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On the Dynamics of a Predator-Prey Model with the Holling-Tanner Functional Response

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Abstract. Dynamic behavior of a two-dimensionnal system modelling a predator-prey problem with a modified Holling-Tanner scheme is analyzed. We establish assumptions under which we have boundedness of solutions, existence of a positively invariant and attracting set, the global stability of the coexisting interior equilibrium via Lyapunov function, finally we study the existence and uniqueness of limit cycle.

1 Introduction and mathematical model

The goal of this paper is to give an improved study of a two-dimensional system of autonomous differential equations modeling a predator-prey system, for which a first study has been done in [1]. This model incorporates a modified version of the Holling-Tanner (or Leslie–Gower) functional response, which recently has recovered some interest, see [2,10–12].

This two-species food chain model describes a prey population X which serves as food for a predator Y. The rate equations for the two components of the chain population can be written as follows :

$$\begin{cases} \frac{dX}{dT} = (r_1 - b_1 X - \frac{a_1 Y}{X+k_1})X \\ \frac{dY}{dT} = (r_2 - \frac{a_2 Y}{X+k_2})Y, \end{cases} \tag{1}$$

with $X(0) \geq 0$ and $Y(0) \geq 0$, where X and Y represent the population densities at time T ; r_1, a_1, b_1, k_1, r_2, a_2 and k_2 are model parameters assuming only positive values. See [1,2] for definitions of all these parameters and for more details concerning the origin of this system.

Let us mention that the first equation of system (1) is standard. By contrast, the second equation is absolutely not standard. It contains a modified Leslie-Gower term, that is the second term on the right hand side in the second equation of (1), the last depicts the loss in the predator population.

To simplify system (1) we introduce some transformations of variables. After applying the rescaling: $t = r_1 T$, $x(t) = \dfrac{b_1}{r_1}X(T)$ and $y(t) = \dfrac{a_2 b_1}{r_1 r_2}Y(t)$, system (1) becomes:

$$\begin{cases} \frac{dx}{dt} = x(1-x) - \frac{axy}{x+e_1} \\ \frac{dy}{dt} = b(1 - \frac{y}{x+e_2})y, \end{cases} \tag{2}$$

where $a = \frac{a_1 r_2}{a_2 r_1}$, $b = \frac{r_2}{r_1}$, $e_1 = \frac{b_1 k_1}{r_1}$ and $e_2 = \frac{b_1 k_2}{r_1}$.

2 Boundedness, permanence and global stability

We denote by $\mathbb{R}^2_+$ the non-negative quadrant, and by $Int(\mathbb{R}^2_+)$ the positive quadrant. For the boundedness of the model and existence of a positively invariant attracting set, see [1], in which the following theorem has been proved :

Theorem 1. *Let A be the set defined by:*
$A = \{(x,y) \in \mathbb{R}^2_+ ; 0 \le x \le 1, 0 \le x + y \le L_1\}$, *where*

$$L_1 = \frac{1}{4b}(5b + (1+b)^2(1+e_2)). \tag{3}$$

Then:

a) A is positively invariant

b) all solutions of (2) initiating in $\mathbb{R}^2_+$ are ultimately bounded with respect to $\mathbb{R}^2_+$ and eventually enter the attracting set A.

In this section we shall prove the permanence, that is uniform persistence plus dissipativity, of system (2) and its global stability by constructing a suitable Lyapunov function. First of all, it is easy to verify that this system has three trivial equilibria, (belonging to the boundary of $\mathbb{R}^2_+$, i.e. at which one or more of populations has zero density or is extinct) :

$$E_0 = (0,0), \quad E_1 = (1,0), \quad \text{and} \quad E_2 = (0, e_2).$$

Eigenvalues associated to E_0 are $\lambda_1 = 1 > 0$ and $\lambda_2 = b > 0$, hence E_0 is an unstable node.
For E_1 we have $\lambda_1 = -1 < 0$ and $\lambda_2 = b > 0$,thus it is a saddle point. Its stable manifold is $x - axis$.
Eigenvalues associated to E_2 are $\lambda_1 = 1 - \frac{ae_2}{e_1}$ and $\lambda_2 = -b < 0$ and we have two cases:

i) if $ae_2 > e_1$, then $\lambda_1 < 0$, and E_2 is a stable node,

ii) if $ae_2 < e_1$,then $\lambda_1 > 0$, and in this case E_2 is a saddle point. Its stable manifold is $y - axis$.

