On the Neimark-Sacker bifurcation in a discrete predator-prey system

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Abstract

A two-parameter family of discrete models describing a predator-prey interaction is considered, which generalizes a model presented by Murray, consisting of two coupled nonlinear difference equations. In contrast to the original case treated by Murray, where the two populations either die out or may display unbounded growth, the general member of this family displays a somewhat wider range of behaviour. In particular, the model has a nontrivial steady state which is stable for a certain range of parameter values, which is explicitly determined, and also undergoes a Neimark-Sacker bifurcation that produces an attracting invariant curve in some areas of the parameter space, and a repelling one in others.

Keywords: Predator-prey system; difference equations; Neimark-Sacker bifurcation.

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1 Introduction

Murray's book [7] is one of the classics of mathematical biology. The range of topics and examples covered reflects the wide-ranging interests of the author. It is one of the first text books to include a detailed account of the theory of bifurcations and chaos for real one-dimensional maps (or equivalently, for first-order difference equations) at a level that is accessible to the student or non-expert who wishes to understand how this theory may be applied to model the dynamics of a single population. However, when it comes to discrete models for interacting populations, it is fair to say that both the original book and the updated two-volume version [8] provide a rather terse account, and mainly concentrate on the stability analysis of fixed points via linearization. (Although the latest version [8] does include a new fifth chapter on the application of difference equations to marital interaction.) A much fuller account of the theory of difference equations and their applications to diverse areas of science (including biology) is provided by Elaydi's two books [2, 3]; the first of these texts deals primarily with linear theory, while the second one covers bifurcations and chaos in nonlinear maps.

A very simple discrete model of the interaction between a predator P and a prey N, where it is assumed that the predator can consume the prey without limit, is given by

$$\begin{aligned} N_{t+1} &= r\,N_t \exp(-bP_t), \\ P_{t+1} &= N_t(1-\exp(-aP_t)), \end{aligned} \tag{1}$$

where $a, b, r > 0$. In chapter 4 of Murray's book [7], this system is given in the special case $b = a$, and it is noted that the model is unrealistic in the sense that solutions can grow unboundedly with t. (The linear stability analysis for this special case is also the third problem given in the exercises for section 4.11, chapter 4 of [3].) Here we consider the model (1) in the case where $b = 1$. In fact, there is no loss of generality in doing this: by rescaling N_t and P_t by the same factor (i.e. by nondimensionalizing), it is always possible to arrange it so that the parameter inside the first exponential is 1; but the parameter in the other exponential (which will still be denoted a) cannot be simultaneously removed.

Henceforth we consider the model in the nondimensional form

$$\begin{aligned} x_{t+1} &= r\,x_t \exp(-y_t), \\ y_{t+1} &= x_t(1-\exp(-ay_t)), \end{aligned} \tag{2}$$

which contains the two positive parameters a, r (which cannot be removed by rescaling). The original discrete predator-prey model discussed by Murray corresponds to the special case $a = 1$. Further analysis of this generalized model reveals a richness of behaviour not present in the original model. For the special case $a = 1$ the dynamics is uninteresting in the sense that either the two species can both die out, or the solutions can grow without bound. However, in general the model displays the more biologically relevant possibilities that the two populations can asymptotically approach positive steady state values, or move towards an attracting invariant curve in the phase plane. The latter scenario arises from a Neimark-Sacker bifurcation that takes place in the (r, a) parameter space.

The Hopf bifurcation is a well known phenomenon for a system of ordinary differential equations in two or more dimensions, whereby, when some parameter is varied, a pair of complex conjugate eigenvalues of the Jacobian at a fixed point crosses the imaginary axis, so that the fixed point changes its behaviour from stable to unstable and a limit cycle appears. In the discrete setting, the Neimark-Sacker bifurcation is the analogue of the Hopf bifurcation.

The Neimark-Sacker bifurcation occurs for a discrete system depending on a parameter, ϵ say, with a fixed point whose Jacobian has a pair of complex conjugate eigenvalues $\lambda(\epsilon)$, $\overline{\lambda}(\epsilon)$ which cross the unit circle transversally at $\epsilon = 0$; so $\rho = |\lambda|$ satisfies $\rho(0) = 1$, $\rho'(0) \neq 0$. In the two-dimensional case of a map in the (x, y) plane, if the origin of coordinates is chosen to be at the fixed point, then upon taking a complex coordinate $z = x + iy$ it can be shown that locally (near the fixed point) the map is conjugate to one of the form

$$z_{t+1} = \lambda\, z_t + \beta |z_t|^2 z_t + O(|z_t|^4), \tag{3}$$

provided that certain resonance conditions do not hold. To be more precise, any such map has the normal form (3) near $\epsilon = 0$ provided that $\lambda(0)^k \neq 1$ for $k = 1, 2, 3, 4$. Subject to the further condition that $\mathrm{Re}(\beta(0)/\lambda(0)) \neq 0$, for sufficiently small ϵ the map has an invariant closed curve enclosing the origin when $\epsilon/\mathrm{Re}(\beta(\epsilon)/\lambda(\epsilon)) < 0$. In the case that $\mathrm{Re}(\beta(0)/\lambda(0)) < 0$, the bifurcation is said to be supercritical, and there is a stable attracting invariant curve for small enough $\epsilon > 0$, while a subcritical bifurcation arises for $\mathrm{Re}(\beta(0)/\lambda(0)) > 0$, when there is a repelling invariant curve for small $\epsilon < 0$. (For more details see Theorem 5.11 in [3], and Theorems 4.5 and 4.6 in [4].)

