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PHASE ANALYSIS FOR THE PREDATOR-PREY SYSTEMS WITH PREY DENSITY DEPENDENT RESPONSE

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Abstract. This paper looks into phase plane behavior of the solution near the positive steady-state for the system with prey density dependent response functions. The positive invariance and boundedness property of the solution to the objective model are proved. The existence result of a positive steady-state and asymptotic analysis near the positive constant equilibrium for the objective system are of interest. The results of phase plane analysis for the system are proved by observing the asymptotic properties of the solutions. Also some numerical analysis results for the behaviors of the solutions in time are provided.

1. Introduction

In 1910, Alfred J. Lotka[5] had proposed a mathematical model for predator and prey relationship in the theory of autocatalytic chemical reactions, which has been called later as "Lotka-Volterra predator-prey model" :

$$(1) \qquad \begin{cases} U_t = U(a_1 - b_1 U - c_1 V), & t \in (0, \infty), \\ V_t = V(a_2 + b_2 U - c_2 V), & t \in (0, \infty) \\ U(0) = U_0 \geq 0 \quad \text{and} \quad V(0) = V_0 \geq 0. \end{cases}$$

The parameters b_i, c_i $(i = 1, 2)$, a_1 and q represent positive constants. Here only the coefficient a_2 might be a nonpositive constant. Lotka[6] extended this model in

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1920 to the predator-prey type reaction phenomena between two species of a plant and a herbivorous animal. The same model was independently published in 1926 by Vito Volterra as a mathematical representation for the observation of predator and prey fish population changes in Adriatic Sea after World War I(1914-1918).

C. S. Holling extended the Lotka-Volterra predator-prey model to include functional response in his classical paper published in 1959[2] and 1965[3]. This extended model has become recognized as a the RosenzweigMcArthur model[7] which have been applied to the dynamical behaviors of natural populations of predator and prey, for example the lynx and snowshoe hare data which had been constructed by the Hudson's Bay Company in [1] and the moose and wolf populations which had been observed in Isle Royale National Park[4].

In this work we analyze the phase plane dynamical behavior of the following predator-prey model with density dependent functional response which is reduced to RosenzweigMcArthur model by scalings of the variables :

$$(2) \qquad \begin{cases} U_\tau = U(a_1 - b_1 U) - \dfrac{c_1 UV}{1+qU}, & \tau \in (0,\infty), \\ V_\tau = a_2 V + \dfrac{b_2 UV}{1+qU}, & \tau \in (0,\infty) \\ U(0) = U_0 \geq 0 \quad \text{and} \quad V(0) = V_0 \geq 0. \end{cases}$$

where a_1, b_1, b_2, c_1, q represent positive constants, and here a_2 might be a nonpositive constant. The detailed explanations for the meanings of the coefficients and the form of the response functions of the given type may be found in [8] and references therein.

The existence result of a positive constant equilibrium $(\overline{U}, \overline{V})$ to the model (2) has been obtained in [8]. An analysis on the stability for the positive equilibrium point $(\overline{U}, \overline{V})$ also practiced in [8] under certain conditions. The present paper investigate phase plane behavior of the solution (U, V) near the positive constant equilibrium $(\overline{U}, \overline{V})$ for the model (2) with $a_2 < 0$ and $0 \leq q < -\left(\dfrac{b_1}{a_1} + \dfrac{b_2}{a_2}\right)$. We also observe some numerical analysis results.

In the course the system (2) is nondimensionalized to a simpler form (1) as shown in Section 2. In Section 3 the positive invariance and boundedness properties of the solution function (u, v) of the model (1) are proved. Section 4 deals the existence of a positive constant equilibrium $(\overline{u}, \overline{v})$ and asymptotic analysis near $(\overline{u}, \overline{v})$ with the model (1). The results of phase plane analysis for the system (1) are also shown in Section 4.

2. Nondimensionalization of the System

The predator-prey system with density dependent functional response (2) can be nondimensionalized to the following simplified system :

$$
(1) \qquad \begin{cases} u_t = u\left(1 - \dfrac{u}{\alpha}\right) - \dfrac{uv}{1+u}, & t \in (0,\infty), \\ v_t = \beta\gamma v + \dfrac{\beta uv}{1+u}, & t \in (0,\infty), \\ u(0) = u_0 \geq 0 \quad \text{and} \quad v(0) = v_0 \geq 0 \end{cases}
$$

by scaling variables as $U = \dfrac{1}{q}u$, $V = \dfrac{a_1}{c_1}v$, $\tau = \dfrac{1}{a_1}t$. This is checked as follows.

