ISSN 0965-5425, Computational Mathematics and Mathematical Physics, 2010, Vol. 50, No. 2, pp. 322–329. © Pleiades Publishing, Ltd., 2010.
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Selection Functionals in Autonomous Models of Biological Systems with a Continuous Age and Spatial Structure

V. N. Razzhevaikin

Dorodnicyn Computing Center, Russian Academy of Sciences, ul. Vavilova 40, Moscow, 119333 Russia
e-mail: razzh@mail.ru

Received April 1, 2009

Abstract—The theory of the relation between evolutionary optimality and the stability of equilibrium states is described. The main result of the theory is stated in the case of quasilinear dynamical systems in normed spaces. Applications of the theory to models of structured biological communities are discussed. Functionals for communities with an age and spatial structure are computed on the basis of available information on steady-state stationary distributions. The functionals are optimized with respect to the parameters of evolutionary selection.

DOI: 10.1134/S0965542510020132

Key words: models of biological systems, stability, evolutionary optimality, age structure, spatial structure.

1. INTRODUCTION

For the last several decades, the construction of extreme principles has remained a central problem in mathematical biology. This interest is explained by a number of reasons, of which the most important are internal (biological) determination and high efficiency. Reviews on this subject can be found in [1, 2].

Interest in this direction is associated with describing the behavior of biological systems and is motivated by the possibility of finding a time-monotone function computed in terms of the parameters of the system, which substantially simplifies the problem of determining the sector of its motion and sometimes its direction. This underlies numerous phenomenological extreme principles constructed in biology, which become teleological concepts when we ignore the situation described in the following section, which is based on the idea of stability. Their application sometimes gives results that are fairly effective from the simulation point of view (see [1]).

Extreme principles arise from the formalization of the idea of evolutionary selection and its consequence—evolutionary optimality, which goes back to Darwin's fundamental work [3]. He managed to identify some possible triggers and, more importantly, the concept of uncovering internal (at the level of a population, community, etc.) mechanisms that determine the direction of evolution. The fact that the competitive struggle within a limited space leads to the elimination of all the species, except for a small number of ones that are most adapted to the given conditions, makes it possible to construct fundamental principles of functioning of biological systems.

These principles are based on the hypothesis that stationary states of biological communities formed in the course of evolution are stable. The ideas underlying the use of this hypothesis in the construction of evolutionary optimality principles are well known to biologists (see [2]) and are formulated in Section 2. Within the framework of the simplest finite-dimensional mathematical model, we can uncover the essence of necessary stability conditions that have the form of extreme relations. The objects to be optimized are the values of Malthusian functions computed on formed stable equilibrium states. Later, these functions play the role of reference points in the construction of functionals for more complicated systems.

However, despite the fundamental character of works concerning evolutionary optimality and the serious mathematical depth of many of them [2, 4], the range of their applications has remained extremely narrow until recently. As a rule, natural systems equipped with a structure were eliminated from consideration.

First, this is associated with the fact that the most frequently used total population sizes turn out to be inadequate to reality because of the difference between the population roles of juvenile and adult individuals. A similar problem arises concerning biological communities, whose properties change noticeably with changing habitat.

Second, the replacement of continuous distributions by discrete ones (in the case of an age structure, the Lotka model [5] is replaced by the Leslie model [6]) assumes the presence of a "natural" discretization scheme, which is absent for most large-scale processes.

Third, attempts to construct acceptable theories directly for continuously distributed systems encountered serious difficulties of a purely mathematical character. For example, results presented in some publications that take into account the age structure of populations (see, e.g., [7, 8]) are based on a rescaling of the linear model. Due to its simplicity, leading asymptotics can be found for each species. However, the rather natural idea that species with maximal asymptotic characteristics have advantages becomes not obvious when attempts are made to fit them into the scheme of evolutionary optimality based on the stability hypothesis. The problem is that we implicitly hypothesize the separation of characteristic times of age stabilization (fast processes) and evolutionary selection (slow processes). This approach seems quite natural in the case of appeals to adequate infinite-dimensional analogues of theorems on singularly perturbed systems of equations. The lack of indications for the possibility of using such appeals leaves considerable gaps in theories constructed on the basis of this scheme.

