# Secondary Bifurcations in Systems with All-to-All Coupling

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**Abstract**

We study the existence, branching geometry, and stability of secondary branches of equilibria in all-to-all-coupled systems of differential equations, that is, equations that are equivariant under the permutation action of the symmetric group $\mathbf{S}_N$. Specifically, we consider the most general cubic-order system of this type, which arises in models of polymorphism in evolutionary biology. Primary branches in such systems correspond to partitions of $N$ into two parts, and secondary branches correspond to partitions of $N$ into three parts of sizes $a, b, c$, respectively. If $a = b = c$ then the cubic-order system is too degenerate to provide secondary branches. The cases when one of $a, b, c$ is equal to $N/3$ are special, and are not treated here. In all other cases, secondary branches exist, and the secondary branch corresponding to $(a, b, c)$ intersects the primary branches corresponding to $(a+b, c), (a, b+c)$, and $(a+c, b)$. All such secondary branches are globally unstable in the cubic-order system. Abstract considerations suggest that such secondary branches are locally unstable, which would explain the common occurrence of jump bifurcations between primary branches in numerical simulations of the cubic-order system. However such considerations do not prove instability due to the possible existence of hidden symmetries. In this paper, we carry out the calculations required to verify that the secondary branches are unstable, and we show moreover that these branches are globally unstable.

## 1 Introduction

The original motivation for this paper came from numerical simulations of differential equations modelling polymorphism in evolutionary biology. Standard models of polymorphism

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(or, on a larger scale, speciation) focus on changes in the frequency distribution of genes in response to selective pressures, Maynard Smith (1974), Hofbauer and Sigmund (1988). An alternative approach attempts to model the dynamics of phenotypes in response to changes in environmental parameters: see Vincent and Vincent (2000), Cohen and Stewart (2000), Elmhirst (1998,2001), and Stewart *et al.*(2002). Here the population is aggregated into $N$ discrete 'cells', with a vector $x_j$ representing the (mean or typical) phenotype of the $j$th cell. If the initial population is monomorphic then the ODEs representing the time-evolution of the phenotypes should be equivariant under the action of the symmetric group $\mathbf{S}_N$; that is, the model is an example of an *all-to-all coupled system.*

Typical phenomena in steady-state bifurcation of all-to-all coupled systems involve *clustering*, see Golubitsky and Stewart (2002). The cells split into two or more subsets, and all cells in a given subset behave identically. In many applications, these clustering phenomena are central to the problem. For example, in the above polymorphism models, clusters correspond to distinct morphs. In the strain structure of pathological microorganisms, Gomes and Medley (2002), clusters correspond to strains that are closely related genetically. In neurobiology, clusters correspond to groups of nerve cells that fire together, Kopell and LeMasson (1994), and it is widely believed that such synchrony has significance for neural processing function and the architecture of neural networks in the brain.

Such clustering can be explained in terms of generic symmetry-breaking bifurcations, which possess a number of 'universal' or 'model-independent' features. Typically, primary bifurcations occur to branches corresponding to dimorphism (two clusters); the bifurcations are jumps; and the mean phenotype changes smoothly but the standard deviation changes discontinuously. By 'universal' we mean that these phenomena depend only on the overall symmetry of the model and the occurrence of a suitable symmetry-breaking bifurcation, Golubitsky and Stewart (2002).

The most widely studied system of this type is the general cubic truncation of a centre manifold reduction, which takes the form (Cohen and Stewart (2000), Stewart *et al.*(2002), Golubitsky and Stewart (2002))

$$\frac{dx_i}{dt} = \lambda x_i + B(Nx_i^2 - \pi_2) + C(Nx_i^3 - \pi_3) + Dx_i\pi_2 \tag{1.1}$$

for $i = 1, \ldots, N$. Here $\lambda, B, C, D \in \mathbf{R}$ are parameters, $x_i \in \mathbf{R}$ for all $i$, the coordinates satisfy $x_1 + \cdots + x_N \equiv 0$, and

$$\pi_2 = x_1^2 + \cdots + x_N^2 \qquad \pi_3 = x_1^3 + \cdots + x_N^3$$

FIGURE 1 NEAR HERE

Simulations of (1.1) often show jump bifurcations between primary branches; Figure 1 is a typical example. This figure shows how the values of $x_1, \ldots, x_{25}$ bifurcate in the case $N = 25$. There is a rapid jump at $\lambda \sim 720$. Prior to the jump 6 of the $x_j$ are equal and positive while the other 19 are equal and negative (a typical instance of clustering). After the jump, 8 of the $x_j$ are equal and positive while the other 17 are equal and negative. Stewart *et al.*(2002) show that these jumps correspond to the loss of stability of a primary branch. They should therefore (see Golubitsky and Stewart (2002) pages 11-13) be associated with *secondary bifurcations*, in which the population is trimorphic (three distinct clusters). Specifically, in this example it corresponds to the onset of instability in the primary branch with isotropy subgroup $\mathbf{S}_6 \times \mathbf{S}_{19}$, when an eigenvalue passes through zero. In this case the kernel of the Jacobian corresponds to a $\mathbf{S}_{19}$-irreducible vector space. This breaks the $\mathbf{S}_{19}$-symmetry but not the $\mathbf{S}_6$-symmetry causing a jump bifurcation. See end of Section 2 for more details.

The aim of this paper is to make this association explicit, and to determine the geometry and stabilities of these secondary branches. On symmetry grounds we expect any secondary branches to be transcritical and unstable near the bifurcation point (see below for details); we show that in fact these branches are globally unstable. This instability provides an explanation for the prevalence of jump bifurcations in simulations.

# 2 Background

Our analysis is organized according to general principles of equivariant bifurcation theory. In this section we review the required concepts, together with some basic properties of $\mathbf{S}_N$-symmetric systems. For a detailed discussion of the basics of equivariant bifurcation theory see Golubitsky *et al.*(1988).

Consider a system of differential equations

$$\frac{dx}{dt} = F(x, \lambda) \tag{2.2}$$

where $x \in V = \mathbf{R}^N$, the vector field $F : V \times \mathbf{R} \to V$ is smooth, and $\lambda \in \mathbf{R}$ is a bifurcation parameter. Suppose that a compact Lie group $\Gamma$ acts linearly (and without loss of generality orthogonally) on $V$. Recall that $F$ *commutes* with the action of $\Gamma$ (or is $\Gamma$-*equivariant*) if

$$F(\gamma x, \lambda) = \gamma F(x, \lambda)$$

for all $\gamma \in \Gamma$ and $x \in V$. Henceforth we assume $F$ to be $\Gamma$-equivariant. The group

$$\Sigma_x = \{\gamma \in \Gamma \ : \ \gamma x = x\} \subseteq \Gamma$$

is the *isotropy subgroup* of $x \in V$. The *fixed-point space* of a subgroup $\Sigma \subseteq \Gamma$ is the subspace of $V$ defined by

$$\mathrm{Fix}(\Sigma) = \{x \in V \ : \ \gamma x = x, \ \forall\, \gamma \in \Sigma\}$$

For any $\Gamma$-equivariant mapping $F$ and any subgroup $\Sigma \subseteq \Gamma$ we have

$$F(\mathrm{Fix}(\Sigma) \times \mathbf{R}) \subseteq \mathrm{Fix}(\Sigma)$$

An isotropy subgroup of $\Gamma$ is *axial* if it has a 1-dimensional fixed-point space. An equilibrium with axial isotropy is called an *axial equilibrium*, and a branch of axial equilibria is an *axial branch*.

