Journal of Biological Dynamics Vol. 00, No. 00, Month-Month 200x, 1–15

Dynamic Reduction with applications to Mathematical Biology and other areas

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(26 March 2007,12 June 2007)

In a difference or differential equation one is usually interested in finding solutions having certain properties, either intrinsic properties (e.g. bounded, periodic, almost periodic) or extrinsic properties (e.g. stable, asymptotically stable, globally asymptotically stable). In certain instances it may happen that the dependence of these equations on the state variable is such that one may (1) alter that dependency by replacing part of the state variable by a function from a class having some of the above properties and (2) solve the "reduced" equation for a solution having the remaining properties and lying in the same class. This then sets up a mapping \mathcal{T} of the class into itself thus reducing the original problem to one of finding a fixed point of the mapping. The procedure is applied to obtain a globally asymptotically stable periodic solution for a system of difference equations modeling the interaction of wild and genetically altered mosquitoes in an environment yielding periodic parameters. It is also shown that certain coupled periodic systems of difference equations of extended Ricker type and also rational difference equations with a finite number of delays are also considered by reducing them to equations without delays but with a larger period. Conditions are given guaranteeing the existence and global asymptotic stability of periodic solutions.

Keywords: Dynamic Reduction, periodic difference equation, global stability, discrete delay equations, Ricker map

AMS Subject Classification: 39A11, 92D25

1. Introduction

Dynamic reduction is a problem dependent algorithm or procedure which allows one to find a solution to a problem having specified properties by reducing the problem to a sequence of simpler ones, each having a solution with the desired properties. To illustrate the technique, consider the problem of finding a *p*-periodic solution of the *p*-periodic difference equation

$$x_{n+1} = f_n(x_n), \qquad f_n : \mathbb{R}^d \to \mathbb{R}^d, \quad f_{n+p} = f_n, \ \forall n \in \mathbb{Z}^+.$$

$$(1.1)$$

We will show in certain applications that the dependence of $f_n(x)$ on x can be decomposed into a convenient form

$$f_n(x) = F_n(x, g_n(x)) \tag{1.2}$$

such that for each $v = \{v_0, v_1, \ldots, v_{p-1}\}$ in a certain class of *p*-periodic sequences \mathcal{P}_p , the "reduced" equation

$$x_{n+1} = F_n(x_n, g_n(v_n))$$
(1.3)

Journal of Biological Dynamics ISSN: 1751-3758 print/ISSN 1751-3766 online © 200x Taylor & Francis http://www.tandf.co.uk/journals DOI: 10.1080/1751375YYxxxxxxx

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 $^{^{\}dagger}$ Supported by University of Southern California, Letters Arts and Sciences Faculty Development Grant. The author thanks Cymra Haskell for several helpful discussions and the referees for several constructive suggestions.

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has a unique p-periodic solution $v^* \in \mathcal{P}_p$. One then has an induced mapping

$$\mathcal{T}: \mathcal{P}_p \to \mathcal{P}_p, \qquad v^* = \mathcal{T}(v).$$
 (1.4)

Clearly, a fixed point of the map (1.4) is equivalent to a *p*-periodic solution of (1.1). Throughout the presentation the function "g" will be used solely to indicate the grouping of the state variables on which the reduction is performed. In certain cases, with proper choice of the function "g", the image under the map \mathcal{T} will have all the desired stability properties.

Linearization of a difference or differential equation is a form of dynamic reduction : about a solution $\phi(t) \equiv 0$,

$$x_{n+1} = f_n(x_n) = Ax_n + g_n(x_n), \quad \text{or}$$
$$x' = f(t, x) = Ax + g(t, x)$$

or about a periodic solution $\phi(t)$,

$$y_{n+1} = f'_n(\phi_n)y_n + g_n(y_n), \quad \text{or}$$

$$y' = \partial_x f(t, \phi(t))y + g(t, y).$$

In the following sections we consider some applications of the technique to various problems. The first involves a model describing the interaction between wild and genetically altered mosquitoes in a periodically varying environment. Under certain conditions we find a globally attracting periodic state yielding a solution to a coupled system of two equations of Ricatti/Ricker type. In subsequent sections we apply dynamic reduction to other systems including systems of Ricker equations with delays and rational difference equations with delays. In certain instances large systems may be completely decoupled thus reducing their solution to an application of known results.

1.1. Stability

Throughout this work, we mean $\mathbb{R}^+ = [0, \infty)$ and $\mathbb{R}^+_0 = (0, \infty)$. While the theorem to follow is quite general, we will restrict ourselves to the setting most common in problems in Mathematical Biology where the state variable x lies in $(\mathbb{R}^+_0)^d$ or $(\mathbb{R}^+)^d$. By global asymptotic stability (GAS) of a periodic orbit $v = \{v_0, v_1, \ldots, v_{p-1}\}$ we shall mean that v globally attracts all solutions starting in $(\mathbb{R}^+)^d$ and is locally exponentially asymptotically stable.

That GAS of a periodic solution of (1.1) (or equivalently (1.2)) does not immediately follow from the GAS of the same solution of (1.3) is seen from the following simple example. Consider an autonomous Ricker equation

$$x_{n+1} = x_n e^{g(x_n) - x_n} \doteq F(x_n, g(x_n)), \qquad 0 < g(x) < 2.$$
(1.5)

If we let g(x) = x then every $v \in (0, 2)$ is a GAS fixed point of (1.3) on \mathbb{R}_0^+ , but not of (1.2). However, with a smallness condition on g', e.g. $g(x) = \alpha + \epsilon x$, $\alpha \in (0, 2), 0 < \epsilon << 1$, the fixed point $x^* = \alpha/(1-\epsilon) \in (0, 2)$ and is a GAS solution of (1.2) with respect to \mathbb{R}_0^+ .

In order to quantify this smallness condition let $x^* = \{x_n^*\}$ be a fixed point of \mathcal{T} and hence a periodic point of (1.1) which we write, taking into account (1.2), as

$$x_{n+1}^* = F_n(x_n^*, g_n(x_n^*)).$$
(1.6)

Notation: For $\mathcal{U} \subset (\mathbb{R}^+_0)^d$ and a periodic vector valued sequence of functions $V = \{V_1, V_2, \ldots, V_{p-1}, V_p = V_0\}$ with $V_n : \mathcal{U} \to (\mathbb{R}^+)^d$ we define $|V|_0 \doteq \max_{n=1,\ldots,p} \sup_{u \in \mathcal{U}} |V_n(u)|$. For a fixed $g = \{g_1, g_2, \ldots, g_{p-1}\}$ with $g_n : \mathcal{U} \to (\mathbb{R}^+)^s$, and $F = \{F_1, \ldots, F_{p-1}\}$ with $F_n = F_n(\xi, g_n(\eta))$ define

 $|F|_0 \doteq \max_{n=1,\dots,p} \sup_{\xi,\eta \in \mathcal{U}} |F_n(\xi, g_n(\eta))|$. For $F = F(x, g(\xi))$, we will use $\partial_2 F$ and $\partial_g F$ interchangeably to mean differentiation with respect to the second argument.

