

UNIQUENESS OF LIMIT CYCLES IN A ROSENZWEIG–MACARTHUR MODEL WITH PREY IMMIGRATION*

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Abstract. Many natural predator and prey populations persist while their densities show sustained oscillations. Hence these populations must be regulated in such a way that the densities are kept away from the values where extinction is likely to occur. On the other hand, nonspatial simple predator-prey models show vigorous oscillations that can bring the populations to the brink of extinction or beyond. Predator-prey systems that are kept in the laboratory also tend to show fluctuations in densities that are severe enough to drive them to extinction. Since the amount of space that laboratory populations live in is small compared to that of natural populations, one is readily led to the hypothesis that spatial interactions must contribute to the regulation of natural predator-prey systems. In this paper, we construct a simplest type of spatially interacting populations by taking into account constant immigration of prey for a predator-prey model with a Holling type II functional response and derive necessary and sufficient conditions for both the uniqueness of limit cycles and the global asymptotic stability of a positive equilibrium. From these results, it is fully suggested (mathematically) that the prey immigration dampens the large fluctuations emerging in the predator-prey model and also stabilizes a positive equilibrium globally.

Key words. predator-prey system, limit cycles, Holling type II functional response, regulation of populations, prey immigration, global asymptotic stability, Liénard system

AMS subject classifications. Primary, 34D05, 34D23, 92D25; Secondary, 34C60, 37G15, 37N25

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1. Introduction. Oscillations in densities have been observed in populations of predator-prey, host-parasite, and host-pathogen. Simple models of such systems with well-mixed populations also show vigorous oscillations that can bring the populations to the brink of extinction or beyond. For instance, based on a standard generalization of the Lotka–Volterra-derived model of Rosenzweig and MacArthur [19], when the prey carrying capacity of a stable predator-prey system is increased sufficiently, the system begins to cycle (see [18]). In fact, mathematically, the emerging structure is a limit cycle. As prey carrying capacity is increased further, this cycle brings both populations closer and closer to zero. As conventionally interpreted, when the limit cycle is sufficiently large, population extinction becomes more probable due to stochastic environmental perturbations. Predator extinction will follow if the prey species disappears, while a trophic level is lost if the predator species goes. Enrichment of the environment for the prey species thus predicts the loss of one or more trophic levels. This has become known as “the paradox of enrichment” (refer to [18]).

However, the oscillations observed in many data series of natural predator-prey populations are normally not as vigorous as the fluctuations predicted by mathematical models. Therefore, natural predator-prey systems must be regulated through a

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mechanism that is not described in the Rosenzweig–MacArthur predator-prey models. In contrast to those of natural populations, predator-prey populations that are kept in laboratory environments, where the amount of space available is much smaller than in a natural population, often do show oscillations which drive the populations to extinction (see [8, 9, 15]). This suggests that spatial elements are important in the regulation of populations.

In this paper, we consider a simplest type of spatially interacting populations by taking into account constant immigration of prey for a Rosenzweig–MacArthur predator-prey model with a Holling type II functional response. Using a theory of a generalized Liénard system which is transformed into the predator-prey models, we derive necessary and sufficient conditions for the uniqueness of limit cycles. With this framework, a limit cycle also emerges when carrying capacity of the prey population increases, and the amplitude can increase with the prey carrying capacity as well. However, because of the prey immigration, the amplitude of the fluctuations can be regulated in such a way that the densities are kept away from the values where extinction is likely to occur, which is clearly suggested by the necessary and sufficient conditions we presented.

2. Mathematical model and results. A Rosenzweig–MacArthur predator-prey model is based on the assumptions that the prey population grows logistically and that the predator has a Holling type II functional response. For a simplest spatial Rosenzweig–MacArthur predator-prey model, the additional assumption has to be made here that prey immigration occurs only outside the system. The immigration rate is assumed to be constant. That gives the following system of equations:

$$(P) \quad \begin{aligned} \frac{dx}{dt} &= r x \left(1 - \frac{x}{k}\right) - \frac{xy}{a+x} + b, \\ \frac{dy}{dt} &= y \left(\frac{\mu x}{a+x} - D\right), \end{aligned}$$

where x , y are the population sizes of prey and predator, respectively, r stands for the intrinsic growth rate of prey, and k is the carrying capacity. The saturation value of the functional response is set to 1 by a scaling, a is the half-saturation constant, μ is the conversion efficiency of the predator, and D is the predator death rate. The prey immigration rate is given by $b \geq 0$. All parameters except b are assumed to be positive.