A basic existence theorem is the Equivariant Branching Lemma of Vanderbauwhede and Cicogna, see Golubitsky *et al.*(1988) Theorem XXIII 3.3. This states that under suitable genericity hypotheses (which we do not repeat here), steady-state bifurcation from a trivial equilibrium leads to 'primary' branches of axial equilibria for all axial subgroups of $\Gamma$.

## The Symmetric Group

We now specialize to the symmetric group, which by definition is the symmetry group for an all-to-all coupled system. Here $\Gamma = \mathbf{S}_N$ acts on $V = \mathbf{R}^N$ by permutation of coordinates:

$$\rho(x_1, \ldots, x_N) = \left(x_{\rho^{-1}(1)}, \ldots, x_{\rho^{-1}(N)}\right)$$

It is a classical result that the sums of $k$th powers

$$\pi_k = \sum_{i=1}^{N} x_i^k$$

where $k = 1, \ldots, N$ generate the polynomial $\mathbf{S}_N$-invariants over $\mathbf{R}$. Let

$$E_k = \left[x_1^k, x_2^k, \ldots, x_N^k\right]^T$$

Then the $\mathbf{S}_N$-equivariant polynomial mappings are generated over the $\mathbf{S}_N$-invariant polynomial function by $E_0, E_1, \ldots, E_{N-1}$, see Golubitsky and Stewart (2002).

In order to compute the isotropy subgroups $\Sigma_x$ of $\mathbf{S}_N$ acting on $\mathbf{R}^N$, we partition $\{1, \ldots, N\}$ into disjoint blocks $B_1, \ldots, B_k$ with the property that $x_i = x_j$ if and only if $i, j$ belong to the same block. Let $b_l = |B_l|$. Then

$$\Sigma_x = \mathbf{S}_{b_1} \times \cdots \times \mathbf{S}_{b_k}$$

where $\mathbf{S}_{b_l}$ is the symmetric group on block $B_l$. Up to conjugacy we may assume that $B_1 = \{1, \ldots, b_1\}$, $B_2 = \{b_1 + 1, \ldots, b_1 + b_2\}, \ldots, B_k = \{b_1 + b_2 + \cdots + b_{k-1} + 1, \ldots, N\}$, and that $b_1 \leq b_2 \leq \cdots \leq b_k$. Therefore conjugacy classes of isotropy subgroups of $\mathbf{S}_N$ are in one-to-one correspondence with partitions of $N$ into nonzero natural numbers arranged in ascending order. If $\Sigma$ corresponds to a partition of $N$ into $k$ blocks, then $\dim \mathrm{Fix}(\Sigma) = k$.

We restrict the action of $\mathbf{S}_N$ onto the standard irreducible $\mathbf{R}^{N-1}$, that is,

$$V_1 = \{(x_1, x_2, \ldots, x_N) \in V : \; x_1 + x_2 + \cdots + x_N = 0\} \;\cong\; \mathbf{R}^{N-1}$$

Note that

$$V = \{(x, x, \ldots, x) : \; x \in \mathbf{R}\} \oplus V_1$$

where the action of $\Gamma$ on $\{(x, x, \ldots, x) : \; x \in \mathbf{R}\}$ is trivial. The isotropy subgroups on $V_1$ remain the same as on $\mathbf{R}^N$, but the dimension of every fixed-point subspace is reduced by 1. In particular, the isotropy subgroups $\mathbf{S}_p \times \mathbf{S}_q$ where $p + q = N$ have one-dimensional fixed-point subspaces, that is, they are axial.

Let $F(x, \lambda)$ be an $\mathbf{S}_N$-equivariant vector field on $\mathbf{R}^N \times \mathbf{R}$, where $\lambda$ is a bifurcation parameter and the Jacobian $dF|_x$ is singular at $\lambda = \lambda_0$. The Equivariant Branching Lemma (Golubitsky *et al.*(1988)) implies that generically there exist branches of equilibria of $\dot{x} = F(x, \lambda)$ emanating from $\lambda = \lambda_0$, with isotropy subgroups $\mathbf{S}_p \times \mathbf{S}_q$. We call these the *primary branches.*

Elmhirst (1998, 2001) studied the Liapunov-Schmidt reduced equations for such a symmetry-breaking bifurcation (see Golubitsky *et al.*(1988)). These equations can also be interpreted as the centre manifold reduction of the ODE (Carr (1981)). Both of these reductions capture the essential features of the bifurcation by restricting and/or projecting it on to a subspace of the smallest possible dimension. The two reductions both have the same symmetry properties and hence the same general form. The centre manifold reduction preserves all dynamics, whereas the Liapunov-Schmidt reduction preserves equilibria; on the other hand the Liapunov-Schmidt reduction is smooth, whereas the centre manifold reduction can be made $C^k$ for any finite $k$. Each reduction procedure has technical advantages and disadvantages: here we prefer the center manifold reduction since this preserves stabilities.

Low order truncations of bifurcation equations can often remove structure that is present at higher order. For example, all primary branches of equilibria are unstable in any quadratic-order $\mathbf{S}_N$-equivariant system. See Golubitsky and Stewart (2002) Example 2.15, page 39. We therefore ask whether the cubic truncation (1.1) adequately captures the presence of such secondary branches and their stabilities. We will show that unless $a = b = c = N/3$, the cubic truncation is adequate in this sense (though we make no claims regarding determinacy in the sense of singularity theory, Golubitsky and Schaeffer (1985)). In this exceptional case, the question can be reduced to the known case $N = 3$, where fifth order terms are required to represent secondary branches and their stabilities adequately, Golubitsky *et al.* (1988). When truncated at cubic order— the lowest order for which the truncated equations stand any chance of being representative of generic bifurcations— the most general all-to-all coupled system on $\mathbf{R}^N$ can be written in the form (1.1), see Cohen and Stewart (2000), Stewart *et al.*(2002). Call this vector field $G$.

It turns out that this reduced system is gradient. Specifically, $G$ is the gradient of the function

$$H(x) = \frac{1}{2}\lambda\pi_2 + B\left(\frac{1}{3}N\pi_3 - \pi_2\pi_1\right) + C\left(\frac{1}{4}N\pi_4 - \pi_3\pi_1\right) + \frac{1}{4}D\pi_2^2.$$

where $\pi_i = x_1^i + \cdots + x_N^i$. The gradient nature of the dynamic implies that all attractors of $G$ are equilibria. In models of polymorphism we can view $-H$ as a 'fitness function': the stable equilibria are the local maxima of $-H$ (local minima of $H$). However, the 'fitness' of a phenotype $x_j$ is not just a function of $x_j$, but of $x_j$ in the context of $x_1, \ldots, x_N$. It can be argued that this feature of the model is biologically sensible.

Analytical computations of eigenvalues along the primary branches (Elmhirst (1998, 2001)) reveal the occurrence of zero eigenvalues, which are typically associated with secondary bifurations. For group-theoretic reasons, we expect any secondary branch to represent a split of the population into *three* subsets, on each of which $x_j$ takes the same value (depending on $\lambda$), with the three values being distinct.

Specifically, the system (1.1) is $\mathbf{S}_N$-equivariant. Primary branches correspond to axial subgroups of $\mathbf{S}_N$, which are conjugate to $\mathbf{S}_p \times \mathbf{S}_q$ where $p + q = N$. Secondary branches correspond to subgroups conjugate to $\mathbf{S}_a \times \mathbf{S}_b \times \mathbf{S}_c$ where $a + b + c = N$.

