Global asymptotic behaviour of solutions to differential system models of the transmission of helminthic infections

Autor(en): **Khanmy, Christian**

Objekttyp: **Article**

Zeitschrift: **Mémoires de la Société Vaudoise des Sciences Naturelles**

Band (Jahr): **18 (1987-1991)**

Heft 3

PDF erstellt am: **21.06.2024**

Persistenter Link: https://doi.org/10.5169/seals-259827

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MÉM. SOC. VAUD. SC. NAT. 18.3, 1990

MODÈLES DYNAMIQUES EN BIOLOGIE, R. ARDITI (DIR.)
DYNAMICAL MODELS IN BIOLOGY, R. ARDITI (ED.)

Global Asymptotic Behaviour of Solutions to Differential System Models of the Transmission of Helminthic Infections

BY

CHRISTIAN KHANMY[1]

Abstract.– KHANMY C., 1990. Global Asymptotic Behaviour of Solutions to Differential System Models of the Transmission of Helminthic Infections. *In*: Dynamical Models in Biology, R. Arditi (ed.). *Mém. Soc. vaud. Sc. nat. 18.3*: 265-284.
A system of ordinary differential equations is derived from models of the transmission of helminthic infections. We establish in this study the global asymptotic behaviour of the solutions which describe the course of the infestation.

Résumé.– KHANMY C., 1990. Comportement asymptotique global des solutions d'un système différentiel lié à la transmission de certaines helminthiases. *In*: Modèles dynamiques en biologie, R. Arditi (éd.). *Mém. Soc. vaud. Sc. nat. 18.3*: 265-284.
Un système d'équations différentielles ordinaires est dérivé de modèles de transmission de certaines helminthiases. On établit dans cette étude le comportement asymptotique global des solutions qui décrivent l'évolution de l'infestation.

INTRODUCTION

Stimulated by the influential work of MACDONALD (1965) on schistosomiasis, various investigators have proposed mathematical approaches to the study of the transmission of helminthic infections. We cite in the bibliography only the works relevant to this paper (GABRIEL 1983, GABRIEL *et al.* 1981, HIRSCH *et al.* 1985, NÅSELL, NÅSELL *et al.* 1972, 1973).

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[1] Department of Mathematics, University of California, Berkeley, CA 94720, USA and Laboratoire d'enseignement assisté par ordinateur, Ecole polytechnique fédérale, CH-1015 Lausanne, Suisse (*present address*).

The parasites concerned in these models obey a cycle involving two host populations: the definitve host (vertebrates) in which the parasite lives its adult stage in the guise of worms and produces eggs, and the intermediate host (fresh-water snails) in which the parasite is in transit while undergoing a larval transformation accompanied by an asexual reproduction process. During this developmental stage called prepatent period and which constitutes a significant fraction of the average life of the intermediate host, snails are infected but not infectious. Outside its definitive host, the parasite is found in larval form and the dynamics of its transmission consists of its flow from the vertebrate to the snail population and back again. The infective larva ensuring the transmission from vertebrates to snails is called «miracidium» and the one allowing the return to vertebrates after passing through snails is called «cercaria».

In this paper we present a model, proposed by Gabriel in a personal communication, which incorporates the prepatent period of the snails into the models previously studies by NÅSELL and HIRSCH (1972, 1973).

There are at least two ways of representing this phenomenon: by introducing a delay in the models (GABRIEL 1983, GABRIEL *et al.* 1981) or by recognizing a prepatent state in the snail population, which is the approach considered here, see also NÅSELL (1976).

Although the original Nåsell-Hirsch models derive from probabilistic assumptions, they can also be made plausible from a purely deterministic point of view; for a discussion of this apsect, see GABRIEL *et al.* (1983, 1981). In the sequel we describe a deterministic model for the transmission of helminthic infections leading to a system of ordinary differential equations and concentrate on the course of the infection over time. Accordingly we study the asymptotic behaviour of its trajectories by exploiting their intrinsic properties in conjunction with some results from the general theory of monotone systems developed by HIRSCH (1982, 1985, 1988).

Besides the papers mentioned above, we have also been inspired by useful tools and results proposed by HIRSCH *et al.* (1983, 1985) and SMITH (1986).

A general conclusion to this study is that under reasonable hypotheses, either the infection ultimately dies out, or else it is driven to a positive level of endemicity.

MODEL FORMULATION

The assumptions underlying the following model are essentially identical to those presented by GABRIEL *et al.* (1983, 1981, 1985).

Consider a community constituted of a vertebrate population and a snail population whose individuals are treated homogeneously and which is submitted to infestation.

We idealize the vertebrate population by assuming that its size remains constant and denote the number of vertebrates by N_0. While adult worms reproduce sexually in the definitive host, exhibiting diverse patterns of sexual behaviour, we identify two types of sexuality: hermaphroditism (single sex) and dioeciousness (two sexes).

In order to represent the number of ovipositing worms per vertebrate host, GABRIEL *et al.* (1983, 1981, 1985) introduced the concept of an *oviposition function.* Any such function denoted by ψ is required to be continuously differentiable on the set of non-negative numbers $\mathbb{R}_+$, to be strictly increasing and to satisfy $\psi(0) = 0$.

From a mathematical viewpoint, dioecious worms are distinguished from hermaphroditic worms by the classification of oviposition functions according to the following definition (HIRSCH *et al.* 1985): *An oviposition function ψ is called «hermaphroditic» if*

$$\left(\frac{\psi(x)}{x}\right)' \leq 0, \quad \textit{for} \quad x > 0 .$$

An oviposition function ψ is called «dioecian» if it is not hermaphroditic and if

$$\psi'(0) = 0 .$$

The unit of infection in the vertebrate population is taken to be the worm pair in the dioecious case and the worm in the hermaphroditic case.

Let $W(t)$ denote the worm burden per vertebrate host at time t. Following the work of Hirsch, Hanisch and Gabriel, the number of ovipositing worms per vertebrate host at time t is represented by $\psi(W(t))$.

In the snail population, we recognize three different states: susceptible, prepatent and infective snails. We denote the number of snails in each of these states at time t by $S(t)$, $E(t)$ and $I(t)$ respectively.

We allow births and deaths of snails, but under the simplifying assumption that each death, whether of a susceptible or prepatent or infective snail, is accompanied by the birth of an uninfected snail; accordingly, the size of the snail population is constant, we denote it by N. We assume that the cercarial shed rate resulting from a miracidial infection is so large that a possible increase due to mutliple infections is unimportant. Therefore a unit of infection in the snail population is an infective snail, not a miracidial infection.