The rest of this article is concerned with the analysis of the predator-prey model (2). In the next section we consider the realistic steady states of the model, determining their linear stability. It is easily seen that apart from the origin $(0, 0)$, the model has another realistic steady state (x^*, y^*) for $r > 1$ only, and to study this it is more convenient to use a together with the quantity

$$v = r^a - 1, \qquad v > 0, \tag{4}$$

instead of r, as a parameter in this range. The Neimark-Sacker bifurcation around this fixed point occurs along the curve $a = a_2(v)$ in the (v, a)

parameter space, where

$$a_2(v) := \left(\frac{1}{\log(1+v)} - \frac{1}{v} \right)^{-1}. \tag{5}$$

The main result proved is the following.

Theorem 1.1. *For sufficiently small ϵ, with*

$$a = \left(\frac{1}{a_2(v)} + \frac{\epsilon}{\log(1+v)} \right)^{-1}, \tag{6}$$

there is a number $v^* \approx 90.494$ such that the discrete predator-prey model (2) has an invariant closed curve encircling a positive steady state (x^*, y^*) in each of the following cases: (i) $v > v^*$, $\epsilon > 0$; (ii) $0 < v < v^*$, $\epsilon < 0$. In the first case the curve is attracting, and in the second case it is repelling.

The third section is devoted to proving the above result, and some conclusions are given in the final section.

2 Steady state analysis

We consider the discrete predator-prey system in the positive quadrant $\mathbb{R}^2_{\geq 0} = \{ (x,y) \in \mathbb{R}^2 | x \geq 0, \, y \geq 0 \}$; the equations (2) define a map from $\mathbb{R}^2_{\geq 0}$ to itself. The system has a steady state at $(0,0)$, and the linearized equations around this point take the form

$$\hat{x}_{t+1} = r \hat{x}_t, \qquad \hat{y}_{t+1} = 0.$$

This linear system is already in diagonal form, with eigenvalues $r, 0$, and so it is clear that for $r < 1$ the origin is an asymptotically stable fixed point for the nonlinear system, while it is unstable for $r > 1$.

If $x^* \neq 0$ then the steady state values (x^*, y^*) must satisfy

$$1 = r \, e^{-y^*}, \qquad y^* = x^* \, (1 - e^{-ay^*}). \tag{7}$$

Thus there are no realistic (non-negative) steady states apart from the origin if $r < 1$, while for $r > 1$ we have

$$x^* = \frac{r^a \log r}{r^a - 1}, \qquad y^* = \log r. \tag{8}$$

Henceforth we will use (x^*, y^*) to denote these values. Using the equations (7), the community matrix A (the Jacobian) at this fixed point can be written concisely as

$$A = \begin{pmatrix} 1 & -x^* \\ 1 - r^{-a} & ax^* r^{-a} \end{pmatrix}.$$

In order to analyze the characteristic polynomial $\det(A-\lambda 1)=\lambda^2-\operatorname{tr}A\,\lambda+\det A$ for $r>1$, it is most convenient to use the quantity v defined by (4), so that we have

$$\operatorname{tr}A = 1+ax^*r^{-a} = 1+\frac{\log(1+v)}{v}>0$$

and

$$\det A = x^*(1+(a-1)r^{-a}) = \left(\frac{1}{a}+\frac{1}{v}\right)\log(1+v)>0$$

for a and v both positive. The discriminant of the characteristic quadratic is

$$\Delta = \left(1-\frac{\log(1+v)}{v}\right)^2-\frac{4}{a}\log(1+v).$$

Performing a Taylor expansion in v around $v=0$, we find $\Delta=-4v/a+O(v^2)$, so that for $a>0$ we have $\Delta(v)<0$ for small enough $v>0$. More precisely, for each value of a there is a small enough value of v such that the eigenvalues λ,μ of A are a complex conjugate pair.

In general, to see where the eigenvalues are real/complex, it suffices to consider the vanishing of the discriminant, $\Delta\equiv\Delta(a,v)=0$, which defines a curve in the (v,a) parameter space. Upon solving the latter equation for a, this curve is given by

$$a=a_1(v):=\frac{4\log(1+v)}{\left(1-\frac{\log(1+v)}{v}\right)^2}. \tag{9}$$

The function $a_1(v)$ is positive for $v>0$, and has the asymptotic behaviour $a_1(v)\sim 16/v\to\infty$ as $v\to 0+$, and $a_1(v)\sim 4\log(1+v)$, as $v\to\infty$. The uppermost curve in Figure 1 is the graph of the function $a_1(v)$; it has an unique local minimum at the point $(v^\dagger,a^\dagger)$ in the parameter space, where

$$a_1'(v^\dagger)=0,\qquad v^\dagger\approx 10.955,\qquad a_1(v^\dagger)=a^\dagger\approx 16.587$$

(with the numerical values, found with Maple, being given to 3 d.p.). Clearly the eigenvalues of A are always complex for $a<a^\dagger$. Now since the discriminant can be written as $\Delta=4\log(1+v)(a_1(v)^{-1}-a^{-1})$, it is clear that the eigenvalues are complex for $a<a_1(v)$ and real for $a\geq a_1(v)$. The case of complex eigenvalues will be the most interesting for the sequel, but first we consider the case of real eigenvalues.

