Stability of coexistence states in a periodic prey-predator system

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Autonomous prey-predator system 1

$$\dot{u} = u(a - bu - cv), \quad \dot{v} = v(d + eu - fv)$$

a, d growth rates, $\quad b, f > 0$ intraspecific competition,

$c, e > 0$ interaction coefficients

$u = u(t) \geq 0$ prey, $\quad v = v(t) \geq 0$ predator

trivial equilibrium $O = (0, 0)$

semi- trivial equilibria $S_1 = (\frac{a}{b}, 0)$ *if* $a > 0$, $S_2 = (0, \frac{d}{f})$ *if* $d > 0$

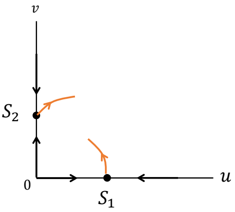
coexistence state $E = (E_1, E_2)$, $E_1 > 0$, $E_2 > 0$

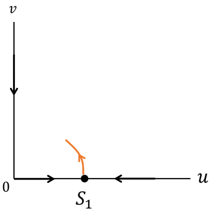
Autonomous prey-predator system 2

$$\dot{u} = u(a - bu - cv), \quad \dot{v} = v(d + eu - fv)$$

$\exists$ coexistence state $E = (E_1, E_2) \iff af - cd > 0,\ bd + ae > 0$

$\iff a > 0$ and semi-trivial states are hyperbolic saddles





Coexistence states are unique and asymptotically stable

Time-dependent systems: seasonal effects

$$\dot{u} = u(a(t) - b(t)u - c(t)v), \quad \dot{v} = v(d(t) + e(t)u - f(t)v)$$

$a = a(t),\ b = b(t), \ldots,\ f = f(t)$ T-periodic and continuous (or locally integrable)

$b(t),\ c(t),\ e(t),\ f(t)$ positive everywhere

Cushing 1977

trivial equilibrium $O = (0, 0)$

semi- trivial states $S_1(t)$, $S_2(t)$ *T-periodic solutions of*
$\dot{S}_1 = S_1(a(t) - b(t)S_1),\ S_1 > 0$ *if* $\overline{a} = \frac{1}{T}\int_0^T a(t)dt > 0$,

$\dot{S}_2 = S_2(d(t) - f(t)S_2),\ S_2 > 0$ *if* $\overline{d} > 0$

coexistence state $E(t) = (E_1(t), E_2(t))$, *T-periodic solution* $E_1 > 0$, $E_2 > 0$

Some literature on coexistence states

$$\dot{u} = u(a(t) - b(t)u - c(t)v), \quad \dot{v} = v(d(t) + e(t)u - f(t)v)$$

$\exists$ coexistence state $\iff \bar{a} > 0$ and semi-trivial states are hyperbolic saddles (Floquet multipliers $|\mu_1| < 1 < |\mu_2|$)
Brown-Hess (1991), López Gómez (1992)

examples with several coexistence states (non-uniqueness)
Dancer (1994), Amine-O. (1994)

finite number of coexistence states
López Gómez-O.-Tineo (1996)

example with a unique coexistence state that is Lyapunov unstable
López Gómez-O.-Tineo (1996)

Uniqueness and asymptotic stability criteria
Tineo (1992), Amine-O. (1994)

A new criterion (2021)

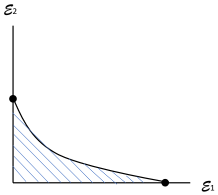
$$\dot{u} = u(a(t) - bu - cv), \quad \dot{v} = v(d(t) + eu - fv)$$

$\exists$ coexistence state $\iff$ the averaged system has a positive equilibrium $\mathcal{E} = (\mathcal{E}_1, \mathcal{E}_2)$, $\mathcal{E}_1 > 0$, $\mathcal{E}_2 > 0$

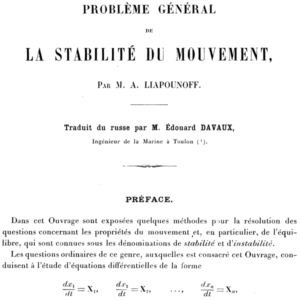
Theorem *The coexistence state is unique and asymptotically stable if*

$$T(\sqrt{ce\mathcal{E}_1\mathcal{E}_2} + \frac{1}{2}(b\mathcal{E}_1 + f\mathcal{E}_2)) \leq 2$$

the number 2 is optimal



Liapounoff stability criterion for Hill's equation (1907)



PROBLÈME GÉNÉRAL

DE

LA STABILITÉ DU MOUVEMENT,

PAR M. A. LIAPOUNOFF.

Traduit du russe par M. Édouard DAVAUX,

Ingénieur de la Marine à Toulon (¹).

PRÉFACE.

Dans cet Ouvrage sont exposées quelques méthodes pour la résolution des questions concernant les propriétés du mouvement et, en particulier, de l'équilibre, qui sont connues sous les dénominations de *stabilité* et d'*instabilité*.