In the first equation of the system (2)

$$
\begin{aligned}
U_\tau &= \frac{1}{q}u_t \cdot \frac{dt}{d\tau} \\
&= \frac{a_1}{q}u_t, \\
U(a_1 - b_1U) - \frac{c_1UV}{1+qU} &= \frac{1}{q}u\left(a_1 - \frac{b_1}{q}u\right) - \frac{a_1uv}{q(1+u)} \\
&= \frac{a_1}{q}u\left(1 - \frac{b_1}{a_1q}u\right) - \frac{a_1}{q}\cdot\frac{uv}{1+u},
\end{aligned}
$$

thus it is reduced to

$$u_t = u\left(1 - \frac{u}{\alpha}\right) - \frac{uv}{1+u},$$

where $\alpha = \dfrac{a_1q}{b_1}$.

In the second equation of the system (2)

$$
\begin{aligned}
V_\tau &= \frac{a_1}{c_1}v_t \cdot \frac{dt}{d\tau} \\
&= \frac{a_1^2}{c_1}v_t, \\
a_2V + \frac{b_2UV}{1+qU} &= \frac{a_1a_2}{c_1}v + \frac{a_1b_2uv}{c_1q(1+u)} \\
&= \frac{a_1}{c_1}\left(a_2v + \frac{b_2uv}{q(1+u)}\right),
\end{aligned}
$$

thus it is reduced to

$$v_t = \beta\gamma v + \frac{\beta uv}{1+u},$$

where $\beta = \dfrac{b_2}{a_1 q}$, $\gamma = \dfrac{a_2 q}{b_2}$. Here notice that $\gamma < 0$ if $a_2 < 0$.

3. Positivity and Boundedness of the Solutions

Let us define two functions of vector variable f, $g : \mathbb{R}^2 \to \mathbb{R}^2$ as

$$f(u,v) = u\left(1 - \frac{u}{\alpha}\right) - \frac{uv}{1+u}, \qquad g(u,v) = \beta\gamma v + \frac{\beta uv}{1+u}$$

which are the response functions of the first and second equation in the system (1).

We see that the response functions $f(u,v)$ and $g(u,v)$ are smooth in the domain $\Omega = \{(u,v) \mid u > 0,\, v > 0\}$. The line $v = 0$, that is the u-axis, is the nullcline(zero set) of the response function $g(u,v)$, and the first equation of the system (1) becomes

$$u_t = u\left(1 - \frac{u}{\alpha}\right) \qquad \text{for } t \in (0,\infty)$$

which has a nonnegative bounded solution. This implies that the nonnegative part of the u-axis is invariant for the system (1). The line $u = 0$, that is the v-axis, is the nullcline(zero set) of the response function $f(u,v)$, and the second equation of the model (1) becomes

$$v_t = -\beta\gamma v \qquad \text{for } t \in (0,\infty)$$

which has a nonnegative bounded solution. This implies that the nonnegative part of the v-axis is also invariant for the system (1). Therefore the u-axis and v-axis are orbits of the system (1), respectively. Since different orbits cannot intersect, it is concluded that the first quadrant Ω is invariant for the system (1). Thus we have the local existence result of the solution to the system (1) in Ω.

Now in the following lemma we prove the boundedness of the solution.

Lemma 3.1. *For the system* (1) *with* $\alpha > 0$, $\beta > 0$, *and* $\gamma < 0$, *it hold that*

$$\left(u + \frac{1}{\beta}v\right)_t < 0 \qquad \text{for } u > \alpha$$

and therefore every orbit $(u(t), v(t))$ *stays in a bounded and closed region in the set* $\{(u,v) \mid u > 0, v > 0\}$ *for every* $t \geq 0$.