Proposition 2.1. *For $v>0$ the fixed point (x^*,y^*) of the system (2) is a stable node whenever $a\geq a_1(v)$.*

Proof: When $a\geq a_1(v)$ the real eigenvalues of A are $\lambda=\frac{1}{2}(\operatorname{tr}A+\sqrt{\Delta})$, $\mu=\frac{1}{2}(\operatorname{tr}A-\sqrt{\Delta})$, with $\Delta=(\operatorname{tr}A)^2-4\det A\geq 0$, and since both the trace

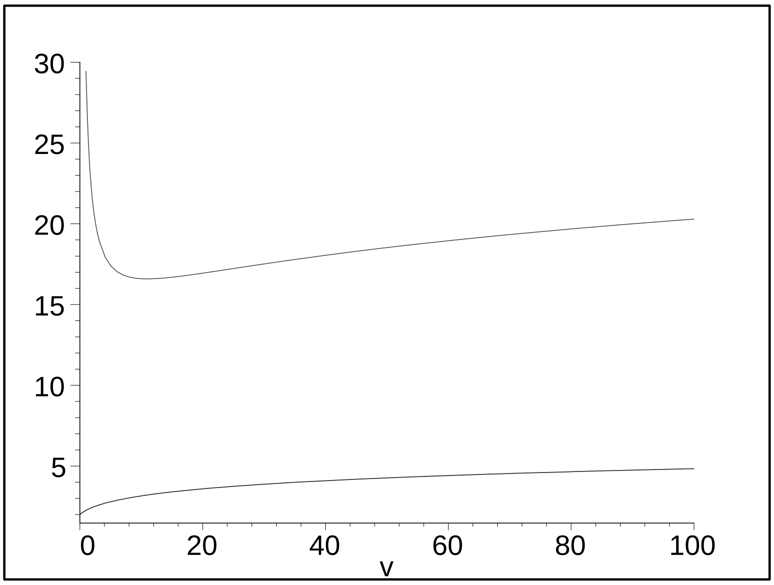

Figure 1: *The curves $a = a_1(v)$ (topmost curve) and $a = a_2(v)$ (bottom curve). For the points above the top curve, the steady state (x^*, y^*) is a stable node, while in the region in between the curves it is a stable spiral, and below the bottom curve it is an unstable spiral.*

and determinant are positive it is clear that $\lambda \geq \mu > 0$. A direct calculation shows that $2(1-\lambda) + \sqrt{\Delta} = 1 - v^{-1}\log(1+v) > 0$, and $(2(1-\lambda) + \sqrt{\Delta})^2 - \Delta = 4a^{-1}\log(1+v) > 0$, so the largest eigenvalue is $\lambda < 1$ and the result follows. $\square$

A particular example of a stable node is illustrated in Figure 2, showing an orbit of the system for $v = 2$, $a = 40$, which converges to the fixed point at $(x^*, y^*) \approx (0.04, 0.03)$.

Having dealt with the regime where the eigenvalues are real, we now treat the complex case where $\mu = \overline{\lambda}$, $\Delta < 0$. The fixed point (x^*, y^*) is a spiral in this case, and in order to determine its stability it is necessary to consider when the pair of eigenvalues have modulus one, that is when $\det A = |\lambda|^2 = |\mu|^2 = 1$, which gives $(a^{-1} + v^{-1})\log(1+v) = 1$. Solving the latter equation for a yields the curve $a = a_2(v)$ in the parameter space, with a_2 as defined in (5). This function satisfies $a_2(0) = 2$, and upon writing

$$a_2(v) = 2 + \frac{h(v)}{v - \log(1+v)}, \qquad h(v) = (v+2)\log(1+v) - 2v$$

one sees that $h'(v) = \frac{1}{v+1} + \log(1+v) - 1$, $h'(0) = 0$ and $h''(v) = \frac{v}{(v+1)^2} > 0$ for $v > 0$, so that h' is monotone increasing in this range, and hence also h is, which implies that $a_2(v) > 2$ for all positive v. Furthermore we have $a_2(v) \sim$

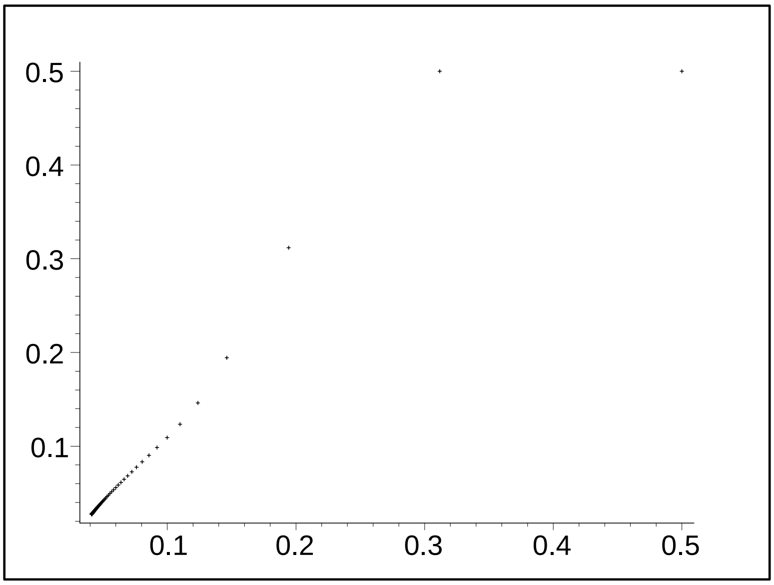

Figure 2: *An orbit of the system (2) with* $a = 40$, $r = 3^{1/40}$ *and initial values* $x_0 = 0.5 = y_0$.

