx + dy) \tag{2.15}$$

written in local infinitesimal coordinates. The Hopf circle, small by nature, is given by

$$dz\;d\bar{z} = R^2, \tag{2.16}$$

where R^2 is determined by (2.14). Substitution of (2.15) gives an ellipse described in local infinitesimal coordinates dx,dy by

$$a(a-1)\,dx^2 - (a-1)dxdy + dy^2 = \frac{(3a+1)\,c^2R^2}{a}. \tag{2.17}$$

Its position, semi-axes, etcetera can be derived from this equation by standard analysis. However, no simple expressions can be obtained for the general case. Its area is given by

$$\frac{2\pi c^2 R^2}{a}\;\sqrt{\frac{3a+1}{a-1}}, \tag{2.18}$$

perhaps the simplest formula of this kind.

It should be noted that a Hopf circle, or better a Hopf ellipse, is merely an invariant curve in the x,y -plane. For a starting point x_0,y_0 on the Hopf curve the two-dimensional dynamic behaviour of the model is reduced to one-dimensional dynamic behaviour. The motion can be aperiodic with a dense covering of the Hopf curve by successive points. However, if $\lambda = (1+\mu)\exp i\alpha$ is close to a point of the unit circle with a low-order rational rotation number, i.e. if $\alpha \approx m/n$, we may have periodic orbits. This is a case of weak resonance. The simplest cases are here 1:7, 1:8, 2:15, etcetera. According to Arnold, the regions in the parameter plane, for which a case of weak resonance occurs, have the shape of thin tongues or horns, with their pointed end at the Hopf line, and fanning well out in the unstable region. Tongues with a different rotation may even intersect each other. The general situation is sketched in Fig. 1.

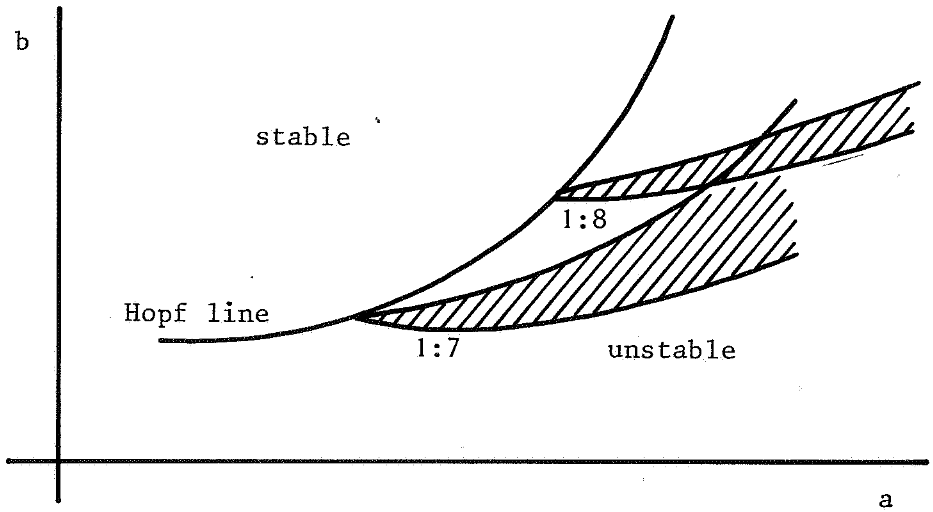

Fig. 1 Hopf bifurcation and Arnold tongues

We conclude this section by giving an alternative expression for the Hopf radius when the given model is of the form

$$\begin{cases} x_{n+1} = x_n \exp(-f(y_n)), \\ y_{n+1} = ax_n - x_{n+1}, \end{cases} \tag{2.19}$$

where

$$f(c(1+t)) = At + AB_1t^2 + AC_1t^3 + \cdots . \tag{2.20}$$

Then we have

$$B = \tfrac{1}{2}A - B_1 \ , \ C = \tfrac{1}{6}A^2 - AB_1 + C_1,$$

and (2.14) passes into

$$\frac{2\mu}{R^2} = \frac{1}{2}A + B_1 + 4B_1^2 - 3C_1. \tag{2.21}$$

3. A simple model

In this section we consider the model

$$\begin{cases} x_{n+1} = \dfrac{ax_n}{1+y_n^b}, \\ y_{n+1} = \dfrac{ax_ny_n^b}{1+y_n^b}, \quad b>0. \end{cases} \tag{3.1}$$

This is perhaps the simplest possible model, as we soon shall see. So we call it the S-model (S=simple). The non-trivial equilibrium is given by

$$(a-1)^{1/b-1} \ , \ c = (a-1)^{1/b}. \tag{3.2}$$

The eigenvalue equation is

$$\lambda^2 - (1 + b/a)\,\lambda + b = 0. \tag{3.3}$$

Thus in the a,b-parameter plane the regions of stability and instability are separated by the Hopf line $b=1$. The expansion

$$\phi(c(1+t)) = \frac{a}{a+ct} = 1 - ct/a + c^2t^2/a^2 - c^3t^3/a^3 + \cdots \tag{3.4}$$

with $c=a-1$ on the Hopf line gives

$$A = c/a \ , \ B = c/a, \ C=c^2/a^2. \tag{3.5}$$

Substitution of these values in (1.12) gives

$$\frac{2\mu}{R^2}' = 0, \tag{3.6}$$

for all values of a. Thus we have no Hopf bifurcation in this case. Computer experiments suggest that for $b < 1$ all orbits converge to the equilibrium (3.2), and that for $b > 1$ all orbits disappear into infinity. For $b = 1$ we have the very simple model

$$\begin{cases} x_{n+1} = \dfrac{ax_n}{1+y_n}, \\ y_{n+1} = \dfrac{ax_ny_n}{1+y_n}. \end{cases} \tag{3.7}$$