In a previously constructed theory (see [9, 10]), the author tried to overcome the above shortcomings and proposed a construction that relates the stability of steady states of distributed biological systems to the extremality of values of inherited traits in species surviving in these states. Despite its artificial character (the purely technical hypothesis of quasilinearity, i.e., the linearity of unbounded components of the operators on the right-hand sides of the equations leads to rather unnatural constraints in continuous-time problems), this theory yields interesting and practically useful results for many important problems. Some of them are discussed in this paper.

Section 3 gives the most general mathematical statement of the main applied result in the theory of [9] for the case of autonomous quasilinear systems with continuous time. When constructing this theory, the author used the possibility of considering, in a unified manner, the relation between stability and evolutionary optimality for systems with a continuous age structure and a continuous spatial structure. These problems are matched for dynamical systems in Banach spaces with unbounded operators on the right-hand side. At this level of abstractness, the main result (a necessary stability condition for a stationary distribution) can be formulated in terms of the localization properties of the spectrum of the explicitly specified operator on the right-hand side of the system calculated for this distribution. Further elaboration associated with the possibility of constructing optimized functionals requires more specific formulations. Two of them are considered in the subsequent sections.

In Section 4, the theory of [9] is applied to systems of equations describing communities of biological populations with a continuous age structure. For them, the functional to be optimized is a specially constructed one (reproductive population potential) that is calculated in terms of the original functions on the considered distribution.

Section 5 deals with applications of the theory to spatially distributed biological systems. The basic model is a system of reaction–diffusion equations with diffusivities independent of the phase variables. The right-hand sides of the equations can involve bounded functions depending not only on the phase variables but also on their functionals over space. In this case, the functional to be optimized is a quadratic one depending on the distributions and their first derivatives with respect to spatial variables.

In Section 6, the reader can find references to some applications of the theory and to its connection with important areas of modern theoretical biology.

2. PRINCIPLE OF EVOLUTIONARY OPTIMALITY

The direction of natural selection in competitive conditions on segments of intersecting ecological niches leads at stabilization times to the formation of structures that can be regarded as stable (in mathematical terminology). Consider the simplest model of the interaction of n biological species:

$$\frac{dx_i}{dt} = x_i f_i(x), \quad i = 1, 2, \ldots, n, \quad x = (x_1, \ldots, x_n). \tag{1}$$

A necessary condition for the stability of the equilibrium

$$\bar{x} = (\bar{x}_1, \ldots, \bar{x}_m, 0, \ldots, 0), \quad \bar{x}_i > 0, \quad i = 1, 2, \ldots, m,$$

which represents a species structure of the community in which only the first m species are present out of all the possible ones, is given by the equality

$$f_i(\bar{x}) = \max_j \{f_j(\bar{x})\}, \quad 1 \le i \le m, \quad 1 \le j \le n$$

(the Jacobian of system (1) at $x = \bar{x}$ has the block structure $\left(\frac{\partial(x_i f_i(x))}{\partial x_j}\right)\Big|_{x = \bar{x}} = \begin{pmatrix} A & B \\ 0 & D \end{pmatrix}$ with a diagonal $(n - m) \times (n - m)$ matrix D; its main diagonal contains elements $f_j(\bar{x}), j > m$ such that $f_j(\bar{x}) = 0, j \le m$.) This condition has the character of an extreme relation and expresses the principle of *evolutionary optimality*. Biologically, it means that the species surviving in an equilibrium state must have the maximum values of the Malthusian functions calculated in this state among all the potentially admissible species characterized by inherited values of the evolutionary selection parameters (in the above example, these are the indices j). It is these parameters that specify the "power of species" in its Darwinian sense if we mean the heuristic formulation of the principle of survival for the strongest.

