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R J Knops (Editor)

Nonlinear analysis and mechanics: Heriot-Watt Symposium

VOLUME III

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Heriot-Watt University

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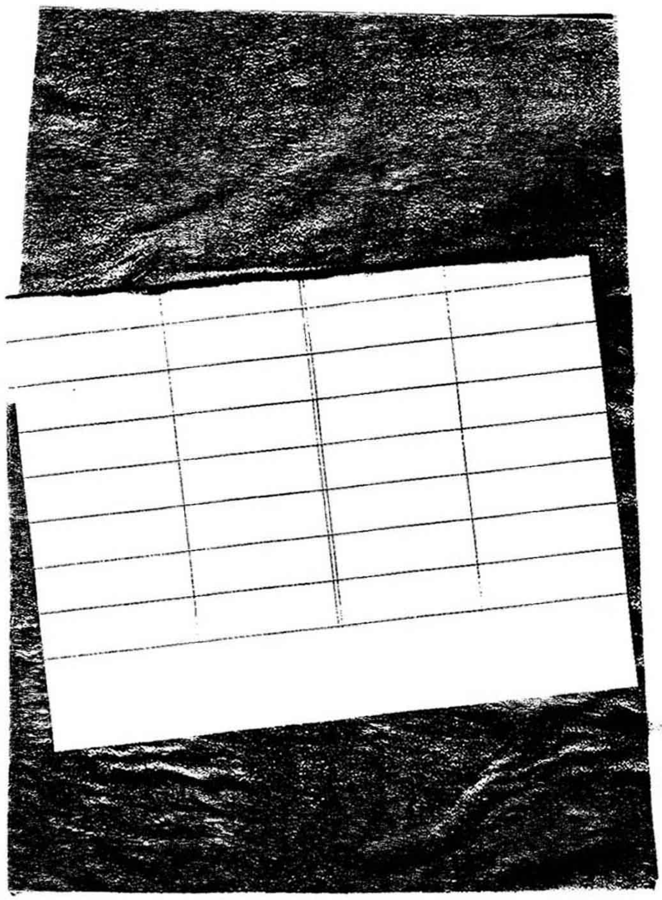

Preface

This is another volume in the series based on invited lectures delivered at Heriot-Watt University as part of an extended research programme under the general sponsorship of the Science Research Council of Great Britain. The articles in the present volume are devoted to a discussion of recent results in population dynamics and viscoelasticity, and also to a comprehensive survey of modern developments in semigroups of nonlinear contractions.

The authors have once again been extremely helpful in the preparation of the typescript. It is a pleasure to acknowledge their assistance and also that of Mr. G. Andrews who prepared the written version of the lectures by Professor Pazy. Thanks must also be expressed to Mrs. M. Gardiner and Mrs. M. E. Crawford for their painstaking and expert typing, and to Lynda Robertson for the diagrams in the article by Professor Pazy.

Edinburgh
July 1978

R. J. Knops

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Suggestions for publication, in the form of outlines and representative samples, are invited by the editorial board for assessment. Intending authors should contact either the main editor or another member of the editorial board, citing the relevant AMS subject classifications. Refereeing is by members of the board and other mathematical authorities in the topic concerned, located throughout the world.

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Population dynamics with age dependence

1 CLASSICAL THEORIES

The simplest model of population dynamics is based on the Malthusian law[†]

$$\dot{P} = \delta P \qquad (\delta = \text{constant}),$$

where $P(t)$ is the total population at time t and δ is the growth modulus. This law is clearly inapplicable to situations in which the population competes for resources, for in those situations δ should depend on the size of the population: the larger the population, the slower should be its rate of growth.

To overcome this deficiency in the Malthusian law, Verhulst [2,3] assumed that

$$\dot{P} = (\delta_0 - \omega_0 P)P \qquad (\delta_0, \omega_0 = \text{constant}). \tag{1.1}$$

For δ_0 and ω_0 positive this differential equation has a stable equilibrium point $P_0 = \delta_0/\omega_0$, and populations with $P(0) < P_0$ grow monotonically to P_0 as $t \longrightarrow \infty$. The solution of (1.1) has been applied, with remarkable success, to fit the growth curves of various types of populations.[††]

[†]Malthus [1], p.13, asserts that: "Population, when unchecked, increases in a geometrical ratio."

[††]See, e.g., Lotka [6], pp. 66-76.