In the case $b = 0$, the dynamics are well known: a positive equilibrium that has stably existed when $\mu > D$ and $a(\mu + D)/(\mu - D) > k > aD/(\mu - D)$ is bifurcated at $k = a(\mu + D)/(\mu - D)$, around which a stable limit cycle emerges when $k > a(\mu + D)/(\mu - D)$. As prey carrying capacity k is increased further, this cycle brings one or both populations closer and closer to zero. For large carrying capacities the densities can reach values where natural populations would certainly become extinct (which is “the paradox of enrichment”).

For spatial predator-prey models, there have been many studies on predator-prey dynamics in a single patch with a constant input (or output) of predator/prey from outside (or to outside) the system (for example, see [1, 2, 3, 4, 6, 7, 12, 13, 14, 17]). Brauer and Soudack [1, 2, 3, 4] examined the qualitative effects of constant-rate stocking of either or both species in a general type of predator-prey system, where the asymptotic behavior of such a system and the domains of attraction for stable equilibrium states were discussed. They also investigated the change in the nature of

equilibria as harvesting and stocking rates change, which was extended by Myerscough et al. [14] to obtain a much more comprehensive overall picture of predator-prey populations for the Rosenzweig-MacArthur model with constant-rate harvesting and stocking. For bifurcation analysis on a general Gause-type predator-prey model with prey harvesting, see Etoua and Rousseau [7]. Also, Li [12, 13] obtained sufficient conditions on the global asymptotic stability of a positive equilibrium and the uniqueness of limit cycles for system (P) (which were also discussed for the model derived by replacing a Holling type II functional response with a Holling type III one in system (P)). However, most studies are concerned only with local analysis around a positive equilibrium and solution behaviors in bifurcations, or with deriving sufficient conditions on global stability or the uniqueness of limit cycles in their systems. Therefore, the effects of spatial elements on the regulation of populations remain unclear. In this paper, we give necessary and sufficient conditions on both the global asymptotic stability of a positive equilibrium and the uniqueness of limit cycles for system (P), by which it is fully clarified mathematically (not by numerical works) how the prey constant immigration dampens the large amplitude of the fluctuations emerging around a positive equilibrium.

Set

$$\Omega = \{(x, y) : x > 0 \text{ and } y > 0\}.$$

From the vector field of (P), we see that all the solutions starting with $x(0) > 0$, $y(0) > 0$ are bounded and remain in Ω for all future time. System (P) has a boundary equilibrium $E_+(k/2 + c, 0)$, where $c = \sqrt{(k/2)^2 + bk/r}$. The origin can be an equilibrium of (P) only when $b = 0$. If $\mu \leq D$, or

$$\mu > D \quad \text{and} \quad k \leq \frac{r\lambda^2}{r\lambda + b},$$

then no equilibria exist in Ω , which implies that system (P) has no limit cycles, where

$$\lambda = \frac{aD}{\mu - D}.$$

On the other hand, if

$$(2.1) \quad \mu > D \quad \text{and} \quad k > \frac{r\lambda^2}{r\lambda + b},$$

then a positive equilibrium $E^*(\lambda, \nu)$ appears in Ω , where

$$(2.2) \quad \nu = \frac{\mu}{D} \left\{ r\lambda \left(1 - \frac{\lambda}{k} \right) + b \right\}.$$

System (P) does not always have a limit cycle even if the positive equilibrium E^* exists. In fact, as shown in the following result, there are no limit cycles for k close to $r\lambda^2/(r\lambda + b)$.

THEOREM 2.1. *If*

$$\mu > D \quad \text{and} \quad k \leq \lambda,$$

then system (P) has no limit cycles in Ω .

The proof of this theorem is given in section 5. Hence, to discuss limit cycles of (P), we need the assumption that

$$(2.3) \quad \mu > D \quad \text{and} \quad k > \lambda.$$

Then we obtain a necessary and sufficient condition for the existence of a unique limit cycle as follows.

THEOREM 2.2. *Suppose that (2.3) holds. If*

$$(2.4) \quad (\mu + D)\lambda + \frac{bk(\mu - D)}{r\lambda} < Dk,$$

then system (P) has a unique limit cycle in Ω ; otherwise it has no limit cycles in Ω .

