Comp & Maths with Appls Vol 11 Nos 1-3 pp 175-188 1985
Printed in the U S A

0097-4943/85 $3.00+.00

GLOBAL BRANCHES OF EQUILIBRIUM SOLUTIONS OF THE McKENDRICK EQUATIONS FOR AGE-STRUCTURED POPULATION GROWTH

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Communicated by Matthew Witten

Abstract—The existence of positive equilibrium solutions of the McKendrick equations for the dynamics of an age-structured population is studied as a bifurcation phenomenon using the inherent net reproductive rate n as a bifurcation parameter Under only continuity assumptions on the density dependent death and fertility rates, it is shown that a global continuum of positive equilibria exists in a certain Banach space This continuum connects from the trivial solution at $n = 1$ to the boundary of the domain on which the problem is posed Results concerning the spectrum are given In particular, some circumstances are described under which positive equilibria exist for all n values greater than the critical value $n = 1$

1 INTRODUCTION

If $\rho = \rho(t, a) \geq 0$ is the density of reproducing individuals of age a in a population at time t, then the equations

$$\begin{aligned} \partial\rho/\partial t + \partial\rho/\partial a + \mu(a, \rho)\rho &= 0, \quad t > 0, \quad 0 < a < A \leq +\infty \\ \rho(t, 0) &= \int_0^A F(a, \rho)\rho(t, a)\,\mathrm{d}a, \quad t > 0 \end{aligned} \tag{1 1}$$

describe respectively the removals and additions to the population, which is assumed closed to immigration and emigration, in terms of the (per unit density per unit time) death and fertility rates μ and F These vital rates are assumed dependent upon a and ρ, but independent of t The number $A \leq +\infty$ is a maximal age for any member of the population and it is required that

$$\rho(t, A) = 0, \quad t > 0$$

Coupled with an initial condition $\rho(0, a) = \bar{\rho}(a)$, $0 < a < A$, these equations determine the future time evolution of the age-specific population density ρ These equations have come to be called the McKendrick equations

In recent years (particularly since the seminal paper of Gurtin and MacCamy[3]) there has been a rapidly growing literature dealing with various aspects of this model system of equations and its implications concerning age-structured population dynamics One fundamental question is that of the existence of positive equilibrium solutions $\rho(t, a) = \rho(a)$ (sometimes misleadingly called "stable age distributions" although they may be mathematically unstable) with which this paper deals solely The goal is to give a general "global" existence result under mild assumptions on the vital rates μ and F and to do so within the framework of bifurcation theory

An equilibrium solution $\rho = \rho(a) \geq 0$ must satisfy the equilibrium equations

$$\begin{aligned} \rho'(a) + \mu(a, \rho)\rho(a) &= 0, \quad 0 < a < A \leq +\infty \\ \rho(0) &= \int_0^A F(a, \rho)\rho(a)\,\mathrm{d}a, \quad \rho(A) = 0 \end{aligned}$$

In accordance with the approach taken here which will utilize certain global bifurcation techniques, the existence of solutions of these equations will be studied as a function of a selected parameter This bifurcation parameter will be taken to be the *inherent net reproductive rate* n at low density (technically at $\rho \equiv 0$) as defined by

$$n = \int_0^A F(a, 0) \exp(-M(a, 0))\, da, \quad M(a, \rho) = \int_0^a \mu(a, \rho)\, da$$

This inherent net reproductive rate is the expected (per unit) number of offspring over a life-span In order to introduce this parameter into the equations, the *normalized fertility rate* $f = f(a, \rho)$ is defined to be the ratio of the (per unit) fertility at age a to the (per unit) expected number of offspring Then $F = nf$ and the equilibrium equations can be written

$$\begin{aligned} &(a)\ \rho'(a) + \mu(a, \rho)\rho(a) = 0, \quad 0 < a < A \leq +\infty \\ &(b)\ \rho(0) = n \int_0^A f(a, \rho)\rho(a)\, da \\ &(c)\ \rho(A) = 0 \end{aligned} \tag{1 2}$$

Note that under this normalization

$$\int_0^A f(a, 0) \exp(-M(a, 0))\, da = 1 \tag{1 3}$$

The equilibrium equations (1 2) have the trivial solution $\rho \equiv 0$ for all values of the parameter n Of primary interest in understanding the time evolution of an age-structured population whose dynamics are governed by the model equations (1 1) is a knowledge of the set of values of n for which the equilibrium equations (1 2) have a nontrivial, positive solution ρ After some preliminary matters in Section 2, including the prerequisite linear theory when $A < +\infty$, an existence result when $A < +\infty$ is given in Section 3 for a global continuum C^+ of pairs (n, ρ) lying in a certain Banach space where ρ is a nontrivial, positive solution of (1 2) corresponding to the inherent net reproductive rate n More specifically the main result of this paper (Theorem 1) shows that under mild conditions on μ and f, a continuum C^+ of positive solutions (n, ρ) of (1 2) bifurcates from the trivial solution $(n, \rho) = (1, 0)$ and connects to the boundary of the domain on which the problem (1 2) is posed The critical solution $(n, \rho) = (1, 0)$ is the biologically meaningful trivial solution at which the inherent net reproductive rate n equals one, a point at which birth and death processes combine to yield exact per unit replacement

In Section 4 it is shown how these results for $A < +\infty$ can be extended to the technically more complicated case $A = +\infty$ In Section 5 the spectrum associated with the continuum of positive equilibria is studied and in Section 6 these results (as well as a few other points) are illustrated by means of an example

There are many recent papers which contain existence results for equilibrium solutions of (1 1) For example, see [5–8, 10, 11] and the refrences cited in these papers None of these papers take the bifurcation approach taken here and all require much stronger restrictions on μ and f than are required here in hypothesis H1 or H2 below In H1 or H2 no special functional dependence of μ and f on ρ is assumed as is frequently the case in the literature (where, for example, either μ or f is often assumed independent of ρ or it is assumed that the functional dependence on ρ is through a dependence on total population size $P(t) = \int_0^A \rho(a)\, da$ only) Nor do we need here any monotonicity or Lipschitz or boundedness conditions on μ or f as are needed in these references

2 THE LINEAR THEORY FOR $A < +\infty$

In this section certain Banach spaces and operators are defined and the necessary linear theory is developed when $A < +\infty$ Let R and R^+ denote the set of reals and nonnegative reals respectively and let Δ denote the set of continuous functions $\mu \in C^0([0, A), R)$ which satisfy

$$\lim_{a \to A-} M(a) = +\infty \quad \text{where} \quad M(a) = \int_0^a \mu(a)\, da$$

For $\mu \in \Delta$ define B_μ to be the linear space of continuous functions $h \in C^0([0, A], R)$ for which $h(a) \exp M(a)$ is continuous on $[0, A]$ It is not difficult to see that B_μ is a Banach space when endowed with the norm

$$\|h\|_\mu = \max_{[a\ A]} |h(a)|/\rho_0(a)$$

where

$$\rho_0(a) = \begin{cases} \exp(-M(a)), & 0 \leq a < A \\ 0, & a = A \end{cases}$$