Its inverse is even simpler

$$\begin{cases} x_n = (x_{n+1} + y_{n+1}) \,/\, a, \\ y_n = y_{n+1} \,/x_{n+1}. \end{cases} \tag{3.8}$$

Computer experiments show that for $a > 1$ the map (3.7) is very much like a Hamiltonian map. A few typical orbits are shown in Fig 2. There are periodic cycles of any order from 9 upwards. In particular the point $x_0 = 0.713$, $y_0=2.090$ is an element of a 9-cycle, and $x_0=0.469$, $y_0=3.796$ is an element of a 10-cycle. It is perhaps a surprise that on a logarithmic scale the map (3.8) is indeed Hamiltonian, i.e. area-preserving. With the variables u,v defined by

$$u = \log x \ , \ v = \log(y/(a-1)), \tag{3.9}$$

the map (3.8) takes the form

$$\begin{cases} u \rightarrow \log \dfrac{e^u + (a-1)e^v}{a}, \\ v \rightarrow v-u. \end{cases} \tag{3.10}$$

In Fig. 3 an illustration is given, again for $a=2$. An orbit consisting of an island chain is clearly visible. The parameter a is a sort of degree of stochasticity. As a increases more and more orbits disintegrate into stochastic rings. An extreme case is shown in Fig. 4 for $a=8$, where a single orbit is shown, starting from $x_0 = 0$, $y_0 = -20$. Of course, such extreme situations have hardly any biological meaning.

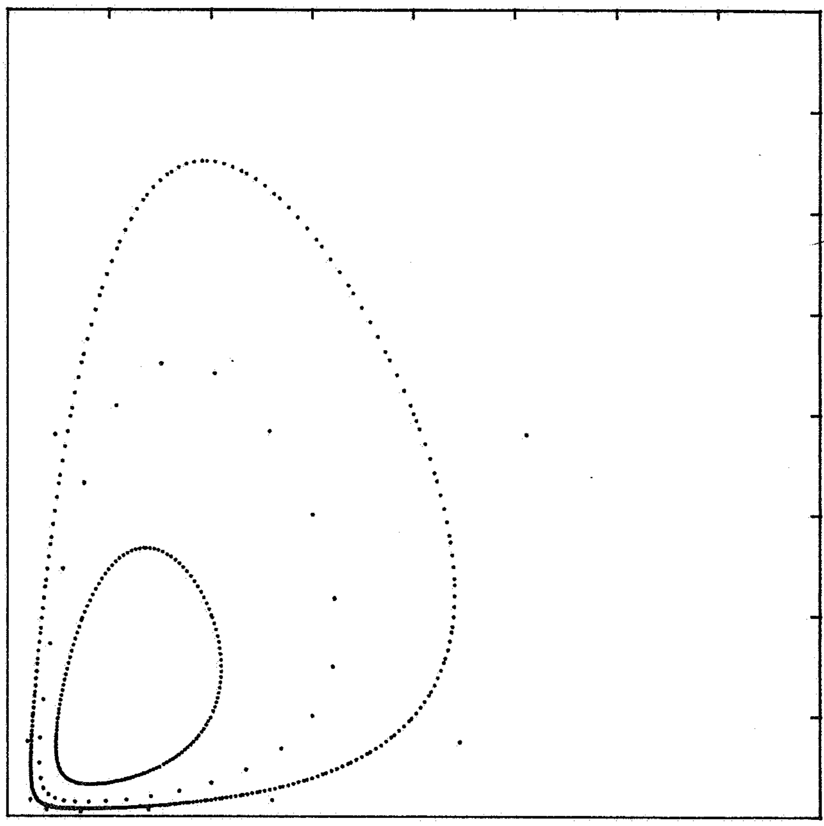

Fig. 2

X'=AX/(1+Y)

Y'=AX-X'

