Local Bifurcations in the Symmetric Model of Selection with Fertility Differences

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Abstract

The analysis of difference equations in population dynamics is frequently confined to the calculation of fixed points and the determination of their stability. In general it is not possible to deduce much about the global behavior of the system from such information. This paper presents a study of the bifurcations of fixed points in the symmetric model of selection with fertility differences. Equivalent methods can be applied to other continuous and discrete models to study the dynamics in the vicinity of fixed points in a systematic way and as a first step in an analysis of the global dynamics.

1 Introduction

Many examples of selection through fertility differences can be found in nature and it is very likely that this form of selection plays a major role in evolution. Due to the complexity of the general model several simplifications have been proposed and studied. The analysis of simplified models by Penrose (1945), Bodmer (1965) and Hadeler and Liberman (1975) is based on calculations of the location and stability of fixed points. Although this approach is standard in biology, the mathematical literature of the last 20 years provides many examples of systems exhibiting exceedingly complex and diverse behavior that cannot be analyzed in this way. Similar examples can be found in relatively simple biological models as demonstrated by May (1975, 1976). An experimental realization of complex behavior predicted by a population model can be found in Constantino, et. al. (1995, 1997). These examples provide evidence that more sophisticated methods should be employed in the study of differential and difference equations in population dynamics.

The first step in a mathematical study of a dynamical system is the analysis of local bifurcations. This information can lead to an understanding of the global bifurcations and sometimes to the complete analysis of a system. This paper provides an analysis of the local bifurcations in the symmetric model of differential fertility introduced by Hadeler and Liberman. Coefficient values at which saddle-node, period-doubling and pitchfork bifurcations occur are given.

2 The models

Consider a diploid population with discrete, non-overlapping generations. Let the genetics be governed by one locus with two alleles, labeled a and A. Moreover assume random mating and Mendelian segregation. Let x, y, and z denote the frequencies of the genotypes AA, Aa and aa respectively. In this situation we can distinguish nine mating types and in the general model of fecundity selection each mating type is assigned a fertility coefficient (see Table 1).

Using these coefficients the general model of fecundity selection takes the form

$$\begin{aligned} \phi x' &= f_{11}x^2 + \tfrac{1}{2}(f_{12}+f_{21})xy + \tfrac{1}{4}f_{22}y^2 \\ \phi y' &= \tfrac{1}{2}(f_{12}+f_{21})xy + (f_{13}+f_{31})xz + \tfrac{1}{2}f_{22}y^2 + \tfrac{1}{2}(f_{23}+f_{32})yz \\ \phi z' &= f_{33}z^2 + \tfrac{1}{2}(f_{23}+f_{32})yz + \tfrac{1}{4}f_{22}y^2 \end{aligned} \tag{1}$$

where ϕ is chosen so that $x'+y'+z'=1$.

There are at most five fixed points in this model, as shown in sections 3.3. The general model is hard to treat analytically due to the number of parameters involved and therefore several simplifications were proposed. Penrose (1949) assumed that the fertility coefficients of a mating pair is the sum of female fecundity (f_i) and male virility (m_i) and Bodmer (1965) introduced a multiplicative variation of the same assumption letting $f_{ij} = f_i m_j$. The column labeled *symmetric* in table 1 presents the assumptions made in the symmetric model proposed by Hadeler and Liberman (1975). A special case of the continuous version of the symmetric model was fully analyzed by Butler, et. al. (1982).

The symmetric model is described by the equations

$$\begin{aligned} \phi x' &= \alpha x^2 + \beta xy + \tfrac{1}{4}\delta y^2 \\ \phi y' &= \beta xy + \beta yz + \tfrac{1}{2}\delta y^2 + 2\gamma xz \\ \phi z' &= \alpha z^2 + \beta yz + \tfrac{1}{4}\delta y^2. \end{aligned} \tag{2}$$

Hadeler and Liberman give a thorough analysis of the fixed points and the following theorem summarizes their results.

