

ON A PREDATOR-PREY SYSTEM OF HOLLING TYPE

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ABSTRACT. We consider the predator-prey system with a fairly general functional response of Holling type and give a necessary and sufficient condition under which this system has exactly one stable limit cycle. Our result extends previous results and is an answer to a conjecture which was recently presented by Sugie, Miyamoto and Morino.

1. INTRODUCTION

The purpose of this paper is to give a necessary and sufficient condition for the uniqueness of limit cycles of a predator-prey system of the form

$$(1.1) \quad \begin{aligned} \dot{x} &= rx \left(1 - \frac{x}{k}\right) - \frac{x^p y}{a + x^p}, \\ \dot{y} &= y \left(\frac{\mu x^p}{a + x^p} - D\right), \end{aligned}$$

where $\dot{} = d/dt$; x and y represent the prey population (or density) and the predator population (or density), respectively; r , k , a , μ , D and p are positive parameters (p is not always an integer). The parameters are as follows:

- (i) r and k are the intrinsic rate of increase and the carrying capacity for the prey population, respectively;
- (ii) $\sqrt[p]{a}$ is the half-saturation constant for the predator;
- (iii) μ and D are the birth rate and the death rate for the predator, respectively.

The function $\frac{x^p}{a + x^p}$ is often called a functional response of Holling type when $p = 1$ or $p = 2$. System (1.1) is an important model on population dynamics (refer to [3], [5], [8]–[10] and references therein). If

$$(1.2) \quad \mu > D \quad \text{and} \quad k > \lambda_p \stackrel{\text{def}}{=} \sqrt[p]{\frac{aD}{\mu - D}},$$

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then system (1.1) has the only critical point (λ_p, ν_p) in the first quadrant $\{(x, y) : x > 0 \text{ and } y > 0\}$, where

$$\nu_p = \frac{r\mu}{D} \left(1 - \frac{\lambda_p}{k} \right) \lambda_p.$$

It is clear that system (1.1) has no limit cycles when assumption (1.2) fails.

Many attempts have been made to give sufficient conditions and necessary conditions to guarantee the existence and the uniqueness of limit cycles of (1.1). For example, see [1], [2], [4], [6]. The following theorems are well-known. (Results in [1], [2], [4], [6] were stated in a slightly different form.)

Theorem A. *Let $p = 1$. Then, under the assumption (1.2), system (1.1) has a unique stable limit cycle if and only if*

$$(D + \mu)\lambda_1 < Dk.$$

Theorem B. *Let $p = 2$. Then, under the assumption (1.2), system (1.1) has a unique stable limit cycle if and only if*

$$2D\lambda_2 < (2D - \mu)k.$$

In a recent paper [12], Sugie, Miyamoto and Morino gave a necessary condition for the existence of limit cycles of (1.1) with $p = 3$ and made the following conjecture.

Conjecture. *Let p be any positive integer. Then, under the assumption (1.2), system (1.1) has no limit cycles if and only if*

$$(1.3) \quad (pD - (p - 2)\mu)\lambda_p \geq (pD - (p - 1)\mu)k.$$

In this paper we prove that the conjecture is true and extend any positive integer p in the conjecture to any positive real number p satisfying a certain condition (Theorems 2.1 and 3.1). To be exact, if condition (1.3) holds, then system (1.1) has no limit cycles; otherwise, system (1.1) has a unique limit cycle. Since the solutions of (1.1) are positive and bounded for all future time, from the Poincaré-Bendixson theorem, we see that under the assumption (1.2), condition (1.3) is necessary and sufficient for the equilibrium (λ_p, ν_p) to be globally asymptotically stable.

2. UNIQUENESS OF LIMIT CYCLES

Kuang and Freedman [8] gave the following result on the uniqueness of limit cycles of the system:

$$(2.1) \quad \begin{aligned} \dot{x} &= x\rho(x) - y\phi(x), \\ \dot{y} &= y(-\nu + \psi(x)), \end{aligned}$$

where $\nu > 0$; all the functions are sufficiently smooth on $[0, \infty)$ and satisfy

$$(2.2) \quad \phi(0) = \psi(0) = 0 \quad \text{and} \quad \phi'(x) > 0, \quad \psi'(x) > 0 \quad \text{for } x > 0.$$

