

On semigroups and populations

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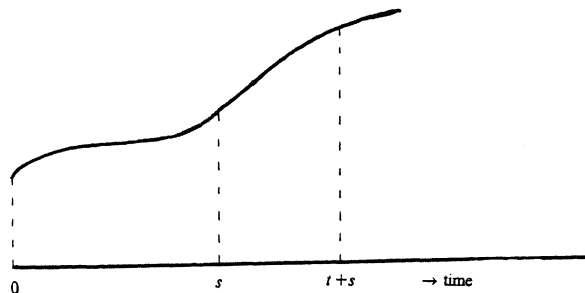
In this paper, which is based on joint work with PH. CLÉMENT, M. GYLLENBERG, H.J.A.M. HEIJMANS and H.R. THIEME, we discuss continuity and differentiability properties of orbits as well as perturbation theorems in the context of dual semigroups. The motivation from structured population dynamics is explained and some still open problems in this area are briefly indicated.

1. REMARKS ON ONE-PARAMETER SEMIGROUPS OF BOUNDED LINEAR OPERATORS

First remark. Consider an autonomous (= time translation invariant) system. Let x_0 be the state at time t_0 and x the state at time t . By writing $x = T(t - t_0)x_0$ we introduce a collection of operators which, because of the interpretation, should have the following *algebraic* properties:

- i) $T(0) = I$
- ii) $T(t)T(s) = T(t+s)$, $t, s \geq 0$.

The first property expresses that the operators act on the state we start from (the initial state) and the second expresses that the state, by definition, *uniquely* fixes the future of the system, such that, when time goes from 0 to $t+s$, it makes no difference whether or not we make an imaginary stop at time s .



A collection of operators $\{T(t)\}_{t>0}$, acting on a Banach space X , with these algebraic properties is called a *semigroup of operators*.

When we draw a picture of an orbit $t \mapsto T(t)x$ we tend to draw a *continuous* curve. But continuity involves *topology* and the interpretation gives no clue concerning a natural topology. Likewise if we discuss the *differentiability* of orbits and introduce the *infinitesimal generator*

$$Ax = \lim_{t \downarrow 0} \frac{1}{t} (T(t)x - x)$$

$$D(A) = \{x: \text{this limit exists}\}$$

we have to specify the topology in which we require *convergence*. And there may be more than one natural topology.

The so-called strongly continuous or C_0 semigroups are defined by the requirement that the orbits are *norm* continuous. And when defining the generator one considers norm convergence.

A well known result (see, for instance, PAZY, 1983, section 2.1) states that “weak equals strong”: if we take weak continuity and convergence instead we obtain exactly the same category of semigroups and exactly the same generator. Seemingly the algebraic properties dominate and the topology is not too important after all.

However, the category of C_0 -semigroups is not invariant under duality. If X is non-reflexive the semigroup of adjoint operators $\{T^*(t)\}_{t>0}$ acting on the dual space X^* is, in general, not strongly continuous. As shown by PHILLIPS (1955; also see BUTZER & BERENS, 1967, section 1.4) it is for these semigroups more appropriate to consider weak $*$ continuity and differentiability of orbits.

The following easy example shows that working with the weak $*$ topology requires some extra caution. Let X^* be the space of regular Borel measures on \mathbb{R} and denote by $T^*(t)$ the usual *translation* semigroup. We know that

$$X^* = AC \oplus S$$

where the direct sum corresponds to the Lebesgue decomposition of a measure into an absolutely continuous part and the part which is singular (with respect to the Lebesgue measure). Both subspaces AC and S are invariant under translation, and AC is precisely the subspace of initial states which yield norm continuous orbits (cf. BUTZER & BERENS, 1967, subsection 1.4.2). The main point of this example is that, because of the invariance, we can translate the AC part and the S part with different speeds and still obtain a semigroup with weak $*$ continuous orbits:

$$T_\alpha^\times(t)x^* := T^*(t)x_{AC}^* + T^*(\alpha t)x_S^*$$

(we use the symbol \times to indicate that the operator acts on X^* but does not necessarily have a pre-adjoint acting on X). To calculate the weak $*$ generator we can restrict ourselves to the AC subspace and here the action does not depend on α . We conclude that in this general setting the one-to-one correspondence between semigroup and generator is lost! Note that only in the “natural” case $\alpha=1$ we can reconstruct the action of the semigroup on X^* from its restriction to AC by the *intertwining formula*

$$T^*(t) = (\lambda I - A^*) T_{AC}^*(t) (\lambda I - A^*)^{-1}$$

See CLÉMENT et al. (to appear) for further discussions on weakly $*$ continuous semigroups.