Note that $\rho_0 \in B_\mu$ and that $h \in B_\mu$ implies $h(A) = 0$

Also needed will be the product space $R \times B_\mu$ subject to the norm $\| \ \|_+ = | \ | + \|\cdot\|_\mu$ and the Banach space $L_1 = L_1([0, A], R)$ with the norm $\|h\|_L = (\int_0^A |h(a)| da)$

Consider the nonhomogeneous linear system of equations

$$\begin{aligned} \rho'(a) + \mu(a)\rho(a) &= h_2(a), \quad 0 < a < A \\ \rho(0) &= \int_0^A g(a)\rho(a)\, da + h_1 \end{aligned} \tag{2 1}$$

and the associated homogeneous system

$$\begin{aligned} \rho'(a) + \mu(a)\rho(a) &= 0, \quad 0 < a < A \\ \rho(0) &= \int_0^A g(a)\rho(a)\, da \end{aligned} \tag{2 2}$$

In these equations $\mu \in \Delta$, $(h_1, h_2) \in R \times B_\mu$ and $g\rho_0 \in L_1$ By a *solution of* (2 1) *or* (2 2) *in* B_μ is meant a function $\rho \in B_\mu$ which is also continously differentiable on $(0, A)$, i e a function $\rho \in B_\mu \cap C^1((0, A), R)$

An integration of the differential equation in (2 2) easily shows that (2 2) has a nontrivial solution in B_μ if and only if

$$\int_0^A g(a)\rho_0(a)\, da = 1 \tag{2 3}$$

in which case all solutions have the form $\rho(a) = c\rho_0(a)$, $c \in R$

All solutions of the nonhomogeneous differential equation in (2 1) have the form

$$\rho(a) = \rho_0(a)\left[c + \int_0^a h_2(a)/\rho_0(a)\, da\right], \quad c \in R \tag{2 4}$$

and lie in $B_\mu \cap C^1$ Thus, the nonhomogeneous system (2 1) is solvable in B_μ if and only if the equation

$$\left[1 - \int_0^A g(a)\rho_0(a)\, da\right]c = h_1 + \int_0^A g(a)\rho_0(a) \int_0^a h_2(a)/\rho_0(a)\, da\, da \tag{2 5}$$

is solvable for $c \in R$

These facts can be summarized in the following Fredholm-type alternative for the linear nonhomogeneous system (2 1) *either the homogeneous system* (2 2) *has no nontrivial solution in* B_μ *in which case the nonhomogeneous system* (2 1) *has a unique solution* B_μ *for each* $(h_1, h_2) \in R \times B_\mu$ *or* (2 2) *has nontrivial solutions in* B_μ *in which case* (2 1) *has a solution in* B_μ *if and only if* $(h_1, h_2) \in R \times B_\mu$ *satisfies*

$$h_1 + \int_0^A g(a)\rho_0(a) \int_0^a h_2(a)/\rho_0(a)\, da\, da = 0 \tag{2 6}$$

In the first case (which occurs when (2 3) fails to hold), the unique solution of (2 1) is given by $\rho = S(h_1, h_2) \in B_\mu \cap C^1$ where the solution operator S is defined by

$$\begin{aligned} S(h_1, h_2) &= \rho_0(a)\left[c + \int_0^a h_2(a)/\rho_0(a)\, da\right] \\ c &= \left[h_1 + \int_0^A g(a)\rho_0(a) \int_0^a h_2(a)/\rho_0(a)\, da\, da\right]\left[1 - \int_0^A g(a)\rho_0(a)\, da\right]^{-1} \end{aligned} \tag{2 7}$$

LEMMA

Assume that $\mu \in \Delta$, $g\rho_0 \in L_1$ *and* (2 2) *has no nontrivial solution in* B_μ (*i e* (2 3) *fails to hold*) *The solution operator* S $R \times B_\mu \to B_\mu$ *is linear and compact Moreover, the range of* S *lies in* $B_\mu \cap C^1((0, A), R)$

Proof That $S(h_1, h_2)$ is linear in (h_1, h_2) and belongs to C^1 are obvious The inequalities

$$\begin{aligned} |S(h_1, h_2)|\rho_0(a) &\le |c| + A\|h_2\|_\mu \le [|h_1| + k_1\|h_2\|_\mu]k_2 + A\|h_2\|_\mu \\ &\le k\|(h_1, h_2)\|_+ \end{aligned} \tag{2 8}$$

where $k_1 = A\|g\rho_0\|_L$, $k_2 = |1 - \int_0^A g(a)\rho_0(a)\, da|^{-1}$ and $k = \max(k_2, k_1k_2 + A)$ show that $\|S(h_1, h_2)\|_\mu \le k\|(h_1, h_2)\|_+$ or, in other words, that S is a bounded operator All that remains to demonstrate is the compactness of S

Suppose (h_1^m, h_2^m) is a bounded sequence in $R \times B_\mu$ It is to be shown that the sequence $\rho_m = S(h_1^m, h_2^m)$ has a convergent subsequence in B_μ From (2 8) it follows that the sequence $s_m(a) = \rho_m(a)/\rho_0(a)$ is a uniformly bounded sequence of functions continuous on $[0, A]$ Moreover, the first equation in the system (2 1) shows that $s_n'(a) = h_2^m(a)/\rho_0(a)$ which implies that the sequence of derivatives $s_m'(a)$ is also uniformly bounded on $[0, A]$ Consequently, there exists a sequence $s_{m_i}(a)$ which converges uniformly on $[0, A]$ to a continuous function $s(a)$ Define

$$\rho(a) = \begin{cases} s(a)\rho_0(a), & 0 \le a < A \\ 0, & a = A \end{cases}$$

Clearly $\rho \in B_\mu$ and $\rho_{m_i} \to \rho$ in B_μ Thus S is compact □

3 GLOBAL BRANCHES OF POSITIVE EQUILIBRIA WHEN $A < +\infty$

By a solution of the equilibrium equations (1 2) in $R \in B_\mu$ will be meant an ordered pair $(n, \rho) \in R \times B_\mu$ for which ρ also belongs to $C^1([0, A], R)$ For example, $(n, 0)$ is a solution for all $n \in R$ This section deals with *positive solutions* in $R \times B_\mu$, that is with solutions (n, ρ) for which $\rho(a) > 0$ on $[0, A)$

Let $\Omega \subseteq B_\mu$ be an open set containing $0 \in \Omega$ The assumptions needed on μ and f are the following

H1 *f and* μ *can be written*

$$f = f(a) + r_1(\rho), \quad \mu = \mu(a) + r_2(\rho), \quad r_i(0) = 0$$

where $\mu(a) \in \Delta$, $f(a)\rho_0(a) \in L_1$, $\int_0^A f(a)\rho_0(a)\,da = 1$ and the operators n_1 $\Omega \to L_1$ and n_2 $\Omega \to B_\mu$ defined by $n_i(\rho) = \rho r_i(|\rho|)$ are continuous and satisfy $\|n_1(\rho)\|_L = 0(\|\rho\|_\mu)$ and $\|n_2(\rho)\|_\mu = 0(\|\rho\|_\mu)$ near $\rho = 0$

