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A predator-prey system with Holling-type functional response

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25 In (H1) the value k is interpreted as the carrying capacity of the prey species in
 26 the absence of the predators. The system (1.1) admits two boundary equilibrium
 27 points, $E_0 = (0, 0)$ and $E_1 = (k, 0)$. It follows from (H2) that there is a unique x^*
 28 such that $0 < x^* < k$ and $g(x^*) = D/\mu$. The predator isocline in the positive cone,
 29 i.e., the curve determined by the equation $\mu g(x) - D = 0$, is a vertical line $x = x^*$.
 30 Meanwhile, the prey isocline is the graph of the function $y = \varphi(x)$ where

$$(1.2) \quad \varphi(x) = \frac{xf(x)}{g(x)}.$$

31 It is easy to see that $\varphi(k) = 0$ and $\varphi(x) > 0$ for $0 < x < k$. The value of $\varphi(0)$
 32 depends on additional properties on g near the origin. The intersection point of
 33 the isoclines, $E^* = (x^*, y^*)$ with $y^* = \varphi(x^*)$, is the only positive equilibrium point
 34 of system (1.1).

35 Since g is not assumed to be smooth at 0, E_0 is not a hyperbolic equilibrium.
 36 Using linear stability analysis (Jacobian) it is easy to see that E_1 is always a saddle
 37 point, while E^* can be a stable or unstable focus or node depending on the sign
 38 of $\varphi'(x^*)$, where φ is defined by (1.2). For $\varphi'(x^*) < 0$, E^* is an attractor. For
 39 $\varphi'(x^*) > 0$, E^* is a repeller.

40 A prototype of $f(x)$ and $g(x)$ in (1.1) is given by the logistic growth and the
 41 Holling functional response, see [12, 13],

$$(1.3) \quad f(x) = r \left(1 - \frac{x}{k}\right), \quad g(x) = \frac{x^p}{a + x^p},$$

42 where r , k , a and p are positive parameters (p is not always an integer). In this
 43 case, if $0 < p < 1$, the function $x \mapsto g(x)$ is not smooth at $x = 0$. Using numerical
 44 simulations, it was observed in [2] that, if $0 < p < 1$, some results of [12, 13] on
 45 the existence of a limit cycle or on the global stability of the positive equilibrium,
 46 are not true. We show in this paper why the classical arguments of dynamical
 47 systems do not apply, and why the results on existence and uniqueness of limit
 48 cycle, together with the result on global attractivity of the positive equilibrium or
 49 the limit cycle obtained in [12, 13] are not true when $0 < p < 1$.

50 Liu [9] considered the system (1.1). This author did not required the smoothness
 51 of $g(x)$ at $x = 0$, because (see the lines following Hypothesis (H2) in [9]), in some
 52 models it may happen that

$$(1.4) \quad g'(0^+) := \lim_{x \rightarrow 0^+} \frac{g(x)}{x} = +\infty.$$

53 For instance, for Holling functions (1.3) with $0 < p < 1$, (1.4) holds.

54 The purpose of this paper is to consider the case where $g(x)$ is not smooth at
 55 $x = 0$ and to study the global asymptotic stability of the positive equilibrium
 56 point (when it is locally exponentially stable), and also to study the existence of
 57 limit cycles (when the positive equilibrium is unstable) and the orbital asymptotic
 58 stability, and hence uniqueness, of the limit cycle (when the limit cycle exists).

59 The paper is organized as follows. In the next section we give a condition on
 60 the response function g , which is satisfied by the Holling function (1.3), with $0 <$
 61 $p < 1$, such that all points of the positive y -axis are points of non-uniqueness of
 62 the solutions of (1.1), that is to say the Cauchy problem (1.1) and the conditions
 63 $x(0) = 0$, $y(0) > 0$ has not only the trivial solution $x(t) \equiv 0$, but also has solutions
 64 satisfying $x(t) > 0$ for some $t < 0$. In Section 3 we discuss the global results on
 65 (1.1) and we describe the basin of attraction of the limit cycle, if it exists, and the

66 basin of attraction of the positive equilibrium point, when it is a local attractor. In
 67 Section 4 we apply our results to the system (1.1) where f and g are given by (1.3)
 68 and we correct some of the results in the existing literature which asserted that the
 69 system has a unique limit cycle (which is hence globally attracting), if and only if
 70 the positive equilibrium is a repeller, and that the positive equilibrium is globally
 71 attracting if and only if it is a local attractor. Some complements and technical
 72 proofs are given in the appendix.

73 2. NON UNIQUENESS OF SOLUTIONS

74 The function $g(x)$ is assumed to satisfy the following hypothesis.

75 (H3) $g(x)$ is not smooth for $x = 0$, (1.4) holds and the integral $\int_{\varepsilon}^{\alpha} \frac{dx}{g(x)}$ converges
 76 as $\varepsilon \rightarrow 0$, where $\alpha > 0$ is fixed.

77 It follows from (1.4) that $\varphi(0) = 0$. The condition on the convergence of the
 78 integral in (H3) is a technical condition that will be useful for the proofs presented in
 79 this paper. For instance, for Holling functions (1.3) with $0 < p < 1$, (H2) and (H3)
 80 hold. However, it should be noticed that (1.4) does not imply that the improper
 81 integral $\int_{\varepsilon}^{\alpha} \frac{dx}{g(x)}$ converges. For instance if function g is equivalent to $-x \ln(x)$ near
 82 0, then (1.4) holds and the improper integral does not converge.