Proof. Considering the second equation of the model (1), we have that

$$\frac{1}{\beta}v_t = \gamma v + \frac{uv}{1+u} \tag{1}$$

By adding the first equation of the model (1) and equation (1), it is obtained that

$$\left(u + \frac{1}{\beta}v\right)_t = \left(1 - \frac{u}{\alpha}\right)u + \gamma v$$

From the given condition that $\alpha > 0$, $\beta > 0$, and $\gamma < 0$, it is concluded that

$$\left(u + \frac{1}{\beta}v\right)_t < 0$$

for $u > \alpha$. □

4. Phase Plane Analysis

Now we analyze the phase plane of the model (1) under the condition that :

$$\alpha > 0, \quad \beta > 0, \quad -1 < \gamma < 0 \quad \text{and} \quad \alpha\gamma + \alpha + \gamma > 0 \tag{1}$$

Lemma 4.1. *Assume the condition* (1) *for system* (1). *Then the model* (1) *possesses a unique positive constant equilibrium* $(\overline{u}, \overline{v})$, *where*

$$\overline{u} = \frac{-\gamma}{1+\gamma}, \qquad \overline{v} = \frac{\alpha + \alpha\gamma + \gamma}{\alpha(1+\gamma)^2}. \tag{2}$$

Proof. Computing the positive roots of the response function of the second equation of the model (1) we have

$$\beta\gamma + \frac{\beta\overline{u}}{1+\overline{u}} = 0, \tag{3}$$

that is,

$$\overline{u} = \frac{-\gamma}{1+\gamma}.$$

From the response function of the first equation of the system (1) to solve for the positive steady-state $(\overline{u}, \overline{v})$ the following equation should hold :

$$1 - \frac{\overline{u}}{\alpha} - \frac{\overline{v}}{1+\overline{u}} = 0. \tag{4}$$

Since

$$1 + \overline{u} = \frac{1}{1+\gamma}$$

equation (4) is reduced to

$$1 + \frac{\gamma}{\alpha(1+\gamma)} - (1+\gamma)\overline{v} = 0,$$

so it is obtained that

$$\overline{v} = \frac{\alpha + \alpha\gamma + \gamma}{\alpha(1+\gamma)^2}.$$

By the condition (1), $\overline{u} > 0$ and $\overline{v} > 0$. Thus it concludes the proof. □

Now we investigate asymptotic behaviors of the solution to the system (1) near $(\overline{u}, \overline{v})$ in the theorem given below.

Theorem 4.1. *Let us assume the condition* (1) *for system* (1). *Then the model* (1) *displays a Hopf bifurcation phenomenon around* $(\overline{u}, \overline{v})$ *at the parameter value* $\alpha = \alpha^*_\gamma$, *where*

$$\alpha^*_\gamma = \frac{1-\gamma}{1+\gamma}.$$

That means, $(\overline{u}, \overline{v})$ *becomes an asymptotically stable constant equilibrium if* $0 < \alpha < \alpha^*_\gamma$, *but an unstable constant equilibrium if* $\alpha > \alpha^*_\gamma$.

Proof. The response function of the equations in the model (1) are defined to be functions of two variables (u, v) as follows :

$$f(u, v) = u\left(1 - \frac{u}{\alpha}\right) - \frac{uv}{1+u}$$

and

$$g(u, v) = \beta\gamma v + \frac{\beta uv}{1+u}.$$

The system (1) is linearized around the positive constant equilibrium $(\overline{u}, \overline{v})$ that was obtained in Lemma 4.1. The linearized system is written with new variables $\eta(t) = u(t) - \overline{u}$ and $\zeta(t) = v(t) - \overline{v}$ as follows :

$$\begin{pmatrix} \dfrac{d\eta}{dt} \\ \dfrac{d\zeta}{dt} \end{pmatrix} = A \begin{pmatrix} \eta \\ \zeta \end{pmatrix}, \tag{5}$$

where

$$A = \begin{pmatrix} \dfrac{df}{du} & \dfrac{df}{dv} \\ \dfrac{dg}{du} & \dfrac{dg}{dv} \end{pmatrix}_{(\overline{u}, \overline{v})} = \begin{pmatrix} 1 - \dfrac{2\overline{u}}{\alpha} - \dfrac{\overline{v}}{(1+\overline{u})^2} & -\dfrac{\overline{u}}{1+\overline{u}} \\ \dfrac{\beta\overline{v}}{(1+\overline{u})^2} & \beta\gamma + \beta\dfrac{\overline{u}}{1+\overline{u}} \end{pmatrix}.$$