Second remark.

There are at least three ways to define semigroups:

- i) explicit expressions
- ii) verifying the Hille-Yosida conditions
- iii) perturbations

In structured population theory (see section 4 below) one uses i and iii. The most easy example of iii is:

THEOREM: Let A_0 be the generator of a C_0 -semigroup $T_0(t)$ and let B be a bounded linear operator. Then $A = A_0 + B$ with $D(A) = D(A_0)$ generates a C_0 -semigroup $T(t)$ and the variation-of-constants relation

$$T(t)x = T_0(t)x + \int_0^t T_0(t-\tau)BT(\tau)x d\tau$$

holds.

One can prove this theorem in various ways, but one proof starts from the variation-of-constants equation and shows that it can be solved by successive approximations:

$$T(t)x = \sum_{j=0}^{\infty} T_j(t)x$$

with

$$T_j(t)x = \int_0^t T_0(t-\tau)BT_{j-1}(\tau)x d\tau, \quad j \geq 1.$$

Subsequently one uses that

$$\frac{1}{t} \int_0^t T_0(t-\tau)BT(\tau)x d\tau \xrightarrow{t \downarrow 0} Bx$$

to deduce that $T(t)$ is generated by $A = A_0 + B$.

Now let's look at an example in the context of population dynamics. The so-called Kolmogorov backward equation of age-dependent population growth is

$$\frac{\partial m}{\partial t}(t, a) = \frac{\partial m}{\partial a}(t, a) - \mu(a)m(t, a) + \beta(a)m(t, 0)$$

$$m(0, a) = \phi(a)$$

Here $\phi \in X = C_0(\mathbb{R}_+)$ is the initial state, μ is the per capita death rate and β is the per capita birth rate. The fact that every newborn individual has age zero (by the very definition of age) is reflected in the second argument of m in the birth term.

If we neglect birth and death (i.e. take $\mu = \beta = 0$) the semigroup is simply translation and the generator is differentiation. If we take death into account then the solution is

$$\phi(a+t) e^{-\int_0^t \mu(\alpha) d\alpha}$$

with generator $\phi' - \mu\phi$. If μ is continuous we can, if we wish, apply the theorem above and the successive approximations correspond precisely to the Taylor expansion of the exponential function. Note, however, that this Taylor expansion makes perfectly sense if μ is not continuous but belongs to L_∞ ! (Of course there is then an interaction between the ϕ' term and the $\mu\phi$ term in the precise definition of the domain of the generator.)

In order to solve the problem with the birth term taken into account it is convenient to baptize $m(t, 0) = b(t)$ and pretend, for the time being, that b is a known function. Then

$$m(t, a) = \phi(a+t) e^{-\int_0^t \mu(\alpha) d\alpha} + \int_0^t \beta(a+t-\tau) e^{-\int_0^{\tau} \mu(\alpha) d\alpha} b(\tau) d\tau.$$

By taking $a=0$ we get a renewal (i.e., Volterra convolution integral) equation for b :

$$b(t) = \phi(t) e^{-\int_0^t \mu(\alpha) d\alpha} + \int_0^t \beta(t-\tau) e^{-\int_0^{\tau} \mu(\alpha) d\alpha} b(\tau) d\tau,$$

which one can solve by successive approximations to obtain a continuous solution b even when the birth rate β is defined as an L_∞ -element only. On the other hand

$$(B\psi)(a) = \beta(a)\psi(0)$$

clearly maps $C_0(\mathbb{R}_+)$ into itself if and only if $\beta \in C_0(\mathbb{R}_+)$.