We now state a theorem which will be used to establish GAS in the applications to follow.

THEOREM 1.1 Assume there are convex compact $K_n \in (\mathbb{R}^+)^d$ such that $f_n : K_n \to K_{n+1}, g : K_n \to \Gamma$ (where the subscripts are interpreted mod p and $\Gamma \subset (\mathbb{R}^+)^s$ is convex and compact) and assume every initial point $x_0 \in (\mathbb{R}^+_0)^d$ is ultimately mapped by (1.1) into one of the K_n . Assume F_n and g_n are C^1 functions. Define \mathcal{P}_p to be that subset of p-periodic sequences such that

$$v \in \mathcal{P}_p \implies v = (v_0, v_1, \dots, v_{p-1}) \in \mathcal{D} = K_0 \times K_1 \times \dots \times K_{p-1}$$

Then, if $|\partial_2 F g'|_0$ is sufficiently small,

(i) the mapping $\mathcal{T}: \mathcal{P}_p \to \mathcal{P}_p$ is a contraction and thus there is a unique fixed point $\mathcal{T}(v^*) = v^*$ and (ii) v^* is a GAS periodic point of (1.1).

Remark 1.1 Item (ii) does not immediately follow from (i). A further reduction on the size of $|\partial_2 F g'|_0$ may be required.

Proof : For $v \in \mathcal{P}_p$ let us denote by y(v) the image of v under \mathcal{T} , $y(v) = \mathcal{T}(v)$, i.e. $y_{n+1}(v) = F_n(y_n(v), g_n(v)) \doteq H_n(y_n(v))$. Then expressing the periodicity of y(v), one has

$$y_{0}(v) = H_{p-1} \circ H_{p-2} \circ \cdots \circ H_{1} \circ H_{0}(y_{0}(v))$$

$$y_{1}(v) = H_{0} \circ H_{p-1} \circ \cdots \circ H_{2} \circ H_{1}(y_{1}(v))$$

$$\cdots \qquad \cdots$$

$$y_{p-1}(v) = H_{p-2} \circ H_{p-3} \circ \cdots \circ H_{0} \circ H_{p-1}(y_{p-1}(v))$$
(1.7)

Letting D_v denote differentiation,

$$D_{v}y_{n+1}(v) = D_{v}H_{n}(y_{n}(v)) = D_{v}F_{n}(y_{n}(v), g_{n}(v))$$

$$= \partial_{1}F_{n}(y_{n}(v), g_{n}(v))D_{v}y_{n}(v) + \partial_{2}F_{n}(\cdots)D_{v}g_{n}(v)$$

$$= \Delta_{n}D_{v}y_{n}(v) + h_{n}, \quad \text{where}$$

$$|h_{n}| \leq \sup_{v} |\partial_{2}F_{n}(y_{n}(v), g_{n}(v))| = \mathcal{O}(|\partial_{2}F|g'|_{0}), \quad \text{and} \quad (1.8)$$

$$\Delta_n = \Delta_n(y, v) \doteq \partial_1 F_n(y_n(v), g_n(v)).$$
(1.9)

Thus, from (1.7),

$$D_v y_0(v) = \Delta_{p-1} \Delta_{p-2} \cdots \Delta_1 \Delta_0 D_v y_0(v)(v) + \mathcal{O}(|\partial_2 F g'|_0)$$
$$\doteq \Delta^{(0)} D_v y_0(v)(v) + \mathcal{O}(|\partial_2 F g'|_0) .$$

Repeating this for subsequent expressions under (1.7) one obtains

$$D_{v}y_{k}(v) = \Delta^{(k)}D_{v}y_{k}(v)(v) + \mathcal{O}(|\partial_{2}F g'|_{0}), \quad k = 0, \dots, p-1, \quad \text{where}$$
(1.10)
$$\Delta^{(k)} = \Delta^{(k)}(y, v) = \Delta_{k+p-1}\Delta_{k+p-2}\cdots\Delta_{k+1}\Delta_{k},$$

where all subscripts are interpreted "mod p". The $\Delta^{(k)}$ all share the same characteristic polynomial [3, p. 320] and hence the same spectrum $\sigma(*)$. From the assumed *exponential* asymptotic stability of y(v) as a periodic point of (1.3), one has

$$\sigma(\Delta^{(k)}) \subset \{ z \in \mathbb{C} : |z| \le \alpha < 1 \} .$$

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Thus $(I - \Delta^{(k)})$ has a bounded inverse and from (1.10),

$$D_v y_k(v) = (I - \Delta^{(k)})^{-1} \mathcal{O}(|\partial_2 F g'|_0) .$$
(1.11)

Next we define a norm in \mathcal{P}_p to be

$$||v|| \doteq \max(|v_0|, |v_1|, \dots, |v_{p-1}|)$$

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Then it follows from (1.11) that for $\delta \in (0, 1)$ and $|\partial_2 F g'|_0$ sufficiently small,

$$|D_v y_k(v)| \le \delta,$$

and from the Mean Value estimate,

$$|y_k(u) - y_k(w)| \le \sup_{t \in [0,1]} |D_v y_k(v_t)| \ \|u - w\| \le \delta \|u - w\|, \qquad v_t = tw + (1-t)u, \tag{1.12}$$

for any pair $u, w \in \mathcal{P}_p$. Thus,

$$||y(u) - y(w)|| \le \delta ||u - w||,$$
 i.e. $||\mathcal{T}(u) - \mathcal{T}(u)|| \le \delta ||u - w||$

and \mathcal{T} is a contraction.

It remains to prove that the unique fixed point v^* of \mathcal{T} is GAS as a solution of (1.2). We first prove v^* is asymptotically stable. The matrix of the equation of first variation of (1.2) at v^* is

$$= \partial_1 F_n(v_n^*, g_n(v_n^*)) + \partial_2 F_n(v_n^*, g_n(v_n^*)) D_v g_n(v_n^*)$$

$$= \Delta_n(v^*, v^*) + \mathcal{O}(|\partial_2 F g'|_0) .$$
(1.13)

By the same argument given above we see that the spectrum of $\Delta^{(n)}(v^*, v^*)$ is independent of n and lies inside the unit circle in the complex plane.