This hypothesis H1 is basically a continuity assumption on the death and fertility rates μ and f, or more precisely on the remainder terms r_i, as operators between certain ρ spaces It is stated in terms of the defined operators n_i for reasons of simplicity, because this is precisely the requirement needed for the proof of Theorem 1 below In any case, the continuity of the n_i is as easy in general to verify in applications as that of the r_i One can easily write down conditions on the remainder terms r_i (or, what amounts to the same thing, on μ and f) under which H1 holds, if desired For example, the remainders r_i need only be defined on *the cone B_μ^+ of nonnegative functions* $0 \le \rho \in B_\mu$, in which case the continuity of r_1 $B_\mu^+ \to L_1$ and r_2 $B_\mu^+ \to B_\mu$ and the order conditions $\|r_1(\rho)\|_L = 0(\|\rho\|_\mu^\gamma)$, $\|r_2(\rho)\|_\mu = 0(\|\rho\|_\mu^\gamma)$, $0 < \gamma$, suffice More will be said about H1 in Section 7

Recall that a continuum is a closed, connected set The notation $\partial(\Gamma)$ denotes the boundary of a set Γ

THEOREM 1

Assume that $A < +\infty$ and that the death and fertility rates $\mu(a, \rho)$ and $f(a, \rho)$ satisfy hypothesis H1 *There exists a maximal continuum $C^+ \subset R \times \Omega$ with the following properties*

(a) $(1, 0) \in C^+$

(b) $(n, \rho) \in C^+/\{(1, 0)\}$ is a positive solution of the equilibrium equations (1 2) with $A < +\infty$

(c) $C^+ \cap \partial(R \times \Omega) \neq \emptyset$

By (b), C^+ is a continuum of positive equilibrium solutions of the general McKendrick system (1 1) with $A < +\infty$ Conclusion (a) says that this continuum of positive equilibria bifurcates from (i e intersects) the branch of trivial equilibria $(n, 0)$, $n \in R$, at the critical inherent net reproductive rate value of $n = 1$ It follows from the proof of Theorem 1 given below and from general bifurcation principles that $n = 1$ is the only possible such critical value of the bifurcation parameter n Property (c) states that the continuum of positive equilibria exists globally in the sense that it reaches the boundary of the set $R \times \Omega$ on which the problem has been posed and on which H1 holds The open set Ω is allowed to be the whole space B_μ in H1 and Theorem 1, in which case $\partial(R \times \Omega) = \infty$ and (c) is to be interpreted as stating that the continuum C^+ is unbounded in $R \times B_\mu$

Before giving the proof of Theorem 1 we note that from (1 2a) follows $\rho(a) = \rho(0) \exp(-M(a, \rho))$ Thus, nontrivial solutions of (1 2) have the following *invariant sign property* if $(n, \rho) \in R \times \Omega$, $\rho \not\equiv 0$, is a solution of (1 2) then either $\rho(a) > 0$ or $\rho(a) < 0$ for all $0 \le a < A \le +\infty$, i e any nontrivial solution is either positive or negative on $[0, A)$

Proof of Theorem 1 The equilibrium equations (1 2a, b) can be written, by use of the hypotheses on μ and f in H1, in the form

$$\begin{aligned} \rho'(a) + \mu(a)\rho(a) &= -\rho r_2(\rho) \\ \rho(0) &= \int_0^A g(a)\rho(a)\,da + \lambda \int_0^A f(a)\rho(a)\,da + \left(\lambda + \frac{1}{2}\right) \int_0^A \rho r_1(\rho)\,da \qquad (3\ 1) \\ g(a) &= \frac{f(a)}{2}, \quad \lambda = n - \frac{1}{2} \end{aligned}$$

Equation (1 2c) is automatically satisfied by solutions $\rho \in B_\mu$ Note that

$$\int_0^A g(a)\rho_0(a)\,da = \frac{1}{2}$$

and thus (2 3) fails to hold Thus, by means of the compact linear operator S define in Section 2, (3 1) can be reformulated, for nonnegative solutions at least, in the operator form

$$\rho = \lambda L\rho + H(\lambda, \rho) \qquad (3\ 2)$$

where

$$L\rho = S\left(\int_0^A f(a)\rho(a)\,da,\ 0\right)$$
$$H(\lambda, \rho) = S\left(\left(\lambda + \frac{1}{2}\right)\int_0^A n_1(\rho)\,da,\ -n_2(\rho)\right)$$

Note that by the Lemma of Section 2 any solution $\rho \in B_\mu$ of (1 2) must lie in C^1 Because S is linear and compact, it follows that the linear operator $L\ B_\mu \to B_\mu$ is compact and the operator $H\ R \times \Omega \to B_\mu$ is completely continuous Moreover, by H1 the operator H satisfies $\|H(\lambda, \rho)\|_+ = o(\|\rho\|_\mu)$ near $\rho = 0$ uniformly on bounded $\lambda \in R$ intervals

If $(\lambda, \rho) \in R \times \Omega$ is a positive solution of (3 1), then (n, ρ) where $n = \lambda + 1/2$ is a positive solution of the equilibrium Equations (1 2) (the absolute values in the n_i defined in H1 being irrelevant if $\rho \geq 0$) On the other hand, if $(\lambda, \rho) \in R \times \Omega$ is a negative solution of (3 2), then $(\lambda, -\rho) \in R \times \Omega$ is a positive solution This follows because $H(\lambda, \rho) = -H(\lambda, -\rho)$ for all $(\lambda, \rho) \in R \times \Omega$ with $\rho \leq 0$

The goal of the proof is to apply Rabinowitz's alternative[9] to (3 2) To do this we must first establish some facts concerning the linear operator L To find the characteristic values λ of L, note that $\rho = \lambda L\rho$ is equivalent to the linear homogeneous system (2 2) with $g(a)$ replaced by $nf(a)$ As observed in Section 2 nontrivial solutions exist if and only if (2 3) holds, i e if and only if $n = 1$ (or $\lambda = 1/2$), in which case the characteristic solutions $\rho \in B_\mu$ are constant multiples of $\rho_0(a)$

This *sole* characteristic value $\lambda = 1/2$ of L is simple For, suppose that $\rho \in B_\mu$ is such that $(1/2L - I)^2\rho = 0$ Then $(1/2L - I)\rho = k\rho_0 = 1/2kL\rho_0$ for some $k \in R$ Thus $\rho = L(1/2\rho - 1/2k\rho_0)$ which is equivalent to the equations

$$\rho'(a) + \mu(a)\rho(a) = 0, \quad \rho(0) = \int_0^A f(a)\rho(a)da - \frac{1}{2}k$$