SCALE Ø,8,Ø,8

A=2

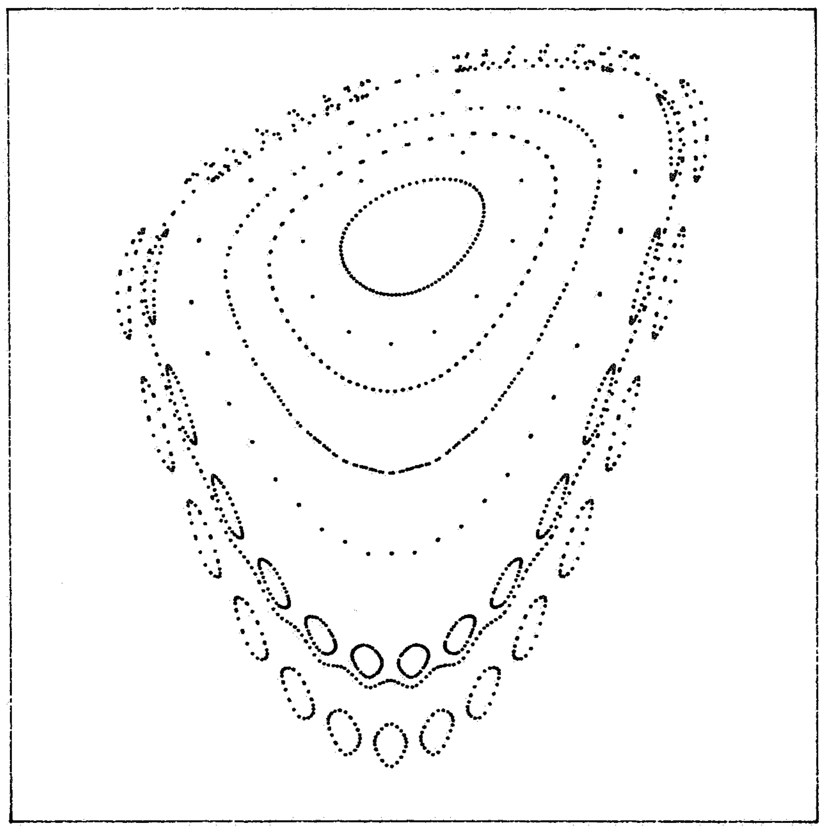

Fig. 3

A=2

SCALE -6,6,-16,6

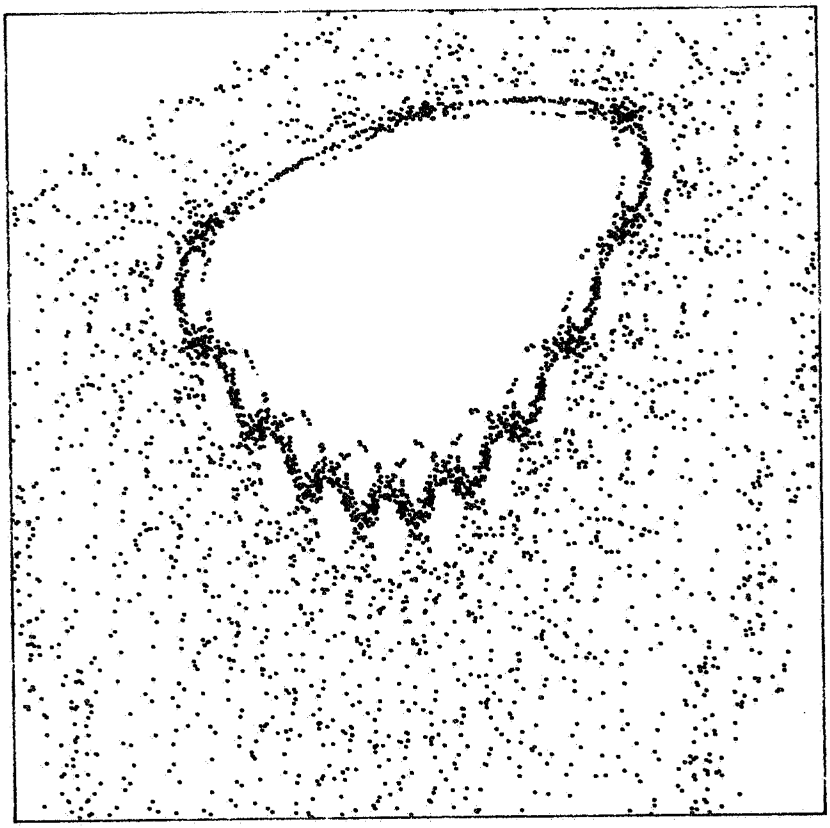

Fig. 4

A=8

SCALE -15, 15, -4Ø, 15

START Ø, -2Ø

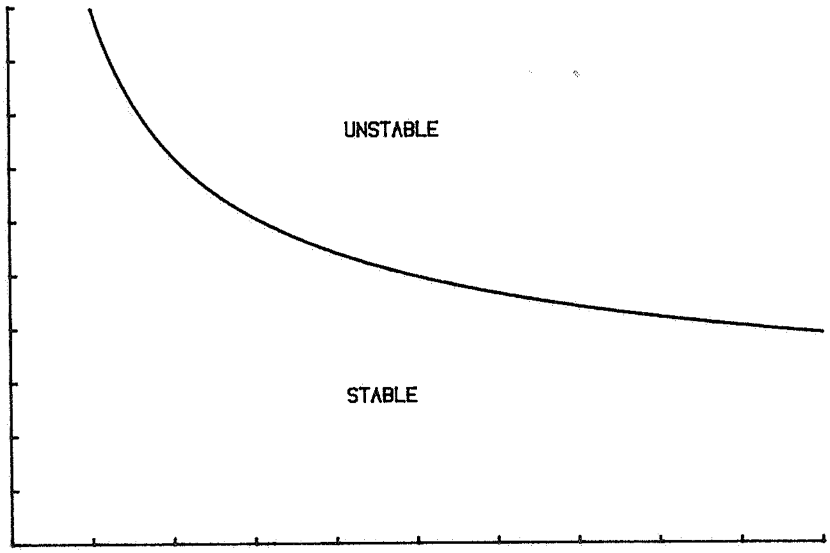

Fig. 5

HASSELL-VARLEY

STABILITY REGION

SCALE Ø, 1Ø, Ø, 1

4. The Hassel-Varley model

The HV-model

$$\begin{cases} x_{n+1} = ax_n \exp(-y_n^b), \\ y_{n+1} = ax_n - x_{n+1}, \quad 0 < b \leqslant 1, \end{cases} \tag{4.1}$$