In order for a secondary branch with isotropy group $\mathbf{S}_a \times \mathbf{S}_b \times \mathbf{S}_c$ to bifurcate from a primary branch with isotropy group $\mathbf{S}_p \times \mathbf{S}_q$, we require $p = a+b, a+c$, or $b+c$. In particular, the most plausible explanation of the secondary transition in Figure 1 is that it corresponds to the onset of instability in the primary branch with isotropy subgroup $\mathbf{S}_6 \times \mathbf{S}_{19}$, when an eigenvalue passes through zero. This breaks the $\mathbf{S}_{19}$ symmetry but not the $\mathbf{S}_6$ symmetry, causing a jump bifurcation, and the most likely end result is that the state jumps to some other primary branch. In this instance, the jump takes the system to a state with $\mathbf{S}_8 \times \mathbf{S}_{17}$

symmetry, which is one of the stable primary branches at this value of $\lambda$ and is itself $\mathbf{S}_6$-invariant.

In general, the result of the jump must be some stable equilibrium (recall, the system is gradient so all attractors are equilibria). Which branch occurs depends on the geometry of the basins of attraction of any competing equilibria, and is not directly related to which secondary branches bifurcate.

If this explanation is correct (as our detailed analysis confirms) then we expect the loss of stability of the primary branch to correspond to the bifurcation of one or more secondary branches with isotropy subgroups of the form $\mathbf{S}_6 \times \mathbf{S}_b \times \mathbf{S}_{19-b}$. In fact, all such branches should bifurcate simultaneously and all of them should be unstable near bifurcation, for reasons that we now indicate.

## Local Instability of Secondary Branches

Some features of the secondary branches in this problem can be 'predicted' on general grounds of symmetry. Our computations provide considerable extra detail, but these generalities put the results in context, so we explain them briefly here.

It is known that generically, all branches of axial equilibria in an $\mathbf{S}_N$-equivariant system of ODEs are unstable close to the bifurcation point. See Golubitsky *et al.*(1988) Theorem XIII 4.4 and Golubitsky and Stewart (2002).

Primary branches in $\mathbf{S}_N$-equivariant systems (in the stated representation) are axial, with isotropy subgroups of the form $\mathbf{S}_p \times \mathbf{S}_q$ with $p+q=N$. The representation of this subgroup decomposes (see section 4) into three irreducible subspaces, of dimensions $1, p-1, q-1$ respectively: call these $W_0, W_1, W_2$. Both $\mathbf{S}_p$ and $\mathbf{S}_q$ act trivially on $W_0$. On $W_1$, the subgroup $\mathbf{S}_q$ acts trivially and $\mathbf{S}_p$ acts by its standard irreducible representation; and the same goes with $p, q$ interchanged for $W_2$.

Follow a primary branch until an eigenvalue of the Jacobian changes sign. Generically, the kernel (eigenspace) is one of $W_0, W_1, W_2$. If it is $W_0$ then the symmetry remains unbroken, and we expect a fold point in the branch. If it is $W_1$ then the $\mathbf{S}_q$ symmetry remains unbroken, but the $\mathbf{S}_p$ symmetry breaks; correspondingly for $W_2$. Consider the case $W_1$. Liapunov-Schmidt or centre manifold reduction near this bifurcation point reduces the problem to a bifurcation problem on $W_1$. This problem is equivariant under the normalizer quotient $N(\Sigma)/\Sigma$ where $\Sigma = \mathbf{S}_q$, and this quotient is isomorphic to $\mathbf{S}_p$. Therefore we expect to find a generic $\mathbf{S}_p$-equivariant bifurcation in the reduction. The generalities of equivariant bifurcation theory predict the occurrence of branches of equilibria for all axial subgroups of $\mathbf{S}_p$; that is, all subgroups $\mathbf{S}_a \times \mathbf{S}_b$ with $a+b=p$. Moreover, generically all such branches are locally unstable.

Lifting back to the original space, we obtain the generic existence of secondary branches, with isotropy subgroups $\mathbf{S}_a \times \mathbf{S}_b \times \mathbf{S}_q$ with $a+b=p$, so $a+b+q=N$. Again, generically all such branches are locally unstable.

In order to make this argument rigorous we must show that there are no 'hidden symmetries' in the sense of Stewart and Dias (2000), and check that the relevant genericity conditions hold. There seems to be no obstacle to carrying out such an analysis, but the results would still be local near the secondary bifurcation points. We therefore prefer to analyse the cubic truncation from a global point of view. This also provides explicit expressions for the eigenvalues along the secondary branches and reveals phenomena that cannot be found by a purely local analysis.

# 3 Secondary Branches: Existence

We now begin detailed computations to determine the existence, geometry, and stability of secondary branches for the system (1.1).

Any secondary branch of equilibria of (1.1) must live in some two-dimensional fixed-point subspace of the form $\mathrm{Fix}(\mathbf{S}_a \times \mathbf{S}_b \times \mathbf{S}_c)$ inside $V_1$, where $a, b, c$ are positive integers such that $a+b+c=N$. Note that we are assuming (1.1), which by definition is an ODE on the centre subspace $V_1$, so these fixed-point subspaces lie inside $V_1$. We prove that generically there are bifurcations to secondary branches of equilibria from primary branches of equilibria (guaranteed by the Equivariant Branching Lemma and existing in the two-dimensional space $\mathrm{Fix}(\mathbf{S}_a \times \mathbf{S}_b \times \mathbf{S}_c)$). In this section we determine the appropriate branching equations and find their solutions; in Section 4 we identify these solutions as forming a secondary branch of the expected kind, see Table 2.

Let $N$ be a fixed positive integer, and $a, b, c$ positive integers such that $a+b+c=N$. Define $\Sigma_1 = \mathbf{S}_a \times \mathbf{S}_{b+c}$, $\Sigma_2 = \mathbf{S}_b \times \mathbf{S}_{a+c}$, $\Sigma_3 = \mathbf{S}_c \times \mathbf{S}_{a+b}$, $\Sigma = \mathbf{S}_a \times \mathbf{S}_b \times \mathbf{S}_c$. The $\Sigma_j$ are the axial subgroups of $\mathbf{S}_N$ that contain $\Sigma$. Let

$$\mathrm{Fix}(\Sigma) = \left\{ \left( \underbrace{-\frac{c}{a}x - \frac{b}{a}y, \ldots}_{a}; \underbrace{y, \ldots}_{b}; \underbrace{x, \ldots}_{c} \right) : x, y \in \mathbf{R} \right\}$$

We restrict to $\mathrm{Fix}(\Sigma)$ the general $\mathbf{S}_N$-equivariant vector field $G$ with components of degree less than or equal to 3, see (1.1). That is, we consider the equations

$$\begin{aligned} \frac{dx}{dt} &= \lambda x + B(Nx^2 - \pi_2) + C(Nx^3 - \pi_3) + Dx\pi_2 \\ \frac{dy}{dt} &= \lambda y + B(Ny^2 - \pi_2) + C(Ny^3 - \pi_3) + Dy\pi_2 \end{aligned} \tag{3.3}$$

where

$$\pi_i = a\left(-\frac{c}{a}x - \frac{b}{a}y\right)^i + by^i + cx^i \tag{3.4}$$

for $i = 2, 3$.