Inasmuch as H1 implies that (2 3) holds with $g(a)$ replaced by $f(a)$ (i e the associated homogeneous system has a nontrivial solution) the "orthogonality condition" (2 6) of the Fredholm alternative stated in Section 2 must hold for this system This means that $k = 0$ and hence that $(1/2L - I)\rho = 0$ In summary, $(1/2L - I)^2\rho = 0$ implies $(1/2L - I)\rho = 0$ which in turn implies that $\lambda = 1/2$ is simple

Corollary 1 12 of [9] now implies the existence of a continuum $C \subset R \times \Omega$ satisfying

$$\left(\frac{1}{2}, 0\right) \in C, \quad C \cap \partial(R \times \Omega) \neq \emptyset$$
$$(\lambda, \rho) \in C / \left\{\left(\frac{1}{2}, 0\right)\right\} \text{ solves (3 2) and } 0 \neq \rho \in B_\mu$$

The second alternative in the Corollary 1 12, namely that C connects to another characteristic solution $(\lambda, 0)$, $\lambda \neq 1/2$, is ruled out here by the uniqueness of the characteristic value $\lambda = 1/2$ of L

Now $(\lambda, \rho) \in C$ implies $\rho' + (\mu + r_1(|\rho|))\rho = 0$ and hence that the invariant sign property holds, i e if $\rho \not\equiv 0$ then either $\rho > 0$ or $\rho < 0$ on $[0, A)$ Thus $C = \{(1/2, 0)\} \cup C_+ \cup C_-$ where $(\lambda, \rho) \in C_+$ implies $\rho > 0$ and $(\lambda, \rho) \in C_-$ implies $\rho < 0$ on $[0, A)$ Theorem 1 is proved by setting

$$C^+ = \{(1, 0)\} \cup \left\{(n, \rho) \Big| \left(n - \frac{1}{2}, \rho\right) \in C_+\right\} \cup \left\{(n, -\rho) \Big| \left(n - \frac{1}{2}, \rho\right) \in C_-\right\} \quad \square$$

If $\Omega = B_\mu$ in H1 and Theorem 1, that is to say if μ and f are globally defined functionals of the density $\rho \in B_\mu$, then the continuum C^+ is unbounded in $R \times B_\mu$. This means that either the *spectrum* of C^+

$$\sigma = \{n \in R \mid (n, \rho) \in C^+/\{(1, 0)\} \text{ for some } \rho \in B_\mu\} \tag{3.3}$$

or the *positive equilibrium solution set* associated with C^+

$$\Sigma^+ = \{\rho \in B_\mu \mid (n, \rho) \in C^+/\{(1,0)\} \text{ for some } n \in R\}$$

is unbounded (or both). The closures of σ and Σ^+ are continua.

The spectrum σ is connected and is consequently an interval of reals. Note that the interval σ is not necessary the "spectrum" of the system (1.1) nor is Σ^+ necessarily the positive solution set of (1.1) because there might well exist positive solutions of (1.1) not lying on the continuum C^+ of positive solutions connecting to the bifurcation point $(n, \rho) = (1, 0)$. For example see Section 6. In Section 5 some results concerning the spectrum σ are given. First, however, we briefly show how the results of this section and of Section 2 can be extended to include the case $A = +\infty$.

4. THE CASE $A = +\infty$

For simplicity of presentation A was taken to be a finite real number in Sections 2 and 3. Quite often however the McKendrick model (1.1) is studied with $A = +\infty$. In this section it is shown how the results of Sections 2 and 3 can be extended to the more technically complicated case when $A = +\infty$.

Let Δ_∞^+ denote the set of nonnegative functions $\rho \in C^0([0, +\infty), R^+)$ for which

$$\boldsymbol{\mu} = \liminf_{a \to +\infty} \mu(a) > 0$$

Then $\mu \in \Delta_\infty^+$ implies $\lim_{a\to+\infty} M(a) = +\infty$. For $\mu \in \Delta_\infty^+$ and $0 < \nu \le 1$ define $B_{\mu\nu}$ to be the Banach space of continuous functions $h \in C^0([0, +\infty), R)$ for which $\|h\|_{\mu\nu} < +\infty$ where

$$\|h\|_{\mu\nu} = \sup_{[0, +\infty)} |h(a)|/\rho_{0\nu}(a), \quad \rho_{0\nu}(a) = \exp(-\nu M(a))$$

Note that $\rho_{0\beta}(a) \in B_{\mu\nu}$ for all $\nu \le \beta \le 1$. Also note that $h \in B_{\mu\nu}$ implies $\lim_{a\to+\infty} h(a) = 0$. Denote $\rho_0(a) = \rho_{01} = \exp(-M(a))$.

The product space $R \times B_{\mu\nu}$ will be given the norm $\|\ \|_+ = |\ | + \|\ \|_{\mu\nu}$ and L_1 will now denote the space $L_1([0, +\infty), R)$ under the norm $\|h\|_L = (\int_0^\infty |h(a)| da)$.

First consider the linear theory for systems (2.1) and (2.2) with $A = +\infty$ in which case all solutions again have the form $\rho = c\rho_0(a)$, $c \in R$. All solutions of the nonhomogeneous system (2.1) again have the form (2.4). To see that this general solution lies in $B_{\mu\nu}$ for $h \in B_{\mu\nu}$ consider the following inequalities

$$\begin{aligned} &\left|\rho_0(a) \int_0^a h_2(a)/\rho_0(a)\, da\right| / \rho_{0\nu}(a) \\ &\quad \le \int_0^a [|h_2(\alpha)|/\rho_{0\nu}(\alpha)]\rho_{0\nu}(\alpha) \exp\left(-\int_\alpha^a \mu(s) ds\right) d\alpha / \rho_{0\nu}(a) \\ &\quad \le \|h_2\|_{\mu\nu} \int_0^a \exp\left((\nu - 1)\int_\alpha^a \mu(s) ds\right) d\alpha \le \|h_2\|_{\mu\nu} k_{\mu\nu} < +\infty \end{aligned} \tag{4.1}$$

The last integral is bounded by a constant $k_{\mu\nu} < +\infty$ for $a \geq 0$ because if $\mathbf{a} \geq 0$ is so large that $\mu(a) \geq \boldsymbol{\mu}/2$ for $a \geq \mathbf{a}$ then for $a \geq \mathbf{a}$

$$0 < \int_0^a \exp\left((\nu - 1)\int_a^a \mu(s)\,ds\right) da = \int_0^{\mathbf{a}} + \int_{\mathbf{a}}^a \exp\left((\nu - 1)\int_a^a \mu(s)\,ds\right) da$$
$$\leq \mathbf{a} + \int_{\mathbf{a}}^a \exp\left((\nu - 1)\frac{1}{2}\boldsymbol{\mu}(a - a)\right) da \leq \mathbf{a} + 2/(1 - \nu)\boldsymbol{\mu} < +\infty$$

The general solution (2 4) in fact lies in $B_{\mu\nu} \cap C^1([0, +\infty), R)$