2 LINEAR THEORY WITH AGE DEPENDENCE

(a) Basic Equations The chief disadvantage of the models of Malthus and Verhulst is that they yield no information whatsoever concerning the distribution of ages in the population and are, in fact, based on the tacit assumption that the birth and death processes are independent of age.

To discuss age dependence we introduce the age distribution $\rho(a,t)$. This field represents the density of individuals of age a at time t; when integrated over all[†] ages it yields the total population $P(t)$:

$$P(t) = \int_0^\infty \rho(a,t)\,da. \tag{2.1}$$

Consider the group of individuals who are of age a at time t. If t is increased by h units, these individuals age by h units; thus

$$D\rho(a,t) = \lim_{h \downarrow 0} \frac{\rho(a+h,t+h) - \rho(a,t)}{h} \tag{2.2}$$

is the rate at which the population of this group is changing in time. Of course, when ρ is differentiable,[††]

$$D\rho = \rho_a + \rho_t.$$

Let $\sigma(a,t)$ denote the population supply; that is, the number of individuals, per unit age, of age a added to the population at time t. Balance of population then requires that

$$D\rho = \sigma. \tag{2.3}$$

[†]For convenience, we allow all ages in the interval $[0,\infty)$.

[††]Subscripts denote partial differentiation with respect to the corresponding argument.

We assume that the supply σ is due only to deaths (and hence is negative). In fact, we assume that (for each a) $\sigma(a,t)$ is proportional to the density $\rho(a,t)$ with constant of proportionality independent of time:

$$\sigma(a,t) = -\mu(a)\rho(a,t).$$

With this assumption equation (2.3) takes the form

$$D\rho(a,t) + \mu(a)\rho(a,t) = 0. \tag{2.4}$$

We call $\mu(a) \geqslant 0$ the <u>survival function</u>. Of importance is the probability

$$\pi(a_0,a) = \exp\{-\int_{a_0}^{a}\mu(\alpha)d\alpha\} \tag{2.5}$$

of an individual of age a_0 living to age a.

The quantity

$$B(t) = \rho(0,t) \tag{2.6}$$

is the <u>birth-rate</u> at time t. We assume that the birth process is governed by a renewal equation of the form

$$B(t) = \int_0^\infty \beta(a)\rho(a,t)da, \tag{2.7}$$

where $\beta(a) \geqslant 0$, called the <u>maternity function</u>, is the expected number of children (per unit age and population) to be born to an individual of age a.† If we multiple $\beta(a)$ by $\pi(0,a)$, the probability of living to age a, and integrate over all ages we get the <u>net reproduction rate</u>

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† See, e.g., Andrewartha and Birch [12], where curves of $\beta(a)$ and $\pi(0,a)$ are given for the vole mouse (microtus agrestis) and for the rice weevil (calandra oryzae).

$$R = \int_0^\infty \pi(0,a)\beta(a)da, \tag{2.8}$$

which is the expected number of offspring to be born to an individual.

Equations (2.4) and (2.7) are the basic equations of the linear theory.[†] To these equations we adjoin the initial condition

$$\rho(a,0) = \phi(a), \tag{2.9}$$

where ϕ is the prescribed <u>initial age distribution</u>.

(b) <u>The Integral Equation</u> We now establish an important alternative formulation of the above system by integrating the partial differential equation (2.4) along characteristics. Thus let ρ be a solution of (2.4), (2.7), and (2.9), let $a_0, t_0 > 0$, and let

$$\bar{\rho}(h) = \rho(a_0 + h, t_0 + h), \quad \bar{\mu}(h) = \mu(a_0 + h).$$

Then (2.2) and (2.4) imply that

$$\frac{d\bar{\rho}}{dh} + \bar{\mu}(h)\bar{\rho} = 0,$$

and hence

$$\rho(a_0 + h, t_0 + h) = \rho(a_0, t_0)\pi(a_0, a_0 + h),$$

where we have used (2.5). This relation gives the values of ρ at all points on the characteristic through (a_0, t_0) in terms of the value of ρ

[†]The basic ideas underlying this theory are due to Sharpe and Lotka [4] (see also Lotka [6], McKendrick [7], Kermack and McKendrick [8,9], Rhodes [10], Scherbaum and Rasch [13], Fisher [14], von Foerster [15], Lopez [16], Fredrickson and Tsuchiya [17], Trucco [18], Fredrickson, Ramkrishna, and Tsuchiya [19], Keyfitz [20], Rubinow [21], Crow and Kimura [22], Coale [24], Langhaar [25], Pollard [27]).