The Equivariant Branching Lemma guarantees that (3.3) has branches of steady-state solutions with symmetry $\Sigma_j$, for $j = 1, 2, 3$ (since the $\Sigma_j$ are axial). Clearly

$$\mathrm{Fix}(\Sigma_1) = \left\{ \left( \underbrace{-\frac{b+c}{a}x, \ldots}_{a}; \underbrace{x, \ldots}_{b+c} \right) : x \in \mathbf{R} \right\}$$

$$\mathrm{Fix}(\Sigma_2) = \left\{ \left( x, \ldots; \underbrace{-\frac{a+c}{b}x, \ldots}_{b}; x, \ldots \right) : x \in \mathbf{R} \right\}$$

$$\mathrm{Fix}(\Sigma_3) = \left\{ \left( \underbrace{-\frac{c}{a+b}x, \ldots}_{a+b}; x, \ldots \right) : x \in \mathbf{R} \right\}$$

That is, the solutions of (3.3) with $\Sigma_1$-symmetry satisfy

$$y = x \tag{3.5}$$

those with $\Sigma_2$-symmetry satisfy

$$y = -\frac{a+c}{b}x \tag{3.6}$$

and finally those with $\Sigma_3$-symmetry satisfy

$$y = -\frac{c}{a+b}x \tag{3.7}$$

Equations (3.3) are equivariant under the normalizer quotient group $N(\Sigma)/\Sigma$, see Golubitsky *et al.*(1988). There are three possibilities for this group, depending on how $a, b, c$ are related:
(i) If $a = b = c$, then $N(\Sigma)/\Sigma \cong \mathbf{S}_3 \cong \mathbf{D}_3$.
(ii) If any two of $a, b, c$ are equal, and different from the third, then $N(\Sigma)/\Sigma \cong \mathbf{Z}_2$.
(iii) If $a \neq b \neq c \neq a$, then $N(\Sigma)/\Sigma \cong \mathbf{1}$.
Here $\mathbf{D}_3$ is the dihedral group of order 6, and $\mathbf{Z}_2$ is the cyclic group of order 2.

In the second and third cases, the cubic truncation possesses secondary branches:

**Theorem 3.1** *Suppose that $N(\Sigma)/\Sigma$ is isomorphic to $\mathbf{Z}_2$ or $\{\mathbf{1}\}$. Then equations (3.3) have a branch of equilibria with symmetry $\Sigma$. This is described by*

$$\begin{aligned} &\lambda + BN(x+y) + CN(x^2+y^2+xy) + D\pi_2 = 0 \\ &Ba + C(a-c)x + C(a-b)y = 0 \end{aligned} \tag{3.8}$$

*where*

$$\pi_2 = a\left(-\frac{c}{a}x - \frac{b}{a}y\right)^2 + by^2 + cx^2$$

**Proof:** We look for steady-state solutions of (3.3). That is, solutions of

$$\begin{aligned} &\lambda x + B(Nx^2 - \pi_2) + C(Nx^3 - \pi_3) + Dx\pi_2 = 0 \\ &\lambda y + B(Ny^2 - \pi_2) + C(Ny^3 - \pi_3) + Dy\pi_2 = 0 \end{aligned} \tag{3.9}$$

We distinguish two cases:

(i) Equilibria with $x = 0$. Then (3.9) implies

$$\begin{aligned} &B\pi_2 + C\pi_3 = 0 \\ &\lambda y + B(Ny^2 - \pi_2) + C(Ny^3 - \pi_3) + Dy\pi_2 = 0 \end{aligned}$$

where $\pi_i = a[-(b/a)y]^i + by^i$ for $i = 2, 3$. If $y = 0$, we have $(x, y, \lambda) = (0, 0, \lambda)$, the trivial solution of (3.9) for all $\lambda \in \mathbf{R}$ with the full $\mathbf{S}_N$-symmetry. If $y \neq 0$, then if $a \neq b$ we get

$$(x, y, \lambda) = \left(0, \frac{Ba}{C(b-a)}, -\frac{B^2ab(CN + Da + Db)}{C^2(b-a)^2}\right)$$

and if $a = b$ we obtain no new solutions.

(ii) If $x \neq 0$, then the first equation of (3.9) implies that

$$\lambda = B\left(\frac{\pi_2}{x} - Nx\right) + C\left(\frac{\pi_3}{x} - Nx^2\right) - D\pi_2 \tag{3.10}$$

Substituting in the second equation, we obtain

$$(y - x)[B\pi_2 + C\pi_3 + xyN(B + Cy + Cx)] = 0$$

The zeros satisfying $y = x$ have $\Sigma_1$-symmetry. We now solve

$$B\pi_2 + C\pi_3 + xyN(B + Cy + Cx) = 0 \tag{3.11}$$

This equation is equivalent to

$$[cx + (a + b)y]\, P(x, y) = 0 \tag{3.12}$$

where

$$P(x, y) = B(y - x) + C(2y^2 - x^2 - xy) + \frac{C\,[cx + (a + b)y]^2}{a^2} - \frac{(B + 3Cy)\,[cx + (a + b)y]}{a}$$

Solutions such that $cx + (a + b)y = 0$ have $\Sigma_3$-symmetry. Now $P(x, y) = 0$ implies that

$$[by + (a + c)x]\,[Ba + C(a - c)x + C(a - b)y] = 0 \tag{3.13}$$

The solutions with $\Sigma_2$-symmetry satisfy $by+(a+c)y = 0$. From $Ba+C(a-c)x+C(a-b)y = 0$ we obtain a branch of equilibria with $\Sigma$-symmetry. Finally, (3.10,3.11) imply that

$$\lambda + BN(x + y) + CN(x^2 + y^2 + xy) + D\pi_2 = 0$$

□

**Remark 3.2** Suppose that $N(\Sigma)/\Sigma \cong \mathbf{D}_3$, that is, $a = b = c$. Then (3.13) implies that there are no steady-state solutions of (3.3) except those with $\Sigma_i$-symmetry, $i = 1, 2, 3$, and the branch of trivial equilibria with $\mathbf{S}_N$-symmetry. For this case, the cubic truncation (1.1) is too degenerate to provide secondary branches. Henceforth, we exclude this case from consideration.

# 4 Secondary Branches: Stability

In this section we derive the stabilities of the secondary branch whose existence is proved in Theorem 3.1, and show that it bifurcates from the appropriate primary branches when an eigenvalue changes sign; that is, it is a genuine secondary branch. Throughout, we assume that at least two of $a, b, c$ are distinct, or equivalently that the normalizer quotient for the secondary branch under consideration is $\mathbf{1}$ or $\mathbf{Z}_2$. We begin by reviewing the stability of the solutions of the primary branches (with symmetry $\Sigma_1, \Sigma_2, \Sigma_3$). We need that information to calculate the stability of the solutions with symmetry $\Sigma$.

## Primary Branches

By Elmhirst (1998), Golubitsky and Stewart (2002), or Stewart *et al.*(2002), the equations for the branches of equilibria with $\mathbf{S}_p \times \mathbf{S}_{N-p}$-symmetry are

$$\lambda + B\mathcal{P}_1(N,p)\left(\frac{x}{p}\right) + C\mathcal{P}_2(N,p)\left(\frac{x}{p}\right)^2 + D\mathcal{P}_3(N,p)\left(\frac{x}{p}\right)^2 = 0 \tag{4.14}$$

where

$$\mathcal{P}_1(N,p) = N(2p-N), \quad \mathcal{P}_2(N,p) = N(N^2 - 3Np + 3p^2), \quad \mathcal{P}_3(N,p) = N(N-p)p$$

In order to compute the eigenvalues along this primary branch, we use the isotypic components of the action of the isotropy subgroup $\mathbf{S}_p \times \mathbf{S}_{N-p}$ to block-diagonalize the Jacobian, see Golubitsky *et al.*(1988) Theorem XII 3.5. The isotypic decomposition of $V_1$ for the action of $\mathbf{S}_p \times \mathbf{S}_{N-p}$ is

$$V_1 = W_0 \oplus W_1 \oplus W_2$$

where

$$W_0 = \mathrm{Fix}(\mathbf{S}_p \times \mathbf{S}_{N-p})$$

$$W_1 = \{(x_1, \ldots, x_p; \underbrace{0, \ldots, 0}_{N-p}) \in V_1 : \; x_1 + \cdots + x_p = 0\}$$

$$W_2 = \{(\underbrace{0, \ldots, 0}_{p}; x_{p+1}, \ldots, x_N) \in V_1 : \; x_{p+1} + \cdots + x_N = 0\}$$

The action of $\Sigma_i$ is absolutely irreducible on each $W_i$ (and trivial on $W_0$). When $p = 1$ the component $W_1$ should be omitted. Thus there are (at most) three distinct real eigenvalues, $\mu_j$, one for each $W_j$, with multiplicities $1,\ p-1,\ N-p-1$ respectively.