Using (2 4) one finds that the nonhomogeneous system (2 1) is solvable for $(h_1, h_2) \in R \times B_{\mu\nu}$ if and only if (2 5) with $A = +\infty$ is solvable for $c \in R$ The integral on the r h s of (2 5) is finite and in fact satisfies

$$\left|\int_0^\infty g(a)\rho_0(a)\int_0^a h_2(a)/\rho_0(a)\,da\,da\right| \leq \|g\rho_{0\nu}\|_L\|h_2\|_{\mu\nu}k_{\mu\nu} \tag{4 2}$$

Thus, *the Fredholm alternative for Section 2 remains valid for* (2 1) *when* $A = +\infty$ *provided* $\mu \in \Delta_\infty^+$, $g\rho_{0\nu} \in L_1$ *for* $0 < \nu < 1$ *and the Banach space* B_μ *is replaced by* $B_{\mu\nu}$

If the homogeneous system (2 2) has no nontrivial solution (i e (2 3) with $A = +\infty$ fails to hold), then the unique solution of the nonhomogeneous system (2 1) is given again by (2 7) (with $A = +\infty$) Using (4 1) and (4 2) one finds that the linear solution operator S $R \times B_{\mu\nu} \to B_{\mu\nu}$ is bounded

$$\|S(h_1, h_2)\|_{\mu\nu} \leq K_{\mu\nu}\|(h_1, h_2)\|_+$$
$$K_{\mu\nu} = \max\left\{\left|1 - \int_0^\infty g\rho_0\,da\right|^{-1},\ k_{\mu\nu}\left[1 + \|g\rho_{0\nu}\|_L\left|1 - \int_0^\infty g\rho_0\,da\right|^{-1}\right]\right\} \tag{4 3}$$

All that remains to show for the validation of the Lemma in Section 2 for the case $A = +\infty$ is the key property of compactness for S Suppose that (h_1^m, h_2^m) is a bounded sequence in $R \times B_{\mu\beta}$, $\beta > \nu$ We wish to show that the sequence of solutions $\rho_m(a) = S(h_1^m, h_2^m)$ of (2 1) has a convergent subsequence in $B_{\mu\beta}$ By (4 3) the sequence $s_m(a) = \rho_m(a)/\rho_{0\beta}(a)$ is uniformly bounded in $a \geq 0$ and m Moreover

$$|ds_m/da| = |h_2^m(a)/\rho_{0\beta}(a) + (\beta - 1)\mu(a)\rho_m(a)/\rho_{0\beta}(a)|$$
$$\leq \|h_2^m\|_{\mu\beta} + (1 - \beta)\mu^* K_{\mu\beta}\|(h_1^m, h_2^m)\|_+$$

shows that the sequence of derivatives of $s_m(a)$ is uniformly bounded Here it is assumed that $\mu \in \Delta_\infty^+$ is a bounded function $0 \leq \mu(a) \leq \mu^* < +\infty$ Consequently, there exists a subsequence s_{m_i} which converges uniformly for $a \geq 0$ to a bounded on compact sets to a continuous function $s(a)$ Define $\rho(a) = s(a)\exp(-\beta M(a))$, which clearly belongs to $B_{\mu\beta}$ Moreover, it is clear that $\rho_{m_i} \to \rho$ in $B_{\mu\beta}$

Thus, *if* $\mu \in \Delta_\infty^+$, $g\rho_{0\nu} \in L_1$ *for* $0 < \nu < 1$ *and if* μ *is bounded for* $a \geq 0$, *then the Lemma of Section* 2 *remains valid for* $A = +\infty$ *provided* B_μ *is replaced by* $B_{\mu\nu}$ *and* $R \times B_\mu$ *by* $R \times B_{\mu\beta}$, $\beta > \nu$

Having now seen that the linear results of Section 2 can be extended to analogous results for the case $A = +\infty$, we turn to the nonlinear equilibrium equations (1 2) when $A = +\infty$ For this case, hypothesis H1 is modified as follows

H2 *f and* μ *can be written*

$$f = f(a) + r_1(\rho), \quad \mu = \mu(a) + r_2(\rho), \quad r_i(0) = 0$$

where $\mu(a) \in \Delta_\infty^+$ *is bounded for* $a \geq 0$, $f(a)\rho_{0\nu}(a) \in L_1$ *for* $0 < \nu < 1$, $\int_0^\infty f(a)\rho_0(a)\,da = 1$ *and the operators* n_1 $\Omega \to L_1$ *and* n_2 $\Omega \to B_{\mu\nu}$ defined by $n_i(\rho) = \rho r_i(|\rho|)$ *are continuous and satisfy* $\|n_1(\rho)\|_L = 0(\|\rho\|_{\mu\nu})$ *and* $\|n_2(\rho)\|_{\mu\nu} = 0(\|\rho\|_{\mu\nu})$ *near* $\rho = 0$

Here $\Omega \ni 0$ is an open set $0 \in \Omega \subseteq B_{\mu,\nu}$ in $B_{\mu,\beta}$, $\beta > \nu$ With this hypothesis in place of H1 the proof of Theorem 1 remains valid as given in Section 3 with $A = +\infty$ and B_μ replaced by $B_{\mu,\nu}$

Thus *with* $A = +\infty$, H1 *replaced by* H2 *and* B_μ *replaced by* $B_{\mu,\nu}$ *the conclusions of Theorem* 1 *remain valid for the equilibrium equations* (1 2) *with* $A = +\infty$ All of the remarks following Theorem 1 and its proof in Section 3 also remain valid from $A = +\infty$ and B_μ is replaced by $B_{\mu,\nu}$ (including the invariant sign property and the definitions of the sets σ and Σ^+)

5 SOME RESULTS CONCERNING THE SPECTRUM σ

Define the *reproductive ratio* $R(\rho)$ *at an equilibrium density* ρ to be the ratio of the net reproductive rate at ρ to the inherent net reproductive rate Thus

$$R(\rho) = \int_0^A f(a, \rho) \exp(-M(a, \rho))\, da \tag{5 1}$$

Equation (1 2a) is equivalent to $\rho(a) = \rho(0) \exp(-M(a, \rho))$ which when substituted into (1 2b) yields, for nontrivial solutions $\rho \not\equiv 0$, the invariance result that

$$n\, R(\rho) = 1 \tag{5 2}$$

This identity means that the population's net reproductive rate at any equilibrium density ρ is always one, i e at exact replacement

Recall that n is the inherent net reproductive rate, i e the net reproductive rate at $\rho = 0$ The normalization (1 3) implies that $R(0) = 1$ Thus (5 2) holds for all $(n, \rho) \in C^+$ and hence it allows for some rather straightforward conclusions regarding the spectral interval σ

(i) *Some general properties of* σ Define

$$\sigma_s = \sup \sigma \quad \text{and} \quad \sigma_i = \inf \sigma$$
$$R_s = \sup_{\rho \in \Sigma^+} R(\rho) \quad \text{and} \quad R_i = \inf_{\rho \in \Sigma^+} R(\rho)$$

THEOREM 2

Let C^+ *be the continuum of solutions in Theorem* 1 (*or in the extension of Theorem* 1 *described in Section* 2 *for the case* $A = +\infty$) *Let* σ *be the spectrum associated with* C^+ *as defined by* (3 3) *Then*