We conclude that in the context of structured population models there is a need for a generalized version of the perturbation theorem stated above. It has turned out that the generalized version is useful in the theory of delay differential equations as well (DIEKMANN, 1987). Note that in the example above we were led to consider $C_0(\mathbb{R}_+)$ as a subspace of $L_\infty(\mathbb{R}_+)$.

Third remark. When an operator A satisfies the Hille-Yosida conditions, but is not necessarily densely defined, it generates a C_0 -semigroup on the closure of its domain. Can we extend the semigroup to the whole space by the *intertwining formula*

$$(\lambda I - A) T(t) (\lambda I - A)^{-1}$$

The answer is yes if $D(A)$ is invariant under $T(t)$.

Fourth remark. By taking restrictions and duals we can embed a space in a larger space which is, by definition, a dual space (for example, rigged Hilbert spaces like $H_0^1 \subset L_2 \subset H^{-1}$). If we perform such a procedure in a way which is canonically related to some easy prototype semigroup we may subsequently exploit the enlarged “vocabulary” to deal with perturbation problems.

2. DUAL SEMIGROUPS

Let $T(t)$ be a C_0 -semigroup on a Banach space X and let A denote its generator. Let $T^*(t)$ be the semigroup of adjoint operators acting on the dual space X^* and let A^* be the adjoint of A . Then:

- i) $t \mapsto \langle x, T^*(t)x^* \rangle$ is continuous for all $x \in X$ (i.e. orbits of T^* are weak $*$ continuous)
- ii) $\frac{1}{t} \langle x, T^*(t)x^* - x^* \rangle$ converges for all $x \in X$ as $t \downarrow 0$ iff $x^* \in D(A^*)$ and in that case the limit equals $\langle x, A^*x^* \rangle$. Moreover $D(A^*)$ is invariant under $T^*(t)$ and an orbit of T^* is weak $*$ differentiable iff it starts at an element of $D(A^*)$.

When X is non-reflexive, T^* need not be strongly continuous and related to that is the fact that A^* need not be densely defined. On the one hand we can now restrict T^* to the maximal subspace of strong continuity

$$X^\circ := \{x^* : \|T^*(t)x^* - x^*\| \rightarrow 0 \text{ as } t \downarrow 0\},$$

on the other hand we can take the part of A^* in the closure of its domain. The next result states that these two procedures are canonically related.

THEOREM 2.1. $X^\circ = \overline{D(A^*)}$ and the C_0 -semigroup $T^\circ(t)$ obtained by restricting $T^*(t)$ to the invariant subspace X° is generated by A° , the part of A^* in X° . Moreover one can recover $T^*(t)$ from its restriction to X° by the intertwining formula

$$T^*(t) = (\lambda I - A^*)T^\circ(t)(\lambda I - A^*)^{-1}$$

The concept of the Favard class of a semigroup was introduced in the context of approximation theory, but by now it has become clear (cf. DESCH & SCHAPPACHER, 1984) that in the theory of dynamical systems it is very useful too. Elements of the Favard class yield Lipschitz continuous (in norm) orbits. The following equivalence result tells us that Lipschitz in norm corresponds precisely to weak $*$ differentiability (in view of Alaoglu’s theorem on the compactness of the unit ball with respect to the weak $*$ topology this is not too surprising).

DEFINITION 2.2. $Fav(T^*) := \{x^* : \limsup_{h \downarrow 0} \frac{1}{h} \|T^*(h)x^* - x^*\| < \infty\}$

THEOREM 2.3. $Fav(T^*) = D(A^*)$

Starting from the C_0 -semigroup $T^\odot(t)$ on X^\odot we can now repeat our procedure: introduce $X^{\odot*}$ and the weak $*$ continuous semigroup $T^{\odot*}(t)$ and subsequently $X^{\odot\odot} = \overline{D(A^{\odot*})}$ and the restriction $T^{\odot\odot}(t)$ generated by the part $A^{\odot\odot}$ of $A^{\odot*}$ in $X^{\odot\odot}$.