Theorem 1 *In the symmetric fertility model there are*

1. *two corner (homozygotic) equilibria*
2. *at least one and at most three symmetric equilibria ($x = z$) all of which are polymorphic*
3. *none or two non-symmetric equilibria.*

The model is invariant under the transformation $x \to z$ and $z \to x$ so that the set $S_0 = \{(x,y,z) : x = z\}$ is invariant under the dynamics of system (2). The sets $x < z$ and $x > z$ are also invariant and the dynamics in $x < z$ is the mirror image of the dynamics in

$x > z$. Introducing a new variable $w = 2\frac{x}{y}$ and restricting to S_0 results in the following 1 dimensional dynamical system

$$w' = f(w) = 1 + \frac{(\alpha - \gamma)w^2}{\gamma w^2 + 2\beta w + \delta} \tag{3}$$

The original variables can be recovered using the condition that $x+y+z = 1$ which implies $x = z = w/2(1+w)$, $y = 1/(1+w)$. Setting $f(w) = w$ gives a cubic polynomial and therefore the maximum number of symmetric fixed points (i.e. fixed points on S_0) is three. Hadeler and Liberman further establish that a symmetric equilibrium $\hat{w}$ is stable in a direction transverse to S_0 if and only if $\hat{w} < (\delta/\alpha)^{\frac{1}{2}}$. The non-symmetric equilibria can be analyzed in a similar way, although conditions on their stability are rather involved.

Feldman, et. al. (1982) show that under certain restrictions the symmetric and multiplicative model are equivalent.

3 Bifurcations of Equilibria

In this section results of local bifurcation theory are applied to the symmetric model to establish the existence of saddle-node, period-doubling and pitchfork bifurcations for a range of coefficient values.

3.1 Saddle-Node Bifurcations

Consider equation (**??**) which describes the behavior of orbits of the symmetric model on the invariant subset S_0. The fixed points of this equation are the real roots of the cubic polynomial

$$Q(w) = \gamma w^3 + (2\beta - \alpha)w^2 + (\delta - 2\beta)w - \delta$$

The degenerate case in which $Q(w)$ has two real roots is of interest here. As the fertility coefficients are changed through these critical coefficient values the number of symmetric fixed points changes from 1 to 3. In general one of the new equilibria will be attracting and the other repelling in S_0 and therefore a *saddle-node* bifurcation takes place.

A 3-parameter family of the coefficients α, β, γ and δ at which such a bifurcation takes place can be obtained by expanding the polynomial $c(w-a)(w-b)^2$ and matching coefficients with $Q(w)$ leading to the following expressions for the coefficients:

$$\begin{array}{ll} \delta = b^2 ac & \beta = -\frac{c}{2}(2ab + b^2 - b^2 a) \\ \gamma = c & \alpha = (-2ba - b^2 + b^2 a + 2b + a)c \end{array}$$

Here only positive coefficients make biological sense and it is assumed that $a \neq b$. These expressions describe a codimension 1 surface in the space of positive coefficients at which the polynomial $Q(w)$ has only two roots. If the coefficients α, β, γ and δ are changed in a direction transversal to this surface a saddle-node bifurcation takes place. Since the bifurcation parameters form a codimension 1 surface in parameter space this is what will typically happen when one of the coefficients is varied and all others are held constant. As discussed in section 2 the stability of the new equilibria in the direction transversal to S_0 can be determined by checking $\hat{w}_i < (\delta/\alpha)^{\frac{1}{2}}$.

The condition that the fertility coefficient be positive implies a restriction on the values of a, b, and c used to define the bifurcation coefficients. Taking this into account a straightforward calculation implies that the bifurcation coefficients must satisfy $\delta \geq 27\,\gamma$. So if the symmetric model is assumed saddle-node bifurcations occur only for such large differences in the fecundity of mating types. This situation is unusual, but may occur during interspecific hybridization or in instances of isolated populations coming together. When $\delta < 27\gamma$ there is only one symmetric equilibrium.

A typical saddle-node bifurcation can be observed for the coefficient values $\alpha = 26$, $\beta = 6$, $\gamma = 1$ and $\delta = 72$. As δ is increased through the bifurcation value the number of symmetric fixed points changes from one to three.

3.2 Flip (period doubling) bifurcation

Hadeler and Liberman proved the existence of a period two orbit for a range of fertility coefficients. One of the ways a period two orbit can appear in a discrete dynamical system is via a period doubling bifurcation. A standard theorem of bifurcation theory (see for example Guckenheimer and Holmes, theorem 3.5.1) specifies the conditions for such bifurcation to take place. If $f_\rho : R \to R$ is a one-parameter family of mappings such that f_ρ has a fixed point w_0 with eigenvalue -1 and certain non-degeneracy conditions are satisfied, changing the parameter ρ through the value ρ_0 results in a change of stability of the family of fixed points corresponding to w_0 and in the birth of a period two orbit. The new period two orbit will emerge from the fixed point w_0 at $\rho = \rho_0$ and its stability is determined by the sign of

$$a = \left(\frac{1}{2} \left(\frac{\partial^2 f}{\partial x^2} \right)^2 + \frac{1}{3} \left(\frac{\partial^3 f}{\partial x^3} \right) \right). \tag{4}$$