We postulate that infected snails are increasing at a rate proportional to the product of the number of infective units and the number of susceptible units in, respectively, the vertebrate and snail populations. This reflects the law of mass action of epidemiology.

The dynamics of the infestation is described by the following system of differential equations

$$\begin{aligned} \dot{W} &= -\mu_0 W + \alpha I \\ \dot{E} &= -(\gamma + \mu_2)E + \beta N_0 \psi(W) S \\ \dot{I} &= -\mu_3 I + \gamma E \\ \dot{S} &= -\mu_1 S - \beta N_0 \psi(W) S + \mu_1 S + \mu_2 E + \mu_3 I \ . \end{aligned}$$

In the first equation, the first term expresses death among worms at a constant rate and the second term means that worm burden *per vertebrate* is increasing at a rate proportional to the number of infective units in the snail population.

In the second equation, the first term indicates disappearance of prepatent snails by death and because they become infective at a constant rate γ and the second term describes the snail infection rate resulting from the law of mass action.

In the third equation, the first term indicates death of infective snails at the constant rate μ_3 and the second term corresponds to the fact that prepatent snails become infective at the rate γ.

In the fourth equation, the first two terms indicate disappearance of susceptible snails by death and because they become prepatent and the remaining terms express the replacement rule stated above. The transmission parameters α and β are respectively interpreted as the potential of the snail (respectively vertebrate) population to deliver *cercariae* (respectively *miracidia*) to vertebrates (respectively snails).

Since $S + E + I = N$ at any time, we content ourselves with discussing the following reduced system

$$(S) \qquad \begin{aligned} \dot{W} &= -\mu_0 W + \alpha I \\ \dot{E} &= -(\gamma + \mu_2)E + \beta N_0 \psi(W)(N - E - I) \\ \dot{I} &= -\mu_3 I + \gamma E \end{aligned}$$

with initial conditions $W(0) \geq 0$, $E(0) \geq 0$, $I(0) \geq 0$ and $E(0) + I(0) \leq N$. The parameters μ_0, μ_2, μ_3, α, β, γ, N and N_0 are positive constants.

BASIC RESULTS FOR SYSTEM (S)

In this section we establish some basic properties of the solutions of the initial value problem for (S) .

The phase space of system (S) consists of the biological domain $B = \{(X_1, X_2, X_3) \in \mathbb{R}^3_+ : X_2 + X_3 \leq N\}$. The boundary ∂B of B is defined by

$$\partial B = \{(X_1, X_2, X_3) \in B : X_1 = 0, \text{ or } X_2 = 0, \\ \text{ or } X_3 = 0, \text{ or } X_2 + X_3 = N\}$$

and the interior B^0 of B is defined by $B^0 = B - \partial B$.

For each initial condition belonging to B^0, the Picard-Lindelöf theorem ensures the existence of a right maximal interval $J \subset \mathbb{R}_+$ on which the initial value problem for (S) possesses a unique solution denoted by $(W(t), E(t), I(t))$. Moreover, either $J = \mathbb{R}_+$ or $J = [0, \epsilon)$ with $\epsilon < \infty$ and $\lim_{t \to \epsilon}(|W(t)| + |E(t)| + |I(t)|) = \infty$, or $J = [0, \epsilon]$ with $\epsilon < \infty$ and $(W(\epsilon), E(\epsilon), I(\epsilon)) \in \partial B$. The last two possibilities are ruled out as a consequence of the following proposition.

PROPOSITION 1. *If* $(W(0)), E(0), I(0)) \in B^0$, *then*
(i) $(W(t), E(t), I(t)) \in B^0$, *for all* $t \in J$*;*
(ii) $W(t) \leq \max(W(0), \frac{\alpha N}{\mu_0})$ *and* $E(t) + I(t) < N$, *for all* $t \in J$.

Proof. (i) Assume that the solution leaves B^0 after finite time. Then there is a first epoch $s \in J$, $s > 0$ such that $(W(t), E(t), I(t)) \in B^0$, for all $t \in [0, s)$ and $(W(s), E(s), I(s)) \in \partial B$.
Thus suppose that $W(s) = 0$. From the definition of s it follows that $\dot{W}(s) \leq 0$ and the first equation of system (s) provides $\dot{W}(s) \geq 0$. Therefore $\dot{W}(s) = 0$ and consequently $I(s) = 0$. Applying the same argument to $I(s)$, we get $E(s) = 0$. Accordingly, the solution reaches a singularity of the vectorfield defined by (S) at time s, which is impossible. It remains to show that the other possibilities also lead to contradictions.
Assume that $E(s) = 0$. From the definition of s, it follows that $\dot{E}(s) \leq 0$ and the second equation of system (s) implies that $\dot{E}(s) \geq 0$. Thus $\psi(W(s))(N - I(s)) = 0$. If $\psi(W(s)) = 0$, then monotonicity of ψ gives $W(s) = 0$, which has already been ruled out. Therefore $I(s) = N$, and using the second and third equations, we obtain $\dot{E}(s) + \dot{I}(s) < 0$. Hence, by continuity, $E + I > N$, in a left neighborhood of s, contradicting the definition of s.
Assume that $I(s) = 0$. Once more by the argument above, we get $E(s) = 0$, $\dot{E}(s) = \beta N_0 N \psi(W(s)) \leq 0$ and therefore $W(s) = 0$, an impossibility. Finally, suppose that $E(s) + I(s) = N$. From the definition of s, it follows that $\dot{E}(s) + \dot{I}(s) \geq 0$, which contradicts the fact that $\dot{E}(s) + \dot{I}(s) = -\mu_2 E(s) - \mu_3 I(s) \leq -\min(\mu_2, \mu_3) N < 0$.

(ii) It follows from (i) that for all $t \in J$, $E(t) + I(t) < N$, thus $\dot{W} < -\mu_0 W + \alpha N$. Integrating this differential inequality, we find that

$$W(t) \leq W(0)\, e^{-\mu_0 t} + \frac{\alpha N}{\mu_0}\left(1 - e^{-\mu_0 t}\right), \quad \text{for all } t \in J\,.$$

Thus if $W(0) \geq \frac{\alpha N}{\mu_0}$ then $W(t) \leq W(0)$, for all $t \in J$ and if $W(0) < \frac{\alpha N}{\mu_0}$ then $W(t) < \frac{\alpha N}{\mu_0}$, for all $t \in J$. Hence $W(t) \leq \max(W(0), \frac{\alpha N}{\mu_0})$, for all $t \in J$.