Before the study of the permanence of system (2) we introduce some necessary definitions. Suppose that Y is a complete metric space with $Y = Y_0 \cup \partial Y_0$ for an open set Y_0. We will choose Y_0 to be the positive cone in $\mathbb{R}^2$. For the following definitions and theorem, one can see [3] and, for the proof of the theorem, see [7].

Definition 1. A flow or semiflow on Y under wich Y_0 and ∂Y_0 are forward invariant is said to be permanent if it is dissipative and if there is a number $\varepsilon > 0$ such that any trajectory starting in Y_0 will be at least a distance ε from ∂Y_0 for all sufficiently large t.

Let $\omega(\partial Y_0) \subset_{=} \partial Y_0$ denotes the union of the sets $\omega(u)$ over $u \in \partial Y_0$.

Definition 2. The set $\omega(\partial Y_0)$ is said to be isolated if it has a covering $M = \cup_{k=1}^{N} M_k$ of pairwise disjoint sets M_k wich are isolated and invariant with respect to the flow or the semi-flow both on ∂Y_0 and on $Y = Y_0 \cup \partial Y_0$, ($M$ is called an isolated covering).

The set $\omega(\partial Y_0)$ is said to be acyclic if there exists an isolated covering $\cup_{k=1}^{N} M_k$ such that no subset of $\{M_k\}$ is a cycle.

Theorem 2. *Suppose that a semiflow on Y leaves both Y_0 and ∂Y_0 forward invariant, maps bounded sets in Y to precompact set for $t > 0$, and it is dissipative. If in addition:*

(i) $\omega(\partial Y_0)$ is isolated and acyclic,

(ii) $W^s(M_k) \cap Y_0 = \emptyset$ for all k, where $\cup_{k=1}^{N} M_k$ is the isolated covering used in the definition of acyclicity of ∂Y_0, then the semiflow is permanent, (W^s denotes the stable manifold).

Theorem 3. *Let us assume the following condition:*

$$ae_2 < e_1 \tag{4}$$

Then, system (2) is permanent.

Proof. If we take Y_0 to be the positive quadrant, then $\omega(\partial Y_0)$ consists of the equilibra $(0,0), (1,0)$ and $(0, e_2)$.

$(0,0)$ is an unstable node;$(1,0)$ is a saddle point, its stable manifold is x-axis and its unstable manifold is y-axis; and if $ae_2 < e_1, (0, e_2)$ is a saddle point stable along the y-axis and unstable along the x-axis.

All trajectories on the x-axis other than $(0,0)$ approach $(1,0)$ and all trajectories on the y-axis other than $(0,0)$ approach $(0, e_2)$.

It follows from these structural features that the in ∂Y_0 is acyclic. So $\omega(\partial Y_0)$ is isolated and acyclic. The stable manifold of $(1,0)$ is the x-axis and the stable manifold of $(0, e_2)$ is the y-axis, and we know, from theorem 1, that these stable manifolds cannot intersect the interior of Y_0. In that case, theorem 2 implies permanence.

Theorem 4. *If (4) holds, then system (2) has a unique interior equilibrium $E^*(x^*, y^*)$.*

Proof. It is straight'forward to show that system (2) has only one interior equilibrium point. Indeed, from system (2), such a point satisfies,

$$(1 - x^*)(x^* + e_1) = ay^*. \tag{5}$$

Therefore, the coordinates of the interior equilibrium are,

$$x^* = x_+^* = \frac{1}{2}(1 - (a + e_1) + \triangle^{\frac{1}{2}}), \tag{6}$$

$$y^* = x^* + e_2. \tag{7}$$

where $\triangle = (a + e_1 - 1)^2 - 4(ae_2 - e_1)$.