From equation (3) and (4),

$$\begin{aligned} \left.\frac{df}{du}\right|_{(\overline{u}, \overline{v})} &= 1 - \frac{2\overline{u}}{\alpha} - \frac{1}{(1+\overline{u})}\left(1 - \frac{\overline{u}}{\alpha}\right) \\ &= \frac{(\alpha - 1 - 2\overline{u})\overline{u}}{(1+\overline{u})\alpha}, \\ &= -\frac{(\alpha\gamma + \alpha + \gamma - 1)\gamma}{(1+\gamma)\alpha}, \end{aligned}$$

$$\left.\frac{df}{dv}\right|_{(\overline{u}, \overline{v})} = \gamma,$$

$$\left.\frac{dg}{du}\right|_{(\overline{u},\overline{v})} = \frac{(\alpha\gamma+\alpha+\gamma)\beta}{\alpha},$$

and

$$\left.\frac{dg}{dv}\right|_{(\overline{u},\overline{v})} = 0.$$

Thus it is simplified to

$$A = \begin{pmatrix} -\dfrac{(\alpha\gamma+\alpha+\gamma-1)\gamma}{(1+\gamma)\alpha} & \gamma \\ \dfrac{(\alpha\gamma+\alpha+\gamma)\beta}{\alpha} & 0 \end{pmatrix}.$$

Here we see that

$$\det A = -\frac{(\alpha\gamma+\alpha+\gamma)\beta\gamma}{\alpha} > 0$$

by the condition (1). Now we observe that

$$\operatorname{tr} A = -\frac{(\alpha\gamma+\alpha+\gamma-1)\gamma}{\alpha(1+\gamma)}.$$

Thus

$$\operatorname{tr} A < 0 \quad \text{if and only if} \quad \alpha\gamma+\alpha+\gamma > 1 \tag{6}$$

and

$$\operatorname{tr} A > 0 \quad \text{if and only if} \quad 0 < \alpha\gamma+\alpha+\gamma < 1. \tag{7}$$

For the purpose to determine the bifurcation value α^*_γ for α, we solve the equation $\operatorname{tr} A = 0$, that is,

$$\alpha\gamma+\alpha+\gamma = 1, \quad \text{or equivalently} \quad (\alpha+1)(\gamma+1) = 2.$$

Hence we obtain that

$$\alpha^*_\gamma = \frac{1-\gamma}{1+\gamma}. \tag{8}$$

Furthermore we have to check the following transversality condition to confirm the Hopf bifurcation phenomenon at $\alpha = \alpha^*_\gamma$:

$$\left.\frac{d(\operatorname{Re}\xi_+)}{d\alpha}\right|_{\alpha=\alpha^*_\gamma} \neq 0, \tag{9}$$

where ξ_+ is the positive root of the characteristic equation $\xi^2 - (\operatorname{tr} A)\xi + \det A = 0$ corresponding to the linearized system (5). The positive eigenvalue ξ_+ of the matrix

A is $\xi_+ = \frac{1}{2}\left(\operatorname{tr} A + \sqrt{(\operatorname{tr} A)^2 - 4\det A}\right)$. From the facts that $\det A > 0$ and $\operatorname{tr} A = 0$ at $\alpha = \alpha^*_\gamma$, we have that $(\operatorname{tr} A)^2 - 4\det A < 0$ around $\alpha = \alpha^*_\gamma$. Therefore

$$\operatorname{Re}\xi_+ = \frac{1}{2}\operatorname{tr} A,$$

and the transversality condition (9) is expressed as

$$\frac{d}{d\alpha}(\operatorname{tr} A)\Big|_{\alpha=\alpha^*_\gamma} = \frac{d}{d\alpha}\left(-\frac{\gamma(\alpha\gamma+\alpha+\gamma-1)}{\alpha(1+\gamma)}\right)\Big|_{\alpha=\alpha^*_\gamma} \neq 0, \tag{10}$$

Now it requires some standard computations to check that

$$\frac{d}{d\alpha}(\operatorname{tr} A)\Big|_{\alpha=\alpha^*_\gamma} = -\frac{(1-\gamma)\gamma}{(1+\gamma)\alpha^2}\Big|_{\alpha=\alpha^*_\gamma} = -\frac{(1+\gamma)\gamma}{1-\gamma} \neq 0.$$