83 Let x_0 be such that $0 < x_0 < x^*$. Let $(X(t, x_0), Y(t, x_0))$ be the solution of (1.1)
 84 with initial condition $(x_0, \varphi(x_0))$. As long as $x^* > x > 0$ and $y > \varphi(x)$, the solution
 85 $(X(t, x_0), Y(t, x_0))$ can be parametrized by x , that is to say its orbit is the graph
 86 of a function of x :

$$(2.1) \quad y = \eta(x, x_0), \text{ for } x_0 \leq x \leq x^*.$$

87 Our aim is to show that the limit of these orbits (2.1) exists when $x_0 \rightarrow 0$ and is a
 88 positive orbit. If the equilibrium point E_0 was hyperbolic, then the limit of orbits
 89 (2.1) is simply the y -axis, which is the stable separatrix of E_0 . However, under
 90 hypothesis (H3) all points $(0, y_0)$, with $y_0 > 0$ are non uniqueness points and some
 91 solutions with initial conditions $x(0) > 0$, $y(0) > 0$ can reach in finite time the
 92 y -axis at some point $(0, y_0)$ after with y decreases to 0. Therefore the orbits (2.1)
 93 are bounded above, so that their limit exists and is a positive orbit.

94 More precisely, we consider the initial value problem

$$(2.2) \quad \begin{aligned} \dot{x} &= xf(x) - yg(x), & x(0) &= 0, \\ \dot{y} &= y(\mu g(x) - D), & y(0) &= y_0. \end{aligned}$$

95 Besides the trivial solution $(x(t) = 0, y(t) = y_0 e^{-Dt})$, the initial value problem (2.2)
 96 admits nontrivial positive solutions $(x_1(t), y_1(t))$, where $x_1(t)$ is not identically 0,
 97 which tends also to E_0 as $t \rightarrow +\infty$, as shown in the following result.

98 **Theorem 2.1.** *For any $y_0 > 0$, $(0, y_0)$ is a non uniqueness point for (2.2). The*
 99 *system admits a maximal solution $(X_1(t, y_0), Y_1(t, y_0))$ satisfying*

- 100 (1) $X_1(t, y_0) > 0$ and $Y_1(t, y_0) > 0$ for $t < 0$.
 101 (2) $X_1(t, y_0) = 0$ and $Y_1(t, y_0) = y_0 e^{-Dt}$ for $t \geq 0$.

102 *Proof.* The concept of maximal solution used in this theorem should not be con-
 103 fused with the usual concept of *maximal solution*, defined on a maximal interval
 104 of definition. Here the solution is said to be *maximal* in the sense that it is the
 105 solution $(X_1(t), Y_1(t))$ of the initial value problem (2.2), which is non trivial (i.e.

106 $X_1(t) > 0$), on the maximal possible interval, that is to say for all $t < 0$. The
 107 details of the proof is given in Appendix B. \square

108 As long as $0 < x < x^*$ and $y > \varphi(x)$, the solution $(X_1(t, y_0), Y_1(t, y_0))$ can be
 109 parametrized by x , that is to say, its orbit is the graph of a function of x :

$$(2.3) \quad y = \eta_1(x, y_0), \text{ for } 0 \leq x \leq x^*.$$

Hence, we have the following inequalities, see Fig. 1(a):

$$\varphi(x) < \eta(x, x_0) < \eta_1(x, y_0), \text{ for } x_0 > 0, y_0 > 0 \text{ and } x_0 \leq x \leq x^*.$$

Therefore the following limits

$$w(x) = \lim_{x_0 \rightarrow 0} \eta(x, x_0) = \sup_{0 < x_0 < x^*} \eta(x, x_0),$$

$$w_1(x) = \lim_{y_0 \rightarrow 0} \eta_1(x, y_0) = \inf_{y_0 > 0} \eta_1(x, y_0),$$

110 exit and satisfy $\varphi(x) < w(x) \leq w_1(x)$, for $0 < x < x^*$, see Fig. 1(a). Since the
 111 graphs of functions $y = w(x)$ and $y = w_1(x)$ are limits, when $x_0 \rightarrow 0$ and $y_0 \rightarrow 0$
 112 respectively, of orbits of (1.1), they themselves are orbits of (1.1). We denote by
 113 $W^s(E_0)$ and $W_1^s(E_0)$ the global orbits corresponding to the local orbits $y = w(x)$
 114 and $y = w_1(x)$ respectively, see Fig. 1(b).

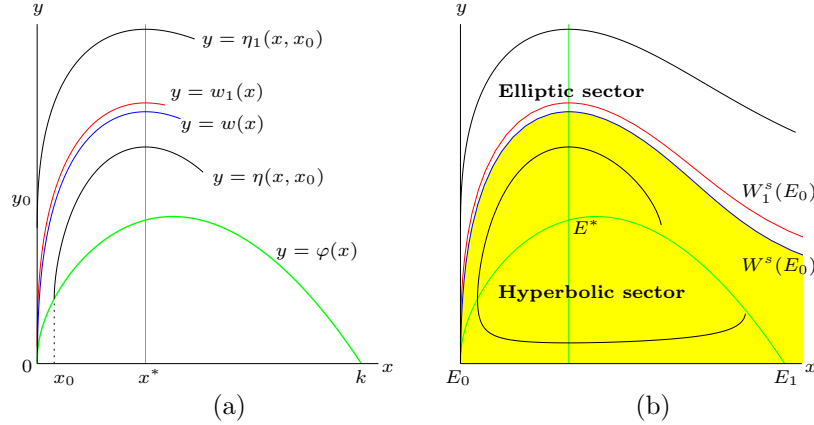


FIGURE 1. (a): The definitions of the local orbits $y = w(x)$ (colored in blue) and $y = w_1(x)$ (colored in red). (b): The global corresponding orbits $W^s(E_0)$ (colored in blue) and $W_1^s(E_0)$ (colored in red) and the elliptic sector, above $W^s(E_0)$, and hyperbolic sector, below $W^s(E_0)$ (colored in yellow), of E_0 .