It is easy to verify that this fixed point belongs to $\mathcal{A}$. From system (2), we get : $\det J(x^*, y^*) = \frac{bx^*}{x^*+e_1}(2x^*+a+e_1-1)$, since $x^* = \frac{1}{2}\left[1-(a+e_1)+\triangle^{\frac{1}{2}}\right]$, we have $x^* > \frac{1}{2}[1-(a+e_1)]$, hence $\det J(x^*, y^*) > 0$; and $\mathrm{tr} J(x^*, y^*) = -\frac{1}{x^*+e_1}(2x^{*2} + (b+e_1-1)x^* + be_1)$. Let

$$P(x) = 2x^2 + (b+e_1-1)x + be_1, \tag{8}$$

by Routh-Hurwitz's criteria, we get the following lemma:

Lemma 1. *The equilibrium $E^*(x^*, y^*)$ is locally asymptotically stable if $P(x^*) > 0$ and it is an unstable focus if $P(x^*) < 0$.*

It is obvious that if $b+e_1 \geq 1$ or if $b+e_1 < 1$ and $(1-(b+e_1))^2 - 8be_1 < 0$, then $P(x) > 0$, and if $b+e_1 < 1$ and $(1-(b+e_1))^2 - 8be_1 > 0$, then $P(x)$ has two positive roots $0 < \alpha_1 < \alpha_2 < 1$ with,

$$\alpha_{1,2} = \frac{1-(b+e_1) \mp \triangle^{\frac{1}{2}}}{4} \quad \text{where } \triangle = (1-(b+e_1))^2 - 8be_1 \tag{9}$$

Moreover, $P(x) > 0$ if $0 < x < \alpha_1$ or $\alpha_2 < x < 1$, and $P(x) < 0$ if $\alpha_1 < x < \alpha_2$. Thus, we obtain the following result:

Lemma 2. *(a) If $b+e_1 \geq 1$, or $0 < x^* < \alpha_1$ or $\alpha_2 < x^* < 1$, then $E^*(x^*, y^*)$ is asymptotically stable. (b) If $\alpha_1 < x^* < \alpha_2$, then $E^*(x^*, y^*)$ is unstable.*

Now we will prove that, under some assumptions, this steady state is globaly asymptotically stable.

Theorem 5. *If $e_1 \geq 1$, then the interior equilibrium $E^*(x^*, y^*)$ is globally assymptotically stable*

Proof. The proof is based on a positive definite Lyapunov function. Let

$$V(x,y) = \int_{x^*}^{x} \frac{\zeta - x^*}{(\zeta+e_2)p(\zeta)} d\zeta + \frac{x^*+e_2}{by^*} \int_{y^*}^{y} \frac{\eta - y^*}{\eta} d\eta.$$

This function is defined and continuous on $Int(\mathbb{R}_+^2)$. It can be easily verifed that the function $V(x,y)$ is zero at the equilibrium (x^*, y^*) and is positive for all positive values of x and y, and thus $E^*(x^*, y^*)$ is global minimum of V. Since the solutions of the system are bounded and ultimately enter the set A, we restrict the study for this set. The time derivate of V along the solutions of system (2) is:

$$\begin{aligned} \frac{dV}{dt} &= \frac{x-x^*}{(x+e_2)p(x)}\left[xg(x) - p(x)y\right] + \frac{x^*+e_2}{by^*}\frac{y-y^*}{y} by(1-\frac{y}{x+e_2}) \\ &= \frac{x-x^*}{x+e_2}\left[\frac{xg(x)}{p(x)} - y\right] + \frac{x^*+e_2}{y^*}(y-y^*)(1-\frac{y}{x+e_2}). \end{aligned}$$

Since $y^* = x^* + e_2$

$$\begin{aligned}\frac{dV}{dt} &= \frac{x-x^*}{x+e_2}\left[\frac{xg(x)}{p(x)} - y^*\right] - \frac{(x-x^*)(y-y^*)}{x+e_2} + \frac{x^*+e_2}{y^*}(y-y^*)(\frac{y^*}{x^*+e_2} - \frac{y}{x+e_2}) \\ &= \frac{x-x^*}{x+e_2}\left[\frac{x(1-x)(x+e_1)}{ax} - y^*\right] - \frac{(x-x^*)(y-y^*)}{x+e_2} \\ &+ \frac{x^*+e_2}{y^*}(y-y^*)(\frac{xy^*-yx^*+e_2(y^*-y)}{(x+e_2)(x^*+e_2)}) \\ &= \frac{x-x^*}{a(x+e_2)}((1-x)(x+e_1) - ay^*) - \frac{(x-x^*)(y-y^*)}{x+e_2} \\ &+ \frac{y-y^*}{y^*}(\frac{y^*(x-x^*)-x^*(y-y^*)-e_2(y-y^*)}{(x+e_2)})\end{aligned}$$