proposed by Hassell and Varley [1] is a generalization of the Nicholson-Bailey model, to which it reduces for $b=1$. The non-trivial equilibrium is here

$$(\log a)^{1/b} \,/(a-1) \ , \ c = (\log a)^{1/b}. \tag{4.2}$$

The eigenvalue equation

$$(a-1)\lambda^2 - (a-1 + b\log a)\lambda + ab\log a = 0 \tag{4.3}$$

shows stability for

$$ab\log a < a - 1. \tag{4.4}$$

The corresponding regions of stability and instability are sketched in Fig. 5. On the Hopf line the Taylor expansion of

$$f(c(1+t)) = ((1+t)^b - 1)\log a \tag{4.5}$$

gives in the notation of (2.19), (2.20) the coefficients

$$A = b\log a, \ B_1 = \tfrac{1}{2}(b-1), \ C_1 = \tfrac{1}{6}(b-1)(b-2). \tag{4.6}$$

Then from (2.21) we obtain at once the simple result

$$\frac{4\mu}{R^2} = b^2 + b\log a - 1, \tag{4.7}$$

or expressed in a only

$$\frac{\mu}{R^2} = \frac{(a-1)^2 - a\log^2 a}{4a^2\log^2 a}. \tag{4.8}$$

Elementary calculus shows that for $a>1$ this expression is always positive. In Table 1 we have collected a few values of α, a and b on the Hopf line, together with the equilibrium x_0, y_0 and the quantity μ/R^2 determining the size of the Hopf curve. A typical orbit is given in Fig. 6

α	a	b	x_{eq}	y_{eq}	μ/R^2
30	1.366	0.859	0.704	0.258	0.0015
40	1.879	0.742	0.611	0.537	0.0045
45	2.414	0.664	0.585	0.827	0.0069
50	3.502	0.570	0.594	1.486	0.0098
53	4.911	0.500	0.647	2.531	0.0117
56	8.447	0.413	0.841	6.261	0.0131
59	33.25	0.277	2.876	92.76	0.0117

Table 1

5. The parasitoid-parasitoid interaction model

According to Metz, the parasitoids are divided into two groups. The first group consists of single individuals looking for a host. The second group consists of pairs of parasitoids more interested in fighting each other. It is like a chemical reaction of the kind

$$P + P \rightleftarrows P_2.$$

If u is the number of single parasitoids, v the number of competing pairs, so that $P = u + 2v$, then

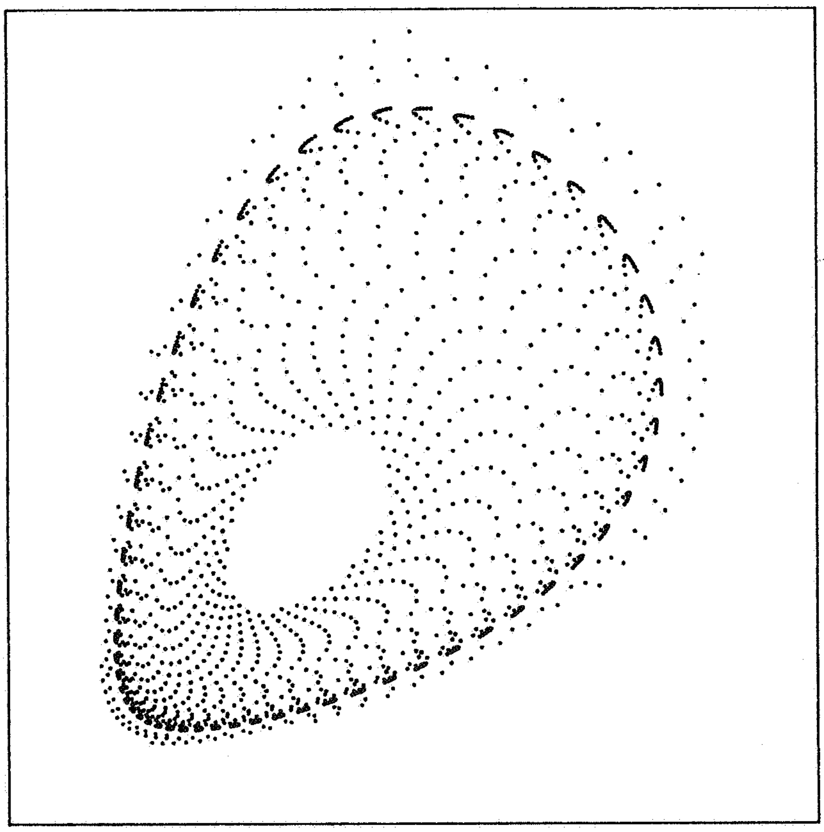

Fig. 6

reaction kinetics requires an equation of the form

$$\dot{u} = -\alpha_1 u^2 + 2\alpha_2 v.$$

Equilibrium, on a small time scale, requires that

$$\alpha_1 u^2 - 2\alpha_2 v = 0,$$

or

$$\alpha_1 u^2 + \alpha_2 u - \alpha_2 P = 0.$$

Solving this for u we have

$$2\alpha_1 u = -\alpha_2 + \sqrt{\alpha_2^2 + 4\alpha_1\alpha_2 P}. \tag{5.1}$$

If this expression is used in combination with the Nicholson-Bailey model

$$x' = ax \exp(-u),\ y' = ax - x',$$

we obtain after some scaling the following so-called parasitoid-parasitoid interaction (PP) model

$$\begin{cases} x' = ax \exp\left(-\dfrac{\sqrt{1+y} - 1}{b}\right), \\ y' = ax - x', \quad b > 0. \end{cases} \tag{5.2}$$