We obtain (4.14) with $p = a$ for the $\Sigma_1$-symmetric branch of solutions, $p = b$ for the $\Sigma_2$-symmetric branch, and $p = a+b$ for the $\Sigma_3$-symmetric solutions. Since we are restricting (1.1) to the two-dimensional space $\mathrm{Fix}(\Sigma)$, the stability in $\mathrm{Fix}(\Sigma)$ for each branch $\Sigma_i$ is determined by the eigenvalue associated with $W_0 = \mathrm{Fix}(\Sigma_i)$ and one more $\mu_i$ related to $W_1$ or $W_2$ according to $\mathrm{Fix}(\Sigma) \cap W_1 \neq \{0\}$ or $\mathrm{Fix}(\Sigma) \cap W_2 \neq \{0\}$. See Table 1.

**Remark 4.1** The eigenvalue $\mu_2$ determining the stability of the solutions with symmetry $\Sigma_1$ has multiplicity $N-a-1$, and for those with $\Sigma_2$-symmetry it has multiplicity $N-b-1$. Finally, the eigenvalue $\mu_1$ in the stability of the solutions with symmetry $\Sigma_3$ has multiplicity $a+b-1$.

## Secondary Branches: Stability in Fix($\Sigma$)

In order to obtain the stability of the solutions $X_0$ with symmetry $\Sigma$ obtained in Theorem 3.1, we begin by describing their stability in $\mathrm{Fix}(\Sigma)$ (Lemma 4.2 below).

We consider the derivative $A$ of $G$ restricted to $\mathrm{Fix}(\Sigma)$ at $X_0$, and calculate the trace and the determinant of $A$. Since $A$ is a $2 \times 2$ matrix, these specify the eigenvalues of $A$; in

| Symmetry | Stability |
|---|---|
| $\Sigma_1$ | $\mu_0 = B\mathcal{P}_1(N,a)\left(\frac{x}{a}\right) + 2\left(C\mathcal{P}_2(N,a) + D\mathcal{P}_3(N,a)\right)\left(\frac{x}{a}\right)^2$ <br> $\mu_2 = BN^2\left(\frac{x}{a}\right) + CN^2(3a-N)\left(\frac{x}{a}\right)^2$ |
| $\Sigma_2$ | $\mu_0 = B\mathcal{P}_1(N,b)\left(\frac{x}{b}\right) + 2\left(C\mathcal{P}_2(N,b) + D\mathcal{P}_3(N,b)\right)\left(\frac{x}{b}\right)^2$ <br> $\mu_2 = BN^2\left(\frac{x}{b}\right) + CN^2(3b-N)\left(\frac{x}{b}\right)^2$ |
| $\Sigma_3$ | $\mu_0 = B\mathcal{P}_1(N,a+b)\left(\frac{x}{a+b}\right) + 2\left(C\mathcal{P}_2(N,a+b) + D\mathcal{P}_3(N,a+b)\right)\left(\frac{x}{a+b}\right)^2$ <br> $\mu_1 = -BN^2\left(\frac{x}{a+b}\right) + CN^2(2N-3(a+b))\left(\frac{x}{a+b}\right)^2$ |

Table 1: Symmetry and stability (in $\mathrm{Fix}(\Sigma)$) of axial equilibria of (3.3).

particular the equilibrium is stable (within the fixed-point space) if and only if the trace is negative and the determinant is positive.

By equation (3.8)

$$\begin{aligned}
\mathrm{tr}(A) &= -B\left(\frac{\partial\pi_2}{\partial x} + \frac{\partial\pi_2}{\partial y}\right) - C\left(\frac{\partial\pi_3}{\partial x} + \frac{\partial\pi_3}{\partial y}\right) + D\left(x\frac{\partial\pi_2}{\partial x} + y\frac{\partial\pi_2}{\partial y}\right) + CN(x-y)^2 \\
\det(A) &= \left[BN(x-y) + (Dx-B)\frac{\partial\pi_2}{\partial x} - C\frac{\partial\pi_3}{\partial x} + CN(x-y)(2x+y)\right] \times \\
&\quad \left[-BN(x-y) + (Dy-B)\frac{\partial\pi_2}{\partial y} - C\frac{\partial\pi_3}{\partial y} + CN(y-x)(2y+x)\right] \\
&\quad - \left[(Dx-B)\frac{\partial\pi_2}{\partial y} - C\frac{\partial\pi_3}{\partial y}\right]\left[(Dy-B)\frac{\partial\pi_2}{\partial x} - C\frac{\partial\pi_3}{\partial x}\right]
\end{aligned} \tag{4.15}$$

Here

$$\begin{aligned}
\frac{\partial\pi_2}{\partial x} &= \frac{2c}{a}(cx+by) + 2cx & \frac{\partial\pi_2}{\partial y} &= \frac{2b}{a}(cx+by) + 2by \\
\frac{\partial\pi_3}{\partial x} &= -\frac{3c}{a^2}(cx+by)^2 + 3cx^2 & \frac{\partial\pi_3}{\partial y} &= -\frac{3b}{a^2}(cx+by)^2 + 3by^2
\end{aligned} \tag{4.16}$$

Recall that $x$ and $y$ satisfy $Ba + C(a-c)x + C(a-b)y = 0$.

The $\Sigma$-branch intersects each of the $\Sigma_i$-branches, except for certain special cases. The cases where there is no intersection between the $\Sigma$ and $\Sigma_i$ branches are: $N = 3a$ and $i = 1$, or $N = 3b$ and $i = 2$, or $2N = 3(a+b)$ (that is, $N = 3c$) and $i = 3$. For example, the $\Sigma$-branch intersects the $\Sigma_1$-branch if $x = y$ and $x = Ba/C(N-3a)$ (recall (3.5) and (3.8)). Then the value of $\lambda$ is the solution of the first equation in (3.9) when $x = y = Ba/C(N-3a)$. Similarly for $\Sigma_2$ and $\Sigma_3$. See Table 2.

In the chosen projections, the $\Sigma_3$-branches are tangent to the $\Sigma$-branch at the intersection point. This apparent tangency is an artefact of projection onto the $x$-variable.

FIGURE 2 NEAR HERE

| Branch | $x$-coordinate | Branch | $x$-coordinate | Branch | $x$-coordinate |
|---|---|---|---|---|---|
| $\Sigma_1$ | $x_1 = \frac{Ba}{C(N-3a)}$ | $\Sigma_2$ | $x_2 = \frac{Bb}{C(N-3b)}$ | $\Sigma_3$ | $x_3 = \frac{B(a+b)}{C(2N-3(a+b))}$ |

Table 2: Intersections between the branches with symmetry $\Sigma$ and the $\Sigma_i$, for $i = 1, 2, 3$.

To avoid distracting complications, we exclude from consideration the special cases $N = 3a,\ N = 3b,\ 2N = 3(a+b)$. A similar analysis can be carried out in these cases, except when $N = 3a = 3b = 3c$, which we have already excluded in Remark 3.2.