115 *Remark 2.2.* Although the origin E_0 is not a hyperbolic singular point, we use the
 116 notations $W^s(E_0)$ and $W_1^s(E_0)$ since the solutions corresponding to these orbits
 117 tend to E_0 as $t \rightarrow +\infty$. The description of the behavior of the system near E_0 is as
 118 follows: The region between $W^s(E_0)$ and the x -axis is a hyperbolic sector and the
 119 region between $W^s(E_0)$ and the y -axis is an elliptic sector, see Fig. 1(b). Orbits
 120 who are between $W^s(E_0)$ and $W_1^s(E_0)$ tend toward E_0 when $t \rightarrow +\infty$ and those
 121 who are between the y axis and $W_1^s(E_0)$ reach the y axis in finite time and then,
 122 go toward the origin when $t \rightarrow +\infty$.

123

3. GLOBAL BEHAVIOUR

124 Assume that E^* is a repeller, that is to say $\varphi'(x^*) > 0$. If g were smooth at 0,
 125 then the system would necessarily have a limit cycle surrounding E^* . The existence
 126 of a limit cycle results from the Poincaré-Bendixson Theorem and the fact that E_0 is
 127 a saddle point, see Appendix A. Is this limit cycle globally orbitally asymptotically
 128 stable (GOAS) ? If the system has at most one cycle, then this cycle is necessarily
 129 GOAS.

130 Assume that E^* is an attractor, that is to say $\varphi'(x^*) < 0$. Is E^* globally
 131 asymptotically stable (GAS) ? In the case where g is smooth at 0, if a solution with
 132 positive initial condition does not converge toward E^* , then, from the Poincaré-
 133 Bendixson Theorem and the fact that E_0 is a saddle point, it must converge toward
 134 a limit cycle, see Appendix A. If the system cannot have a cycle, then E^* is
 135 necessarily GAS.

136 In both cases the argument that the system has a limit cycle that must surround
 137 E^* uses the fact that E_0 is a saddle point, which does not hold when g is not
 138 smooth at 0, as shown in the preceding section, see Remark 2.2. In the case where
 139 hypothesis (H3) holds, E_0 is not a saddle point and the Poincaré-Bendixson theorem
 140 is inapplicable. In this case, the description of the global behavior of the system is
 141 obtained by considering the relative position of the orbit $W^s(E_0)$ with respect to
 142 the unstable separatrix $W^u(E_1)$ of the saddle point E_1 .

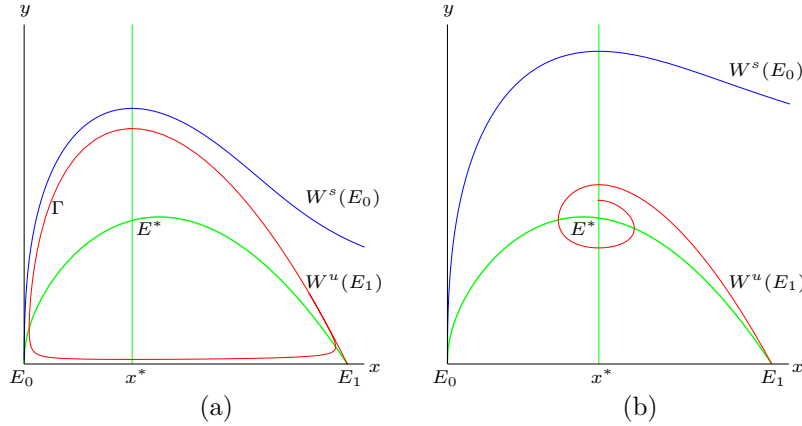


FIGURE 2. $W^s(E_0)$ (in blue) is above $W^u(E_1)$ (in red). The iso-
 clines $\dot{x} = 0$ and $\dot{y} = 0$ are represented in green. (a): E^* is a
 repeller; (b): E^* is an attractor.

143 **3.1. The case where $W^s(E_0)$ is above $W^u(E_1)$.** We have the following result

144 **Proposition 3.1.** *Assume that $W^s(E_0)$ is above $W^u(E_1)$. If E^* is a repeller,*
 145 *then it is surrounded by at least one limit cycle. If the system can have at most one*
 146 *cycle, then E^* is surrounded by a unique limit cycle which is orbitally asymptotically*
 147 *stable. This limit cycle is not GOAS, even if it is unique. If E^* is an attractor and*
 148 *if the system has no cycles, then all orbits below $W^s(E_0)$ converge towards E^* . E^**
 149 *is not GAS, even if it is not surrounded by any unstable limit cycle.*

150 *Proof.* Assume that E^* is a repeller. The orbit $W^u(E_1)$ lies in the hyperbolic
 151 sector. Therefore, its ω -limit set is a limit cycle Γ surrounding E^* . This limit
 152 cycle is attracting at least on its exterior, see Fig. 2(a). Since E^* is repelling, it is
 153 surrounded also by a limit cycle Γ_1 which is attracting at least on its interior. If
 154 the system can have at most one cycle then $\Gamma_1 = \Gamma$. Therefore a limit cycle exists
 155 but it is not GOAS: all orbits above $W^s(E_0)$ converge toward E_0 and all positive
 156 orbits below $W^s(E_0)$, excepted for E^* , converge toward the limit cycle Γ .