For a small value of b also x and y are small and then $\sqrt{1+y} - 1 \approx y/2$. This shows that in that case the model is very close to the Nicholson-Bailey model. If b is large, then also y is large, and then $\sqrt{1+y} \approx y^{\frac{1}{2}}$. In that case the model is an approximation of the Hassell-Varley model with exponent $\frac{1}{2}$. The non-trivial equilibrium is here $c/(a-1)$, c with

$$c = (1 + b \log a)^2 - 1. \tag{5.3}$$

The eigenvalues follow from

$$\lambda_1\lambda_2 = \frac{a \log a\,(2 + b \log a)}{2(a-1)\,(1 + b\log a)} \tag{5.4}$$

and

$$\lambda_1 + \lambda_2 = 1 + \lambda_1\lambda_2/a. \tag{5.5}$$

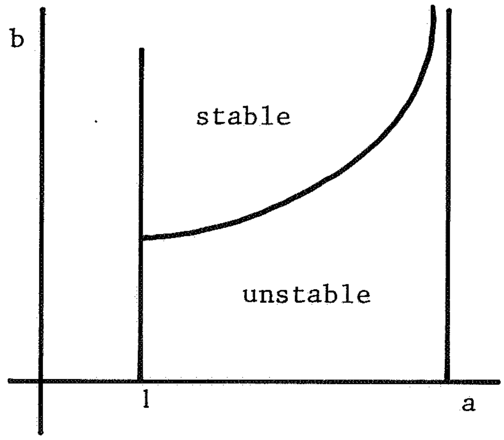

Fig. 7

The stability condition $\lambda_1\lambda_2 < 1$ can be written as

$$b > \frac{a}{2(a-1)-a \log a} - \frac{1}{\log a}, \tag{5.6}$$

with $a < 4.92155$, the value for which $2(a-1) = a \log a$. The corresponding regions of stability and instability are illustrated in Fig. 7. On the Hopf line, the Taylor expansion of

$$f(c(1+t)) = ((1+c+ct)^{\frac{1}{2}} - (1+c)^{\frac{1}{2}})/b \tag{5.7}$$

leads to the following expansion for the Hopf radius

$$\frac{\mu}{R^2} = \frac{c}{8b\sqrt{1+c}} - \frac{3c^2+2c}{16(1+c)^2}. \tag{5.8}$$

On the Hopf line the relations (5.3) and

$$b = \frac{a}{2(a-1)-a \log a} - \frac{1}{\log a} \tag{5.9}$$

enable us to express μ/R^2 as a function of a only. Then the following Table 2 can be constructed

α	a	b	x_{eq}	y_{eq}	μ/R^2
24	1.209	1.144	2.302	0.481	-0.00399
30	1.366	1.258	2.565	0.939	-0.00820
40	1.879	1.695	3.733	3.283	-0.01556
45	2.414	2.311	5.815	8.224	-0.01469
50	3.502	4.897	19.96	49.94	-0.00401
51	3.866	6.929	37.17	106.5	0.00016
52	4.323	12.938	119.4	396.6	0.00530
53	4.911	774.88	3.895E5	1.523E6	0.01159

Table 2

It appears that here (5.8) changes sign at the critical value $\alpha = \alpha_0 = 50^0.96$. This means that for $\alpha > \alpha_0$ we have forward Hopf bifurcation, and for $\alpha < \alpha_0$ backward Hopf bifurcation. According to the theory, for $\alpha > \alpha_0$ and α close to α_0 we may expect two invariant Hopf curves. The inner Hopf curve is attracting, and it is either densely filled by successive iteration points, or it contains a periodic cycle with a rotation number close to 1:7. The outer Hopf curve is repelling and seperates the bounded orbits from the unbounded ones. A typical case is illustrated in Fig. 8 for $a = 4.2$, $b = 10$ corresponding to $\alpha = 51^0.8$, $\mu = 0.00156$. The equilibrium is at $x = 73.3$, $y = 234.6$. The start 125, 929 gives the stable Hopf curve. The start 125, 1284 gives the separatrix, the unstable Hopf curve.

6. Hassell's model

In his recent paper on parasitism in patchy environments [5], Hassell considers the model

$$\begin{cases} N_{n+1} = F\, N_n f(P_n), \\ P_{n+1} = c\, N_n\, (1 - f(P_n)), \end{cases} \tag{6.1}$$

where

$$f(P) = \alpha\, e^{-\alpha\beta P} + (1-\alpha) e^{-g\alpha\beta P}, \tag{6.2}$$