With f as in (**??**) finding the coefficient values for which f' is -1 at a symmetric fixed point leads to computational difficulties since the fixed points are expressed as roots of a cubic polynomial. In the present instance the period two orbit can be calculated directly by factoring the numerator of $f^{(2)} - w$ to obtain

$$Q(w)[(\gamma\delta + 2\beta\alpha + \alpha^2)w^2 + (4\beta^2 - \gamma\delta + 2\beta\delta + 2\beta\alpha + \delta\alpha)w + \delta\alpha + 2\beta\delta + \delta^2] = Q(w)P(w).$$

Since the roots of $Q(w)$ are the fixed points of f the roots of $P(w)$ represent a period two orbit whenever they are real. The period-doubling bifurcation occurs at the coefficient values at which $P(w)$ has exactly one real root, that is when:

$$\left[(\delta\alpha + 2\beta\delta + \delta^2)(\gamma\delta + 2\beta\alpha + \alpha^2)\right]^{\frac{1}{2}} = -\frac{1}{2}(4\beta^2 - \gamma\delta + 2\beta\delta + 2\beta\alpha + \delta\alpha)$$

In general, this condition will define a codimension 1 surface in the coefficient space. Period-doubling bifurcations occur with changes in coefficients that are transversal to this manifold.

The stability of the new period 2 orbit within S_0 can be determined directly by evaluating the quantity a defined in (4). The conditions for stability in the direction transversal to S_0 are harder to determine; however, if the equilibrium that gave birth to the period two orbit is stable (respectively unstable) in this direction, then the period two orbit will also be transversally stable (respectively unstable) for coefficients sufficiently close to the bifurcation coefficients.

In their paper on the symmetric model Hadeler and Liberman propose the coefficient values $\alpha = 1$, $\beta = 2$, $\gamma = 55$, $\delta = 4$ as an example where no stable equilibria exist. However this is a case in which there is only one symmetric fixed point which is in fact "weakly" attracting. The unique real root of $Q(w)$ for these coefficient values is $\frac{2}{5}$ and the Taylor series of $f^{(2)}$ around $w = \frac{2}{5}$ is:

$$f(f(w)) = \frac{2}{5} + (w - \frac{2}{5}) - \frac{625}{288}(w - \frac{2}{5})^3 + O((w - \frac{2}{5})^4)$$

so that this point is stable in S_0. Moreover for these coefficient values $P(w)$ has only one root, $f'(\frac{2}{5}) = -1$, $a = 225/32$ and

$$\left(\frac{\partial f}{\partial \gamma}\frac{\partial^2 f}{\partial x^2} + 2\frac{\partial^2 f}{\partial x \partial \gamma} \right) = -\frac{1}{108}$$

Therefore the non-degeneracy conditions for a period-doubling bifurcations are satisfied. As γ is changed past the value of 55 the equilibrium changes stability and a new stable period two orbit appears. Numerical computations show that the new period two orbit is globally attracting. As the coefficient γ is increased further the two points of this orbit spread apart approaching some limiting values without changing stability.

Note that for the coefficient values given above with $\gamma > 55$ there are no stable fixed points. However the stable period two orbit is globally attracting and a protected polymorphism exists. This example indicates that when looking for protected polymorphisms the existence and stability of periodic orbits or even larger invariant subsets is as important as the existence and stability of fixed points. In the examples of a stable period two orbit, the population will not converge to a stable ratio of the AA, Aa and aa genotypes, but rather this ratio will oscillate with a period of two generations.

Periodic and non-periodic oscillations in population size have been induced by changing the mortality rate in a laboratory culture of the flour beetle *Tribolium* (Constantino, et. al. (1995, 1997)). In their model the initial period-doubling bifurcation is followed by a Feigenbaum (period-doubling) cascade. Since in the present case f is either strictly increasing or strictly decreasing, $f^{(2)}$ is always strictly increasing and therefore a period doubling cascade may not occur.

Hadeler and Glas (1983) have shown that in the continuous model with differential fertility every solution tends to an equilibrium. Therefore the two assumptions of discrete and continuous reproduction in time lead to models with fundamentally different behavior.

3.3 Pitchfork bifurcation

Due to the invariance of the symmetric system under the transformation $x \to z$ and $z \to x$ a saddle-node bifurcation can not occur in a direction transverse to S_0. In systems with such symmetry a pitchfork bifurcation is generic at fixed points with one eigenvalue equal to 1 (see Guckenheimer and Holmes). General results of bifurcation theory could be used to study the pitchfork bifurcation, but in the case under consideration it is simpler to use a direct approach.