Since the equilibrium $\bar{x}$ lacks the species indexed by $m + 1 \le j \le n$, they can be regarded as virtual; i.e., they can be supplemented with any other species having the hypothetical possibility of being in the original collection. Moreover, in contrast to the above example, the indices distinguishing species do not need to be chosen from a finite set but can have an entirely arbitrary nature. Specifically, they can be elements of a (usually bounded) domain Λ of a finite-dimensional (or sometimes infinite-dimensional comprising, for example, a class of functions) space so that the optimization problem is solved with respect to this domain. (For this reason, the term "index" is replaced in this paper by its synonym "selection parameter," which is more suitable in a continuous interpretation.) Due to this extension, in a typical case when solving an optimization problem, we can find isolated points in Λ that contain those values of the selection parameters $\bar{\lambda} \in \Lambda$ for which the equilibrium $\bar{x}$ is stable.

Note that, in addition to the above necessary stability condition, which corresponds to *external* stability (a synonym of evolutionary stability) and characterizes the stability of the community's equilibrium with respect to species not presented in this state, we need *internal* stability, which characterizes stability with respect to small deviations of sizes of the present species. The determination of $\bar{\lambda} \in \Lambda$ corresponding to species observed in the specified conditions (including the species structure of the communities) can be used as a methodological foundation for identifying the values of those parameters of actually observed (quasi-)stationary biological systems for which field measurements are impossible or very difficult.

In mathematical models of particular structured biological communities, the most difficult task in practice is the construction of maximized functionals of distributions. Their role in the above point example is played by the functions $f_i(x)$ of species sizes. If such functionals can be found, then analogues of the above results (and the schemes for the subsequent computations) can be obtained from a more general theory of the relation between stability and optimality for the case of distributed quasilinear systems (see [9, 10]). Below, this theory is applied to dynamic models of communities consisting of populations with a continuous structure for which we managed to find these functionals.

3. SOME RESULTS OF THE GENERAL THEORY

In this section, we formulate fundamental results concerning the theory relating stability and evolutionary optimality in models of distributed biological systems. The consideration is restricted to continuous-time autonomous systems, which are constructively covered by the description of quasilinear dynamical systems in Banach spaces. The proofs can be found in [9].

The original autonomous dynamical system has the form

$$\begin{aligned} d_t x &= (h_x + a(x, y))x, \\ d_t y &= h_y y + b(x, y), \end{aligned} \tag{2}$$

where $t \in J = [0, T]$, $T > 0$, $d_t = d/dt$, $x \in X$, $y \in Y$, X and Y are Banach spaces, $a \in C^1(X \oplus Y, B(X))$, $b \in C^1(X \oplus Y, Y)$, and $B(Y)$ is the space of bounded linear operators in X. The linear operators $h_{x,y}$ are infinitesimal generators of strongly continuous semigroups of linear bounded operators acting in X and Y, respectively. Recall that a family of such operators $T(t)$, $t \ge 0$, acting in X is called a semigroup if $T(t + s) = T(t)T(s)$ for any $t, s \ge 0$. Strong continuity means the continuity of $T(t)x$, $t \ge 0$, for any $x \in X$. Its infinitesimal generator h_x is defined for $x \in X$ as the limit $h_x x = \lim_{t \searrow 0} \{[T(t)x - T(0)x]/t\}$ with a domain $D(h_x) \subset X$ for which this limit exists for $x \in D(h_x)$. Specifically, such operators are closed (i.e., $\{(x, h_x x), x \in D(h_x)\}$ is closed in $X \oplus X$) and their domain $D(h_x) \subset X$ is dense.

The variables of system (2) are initially divided into two groups: evolutionary x (their variation vanishes at zero values) and nonevolutionary y (required only for the generality necessary in applications; in mathematical constructions, they can be discarded for brevity). The reduced formulation of system (2) has the form

$$d_t w = hw + K(w), \quad \text{where} \quad w = (x, y) \in W = X \oplus Y, \quad h = \begin{pmatrix} h_x & 0 \\ 0 & h_y \end{pmatrix}.$$

Well-posedness, extendability in time, positiveness (construction of invariant cones), and (Hölder) smoothness with respect to initial conditions were discussed in detail in [9]. Concerning some of these issues, the reader is referred to classical results (see, e.g., [11]).