157 Assume that E^* is an attractor. The orbit $W^u(E_1)$ lies in the hyperbolic
 158 sector. Therefore, its ω -limit set, if it does not contain E^* , is necessarily a limit cycle
 159 surrounding E^* . If the system cannot have a cycle then the limit set of $W^u(E_1)$
 160 is equal to E^* . Therefore E^* is not GAS since: all orbits above $W^s(E_0)$ converge
 161 toward E_0 and all positive orbits below $W^s(E_0)$ converge toward E^* , see Fig.
 162 2(b). \square

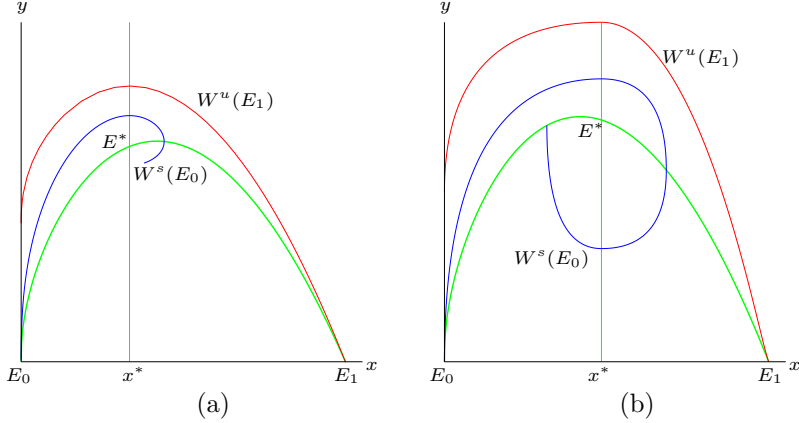


FIGURE 3. $W^s(E_0)$ (in blue) is below $W^u(E_1)$ (in red). The iso-
 clinics $\dot{x} = 0$ and $\dot{y} = 0$ are represented in green. (a): E^* is a
 repeller; (b): E^* is an attractor.

163 **3.2. The case where $W^s(E_0)$ is below $W^u(E_1)$.** We have the following result

164 **Proposition 3.2.** *Assume that $W^s(E_0)$ is below $W^u(E_1)$. If E^* is a repeller and*
 165 *assuming that the system can have at most one cycle and, if it exists, this cycle*
 166 *cannot be semi-stable (i.e stable on one side and unstable in another side), then all*
 167 *positive orbits, excepted for E^* , converge toward E_0 . If E^* is an attractor then it*
 168 *is surrounded by an unstable limit cycle.*

169 *Proof.* Assume that E^* is a repeller. The orbit $W^s(E_0)$ lies in the hyperbolic
 170 sector. Therefore, its α -limit set, if it does not contain E^* , is necessarily a limit cycle Γ
 171 surrounding E^* . This limit cycle is repelling on its exterior. Since E^* is repelling,
 172 it is surrounded also by a limit cycle Γ_1 which is attracting on its interior. Since
 173 the system can have at most one cycle, $\Gamma_1 = \Gamma$. Therefore Γ is attracting on one
 174 side and repelling on the other side. Since this situation is impossible, the α -limit
 175 set of $W^s(E_0)$ is equal to E^* . Therefore no limit cycle can exist and all positive
 176 solutions, excepted for E^* , converge toward E_0 .

177 Assume that E^* is an attractor. The orbit $W^s(E_0)$ lies in the hyperbolic sector.
 178 Therefore, its α -limit set is necessarily a limit cycle Γ surrounding E^* . This limit
 179 cycle is repelling on its exterior. \square

180 The first case of the proposition (E^* is a repeller) is depicted in Fig.3(a). This
 181 case presents an unstable positive equilibrium, which is not surrounded by a cycle.
 182 The second case of the proposition (E^* is an attractor) is depicted in Fig. 3(b). If
 183 the system cannot have a cycle then the situation where E^* is an attractor and in
 184 the same time $W^s(E_0)$ is below $W^u(E_1)$ cannot hold.

185 4. APPLICATIONS

186 The purpose of this section is to clarify the necessary and sufficient conditions
 187 for the existence and uniqueness of limit cycles of the predator-prey system (1.1),
 188 where f and g are given by (1.3), with $0 < p < 1$. The system is written

$$(4.1) \quad \begin{aligned} \dot{x} &= rx \left(1 - \frac{x}{k}\right) - \frac{x^p y}{a + x^p}, \\ \dot{y} &= y \left(\frac{\mu x^p}{a + x^p} - D\right). \end{aligned}$$

189 The condition $\mu g(k) > D$ in (H2) is equivalent to $k > x^*$, where x^* is defined by
 190 $g(x^*) = D/\mu$, that is to say

$$(4.2) \quad \mu > D, \quad k > x^* := \left(\frac{aD}{\mu - D}\right)^{\frac{1}{p}}.$$

191 Hence functions f and g satisfy the hypotheses (H1), (H2) and (H3) if and only if
 192 $0 < p < 1$ and (4.2) is satisfied. Therefore the results in Propositions 3.1 and 3.2,
 193 have the corollary that if E^* is a repeller, the system does not always have a limit
 194 cycle, and if E^* is a attractor, it is not GAS.

195 **4.1. Existence of a limit cycle.** Sugie, Kohno and Miyazaki have stated (see
 196 Theorem 2.1 in [13]) that if

$$(4.3) \quad (pD - (p-1)\mu)k > (pD - (p-2)\mu)x^*,$$

197 then the system (4.1) has a unique limit cycle. Owing the the non uniqueness of
 198 the solution, this claim is not true. We have the following result:

199 **Proposition 4.1.** *Assume that (4.2) and (4.3) hold. Then, if $W^s(E_0)$ is above*
 200 *$W^u(E_1)$, the system (4.1) has a unique limit cycle whose basin of attraction is the*
 201 *positive region of the plane located below $W^s(E_0)$. If $W^s(E_0)$ is below $W^u(E_1)$, the*
 202 *system (4.1) has no limit cycle and all positive solutions, excepted for E^* converge*
 203 *toward E_0 .*