Thus the transversality condition (9) holds. Finally from (6) and (7) we have that

$$\operatorname{tr} A < 0 \quad \text{if} \quad 0 < \alpha < \alpha^*_\gamma \quad \text{and} \quad \operatorname{tr} A > 0 \quad \text{if} \quad \alpha > \alpha^*_\gamma,$$

and thus $(\overline{u}, \overline{v})$ is an asymptotically stable constant equilibrium if $0 < \alpha < \alpha^*_\gamma$, but an unstable constant equilibrium if $\alpha > \alpha^*_\gamma$. □

Now we analyze the system (1) numerically to confirm the results obtained in Theorem 4.1. Let us fix the value of the parameter $\beta = 1$ and $\gamma = -0.5$ and compute to obtain the the bifurcation value $\alpha^*_{-0.5} = 3$ for the positive parameter α using (8) in Theorem 4.1. From the result of Theorem 4.1 we see that $(\overline{u}, \overline{v})$ is an asymptotically stable constant equilibrium if $0 < \alpha < 3$, but an unstable constant equilibrium if $\alpha > 3$ in this setting.

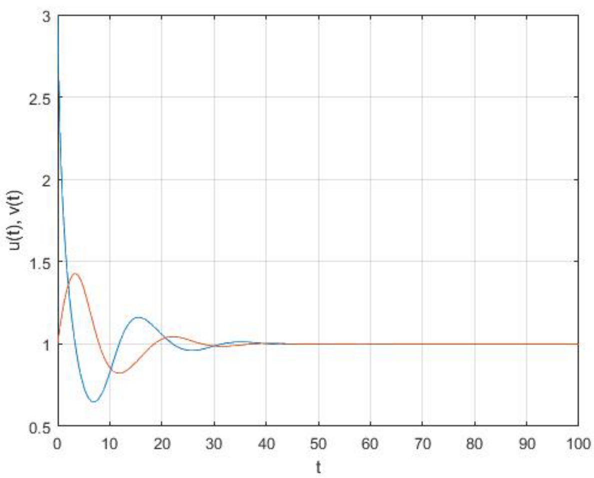

Figure 1. The graphs of the function $u(t)$ and the function $v(t)$ for the model (1) with $\alpha = 2$, $\beta = 1$, $\gamma = -0.5$, and $u(0) = 3$, $v(0) = 1$

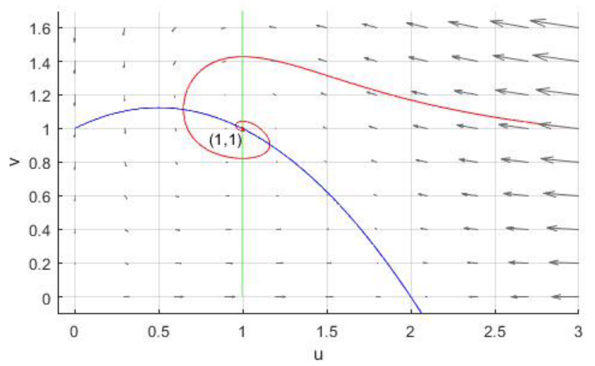

Figure 2. The phase plane behavior of $(u(t), v(t))$ for the model (1) with $\alpha = 2$, $\beta = 1$, $\gamma = -0.5$, and $u(0) = 3$, $v(0) = 1$

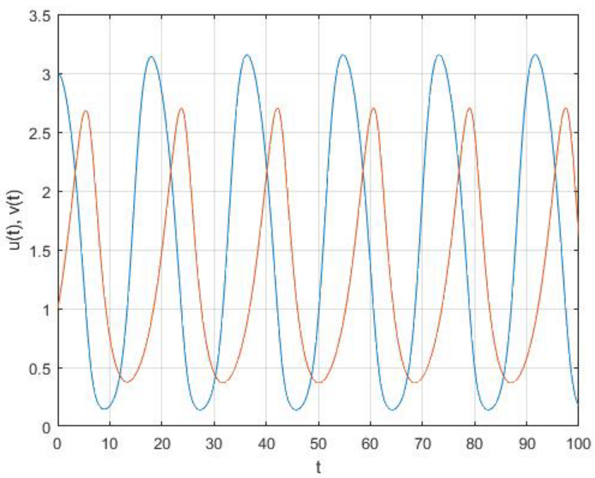

Figure 3. The graphs of the function $u(t)$ and the function $v(t)$ for the model (1) with $\alpha = 4$, $\beta = 1$, $\gamma = -0.5$, and $u(0) = 3$, $v(0) = 1$