In order to consider initial conditions belonging to ∂B, we extend ψ arbitrarily as a continuously differentiable function to $(-\infty, 0)$. By Picard-Lindelöf theorem again, for any initial condition belonging to B, there is a unique solution to the initial value problem for (S), which exists on a right maximal interval $J^* \subset \mathbb{R}_+$.

PROPOSITION 2. *If* $(W(0), E(0), I(0)) \in B$, *then*

(i) $(W(t), E(t), I(t)) \in B$, *for all* $t \in J^*$;

(ii) $(W(t) \leq \max(W(0), \frac{\alpha N}{\mu_0})$ *and* $E(t) + I(t) \leq N$, *for all* $t \in J^*$;

(iii) $J^* = \mathbb{R}_+$;

(iv) *If* $(W(0), E(0), I(0)) \neq (0,0,0)$, *then* $W(t) > 0$, $E(t) > 0$ *and* $I(t) > 0$, *for all* $t \in (0, \infty)$.

Proof. Assertions (i), (ii) and (iii) follow from Proposition 1 using continuity of solutions in initial conditions. To establish statement (iv), we use the variation of constants formula. For any $t > 0$ it follows that

$$(*) \quad W(t) = W(0)\ e^{-\mu_0 t} + \alpha e^{-\mu_0 t} \int_0^t e^{\mu_0 s} I(s)\ ds;$$

$$(**) \quad E(t) = E(0)\ e^{-\int_0^t \theta(s)\ ds} + e^{-\int_0^t \theta(s)\ ds} \int_0^t e^{\int_0^s \theta(r)\ dr} \beta N_0 \psi(W(s))(N - I(s))\ ds,$$

where $\theta(s) = \gamma + \mu_2 + \beta N_0 \psi(W(s))$;

$$(***) \quad I(t) = I(0)\ e^{-\mu_3 t} + \gamma\ e^{-\mu_3 t} \int_0^t e^{\mu_3 s}\ E(s)\ ds.$$

Thus assume that $W(0) > 0$. Since $I(s) \geq 0$, for $s > 0$, it follows from (*) that $W(t) > 0$, for all $t > 0$. We now show that $E(t) > 0$, for all $t > 0$. Assume *per contra* that there exists $\tau > 0$ such that $E(\tau) = 0$. It follows then from (**) that $I(s) = N$ for all $s \in [0, \tau]$, thus $\dot{I}(\tau) = 0$ which contradicts the fact that, by the third equation of system (S), $\dot{I}(\tau) = -\mu_3 N$. Accordingly $E(t) > 0$, for all $t > 0$ and, using (***), we get $I(t) > 0$, for all $t > 0$, which proves assertion iv). The cases $E(0) > 0$ or $I(0) > 0$ are treated similarly.

Remark. By differentiating each question of (S) and using the facts that ψ is continuously differentiable and that W, E and I are uniformly bounded, we obtain the uniform boundedness of $\ddot{W}$, $\ddot{E}$ and $\ddot{I}$. This property will be used in later arguments.

We show next that (S) can be converted into systems which are *cooperative* (HIRSCH 1982), in the sense that the resulting vector fields are such that the off-diagonal entries of their Jacobian matrix are nonnegative.

The transformation $X_1 = W$, $X_2 = E + I$ and $X_3 = I$ converts the biological domain B into $B^* = \{(X_1, X_2, X_3) \in \mathbb{R}_+^3 : X_3 \leq X_2, X_2 \leq N\}$, and (S) into the following system

$$(S^*) \qquad \begin{aligned} \dot{X}_1 &= -\mu_o X_1 + \alpha X_3 \\ \dot{X}_2 &= -\mu_2 X_2 + (\mu_2 - \mu_3) X_3 + \beta N_0 \psi(X_1)(N - X_2) \\ \dot{X}_3 &= -(\gamma + \mu_3) X_3 + \gamma X_2 \end{aligned}$$

whereas system (S^*) is converted by the change of variables $Y_1 = X_1$, $Y_2 = X_2 + \frac{1}{\alpha}(\mu_3 - \mu_2) X_1$, and $Y_3 = X_3 + \frac{1}{2\alpha}(\gamma + \mu_3 - \mu_0) X_1$ into

$$(S^{**}) \qquad \begin{aligned} \dot{Y}_1 &= -\tfrac{1}{2}(\gamma + \mu_0 + \mu_3) Y_1 + \alpha Y_3 \\ \dot{Y}_2 &= -\mu_2 Y_2 + \tfrac{1}{\alpha}(\mu_3 - \mu_2)(\mu_2 - \mu_0) Y_1 + \\ &\quad + \beta N_0 \psi(Y_1)(N - Y_2 + \tfrac{1}{\alpha}(\mu_3 - \mu_2) Y_1) \\ \dot{Y}_3 &= -\tfrac{1}{2}(\gamma + \mu_3 + \mu_0) Y_3 + \gamma Y_2 + \\ &\quad + \tfrac{1}{4\alpha}((\gamma + \mu_0 - \mu_3)^2 - 4\gamma(\mu_0 - \mu_2)) Y_1 \end{aligned}$$

while B^* is transformed into a domain B^{**}.

Since ψ is increasing, we notice that the off-diagonal elements of the Jacobian matrix of the vector field appearing in (S^*) are nonnegative for all $(X_1, X_2, X_3) \in B^*$, provided that $\mu_2 \geq \mu_3$. The vector field appearing in (S^{**}) enjoys likewise that property for all $(Y_1, Y_2, Y_3) \in B^{**}$, provided that $\mu_2 < \mu_3$ and $\mu_2 \geq \mu_0$.

In brief, (S) can be imbedded into the class of cooperative systems when $\mu_2 \geq \mu_0$. Since $\frac{1}{\mu_0}$ and $\frac{1}{\mu_2}$ may be interpreted respectively as the expected lifetimes of the adult worms and the prepatent snails, the restriction on the epidemiological parameters μ_0 and μ_2 is mild from a biological viewpoint, because $\frac{1}{\mu_2}$ is a few weeks and $\frac{1}{\mu_0}$ is several years.

The rest of this paper is devoted to the study of the limiting behaviour of every solution of system (S^*), under the assumption $\mu_2 \geq \mu_3$; the arguments apply in the same way to system (S^{**}), if $\mu_2 < \mu_3$ and $\mu_2 \geq \mu_0$, yielding similar conclusions.