In the original version in [9], the system was nonautonomous with periodic coefficients. Periodicity was necessary to reduce the original problem (for fluxes) to a simpler problem (with bounded operators on the right-hand side) for cascades (over a period). The autonomous case is covered by the general scheme for any positive value of the period. For it, the stability of a stationary solution $\bar{w} = (\bar{x}, \bar{y})$ is understood in the sense that the spectrum of the Jacobian of the mapping calculated over positive time at $\bar{w}$ lies inside the unit disk.

A projector P, i.e., a linear bounded idempotent ($P^2 = P$) operator in W is called *admissible* with respect to h if the domain of the latter satisfies $D(Ph) \subset D(h)$ and, additionally, $hP = PhP$ (i.e., the operator h in coordinates $(P, I - P)$, where I is the identity operator in W, has a upper triangular form).

A projector P in W is called *admissible with respect to* $w \in W$ if $Pw = w$, P is admissible with respect to h and commutes with I_Y (projector onto Y), and, for some neighborhood $O(w) \subset W$, $v \in PW \subset O(w)$ implies $K(v) \in PW$.

The Jacobian of system (2) calculated at the equilibrium $\bar{w} = (\bar{x}, \bar{y})$ is decomposed into the sum

$$l(\bar{w}) = l_0(\bar{w}) + l_1(\bar{w}), \quad \text{where} \quad l_0(\bar{w}) = \begin{pmatrix} h_x + a(\bar{w}) & 0 \\ 0 & 0 \end{pmatrix}$$

Let $\mathbb{C}_{-\delta}$, $\delta > 0$, denote the left complex half-plane shifted to the left by δ. In the autonomous case, the most interesting result of the theory of [9] (minus some generalizations aimed at larger adequacy for biological setting) can be formulated as follows.

Theorem 1. *Let* $\bar{w} = (\bar{x}, \bar{y})$ *be a stable stationary solution to system* (2). *Then, for any projectors* P_1, P_2 *in* $\bar{w}$ *that are admissible with respect to* W *and such that* $P_1P_2 = P_2P_1 = P_2$ *and* $P_2I_Y = P_1I_Y$, *there* is $\delta > 0$ *such that* $\sigma((Ql_0(\bar{w}))_{QW}) \subset \mathbb{C}_{-\delta}$.

Here, $Q = P_1 - P_2$ is a projector in W, A_V is the restriction of a linear operator $A : W \longrightarrow W$ to a subspace $V \subset W$ that is invariant with respect to it, and $\sigma(A)$ is the spectrum of the operator A.

By virtue of (2), $\bar{x} \in \operatorname{Ker}(h_x + a(\bar{w}))$ (the kernel of the operator). Therefore, the following result holds in the case $\bar{x} \neq 0$, which is of interest for applications.

Corollary (extreme principle). The zero maximum of the upper bound for the real part of the spectrum of restrictions of the operator $h_x + a(\bar{w})$ is reached at the vector $\bar{x} \neq 0$ realized in the stable equilibrium $\bar{w} = (\bar{x}, \bar{y})$.

This assertion is a direct generalization of the necessary condition for external stability (formulated in extreme form) to the case under study (see Section 3).

4. MODEL WITH A CONTINUOUS AGE STRUCTURE

The original system of equations describing the dynamics of a community of species with a continuous age structure has the form

$$\begin{aligned} \partial x_\lambda &= -\mu_\lambda x_\lambda, \quad \lambda \in \Lambda, \\ \partial y_i &= b_i, \quad i \in I = \{1, 2, \dots, J_1\}, \\ \partial_t y_j &= b_j, \quad j \in J = \{J_1 + 1, \dots, J_2\}, \end{aligned} \tag{3}$$

with the boundary conditions

$$x_\lambda(0, t) = \int_0^\infty \beta_\lambda(a) x_\lambda(a, t) da, \quad \lambda \in \Lambda, \quad y_i(0, t) = \int_0^\infty g_i(a) y_i(a, t) da, \quad i \in I,$$

and with suitable initial conditions. Here, t is time, a is age, $\partial_i = \partial/\partial t$, $\partial = \partial_t + \partial_a$, λ is the index (possibly from the infinite set Λ) of an evolving species with an age population density $x_\lambda = x_\lambda(a, t)$, and i is the index (from a finite set) of a not evolving species with an age density $y_i = y_i(a, t)$. The difference between the first and the second is that the second can be controlled externally. Moreover, the system can contain external (i.e., not evolving) variables $y_j = y_j(t)$ with no age structure.