We finally show v^* is globally attracting. Let $\mathcal{B} = \mathcal{B}(v^*)$ be the basin of attraction of v^* . Since \mathcal{B} is open, from (1.12) with $w = v^*$, it follows that for δ sufficiently small the entire image under \mathcal{T} of \mathcal{P}_p lies in \mathcal{B} , $\mathcal{T}(\mathcal{P}_p) \subset \mathcal{B}$. Thus for each $v \in \mathcal{P}_p$ there exists a $T(v) \in \mathbb{Z}^+$ such that the solution x_n of (1.3) with $x_0 = v_0$ lies in \mathcal{B} for n = T(v) and by continuity, some open neighborhood of v, $\mathcal{U}(v)$ is carried into \mathcal{B} in the same number of iterations : symbolically,

$$\mathcal{U}(v) \cdot T(v) \subset \mathcal{B} .$$

Let $\{\mathcal{U}_1 \doteq \mathcal{U}(v^{(1)}), \mathcal{U}_2, \ldots, \mathcal{U}_k\}$ be a finite sub-cover of \mathcal{P}_p and define $T = \max_{i=1,\ldots,k} \{T_i \doteq T(v^{(i)})\}$. Thus every initial point $v \in \mathcal{P}_p$ is mapped by (1.3) into \mathcal{B} upon τ iterations, $0 \leq \tau \leq T$ and the same will remain true for (1.2) provided $|\partial_2 F g'|_0$ is sufficiently small. A sufficient (but not necessary) condition to accomplish this would be to assume |g'| small.

Remark 1.2

- (a) The estimate (1.12) is the very raison $d \hat{e}tre$ for the reduction method. The spectrum σ of the product of $F_x(x, y)$'s along a periodic sequence does not, in general, lie inside the unit circle in the complex plane. What the reduction method accomplishes is that for each fixed $t \in (0, 1)$ the solution of (1.3) with $v = u_t$ "runs" over to the GAS periodic orbit y(v) of that system and it is there that $|\sigma| < 1$.
- (b) In certain cases, notably rational difference equations (Section 3.3), it is possible it achieve the smallness condition on $|\partial_2 F g'|_0$ without making $|g'|_0$ small, c.f. (3.13).

The next lemma is needed in the sections to follow.

LEMMA 1.2 [5] The periodic Ricker equation,

$$x_{n+1} = x_n e^{\sigma_n - x_n}, \qquad \sigma_{n+p} = \sigma_n, \quad x_n \in \mathbb{R}$$

with $\sigma_n \in (0,2)$ has a globally asymptotically stable p-periodic solution $\{x_n^*\}$. Moreover,

$$\frac{1}{p}\sum_{i=0}^{p-1}x_i^* = \frac{1}{p}\sum_{i=0}^{p-1}\sigma_i$$

i.e. neither attenuation nor resonance prevails.

2. Genetically Altered Mosquitos

This model was first introduced in the time independent or autonomous case by Jia Li [4] and later considered in [6,7] by the authors where the technique of "ratio dynamics" was introduced. In an attempt to describe more accurately a periodically varying environment we consider the following *p*-periodic system where x and y represent, respectively, the populations of wild (W) and genetically altered (GA) mosquitos

$$x_{n+1} = \frac{\alpha_{1,n}x_n + \beta_{1,n}y_n}{x_n + y_n} x_n e^{-d_{1,n} - k_{1,n}(x_n + y_n)},$$
$$y_{n+1} = \frac{\alpha_{2,n}x_n + \beta_{2,n}y_n}{x_n + y_n} y_n e^{-d_{2,n} - k_{2,n}(x_n + y_n)},$$

where the initial conditions x_0, y_0 and all the coefficients are positive and thus x_n and y_n remain positive for all $n \in \mathbb{Z}^+$. We assume all the coefficients to be periodic of period p in the integer variable n. The expressions

$$\frac{\alpha_{i,n}x_n + \beta_{i,n}y_n}{x_n + y_n} \doteq f_{i,n}(x_n, y_n) \qquad i = 1,2$$

$$(2.1)$$

are the growth functions, i.e. the per-capita rate of offspring production and are derived (following [4]) as follows. Let $N_n = x_n + y_n$ represent the total population at generation n and $c(N_n)$ be the total number of encounters or matings per individual, per unit of time. Concentrating first on the x equation governing the wild (W) mosquitoes,

$$x_{n+1} = f_{1,n}(x_n, y_n) s_{1,n}(x_n, y_n) x_n$$

the number of matings that are with W or GA mosquitoes at generation n is $c(N_n)x_n/N_n$ or $c(N_n)y_n/N_n$ respectively. Let $A_{1,n}$ and $B_{1,n}$ be the number of W offspring that a W produces through a mating with a W and a GA at generation n. Similarly, let $A_{2,n}$ and $B_{2,n}$ be the number of GA offspring that a GA produces through a mating with a W and a GA respectively, at generation n. Then the total number of W offspring produced by a single W at generation n is just

$$c(N_n)\frac{A_{1,n}x_n + B_{1,n}y_n}{x_n + y_n}$$

For large populations it is reasonable to assume that the function $c(N_n)$ reaches a constant saturation level, $c(N_n) = c_0$. Defining $\alpha_{i,n} = c_0 A_{i,n}$ and $\beta_{i,n} = c_0 B_{i,n}$ we obtain (2.1).

The expressions

$$e^{-d_{i,n}-k_{i,n}(x_n+y_n)} \doteq s_{i,n}(x_n, y_n)$$
 $i = 1, 2$

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are the survival probabilities. The $d_{i,n}$ are the ambient mortality rates while the $k_{i,n}$ are the rates of density dependent mortality and characterize the instantaneous carrying capacity at generation n.

We first eliminate the "exp $(-d_{i,n})$ " terms by absorbing them into the coefficients a_i, b_i $(a_i = \alpha_i e^{-d_i}, a_i = \beta_i e^{-d_i})$ to obtain

$$x_{n+1} = \frac{a_{1,n}x_n + b_{1,n}y_n}{x_n + y_n} x_n e^{-k_{1,n}(x_n + y_n)} , \qquad (2.2)$$

$$y_{n+1} = \frac{a_{2,n}x_n + b_{2,n}y_n}{x_n + y_n} y_n e^{-k_{2,n}(x_n + y_n)} .$$
(2.3)

Remark 2.1 We assume that each species is self sustaining in the sense that if (2.2)-(2.3) evolves with the parameters all fixed at any $n \in \{1, 2, ..., p-1\}$ then each species, in the complete absence of the other, can grow to a non-extinction state. This imposes the conditions $a_{1,n} > 1$ and $b_{2,n} > 1$, $\forall n$.