at (a_0,t_0). In particular, if we take $(a_0,t_0) = (a-t,0)$ and $h = t$, we conclude, with the aid of (2.9), that

$$\rho(a,t) = \phi(a-t)\pi(a-t,a) \qquad (a \geqslant t). \tag{2.10}$$

On the other hand, the substitutions $(a_0,t_0) = (0,t-a)$ and $h = a$ lead to

$$\rho(a,t) = B(t-a)\pi(0,a) \qquad (t > a). \tag{2.11}$$

We have yet to use the birth law (2.7); if we substitute (2.10) and (2.11) into (2.7) we arrive at the following linear Volterra integral equation for B:

$$B(t) = \int_0^t \pi(0,a)\beta(a)B(t-a)da + \Phi(t), \tag{2.12}$$

where

$$\Phi(t) = \int_0^\infty \pi(a,a+t)\beta(a+t)\phi(a)da \tag{2.13}$$

depends only on the initial data ϕ. Conversely, if B satisfies (2.12), then ρ defined by (2.10) and (2.11) satisfies our original system (2.4), (2.7) and (2.9).

(c) Some Simple Solutions By a persistent† age distribution we mean a product solution of (2.4) and (2.7):

$$\rho(a,t) = A(a)T(t).$$

We may, without loss in generality, add the requirement that

$$\int_0^\infty A(a)da = 1;$$

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†In the literature solutions of this type are called stable.

then $T(t)$ becomes the total population $P(t)$ and

$$\rho(a,t) = A(a)P(t). \tag{2.14}$$

Thus for any persistent age distribution the proportion $\rho(a,t)/P(t)$ of the population of age a is independent of time. If we substitute (2.14) into (2.4) and (2.8), we easily verify that

$$\begin{aligned} A(a) &= Ce^{-pa}\pi(0,a) \qquad (C = \text{constant}), \\ P(t) &= P_0 e^{pt} \end{aligned} \tag{2.15}$$

with p a solution of

$$\int_0^\infty \pi(0,a)\beta(a)e^{-pa}da = 1. \tag{2.16}$$

Note that, by (2.16), $p = 0$, $p < 0$, or $p > 0$ accordingly as the net reproduction rate (2.8) satisfies $R = 1$, $R < 1$, or $R > 1$. Thus, for $R = 1$, (2.14) reduces to the <u>equilibrium age distribution</u>

$$\rho(a) = B\pi(0,a)$$

with B the (constant) birth-rate.

(d) <u>Asymptotic Behavior of Solutions</u>† The integral equation (2.12) is easily analyzed by means of Laplace transforms. We write

$$f\hat{}(s) = \int_0^\infty e^{-st}f(t)dt$$

for the Laplace transform of a function f. If we transform (2.12) and use

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†This section follows Hoppensteadt [30]. See also Lotka [5], Feller [11, 23] and Coale [24].

the convolution theorem, we arrive at the expression

$$[1 - \hat{k}(s)]\hat{B}(s) = \hat{\Phi}(s), \tag{2.17}$$

where

$$k(a) = \pi(0,a)\beta(a).$$

Equation (2.17), although formal, can be used under appropriate hypotheses to establish the existence of a solution to (2.12). Let us assume that $\phi \in L_1(\mathbb{R}^+)$ $(\mathbb{R}^+ = [0,\infty))$ and

$$\beta(a) = 0 \quad \text{for} \quad a \geqslant a_0 > 0.$$

The first assumption is simply the requirement that the initial population be finite, while the second asserts that there be no reproduction for ages greater than a_0. The second condition insures that both k and Φ (cf. (2.13)) have compact support; hence $\hat{k}(s)$ and $\hat{\Phi}(s)$ are entire functions of s, and both tend to zero as $s \to \infty$ in $\mathcal{Re}(s) \geqslant \delta$ for any δ.

Now define $\hat{B}(s)$ by the formula

$$\hat{B}(s) = \frac{\hat{\Phi}(s)}{1 - \hat{k}(s)} ;$$

then $\hat{B}(s)$ is a meromorphic function of s with poles at exactly those values of s which satisfy

$$1 = \hat{k}(s) = \int_0^\infty e^{-st}\pi(0,t)\beta(t)dt$$

(cf. (2.16)). Since $\hat{k}(s) \to 0$ as $s \to \infty$ in $\mathcal{Re}(s) \geqslant 0$, it follows that there is an s_0 such that $\hat{B}(s)$ is analytic in $\mathcal{Re}(s) \geqslant s_0$. It therefore makes sense to define $B(t)$ through the complex inversion formula