System (3) is assumed to be autonomous in time, so each of the death rates $\mu_\lambda = \mu_\lambda(a, x, y)$ of individuals of the species indexed by λ and the current variations (death rate, migration, etc.) of the nonevolving species are assumed to depend only on the age of these individuals and the values of the distribution vectors $x = x(t) = \{x_\rho(\cdot, t)\}$, $\rho \in \Lambda$, $y = (y_I, y_J)$, $y_I = y_I(t) = \{y_i(\cdot, t)\}$, $i \in I$, $y_J = y_J(t) = \{y_j(t)\}$, $i \in J$, which describe the current state of the community structure (i.e., at a fixed time). Here and below, a dot placed instead of a distribution variable means that the distribution is treated as a whole, i.e., as an element of a suitable function space. More specifically, this means that the death rates are functions of the state of the community as a whole. The birth rates $\beta_\lambda(a)$ and $g_i(a)$ are assumed to be independent of the current form of the distributions (quasilinearity condition).

To use the results of the previous section, all the functions are assumed to be twice uniformly continuously differentiable with respect to their arguments. As suitable Banach spaces, we can use $X = l_\infty(\Lambda) \oplus L_1(\mathbb{R}_+)$ and $Y = \mathbb{R}^{|J_1|} \otimes \otimes L_1(\mathbb{R}_+) \oplus \mathbb{R}^{|J_2|}$. Here, $l_\infty(\Lambda)$ denotes the space of real-valued functions on Λ with a countable support that are summable on the support in the l_∞ norm. Integral summability with respect to $a \in \mathbb{R}_+$ reflects the natural requirement that the total population size be bounded. The operator h_x is assumed to be diagonal in the structure of $l_\infty(\Lambda)$, and its nonzero component indexed by λ is a closed operator of the form $-\partial_a$ with the domain consisting of bounded absolutely continuous functions from $L_1(\mathbb{R}_+)$ that satisfy the first boundary condition in (2). In a similar manner, the second of these conditions defines the domain of the corresponding diagonal components of h_y. The remaining components on the right-hand side of (3) (death rate, etc.) are described by bounded operators and functions. Since the general quasilinear theory does not prevent their dependence on the phase variables, this dependence (possibly even on the age distributions overall) is admissible in the application under study.

Let $(\bar{x}, \bar{y})$ be a stationary solution of system (3) that is stable in the sense of the previous section. Let $\bar{\lambda} \in \operatorname{supp}\bar{x}$ (the subset of those values of $\lambda \in \Lambda$ for which $\bar{x}_\lambda(a)$ does not vanish identically). For the above construction, the verification of the conditions of Theorem 1 is a technical task, which is omitted (see [10]). By the Lotka theorem (see, e.g., Theorem 4.1 in [12]), having the maximum real part, the eigenvalue of the operator $h_\lambda - M_\lambda$, where M_λ is the operator of pointwise multiplication (with respect to a) by the function $\mu_\lambda(a, \bar{x}, \bar{y})$, is real and the corresponding eigenfunction is positive. This eigenvalue is determined for every $\lambda \in \Lambda$ from the characteristic equation for κ, which has the form

$$1 = \Phi(\lambda, \kappa, \bar{x}, \bar{y}), \quad \text{where} \quad \Phi(\lambda, \kappa, \bar{x}, \bar{y}) = \int_0^\infty \beta_\lambda(a) \exp\left(-\kappa a - \int_0^a \mu_\lambda(s, \bar{x}, \bar{y}) ds\right) da.$$

By Theorem 1, its solution satisfies $\kappa_\lambda \le 0$. Therefore, $\Phi(\lambda, 0, \bar{x}, \bar{y}) \le \Phi(\lambda, \kappa_\lambda, \bar{x}, \bar{y}) = 1 = \Phi(\bar{\lambda}, 0, \bar{x}, \bar{y})$. The functional $\varphi(\lambda) = \Phi(\lambda, 0, \bar{x}, \bar{y})$ reaches its maximum value at $\bar{\lambda}$. Hence, in terms of the model of this section, the extreme principle can be formulated as follows.