Les questions ordinaires de ce genre, auxquelles est consacré cet Ouvrage, conduisent à l'étude d'équations différentielles de la forme

$$\frac{dx_1}{dt} = X_1, \quad \frac{dx_2}{dt} = X_2, \quad \ldots, \quad \frac{dx_n}{dt} = X_n,$$

Stability for the equation

$$\ddot{y} + \alpha(t) y = 0$$

it $\alpha(t)$ is T-periodic, $\alpha(t) > 0$, $T \int_0^T \alpha(t)dt \leq 4$ the number 4 is optimal

1 Proof of the Theorem

Linearization at the coexistence state $(E_1(t), E_2(t))$,

$$\dot{y} = A(t)y, \quad y \in \mathbb{R}^2$$

$a_{ij}(t)$ is a linear combination of $E_1(t)$ and $E_2(t)$

$A(t)$ is T-periodic

$$\mu_1, \mu_2 \in \mathbb{C} \text{ Floquet multipliers}$$

GOAL:

$$|\mu_i| < 1, \quad = 1, 2$$

2 Proof: a class of linear systems

Change of variables $x_1 = E_1(t)y_1$, $x_2 = E_2(t)y_1$

$$\dot{x} = B(t)x, \quad x \in \mathbb{R}^2$$

Linear prey-predator systems: $b_{12}(t) < 0, \quad b_{21}(t) > 0$ for all $t \in \mathbb{R}$

Lyapunov's framework is in this class

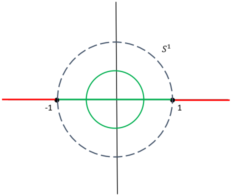
$$\dot{x}_1 = -x_2, \quad \dot{x}_2 = \alpha(t)x_1$$

$\alpha(t)$ is T-periodic and positive

$$\dot{x} = [\lambda B(t) + (1-\lambda)\overline{B}]x, \quad \lambda \in [0,1]$$

$\nexists$ periodic solutions of period $2T$ $(x \neq 0) \implies |\mu_i| < 1,\ i = 1,2$

$trace(\overline{B}) < 0$ implies...



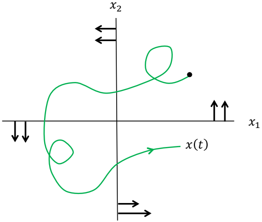
$\dot{x} = \overline{B}x$ is asymptotically stable $|\mu_i(0)| < 1$ and $|\mu_i(\lambda)| \neq 1$ for each $\lambda \in [0,1]$

4 Proof: Following the argument

$$\dot{x} = B(t,\lambda)x$$

elliptic-polar coordinates $x_1 = \sqrt{\mu}\, r\cos\theta, \quad x_2 = \frac{1}{\sqrt{\mu}} r\sin\theta$

$$\dot{\theta} = \mu b_{21}(t,\lambda)\cos^2\theta - \frac{1}{\mu} b_{12}(t,\lambda)\sin^2\theta + (b_{11}(t,\lambda) - b_{22}(t,\lambda))\cos\theta\sin\theta$$



$x(t)$ is $2T$-periodic $\iff \theta(t+2T) = \theta(t) + 2\pi m,\ m = 0, 1, 2, \dots$

Task: to control $\theta(2T) - \theta(0)$ in terms of $\overline{b}_{12}$, $\overline{b}_{21}$ and $\int_0^T |b_{11} - b_{22}|$, hence in terms of $\overline{E}_1$ and $\overline{E}_2$

5 Proof: back to the original equation

$$\dot{E}_1 = E_1(a(t) - bE_1 - cE_2), \quad \dot{E}_2 = E_2(d(t) + eE_1 - fE_2)$$

$$0 = \int_0^T \frac{\dot{E}_1}{E_1} = \int_0^T (a(t) - bE_1 - cE_2)$$

$$0 = \int_0^T \frac{\dot{E}_2}{E_2} = \int_0^T (d(t) + eE_1 - fE_2)$$

$$\overline{a} = b\overline{E}_1 + c\overline{E}_2$$

$$\overline{d} = -e\overline{E}_1 + f\overline{E}_2$$

$$(\overline{E}_1, \overline{E}_2) = (\mathcal{E}_1, \mathcal{E}_2)$$

A trick to control the argument

$$\dot{\theta} = \mu b_{21}(t,\lambda)\cos^2\theta - \frac{1}{\mu} b_{12}(t,\lambda)\sin^2\theta + (b_{11}(t,\lambda) - b_{22}(t,\lambda))\cos\theta\sin\theta$$

$$\text{If } |\theta(t) - 2\pi n| \leq \tfrac{\pi}{4} \implies |\sin\theta(t)| \geq |\cos\theta(t)|$$

$$\dot{\theta} \leq \left(\mu b_{21}(t,\lambda) - \frac{1}{\mu} b_{12}(t,\lambda) + |b_{11}(t,\lambda) - b_{22}(t,\lambda)|\right)\cos^2\theta$$

separation of variables

The proof of uniqueness

Poincaré map: $P(u_0, v_0) = (u(T; u_0, v_0), v(T; u_0, v_0))$

$\exists \Gamma$ Jordan curve in $int(\mathbb{R}^2_+)$:

$$\mathrm{Fix}(P) \subset \Omega$$

Ω bounded connected component of $\mathbb{R}^2 \setminus \Gamma$

$$\deg(id - P, \Omega, 0) = 1$$

$$\deg(id - P, \Omega, 0) = \sum_{x \in \mathrm{Fix}(P)} I(P, x)$$

$I(P, x)$ fixed point index, $|\mu_i| < 1 \implies I(P, x) = 1$

An open question

Given a coexistence state that is locally asymptotically stable and unique, can we say that it is a global attractor?