Let F^* denote the vetor field appearing in (S^*). Since ψ is strictly increasing, it follows that the Jacobian matrix $F^{*\prime}$ of F^* is irreducible in the interior of B^*, that is for any proper subset E of $\{1, 2, 3\}$, there exist $i \in E$ and $j \in \{1, 2, 3\} - E$ such that $(F^{*\prime})_{ij} \neq 0$, for all $(X_1, X_2, X_3) \in (B^*)^\circ$. Thus, $S^*$is cooperative and irreducible in the interior $(B^*)^\circ$ of B^*.

From now on, we consider initial conditions belonging to $(B^*)^\circ$, which is not a restriction according to Proposition 2.

We turn now to a review of some standard notions from dynamical systems theory and some general results on monotone systems.

BACKGROUND AND GENERAL RESULTS

Let $\dot{X}(t) = F^*(X(t))$, $X(0) = Z$, $Z \in (B^*)^\circ$ denote systems (S^*) in vector form. A solution is alternatively denoted by $Z(t)$ or $\phi_t(Z)$. A subset S of B^* is called positively invariant if for each $Z \in S$, $\phi_t(Z) \in S$ for $t \in \mathbb{R}_+$.

It is well known that the long term behaviour of a solution often reduces to the study of its omega-limit set

$$\omega(Z) = \Big\{Y \in B^* : \text{there exists a sequence } (t_k) \text{ with } \lim_{k\to\infty} t_k = \infty \\ \text{and } \lim_{k\to\infty} Z(t_k) = Y\Big\} .$$

This set is positively invariant and consists of a single element P, namely an equilibrium point, that is $F^*(P) = 0$, if and only if $\lim_{t\to\infty} Z(t) = P$.

An equilibrium point P is called a «trap» (HIRSCH 1985) if there is some open set $M \subset (B^*)^\circ$, not necessarily containing P, such that

$$\lim_{t\to\infty} Z(t) = P, \quad \text{for all } Z \in M .$$

If P is a trap, then $\mathrm{Re}\,\lambda \leq 0$ for all eigenvalue λ of the Jacobian matrix $F^{*\prime}(P)$.

We use the following notation. For $X, Y \in \mathbb{R}^3$, we write

$$X \geq Y \;\text{ if } X - Y \in \mathbb{R}^3_+ \quad \text{and} \quad X > Y \;\text{ if } X - Y \in \mathring{\mathbb{R}}^3_+ ,$$

where $\mathring{\mathbb{R}}^3_+$ is the interior of $\mathbb{R}^3_+$. Replacing X, Y by $-X, -Y$, we get the corresponding notions $\leq$ and $<$. If $X \leq Y$ we set

$$[X, Y] = \{Z \in \mathbb{R}^3 : X \leq Z \leq Y\} .$$

Kamke's comparison principle expresses that solutions of cooperative systems enjoy a monotonicity property (KAMKE 1932). A stronger result can be proved in case irreducibility occurs (KRASNOSEL'SKII 1968 and HIRSCH 1985). Thus the solutions of our system satisfy the following property: for $Z, Y \in (B^*)^\circ$, $Z \geq Y$ and $Z \neq Y$ imply $Z(t) > Y(t)$ for $t > 0$. The following result is a well known convergence criterion (SELGRADE 1979, 1980).

PROPOSITION 3. *Suppose that* $Z \in B^*$ *is such that* $F^*(Z) \geq 0$ *(or* $F^*(Z) \leq 0$*). Then all coordinates of the solution* $Z(t)$ *are nondecreasing (or nonincreasing) for* $t \geq 0$. *In either case, since* $\omega(Z)$ *is not empty,* $Z(t)$ *converges to an equilibrium point at* $t \to \infty$.

The following result is an immediate consequence of an important theorem due to HIRSCH (1985, Theorem 4.1.).

PROPOSITION 4. *Suppose that the set of equilibrium points of* (S^*) *in* B^* *is discrete. Then the set of initial conditions* $Z \in B^*$ *for which* $Z(t)$ *does not converge to an equilibrium point at* $t \to \infty$ *has Lebesgue measure zero.*

We end the section with two very useful results proved by GABRIEL (1983) and HIRSCH *et al.* (1985) concerning the asymptotic behaviour of functions of a real variable.

PROPOSITION 5. *Let* $f : \mathbb{R}_+ \to \mathbb{R}$ *be a function such that*
(i) $\dot{f}(t)$ *exists and is bounded for* $t \in \mathbb{R}_+$ *;*
(ii) $\int_0^\infty f(t)\, dt \in \mathbb{R}$, *then* $\lim_{t\to\infty} f(t) = 0$.

PROPOSITION 6. *Suppose that a function* $f : \mathbb{R}_+ \to \mathbb{R}$ *is differentiable and uniformly bounded. Then*
(i) There are sequences t_k *and* s_k *such that*

$$\begin{aligned}
\lim_{k\to\infty} t_k &= \lim_{k\to\infty} s_k = \infty, \\
\lim_{k\to\infty} f(t_k) &= \lim_{t\to\infty} \sup f(t), \\
\lim_{k\to\infty} \dot{f}(t_k) &= 0, \\
\lim_{k\to\infty} f(s_k) &= \lim_{t\to\infty} \inf f(t), \\
\lim_{k\to\infty} \dot{f}(s_k) &= 0\,.
\end{aligned}$$

(ii) Moreover, if f *is twice differentiable and its second derivative* $\ddot{f}$ *is uniformly bounded, then for any sequence* (r_k) *such that*

$$\begin{aligned}
&\lim_{k\to\infty} r_k = \infty \\
\textit{and } &\lim_{k\to\infty} f(r_k) = \lim_{t\to\infty} \sup f(t)\,, \\
\textit{or } &\lim_{k\to\infty} f(r_k) = \lim_{t\to\infty} \inf f(t)\,, \\
\textit{then } &\lim_{k\to\infty} \dot{f}(r_k) = 0\,.
\end{aligned}$$

EQUILIBRIUM POINTS OF (S^*)

To make writing simpler, we first put

$$T_1 = \frac{\alpha\gamma N}{\mu_0(\gamma+\mu_3)} , \quad T_2 = \frac{\beta N_0(\gamma+\mu_3)}{\mu_3(\gamma+\mu_2)}$$

and following HIRSCH *et al.* (1985), we introduce the function

$$g_{T_1}(x) = \frac{\psi(x)(T_1 - x)}{x} , \quad 0 < x < T_1 .$$

It results from (S^*) that a point P_x is an equilibrium point of (S^*) if and only if

$$P_x = x\left(1, \frac{\mu_0(\gamma+\mu_3)}{\alpha\gamma}, \frac{\mu_0}{\alpha}\right)$$

where either $x = 0$ or x is a solution of the following equation

$$g_{T_1}(x) = \frac{1}{T_2} . \tag{E}$$

For a hermaphroditic oviposition function, the following general statement can be made about the possible number of equilibrium points.