Theorem 2. *If system* (3) *has a stable stationary equilibrium* $\bar{x} = \{\bar{x}_\lambda(a)\}$, $\lambda \in \Lambda$, *then* $\bar{\lambda} \in \operatorname{supp}(\bar{x})$ *satisfies the relation* $\varphi(\bar{\lambda}) = \max\limits_{\lambda \in \Lambda}(\varphi(\lambda))$ *with the functional*

$$\varphi(\lambda) = \int_0^\infty b_\lambda(a) \exp\left(-\int_0^a m_\lambda(s, \bar{x}) ds\right) da. \tag{4}$$

From a practical point of view, this means that the set of parameters values λ for an a priori known steady-state stationary distribution $\bar{x}$ can be determined by maximizing functional (4) over λ. Note that the theoretical maximum value of this functional is equal to unity.

The meaning of functional (4), which goes back to Lotka's fundamental constructions [5], is the mean number of the newborn per individual with allowance for the age-specific death rate.

5. MODEL WITH A CONTINUOUS SPATIAL STRUCTURE

Starting in this section, for brevity, we ignore the nonevolving variables y.

For spatially distributed biological communities, the most frequently used continuous model is based on systems of second-order quasilinear parabolic equations with homogeneous conditions on the boundary of the considered spatial domain. In the case of an a priori known stationary distribution of biological species, the results of the general theory (see Section 3) can be used to construct the minimization problem for a suitable integral functional in order to determine the selection parameters values corresponding to surviving species.

The original system of equations has the form

$$\partial_t x_\lambda = h_\lambda x_\lambda + \hat{a}_\lambda(x) x_\lambda, \quad \lambda \in \Lambda, \tag{5}$$

where $x_\lambda = x_\lambda(\xi, t)$ is the spatial biomass density of the species indexed by λ at the point $\xi \in \Omega$ at time t (here, $\Omega \subset \mathbb{R}^n$ is a connected bounded domain with a sufficiently smooth boundary $\partial\Omega$ and describes the habitat of the community), h_λ are elliptic operators of the form $h_\lambda x_\lambda = \operatorname{div}\{A_\lambda(\xi)[\operatorname{grad} x_\lambda + x_\lambda \operatorname{grad} q_\lambda(\xi)]\}$ with sufficiently smooth coefficients $\alpha_\lambda^{\iota\kappa}(\xi)$ and $q_\lambda(\xi)$ $(\iota, \kappa = 1, 2, \dots, n)$ in the closure of Ω, and $A_\lambda(\xi) = \|\alpha_\lambda^{\iota\kappa}(\xi)\|$ are symmetric matrices that are uniformly positive definite in Ω (i.e., $(A_\lambda(\xi)\zeta, \zeta) \ge k_\lambda(\zeta, \zeta) > 0$ for $\zeta \in \mathbb{R}^n \backslash \{0\}$). Here, the divergence and the gradient are calculated with respect to ξ and $(u, v) = \sum_{i=1}^n u_i v_i$ is the standard notation for the scalar product in $\mathbb{R}^n$. These operators are used to describe diffusion in the case of an anisotropic space (from the point of view of possible displacements of individuals of the species indexed by λ; the isotropic case corresponds to a diffusion matrix $A_\lambda(\xi)$ that is proportional to the identity matrix) and the presence of a spatial drift defined by the gradient of $q_\lambda(\xi)$ (for example, in chemotaxis problems, this is a species-specific function of the attractant concentration).