204 *Proof.* One can check that the condition (4.3) is equivalent to $\varphi'(x^*) > 0$. Therefore
 205 E^* is a repeller and it can be surrounded by a limit cycle. However, this limit cycle
 206 is not GOAS since it cannot attract the orbits above $W^s(E_0)$. Actually, if it exists,
 207 the limit cycle attracts all the orbits below $W^s(E_0)$. Using the result of [13] that,
 208 in this case, the system can have at most one limit cycle, we obtain as a corollary
 209 of Proposition 3.1 that if $W^s(E_0)$ is above $W^u(E_1)$, then the system has a unique
 210 limit cycle. On the other hand, using Proposition 3.2 we obtain that if $W^s(E_0)$ is
 211 below $W^u(E_1)$, then the system has no cycle and all positive solutions are attracted
 212 by E_0 . \square

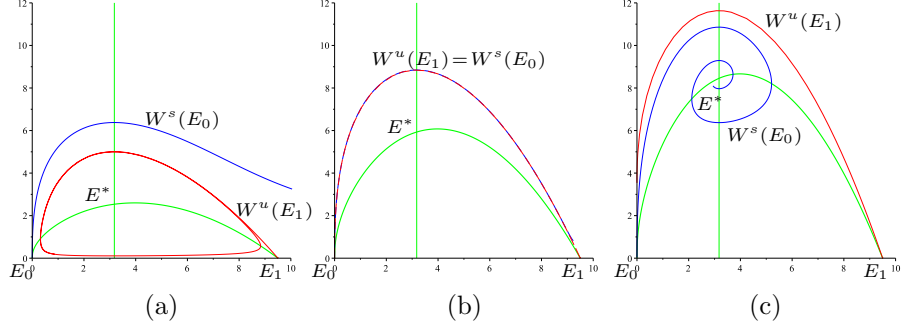


FIGURE 4. The relative positions of $W^s(E_0)$ and $W^u(E_1)$ for (4.1) when the parameter values are $k = 9.5$, $a = 2$, $p = 0.6$, $\mu = 2$, $D = 1$ and (a): $r = 0.6$, (b): The heterocline bifurcation $W^s(E_0) = W^u(E_1)$ holds for $1.4026 < r < 1.4027$, (c): $r = 2$.

213 These results are illustrated in Fig. 4. The numerical simulations show that for
 214 the given values of the parameters, there exists a bifurcation value r_0 for which the
 215 heterocline bifurcation $W^s(E_0) = W^u(E_1)$ occurs: If $r < r_0$ then $W^s(E_0)$ is above
 216 $W^u(E_1)$ and the system has a unique limit cycle which is not GOAS; If $r > r_0$
 217 then $W^s(E_0)$ is below $W^u(E_1)$ and the system has no limit cycle, and the positive
 218 solutions are attracted by the origin.

219 **4.2. Global asymptotic stability of E^* .** Sugie and Katayama have stated (see
 220 Theorem 1.1 in [12]) that the positive equilibrium E^* is GAS if and only if

$$(4.4) \quad (pD - (p-1)\mu)k \leq (pD - (p-2)\mu)x^*.$$

221 Owing to the non uniqueness of the solution, this claim is not true. We have the
 222 following result:

223 **Proposition 4.2.** *Assume that (4.2) and (4.4) hold. Then $W^s(E_0)$ is above
 224 $W^u(E_1)$ and the basin of attraction of E^* is the positive region of the plane lo-
 225 cated below $W^s(E_0)$. Therefore E^* is not GAS.*

226 *Proof.* One can check that the condition (4.4) is equivalent to $\varphi'(x^*) \leq 0$. Therefore
 227 E^* is an attractor. However, it is not GAS since it cannot attract the orbits above
 228 $W^s(E_0)$. Actually, it attracts all the orbits below $W^s(E_0)$. Using the result of [9, 12]
 229 that, in this case the system has no cycle, we obtain as a corollary of Proposition
 230 3.2 that $W^s(E_0)$ is always above $W^u(E_1)$, that is to say, the situation depicted in
 231 Fig. 3 never occurs. Therefore, using Propositions 3.1 we obtain that E^* attracts
 232 all the orbits below $W^s(E_0)$. \square

233 These results are illustrated in Fig. 5, where it is shown that E^* is never GAS.

234 5. DISCUSSION

235 We have shown in this work that the differentiability of g at $x = 0$ could drastically
 236 affect the dynamics of (1.1). For instance, when $0 < p < 1$, and E^* is a
 237 repeller, the system (4.1) does not necessarily have a limit cycle. When $W^s(E_0)$ is
 238 above $W^u(E_1)$, the limit cycle exists. However, it is not GOAS. All solutions with
 239 initial conditions above $W^s(E_0)$ reach the y -axis in finite time. All solutions with
 240 initial conditions below $W^s(E_0)$ excepted the equilibrium point E^* converge to the

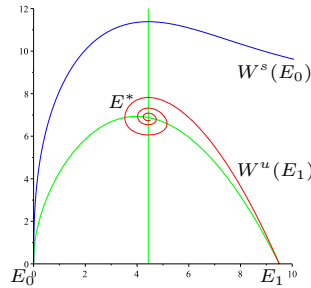


FIGURE 5. When E^* is an attractor, $W^s(E_0)$ is always above $W^u(E_1)$. The parameter values are the same as in Fig. 4, excepted that $D = 1.1$ and $r = 1.6$.

241 limit cycle. When $W^s(E_0)$ is below $W^u(E_1)$, the limit cycle does not exist. All
 242 solutions, excepted the equilibrium point E^* , reach the y -axis in finite time.