Our interest is in establishing the existence of a periodic state (\hat{x}_n, \hat{y}_n) , $n = 0, 1, \ldots, p-1$ which globally attracts all initial states (x, y) with x > 0 and y > 0.

In the case of equal rates of density-dependent mortality we obtain a globally asymptotically stable periodic solution (Section 2.1). When these rates are not the same, ratio dynamics fails. In Section 2.2 we apply dynamic reduction to obtain a new set of equations to which ratio dynamics will apply to give the desired periodic solution and hence the mapping (1.4).

Ratio dynamics ultimately leads to the study of the scalar p-periodic Ricker equation

$$x_{n+1} = x_n e^{\sigma_n - x_n}, \qquad \sigma_{n+p} = \sigma_n$$
(2.4)

to which Lemma 1.2 applies.

2.1. Ratio Dynamics, $k_{1,n} = k_{2,n}, n = 1, 2..., p$

We first describe the case of equal rates of density dependent mortality, $k_{1,n}$ and $k_{2,n}$. This case, while quite artificial in practice, is nevertheless quite useful in solving the more general problem.

In (2.2) we form the ratio, $z_n = x_n/y_n$ to obtain

$$z_{n+1} = \frac{a_{1,n}z_n + b_{1,n}}{a_{2,n}z_n + b_{2,n}} z_n.$$
(2.5)

We then have the following lemma :

LEMMA 2.1 For each fixed n assume $a_{1,n}/a_{2,n} < 1$ and $b_{1,n}/b_{2,n} > 1$. Then (2.5) has a globally asymptotically stable periodic solution $\{\zeta_0, \zeta_1, \ldots, \zeta_{p-1}\}$.

Proof : For each *n* the right hand side of (2.5) is a concave mapping from $\mathbb{R}^+ \to \mathbb{R}^+$ that intersects the diagonal. The rest follows from [2].

Remark 2.2 Referring to equations (2.2)-(2.3), and recalling that x represents Wild type while y represents GA, the conditions $a_{2,*} > a_{1,*}$ imply that the likelihood of a GA producing a GA when mating with a Wild, is greater than the likelihood of a Wild producing a Wild when mating with a Wild. Similarly, the conditions $b_{1,*} > b_{2,*}$ imply that the likelihood of a Wild producing a Wild when mating with a GA, is greater than the likelihood of a GA producing a GA when mating with a GA, is greater than the likelihood of a GA producing a GA when mating with a GA. The conditions preclude an attracting fixed point of (2.2)-(2.3) on one of the axes, i.e. the case in which one of the species reaches extinction. See [4] for a discussion of these extinction cases in the autonomous, or time independent case.

Substituting $x_n = y_n \zeta_n$ into the second equation in (2.2) we obtain

$$y_{n+1} = \frac{a_{2,n}\zeta_n + b_{2,n}}{\zeta_n + 1} y_n e^{-k_{2,n}(\zeta_n + 1)y_n},$$
(2.6)

$$= y_n \exp\left[\rho(n) - K(n)y_n\right] \quad \text{where}$$

$$\rho(n) = \log\left(\frac{a_{2,n}\zeta_n + b_{2,n}}{\zeta_n + 1}\right), \quad \text{and} \ K(n) = k_{2,n}(\zeta_n + 1) \tag{2.7}$$

Using the substitution $u_n = K(n)y_n$ in (2.6) we get, in the same form as in (2.4), the following Ricker equation

$$u_{n+1} = u_n e^{\sigma(n) - u_n}, \quad \text{where}$$

$$\sigma(n) = \log\left(\frac{K(n+1)}{K(n)}\right) + \rho(n).$$
(2.8)

Thus, we have the following theorem :

THEOREM 2.2 Assume $\sigma(n) \in (0,2)$ $\forall n$. Then (2.8) has a globally asymptotically stable (with respect to \mathbb{R}_0^+) p-periodic solution $\{u_0^*, u_1^*, \ldots, u_{p-1}^*\}$ and hence (2.2)-(2.3), with $k_{1,n} = k_{2,n} \forall n$, has a globally asymptotically stable (with respect to the open first quadrant) solution

$$v^* \doteq \{(\frac{\zeta_n u_n^*}{K(n)}, \frac{u_n^*}{K(n)}), n = 0, 1, \dots, p-1\}.$$

Remark 2.3 The condition $\sigma(n) \in (0, 2)$ in Theorem 2.2 is a sufficient condition only and it precludes period doubling bifurcations from occurring (See [4] where these bifurcations were studied in the autonomous case). The condition is, however, not necessary as pointed out in [8] where periodic coefficients were treated and some results, largely numerical, were obtained for periods 2 and 3 where some of the σ_n are allowed to exceed 2, provided their average remains less than 2.

Remark 2.4 In [2] the following was shown : Let two concave maps $f, g : \mathbb{R}^+ \to \mathbb{R}^+$ have fixed points x_f and x_g with $x_f < x_g$. Then $x_f < x_{f \circ g} < x_g$ and $x_f < x_{g \circ f} < x_g$. This is useful in estimating the "spread" of the invariant set of lines in the (x, y) plane determined by the periodic solution given by Lemma 2.1. More precisely, if P_n is the fixed point of the n^{th} map in (2.5), then the slopes of the invariant lines are $1/\zeta_n$ and lie in the open interval (min $S_n, \max S_n$), where $S_n = 1/P_n$. Note that P_n is simply the solution of $(a_{1,n} - a_{2,n})P_n = (b_{2,n} - b_{1,n})$.