The pairing $\langle x, x^\odot \rangle$ defines an embedding j of X into $X^{\odot*}$ (since X^\odot is weak $*$ dense it separates the points of X ; moreover $\|x\| := \sup\{|\langle x, x^\odot \rangle| : \|x^\odot\| \leq 1\}$ defines an equivalent norm on X (which is identical to the old one whenever $T(t)$ is a contraction semigroup) and consequently $j(X)$ is a *closed* subspace of $X^{\odot*}$). Clearly $j(X) \subset X^{\odot\odot}$ and $T^{\odot\odot}(t)j = jT(t)$.

DEFINITION 2.4. X is called \odot -reflexive (pronounce as sun-reflexive) with respect to T iff

$$j(X) = X^{\odot\odot}$$

EXAMPLE 2.5. Let S denote the circle and let $X = C(S)$ be the space of continuous functions on S (or equivalently the space of periodic functions of a given period on the real line). Let $T(t)$ be the translation semigroup. Then

$$X^* = M(S), X^\odot = AC(S) \simeq L_1(S), X^{\odot*} = L_\infty(S) \text{ and } X^{\odot\odot} = C(S) = X$$

(the embedding j assigns to a continuous function its L_∞ -equivalence class, but we usually shall suppress j in our notation).

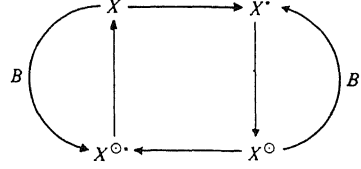
EXAMPLE 2.6. We now take $X = C_0(\mathbb{R})$, the space of continuous functions on \mathbb{R} which tend to zero at $\pm\infty$ and consider once more the translation semigroup. Now $X^* = M(\mathbb{R})$, $X^\odot = AC(\mathbb{R}) \simeq L_1(\mathbb{R})$, $X^{\odot*} = L_\infty(\mathbb{R})$ but $X^{\odot\odot} = BUC(\mathbb{R}) \neq C_0(\mathbb{R}) = X$. Here BUC is the space of bounded uniformly continuous functions. We conclude that this is a non- \odot -reflexive example.

The two closely related examples above seem to indicate that \odot -reflexivity is somehow related to compactness. DE PAGTER (to appear) has recently improved an old characterization of Phillips:

THEOREM 2.7. (PHILLIPS-DE PAGTER) X is \odot -reflexive with respect to T iff the resolvent $(\lambda I - A)^{-1}$ is weakly compact.

3. PERTURBATION THEORY FOR DUAL SEMIGROUPS

In this section we summarize a number of recent results due to CLÉMENT, DIEKMANN, GYLLENBERG, HEIJMANS and THIEME (1987, 1988 and to appear). Our starting point is a C_0 -semigroup $T_0(t)$ on a Banach space X with generator A_0 . We call T_0 the unperturbed semigroup. Let us first concentrate on the case that X is \odot -reflexive with respect to T_0 . On the level of the generator we now introduce the perturbation as a bounded linear operator $B : X \rightarrow X^{\odot*}$



So note in particular that the range of B is in the larger space $X^{\ominus*}$ which we have introduced on the basis of the behaviour of T_0 . Formally at least we can now write a differential equation

$$\begin{aligned} \frac{du}{dt} &= A_0^{\ominus*} u + Bu \\ u(0) &= x \end{aligned} \quad (3.1)$$

for an X -valued function u (so we look for orbits in X but the differential equation is an identity in $X^{\ominus*}$). By integration we obtain the variation-of-constants equation

$$u(t) = T_0(t)x + \int_0^t T_0^{\ominus*}(t-\tau)Bu(\tau)d\tau. \quad (3.2)$$

The following key lemma tells us that we can solve this equation by successive approximations and gives some further information.

LEMMA 3.1. Let $f: \mathbb{R}_+ \rightarrow X^{\ominus*}$ be a given norm continuous function. Define

$$v(t) = \int_0^t T_0^{\ominus*}(t-\tau)f(\tau)d\tau$$

as a weak $*$ Riemann integral, i.e.

$$\langle v(t), x^{\ominus} \rangle = \int_0^t \langle f(\tau), T_0^{\ominus}(t-\tau)x^{\ominus} \rangle d\tau, \quad \forall x^{\ominus} \in X^{\ominus}$$

Then v is norm continuous, takes values in X and

$$\|v(t)\| \leq M \frac{e^{\omega t} - 1}{\omega} \sup_{0 \leq \tau \leq t} \|f(\tau)\|$$

where M and ω are such that $\|T_0(t)\| \leq Me^{\omega t}$.