PROPOSITION 7. *By HIRSCH et al. (1985), let* ψ *be a hermaphroditic oviposition function.*

(i) If

$$T_1 T_2 \leq \frac{1}{\psi'(0)} ,$$

then the origin 0 *is the only equilibrium of* (S^*).

(ii) If

$$T_1 T_2 > \frac{1}{\psi'(0)} ,$$

then (S^*) *has two equilibria, the origin* 0 *and* P_{x_0}, *where* x_0 *is the root of equation* (E).

When ψ is dioecian, the question of its influence on the statics and the dynamics of the transmission model becomes more difficult to tackle. However, an important special case was distinguished by HIRSCH *et al.* (1985), wich motivates the following definition: *a dioecious oviposition function* ψ

is called «triadic» if to each $T_1 > 0$ *there corresponds a positive number* $x(T_1)$ *such that*

$$\begin{aligned}
&g'_{T_1}(x) > 0 \quad if \;\; 0 < x < x(T_1)\\
&g'_{T_1}(x) = 0 \quad if \;\; x = x(T_1)\\
&g'_{T_1}(x) < 0 \quad if \;\; x(T_1) < x < T_1\ .
\end{aligned}$$

It results from the definition that the equilibrium points of (S^*) for such a function are determined in the following way

(i) If

$$\frac{1}{T_2} > g_{T_1}(x(T_1))$$

then the origin 0 is the only equilibrium.

(ii) If

$$\frac{1}{T_2} = g_{T_1}(x(T_1))$$

then (S^*) has two equilibria: 0 and $P_{x(T_1)}$.

(iii) If

$$\frac{1}{T_2} < g_{T_1}(x(T_1))$$

then (S^*) has three equilibria: 0, P_{x_1} and P_{x_2}, where $0 < x_1 < x(T_1) < x_2 < T_1$.

Consider the half line

$$L = \left\{P_x = x\left(1, \frac{\mu_0(\gamma+\mu_3)}{\alpha\gamma}, \frac{\mu_0}{\alpha}\right) : x > 0\right\}.$$

An easy computation gives for any $P_x \in L$,

$$\begin{aligned}
&F_1^*(P_x) = F_3^*(P_x) = 0\\
\text{and}\quad &F_2^*(P_x) = \frac{x\mu_0(\gamma+\mu_3)\beta N_0}{\alpha\gamma}\left(g_{T_1}(x) - \frac{1}{T_2}\right),
\end{aligned}$$

where F_1^*, F_2^*, F_3^* are the coordinates of the vector field F^*.
In particular, when ψ is a triadic oviposition function, we get $F^*(P_x) \le 0$ if $0 < x \le T_1$ and equation (E) has only the root $x(T_1)$, $F^*(P_x) \le 0$ if $0 < x \le x_1$, $F^*(P_x) \ge 0$ if $x_1 \le x \le x_2$ and equation (E) has the roots x_1 and x_2. Thus, using monotonicity of the solutions of (S^*) and proposition 3, we obtain the following proposition.

PROPOSITION 8. *Let ψ be a triadic oviposition function.*

(i) *If (S^*) has two equilibria,*
then $\lim_{t\to\infty} Z(t) = 0,$ *for all* $Z \in [0, P_{x(T_1)}],\ Z \neq P_{x(T_1)}$.

(ii) *If (S^*) has three equilibria,*
then $\lim_{t\to\infty} Z(t) = 0,$ *for all* $Z \in [0, P_{x_1}],\ Z \neq P_{x_1}$
and $\lim_{t\to\infty} Z(t) = P_{x_2},$ *for all* $Z \in [P_{x_1}, P_{x_2}],\ Z \neq P_{x_1}$.

GLOBAL ASYMPTOTIC BEHAVIOR OF SOLUTIONS OF (S^*)

In this section, we establish the convergence of all solutions of (S^*) to equilibrium points as $t \to \infty$, by exploiting their monotonicity properties in conjunction with *ad hoc* arguments stemming from the particular form of (S^*).

In the same spirit (HIRSCH *et al.* 1985), we next associate to (S^*) some inequalities which we call «fundamental inequalities».

PROPOSITION 9. *Let $Z_i(t)$, $i = 1, 2, 3$, be the coordinates of a solution of (S^*) and denote,*

$$\limsup_{t\to\infty} Z_i(t), \quad \liminf_{t\to\infty} Z_i(t) .$$

respectively by $\bar{Z}_i$ and $\underline{Z}_i$. The following inequalities occur

(i) $$\mu_0 \bar{Z}_1 \leq \alpha \bar{Z}_3$$

(ii) $$(\mu_2 + \beta N_0 \psi(\bar{Z}_1))\bar{Z}_2 \leq (\mu_2 - \mu_3)\ \bar{Z}_3 + \beta N_0 N \psi(\bar{Z}_1)$$

(iii) $$(\psi + \mu_3)\bar{Z}_3 \leq \gamma \bar{Z}_2$$

(iv) $$\frac{1}{T_2} \leq g_{T_1}(\bar{Z}_1) \quad \textit{if} \quad \bar{Z}_1 > 0$$

(v) *The above inequalities are reversed if $\bar{Z}_i$, $i = 1, 2, 3$, are replaced by $\underline{Z}_i$, $i = 1, 2, 3$.*

Proof. (i) If (t_k) is a sequence such that

$$\lim_{k\to\infty} t_k = \infty \quad \text{and} \quad \lim_{k\to\infty} Z_1(t_k) = \bar{Z}_1 ,$$

then Proposition 6 implies

$$\lim_{k\to\infty} \dot{Z}_1(t_k) = 0 .$$

By boundedness of the solution, we can choose a convergent subsequence of $Z_3(t_k)$, say

$$\lim_{k\to\infty} Z_3(t_k) = Z_3^* \ .$$

Evaluating the first equation of (S^*) at t_k and letting k go to infinity, we get

$$0 = -\mu_0\bar{Z}_1 + \alpha Z_3^* \leq -\mu_0\bar{Z}_1 + \alpha\bar{Z}_3 \ .$$