Using eq. (5), we get:

$$\begin{aligned}\frac{dV}{dt} &= \frac{x-x^*}{a(x+e_2)}((1-x)(x+e_1) - (1-x^*)(x+e_1)) - \frac{(x-x^*)(y-y^*)}{x+e_2} \\ &+ \frac{y-y^*}{y^*}(\frac{y^*(x-x^*)-(x^*+e_2)(y-y^*)}{(x+e_2)}) \\ &= \frac{x-x^*}{a(x+e_2)}(x + e_1 - x^2 - e_1x - x^* - e_1 + {x^*}^2 + e_1x^*) - \frac{(x^*+e_2)(y-y^*)^2}{y^*(x+e_2)} \\ &= \frac{x-x^*}{a(x+e_2)}(x - x^* - e_1(x-x^*) - (x-x^*)(x+x^*)) - \frac{(x^*+e_2)}{y^*(x+e_2)}(y-y^*)^2 \\ &= \frac{1}{a(x+e_2)}(1 - e_1 - x - x^*)(x-x^*)^2 - \frac{(x^*+e_2)}{y^*(x+e_2)}(y-y^*)^2 \\ &= -(x + x^* + e_1 - 1)\frac{1}{a(x+e_2)}(x-x^*)^2 - \frac{(x^*+e_2)}{y^*(x+e_2)}(y-y^*)^2.\end{aligned}$$

It follows that , if $e_1 \geq 1$, then $\frac{dV}{dt} < 0$ along all trajectories in the first quadrant, except (x^*, y^*), so that $E^*(x^*, y^*)$ is globally assymptotically stable.

3 Limit cycle

To prove that the system has no limit cycle, we will use the Dulac's criterion, see [6]. We also will establish conditions under which system (2) has a limit cycle.

Theorem 6. *Let $D \subseteq \mathbb{R}^2$ be a simply connected open set and $B(x, y)$ be a real-valued C^1 function in D.*

If the function $divBf = \frac{\partial(Bf_1)}{\partial x} + \frac{\partial(Bf_2)}{\partial y}$ is of constant sign and not identically zero in D, then $\frac{dX}{dt} = f(X)$ has no periodic orbit lying entirely in the region D.

Theorem 7. *If $b + e_1 \geq 1$, then the system (2) has no limit cycle.*

Proof. Let $B(x, y) = (\frac{x+e_1}{ax})\frac{1}{y^2}$, $x > 0$, $y > 0$.

We get $divBf = B(\frac{\partial f_1}{\partial x} + \frac{\partial f_2}{\partial y}) + f_1\frac{\partial B}{\partial x} + f_2\frac{\partial B}{\partial y}$, we have:

$$\frac{\partial f_1}{\partial x} = 1 - 2x - \frac{ae_1y}{(x+e_1)^2} \quad \text{and} \quad \frac{\partial f_2}{\partial y} = b(1 - \frac{2y}{x+e_2})$$

$$\frac{\partial B}{\partial x} = -\frac{e_1}{ax^2y^2} \quad \text{and} \quad \frac{\partial B}{\partial y} = -\frac{2}{y^3}(\frac{x+e_1}{ax}).$$

Thus, after some simple algebraic computations, we get,

$$divBf = \frac{B(x,y)}{x+e_1}(-(2x^2 + (b+e_1-1)x + be_1)).$$

It is obvious that, if $b + e_1 \geq 1$, then $divBf$ has a constant sign. By Dulac's criterion, we conclude that system (2) has no limit cycles under this assumption.

With the following theorem, see [5], we can, under some assumptions, establish the existence of at least one limit cycle for system (2).