On the boundary $\partial\Omega$, we set the homogeneous Dirichlet conditions

$$x_\lambda|_{\partial\Omega} = 0, \tag{6}$$

or the impermeability conditions

$$(\operatorname{grad} x_\lambda + x_\lambda \operatorname{grad} q_\lambda(\xi), A_\lambda(\xi)\nu)|_{\partial\Omega} = 0, \tag{7}$$

where ν is the normal vector to the boundary at the point $\xi \in \partial\Omega$. Condition (7), in which the projection of the total flux (due to diffusion and drift) of individuals of species λ through the boundary is set equal to zero, means that, from a biological point of view, the boundary is an insuperable barrier for individuals.

The operator $\hat{a}_\lambda(x)$ defines the pointwise (with respect to ξ) multiplication of $x_\lambda(\xi, t)$ by $a_\lambda(x(\cdot, t), \xi)$, in which $x = x(\cdot, t) = \{x_\rho(\cdot, t)\}$, $\rho \in \Lambda$. At each spatial point, this operator plays the role of a Malthusian function (see Section 2) for the species indexed by λ. The collection of these operators specifies all the intraspecies and interspecies interactions in the community.

As in the previous section, all the introduced functions are assumed to be twice uniformly continuously differentiable with respect to their arguments. As $W = X$, we use the space $l_\infty(\Lambda, \{L_2^\lambda(\Omega)\}_{\lambda \in \Lambda})$ of l_∞-normalized finite-dimensional vectors with the λth component $x_\lambda(\xi)$ from the Hilbert space $L_2^\lambda(\Omega)$ with the norm $\int_\Omega e^{q_\lambda(\xi)} x_\lambda^2(\xi) d\xi$. The operators $h = h_x$ and $a(x)$ act componentwise as h_λ and $\hat{a}_\lambda(x)$, and the domain of h_λ is the space $W_2^\lambda(\Omega) \subset W_2^2(\Omega)$ of functions having second partial derivatives from $L_2^\lambda(\Omega)$ and satisfying the boundary conditions in the sense of the trace. The operators h_λ thus defined are closed and self-adjoint in $L_2^\lambda(\Omega)$, which means that they are sectorial. Therefore, there exists an analytical (and, hence, strongly continuous) semigroup for which they are infinitesimal generators.

Moreover, by using standard methods (see, e.g., [13]), we can check that the variational principle holds for $h_\lambda + \hat{a}_\lambda(x)$. This means that the minimum eigenvalue of $h_\lambda + \hat{a}_\lambda(x)$ is simple and, up to the sign, coincides at its eigenfunction $v^\lambda(\xi)$ with the minimum of the functional

$$\Phi(\lambda, x, v) = \frac{\int\limits_\Omega e^{q_\lambda(\xi)}[(w_\lambda(\xi), A_\lambda(\xi)w_\lambda(\xi)) - a_\lambda(x, \xi)v^2(\xi)]d\xi}{\int\limits_\Omega e^{q_\lambda(\xi)}v^2(\xi)d\xi}, \tag{8}$$

where $w_\lambda(\xi) = \mathrm{grad}\,v(\xi) + v(\xi)\mathrm{grad}\,q_\lambda(\xi)$. The minimum of functional (8) is calculated over $v(\xi) \neq 0$ on the Friedrichs extension of the domain of $h_\lambda + \hat{a}_\lambda(x)$, which coincides with $H_0^1(\Omega)$ in the case of (6) (distributions on Ω with first partial derivatives from $L_2(\Omega)$ vanishing on the domain boundary in the sense of the trace) and with $H^1(\Omega)$ in the case of (7) (the same but without the boundary conditions).

Let $\bar{x}$ be a stationary solution to system (5) that is stable in sense of Section 3, and let $\bar{\lambda} \in \mathrm{supp}\bar{x}$ (see the definition in the previous section). The last inclusion means that the kernel of $h_{\bar{\lambda}} + \hat{a}_{\bar{\lambda}}(\bar{x})$ is not empty, since it includes the nonzero distribution $\bar{x}_{\bar{\lambda}}$. For it, Green's identity gives $\Phi(\bar{\lambda}, \bar{x}, \bar{x}_{\bar{\lambda}}) = 0$. The variational principle also implies the inequality $\Phi(\lambda, \bar{x}, v^\lambda) \le \Phi(\lambda, \bar{x}, \bar{x}_{\bar{\lambda}})$ and the equality $\Phi(\lambda, \bar{x}, v^\lambda) = -\sup\sigma(h_\lambda + \hat{a}_{\bar{\lambda}}(\bar{x}))$ for $\lambda \in \Lambda$. The application of Theorem 1 to supp $\lambda \notin \mathrm{supp}\bar{x}$ yields $\sup\sigma(h_\lambda + \hat{a}_\lambda(\bar{x})) < 0$. Collecting these relations, we obtain the chain