$\log(1+v)$ as $v \to \infty$, and since $|\lambda| = \frac{1}{2}\mathrm{tr}\,A < 1$ on $a = a_1(v)$, by continuity it follows that the graphs of a_1 and a_2 can never meet; the two graphs are compared in Figure 1. The next two statements follow immediately from these observations.

Proposition 2.2. *For $v > 0$ the fixed point (x^*, y^*) of the system (2) is a stable spiral whenever $a_2(v) < a < a_1(v)$, and an unstable spiral for $a < a_2(v)$.*

Corollary 2.3. *When $0 < a < 2$ the steady state (x^*, y^*) is unstable for all values of $v > 0$.*

Remark 2.4. *The preceding statement includes the special case treated by Murray [7], that is the model (2) with $a = 1$, for $r > 1$.*

A particular example of a stable spiral is illustrated in Figure 3, showing an orbit of the system for $v = 8$, $a = 10$, which converges to the fixed point at $(x^*, y^*) \approx (0.25, 0.22)$.

3 Neimark-Sacker bifurcation

The Neimark-Sacker bifurcation for the system (2) occurs on the curve $a = a_2(v)$ in the parameter space, where the complex conjugate pair of eigenvalues satisfy $|\lambda| = |\mu| = 1$, and for fixed v the eigenvalues cross the unit circle as the parameter a moves through the value $a = a_2(v)$. In order to

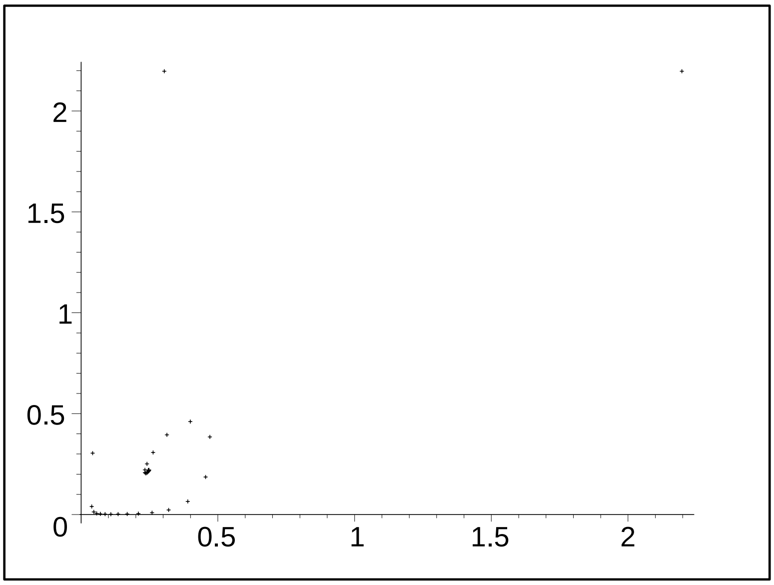

Figure 3: *An orbit of the system (2) with* $a = 10$, $r = 9^{1/10}$ *and initial values* $x_0 = 2.197 = y_0$.

study this bifurcation it is convenient to introduce a new coordinate system that are better adapted to the neighbourhood of the fixed point (x^*, y^*). To begin with we set

$$x = x^* \exp(X/a), \qquad y = y^* + Y/a$$

to obtain the coordinates $(X, Y) \in \mathbb{R}^2$ whose origin coincides with $(x, y) = (x^*, y^*)$. In these new variables the pair of difference equations (2) for the population values $(x, y) = (x_t, y_t)$ at time t is transformed to the system

$$\begin{array}{rcl} X_{t+1} & = & X_t - Y_t, \\ Y_{t+1} & = & -ay^*(1 - \exp(a^{-1}X_t)) + d \exp(a^{-1}X_t)(1 - \exp(-Y_t)), \end{array} \tag{10}$$

where the coefficients y^*, d are expressed in terms of the parameters v, a by

$$y^* = \frac{\log(1+v)}{a}, \qquad d = d(v) := \frac{\log(1+v)}{v}. \tag{11}$$

Upon solving the first equation in (10) for Y_t and substituting into the second, the above system can also be rewritten explicitly as a single second order recurrence relation for X_t, namely

$$X_{t+2} = X_{t+1} + ay^*(1 - \exp(a^{-1}X_t)) - d \exp(a^{-1}X_t)(1 - \exp(X_{t+1} - X_t)) \tag{12}$$

The iteration $t \to t+1$ for the system (10) defines an analytic map from the (X, Y) plane to itself, whose expansion around the fixed point at the origin has the form

$$\begin{pmatrix} X \\ Y \end{pmatrix} \mapsto \begin{pmatrix} 1 & -1 \\ y^* & d \end{pmatrix} \begin{pmatrix} X \\ Y \end{pmatrix} + \begin{pmatrix} 0 \\ N(X,Y) \end{pmatrix}, \tag{13}$$

where $N(X,Y)$ denotes nonlinear terms of degree two and higher. Of course, the eigenvalues of A are the same as the eigenvalues of the Jacobian of this map at the fixed point $(0,0)$, so from the 2×2 matrix

$$J = \begin{pmatrix} 1 & -1 \\ y^* & d \end{pmatrix}$$

on the right hand side of (13) we can read off the formulae

$$\operatorname{tr} A = \lambda + \mu = 1 + d, \qquad \det A = \lambda\mu = y^* + d, \tag{14}$$

which agree with the previous expressions for the trace and determinant of A.