Theorem 8. *Suppose that* $\frac{dx}{dt} = f(x)$ *is a planar system with a finite number of equilibrium points. If the positive orbit* $\delta^+(x_0)$ *of* x_0 *is bounded, then one of the following is true:*

(i) the ω*-limit set* $\omega(x_0)$ *is a single point* $\overline{x}$ *wich is an equilibrium point and* $\delta^+(t, x_0) \to \overline{x}$ *as* $t \to +\infty$,

(ii) $\omega(x_0)$ *is a periodic orbit* Γ *and either* $\delta^+(x_0) = \omega(x_0) = \Gamma$ *or else* $\delta^+(x_0)$ *spirals with increasing time toward* Γ *on one side of* Γ,

(iii) $\omega(x_0)$ *consists of equilibrium points and orbits whose* $\alpha-$*limit and* $\omega-$*limit sets are the equilibrium points.*

Theorem 9. *If condition (4) holds,*

$$b + e_1 < 1, \tag{10}$$

and

$$\alpha_1 < x^* < \alpha_2, \tag{11}$$

(where $\alpha_{1,2}$ *are given by Eq.(9)), then system (2) has at least one limit cycle.*

Proof. If $b + e_1 < 1$ and $\alpha_1 < x^* < \alpha_2$, then, by lemma 2, $E^*(x^*, y^*)$ is unstable.

By theorem 3, we saw that if (4) holds, then system (2) is permanent. Permanence implies that system (2) has a compact attractor lying in the interior of the positive cone wich is globally attracting for positive solutions (the set A). So trajectories leaving the vicinity of (x^*, y^*) must have ω-limit sets in the attractor but distinct from (x^*, y^*) , because it is unstable. Now, by theorem 8, such ω-limit sets are periodic orbits. And hence system (2) has at least one limit cycle.

To study the uniqueness of limit cycle, we will transform system (2) to a Gause-Type model, see [8]. Let $z = yl(x)$, where $l(x) = \left(\frac{1-x}{x}\right)^b$. We obtain the following system,

$$\begin{cases} \dfrac{dx}{dt} = x(1-x) - \dfrac{ax}{x+e_1}\dfrac{z}{l(x)} = g(x) - \varphi(x)z \\ \dfrac{dz}{dt} = \dfrac{b}{l(x)(1-x)(x+e_1)(x+e_2)}(x + \dfrac{e_1 - ae_2}{x^*})(x-x^*)z^2 = \psi(x)z^2, \end{cases} \tag{12}$$

with $x(0) > 0$, $z(0) > 0$. Let $h(x) = \frac{g(x)}{\varphi(x)}$. We get $h(x) = \frac{(1-x)(x+e_1)l(x)}{a}$ and the following system,

$$\begin{cases} \frac{dx}{dt} = \varphi(x)(h(x) - z) = F(x, z) \\ \frac{dz}{dt} = \psi(x)z^2 = G(x, z). \end{cases} \tag{13}$$

Let us consider the prey isocline of (13), $z = h(x) = \frac{(1-x)(x+e_1)l(x)}{a}$. We have $h'(x) = -\frac{l(x)}{ax}P(x)$ where $P(x)$ is given by (8). If $b + e_1 < 1$ and $(1-(b+e_1))^2 - 8be_1 > 0$, then $h'(x) = -\frac{2l(x)}{ax}(x-\alpha_1)(x-\alpha_2)$. Thus the prey isocline $z = h(x)$ has two humps, a local maximum at $x = \alpha_2$ and a local minimum at $x = \alpha_1$. It is obvious that $h(1) = 0$, $\lim h(x) = +\infty$ as $x \to 0$, and $h'(x) > 0$ for $\alpha_1 < x < \alpha_2$. Thus, there exist x_1^*, x_2^* satisfying :

$$0 < x_1^* < \alpha_1, \alpha_2 < x_2^* < 1, \text{ and } h(x_1^*) = h(x_2^*) = h(x^*) = z^* \qquad (14)$$

We introduce $R(x) = b\int_{x^*}^{x} \frac{\zeta - x^*}{q(\zeta)} d\zeta$ where $q(x) = \frac{(x+e_2)(1-x)}{x + \frac{e_1 - ae_2}{x^*}}$. The following theorem proves the uniqueness of limit cycle, see [9].

Theorem 10. *Let $\alpha_1 < x^* < \alpha_2$.*
If $R(x_1^*) \geq R(x_2^*)$ then the (2) has a unique limit cycle.