Inequalities (ii) and (iii) are obtained in the same way and using the fact that ψ is increasing. (iv) It follows from inequalities (ii) and (iii) that

$$(\mu_2 + \beta N_0\psi(\bar{Z}_1))\bar{Z}_2 \leq \frac{\gamma(\mu_2-\mu_3)}{\gamma+\mu_3}\bar{Z}_2 + \beta N_0 N\psi(\bar{Z}_1) \ , \text{ thus}$$

$$\left(\frac{\mu_3(\gamma+\mu_2)}{\gamma+\mu_3} + \beta N_0\psi(\bar{Z}_1)\right)\bar{Z}_2 \leq \beta N_0 N\psi(\bar{Z}_1) \ .$$

Since by inequalities (i) and (iii), we have

$$\bar{Z}_2 \geq \frac{\mu_0(\gamma+\mu_3)}{\alpha\gamma} \ , \text{ we get}$$

$$\left(\frac{\mu_3(\gamma+\mu_2)}{\beta N_0(\gamma+\mu_3)} + \psi(\bar{Z}_1)\right)\bar{Z}_1 \leq \frac{\alpha\gamma N}{\mu_0(\gamma+\mu_3)}\psi(\bar{Z}_1) \ ,$$

which is inequality (iv) in a disguised form. (v) is proved in the same way.

The behaviour of solutions of (S^*) as $t \to \infty$ can now be derived, in the hermaphroditic case, from the last proposition.

PROPOSITION 10. *Let ψ be a hermaphroditic oviposition function and let $Z(t) = (Z_1(t), Z_2(t), Z_3(t))$ be a solution of (S^*) corresponding to an initial condition $Z \in (B^*)^\circ$.*

(i) If $T_1T_2 \leq \dfrac{1}{\psi'(0)}$, *then* $\lim_{t\to\infty} Z(t) = 0$.

(ii) If $T_1T_2 > \dfrac{1}{\psi'(0)}$, *then* $\lim_{t\to\infty} Z(t) = P_{x_0}$.

Proof. (i) We first prove that $\bar{Z}_1 = 0$. To see this suppose *per contra* that $\bar{Z}_1 > 0$. Then by part (iv) of Proposition 9 and assumption (i) we get

$$g_{T_1}(\bar{Z}_1) \geq \frac{1}{T_2} \geq T_1 \ \psi'(0) = \lim_{x\to 0} g_{T_1}(x) \ .$$

Since ψ is hermaphroditic, it is easily seen that the function g_{T_1} is strictly decreasing. Thus $\bar{Z}_1 = 0$, a contradiction. Therefore

$$\lim_{t\to\infty} Z_1(t) = 0$$

and, using Proposition 6 and the first and third equations of (S^*),

$$\lim_{t\to\infty} Z_2(t) = 0 \quad \text{and} \quad \lim_{t\to\infty} Z_3(t) = 0 \, .$$

(ii) We first prove that since $Z \neq 0$, $\bar{Z}_1 > 0$. Assuming *per contra* that $\bar{Z}_1 = 0$ and therefore that $\lim_{t\to\infty} Z(t) = 0$, it follows from monotonicity that for all $X \in [0, Z] - \{0, P_{x_0}\}$, the solution $\phi_t(X)$ converges to 0, as $t \to \infty$. Thus the equilibrium point 0 is a trap and consequently $\mathrm{Re}\,\lambda \leq 0$ for all eigenvalue λ of $F^{*\prime}(0)$. It results from a straightforward computation that the product of these eigenvalue is equal to

$$\alpha\beta\gamma N_0 N \left(\psi'(0) - \frac{1}{T_1 T_2}\right)$$

which is positive by assumption (ii).
Hence one eigenvalue, at least, is positive: a contradiction. Therefore $\bar{Z}_1 > 0$ and by parts iv) and v) of Proposition 9,

$$g_{T_1}(\bar{Z}_1) \geq \frac{1}{T_2} \geq g_{T_1}(\underline{Z}_1) \, .$$

Since the function g_{T_1} is decreasing we get

$$\bar{Z}_1 = \underline{Z}_1 = x_0 \, , \quad \text{that is} \quad \lim_{t\to\infty} Z_1(t) = x_0 \, .$$

Finally, the convergence of $Z(t)$ to P_{x_0} as $t \to \infty$ follows from Proposition 6, using the first and third equations of (S^*).

Remark. It is also possible to establish Proposition 10 by using a general result for monotone systems, stipulating that for any compact omega limit set, there exist equilibrium points P, Q, such that this omega-limit set is contained in $[P, Q]$ (HIRSCH 1982, 1988).

We now turn to the dioecious case and divide the proof into two parts because the case where (S^*) has three equilibrium points requires more analysis.

PROPOSITION 11. *Let ψ be a triadic oviposition function and suppose that (S^*) has at most two equilibrium points. Let $Z(t)$ denote a solution of (S^*) corresponding to an initial condition $Z \in (B^*)^\circ$.*

(i) If $\dfrac{1}{T_2} > g_{T_1}(x(T_1))$, *then* $\lim_{t\to\infty} Z(t) = 0$.

(ii) If $\dfrac{1}{T_2} = g_{T_1}(x(T_1))$*, then* $Z(t)$ *converges to an equilibrium point as* $t \to \infty$. *In particular,*

$$\lim_{t\to\infty} Z(t) = 0, \quad \textit{if } Z \in \left[0, P_{x(T_1)}\right] - \left\{P_{x(T_1)}\right\}$$
$$\textit{and} \quad \lim_{t\to\infty} Z(t) = P_{x(T_1)}, \quad \textit{if } Z \geq P_{x(T_1)} \,.$$