2.2. Dynamic Reduction leads to Ratio Dynamics, the case $k_{1,n} \neq k_{2,n}$ for some n

The whole point of dynamic reduction is to reduce a given problem to one for which a known solution technique is readily available. In order to reduce this case to the one treated in Section 2.1, we rewrite (2.2) as

$$x_{n+1} = \frac{a_{1,n}x_n + b_{1,n}y_n}{x_n + y_n} x_n e^{-k_{2,n}(x_n + y_n)} g_n(x_n, y_n),$$
(2.9)

$$y_{n+1} = \frac{a_{2,n}x_n + b_{2,n}y_n}{x_n + y_n} y_n e^{-k_{2,n}(x_n + y_n)}, \quad \text{where}$$
(2.10)

$$g_n(x_n, y_n) = e^{(k_{2,n} - k_{1,n})(x_n + y_n)},$$
(2.11)

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which has the form (1.2). Our aim is to define a region $\mathcal{D} \subset \mathbb{R}^+ \times \mathbb{R}^+$ as

$$\mathcal{D} \doteq [0, M] \times [0, M] \setminus [0, m) \times [0, m) \tag{2.12}$$

and a subset

$$\mathcal{P}_p = \{p \text{-periodic sequences}, \{(x_n, y_n)\}, \text{ with } (x_n, y_n) \in \mathcal{D}\}$$

such that for each sequence $v = \{(\hat{x}_n, \hat{y}_n)\} \in \mathcal{P}_p$, the "reduced" system,

$$x_{n+1} = \frac{a_{1,n}x_n + b_{1,n}y_n}{x_n + y_n} x_n e^{-k_{2,n}(x_n + y_n)} g_n(\hat{x}_n, \hat{y}_n),$$
(2.13)

$$y_{n+1} = \frac{a_{2,n}x_n + b_{2,n}y_n}{x_n + y_n} y_n e^{-k_{2,n}(x_n + y_n)},$$
(2.14)

with initial conditions $x_0 > 0$ and $y_0 > 0$, has a globally asymptotically stable (with respect to the open first quadrant), and hence unique, periodic solution $v^* = \{(x_n^*, y_n^*)\} \in \mathcal{P}_p$. Thus the mapping (1.4) will be established. If v^* is a fixed point of \mathcal{T} , i.e. a solution of

$$x_{n+1} = \frac{a_{1,n}x_n + b_{1,n}y_n}{x_n + y_n} x_n e^{-k_{2,n}(x_n + y_n)} g_n(x_n^*, y_n^*),$$
(2.15)

$$y_{n+1} = \frac{a_{2,n}x_n + b_{2,n}y_n}{x_n + y_n} y_n e^{-k_{2,n}(x_n + y_n)},$$
(2.16)

then it remains to show that v^* is GAS as a solution of the original system (2.9)-(2.10).

Note that while a fixed point of the mapping \mathcal{T} in (1.4) is a *p*-periodic solution of (2.9)-(2.10) and therefore (2.2)-(2.3), the converse is not true since (2.2)-(2.3) has *p*-periodic points on the two intervals of the boundary of \mathcal{D} where x = 0 or y = 0. It turns out that the mapping \mathcal{T} will send sequences lying on those portions of the boundary to sequences with values in that part of \mathcal{D} lying on the interior of the first quadrant.

Hence, we are interested first in defining the region \mathcal{D} in (2.12) that is mapped into itself by the right side of (2.13)-(2.14) with some mild restrictions on g. Then we explore conditions guaranteeing that the ratio system

$$z_{n+1} = \frac{a_{1,n}z_n + b_{1,n}}{a_{2,n}z_n + b_{2,n}} z_n \ g_n(\hat{x}_n, \hat{y}_n), \tag{2.17}$$

formed from (2.13)-(2.14) by setting z = x/y has a globally asymptotically stable (with respect to \mathbb{R}_0^+) solution. This will establish a positively invariant set of lines in the (x, y) plane which attract every solution starting in the open first quadrant. Finally, the stability of the solution of the system corresponding to (2.6) will be established.

We first consider the following scalar mapping containing a parameter λ ,

$$x \mapsto F_{\lambda}(x) \doteq \frac{ax + b\lambda}{x + \lambda} x e^{-k(x + \lambda)}, \quad x, \lambda \ge 0, \quad x + \lambda > 0,$$
(2.18)

and the the associated family of mappings (simple multiplication by ϕ),

$$\mathcal{F} = \left\{ F_{\lambda}(x)\phi, \quad \frac{1}{\min\left\{a,b\right\}} < \phi < \frac{e}{2} \right\}.$$
(2.19)

Note in particular that $F_{\lambda} \in \mathcal{F}$ when a, b > 1.



Figure 1. Parameter region for which $m \le x \le M$ is invariant.



Figure 2. Parameter region for which $m \leq y \leq M$ is invariant.

LEMMA 2.3 Assume a, b > 1 and let M be such that $M \ge \frac{\max\{a, b\}}{2k}$. Then for $\lambda \le M$ there exist small positive numbers, m and \tilde{m} depending on M, with $m < \tilde{m} < M$ such that each member of the family (2.19) satisfies

- (a) For $\lambda \in [0, M]$ and $x \in [\tilde{m}, M]$ one has $F_{\lambda}(x)\phi \in [m, M]$,
- (b) For $\lambda \in [0, \tilde{m}]$ and $x \in (0, \tilde{m}]$ one has $x < F_{\lambda}(x)\phi \leq M$.

Proof : For x and λ small, $F_{\lambda}(x)$ may be approximated by $g_{\lambda}(x) = \frac{ax + b\lambda}{x + \lambda}x$, and thus

$$g_{\lambda}'(x)\phi = \frac{b\lambda^2 + a(2\lambda x + x^2)}{\lambda^2 + 2\lambda x + x^2}\phi \ge \min{\{a, b\}\phi} > 1,$$

since the above expression is a convex combination of a and b. Thus there exists a small $\tilde{m} > 0$ such that (b) holds. Next observe that

$$0 < F_{\lambda}(x) \le \max_{x,\lambda} \frac{ax+b\lambda}{x+\lambda} \max_{x,\lambda} xe^{-k(x+\lambda)} \le \frac{\max\{a,b\}}{ke},$$

again using convexity on the first "max". Then choose $m, 0 < m \leq \tilde{m}$ such that

$$m < \min_{x,\lambda} F_{\lambda}(x) \frac{1}{\min\{a,b\}}, \qquad x \in [\tilde{m}, M], \quad \lambda \in [0, M],$$

so that (a) follows.

Figure 1 is an interpretation of Lemma 2.3. Part (a) implies that for (x, λ) in the large rectangle, each member f of the family \mathcal{F} maps x to the interval [m, M] while part (b) implies that for (x, λ) in the small rectangle f moves x to the right, but not past M. Thus, in either case the interval [m, M] is invariant under application of $f \in \mathcal{F}$.