As an example, if $\alpha = 2$, $\beta = 1$, $\gamma = -0.5$ then the positive constant equilibrium $(\overline{u}, \overline{v}) = (1, 1)$ which is obtained from the result in Lemma 4.1 is asymptotically stable, and the positive solution $(u(t), v(t))$ to the model (1) stays bounded and shows a convergent behavior to $(\overline{u}, \overline{v}) = (1, 1)$ as $t \to \infty$. Figure 1 shows the graphs of the functions $u(t)$ and $v(t)$ for $t \in (0, 100)$, and Figure 2 shows the phase plane behavior of the solution function $(u(t), v(t))$ in this case with $u(0) = 3$, $v(0) = 1$.

For another example, if $\alpha = 4$, $\beta = 1$, $\gamma = -0.5$ then the positive constant equilibrium $(\overline{u}, \overline{v}) = (1, 1.5)$ is unstable, and the positive solution $(u(t), v(t))$ to the

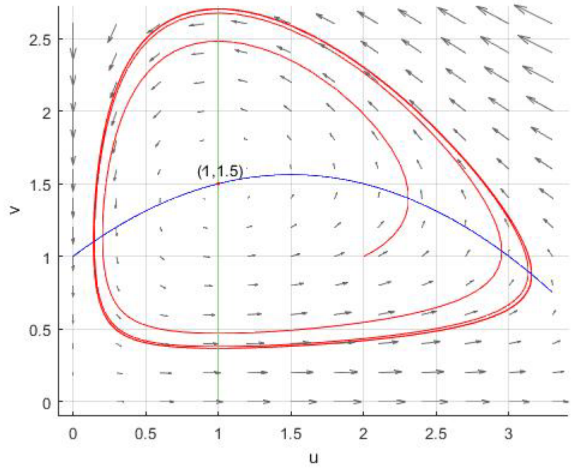

Figure 4. The phase plane behavior of $(u(t), v(t))$ for the model (1) with $\alpha = 4$, $\beta = 1$, $\gamma = -0.5$, and $u(0) = 3$, $v(0) = 1$

model (1) is bounded, but does not converge to $(\overline{u}, \overline{v})$. In this case we see that the solution function $(u(t), v(t))$ converges to an periodic orbit as $t \to \infty$. Figure 3 shows the graphs of the functions $u(t)$ and $v(t)$ in for $t \in (0, 100)$, and Figure 4 shows the phase plane behavior of the solution function $(u(t), v(t)$ in this case with $u(0) = 3$, $v(0) = 1$.

References

1. M.E. Gilpin: Do hares eat lynx?. American Naturalist. **107** (1973), 727-730.
2. C. Holling: The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Can. Entomol. **91** (1959), 293-320.
3. C. Holling: The functional response of predators to prey density and its role in mimicry and population regulation. Mem. Entomol. Soc. Can. **45** (1965), 3-60.
4. C. Jost, G. Devulder, J.A. Vucetich, R. Peterson & R. Arditi: The wolves of Isle Royale display scale-invariant satiation and density dependent predation on moose. J. Anim. Ecol. **74** (2005), no. 5, 809-816.
5. A.J. Lotka: Contribution to the Theory of Periodic Reaction. J. Phys. Chem. **14** (1910), no. 3, 271-274.
6. A.J. Lotka: Analytical Note on Certain Rhythmic Relations in Organic Systems. Proc. Natl. Acad. Sci. U.S.A. **6** (1920), 410-415.
7. M.L. Rosenzweig & R.H. MacArthur: Graphical representation and stability conditions of predator-prey interactions. American Naturalist. **97** (1963), 209-223.

8. S. Shim: Hopf Bifurcation Properties og Holling Type Predator-Prey System. J. Korea Soc. Math. Educ. Ser. B: Pure Appl. Math. **15** (2008), no. 3, 329-342.

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