Let $v = \frac{x}{y}$ and $w = \frac{z}{y}$ so that the original dynamical system becomes

$$\begin{aligned} v' &= \frac{\alpha v^2 + \beta v + \frac{1}{4}\delta}{\beta v + 2\gamma v w + \frac{1}{2}\delta + \beta w} \\ w' &= \frac{\alpha w^2 + \beta w + \frac{1}{4}\delta}{\beta v + 2\gamma v w + \frac{1}{2}\delta + \beta w} \end{aligned} \tag{5}$$

and the original variables can be recovered from the equations $x = \frac{v}{v+w+1}$, $y = \frac{1}{v+w+1}$ and $z = \frac{w}{v+w+1}$. The fixed points of this system correspond to the fixed points of the general system when $y \neq 0$ and are the solutions of the following equations:

$$\begin{aligned} w^2(\beta - \alpha) + w(\frac{1}{2}\delta - \beta) + \beta w v + 2\gamma v w^2 - \frac{1}{4}\delta = 0 \\ v^2(\beta - \alpha) + v(\frac{1}{2}\delta - \beta) + \beta w v + 2\gamma w v^2 - \frac{1}{4}\delta = 0 \end{aligned}$$

The solutions of this system can be expressed as the roots of the cubic polynomial $Q(w)$ (symmetric equilibria), and the roots of a quadratic polynomial $R(w)$ (the non-symmetric equilibria). The coefficients at which $R(w)$ has one root are the bifurcation parameters and they satisfy the following equation:

$$\gamma^2\delta^2 + (2\alpha\delta^2 - 4\alpha\beta\delta)\gamma + 4\alpha^2\beta\delta - 4\alpha^3\delta + \delta^2\alpha^2 - 4\alpha\beta\delta = 0.$$

The bifurcation coefficients again form a codimension 1 surface in the space of coefficients. If $R(w)$ has only one root it must lie on S_0 due to the symmetry of the system. Therefore all non-symmetric equilibria appear via a pitchfork bifurcation of a symmetric equilibrium. A subcritical pitchfork bifurcation can be observed at the coefficient values $\alpha = 2$, $\beta = 1$, $\delta = 2$ and $\gamma = 2$.

The symmetry of the equations also prohibits period-doubling bifurcations transverse to S_0 and Hopf bifurcations of the symmetric equilibria.

Rewriting the general model of differential fertility in the variables v and w defined in this section can be used to prove that there is a maximum of 5 equilibrium points, as conjectured by Hadeler and Liberman.

4 Conclusion

The theory of local bifurcations can be used to predict and analyze changes in the local and global behavior of differential fertility and other population dynamics models. Of particular interest in the present analysis is the flip bifurcation leading to the birth of a stable period two orbit. It shows that the continuous and discrete models of differential fertility can exhibit drastically different behavior. The stable period two orbit is also an example of an attracting set that can not be detected by an approach focusing on the stability of equilibria alone. The analysis of the saddle-node bifurcation indicates that a detailed knowledge of the bifurcation coefficients can provide information about the dynamics occurring in a certain parameter regime that might be of biological interest.

The example of Constantino, et. al. leads us to expect that bifurcations in the dynamics of a population can be induced experimentally. One possible way to change the fertility coefficients of mating pairs is by increasing the density of a population as explained by Clark and Feldman (1981).

It is possible that the global behavior of the differential fertility model is more complicated than the local bifurcation analysis suggests. The next step towards a full analysis of the model would be the computation of the stable and unstable manifolds of each equilibrium. Numerical computations of the stable and unstable manifolds at a number of different coefficient values did not yield any unusual examples.

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Note: The packages Maple V and Mathematica were used for some of the calculations. The dynamical systems analysis toolkit DSTool (v.2) was used for the numerical simulations. DSTool is available by anonymous ftp from the Center for Applied Mathematics at Cornell University, cam.cornell.edu in the pub/dstool subdirectory.

Mating Type	Fertility coefficients		Frequency
male x female	general	symmetric	
AA x AA	f_{11}	α	x^2
AA x Aa	f_{12}	β	xy
AA x aa	f_{13}	γ	xz
Aa x AA	f_{21}	β	xy
Aa x Aa	f_{22}	δ	y^2
Aa x aa	f_{23}	β	yz
aa x AA	f_{31}	γ	xz
aa x Aa	f_{32}	β	yz
aa x aa	f_{33}	α	z^2

Table 1: Fertility coefficients for the general and symmetric model