**Lemma 4.2** *Assume the conditions of Theorem 3.1, and suppose that*

$$N \neq 3a \qquad N \neq 3b \qquad 2N \neq 3(a+b) \qquad a \neq b \tag{4.17}$$

*Let $X_0$ be an equilibrium of (3.3) in the $\Sigma$-branch obtained in Theorem 3.1, and let $A = (dG)_{X_0}|_{\mathrm{Fix}(\Sigma)}$. Then*

$$\det(A) \;=\; (dx+e)\left(x - \tfrac{Ba}{C(N-3a)}\right)\left(x - \tfrac{Bb}{C(N-3b)}\right)\left(x - \tfrac{B(a+b)}{C(2N-3(a+b))}\right) \tag{4.18}$$

*where*

$$\begin{aligned} e = \;& B(N-3a)(N-3b)(2N-3a-3b)(2CNb^2 + 6Dab^2 - CN^2b \\ & -4DNab + 2CNab + 6Da^2b + 2CNa^2 - CN^2a)/(a-b)^4 \\ d = \;& -2C(N-3a)(N-3b)(2N-3a-3b)(DNb^2 - 3CNb^2 - 9Dab^2 \\ & -DN^2b + 3CN^2b + 10DNab - 3CNab - 9Da^2b - CN^3 - DN^2a \\ & +3CN^2a + DNa^2 - 3CNa^2)/(a-b)^4 \end{aligned} \tag{4.19}$$

**Proof:** Theorem 3.1 guarantees the existence of the $\Sigma$-branch of equilibria of (3.3). Conditions (4.17) guarantee that each primary branch with symmetry $\Sigma_i$ for $i = 1, 2, 3$ intersects the $\Sigma$-branch in a unique point, say $x_i$, if its coordinate is $x_i$ (in the $x$-component) as in Table 2. At each point $x_i$ one of the two eigenvalues determining the stability of the branch in $\mathrm{Fix}(\Sigma)$ is zero, so the determinant of $A$ is zero. Note that for the $\Sigma_1$-branch $\mu_2 = 0$ at $x_1$. Also $\mu_1 = 0$ for the $\Sigma_3$-branch at $x_3$, and $\mu_2 = 0$ for the intersection point $x_2$ of the $\Sigma_2$- and $\Sigma$-branches.

We can use this information to decompose $\det(A)$. There are real constants $d$ and $e$ such that

$$\det(A) = (dx+e)(x-x_1)(x-x_2)(x-x_3)$$

Using Maple we obtain the stated expressions for $d$ and $e$. □

Assume the conditions of Lemma 4.2. Thus the $\Sigma$-branch has at least one eigenvalue crossing zero at four distinct points. Three correspond to the values of $\lambda$ where a secondary bifurcation occurs (from each of the primary branches with isotropy subgroups $\Sigma_i$). It is easy to show that the fourth (which exists if $d \neq 0$, a generic condition) corresponds to the unique fold point in the the secondary branch, that is, the vertex of the parabola.

**Remark 4.3** When $a = b$, the condition (3.8) implies that $x$ is constant along the $\Sigma$-branch ($x = Ba/C(c-a)$) and only $y$ varies. Thus the analysis of Lemma 4.2 can be carried out for this case, but now we need to describe $\det(A)$ as a function of $y$. Equivalently, instead of $(a, b, c) = (a, a, N-2a)$, we take $(a', b', c') = (a, N-2a, a)$, and we can then apply Lemma 4.2.

## Secondary Branches: Full Stability

We decompose now $V_1$ into isotypic components and use the action of $\Sigma$ to block-diagonalize the Jacobian on the whole of $V_1$. The isotypic decomposition of $V_1$, for the action of $\Sigma$, is

$$V_1 = \mathrm{Fix}(\Sigma) \oplus U_1 \oplus U_2 \oplus U_3$$

where

$$U_1 = \{(x_1, \ldots, x_a; \underbrace{0, \ldots, 0; 0, \ldots, 0}_{b+c}) \in V_1 : \ x_1 + \cdots + x_a = 0\}$$

$$U_2 = \{(\underbrace{0, \ldots, 0}_{a}; y_1, \ldots, y_b; \underbrace{0, \ldots, 0}_{c}) \in V_1 : \ y_1 + \cdots + y_b = 0\}$$

$$U_3 = \{(\underbrace{0, \ldots, 0; 0, \ldots, 0}_{a+b}; z_1, \ldots, z_c) \in V_1 : \ z_1 + \cdots + z_c = 0\}$$

When $a = 1$ the component $U_1$ should be omitted. Similarly for $U_2$ if $b = 1$, and for $U_3$ if $c = 1$. The action of $\Sigma$ is absolutely irreducible on each isotypic component $U_i$, for $i = 1, 2, 3$, and trivial on $\mathrm{Fix}(\Sigma)$. Moreover, $\dim U_1 = a - 1 = \beta_1$, $\dim U_2 = b - 1 = \beta_2$ and $\dim U_3 = c - 1 = \beta_3$. Thus $(dG)_{X_0}$, when restricted to each of the $U_i$, has a real eigenvalue $\lambda_i$ with multiplicity $\beta_i$. Since $(dG)_{X_0}$ commutes with $\Sigma$,

$$(dG)_{X_0} = \begin{bmatrix} C_1 & C_2 & C_3 \\ C_4 & C_5 & C_6 \\ C_7 & C_8 & C_9 \end{bmatrix}$$

where the blocks correspond to the isotypic decomposition and $C_1, C_5, C_9$ commute with $\mathbf{S}_a, \mathbf{S}_b, \mathbf{S}_c$ respectively. Recall that if we write a square matrix $A$ of order $n$, say with rows $l_1, \ldots, l_n$, and if $A$ commutes with $\mathbf{S}_n$, then

$$A = \begin{bmatrix} l_1 \\ (12) \cdot l_1 \\ \vdots \\ (1n) \cdot l_1 \end{bmatrix}$$

where if $l_1 = (a_1, \ldots, a_n)$, then $(1i) \cdot l_1 = (a_i, a_2, \ldots, a_{i-1}, a_1, a_{i+1}, \ldots, a_n)$. Also $l_1$ is invariant under $\mathbf{S}_{n-1}$ in the last $n - 1$ entries. That is, $l_1$ is of type $(a_1, a_2, \ldots, a_2)$. Applying this to $C_1, C_5, C_9$ we get:

$$C_1 = \begin{bmatrix} \partial_1 & & & \\ & \ddots & \partial_4 & \\ & \partial_4 & \ddots & \\ & & & \partial_1 \end{bmatrix} \qquad C_5 = \begin{bmatrix} \partial_2 & & & \\ & \ddots & \partial_5 & \\ & \partial_5 & \ddots & \\ & & & \partial_2 \end{bmatrix} \qquad C_9 = \begin{bmatrix} \partial_3 & & & \\ & \ddots & \partial_6 & \\ & \partial_6 & \ddots & \\ & & & \partial_3 \end{bmatrix}$$

where

$$\begin{array}{lll} \partial_1 = (\partial G_1/\partial x_1)_{X_0} & \partial_2 = (\partial G_{a+1}/\partial x_{a+1})_{X_0} & \partial_3 = (\partial G_{a+b+1}/\partial x_{a+b+1})_{X_0} \\ \partial_4 = (\partial G_1/\partial x_2)_{X_0} & \partial_5 = (\partial G_{a+1}/\partial x_{a+2})_{X_0} & \partial_6 = (\partial G_{a+b+1}/\partial x_{a+b+2})_{X_0} \end{array}$$

The other symmetry restrictions on the $C_i$, for $i \neq 1,5,9$, imply that the rest of the matrices each have one identical entry. From this we obtain bases for each $U_i$ composed of eigenvectors of $(dG)_{X_0}$:

$$\begin{aligned}
U_1: \quad & \nu_1 = (1,-1,0,\dots,0;0,\dots,0;0,\dots,0)^T \\
& \nu_2 = (0,1,-1,0,\dots,0;0,\dots,0;0,\dots,0)^T \\
& \vdots \\
& \nu_{a-1} = (0,\dots,0,1,-1;0,\dots,0;0,\dots,0)^T \\
U_2: \quad & \psi_1 = (0,\dots,0;1,-1,0,\dots,0;0,\dots,0)^T \\
& \psi_2 = (0,\dots,0;0,1,-1,0,\dots,0;0,\dots,0)^T \\
& \vdots \\
& \psi_{b-1} = (0,\dots,0;0,\dots,0,1,-1;0,\dots,0)^T \\
U_3: \quad & \phi_1 = (0,\dots,0;0,\dots,0;1,-1,0,\dots,0)^T \\
& \phi_2 = (0,\dots,0;0,\dots,0;0,1,-1,0,\dots,0)^T \\
& \vdots \\
& \phi_{c-1} = (0,\dots,0;0,\dots,0;0,\dots,0,1,-1)^T
\end{aligned}$$

Here $T$ indicates the transpose.