Proof. (i) Denote the coordinates of $Z(t)$ by $Z_i(t)$, $i = 1, 2, 3$. We first prove that $\bar{Z}_1 = 0$. Assuming *per contra* that $\bar{Z}_1 > 0$, then by part (iv) of Proposition 9, we get

$$g_{T_1}(\bar{Z}_1) \geq \frac{1}{T_2}$$

which contradicts the fact that by assumption (i)

$$\max_{x\in[0,T_1]} g_{T_1}(x) < \frac{1}{T_2} \,.$$

Therefore $\bar{Z}_1 = 0$, that is

$$\lim_{t\to\infty} Z_1(t) = 0$$

and the convergence of $Z(t)$ to 0 as $t \to \infty$ follows from Proposition 6.
(ii) Arguing as in (i) we obtain the following alternative: either $\bar{Z}_1 = 0$, thus

$$\lim_{t\to\infty} Z(t) = 0, \text{ or } \bar{Z}_1 = x(T_1) \,.$$

In the latter case, considering a sequence (t_k) such that

$$\lim_{t\to\infty} t_k = \infty \quad \text{and} \quad \lim_{k\to\infty} Z_1(t_k) = \bar{Z}_1 \,,$$

we get, by using the fundamental inequalities and Proposition 6,

$$\lim_{k\to\infty} Z(t_k) = P_{x(T_1)} \,,$$

that is

$$P_{x(T_1)} \in \omega(Z) \quad \text{and} \quad X \leq P_{x(T_1)} \quad \text{for all} \quad X \in \omega(Z) \,.$$

The last part of the assertion follows from Proposition 8.
Since $\omega(Z) \subset [0, P_{x(T_1)}]$, we conclude

$$\omega(Z) = P_{x(T_1)} \quad \text{that is} \quad \lim_{t\to\infty} Z(t) = P_{x(T_1)} \,.$$

Finally, we consider the case where (S^*) possesses three equilibria. Using the fundamental inequalities of Proposition 9, it is easy to prove that any solution of (S^*) either converges to the equilibrium point P_{x_2} as $t \to \infty$, or ultimately lies in $[0, P_{x_2}]$. Therefore, we concentrate on initial conditions belonging to $[0, P_{x_2}]$.

Let $B(0)$ and $B(P_{x_2})$ denote respectively the domains of attraction of 0 and P_{x_2} in $[0, P_{x_2}]$, that is

$$B(0) = \left\{Z \in [0, P_{x_2}] : \lim_{t\to\infty} Z(t) = 0\right\}$$

$$B(P_{x_2})) = \left\{Z \in [0, P_{x_2}] : \lim_{t\to\infty} Z(t) = P_{0,x_2}\right\} .$$

Since by Proposition 8, we have

$$\left[0, P_{x_1}\right] - \left\{P_{x_1}\right\} \subset B(0) \quad \text{and} \quad \left[P_{x_1}, P_{x_2}\right] - \left\{P_{x_1}\right\} \subset B\left(P_{x_2}\right) ,$$

we notice that $B(0)$ and P_{x_2} are open sets relatively to $[0, P_{x_2}]$.

The next result shows that the boundaries of $B(0)$ and $B(P_{x_2})$ decompose $[0, P_{x_2}]$.

PROPOSITION 12. *Let ψ be a triadic oviposition function and suppose that (S^*) has three equilibrium points. Then*

$$\left[0, P_{x_2}\right] = \overline{B(0)} \cup \overline{B(P_{x_2})} ,$$

where the bar denotes relative closure in $[0, P_{x_2}]$.

Proof. Let

$$A = \left[0, P_{x_2}\right] - \left(\overline{B(0)} \cup \overline{B(P_{x_2})}\right)$$

and assume *per contra* that A is not empty. Notice that A is open relatively to $[0, P_{x_2}]$. Let $[0, P_{x_2}]^\circ$ denote the interior of $[0, P_{x_2}]$. By Proposition 4, for $P \in A \cap [0, P_{x_2}]^\circ$, there exist $Q, R \in A$ such that $Q < P < R$ and $\phi_t(Q)$, $\phi_t(R)$ converge to equilibria, as $t \to \infty$. It follows from the definition of A that

$$\lim_{t\to\infty} \phi_t(Q) = \lim_{t\to\infty} \phi_t(R) = P_{x_1} ,$$

thus, by monotonicity,

$$\lim_{t\to\infty} \phi_t(Z) = P_{x_1} , \quad \text{for all } Z \in [Q, R] .$$

Hence P_{x_1} is a trap and consequently, $\mathrm{Re}\,\lambda \leq 0$, for all eigenvalue λ of $F^{*\prime}(P_{x_1})$. A straightforward computation shows that the product of these eigenvalues is equal to $\mu_0(\gamma+\mu_3)\beta N_0 x_1\; g'_{T_1}(x_1)$, which is positive by definition of x_1. Therefore, at least one eigenvalue must be positive: a contradiction. Thus A is empty which completes the proof.

Remarks. (i) The result above is true for any cooperative and irreducible system which has three hyperbolic equilibria, provided that its phase space Ω is a lattice, that is, for any $P=(P_1,\ldots,P_n)$ and $Q=(Q_1,\ldots,Q_n)$ belonging to Ω, the points whose i-th coordinate is $\max\{P_i,Q_i\}$ or $\min\{P_i,Q_i\}$ belong to Ω.

(ii) The result above also partakes of the fact that for cooperative and irreducible systems, it is possible to operate a partition of the phase space into invariant open sets in which solutions converge to equilibrium points (HIRSCH 1988 and SMITH 1986).

Proposition 12 implies that it remains to study the dynamics of (S^*) for initial conditions belonging to the boundaries of $B(0)$ and $B(P_{x_2})$. A moments reflection will convince the reader that these boundaries coincide and are positively invariant.

In this situation, we exploite a useful result of SMITH (1986, Prop. 2.4.) which states that the boundary of $B(0)$ for instance can be continuously parametrized by points of the set obtained by projecting this boundary orthogonally onto the X_1X_3 plane. More precisely, there exists a continuous function $H(X_1,X_3)$ defined on a subset of the X_1X_3 plane, strictly decreasing in the sense that $P\le Q$, $P\ne Q$ implies $H(P)>H(Q)$, such that the boundary of $B(0)$ is the graph of H.
Therefore any solution of (S^*) with an initial condition belonging to this boundary obeys the following reduced differential system

$$\begin{aligned}\dot X_1 &= -\mu_0 X_1+\alpha X_3\\ \dot X_3 &= -(\gamma+\mu_3)X_3+\gamma H(X_1,X_3)\,.\end{aligned}\tag{R}$$

To our knowledge, the question of the smoothness of such a function H is still opened. Therefore we cannot apply Bendixson's negative criterion to rule out periodic solutions of (R). Nevertheless it is possible to establish the asymptotic behaviour of solutions of (R) under the assumption that H is merely continuous and decreasing, using the method of the energy integral described by HIRSCH *et al.* (1985).