Now fix n, and consider the mapping (2.13)-(2.14). The first component (2.13) has the form considered in Lemma 2.3. But x and y occur symmetrically in (2.13)-(2.14), so that Lemma 2.3 applies to the family

$$F_{\lambda}(y)\phi \doteq \frac{a\lambda + by}{\lambda + y}ye^{-k(\lambda + y)}\phi, \qquad \frac{1}{\min\{a, b\}} < \phi < \frac{e}{2}$$

which includes the second component (2.14), see Figure 2. Finally we consider the mapping (2.13)-(2.14),

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Figure 3. Region \mathcal{D} in x, y-plane left invariant.

with $|k_2 - k_1|$ sufficiently small so that g satisfies the condition (with n suppressed),

$$\frac{1}{\min\{a_1, a_2, b_1, b_2\}} < \min(1, g) \le \max(1, g) < \frac{e}{2}.$$
(2.20)

If $(x, y) \in \mathcal{D}$ then one of the variables must lie in the interval [m, M] so that Lemma 2.3 implies the image under the right side of (2.13)-(2.14) lies in \mathcal{D} , the two shaded regions in Figure 3. But more can be inferred from Lemma 2.3 which we state as

COROLLARY 2.4 Let condition (2.20) hold and m, and M be defined as in Lemma 2.3. If \mathcal{D} is the region

$$\mathcal{D} \doteq [0, M] \times [0, M] \setminus [0, m) \times [0, m)$$
.

then \mathcal{D} and its convex hull $co\mathcal{D}$ are each invariant under the mapping

$$x_{n+1} = \frac{a_1 x_n + b_1 y_n}{x_n + y_n} x_n e^{-k_2 (x_n + y_n)} g(x_n, y_n), \qquad (2.21)$$

$$y_{n+1} = \frac{a_2 x_n + b_2 y_n}{x_n + y_n} y_n e^{-k_2 (x_n + y_n)}.$$
(2.22)

Proof : From Lemma 2.3(b) it follows that any $(x, y) \in [0, m] \times [0, m]$ that satisfies $y \ge m - x$ is mapped to a point (x_1, y_1) with $x \le x_1 \le M$ and $y \le y_1 \le M$.

Thus we have the following theorem :

Theorem 2.5

(a) In the reduced system (2.13)-(2.14) assume $a_{1,n}, a_{2,n}, b_{1,n}, b_{2,n} > 1$ and define

$$M = \max\{M_1, M_2\}$$
 where $M_i = \max_n \frac{\{a_{i,n}, b_{i,n}\}}{k_{i,n}e}$.

Assume $\max_{n} |k_{2,n} - k_{1,n}|$ sufficiently small so that when $x \leq M$ and $y \leq M$, one has

$$\frac{1}{\min_n \{a_{1,n}, a_{2,n}, b_{1,n}, b_{2,n}\}} < g_n(x, y) < \frac{e}{2}.$$

Then there exists an m, 0 < m < M, such that the region

$$\mathcal{D} \doteq [0, M] \times [0, M] \setminus [0, m) \times [0, m)$$

and its convex hull $co\mathcal{D}$ are invariant under the mapping (2.13)-(2.14), i.e. if $(x_0, y_0) \in \mathcal{D}$ then $(x_n, y_n) \in \mathcal{D}$ and $x_n y_n > 0$ for all $n \in \mathbb{Z}^+$.

(b) Further, if for each n, $|k_{2,n} - k_{1,n}|$ is sufficiently small so that $\max_n \frac{a_{1,n}}{a_{2,n}} \max_{\mathcal{D}} g_n < 1$ and

 $\min_{n} \frac{b_{1,n}}{b_{2,n}} \min_{\mathcal{D}} g_n > 1, \text{ then the ratio equation (2.17) has a globally asymptotically stable (with respect to <math>\mathbb{R}^+_0$) p-periodic solution

$$\{\zeta_0, \zeta_1, \dots, \zeta_{p-1}\}.$$
 (2.23)

(c) Assume $\sigma(n)$ defined in (2.8) and computed from (2.23) satisfies $\sigma(n) \in (0,2)$. Then the reduced system (2.15)-(2.16)) has a globally asymptotically stable (with respect to the open first quadrant) p-periodic solution $v^* = \{v_0^*, v_1^*, \ldots, v_{p-1}^*\}$. If, for each n, $|k_{2,n} - k_{1,n}|$ is sufficiently small, then $v^* = \{x_n^*, y_n^*\}$ is a GAS solution of the original system (2.9)-(2.10)).

Proof : (a) This follows immediately from Corollary 2.4 since each map in the sequence satisfies the conditions of Lemma 2.3.

(b) Toward ultimately defining the mapping

$$\mathcal{T}: \mathcal{P}_p \to \mathcal{P}_p, \qquad v^* = \mathcal{T}(v),$$

let $v = \{(\hat{x}_n, \hat{y}_n)\} \in \mathcal{P}_p$ be chosen and consider (2.13)-(2.14). Letting $z_n = x_n/y_n$ we obtain the "ratio" equation :

$$z_{n+1} = \frac{a_{1,n}g(\hat{x}_n, \hat{y}_n)z_n + b_{1,n}g(\hat{x}_n, \hat{y}_n)}{a_{2,n}z_n + b_{2,n}} z_n \doteq h_n(z_n).$$
(2.24)

From the hypotheses, for each $n, h_n : \mathbb{R}^+ \to \mathbb{R}^+$ is concave and the graph of $\eta = h_n(z)$ crosses the "diagonal", $\eta = z$ in the (z, η) plane. The proof of part (b) follows from the results of Section 2.1.

(c) Theorem 2.2 tells us that the reduced equation (2.13)-(2.14) has a globally asymptotically stable solution v^* thus giving us the mapping \mathcal{T} . It is clearly continuous and carries points in \mathcal{P}_p having values on the axes in $co\mathcal{D}$ (see Figure 3) to points in \mathcal{P}_p having no values on the axes in $co\mathcal{D}$. Clearly a fixed point (periodic sequence in \mathbb{R}^2) has no values lying on either axis.

To see that \mathcal{T} is a contraction and its unique fixed point v^* is GAS as a solution of the original system, we will verify the smallness condition of Theorem 1.1. Noting that F_n is the right hand side of (2.9)-(2.10)), and defining $\Delta k_n = (k_{2,n} - k_{1,n})$, we have

$$\partial_g F_n(x_n, y_n) = \begin{bmatrix} \frac{a_{1,n} x_n + b_{1,n} y_n}{x_n + y_n} x_n e^{-k_{2,n}(x_n + y_n)} \\ 0 \end{bmatrix}, \qquad \partial_{(x,y)} g_n(x, y) = -\Delta k_n e^{-\Delta k_n(x_n + y_n)} \begin{bmatrix} 1 \\ 1 \end{bmatrix}$$

From Lemma 2.3, $|\partial_g F_n| \leq M$. The rest follows from by letting $|\Delta k_n|$ be sufficiently small for each n.