Theorem C. Assume (2.2). If there exist constants x^* and m with $0 < x^* < m$ such that

$$(2.3) \quad \psi(x^*) = \nu \quad \text{and} \quad (x - m)\rho(x) < 0 \quad \text{for } x \neq m;$$

$$(2.4) \quad \left. \frac{d}{dx} \left(\frac{x\rho(x)}{\phi(x)} \right) \right|_{x=x^*} > 0;$$

$$(2.5) \quad \frac{d}{dx} \left(\frac{x\rho'(x) + \rho(x) - x\rho(x)\frac{\phi'(x)}{\phi(x)}}{-\nu + \psi(x)} \right) \leq 0 \quad \text{for } x \neq x^*,$$

then system (2.1) has exactly one limit cycle which is globally asymptotically stable.

By means of Theorem C, we will show that ‘only if’-part of Conjecture in Section 1 is correct.

Theorem 2.1. Let p be a positive number with $p \leq 1$ or $p \geq 2$. If (1.2) and

$$(2.6) \quad (pD - (p - 2)\mu)\lambda_p < (pD - (p - 1)\mu)k$$

are satisfied, then system (1.1) has a unique limit cycle.

Proof of Theorem 2.1. We can rewrite system (1.1) as system (2.1) with $\nu = D$,

$$(2.7) \quad \rho(x) = r \left(1 - \frac{x}{k} \right), \quad \phi(x) = \frac{x^p}{a + x^p} \quad \text{and} \quad \psi(x) = \mu \phi(x).$$

It is clear that $\phi(x)$ and $\psi(x)$ satisfy assumption (2.2).

Let

$$x^* = \lambda_p \quad \text{and} \quad m = k.$$

Then by (1.2) we see that $x^* < m$. Assumption (2.3) is satisfied. In fact, we have $\psi(\lambda_p) = D$;

$$\rho(x) > 0 \quad \text{if } 0 < x < k \quad \text{and} \quad \rho(x) < 0 \quad \text{if } x > k.$$

For the sake of convenience, let

$$H(x) = x\rho'(x) + \rho(x) - x\rho(x)\frac{\phi'(x)}{\phi(x)}$$

and

$$W(x) = -\frac{H(x)}{\psi(x) - D} \quad \text{for } x \neq \lambda_p.$$

Since

$$(2.8) \quad \frac{d}{dx} \left(\frac{x\rho(x)}{\phi(x)} \right) = \frac{H(x)}{\phi(x)} = r \left\{ (1 - p) \left(1 - \frac{x}{k} \right) \frac{a + x^p}{x^p} - \frac{x(a + x^p)}{kx^p} + p \left(1 - \frac{x}{k} \right) \right\},$$

we get

$$\begin{aligned} \left. \frac{d}{dx} \left(\frac{x\rho(x)}{\phi(x)} \right) \right|_{x=\lambda_p} &= r \left\{ (1 - p) \left(1 - \frac{\lambda_p}{k} \right) \frac{\mu}{D} - \frac{\lambda_p \mu}{kD} + p \left(1 - \frac{\lambda_p}{k} \right) \right\} \\ &= \frac{r}{kD} \left\{ (pD - (p - 1)\mu)k - (pD - (p - 2)\mu)\lambda_p \right\} > 0 \end{aligned}$$

by (2.6). Hence, assumption (2.4) holds.

From (2.7) and (2.8) it turns out that

$$\begin{aligned} W(x) &= -\frac{r}{\mu x^p - D(a+x^p)} \left\{ (1-p) \left(1 - \frac{x}{k}\right) (a+x^p) - \frac{x(a+x^p)}{k} + p \left(1 - \frac{x}{k}\right) x^p \right\} \\ &= -\frac{r}{k((\mu-D)x^p - aD)} \{ ak(1-p) + a(p-2)x + kx^p - 2x^{p+1} \}. \end{aligned}$$

Differentiating this equality and using the fact that $aD = (\mu - D)\lambda_p^p$, we obtain

$$\begin{aligned} W'(x) &= \frac{r(\mu-D)}{k((\mu-D)x^p - aD)^2} \left\{ 2x^{2p} - (2(p+1)\lambda_p^p - a(p-1)(p-2))x^p \right. \\ &\quad \left. + kp(\lambda_p^p - a(p-1))x^{p-1} + a(p-2)\lambda_p^p \right\}. \end{aligned}$$