Moreover $\frac{1}{t}v(t) \rightarrow f(0)$ weak $*$ as $t \downarrow 0$.

If f is Lipschitz continuous then v takes values in $D(A_0^{\ominus*})$, is weak $*$ continuously differentiable and

$$\frac{d}{dt} \langle v(t), x^{\ominus} \rangle = \langle A_0^{\ominus*} v(t), x^{\ominus} \rangle + \langle f(t), x^{\ominus} \rangle, \quad \forall x^{\ominus} \in X^{\ominus}$$

COROLLARY 3.2. Equation 3.2 defines a C_0 -semigroup $T(t)$ on X and $\|T(t) - T_0(t)\| = O(t)$ for $t \downarrow 0$.

REMARK 3.3. In DIEKMANN, GYLLENBERG and HELMANS (to appear) the reverse is shown: if T and T_0 are two C_0 -semigroups on X such that $\|T(t) - T_0(t)\| = O(t)$ for $t \downarrow 0$, then both define the same space X^\ominus and a bounded $B: X \rightarrow X^{\ominus*}$ exists such that

$$T(t) = T_0(t) + \int_0^t T_0^{\ominus*}(t-\tau) B T(\tau) d\tau \quad (3.3)$$

COROLLARY 3.4.

- i) $D(A^*) = D(A_0^*)$ and $A^* = A_0^* + B^*$
- ii) $D(A^{\ominus*}) = D(A_0^{\ominus*})$ and $A^{\ominus*} = A_0^{\ominus*} + B$

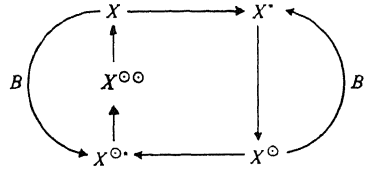
The generator of T is, of course, obtained by taking the part of $A^{\ominus*}$ in X . Since this is basically a condition on the range of $A_0^{\ominus*} + B$ the operator B may (and does in examples) influence the domain.

Alternatively we can start from the dual variation-of-constants equation

$$T^\ominus(t) = T_0^\ominus(t) + \int_0^t T_0^*(t-\tau) B^* T^\ominus(\tau) d\tau \quad (3.4)$$

but this amounts to the same thing since in the \ominus -reflexive case we stay in the realm of dual semigroups when applying bounded perturbations.

In the general case, however, we have to deal with the asymmetric diagram:



Using the dual version of Lemma 3.1 we can still solve equation (3.4). After T^\ominus has thus been defined we can proceed in two ways:

- 1) We can introduce $T^{\ominus*}$ and $T^{\ominus\ominus}$ (note that $X^{\ominus\ominus}$ does not depend on B) but in general X will not be invariant (example: take the age dependent backward population equation and assume that the birth rate β does not tend to zero for $a \rightarrow \infty$).
- 2) the $O(t)$ estimate shows that $D(A_0^*)$ is the Favard class of T^\ominus as well; consequently $D(A_0^*)$ is invariant under T^\ominus and the definition

$$T^\times(t) = (\mathcal{N} - A^\times) T^\ominus(t) (\mathcal{N} - A^\times)^{-1} \quad (3.5)$$

where $A^\times = A_0^* + B^*$ and $D(A^\times) = D(A_0^*)$, makes sense.

The natural question now is: how can we describe the relation between $T^{\odot\odot}$ and T^\times ? Note that in Example 2.6 it is possible to define a pairing between $X^{\odot\odot}$ and X^* : simply integrate the *BUC* function with respect to the measure. As a subspace of $X^{\odot*}$, however, $X^{\odot\odot}$ is in fact the space of L^∞ -equivalence classes which contain a *BUC* function and so the pairing involves picking out the continuous representative. It is not immediately clear how one can define such a procedure abstractly. Yet it is possible, and in fact easy, to give a general definition of a canonical pairing between $X^{\odot\odot}$ and X^* .