Therefore the eigenvalue associated with $\nu_i$ is $\lambda_1 = \partial_1 - \partial_4$, the one associated with $\psi_i$ is $\lambda_2 = \partial_2 - \partial_5$ and the eigenvalue associated with $\phi_i$ is $\lambda_3 = \partial_3 - \partial_6$. The branching conditions (for $\Sigma$) of Theorem 3.1 yield

$$\begin{aligned}
\lambda_1 &= 3BN(x+y) + CN(2x^2+2y^2+5xy) + \tfrac{NB^2}{C} \\
\lambda_2 &= BN(y-x) + CN(y-x)(2y+x) \\
\lambda_3 &= BN(x-y) + CN(x-y)(2x+y)
\end{aligned} \tag{4.20}$$

where $x$ and $y$ are related by

$$Ba + C(a-c)x + C(a-b)y = 0 \tag{4.21}$$

**Lemma 4.4** *Assume the conditions of Lemma 4.2. Then the eigenvalues $\lambda_1, \lambda_2, \lambda_3$ of $(dG)_{X_0}$ are:*

$$\lambda_1 = J_1(x-x_2)(x-x_3) \quad \lambda_2 = J_2(x-x_1)(x-x_3) \quad \lambda_3 = J_3(x-x_1)(x-x_2) \tag{4.22}$$

*where*

$$J_1 = \tfrac{CN(3b-N)(3b+3a-2N)}{(a-b)^2} \quad J_2 = \tfrac{CN(3a-N)(3b+3a-2N)}{(a-b)^2} \quad J_3 = -\tfrac{CN(3b-N)(3a-N)}{(a-b)^2} \tag{4.23}$$

*and $x_1, x_2, x_3$ are as in Table 2.*

**Proof:** If $X_0$ corresponds to the solution of the $\Sigma$-branch (and $\Sigma_1$-branch) denoted by $x_1$ (the $x$-coordinate), then the eigenvalue $\mu_2 = BN^2(x_1/a) + CN^2(3a-N)(x_1/a)^2$ is zero and it is associated with the eigenspace

$$W_2 = \{(\underbrace{0,\dots,0}_{a}; x_{a+1},\dots,x_N) \in V_1 : \; x_{a+1} + \cdots + x_N = 0\}$$

(Recall Remark 4.1, Table 1 and Table 2.) Moreover $U_2 \subseteq W_2$ and $U_3 \subseteq W_2$. Therefore $x = x_1$ is a zero of $\lambda_2$ and $\lambda_3$. Similarly we get that $x = x_2$ is a zero of $\lambda_1$ and $\lambda_3$, and $x_3$ is a zero of $\lambda_1$ and $\lambda_2$. □

The above discussion and Lemma 4.2 lead to:

**Theorem 4.5** *Assume the conditions of Theorem 3.1, and suppose that*

$$N \neq 3a \qquad N \neq 3b \qquad 2N \neq 3(a+b) \qquad a \neq b. \tag{4.24}$$

*Let $X_0$ be an equilibrium of (3.3) in the $\Sigma$-branch obtained in Theorem 3.1, and let $B = (dG)_{X_0}$. Then the eigenvalues of $B$ determining the stability of $X_0$ are $\lambda_i$ for $i = 1, \ldots, 5$, where:*

$$\lambda_1 = J_1 \left(x - \tfrac{Bb}{C(N-3b)}\right)\left(x - \tfrac{B(a+b)}{C(2N-3(a+b))}\right) \quad \text{(multiplicity } a-1)$$

$$\lambda_2 = J_2 \left(x - \tfrac{Ba}{C(N-3a)}\right)\left(x - \tfrac{B(a+b)}{C(2N-3(a+b))}\right) \quad \text{(multiplicity } b-1)$$

$$\lambda_3 = J_3 \left(x - \tfrac{Ba}{C(N-3a)}\right)\left(x - \tfrac{Bb}{C(N-3b)}\right) \quad \text{(multiplicity } c-1)$$

$$\lambda_4\lambda_5 = (dx+e)\left(x - \tfrac{Ba}{C(N-3a)}\right)\left(x - \tfrac{Bb}{C(N-3b)}\right)\left(x - \tfrac{B(a+b)}{C(2N-3(a+b))}\right)$$

$$\lambda_4 + \lambda_5 = -B\left(\tfrac{\partial \pi_2}{\partial x} + \tfrac{\partial \pi_2}{\partial y}\right) - C\left(\tfrac{\partial \pi_3}{\partial x} + \tfrac{\partial \pi_3}{\partial y}\right) + D\left(x\tfrac{\partial \pi_2}{\partial x} + y\tfrac{\partial \pi_2}{\partial y}\right) + CN(x-y)^2$$

*Here $J_1, J_2, J_3$ are as in (4.23), the $d, e$ are as in (4.19) (of Lemma 4.2). The expressions for $\frac{\partial \pi_j}{\partial x}$ and $\frac{\partial \pi_j}{\partial y}$ appear in (4.16), where $x$ and $y$ satisfy (4.21).*

**Theorem 4.6** *Under the conditions of Theorem 4.5, the $\Sigma$-branch solutions are generically unstable. The genericity condition here is $C \neq 0$.*

**Proof:** From Theorem 4.5

$$J_1 J_2 J_3 = -C\frac{C^2 N^3 (3b-N)^2 (3b+3a-2N)^2 (3a-N)^2}{(a-b)^6}$$

and so generically $\lambda_1\lambda_2\lambda_3 = J_1J_2J_3(x-x_1)^2(x-x_2)^2(x-x_3)^2 > 0$ if $C < 0$, for the solutions of the $\Sigma$-branch (where the $x$-component is not $x_i$ for $i = 1, 2, 3$).