Taking (2.6) into account, we have

$$\begin{aligned} kp(\lambda_p^p - a(p-1)) &= \frac{ap}{\mu-D}(pD - (p-1)\mu)k \\ &> \frac{ap}{\mu-D}(pD - (p-2)\mu)\lambda_p \\ &= p\lambda_p(2\lambda_p^p - a(p-2)). \end{aligned}$$

Hence

$$\begin{aligned} W'(x) &> \frac{r(\mu-D)}{k((\mu-D)x^p - aD)^2} \left\{ 2x^{2p} - (2(p+1)\lambda_p^p - a(p-1)(p-2))x^p \right. \\ &\quad \left. + p\lambda_p(2\lambda_p^p - a(p-2))x^{p-1} + a(p-2)\lambda_p^p \right\} \\ &= \frac{r(\mu-D)}{k((\mu-D)x^p - aD)^2} (2x^{p-1}U(x) + a(p-2)V(x)), \end{aligned}$$

where

$$U(x) = x^{p+1} - (p+1)\lambda_p^p x + p\lambda_p^{p+1} \quad \text{and} \quad V(x) = (p-1)x^p - p\lambda_p x^{p-1} + \lambda_p^p.$$

Since $U'(x) = (p+1)(x^p - \lambda_p^p)$ and $V'(x) = p(p-1)x^{p-2}(x - \lambda_p)$, it follows that for $x > 0$

$$U(x) \geq U(\lambda_p) = 0;$$

$$V(x) \leq V(\lambda_p) = 0 \quad \text{if } p \leq 1 \quad \text{and} \quad V(x) \geq V(\lambda_p) = 0 \quad \text{if } p > 1.$$

We therefore conclude that if $p \leq 1$ or $p \geq 2$, then

$$2x^{p-1}U(x) + a(p-2)V(x) \geq 0$$

for $x > 0$. Thus, assumption (2.5) is also satisfied.

Using Theorem C, we see that system (1.1) has a unique stable limit cycle. The proof is complete.

Remark 2.1. In the above proof, if $1 < p < 2$, then $W'(x) < 0$ for x sufficiently small and so assumption (2.5) fails. Hence, we cannot use Theorem C.

3. NON-EXISTENCE OF LIMIT CYCLES

In this section we will show that ‘if’-part of Conjecture in Section 1 is true. To see this, we need Theorem D below which was stated in [11] (we can find a similar result to Theorem D in [7]).

By changing variables

$$u = x - \lambda_p, \quad v = \log y - \log \nu_p \quad \text{and} \quad d\tau = -\frac{x^p}{a + x^p} dt,$$

system (1.1) can be transformed into the system

$$(3.1) \quad \begin{aligned} \frac{du}{d\tau} &= \nu_p(e^v - 1) - F(u), \\ \frac{dv}{d\tau} &= -g(u), \end{aligned}$$

where

$$F(u) = r \left(1 - \frac{u + \lambda_p}{k} \right) \frac{a + (u + \lambda_p)^p}{(u + \lambda_p)^{p-1}} - \nu_p \quad \text{and} \quad g(u) = \mu - D - \frac{aD}{(u + \lambda_p)^p}.$$

Note that $F(u)$ and $g(u)$ are defined for $u > -\lambda_p$ and satisfy

$$F(0) = 0 \quad \text{and} \quad ug(u) > 0 \quad \text{for} \quad u \neq 0.$$

Define

$$G(u) = \int_0^u g(s) ds.$$

Then the inverse function of $w = G(u)$ $\text{sgn} \ u$ exists. Let $G^{-1}(w)$ be the inverse.

Theorem D. *Suppose that*

$$(3.2) \quad F(G^{-1}(-w)) \neq F(G^{-1}(w)) \quad \text{for} \quad 0 < w < M,$$

where $M = G(-\lambda_p + 0)$. Then (3.1) has no limit cycles and neither has (1.1).

Unfortunately, however, it is difficult to construct explicitly the inverse function $G^{-1}(w)$ because

$$G(u) = \begin{cases} (\mu - D)u + \frac{aD}{p-1} \left(\frac{1}{(u + \lambda_p)^{p-1}} - \frac{1}{\lambda_p^{p-1}} \right) & \text{if } p \neq 1, \\ (\mu - D)u - aD(\log(u + \lambda_p) - \log \lambda_p) & \text{if } p = 1. \end{cases}$$

Hence, to prove the following result, we intend to check (3.2) without calculating $G^{-1}(w)$ directly.