$$\Phi(\bar{\lambda}, \bar{x}, \bar{x}_{\bar{\lambda}}) = 0 < \Phi(\lambda, \bar{x}, v^\lambda) \le \Phi(\lambda, \bar{x}, \bar{x}_{\bar{\lambda}}), \tag{9}$$

which implies the extreme principle for $\varphi(\lambda) = \Phi(\lambda, \bar{x}, \bar{x}_{\bar{\lambda}})$. More specifically, the following result holds.

Theorem 3. *If system* (5) *with boundary conditions* (6) or (7*) has a stable stationary equilibrium* $\bar{x} = \{\bar{x}_\lambda(\xi)\}$, $\lambda \in \Lambda$, *then* $\bar{\lambda} \in \mathrm{supp}(\bar{x})$ *satisfies the relation*

$$\varphi(\bar{\lambda}) = \min_{\lambda \in \Lambda}\varphi(\lambda). \tag{10}$$

Note that $\varphi(\lambda)$ in (10) can be replaced by $\phi(\lambda) = \Phi(\lambda, \bar{x}, v^\lambda)$. First, this follows formally from the first inequality in (9) and $\Phi(\bar{\lambda}, \bar{x}, v^{\bar{\lambda}}) \le \Phi(\bar{\lambda}, \bar{x}, \bar{x}_{\bar{\lambda}})$. Second, assuming that $\bar{x}$ is stable with respect to spatial perturbations of the distributions for $\bar{\lambda} \in \mathrm{supp}(\bar{x})$, we obtain $\bar{x}_{\bar{\lambda}} = v^{\bar{\lambda}}$ (otherwise, $\bar{x}_{\bar{\lambda}}$ is unstable with respect to $v^{\bar{\lambda}}$), which makes both formulations of the extreme principle equivalent. However, in the construction of functionals, the second version allows us to take into account the form of the steady-state distribution only in the computation of the coefficients. Specifically, we do not need to determine its spatial derivatives, since, instead of the latter, we use the functions v^λ computed by minimizing the functional $\Phi(\lambda, \bar{x}, v)$.

6. CONCLUSIONS

The constructions discussed above are rather difficult in the sense that the right-hand sides of dynamical systems involve unbounded operators. If there are no such operators (for example, for right-hand sides of integral form), we do not need to invoke the general theory discussed in Section 3, although it naturally covers this case. Such "simple" constructions are rather frequently used to describe the dynamics of probability distributions; numerous examples include various models for the propagation of epidemics [14], epiphytoties, etc. Even "simpler" (constructively but not ideologically) models with a discrete structure can be formally reduced to the problem addressed in Section 2. Moreover, acceptable functionals can be constructed due to the specific features of the arising right-hand sides (see [15]).

The same is true for discrete-time systems. Note that time was initially assumed discrete (see [9]) and, then, the results were extended to time-continuous periodic (specifically, autonomous) systems. The best-known population model with discrete time and age is that of Leslie (see the bibliography in [1, Chapter

II]). Some of its generalizations associated with the possibility of interage (more exactly, interstage) transitions also have found their reflection in the computation of evolutionary selection functionals (see [16]).

Concerning applications of the results presented in this paper, an example is the theory of correlation adaptometry [17] constructed on the basis of the extreme properties of functionals of spatial distributions (Section 5). This theory uncovers the relation between the level of unfavorable actions on a population and the degree of correlation between the distributions of physiological parameters of its terms.

ACKNOWLEDGMENTS

This work was supported by the Russian Foundation for Basic Research, project no. 09-07-00398.

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