Even more convenient is to diagonalize J and thereby replace the (X,Y) coordinates by new variables $z, \overline{z}$ defined by the linear transformation

$$X = z + \overline{z}, \qquad Y = z(1-\lambda) + \overline{z}(1-\mu). \tag{15}$$

At the level of the linearized system, this is just the transformation to the basis of eigenvectors of J. For the case of interest here, with complex conjugate eigenvalues $\mu = \overline{\lambda}$, z is a complex coordinate and $\overline{z}$ is its complex conjugate. (However, note that the formulae are still correct when the eigenvalues are real and distinct, in which case $z, \overline{z}$ should be interpreted as an independent pair of real coordinates.) The inverse of the linear change of variables (15) is given by

$$z = (\lambda - \mu)^{-1}\Big((1-\mu)X - Y\Big)$$

and the analogous (conjugate) formula for $\overline{z}$ obtained by interchanging $\lambda \leftrightarrow \mu$. Upon rewriting it in terms of z the map (13) has the form

$$F: \qquad z \mapsto \lambda\, z + \alpha_1\, z^2 + \alpha_2\, z\overline{z} + \alpha_3\, \overline{z}^2 + O(|z|^3), \tag{16}$$

where the coefficients α_j for $j = 1,2,3$ are determined by the quadratic terms in $N(X,Y)$, and the conjugate part of the map ($\overline{z} \mapsto \ldots$) is found by interchanging $z \leftrightarrow \overline{z}$ and $\lambda \leftrightarrow \mu$ in (16). For completeness, we present the quadratic coefficients here:

$$\begin{aligned} \alpha_1 &= \tfrac{1}{2(\lambda-\mu)}\,\big(d(1-\lambda)^2 - a^{-1}(2d(1-\lambda) + y^*)\big) = -\overline{\alpha}_3, \\ \alpha_2 &= \tfrac{1}{(\lambda-\mu)}\,\big(d(1-\lambda)(1-\mu) - a^{-1}(d(2-\lambda-\mu) + y^*)\big) = -\overline{\alpha}_2 \end{aligned} \tag{17}$$

We also require the explicit form of the coefficient of the cubic term $z^2\overline{z}$ in the formula (16) for the map F, namely

$$\begin{aligned}\hat{\beta} = -\tfrac{1}{2(\lambda-\mu)}\Big(d(1-\lambda)^2(1-\mu) \quad &- \quad a^{-1}(d(1-\lambda)(3-\lambda-2\mu) \\ &+ \quad a^{-2}(d(3-2\lambda-\mu)+y^*)\Big).\end{aligned} \tag{18}$$

In order to determine the nature of the Neimark-Sacker bifurcation precisely, it is necessary to put the map F into the normal form (3) by conjugating it with a suitable diffeomorphism defined locally (that is, in a neighbourhood of the fixed point at $z=0$). This can be achieved in two stages, which are given as exercises 15 and 16 for sections 5.4 and 5.5 in chapter 5 of [3], and also detailed in chapter 4 of [4]; however, the basic steps are outlined here for the sake of clarity.

The first stage is to obtain the map $G = g^{-1}\cdot F\cdot g$, by conjugating with

$$g: \qquad z \mapsto z + c_1 z^2 + c_2 z\overline{z} + c_3\overline{z}^2,$$

where the coefficients c_j are chosen in order to remove the quadratic terms appearing in (16), so that G has the form

$$G: \qquad z \mapsto \lambda\, z + O(|z|^3). \tag{19}$$

A short calculation shows that this is possible provided that $\lambda = \overline{\mu}$ is not a kth root of unity for $k=1$ or 3, in which case the quadratic coefficients of g are given by

$$c_1 = \frac{\alpha_1}{\lambda(\lambda-1)}, \qquad c_2 = \frac{\alpha_2}{\lambda(\mu-1)}, \qquad c_3 = \frac{\alpha_3}{(\mu^2-\lambda)}.$$

Moreover, the coefficients of the cubic terms in G are altered compared with those in F, so that the coefficient of $z^2\overline{z}$ in the formula (19) is

$$\beta = \hat{\beta} + 2\alpha_1 c_2 + \alpha_2(c_1+\overline{c}_2) + 2\alpha_3\overline{c}_3. \tag{20}$$

The second stage is to conjugate once more by a suitable diffeomorphism $h: z\mapsto z+O(|z|^3)$ in the neighbourhood of $z=0$, so that $H = h^{-1}\cdot G\cdot h$ has the form

$$H: \qquad z \mapsto \lambda\, z + \beta z^2\overline{z} + O(|z|^4). \tag{21}$$

Provided that $\lambda=\overline{\mu}$ is not a kth root of unity for $k=2$ or 4, this normal form can always be obtained by making a suitable choice of cubic coefficients in h. Furthermore, it is important to note that β, the coefficient of $z^2\overline{z}$ in the formula (21), is the same as the corresponding coefficient for G, as given in (20). Thus for practical purposes it is sufficient to perform only the first stage of the procedure (as long as λ is not a small root of unity). If it further holds that λ is not a 5th root of unity, then it is possible to conjugate again and reduce the map to the form $z \mapsto \lambda z + \beta z^2 \overline{z} + O(|z|^5)$ (see exercise 17 at the end of chapter 5 in [3]); Theorem 5.11 in [3] is stated under this slightly more stringent assumption, but the condition $\lambda^5 \neq 1$ is not necessary for the conclusion.