PROPOSITION 13. *Suppose that the function H is continuous and decreasing in the sense defined above and assume that (R) has a solution, denoted by $X_1(t)$, $X_3(t)$, which exists for $t>0$ and is bounded. Then*
(i) $\lim_{t\to\infty}\dot X_1(t)=0$;
(ii) $\lim_{t\to\infty}X_1(t)$ *and* $\lim_{t\to\infty}X_3(t)$ *exist.*

Proof. By differentiating the first equation of (R) and using the second equation of (R) we obtain

$$\ddot{X}_1 + (\gamma + \mu_0 + \mu_3)\dot{X}_1 + \mu_0(\gamma + \mu_3)X_1 = \alpha\gamma H\left(X_1, \frac{\dot{X}_1 + \mu_0 X_1}{\alpha}\right) .$$

Multiplying the preceding equation by $\dot{X}_1$ and integrating from 0 to t, we get

$$\begin{aligned}\frac{1}{2}\left(\dot{X}_1^2(t) - \dot{X}_1^2(0)\right) + \\ + \frac{\mu_0}{2}(\gamma + \mu_3)\left(X_1^2(t) - X_1^2(0)\right) + (\gamma + \mu_0 + \mu_3)\int_0^t \dot{X}_1^2(s)\, ds = \\ = \alpha\gamma \int_0^t H\left(X_1(s), \frac{\dot{X}_1(s) + \mu_0 X_1(s)}{\alpha}\right)\dot{X}_1(s)\, ds. \qquad (*)\end{aligned}$$

Since H is decreasing, we obtain

$$H\left(X_1, \frac{\dot{X}_1 + \mu_0 X_1}{\alpha}\right) - H\left(X_1, \frac{\mu_0 X_1}{\alpha}\right) \geq 0$$

(respectively ≤ 0) if $\dot{X}_1 \leq 0$ (respectively $\dot{X}_1 \geq 0$). Therefore

$$H\left(X_1, \frac{\dot{X}_1 + \mu_0 X_1}{\alpha}\right)\dot{X}_1 \leq H\left(X_1, \frac{\mu_0 X_1}{\alpha}\right)\dot{X}_1 , \quad \text{for all } t > 0 .$$

Accordingly, the right-hand side of (*) is bounded above by

$$\alpha\gamma \int_0^t H\left(X_1(s), \frac{\mu_0}{\alpha}X_1(s)\right)\dot{X}_1(s)\, ds = \alpha\gamma \int_{X_1(0)}^{X_1(t)} H\left(u, \frac{\mu_0}{\alpha}u\right) du .$$

Since $X_1(t)$ is uniformly bounded, this last integral is uniformly bounded. Observe also that since X_1 and X_3 are bounded, it follows from (R) that $\dot{X}_1$, $\dot{X}_3$ and $\ddot{X}_1$ are bounded. Considering equation (*), we conclude

$$\int_0^\infty \dot{X}_1^2(s)ds < \infty , \quad \text{thus} \quad \lim_{t\to\infty}\int_0^t \dot{X}_1^2(s)ds \in \mathbb{R} .$$

Applying Proposition 5 to the function $\dot{X}_1^2$, we obtain

$$\lim_{t\to\infty} \dot{X}_1^2(t) = \lim_{t\to\infty} \dot{X}_1(t) = 0 \quad \text{which proves (i)} .$$

(ii) Applying part (i) of Proposition 6 to the function X_3, we get the existence of sequences (t_k) and (s_k) such that

$$\lim_{k\to\infty} X_3(t_k) = \bar{X}_3 \ , \ \lim_{k\to\infty} \dot{X}_3(t_k) = 0 \ , \ \lim_{k\to\infty} X_3(s_k) = \underline{X}_3$$

$$\text{and} \ \lim_{k\to\infty} \dot{X}_3(s_k) = 0 \ ,$$

$$\text{where} \ \bar{X}_3 = \lim_{t\to\infty} \sup X_3(t) \ \text{and} \ \underline{X}_3(t) = \lim_{t\to\infty} \inf X_3(t) \ .$$

$$\text{Since} \ \dot{X}_3 = -(\gamma+\mu_3)X_3 + \gamma H\left(\frac{\alpha X_3 - \dot{X}_1}{\mu_0}, X_3\right) \ ,$$

then evaluating each member of this equation at t_k and s_k, letting $k \to \infty$ and using part (i), we obtain

$$\bar{X}_3 = \frac{\gamma}{\gamma+\mu_3} H\left(\frac{\alpha}{\mu_0}\bar{X}_3, \bar{X}_3\right) \ \text{and} \ \underline{X}_3 = \frac{\gamma}{\gamma+\mu_3} H\left(\frac{\alpha}{\mu_0}\underline{X}_3, \underline{X}_3\right) \ .$$

Since H is decreasing, we deduce $\underline{X}_3 \geq \bar{X}_3$, therefore $\underline{X}_3 = \bar{X}_3$, that is $\lim_{t\to\infty} X_3(t)$ exists. The existence of $\lim_{t\to\infty} X_1(t)$ follows from (R) and part (i). As an immediate consequence of Proposition 13, we conclude the convergence of solutions of (S^*) with initial conditions belonging to the boundary of $B(0)$ and $B(P_{x_2})$ to the equilibrium point P_{x_1} as $t \to \infty$.

Remarks. (i) The case where (S^*) has three equilibrium points can also be treated by methods initiated by SELGRADE (1979, 1980).
(ii) Another approach consists of applying a powerful result due to HIRSCH (1982, Thm. C.) which states that a compact omega-limit set of three dimensional cooperative system which contains no equilibrium must be a periodic orbit. It is then possible to preclude the existence of periodic orbits using the fact that the vector field has negative divergence. We give only an outline of the proof of this assertion. Assuming the existence of a nontrivial periodic orbit, it is possible to construct a set V such that the interior of V is nonempty, V has finite volume and V is negatively invariant (HIRSCH 1982 and SMITH 1986). Since the divergence of the vector field is negative, Liouville's theorem implies that $\phi_t(V)$ has smaller volume than V which contradicts the fact that, by negative invariance of V, $\phi_t(V) \supset V$ for $t > 0$. Accordingly the omega-limit set of any solution of (S^*) contains at least one equilibrium point. This fact makes the study of the asymptotic behaviour of solutions of (S^*) easier and can be used in case (S^*) has more than three equilibrium points. In case the oviposition function ψ is triadic, it yields the convergence result immediately.

ACKNOWLEDGMENTS

This work was supported by the Swiss National Fund for Scientific Research.

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Manuscrit reçu le 3 janvier 1989