(a) $0 \le \sigma_i \le 1 \le \sigma_s \le +\infty$,

(b) $R_i = 0$ *if and only if* $\sigma_s = +\infty$,

(c) $R_i > 0$ *implies* $\sigma_s = 1/R_i$ *and thus* $R_i \le 1$,

(d) $R_s = +\infty$ *if and only if* $\sigma_i = 0$,

(e) $R_s < +\infty$ *implies* $\sigma_i = 1/R_s$ *and thus* $R_s \ge 1$

Proof (a) If $0 \in \sigma$, then there exists a $\rho \in B_\mu$ (or $B_{\mu,\nu}$), $\rho \not\equiv 0$, such that $(0, \rho) \in C^+$ But then (1 2b) implies $\rho(0) = 0$ and (1 2a) in turn implies the contradiction $\rho \equiv 0$ Thus $0 \notin \sigma$ Since $n = 1$ lies in the closure of σ and since σ is a connected interval (a) follows

(b) If $R_i = 0$ then there exists a sequence $(n_m, \rho_m) \in C^+$ for which $R(\rho_m) \to R_i = 0$ By (5 2), $n_m R(\rho_m) = 1$ for all m and hence $n_m \to +\infty$ which in turn implies $\sigma_s = +\infty$

Conversely suppose $\sigma_s = +\infty$ Then there exists a sequence $(n_m, \rho_m) \in C^+$ such that $n_m \to +\infty$ Then $n_m R(\rho_m) = 1$ for all m implies $R(\rho_m) \to 0$ and hence $R_i = 0$

(c) If $R_i > 0$ then $1 = nR(\rho) \ge nR_i$ for all $(n, \rho) \in C^+$ This implies $n \le 1/R_i$ for all $n \in \sigma$ and hence $\sigma_s \le 1/R_i$ On the other hand, $R_i > 0$ implies $\sigma_s < +\infty$ by (b) Then $1 = nR(\rho) \le \sigma_s R(\rho)$ for all $(n, \rho) \in C^+$ or $R(\rho) \ge 1/\sigma_s$ for all $\rho \in \Sigma^+$ This in turn implies $R_i \ge 1/\sigma_s$ Thus $R_i \sigma_s = 1$ Then $R_i \le 1$ follows by (a)

(d) and (e) are proved in a manner quite similar to (b) and (c) respectively □

Theorem 2 relates the endpoints of the spectral interval σ to properties of the reproductive ratio $R(\rho)$ when ρ is an equilibrium solution These properties of R can in turn be related to properties of the vital rates μ and f by means of the definition (5 1), that is to say one can often deduce certain properties of R from properties of μ and f via (5 1)

Although in general the functional dependence of μ and f on population density ρ can take many forms, some broad fundamental properties are nearly always assumed in attempting to make reasonably realistic models Usually the fertility rate f is in some sense a nonincreasing if not a decreasing functional of ρ, at least for "large" ρ (it may increase with ρ for small densities ρ) Similarly the death rate μ is usually taken to be a nondecreasing functional of ρ for large ρ, but may be decreasing for small ρ (a phenomenon often termed "depensation" or an Allee–Robertson effect) Also, in the population dynamical setting, f and μ will always be nonnegative, an assumption not needed in Theorems 1 and 2

(ii) *Some results concerning σ when $A < +\infty$* Some illustrations of the discussion immediately above to some restricted, but still rather general cases are given in Corollaries 2 and 3 below for the case $A < +\infty$ These results are based upon the following simple corollary of Theorem 2

COROLLARY 1

Assume $A < +\infty$

(a) *Suppose that* H1 *holds with $\Omega = B_\mu$ and suppose that $R(\rho_m) \to 0$ for any sequence $\rho_m \in B_\mu^+$ of positive solutions of* (1 2a) *for which $\|\rho_m\| \to +\infty$ Then $\sigma_s = +\infty$ for the continuum C^+ of Theorem* 1

(b) *Suppose that* H1 *holds and that $R(\rho) \leq k$ for some $k \in R$, $1 \leq k < +\infty$, and for all positive solutions $\rho \in B_\mu^+$ of* (1 2a) *Then $\sigma_i \geq 1/k$*

Proof (a) Since $\Omega = B_\mu$, either Σ^+ is unbounded or $\sigma_s = +\infty$ But if Σ^+ is unbounded then $\sigma_s = +\infty$ by Theorem 2(b) Thus, in either case $\sigma_s = +\infty$

(b) Since $R_s \leq k$ follows from the assumption, $\sigma_i \geq 1/k$ follows from Theorem 2(e) □

Note for example that if $k = 1$ in Corollary 1(b) then $\sigma_i = 1$ and the spectral interval has the form $\sigma = (1, \sigma_s)$ or $(1, \sigma_s]$ It follows in this case that the bifurcation is supercritical or "to the right" One case for which this happens is the case when it is assumed that the smallest death rate occurs, for all age classes, at lowest population densities

$$0 \leq \mu(a) = \mu(a, 0) \leq \mu(a, \rho), \quad (a, \rho) \in [0, A] \times B_\mu^+ \tag{5 3}$$

and that the largest fertility rate occurs, for all age classes, at lowest population densities

$$f(a) = f(a, 0) \geq f(a, \rho) \geq 0, \quad (a, \rho) \in [0, A] \times B_\mu^+ \tag{5 4}$$

Under these assumptions it follows from (5 1) and (1 3) that

$$R(\rho) \leq \int_0^A f(a) \exp(-M(a))\, da = 1, \quad \rho \in B_\mu^+$$

Thus $k = 1$ in Corollary 1(b)

COROLLARY 2

If $A < +\infty$, H1 *with $\Omega = B_\mu$ and* (5 3)–(5 4) *hold, then the spectral interval of C^+ in Theorem* 1 *has the form $\sigma = (1, \sigma_s)$ or $(1, \sigma_s]$*

If it also occurs that $\sigma_s = +\infty$, then it would be the case that $\sigma = (1, +\infty)$ and one would have the interesting case that positive equilibria exist for all inherent net reproductive rates n greater than the critical value $n = 1$ One way in which $\sigma_s = +\infty$ can occur is by means of the assumption on $R(\rho)$ in Corollary 1(a), which means roughly that fertility drops to zero as population density increases without bound This is a very common modelling assumption (This occurs also when $R(\rho)$ drops to zero as the death rate μ increases without bound with population density ρ) To see a fairly general example consider the commonly assumed case when the fertility rate is multiplicatively separable $f = f(a)\phi(\rho)$ Specifically, assume the following

H3 (i) $f = f(a)\phi(\int_0^A w(a)\rho(a)\,da) \geq 0$ *where* $0 \leq f(a)\rho_0(a) \in L_1$, $\int_0^A f(a)\rho_0(a)\,da = 1$, $0 \leq w(a)\rho_0(a) \in L_1$, $\int_0^A w(a)\rho_0(a)\,da > 0$ *and* $\phi \in C^0(R^+, R^+)$ *is nonincreasing with* $\lim_{x\to+\infty} \phi(x) = 0$ *and* $|\phi(x) - 1| = 0(|x|^\gamma)$ *for* $0 < \gamma \in R$ *and* x *near* 0, (ii) μ *satisfies* H1, (5 3) *and* $\mu(a, \rho) \leq \bar{\mu}(a) \in \Delta$ *for* $(a, \rho) \in [0, A] \times B_\mu^+$