243 An heterocline bifurcation occurs when $W^s(E_0) = W^u(E_1)$ giving rise to a poly-
 244 cycle: all solutions with initial conditions outside the poly-cycle reach the y -axis in
 245 finite time. All solution with initial conditions inside the poly-cycle excepted the
 246 equilibrium E^* converge to the poly-cycle.

247 On the other hand, when $0 < p < 1$ and E^* is an attractor, it is not GAS. In
 248 this case $W^s(E_0)$ is always above $W^u(E_1)$, and the basin of attraction of E^* is the
 249 positive region below $W^s(E_0)$.

250 Our findings clarify some misunderstandings on the behaviour of this prey preda-
 251 tor model that appeared in the existing literature [12, 13]. It is not true that when
 252 $0 < p < 1$ the system admits a limit cycle as long as its positive equilibrium E^*
 253 is a repeller, nor that this limit cycle is globally attracting whenever it exists, nor
 254 that E^* is GAS, whenever it is an attractor.

255 In [12], the authors consider that the function $g(x) = \frac{x^p}{a+x^p}$ in (4.1) is of Holing
 256 type II if $p \leq 1$ and of Holing type III if $p > 1$. Actually the functional response
 257 belongs to Holling type III if $p > 1$, since its has an inflexion point and the func-
 258 tional response curve is sigmoid [5]. When $0 < p \leq 1$, the function g is strictly
 259 increasing, bounded and convex, although the case $0 < p < 1$ deserves special in-
 260 terest because of the singularity of g in 0. From a biological and ecological point of
 261 view, the functional response g with $0 < p < 1$, defines a class of prey and predator
 262 populations characterized by predators with a very high attack rate for very small
 263 densities prey and a need for a large amount of prey to reach satiety. This response
 264 function has the property that the prey can go extinct in finite time, which never
 265 happens when $p \geq 1$.

266 APPENDIX A. EXISTENCE OF LIMIT CYCLES WHEN g IS SMOOTH AT 0

267 Most of the classical works on (1.1) or (4.1) have employed the transforma-
 268 tion that converts the system into an equivalent generalized Liénard system. This
 269 method requires that $f(x)$ and $g(x)$ are sufficiently smooth so that existence,
 270 uniqueness, and continuation for all positive t are satisfied for initial-value prob-
 271 lems. For instance, the proof of the existence of a cycle, when g is smooth at 0,
 272 and the positive equilibrium is a repeller, needs the Poincaré-Bendixson Theorem

273 and the fact that E_0 is hyperbolic. However, since this proof is standard, it is often
 274 omitted in the existing literature by authors who attempted to extend the results
 275 to functions g which are not smooth at 0. This is precisely the point where these
 276 proofs are not correct.

277 For the convenience of the reader, we give here the details on the proof of the
 278 existence of a limit cycle, when the positive equilibrium point is a repeller and
 279 the function g is smooth at 0. The hypothesis of hyperbolicity of E_0 is crucial to
 280 applying the so-called Butler-MacGehee Theorem which we recall here and whose
 281 proof is given in [10].

282 **Theorem A.1.** (*Butler–MacGehee*). *If an omega (or alpha)-limit set ω contains a*
 283 *hyperbolic equilibrium point a , but it is not equal to $\{a\}$, then ω contains a point*
 284 *$b \neq a$ of the stable manifold $W^s(a)$, as well as a point $c \neq a$ of the unstable manifold*
 285 *$W^u(a)$.*

286 We have the following result

287 **Theorem A.2.** *Assume that (H1) and (H2) hold and in addition g is smooth at*
 288 *0. If E^* is a repeller, then (1.1) has a limit cycle that contains E^* in its interior.*

289 *Proof.* It is known that under the hypotheses (H1) and (H2), all solutions of (1.1)
 290 are positively bounded. Therefore the omega-limit set ω of a positive trajectory is
 291 nonempty, invariant and compact. If g is smooth at $x = 0$ then E_0 is hyperbolic (a
 292 saddle point).

293 The limit set ω does not contain the saddle points E_0 and E_1 . Indeed, if ω
 294 contains E_0 , and since it is different from E_0 , because E_0 is the omega-limit set of
 295 only the trajectories lying in the y -axis, then by the Butler-MacGehee Theorem, it
 296 must contain a point $b = (0, y_0)$ with $y_0 > 0$ of $W^s(E_0)$ which is the positive y -axis.
 297 Since ω is invariant it must contain the whole trajectory of b , which is the positive
 298 y axis. This contradicts the compactness of ω .

299 In the same manner if ω contains E_1 , and since it is different from E_1 , because
 300 E_1 is the omega-limit set of only trajectories lying in the x -axis, then by the Butler-
 301 MacGehee Theorem, it must contain a point $b = (x_0, 0)$ with $x_0 > 0$ of $W^s(E_1)$
 302 which is the positive x -axis. Two cases must be distinguished: If $x_0 > k$ then
 303 ω contains the whole trajectory of b which is unbounded. This contradicts the
 304 compactness of ω ; If $x_0 < k$ then ω contains the whole trajectory of b which is the
 305 segment $(0, k)$ of the x -axis. Since ω is closed, it must contain $[0, k]$, the closure of
 306 $(0, k)$. Therefore ω contains E_0 which is impossible as we have previously seen.

307 Assuming that E^* is a repeller, then it cannot belong to the omega-limit set ω .
 308 Therefore ω contains no equilibrium points. By the Poincaré-Bendixson Theorem,
 309 ω is a cycle. Since in the plane, a cycle must contain an equilibrium point in its
 310 interior, ω surrounds E^* . \square

311 If one have to our disposal the result that (1.1) admits at most one cycle, then
 312 the limit cycle whose existence was proved in the previous theorem is necessarily
 313 GOAS. Therefore, all solutions with positive initial conditions, excepted for E^*
 314 converge toward this limit cycle. The solutions with initial conditions on the y -axis
 315 converge toward E_0 , and the solutions with initial conditions on the positive x -axis
 316 converge toward E_1 .