Having found the normal form of the map in the neighbourhood of the fixed point, we can now describe the bifurcation that occurs near the curve $a = a_2(v)$ in parameter space. If a new parameter ϵ is introduced so that a is given by (6), then we can regard the set of pairs (v, ϵ) as the parameter space for (2), since the transformations from (r, a) to (v, a) and from (v, a) to (v, ϵ) are invertible, and $\epsilon = 0$ corresponds precisely to the bifurcation along $a = a_2(v)$. Then by setting $\rho = |\lambda| = |\mu|$, $\theta = \arg\lambda = -\arg\mu$, we see from (14) that

$$\rho^2 = 1 + \epsilon, \qquad 2\rho\cos\theta = d + 1. \tag{22}$$

In order for the complex conjugate pair of eigenvalues to approach the unit circle transversally, it is sufficient to keep v fixed and just vary ϵ. Then $\rho = \rho(\epsilon) = \sqrt{1+\epsilon}$ satisfies $\rho(0) = 1$, $\rho'(0) \neq 0$ as required, and if the argument of λ is chosen as $\theta = \theta(\epsilon) \in [0, \pi]$ (with the dependence on v suppressed) then from (22) it is clear that $\cos\theta(0) = (d+1)/2$ and $0 < d < 1$ for $v > 0$, so that $0 < \theta(0) < \pi/3$, and hence $\lambda(0) = \exp(i\theta(0))$ is not a kth root of unity for $k = 1, 2, 3, 4$.

Finally, in order to check whether the bifurcation is supercritical or subcritical, it is necessary to find the parameter β appearing in the normal form (21) explicitly as a function of v and ϵ, so that the sign of $\mathrm{Re}(\beta/\lambda)$ at $\epsilon = 0$ can be determined. Indeed, in general, with $z = R\exp(i\phi)$ and $\gamma = \beta/\lambda$ the normal form of such a map can be rewritten as $R\exp(i\phi) \mapsto \lambda R\exp(i\phi)(1 + \gamma R^2) + O(R^4)$, so that the radial part becomes

$$R \mapsto |\lambda| R(1 + \mathrm{Re}(\gamma)R^2) + O(R^4).$$

Thus from the leading order terms one sees that for $|\lambda| > 1$ and $\mathrm{Re}(\gamma) < 0$ there is a stable invariant curve which is approximately a circle of radius $\sqrt{(1-|\lambda|)/\mathrm{Re}(\gamma)}$, corresponding to the supercritical case, while for $|\lambda| < 1$ and $\mathrm{Re}(\gamma) > 0$ there is an unstable invariant curve, approximately circular with the radius given by the same formula, which corresponds to the subcritical bifurcation. By continuity it suffices to determine the sign of γ at $\epsilon = 0$, provided that $\gamma(0) \neq 0$.

For the particular system under consideration, after a certain amount of algebra, substituting the explicit formulae (17) and (18) into (20) and then using (14) to express the numerator in terms of a and d, an expression of the form

$$\mathrm{Re}(\gamma(\epsilon)) = \frac{C_0(\epsilon) + C_1(\epsilon)a^{-1} + C_2(\epsilon)a^{-2}}{D(\epsilon)} \tag{23}$$

results, where a should be regarded as a function of v and ϵ according to (6), and the C_j and D are certain other functions of these parameters. The

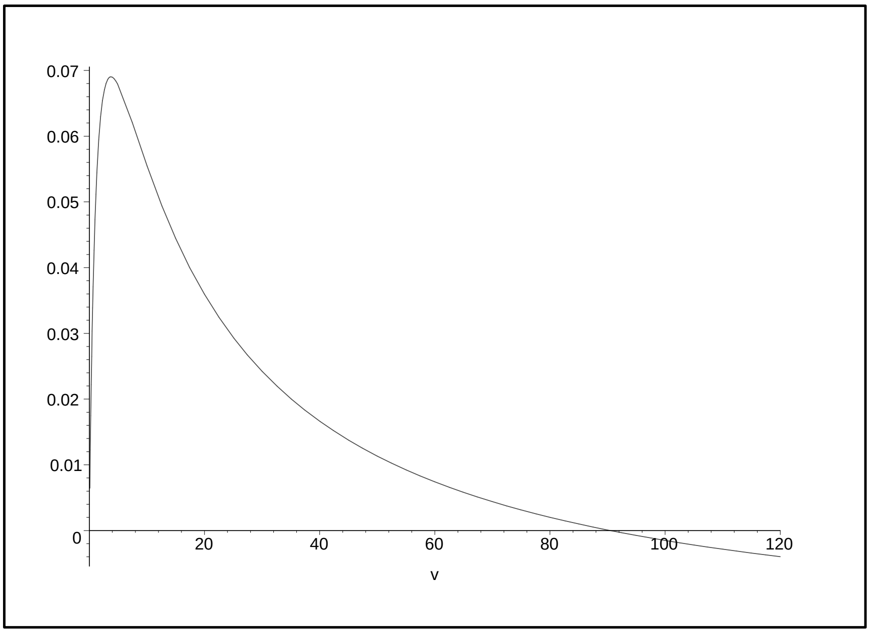

Figure 4: *Part of the graph of the function $f(v)$, defined by (24), whose sign determines the nature of the Neimark-Sacker bifurcation for the map (2). It crosses the horizontal axis at $v = v^* \approx 90.494$, marking the change from a subcritical to a supercritical bifurcation.*