It is easy to show that H3 implies H1, (5 3) and (5 4) Thus $\sigma_i = 1$ by Corollary 2 The following corollary shows that $\sigma_s = +\infty$ under H3

COROLLARY 3

If $A < +\infty$ *and* H3 *hold, then* $\sigma = (1, +\infty)$ *for the continuum* C^+ *of Theorem* 1

Note that (5 3) and (5 4) imply $r_2(\rho) \geq 0$ and $r_1(\rho) \geq 0$ in H1 respectively Thus under H1 and (5 3)

$$d(\rho(a) \exp(M(a)))/da = -\rho r_2(\rho) \exp(M(a)) \leq 0$$

and hence $\|\rho\|_\mu = \rho(0)$ for any positive solution ρ of (1 2a)

Proof of Corollary 3 All that needs be shown is $\sigma_s = +\infty$ and this will be done by an application of Corollary 1(a) Suppose $\rho_m \in B_\mu^+$ is a sequence of positive solutions of (1 2a) for which $\|\rho_m\|_\mu = \rho_m(0) \to +\infty$ as $m \to +\infty$ By H3(ii)

$$\int_0^A w(a)\rho_m(a)\,da = \rho_m(0) \int_0^A w(a) \exp(-M(a, \rho))\,da \geq \|\rho_m\|_\mu w_0$$

where

$$0 < w_0 = \int_0^A w(a) \exp\left(-\int_0^a \bar{\mu}(a)\,da\right) da$$

This implies, together with H3 (i), that

$$\phi_m = \phi\left(\int_0^A w(a)\rho_m(a)\,da\right) \to 0$$

Since

$$0 \leq R(\rho_m) \leq \int_0^A f(a)\phi\left(\int_0^A w(a)\rho_m(a)da\right) \exp(-M(a, \rho_m))\,da \leq \phi_m \int_0^A f(a)\rho_0(a)\,da = \phi_m$$

it follows that $R(\rho_m) \to 0$ as $m \to +\infty$ □

Hypotheses H3 allows for a general dependence of f on a and for a fairly general functional dependence on ρ The key requirement is the multiplicative separability and the requirement that $\lim_{x\to+\infty} \phi(x) = 0$ (It is not difficult to modify H3(i) in an obvious way for non-separable f in such a way as to retain the proof and the Corollary) To (5 3) hypothesis H3(ii) adds an age-specific upper bound on the density dependent death rate μ

(iii) *The case* $A = +\infty$ The general results in (i) concerning σ are valid when $A = +\infty$ Thus Corollary 1 and its proof stand as given when $A = +\infty$ if B_μ and $\|\cdot\|_\mu$ are replaced by $B_{\mu\nu}$ and $\|\ \|_{\mu\nu}$ and H1 is replaced by H2 The same is easily seen to be true of Corollary 2 Corollary 3 with $A = +\infty$ is valid as stated, as is its proof, if in addition to these changes the condition $f\rho_{0\mu} \in L_1$ replaces $f\rho_0 \in L_1$ (It is also necessary to note that $\|\rho\|_{\mu\nu} = \rho(0)$ for positive solutions This follows from

$$d(\rho(a) \exp(\nu M(a)))/da = (-\rho r_2(\rho) + (\nu - 1)\mu\rho) \exp(\nu M(a)) \leq 0$$

which holds for $\rho \geq 0$ because $0 < \nu < 1$, $\mu \geq 0$ under H3 and $r_2(\rho) \geq 0$ by (5 3))

(iv) *An example* An example of a commonly used fertility rate functional of the form required by H3(i) is

$$f = f(a)\left[1 - \int_0^A w(a)\rho(a)\, da\right]_+$$

where $[x]_+ = x$ if $x \geq 0$ and $[x]_+ = 0$ if $x < 0$ (see [4]) By Corollary 3, $\sigma = (1, +\infty)$ for this example For the even simpler case when $\mu(a, \rho) \equiv \mu(a)$, this can be seen by a direct solution of (1 2) for $\rho(a) = (n - 1)\rho_0(a)/\int_0^A w(a)\rho_0(a)da$ This is a special case of the application considered in the next section

6 AN APPLICATION

For $A = 1$ take $\mu(a, \rho) = 1/(1 - a) \in \Delta$ and

$$f = f(a)[1 + \beta W(\rho) - (1 + \beta)W^2(\rho)]_+, \quad \beta \in R, \quad f(a) \geq 0$$

where $f\rho_0 = (1 - a)f(a) \in L_1$ is chosen such that $\int_0^1 (1 - a)f(a)\, da = 1$ and where

$$W(\rho) = \int_0^1 w(a)\rho(a)\, da, \quad w(a) \geq 0$$

Here $w\rho_0 = (1 - a)w(a) \in L_1$ is chosen such that $\int_0^1 (1 - a)w(a)\, da = 1$ H1 is satisfied for these vital rates μ and f The fertility rate is (the positive part of) a quadratic polynomial in the functional $W(\rho)$ and serves as a generalization of the example at the end of the previous section[4] where $\beta = -1$

The equilibrium equations become

$$\begin{aligned} &\text{(a)}\ \rho'(a) + \rho(a)/(1 - a) = 0, \quad 0 < a < 1 \\ &\text{(b)}\ \rho(0) = n\int_0^1 f(a)[1 + \beta W(\rho) - (1 + \beta)W^2(\rho)]_+\, \rho(a)\, da \qquad (6\ 1) \\ &\text{(c)}\ \rho(1) = 0 \end{aligned}$$

Equations (a) and (c) are easily solved $\rho(a) = c(1 - a)$, $c \in R^+$ Substitution of this solution into (b) leads to an algebraic quadratic equation for $c \in R^+$

$$n(1 + \beta)c^2 - \beta nc + (1 - n) = 0 \qquad (6\ 2)$$

the solution c of which, as a function of $n > 0$, depends on the value of β The three qualitatively different cases are graphed in Fig 1 below The continuum of positive equilibria $C^+ = \{(n, c(1 - a))|(n, c) \in C_0^+\}$, where C_0^+ is the solution branch of the quadratic (6 2) connecting to $(n, c) = (1, 0)$ as is indicated in Fig 1, is the continuum of Theorem 1 It is clearly unbounded as guaranteed by Theorem 1(c) In fact Σ^+ is bounded and the spectrum σ is unbounded ($\sigma_s = +\infty$) in every case

Beyond the existence of a global branch of equilibria, this example illustrates some further possible properties of the equilibrium equations Case (a) in Fig 1 when $\beta < -1$ shows that it is not necessarily true that all equilibria lie on the branch C^+ of Theorem 1 nor that the spectrum σ of C^+ is necessarily the spectrum of the equilibrium equations (1 2) (which in case (a) is R^+) Cases (b) and (c) in Fig 1 show that the bifurcation from $(n, \rho) = (1, 0)$ can be super- or subcritical and that σ_i can be <1