with

$$g = \left[\frac{1-\alpha}{(n_0-1)\alpha} \right]^{\mu}. \tag{6.3}$$

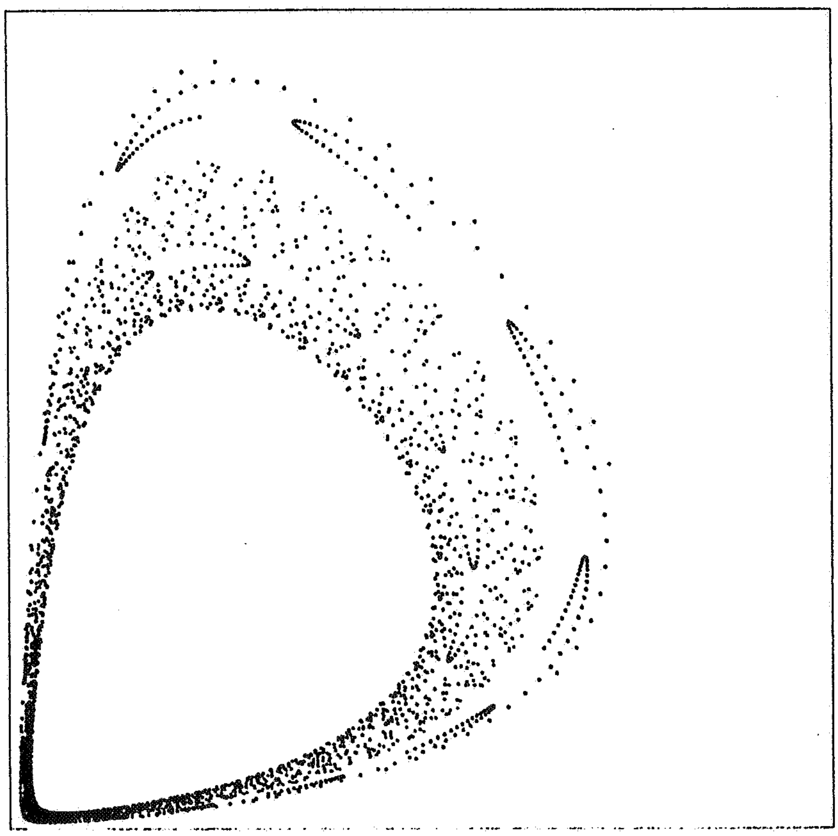

Fig. 8

PP-INTERACTION

A=4.2 , B=10

SCALE 0, 500, 0, 1500

START 250, 1000 & 250, 1100

Realistic values are

$$0.3 \leqslant \alpha \leqslant 0.6\ ,\ n_0 \approx 10\ ,\ F \approx 2\ ,\ -3 \leqslant \mu \leqslant 3.$$

With the following scaling and change of notation

$$\begin{cases} N = F\,x \,/\, (\alpha\beta c)\ \ ,\ \ P = y \,/\, (\alpha\beta), \\ F = a\ ,\ g = b\ ,\ \alpha = \theta, \end{cases} \tag{6.4}$$

we obtain in our notation the model (1.1) with

$$\phi(y) = a\,(\theta e^{-y} + (1-\theta)e^{-by}),\ b > 0,\ \ 0 < \theta < 1. \tag{6.5}$$

In view of the symmetry relations

$$x \rightarrow x/b\ ,\ y \rightarrow y/b\ ,\ \theta \rightarrow 1-\theta\ ,\ b \rightarrow 1/b, \tag{6.6}$$

it is sufficient to consider only the case $b > 1$. The equilibrium of the model is determined by

$$a\,\theta\,e^{-c} + a(1-\theta)e^{-bc} = 1. \tag{6.7}$$

The product L of its eigenvalues is given by

$$L = \frac{a^2 c}{a-1}\,(\theta e^{-c} + (1-\theta)be^{-bc}). \tag{6.8}$$

For given values of θ, α and μ the corresponding values of a,b and c can be determined by solving (6.7) and (6.8), where

$$a = L \,/\, (2(1+\mu)\cos\alpha - 1) \tag{6.9}$$

and

$$L = (1+\mu)^2. \tag{6.10}$$

Perhaps the simplest way of solving these equatons is as follows. We write

$$u = a\,\theta\,e^{-c}\ ,\ v = a(1-\theta)e^{-bc}, \tag{6.11}$$

and replace (6.7), (6.8) by

$$\begin{cases} u + v = 1, \\ u\,\log\dfrac{u}{\theta} + v\,\log\dfrac{v}{1-\theta} = \log a - \dfrac{a-1}{a}\,L, \end{cases} \tag{6.12}$$

with $u,v \in (0,1)$. Then we have to solve

$$f(u) \equiv u\log(u/\theta) + (1-u)\log((1-u) \,/\, (1-\theta)) - \log a + L(a-1)/a = 0. \tag{6.13}$$

A possible root of $f(u) = 0$ should result in a positive value of c and in $b > 1$. This imposes the conditions

$$\theta < u < \theta\,a. \tag{6.14}$$

Since $df/du > 0$ for $\theta < u \leqslant 1$, the equation (6.13) yields a single root, provided

$$f(\theta) < 0,\quad \begin{cases} f(1) > 0 & \text{if}\ \ \theta a > 1, \\ f(\theta a) > 0 & \text{if}\ \ \theta a < 1. \end{cases} \tag{6.15}$$

By these conditions in the a,θ-plane a region of admissible values is determined. For $\mu=0$ this region is sketched in Fig. 9. Its boundaries are determined by

$$\theta a = \exp\,(1-1\,/\,a), \tag{6.16}$$

and

$$a \log (1+\frac{a-1}{1-\theta a}) = \frac{a-1}{1-\theta a}. \tag{6.17}$$

In particular, for $\theta = \frac{1}{2}$ we have $1 < a < 4.3111$.