Theorem 3.1. *Let p be a positive number with $p \leq \frac{1}{2}$ or $p \geq 1$. If (1.2) and*

$$(3.3) \quad (pD - (p - 2)\mu)\lambda_p \geq (pD - (p - 1)\mu)k$$

are satisfied, then system (1.1) has no limit cycles.

Proof of Theorem 3.1. When $p = 1$, the theorem is an immediate consequence of Theorem A. We thus consider only the case $p \neq 1$. By virtue of Theorem D, it is enough to prove that (3.3) implies (3.2). We will show this by way of contradiction. Suppose that

$$F(G^{-1}(-w_0)) = F(G^{-1}(w_0))$$

for some $w_0 \in (0, M)$. Then we have

$$(3.4) \quad F(-\alpha) = F(\beta) \quad \text{and} \quad G(-\alpha) = G(\beta)$$

where $\alpha = -G^{-1}(-w_0)$ and $\beta = G^{-1}(w_0)$. Here we note that $-\lambda_p < -\alpha < 0 < \beta$. For simplicity, let

$$(3.5) \quad \gamma = \lambda_p - \alpha \quad \text{and} \quad \delta = \lambda_p + \beta.$$

Then (3.4) becomes

$$(3.6) \quad (k - \gamma) \left(\frac{a}{\gamma^{p-1}} + \gamma \right) = (k - \delta) \left(\frac{a}{\delta^{p-1}} + \delta \right);$$

$$(3.7) \quad \frac{a}{\delta^{p-1}} = \frac{a}{\gamma^{p-1}} - \frac{(p-1)(\alpha + \beta)(\mu - D)}{D}.$$

Substituting (3.7) into the right-hand side of (3.6) and using the fact that $\alpha + \beta = \delta - \gamma$, we obtain

$$(3.8) \quad \frac{a}{\gamma^{p-1}} + \gamma + \frac{pD - (p-1)\mu}{D}(\delta - k) = 0.$$

Similarly, we get

$$(3.9) \quad \frac{a}{\delta^{p-1}} + \delta + \frac{pD - (p-1)\mu}{D}(\gamma - k) = 0.$$

Hence, from (1.2) and (3.5), it turns out that

$$(3.10) \quad pD - (p-1)\mu > 0.$$

Now, we define the function

$$h(z) = -\frac{D}{pD - (p-1)\mu} \left(\frac{a}{z^{p-1}} + z \right) + k$$

for $z > 0$ and consider two curves $\eta = h(\xi)$ and $\xi = h(\eta)$ in the (ξ, η) -plane. Then the curves are symmetric with respect to the straight line $\eta = \xi$. The equalities (3.8) and (3.9) show that the curves intersect each other at the point (γ, δ) which is in the region $R = \{(\xi, \eta) : 0 < \xi < \lambda_p < \eta\}$. We divide our argument into two cases.

Case (i) $p > 1$. From (3.10) it follows that $h(z)$ has the maximum value $h(z_*)$ with $z_* = \sqrt[p]{a(p-1)}$ because

$$h'(z) = -\frac{D}{pD - (p-1)\mu} \left(1 - \frac{a(p-1)}{z^p} \right).$$

It is clear that

$$h(z) \rightarrow -\infty \quad \text{as} \quad z \rightarrow 0^+.$$

By (3.3) and (3.10) we also see that

$$z_* < \lambda_p \quad \text{and} \quad h(\lambda_p) \leq \lambda_p.$$

In fact, we have

$$\lambda_p^p - z_*^p = \frac{aD}{\mu - D} - a(p-1) = \frac{a}{\mu - D}(pD - (p-1)\mu) > 0;$$

$$\begin{aligned} \lambda_p - h(\lambda_p) &= \lambda_p + \frac{D\lambda_p}{pD - (p-1)\mu} \left(\frac{a}{\lambda_p^p} + 1 \right) - k \\ &= \lambda_p + \frac{\lambda_p \mu}{pD - (p-1)\mu} - k \\ &= \frac{(pD - (p-2)\mu)\lambda_p - (pD - (p-1)\mu)k}{pD - (p-1)\mu} \geq 0. \end{aligned}$$

Thus, the curve $\eta = h(\xi)$ crosses the straight line $\eta = \xi$ at two points $P(z_1, z_1)$ and $Q(z_2, z_2)$ with

$$(3.11) \quad 0 < z_2 < z_* < z_1 \leq \lambda_p.$$

Because of the symmetry of $\eta = h(\xi)$ and $\xi = h(\eta)$, the curve $\xi = h(\eta)$ also passes through the points P and Q (see Figure 1).