317 When E^* is an attractor, we have the following result

318 **Theorem A.3.** *Assume that (H1) and (H2) hold and in addition g is smooth at*
 319 *0 . If E^* is an attractor and (1.1) has no cycles then E^* is GAS.*

320 *Proof.* Assume that E^* is an attractor. If a solution with positive initial condition
 321 does not converge toward E^* , then its omega-limit set ω cannot contain E^* . By
 322 the Butler-McGehee Theorem, it cannot contain E_0 nor E_1 as shown in the proof
 323 of the previous theorem. Therefore ω contain no equilibrium points. From the
 324 Poincaré-Bendixson Theorem, ω is a limit cycle, which contradicts the hypothesis
 325 that (1.1) has no cycles. Therefore $\omega = \{E^*\}$, which proves that E^* is GAS. \square

326 In the case where $g(x)$ is not smooth at $x = 0$, E_0 is not a hyperbolic saddle
 327 point and the arguments used in the proofs of Theorem A.2 and Theorem A.3 do
 328 not apply. For instance, in his proof of Theorem 1 in [9], the author claimed that
 329 $(0, 0)$ is a saddle, which is not true when $g(x)$ is not smooth at $x = 0$. Therefore,
 330 the system does not have necessarily a cycle when (x^*, y^*) is a repeller. Moreover,
 331 the claim of the author following the proof of his Theorem 1, that “local asymptotic
 332 stability of (x^*, y^*) implies its global asymptotic stability” is not true. Indeed Fig.
 333 5 provides a counterexample to this claim.

334 APPENDIX B. PROOF OF THEOREM 2.1

335 The proof needs the following result, known as the Tamarkine’s non uniqueness
 336 theorem (see [1], p. 98).

337 **Theorem B.1.** *Let $F(u, x)$ be a continuous function on $S = [-a, a] \times [-b, b]$, with*
 338 *$a > 0$ and $b > 0$. Assume that for all $(u, x) \in S$*

$$|F(u, x) - F(u, x_0(u))| \geq G(|x - x_0(u)|),$$

339 *where $u \mapsto x_0(u)$ is a solution of the initial value problem*

$$(B.1) \quad \frac{dx}{du} = F(u, x), \quad x(0) = 0.$$

340 *Assume that $z \mapsto G(z)$ is an increasing function for $z \geq 0$, $G(0) = 0$ and the*
 341 *integral $\int_{\varepsilon}^{\alpha} \frac{dz}{G(z)}$, ($\alpha > \varepsilon$) converges as $\varepsilon \rightarrow 0$. Then, the initial value problem*
 342 *(B.1) has at least two solutions in $[-a, a]$.*

343 *Proof. (of Theorem 2.1)* The change of variables $y = y_0 e^u$, transforms (2.2) into
 344 the system

$$(B.2) \quad \begin{aligned} \dot{x} &= x f(x) - y_0 e^u g(x), & x(0) &= 0, \\ \dot{u} &= \mu g(x) - D, & u(0) &= 0. \end{aligned}$$

In the region

$$D = \left\{ (x, u) : 0 \leq x < x^*, u > \ln \frac{\varphi(x)}{y_0} \right\},$$

345 where $\varphi(x)$ is defined by (1.2), we have $x f(x) - y_0 e^u g(x) < 0$ and $\mu g(x) - D < 0$.
 346 Therefore (B.2) is equivalent to the scalar initial value problem

$$(B.3) \quad \frac{dx}{du} = F(u, x, y_0), \quad x(0) = 0,$$

with

$$F(u, x, y_0) = \frac{x f(x) - y_0 e^u g(x)}{\mu g(x) - D},$$

where y_0 is considered as a parameter. Using (1.2), $F(u, x, y_0)$ can be written

$$F(u, x, y_0) = g(x) \frac{y_0 e^u - \varphi(x)}{D - \mu g(x)}.$$

347 Since $g(0) = 0$, $F(u, 0, y_0) = 0$. Therefore $x_0(u) = 0$ is a solution of (B.3). Actually
348 the initial value problem (B.3) has also non trivial solutions.

If $u \geq 0$ then $y_0 e^u \geq y_0$ and hence, for any $u \geq 0$ and $x \in [0, x^*]$, we have

$$|F(u, x, y_0) - F(u, x_0(u), y_0)| = F(u, x, y_0) > G(x),$$

where

$$G(z) = g(z) \frac{y_0 - \varphi(z)}{D - \mu g(z)}.$$

Let us denote by

$$h(z) = \frac{y_0 - \varphi(z)}{D - \mu g(z)}.$$

The function G is written $G(z) = g(z)h(z)$. It satisfies that $G(0) = 0$ and, for z small enough, G is increasing. Indeed, from $h(0) = y_0/D > 0$ we deduce that $h(x) > 0$ for x small enough, and from $g(0) = 0$ we deduce that $g(x)$ is small for x small enough, so that

$$G'(z) = g'(z)h(z) + g(z)h'(z) \approx g'(z)h(z) > 0.$$

For z small enough

$$\frac{1}{G(z)} = \frac{D - \mu g(z)}{g(z)(y_0 - \varphi(z))} \sim \frac{D}{y_0 g(z)}.$$

349 Therefore, using (H3), $\int_\varepsilon^\alpha \frac{dz}{G(z)}$ converges as $\varepsilon \rightarrow 0$. Using Theorem B.1 the initial
350 value problem (B.3) has a positive nontrivial solution $x_1(u)$ such that $x_1(u)$ is not
351 identically 0.