denominator D is given explicitly in terms of λ and μ by

$$\begin{aligned} D &= -4\lambda^2\mu^2(\lambda-\mu)^2(\lambda-\mu^2)(\mu-\lambda^2)(1-\lambda)(1-\mu) \\ &= 4|\lambda|^4|\lambda-\overline{\lambda}|^2|\lambda-\overline{\lambda}^2|^2|1-\lambda|^2 > 0, \end{aligned}$$

so it has no effect on the sign of $\mathrm{Re}(\gamma)$. Upon setting $\epsilon = 0$ in (23), the numerator becomes

$$N_0 := C_0(0) + C_1(0)a_2^{-1} + C_2(0)a_2^{-2} = (1-d)^3(2+d)^2(3+d)\, f(v),$$

where $C_0(0) = d(1-d)^5(2+d)^2(3+d)$, $C_1(0) = d^2(3-2d)(1-d)^3(2+d)^2(3+d)$, $C_2(0) = (d^3-d^2-d-1)(1-d)^3(2+d)^2(3+d)$, and $f = f(v)$ is given by

$$f := d(1-d)^2 + a_2^{-1}d^2(3-2d) + a_2^{-2}(d^3-d^2-d-1). \tag{24}$$

Since $0 < d < 1$ for $v > 0$, the prefactor in front of $f(v)$ in the numerator N_0 is always positive, so the sign of $\mathrm{Re}(\gamma(0))$ just depends on the function $f(v)$ defined by (24) with $d = d(v)$ as in (11) and $a_2 = a_2(v)$ given by (5).

By expanding the terms in (24) around $v = 0$, one sees that this function has the leading order behaviour $f(v) = \frac{1}{12}v + O(v^2)$, and hence is positive for small $v > 0$, while for $v \to \infty$ the main contribution to its asymptotics comes from a_2^{-2}, so that $f(v) \sim -1/(\log(1+v))^2 \to 0-$ and hence is negative for large enough v. So by the intermediate value theorem, there is a positive value v^* where $f(v^*) = 0$, and numerically we find an unique zero of f, that is at $v = v^* \approx 90.494$ (to 3 d.p.). Further numerical calculations reveal that f has two stationary points, namely a maximum at $v \approx 3.753$ and a minimum at $v \approx 954.695$, the former being visible (as well as the zero at v^*) in Figure 4. Hence we see that on the one hand, f is positive for $0 < v < v^*$, corresponding to a subcritical Neimark-Sacker bifurcation for (2), where an unstable invariant curve encircles a stable fixed point for small enough $\epsilon < 0$; and on the other hand, f is negative for $v > v^*$, implying that in this range the bifurcation is supercritical and yields a stable invariant curve for sufficiently small $\epsilon > 0$. Thus the proof of Theorem 1.1 is complete.

Remark 3.1. *The Neimark-Sacker bifurcation occurs in codimension one in the two-dimensional parameter space of the map (2), along the curve* $a = a_2(v)$ *in the* (v, a) *plane. The change from subcritical to supercritical behaviour is a codimension two phenomenon that takes place at the point* (v^*, a^*)*, with* $a^* = a_2(v^*) \approx 4.754$*. Further numerical studies of particular orbits for parameter values near to this point confirm the change in stability of the invariant curves. However, empirically we find that the behaviour of the map is much more evident further away from this double bifurcation; for instance, in Figure 5, with* $v = 3^{40} - 1$*,* $a = 40$*, the stable invariant curve around the unstable fixed point at* $(x^*, y^*) \approx (1.10, 1.10)$ *is clearly visible.*

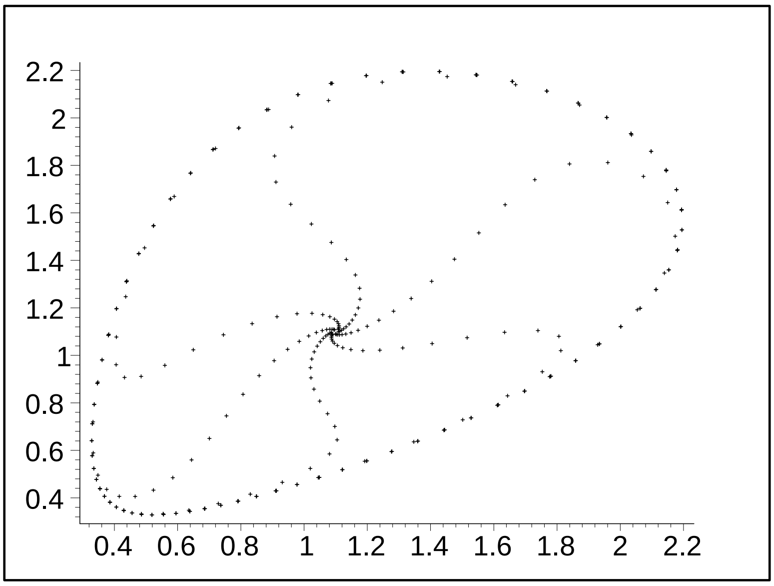

Figure 5: *An orbit for the system (2) with* $a = 40$*,* $r = 3$ *and initial values* $x_0 = 1.09 = y_0$*. The picture shows 300 iterates.*