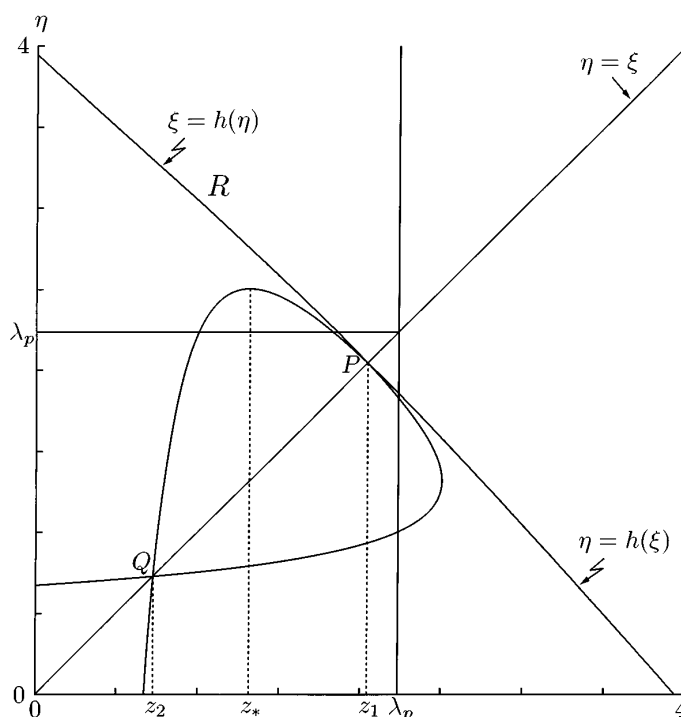


FIGURE 1. The parameters $p = 4, a = 1, D = 25, k = \frac{9}{2}, \mu = 26$ and the function $h(z) = -\frac{25}{22} \left(\frac{1}{z^3} + z \right) + \frac{9}{2}$

Since $h(z)$ is strictly decreasing for $z \geq z_1$, the curve $\xi = h(\eta)$ ($\eta \geq z_1$) can be rewritten as $\eta = h^{-1}(\xi)$ ($\xi \leq z_1$). Taking notice of (3.10), we obtain

$$(3.12) \quad h''(z) < 0 < h'''(z) \quad \text{for } z > 0.$$

Hence, it follows from (3.11) that

$$(3.13) \quad h'(z_1) \geq h'(\lambda_p) = -\frac{D}{pD - (p-1)\mu} \left(1 - \frac{a(p-1)}{\lambda_p^p} \right) = -1,$$

and therefore,

$$(3.14) \quad (h^{-1})'(z_1) = \frac{1}{h'(z_1)} \leq -1.$$

Next, consider the curvature

$$K(\xi) = \frac{h''(\xi)}{\{1 + (h'(\xi))^2\}^{\frac{3}{2}}}$$

at a point $(\xi, h(\xi))$ on the curve $\eta = h(\xi)$. Then we have

$$K'(\xi) = \frac{1}{\{1 + (h'(\xi))^2\}^{\frac{3}{2}}} \left\{ h'''(\xi) \{1 + (h'(\xi))^2\} - 3h'(\xi)(h''(\xi))^2 \right\}.$$

Consequently, by (3.12), the curvature $K(\xi)$ is negative and strictly increasing for $\xi \geq z_*$. This fact means that the absolute value of curvature of $\eta = h(\xi)$ is larger than that of $\eta = h^{-1}(\xi)$ in the interval $[z_*, z_1)$. Hence, together with (3.13) and (3.14), we see that the curve $\eta = h(\xi)$ lies below the curve $\eta = h^{-1}(\xi)$ in this interval. It is obvious that the curves $\eta = h(\xi)$ and $\eta = h^{-1}(\xi)$ do not meet for $0 < \xi \leq z_*$. We therefore conclude that the curves $\eta = h(\xi)$ and $\xi = h(\eta)$ have no common point in the region R . This is a contradiction.