Remark 2.5 We saw in an earlier in Remark 2.1, the assumption that each species is self sustaining imposed the condition $a_{1,n}$, $b_{2,n} > 1$, $\forall n$. In Remark 2.2 the assumptions $\frac{a_{1,n}}{a_{2,n}} < 1$, $\frac{b_{1,n}}{b_{2,n}} > 1$ were interpreted biologically and were seen to preclude extinction states. From these it follows that $a_{2,n}$, $b_{1,n} > 1$, $\forall n$. The condition $\sigma(n) \in (0,2)$ is a *sufficient* condition that precludes period doubling, Remark 2.3.

3. Other Applications

The possible applications of dynamic reduction are limited only by the users imagination. The key point is that the reduced equation should have a solution having all the properties desired of the solution of the original problem. As we saw in the mosquito model, some of these properties (periodicity) are built into the class \mathcal{P}_p on which \mathcal{T} acts while other properties (global asymptotic stability) are obtained by carefully defining the map. Here we state a few applications with just enough details to establish the mapping $\mathcal{T} : \mathcal{P}_p \to \mathcal{P}_p$ on a subset of periodic sequences such that each point in the range of \mathcal{T} is a globally asymptotically stable solution of the reduced system. As noted earlier, a fixed point yields a solution of the original problem. We also calculate the derivatives needed to verify the smallness conditions of the stability theorem, Theorem 1.1.

The first two examples are systems of Ricker equations with coupling and delays. Although Ricker's equation arose in the modeling of problems in Biology, the authors have no specific application in mind. The aim is to illustrate the use of dynamic reduction.

3.1. Systems may be decoupled

Consider

$$x_{n+1} = x_n e^{g_{1,n}(x_n, y_n) - x_n}$$

$$y_{n+1} = y_n e^{g_{2,n}(x_n, y_n) - y_n}$$
(3.1)

where $g_{*,n}$ is periodic in n of period p and $0 < g_i(n, x, y) < 2$ whenever $(n, x, y) \in \mathbb{Z}^+ \times \mathcal{D}$, where

$$\mathcal{D} = [m, M] \times [m, M],$$

and where the constants are chosen as follows. With 0 < c < 2, the maximum of $x \exp(c - x)$ on \mathbb{R}^+ is $x = \exp(c - 1) < e$. Thus we take M = e. Using this value for x and c = 0 gives a lower bound m on how close to the origin a point can be mapped :

$$m < e^{1-e} (3.2)$$

Using these values the region \mathcal{D} is invariant under the action of (3.1). Here g is periodic in n and we seek a globally asymptotically stable periodic solution. To this end define $\mathcal{P}_p \subset \{\text{p-periodic sequences}\}$ such that

$$v = (v_0, v_1, \dots, v_{p-1}) \in \mathcal{P}_p \implies v_j = \begin{pmatrix} x_j \\ y_j \end{pmatrix} \in \mathcal{D}$$

Then for $\hat{v} \in \mathcal{P}_p$, the globally asymptotically stable solution v^* of

$$x_{n+1} = x_n e^{g_{1,n}(\hat{x}_n, \hat{y}_n) - x_n}$$

$$y_{n+1} = y_n e^{g_{2,n}(\hat{x}_n, \hat{y}_n) - y_n}$$
(3.3)

To obtain the contraction property and global asymptotic stability as a solution of (3.1) one then must restrict the size of $|\partial_2 F g'|_0$ in order to verify smallness condition of Theorem 1.1 where

$$\partial_g F_n = \begin{bmatrix} F_{1,n} & 0\\ 0 & F_{2,n} \end{bmatrix} \quad \text{and} \quad g'_n = \begin{bmatrix} \partial_{x_1} g_{1,n} & \partial_{x_2} g_{1,n} \\ \partial_{y_1} g_{2,n} & \partial_{y_2} g_{2,n} \end{bmatrix}.$$

3.2. Periodic systems with delays

These can be handled similarly, e.g. consider

$$x_{n+1} = x_n e^{g_n(x_n, x_{n-1}, \dots, x_{n-k}) - x_n} \doteq F(x_n, g_n(x_n, x_{n-1}, \dots, x_{n-k})), \quad x_j \in (\mathbb{R}_0^+)^d, \tag{3.4}$$

$$g_n: \mathbb{Z}^+ \times \prod_{j=0}^{\kappa} (\mathbb{R}_0^+)^d \to (\mathbb{R}_0^+)^d$$
(3.5)

where multiplication and exponentiation on the right side are done element-wise. In this case, with the same m as in (3.2), we define the region \mathcal{D} and $v \in \mathcal{P}_{\lambda}$ as

$$v = (v_0, v_1, \dots, v_{\lambda-1}) \in \mathcal{P}_{\lambda} \implies v_j \in \mathcal{D} = \prod_{j=1}^d [m, e]$$

where λ is determined as follows. If p is the minimal period of the system (3.4) then $\lambda = \mu p$ where μ is the unique positive integer such that

$$(\mu - 1)p < (k+1) \le \mu p . \tag{3.6}$$

The mapping, $v^* = \mathcal{T}(v)$, is then established by finding the solution v^* of the reduced system

$$x_{n+1} = x_n e^{g_n(v_n, v_{n-1}, \dots, v_{n-k}) - x_n}, \quad x \in (\mathbb{R}_0^+)^d$$

where again we assume $0 < g_{j,n}(\cdots) < 2, \ j = 1, \ldots, d$.

Remark 3.1 Even though a fixed point of \mathcal{T} yields a λ -periodic solution of (3.9), λ need not be the minimal period of that solution.