The three cases in Fig 1 are distinguished by the value of β, i e by the nature of the functional response of the fertility rate f to the weighted density functional $W(\rho)$ These cases are illustrated in Fig 2

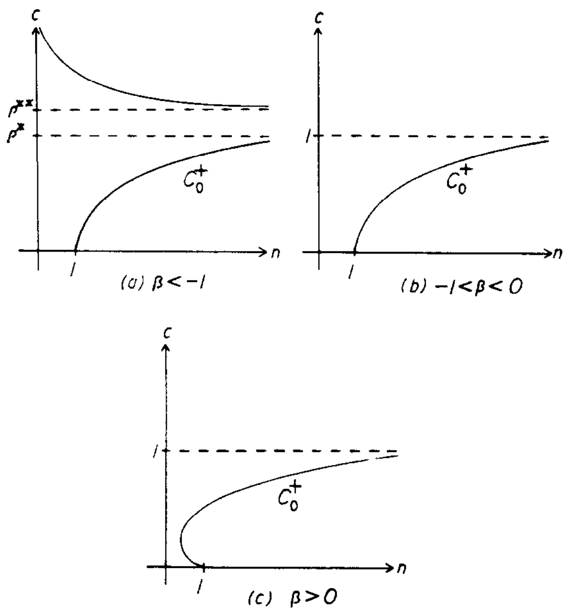

Fig 1 The solution c of (6 2) is plotted as a function of $n > 0$ in the three qualitatively different cases depending on the value of β Equilibrium solutions of (6 1) are given by $\rho = c(1 - a)$ In case (a), $\rho^* = 1$, $\rho^{**} = -1/(1 + \beta)$ if $\beta < -2$ and $\rho^* = -1/(1 + \beta)$, $\rho^{**} = 1$ if $-2 < \beta < -1$

7 CONCLUDING REMARKS

The main result of this paper is contained in Theorem 1 and its extension described in Section 4 to the case when $A = +\infty$ It states that the McKendrick equations (1 1) for the birth and death processes of an age-structured population has, for death rate $\mu = \mu(a, \rho)$ and fertility rate $F = nf(a, \rho)$ where f is normalized by (1 3) and n is the inherent net reproductive rate, a global continuum of positive equilibria $(n, \rho) \in R \times B_\mu$ $(R \times B_{\mu\backslash}$ when $A = +\infty)$ solely under the continuity assumption H1 (H2 when $A = +\infty$) on μ and f This continuum bifurcates from the critical point (1, 0) and connects to the boundary of $R \times \Omega$ where Ω is the domain of definition of μ and f as functionals of population density ρ The simple continuity hypothesis H1 (or H2) is quite mild in comparison to the various monotonicity, boundedness, Lipschitz and differentiability restrictions placed on μ and f in previous literature

H1 and H2 require that f and μ, or more accurately the operators n_1 and n_2, map B_μ and $B_{\mu\backslash}$ respectively into certain Banach spaces In the case of the fertility rate f, the operator n_1 must map into L_1 This is a minimal and quite natural restriction for the McKendrick equations (1 1) It is satisfied, for example, when $A < +\infty$ if the remainder term r_1 satisfies $r_1(\rho)$ exp $(-M(a)) \in L_1$ for $\rho \in B_\mu$

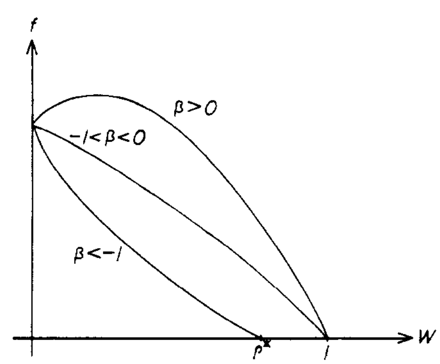

Fig 2 The functional response of the fertility rate f (for fixed age a) is plotted against the weighted density functional W

For the death rate μ, H1 (or H2) requires the operator n_2 to map into B_μ (or $B_{\mu,1}$ when $A = +\infty$) This means roughly that $r_2(\rho)$ must, for $\rho \in \Omega \subseteq B_\mu$ (or $B_{\mu,1}$), be a bounded function of $a \in [0, A)$ In an application this may be the most restrictive requirement of H1 or H2 For example, when $A < +\infty$, H1 cannot be satisfied by a death rate functional for which the remainder term r_2 has the form $\mu(a)W(\rho)$ where W is a functional on B_μ such as $\int_0^A w(a)\rho(a)da$ because in order for n_2 to map into B_μ it would be necessary for $\mu(a)$ to be a bounded function of $a \in [0, A)$ which is imcompatible with $\mu \in \Delta$ Or, as another example if $r_2(\rho) = \mu(a)\rho^\gamma$, $0 < \gamma \in R^+$ then H1 is satisfied only if $\mu \in \Delta$ satisfies some additional restraint such as the boundedness of $|\mu(a)| \exp(-\gamma M(a))$ for $a \in [0, A)$ These simple examples show that the hypotheses H1 or H2 are, at least with regard to the death rate μ, slightly more restrictive than they might first appear to be

The requirements of μ and f are the most natural and straightforward ones for the approach taken here It is possible that other Banach spaces could be used in H1 and H2 and still obtain the general result of Theorem 1 under such mild continuity assumptions only To do this by means of the global bifucation theorem of Rabinowitz[9] used here would require that the linear theory of Sections 2 and 4 remain valid on these spaces and in particular that the crucial compactness property of the solution operator S hold

Theorem 1 is purely an existence result There are several other important and interesting questions which are not addressed here, such as the uniqueness of positive equilibria vs the existence of multiple positive equilibria, the stability of equilibria, the structure of the bifurcating branch of positive equilibria (especially near bifurcation) and the structure of the spectrum σ (with which Section 5 deals) and the set Σ^+

In a forthcoming paper[2] the properties of the bifurcating branch of positive equilibria will be studied in detail locally near the bifurcation point $(n, \rho) = (1, 0)$ A parameterization of the local branch will be developed which will show the nature of the equilibria near bifurcation, the direction of bifurcation and how it depends on the vital rates μ and f, and the stability of the branch equilibria and the trivial equilibrium $\rho \equiv 0$ As is commonly the case, these results will show that the trivial equilibrium loses stability as n increases through the critical bifurcation value $n = 1$ while the stability of the positive branch equilibria depends on the direction of bifurcation (namely, right bifurcating branches are stable and left bifurcating branches are unstable) Even when the local branch equilibria are stable near criticality the stability may not persist globally along the branch however A secondary, Hopf type bifurcation to time periodic solutions of (1 1) can occur[1] The global dynamics and stability picture for (1 1) can be quite complex and remains a challenging problem

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Note added in proof

To H1 and H2 must be added the assumption that n_i takes bounded sets to bounded sets