Let us prove now that the initial value problem (B.3) has a solution $\xi(u, y_0)$ satisfying the following conditions:

$$\xi(u, y_0) > 0, \text{ for } 0 < u < u_0 \text{ and } \xi(u, y_0) = 0, \text{ for } u \leq 0.$$

The set $\Phi(y_0)$ of all solutions $u \mapsto x(u)$ of (B.3) defined on a open interval I containing 0 contains at least two distinct solutions, the trivial solution x_0 for which $x_0(u)$ is identically 0 and a non trivial solution x_1 for which $x_1(u)$ is not identically 0. For each $u \in I$ let

$$\xi(u, y_0) = \sup_{x \in \Phi(y_0)} x(u).$$

It is well known (see [3], section 10.5, problem 7) that ξ belongs to $\Phi(y_0)$. It is called the *maximal solution* of (B.3) on I , corresponding to the initial condition $x(0) = 0$. Let $u_0 \in I$, such that $u_0 > 0$. Using the definition of ξ , we have $\xi(u, y_0) > 0$ for $0 < u < u_0$. The trivial solution $x_0(u) = 0$ of (B.3) corresponds to the trivial solution $(x(t) = 0, y(t) = y_0 e^{-Dt})$ of (2.2) and a nontrivial solution $x_1(u)$ of (B.3) corresponds to a nontrivial positive solution $(x_1(t), y_1(t))$ of (2.2). For instance, to the maximal nontrivial solution $\xi(u, y_0)$ corresponds the maximal solution $(X_1(t, y_0), Y_1(t, y_0))$ of (2.2) constructed as follows. First we consider the second equation in (B.2), where x is replaced by $\xi(u, y_0)$:

$$\dot{u} = \mu g(\xi(u, y_0)) - D, \quad u(0) = 0.$$

Let $U(t, y_0)$ be the solution of this initial value problem. Since $\xi(u, y_0) = 0$ for $u \leq 0$, one has $U(t, y_0) = -Dt$ for $u \leq 0$. Using the change of variables $y = y_0 e^u$, the solution $(X_1(t, y_0), Y_1(t, y_0))$ of (2.2) is defined by

$$X_1(t, y_0) = \xi(U(t, y_0), y_0), \quad Y_1(t, y_0) = y_0 e^{U(t, y_0)}.$$

352 This solution satisfies $X_1(t, y_0) = 0$, $Y_1(t, y_0) = y_0 e^{-Dt}$ for $t \leq 0$ and $X_1(t, y_0) > 0$,
 353 $Y_1(t, y_0) > 0$ for $t < 0$, which are the conditions in the theorem. \square

354

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REFERENCES

- 360 1. R. P. Agarwal and V. Lakshmikantham, *Uniqueness and non uniqueness criteria for Ordinary*
 361 *Differential Equations*, Series in Real Analysis Volume 6, World Scientific 1993.
 362 2. N. Beroual and A. Bendjeddou, *On a Predator-Prey System with Holling Functional Response:*
 363 $\frac{x^p}{a+x^p}$, Natl. Acad. Sci. Lett. **39** (2016), 43–46. MR34351609
 364 3. J. Dieudonné, *Foundations of modern analysis*, Academic Press, New York, 1960.
 365 4. H. I. Freedman, *Deterministic Mathematical Models in Population Ecology*, 2nd ed., HIFR
 366 Consulting LTD, Edmonton, Canada, 1987.
 367 5. C.S. Holling, *The functional response of predators to prey density and its role in mimicry and*
 368 *population regulation*, Mem. Ent. Soc. Can., 45 (1965), 5–60.
 369 6. X.C. Huang and S. J. Merrill, *Conditions for uniqueness of limit cycles in general predator-prey*
 370 *systems*, Math. Biosci., 96 (1989), 47–60. MR1013301 (90m:92056)
 371 7. Y. Kuang, *Global stability of Gause-type predator-prey systems*, J. Math. Biol., **28** (1990),
 372 463–474. MR1057049 (91g:92017)
 373 8. Y. Kuang and H. I. Freedman, *Uniqueness of limit cycles in Gause-type models of predator-prey*
 374 *systems*, Math. Biosci., **88** (1988), 67–84. MR0930003 (89g:92045)
 375 9. Y. Liu, *Geometric criteria for the nonexistence of cycles in Gause-type predator-prey systems.*
 376 Proc. Amer. Math. Soc. **133** (2005), 3619–3626. MR2163598 (2006f:92028)
 377 10. H.L. Smith and P. Waltman, *The Theory of the Chemostat: Dynamics of Microbial Compe-*
 378 *tition*, vol. 13, Cambridge University Press, Cambridge, 1995.
 379 11. J. Sugie *Uniqueness of limit cycles in a predator-prey system with Holling-type functional*
 380 *response*, Quart. Appl. Math. **58** (2000), 577–590. MR1770656
 381 12. J. Sugie, M. Katayama, *Global asymptotic stability of a predator-prey system of Holling type,*
 382 Nonlinear Anal. **38** (1999), 105–121. MR1693000
 383 13. J. Sugie, R. Kohno, R. Miyazaki, *On a predator-prey system of Holling type*, Proc. Amer.
 384 Math. Soc. **125** (1997), 2041–2050. MR1396998 (97m:92005)
 385 14. J. Sugie, K. Miyamoto and K. Morino, *Absence of limit cycles of a predator-prey system with*
 386 *a sigmoid functional response*, Appl. Math. Lett. **9** (1996), 85–90. MR1415457
 387 15. D. Xiao and Z. Zhang, *On the uniqueness and nonexistence of limit cycles for predator-prey*
 388 *systems*, Nonlinearity, **16** (2003), 1185–1201. MR1975802 (2004c:34084)

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