To verify \mathcal{T} is a contraction and that the unique fixed point v^* is a GAS solution of (3.4) one then must restrict the size of $|\partial_2 F g'|_0$ in order to satisfy the conditions of Theorem 1.1. For each n, $\partial_{g_n} F_n$ is the diagonal $d \times d$ matrix

$$\partial_{g_n} F_n = \operatorname{diag} \left[\partial_{g_{1,n}} F_{1,n}, \dots, \partial_{g_{d,n}} F_{d,n} \right]$$

and letting D_j represent differentiation with respect to the j^{th} argument, the term $\partial_x g_n$ in $g_n(x_n, x_{n-1}, \ldots, x_{n-k})$ is interpreted to mean the $d \times k + 1$ matrix

$$\partial_x g_n = [D_j g_{i,n}], \qquad i = 1, \dots, d \quad j = 1, \dots, k+1.$$
 (3.7)

3.3. Rational difference equations

The following equation has been the subject of much attention, [1]

$$x_{n+1} = \frac{\alpha + \sum_{i=0}^{k} \beta_i x_{n-i}}{A + \sum_{i=0}^{k} B_i x_{n-i}} , \qquad x \in \mathbb{R}^+ .$$

where all coefficients are assumed non-negative (other conditions to follow). Adding periodicity gives

$$x_{n+1} = \frac{\alpha_n + \sum_{i=0}^k \beta_{i,n} x_{n-i}}{A_n + \sum_{i=0}^k B_{i,n} x_{n-i}} , \qquad x \in \mathbb{R}^+ .$$
(3.8)

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Separating out the delayed terms, one has

$$x_{n+1} = \frac{\alpha_n + \beta_{0,n} x_n + g_{1,n}(x_{n-1}, \dots, x_{n-k})}{A_n + B_{0,n} x_n + g_{2,n}(x_{n-1}, \dots, x_{n-k})} \doteq F_n(x_n, g_n(x_{n-1}, \dots, x_{n-k})) .$$
(3.9)

Consider, for $\hat{v} \in \mathcal{P}_p$ the reduced equation

$$x_{n+1} = \frac{\alpha_n + \beta_{0,n} x_n + g_{1,n}(\hat{v}_{n-1}, \dots, \hat{v}_{n-k})}{A_n + B_{0,n} x_n + g_{2,n}(\hat{v}_{n-1}, \dots, \hat{v}_{n-k})}$$
$$= \frac{\hat{\alpha}_n + \beta_{0,n} x_n}{\hat{A}_n + B_{0,n} x_n} \doteq \phi_n(x_n) .$$
(3.10)

For each n we assume $\beta_{0,n} > 0$, $B_{0,n} > 0$. Then

$$0 < M_n \doteq \lim_{x \to \infty} \phi_n(x) = \frac{\beta_{0,n}}{B_{0,n}} < \infty, \quad n \in \mathbb{Z}^+ \bmod p .$$

$$(3.11)$$

Our aim is to give additional conditions that guarantee that each ϕ_n is concave so that $M_n = \sup_{x \in \mathbb{R}^+} \phi_n(x)$. Since the values of each ϕ_i are acted on by ϕ_{i+1} , we may restrict the upper boundary of the domain of ϕ_{i+1} to be M_i and thus define the region \mathcal{D} and the subset of λ -periodic sequences, \mathcal{P}_{λ} to be

$$v \in \mathcal{P}_{\lambda} \implies v = (v_0, v_1, \dots, v_{\lambda-1}) \in \mathcal{D} = [m, M_{\lambda-1}] \times [m, M_0] \times \dots \times [m, M_{\lambda-2}],$$

where λ is chosen as in (3.6).

There is some latitude in the choice of m. In order to render (3.10) concave for each n we require

$$\sup_{v \in \mathcal{D}} \frac{\hat{\alpha}_n}{\hat{A}_n} = \sup_{v \in \mathcal{D}} \frac{\alpha_n + g_{1,n}(v_{n-1}, \dots, v_{n-k})}{A_n + g_{2,n}(v_{n-1}, \dots, \hat{v}_{n-k})} < M_n , \quad n \in \mathbb{Z}^+ .$$
(3.12)

Then by the result, [2], the λ -periodic equation

$$x_{n+1} = \frac{\hat{\alpha}_n + \beta_{0,n} x_n}{\hat{A}_n + B_{0,n} x_n}$$

has a globally asymptotically stable periodic solution v^* thus establishing the mapping

$$v^* = \mathcal{T}(\hat{v})$$
.

As noted in Remark 3.1, a fixed point of \mathcal{T} yields a λ -periodic solution of (3.9) but λ need not be the minimal period of that solution.

To verify \mathcal{T} is a contraction and that the unique fixed point v^* is a GAS solution of (3.9) one then must satisfy the smallness conditions of Theorem 1.1. To that end, one needs to evaluate the derivatives $\partial_g F$ and $\partial_x g$ (a $d \times k$ matrix) that are given by

$$\partial_{g_n} F_n = \left[\frac{1}{A_n + B_{0,n} x_n + g_{2,n}(x_{n-1}, \dots, x_{n-k})}, -\frac{\alpha_n + \beta_{0,n} x_n + g_{1,n}(x_{n-1}, \dots, x_{n-k})}{(A_n + B_{0,n} x_n + g_{2,n}(x_{n-1}, \dots, x_{n-k}))^2} \right], \text{ and}$$
$$g'_n = [D_j g_{i,n}] \qquad i = 1, \dots, d \quad j = 1, \dots, k ,$$
(3.13)

where D_j is differentiation with respect to the j^{th} variable.

Remark 3.2 If at least one of the α_n in (3.9) is positive we may actually choose m = 0 since the identically zero solution is then impossible and therefore the zero sequence is not in the range of \mathcal{T} . Even in this case, however, it might be advantageous to use a larger m in order to satisfy the smallness condition on $|\partial_2 F g'|_0$. This would be the case if g_2 was not identically zero. No general statement seems possible.

4. Conclusions

Dynamic reduction is a procedure for solving a difference equation by replacing certain "excess" state variables by a function lying in a class having some of the desired properties of the sought after solution. Done properly, the resulting or reduced equation will have a solution having the remaining properties and lying in the same class. This sets up a mapping \mathcal{T} of the class into itself, a fixed point of which solves the original problem. The technique is illustrated by applying it to various problems.

In the application to the periodic model for wild (W) and genetically altered (GA) mosquitos, it is shown (See Remark 2.2) that if the growth parameters satisfy certain inequalities then neither species goes extinct and in fact their population *ratios* are attracted to a periodically varying state and thus the dynamics of the model takes place on a periodic set of lines in the plane of x, the W population and y, the GA population. When restricted to these lines, further conditions (shown to preclude period doubling by Jia Li [4] in the autonomous case) guarantee the existence of a periodic state to which all initial non-zero populations are attracted. In Remark 2.4 it is noted that the population ratios asymptotically lie between certain easily calculated bounds : solutions ξ of scalar equations of the form $a\xi = b$.

It is also shown that certain coupled periodic systems of difference equations may be completely decoupled so that the mapping \mathcal{T} is established by solving a set of scalar equations. Periodic difference equations of extended Ricker type and also rational difference equations with a finite number of delays are also treated by reducing them to equations without delays but with a larger period.

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