Case (ii) $p \leq \frac{1}{2}$. As in the proof of the case (i), we have

$$(3.15) \quad h(\lambda_p) \leq \lambda_p.$$

The curve $\eta = h(\xi)$ intersects the straight line $\eta = \xi$ at a point because

$$h'(z) < 0 \quad \text{for } z > 0;$$

$$h(z) \rightarrow k \quad \text{as } z \rightarrow 0^+ \quad \text{and} \quad h(z) \rightarrow -\infty \quad \text{as } z \rightarrow \infty.$$

Let $P(z_1, z_1)$ be the point of intersection. Then by (3.15) we see

$$(3.16) \quad 0 < z_1 \leq \lambda_p.$$

The curve $\xi = h(\eta)$ also passes through the point P (see Figure 2).

Rewrite $\xi = h(\eta)$ as $\eta = h^{-1}(\xi)$. Since

$$(3.17) \quad h'''(z) < 0 < h''(z) \quad \text{for } z > 0,$$

it follows from (3.16) that

$$(3.18) \quad h'(z_1) \leq h'(\lambda_p) = -1 \quad \text{and} \quad (h^{-1})'(z_1) = \frac{1}{h'(z_1)} \geq -1.$$

Consider again the curvature $K(\xi)$ at a point $(\xi, h(\xi))$ on the curve $\eta = h(\xi)$. By (3.17), the curvature $K(\xi)$ is positive for $\xi > 0$. Also, a simple calculation yields

$$K'(\xi) < -\frac{ap(1-p)D^3(\xi^p + a(1-p))((p+1)\xi^p + a(1-p)(1-2p))}{\{1 + (h'(\xi))^2\}^{\frac{3}{2}}(pD + (1-p)\mu)^3 \xi^{3p+2}} < 0$$

for $\xi > 0$. Hence, taking into account (3.18), we see that the curves $\eta = h(\xi)$ and $\xi = h(\eta)$ fails to cross in the region R . This contradicts the fact that (γ, δ) is a common point in R .

Thus, we find a contradiction in both cases (i) and (ii). The proof is now complete.

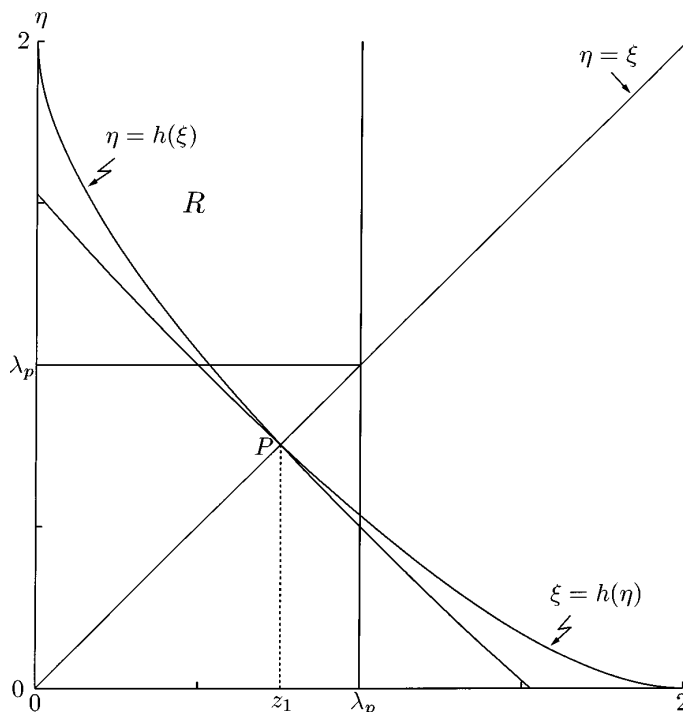


FIGURE 2. The parameters $p = \frac{1}{2}$, $a = 2$, $D = 1$, $k = 2$, $\mu = 3$ and the function $h(z) = -\sqrt{z} - \frac{1}{2}z + 2$.

Remark 3.1. By examining the slope and the curvature of $\eta = h(\xi)$, where

$$h(\xi) = \frac{aD}{\mu - D} (\log(k - a - \xi) - \log \xi) + \xi \quad \text{for } 0 < \xi < k - a,$$

the proof of the case $p = 1$ can be carried out in the same way.

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