THEOREM 3.5.

$$[x^{\odot\odot}, x^*] = \lim_{t \downarrow 0} \frac{1}{t} \langle x^{\odot\odot}, \int_0^t T_0^*(\tau)x^* d\tau \rangle = \lim_{\lambda \rightarrow \infty} \lambda \langle x^{\odot\odot}, (\lambda I - A_0^*)^{-1}x^* \rangle$$

defines a bilinear continuous mapping $X^{\odot\odot} \times X^* \rightarrow \mathbb{C}$ and

$$[T^{\odot\odot}(t)x^{\odot\odot}, x^*] = [x^{\odot\odot}, T^\times(t)x^*]$$

This theorem motivates us to introduce yet another topology on X^* : the $\sigma(X^*, X^{\odot\odot})$ topology or, in abbreviated form, the \odot topology. The theorem tells us that the orbits $t \mapsto T^\times(t)x^*$ are continuous in the \odot topology. Likewise we have

THEOREM 3.6. $\frac{1}{t}[x^{\odot\odot}, T^\times(t)x^* - x^*]$ converges as $t \downarrow 0$ for all $x^{\odot\odot} \in X^{\odot\odot}$ iff $x^* \in D(A_0^*)$ and in that case the limit equals $[x^{\odot\odot}, A^\times x^*]$.

So we now use the \odot topology to characterize the continuity and differentiability properties of orbits. But we still use the weak $*$ topology to define integrals since X^* equipped with the \odot topology is not necessarily sequentially complete. Nevertheless one can prove:

THEOREM 3.7. Let $f: \mathbb{R}_+ \rightarrow X^*$ be norm continuous. Define

$$v(t) = \int_0^t T^\times(t-\tau)f(\tau)d\tau$$

as a weak $*$ integral. Then v is norm continuous and takes values in X^\odot . If f is Lipschitz continuous then v takes values in $D(A_0^*)$, v is continuously \odot differentiable and

$$\frac{d}{dt}[x^{\odot\odot}, v(t)] = [x^{\odot\odot}, A^\times v(t)] + [x^{\odot\odot}, f(t)], \quad \forall x^{\odot\odot} \in X^{\odot\odot}$$

Analogously one can study semilinear problems which are defined by a Lipschitz continuous nonlinear mapping

$$F: X^\odot \rightarrow X^*$$

Again we look at orbits in X° but interpret the differential equation

$$\begin{aligned}\frac{du}{dt} &= A^\times u + F(u) \\ u(0) &= x^\circ\end{aligned}$$

as an identity in X^* . Solutions are defined by a contraction mapping argument applied to the integral equation

$$u(t) = T^\circ(t)x^\circ + \int_0^t T^\times(t-\tau)F(u(\tau))d\tau$$

and for x° in the dense subset $D(A_0^*)$ these satisfy the differential equation in the sunny sense. The integral equation is the key ingredient for a standard proof of the linearized stability principle, the construction of stable, unstable and center manifolds and hence for a standard treatment of Hopf bifurcation.

4. STRUCTURED POPULATION DYNAMICS

The approach of section 3 yields results for nonlinear population dynamics in $L_1(\mathbb{R}_+)$ and for functional differential equations. In METZ & DIEKMANN, eds., 1986, a general class of physiologically structured population models is described in detail, mainly in terms of forward equations for densities. Moreover it is explained how one can use the idea of feedback through the environment to analyse nonlinear models in terms of linear ones and a fixed point argument.

In order to cover this general class the theory of section 3 needs to be extended. First of all we need to deal with backward and forward evolutionary systems rather than dual semigroups. Secondly, in order to treat models with higher dimensional individual state space we have to take into account a certain anisotropy (the individual state space is foliated by characteristics and we translate along these; consequently only discontinuities of birth and death rates which in some sense are transversal to the characteristics are allowed).

We conclude that the theory developed so far constitutes only a first, albeit important, step towards a general mathematical theory for physiologically structured population models and that many questions await a penetrating analysis.

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