4 Discussion

The Neimark-Sacker bifurcation is the discrete analogue of the Hopf bifurcation that occurs in continuous systems. It was discovered by Neimark [9], and independently by Sacker [10, 11], who originally studied it in connection with the stability of periodic solutions of ordinary differential equations, where it arises from the map obtained by taking a Poincaré section transverse to the periodic flow. The Hopf bifurcation is extremely important in the context of realistic continuous models of predator-prey systems and biological oscillators, where one observes periodic solutions corresponding to a closed invariant curve (that is, a limit cycle) in the phase space; see chapter 7 in [8], for a discussion. Similarly the Neimark-Sacker bifurcation is also highly relevant to the modelling of biological systems, both for understanding the stability of periodic solutions of continuous models, and as a basic phenomenon appearing in discrete models of such systems. However, in the latter case there is a slight difference compared with the continuous case, in that the generic motion on the invariant curve is not periodic in the discrete time t, because the time step need not be commensurate with the angular variable around the cycle. Moreover, the problem of computing approximations to the invariant curve is an interesting one [6]. Quite recently, the Neimark-Sacker bifurcation has also appeared in discrete models of business cycles in economics (see [12] and references).

It is worth considering the merits and disadvantages of the model (2) treated here: can the same phenomena be described by a simpler model? A good candidate for such a model is the system

$$x_{t+1} = x_t(a - bx_t - y_t), \qquad y_{t+1} = x_t y_t, \tag{25}$$

which is a rescaled version of a predator-prey model given in the exercises for chapter 5 of [3]. The steady state $(1, a-b-1)$ undergoes a Neimark-Sacker bifurcation along the line segment $a = 2b+1$ for $0 < b < 4$ in the (a, b) parameter space. However, the main disadvantage of this model is that the coordinates (x, y) do not remain non-negative under iteration: while the y coordinate of the image is positive for $x, y > 0$, the x coordinate of the image is negative whenever $a - bx - y < 0$, and if the map is restricted to the region where $a - bx - y > 0$ then it can move outside this region after one iteration.

The system (2) has the advantage that the image of non-negative population sizes is always non-negative, but in a certain parameter region, namely the subset of the area $0 < a < a_2(v)$ (at the bottom of Figure 1) where there is neither a stable fixed point nor a stable bounded invariant curve, it suffers from the same defect as the case $a = 1$ treated by Murray, namely the fact that the solutions can display unbounded growth. The origin of this defect is the existence of another invariant curve for the system, namely the axis $y = 0$, upon which the solutions for the prey population, $x_t = Ar^t$ for

$A > 0$, go to infinity for $r > 1$. However, the precise nature of the dynamics in the relevant parameter regime appears to be quite complicated. Indeed, setting $x_t = Ar^t + \hat{x}_t$, $y_t = \hat{y}_t$ and linearizing gives

$$\hat{x}_{t+1} = r\hat{x}_t - Ar^{t+1}\hat{y}_t \qquad \hat{y}_{t+1} = Aar^t\hat{y}_t,$$

and hence $\hat{y}_t = \hat{y}_0(Aa)^t r^{t(t-1)/2} \to \infty$ as $t \to \infty$ for $r > 1$, so that the solutions lying on this invariant curve are not linearly stable. However, it is rather difficult to perform a precise numerical calculation of orbits that go near to $y = 0$, because the value of y rapidly drops to zero within numerical accuracy and thereafter the dynamics is restricted to the invariant curve; yet more careful numerics shows that y_t can continue to oscillate.

In order to have a more realistic model, one can consider the system

$$\begin{array}{rcl} N_{t+1} & = & N_t \exp\left[\left(r\left(1 - \frac{N_t}{K}\right) - bP_t\right]\right., \\ P_{t+1} & = & N_t(1 - \exp(-aP_t)). \end{array} \tag{26}$$

In the case $b = a$, this is the density-dependent predator-prey model studied by Beddington et al. [1]. As for (1), by rescaling one can arrange it so that $b = 1$, and then the behaviour of the two populations just depends on the three positive parameters a, r, K. This system has the advantage that the dynamics restricted to $P_t = 0$ for all t is given by the Ricker curve $N_{t+1} = e^{r(1-N_t/K)}$, so the growth of the prey is limited and does not become unbounded. Density-dependent models of the general form $N_{t+1} = \lambda N_t g(N_t) f(P_t)$, $P_{t+1} = N_t(1 - f(P_t))$ are considered in [5], where f denotes the fraction of prey surviving predation in each generation; but for $b \neq a$ the system (26) is not of this type. The structure of this system should include both the features of the Neimark-Sacker bifurcation appearing in (1), and the period-doubling bifurcations that are inherited from the Ricker curve, so it is likely to be a rich model for further study.

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