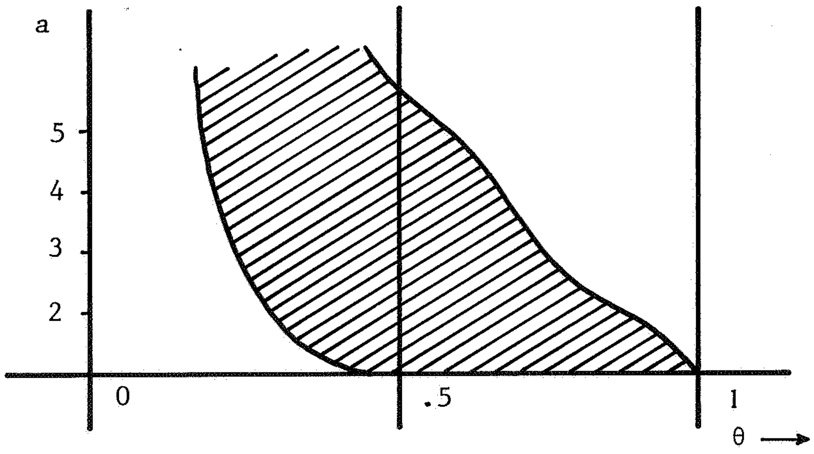

Fig. 9 Admissible values of θ, a

The Hopf line in the a,b-parameter plane is determined by (6.13) with $L=1$, i.e. by

$$u \log (u / \theta) + (1-u) \log ((1-u)/(1-\theta)) = \log a - (a-1)/a.$$

The corresponding illustration for the special case $\theta=\frac{1}{2}$ is given in Fig. 10.

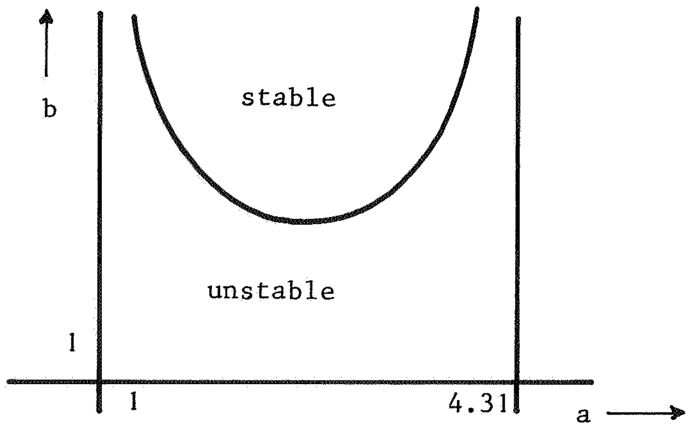

Fig. 10.

The expansion of the Hopf radius is determined by the Taylor expansion of

$$\phi(c(1+t)) = ue^{-ct} + ve^{-bct},$$

from which

$$A = c(u+bv) = 1-1/a,$$
$$AB = \frac{1}{2}c^2(u+b^2v),$$
$$AC = \frac{1}{6}c^3(u+b^3v).$$

Thus the same numerical procedure enables us to calculate (1.12). A few results are collected in Table 3 for the case $\theta=\frac{1}{2}$.

α	a	b	x_{eq}	y_{eq}	μ/R^2
24	1.209	18.373	0.102	0.021	0.01035
30	1.366	12.247	0.147	0.054	0.02376
40	1.879	7.600	0.216	0.190	0.03931
45	2.414	6.531	0.236	0.334	-0.02068
48	2.956	6.282	0.241	0.471	-0.12926
50	3.502	6.521	0.238	0.597	-0.21569
51	3.866	7.096	0.236	0.675	-0.19912
51.9	4.272	10.285	0.232	0.760	0.08046

Table 3

The expression of the Hopf radius changes sign at $\alpha=44^0.05$ ($a=2.286$) and at $\alpha=51^0.79$ ($a=4.220$) close to the boundary $\alpha=51^0.977$ ($a=4.311$). This means that close to the Hopf line we have two regions of forward Hopf bifurcation and backward Hopf bifurcation for $44^0.05<\alpha<51^0.79$. Close to the boundaries $\alpha\approx2.29$, $a \approx 4.22$ we have anomalous Hopf bifurcation with two Hopf curves. A typical case is given in Fig. 11 for $\theta=0.5$, $a=2$, $b=7.1$. In this case there is an attracting Hopf curve and a second unstable Hopf curve separating the bounded and the unbounded orbits. The corresponding position on the Hopf line is $a=2$, $b=7.231$. For $a=2$ and $b=7.06$ the two Hopf curves coalesce, annihilating each other. Thus for $a=2$, $b < 7.06$ all orbits are unbounded.