In order to have stable solutions, thus $C > 0$, we need $\lambda_1\lambda_2 > 0$, $\lambda_1\lambda_3 > 0$ and $\lambda_2\lambda_3 > 0$. The signs of these three products depend on $(x-x_1)(x-x_2)$, $(x-x_1)(x-x_3)$ and $-(x-x_2)(x-x_3)$. Therefore there are no values of $x$ such that all these three expressions have positive values. □

FIGURE 3 NEAR HERE

# 5 Example

Consider the example (b) of Figure 2. Thus $N = 25,\ a = 6,\ b = 2,\ c = 17$ and the parameter values are $B = 1,\ C = -0.8,\ D = -5$. Also $\Sigma = \mathbf{S}_6 \times \mathbf{S}_2 \times \mathbf{S}_{17},\ \Sigma_1 = \mathbf{S}_6 \times \mathbf{S}_{19},\ \Sigma_2 = \mathbf{S}_2 \times \mathbf{S}_{23}$ and $\Sigma_3 = \mathbf{S}_{17} \times \mathbf{S}_8$. Recall Table 2. In this case the eigenvalues of $(dG)_{X_0}$ are given by:

$$\lambda_1 = -\tfrac{1235}{2}(x - x_2)(x - x_3) \quad \lambda_2 = -\tfrac{455}{2}(x - x_1)(x - x_3) \quad \lambda_3 = \tfrac{655}{4}(x - x_1)(x - x_2)$$

$$\lambda_4\lambda_5 = (dx + e)(x - x_1)(x - x_2)(x - x_3) \qquad \lambda_4 + \lambda_5 = -\tfrac{8952}{5}x^2 - \tfrac{1941}{2}x - \tfrac{785}{4}$$

where

$$d = \frac{1118663}{4} \qquad e = \frac{544635}{8} \qquad x_1 = -\frac{15}{14} \qquad x_2 = -\frac{5}{38} \qquad x_3 = -\frac{5}{13}$$

See Figure 3 for graphs of $\lambda_1, \lambda_2, \lambda_3$ and $\lambda_4 + \lambda_5, \lambda_4\lambda_5$. The solutions on the secondary branch are always unstable, as Theorem 4.6 implies.

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# List of Figures



**Short Title**

Secondary bifurcations in coupled systems.

# Figures

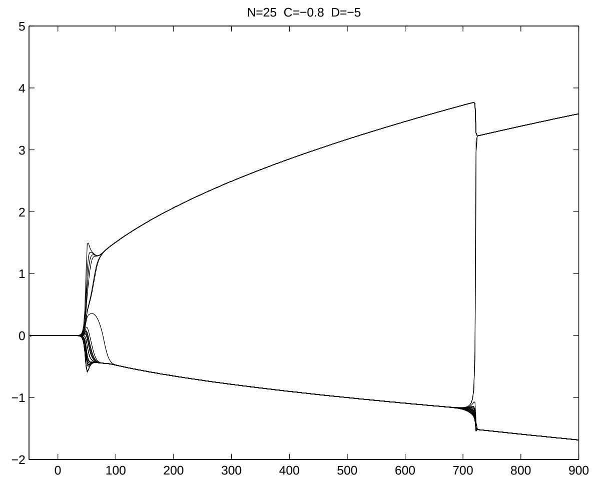
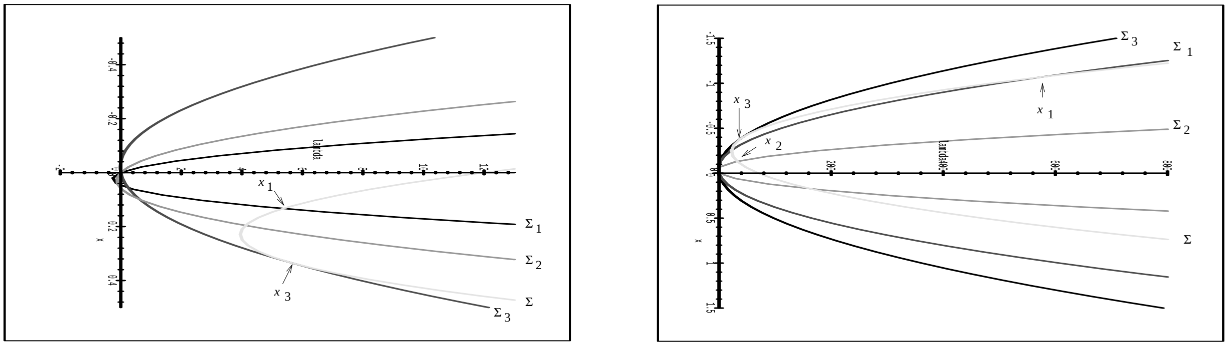
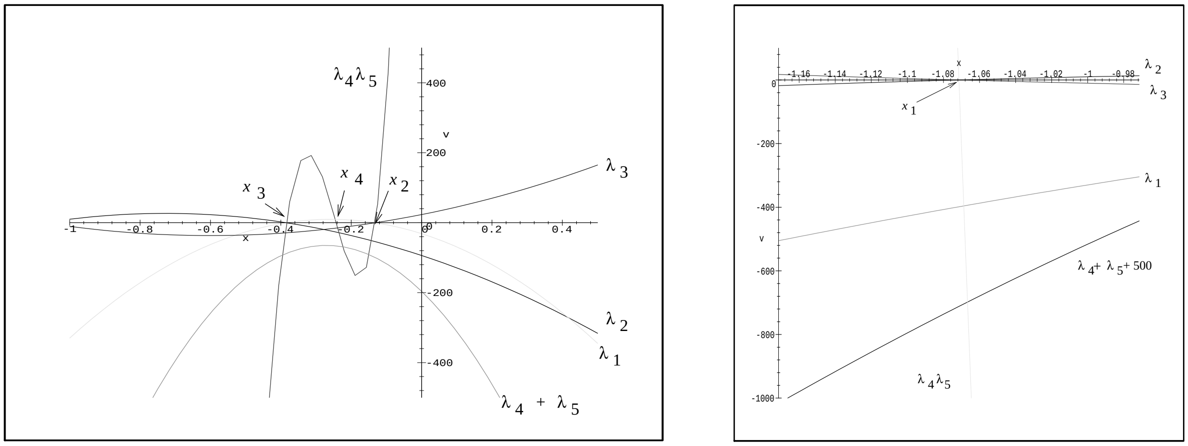



Figure 1: Symmetry-breaking bifurcation in a model with $N = 25$ cells. Time series of all cells are superposed, with $\lambda$ horizontal and $x_j$ vertical for each $j$. Note the jump bifurcation between primary branches when $\lambda \sim 720$. More detailed calculations show that prior to the jump 6 of the $x_j$ are equal and positive while the other 19 are equal and negative. After the jump, 8 of the $x_j$ are equal and positive while the other 17 are equal and negative.




(a) (b)

Figure 2: Branches of steady-state solutions of (3.3) projected on the $(x, \lambda)$-plane for: (a) $N = 9,\ a = 2,\ b = 3,\ c = 4$ and parameter values $B = -1,\ C = -5,\ D = -1$. Here $\Sigma = \mathbf{S}_2 \times \mathbf{S}_3 \times \mathbf{S}_4,\ \Sigma_1 = \mathbf{S}_2 \times \mathbf{S}_7,\ \Sigma_2 = \mathbf{S}_3 \times \mathbf{S}_6$ and $\Sigma_3 = \mathbf{S}_5 \times \mathbf{S}_4$. For this example there is no intersection between the $\Sigma$- and $\Sigma_2$-branches since $N = 3b$; (b) $N = 25,\ a = 6,\ b = 2,\ c = 17$ and parameter values $B = 1,\ C = -0.8,\ D = -5$. Here $\Sigma = \mathbf{S}_6 \times \mathbf{S}_2 \times \mathbf{S}_{17},\ \Sigma_1 = \mathbf{S}_6 \times \mathbf{S}_{19},\ \Sigma_2 = \mathbf{S}_2 \times \mathbf{S}_{23}$ and $\Sigma_3 = \mathbf{S}_8 \times \mathbf{S}_{17}$




(a) (b)

Figure 3: Graphs of $\lambda_1, \lambda_2, \lambda_3$ and $\lambda_4+\lambda_5,\ \lambda_4\lambda_5$, which determine the stability of the solutions in the $\Sigma$-branch (as a function of the $x$-variable). Here $N = 25,\ a = 6,\ b = 2,\ c = 17$ and the parameter values are $B = 1,\ C = -0.8,\ D = -5$: (a) $x \in [-1, 1/2]$ and $x_4 = -315/1294$; (b) $x \in [-15/14 - 1/10, -15/14 + 1/10]$.