This theorem is proved thanks to the following lemmas in wich we use the below notations. We will prove the first lemma, proofs of the others can be found in [9].
$\Omega_1 = [0, \alpha_1] \times \mathbb{R}^+$ $\Omega_2 = [\alpha_1, \alpha_2] \times \mathbb{R}^+$ and $\Omega_3 = [\alpha_2, 1] \times \mathbb{R}^+$; $h_1 : (0, \alpha_1) \to \mathbb{R}$, $h_2 : [\alpha_1, \alpha_2] \to \mathbb{R}$, $h_3 : [\alpha_2, 1] \to \mathbb{R}$, by $h_i(x) = h(x)$ for $i = 1, 2, 3$.
We denote Γ to be a periodic orbit of (13) with period T,
$\Gamma = \{(x(t), z(t)) : 0 \leq t < T\}$, and $\Omega(\Gamma)$ to be the region enclosed by Γ in xz phase plane ;
$x_m = x_m(t) = \min\{x(t); 0 \leq t \leq T\}$ $x_M = x_M(t) = \max\{x(t); 0 \leq t \leq T\}$ and $I(\Gamma) = [x_m, x_M]$.

Lemma 3. *Let $\alpha_1 < x^* < \alpha_2$. Then $\frac{d}{dx}\left[\frac{\varphi(x)h'(x)}{\psi(x)h(x)}\right] < 0$ for $x \in [\alpha_1, x^*) \cup [\alpha_2, 1]$.*

Proof. From (13) and since $h'(x) = -\frac{2l(x)}{ax}(x-\alpha_1)(x-\alpha_2)$, we have : $\varphi(x)h'(x) = -\frac{2(x-\alpha_1)(x-\alpha_2)}{x+e_1}$ and $\psi'(x)h(x) = \frac{b}{a(x+e_1)}(x-x^*)(x+\frac{e_1-ae_2}{x^*})$. Let $Q(x) = \frac{(x+e_2)(x-\alpha_1)}{(x+e_1)(x+\frac{e_1-ae_2}{x^*})}$, then,
$\frac{\varphi(x)h'(x)}{\psi(x)h(x)} = -\frac{2(x-\alpha_1)(x-\alpha_2)}{x+e_1}\frac{a(x+e_2)}{b(x-x^*)(x+\frac{e_1-ae_2}{x^*})} = -\frac{2a}{b}Q(x)\frac{x-\alpha_2}{x-x^*}$
and $\frac{d}{dx}\left[\frac{\varphi(x)h'(x)}{\psi(x)h(x)}\right] = -\frac{2a}{b}\left[Q'(x)\frac{x-\alpha_2}{x-x^*} + Q(x)\frac{\alpha_2 - x^*}{(x-x^*)^2}\right]$.
Since $Q(x)$ is increasing on $(\alpha_1, 1)$, then from the above identity we complete the proof of this lemma.

Lemma 4. *(i)* $\int\int_{\Omega(\Gamma)} \frac{h'(x)}{z^2} dxdz = 0$
(ii) $I(\Gamma)$ is not contained in $[x_1^*, x_2^*]$ where x_1^*, x_2^* are defined in (14).

Lemma 5. *If Int* $I(\Gamma) \supseteq [x_1^*, x_2^*]$, *then* Γ *is orbitally asymptotically stable.*

Lemma 6. *If* $\alpha_1 \leq x_m$, *then* Γ *is orbitally asymptotically stable.*

Lemma 7. *If* $x_1^* \leq x_m < \alpha_1$, *then* Γ *is orbitally asymptotically stable.*

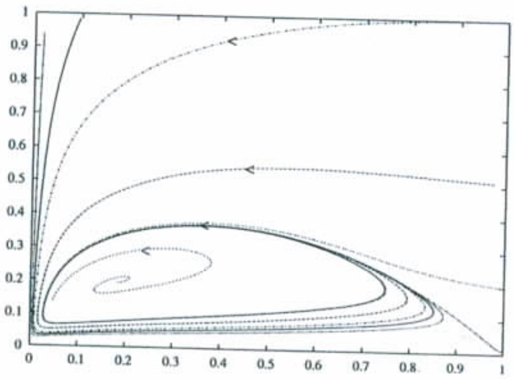

Fig. 1. Phase portrait of system (2), for the parameters $a = 1.1$, $b = 0.2$, $e_1 = 0.08$ and $e_2 = 0.01$. A unique limit cycle exists.

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