Appendix

In this appendix a theory is given of normal and anomalous Hopf bifurcation. Our starting-point is the following normal form in complex coordinates $z,\bar{z}$ where $z=x+iy$ or $z= r\exp i\theta$ in polar coordinates

$$z' = \lambda z - Q\, z^2\bar{z} + h.o.t., \tag{A1}$$

with

$$\lambda = (1+\mu)e^{i\alpha}. \tag{A2}$$

By suitable scaling it can be arranged that $|Q|=1$. Accordingly we write

$$Q = \exp i\gamma. \tag{A3}$$

From (A1) we obtain for the square modulus $s = r^2 = z\bar{z}$ the transformation

$$s' = (1+2\mu)s - 2\cos(\alpha-\gamma)s^2 + h.o.t., \tag{A4}$$

where the higher order terms contain all terms of order μ^3 and higher, assuming that $s=O(\mu)$. For $s'=s$ we obtain the well-known relation for the radius of the Hopf circle

$$s = \mu \,/\, \cos(\alpha-\gamma)$$

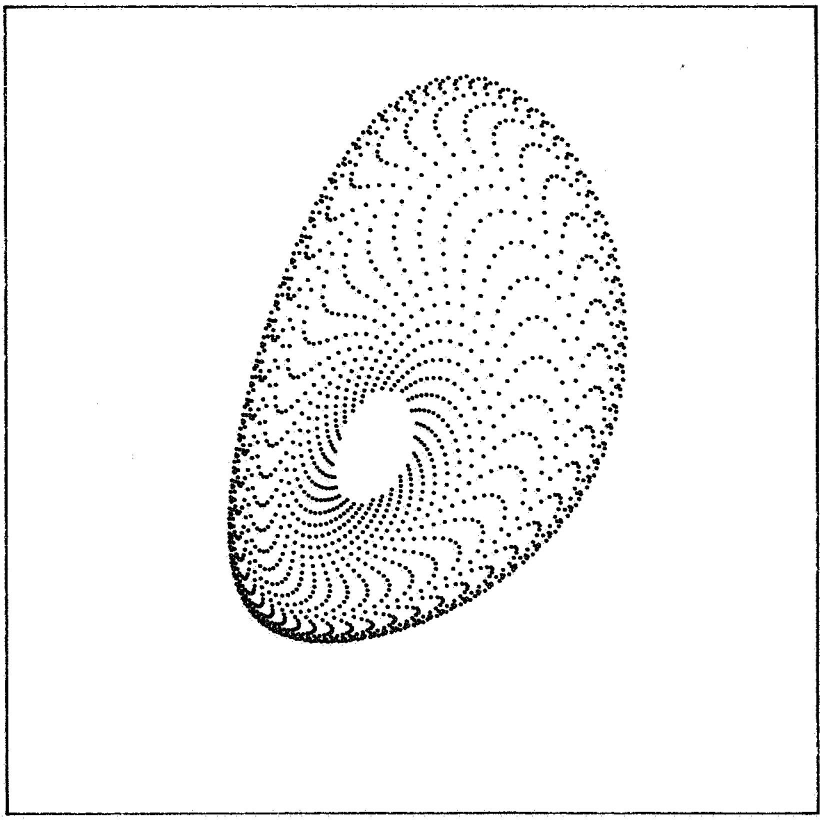

Fig. 11

HASSELL

T=Ø.5 , A=2 , B=7.1

SCALE Ø,Ø.5,Ø,Ø.5

START Ø.25,Ø.25

or

$$\frac{\mu}{R^2} = \cos(\alpha-\gamma). \tag{A5}$$

If $\cos(\alpha-\gamma)$ is not small we obtain either forward or backward Hopf bifurcation depending on the sign of $\cos(\alpha-\gamma)$. However, if $\cos(\alpha-\gamma)$ is small the analysis breaks down. It becomes necessary to extend the normal form (A1) by taking

$$z' = \lambda z - Q\, z^2\bar{z} + Q_1\, z^3\bar{z}^2 + O(z^6). \tag{A6}$$

This normal form holds when lower resonances up to the order 6 are excluded. Fortunately, this is no restriction in the host-parasitoid models. Proceeding as before, we have for $s = r^2$ the transformation

$$s' = (1+2\mu)s - 2\cos(\alpha-\gamma)s^2 + Cs^3 + h.o.t., \tag{A7}$$

where

$$C = 1 + e^{i\alpha}\overline{Q}_1 + e^{-i\alpha}Q_1.$$

For an invariant circle we should have $s'=s$. This gives at the lowest order of approximation the quadratic equation

$$C\,s^2 - 2s\cos(\alpha-\gamma) + 2\mu = 0, \tag{A8}$$

from which

$$C\,s = \cos(\alpha-\gamma) \pm\sqrt{\cos^2(\alpha-\gamma) - 2\mu C}. \tag{A9}$$

Depending on the signs of μ, C and $\cos(\alpha-\gamma)$, there may be two roots, giving two Hopf circles. One of the possibilities is sketched in the bifurcation diagram of Fig. 12

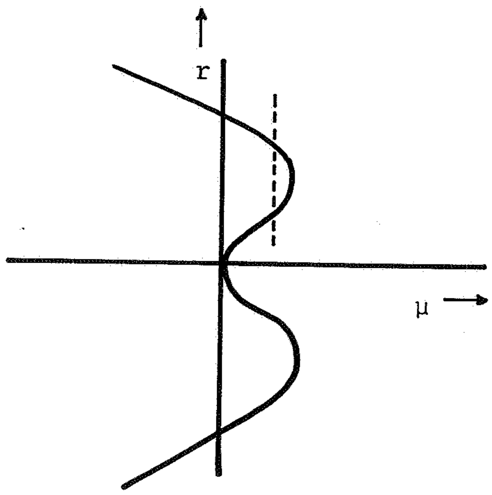

Fig. 12

The bifurcation line is determined by (A8) with $s = r^2$. If $\mu > 0$ and sufficiently small we have two Hopf circles. It can be shown that the inner circle is stable and that the outer one is unstable. If μ increases gradually, the two circles aproach each other, coalesce and disappear.

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