The proof of this theorem is given in section 6. We remark that parameters satisfying

$$(\mu + D)\lambda + \frac{bk(\mu - D)}{r\lambda} = Dk$$

are bifurcation values. As parameters satisfying condition (2.4) approach the bifurcation values, the unique limit cycle of (P) becomes smaller and smaller until reaching positive equilibrium E^* . Hence, by combining Theorems 2.1 and 2.2, under the assumption (2.1), the positive equilibrium E^* is shown to be globally asymptotically stable if and only if (2.4) does not hold. In fact, if (2.4) does not hold, then E^* is globally asymptotically stable when $k > \lambda$ (by Theorem 2.2), while it is also when $k \leq \lambda$ (by Theorem 2.1). Since

$$D\lambda < (\mu + D)\lambda + \frac{bk(\mu - D)}{r\lambda} < Dk,$$

(2.4) implies that $k > \lambda$. Hence, if (2.4) holds, then E^* is not globally asymptotically stable by Theorem 2.2. We therefore conclude the following result.

THEOREM 2.3. *Suppose that (2.1) holds. Then the positive equilibrium E^* is globally asymptotically stable if and only if*

$$(2.5) \quad (\mu + D)\lambda + \frac{bk(\mu - D)}{r\lambda} \geq Dk$$

holds.

3. Ecological interpretations and discussion. In Theorems 2.2 and 2.3, we provide necessary and sufficient conditions on both the uniqueness of limit cycles and the global asymptotic stability of a positive equilibrium for system (P). These mean that (P) has only one limit cycle whenever it exists. A limit cycle emerging from a Hopf bifurcation is kept unique even far from the bifurcation points. Reversing a remark from section 2, we can say that the limit cycle becomes larger and larger as parameters satisfying (2.4) are farther and farther away from the bifurcation points. Let $\mu > D$ here, which is a reasonable assumption for the maintenance of the predator population.

Suppose that $k \leq \lambda$. Then, without prey immigration, there is no positive equilibrium. In the absence of positive equilibrium, Theorem 2.1 tells us that a boundary equilibrium E_+ not only is stable but also attracts all positive solutions of (P). In other words, the equilibrium E_+ is globally asymptotically stable. As the prey immigration rate b is increased from 0, a positive equilibrium becomes feasible when

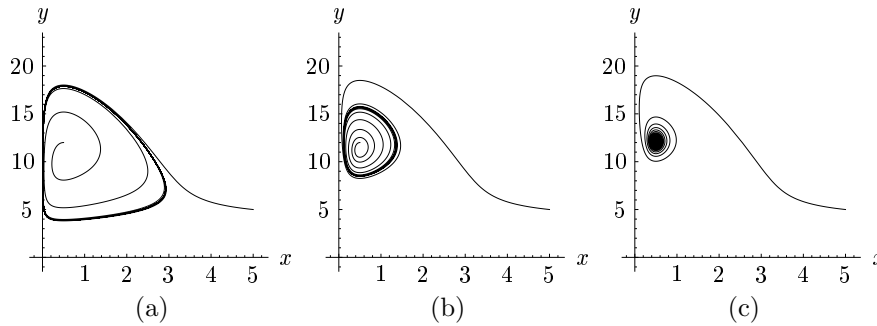


FIG. 1. Phase-plane plots of predators over prey are shown for $r = 6$, $k = 4$, $a = 1.5$, $\mu = 2$, $D = 0.5$, and various values of b : (a) $b = 0$, a unique limit cycle emerges, to which all trajectories are attracted; (b) $b = 0.2$, as (a), but the amplitude of the unique limit cycle is now smaller; (c) $b = 0.4$, all trajectories are attracted to a positive equilibrium. In both (a) and (b), two kinds of positive orbits are drawn where one starts at the point $(5, 5)$ on the outside of the limit cycle and the other at the point $(0.5, 12)$ on the inside (the limit cycle is shown by the thick black line).

$\lambda \geq k > r\lambda^2/(r\lambda + b)$ and is ensured by Theorem 2.3 to be always globally asymptotically stable. Constant-rate prey immigration is suggested as a factor which enables species to stably coexist.

If we suppose that $k > \lambda$, there is a positive equilibrium even without prey immigration. Without prey immigration, the positive equilibrium is globally asymptotically stable for the case $(\mu + D)\lambda/D \geq k > \lambda$, while a unique limit cycle exists for the case $k > (\mu + D)\lambda/D$. As described above, the increase in k amplifies the amplitude of the fluctuations. As the prey immigration rate b is increased from 0, however, the positive equilibrium that has been globally asymptotically stable still has the same properties for the former case, while the limit cycle takes both populations farther and farther from zero for the latter case since it becomes smaller and smaller as it reaches the positive equilibrium (as illustrated in Figure 1).

The prey immigration rate b might increase with an enrichment barometer k . Because of the role of b shown above, this case predicts that the amplitude of emerging fluctuations does not become so large compared with the no prey immigration case even if k increases. Extremely speaking, if b is an increasing function of k that has a particular relationship with k such as

$$b \geq rD\lambda/(\mu - D) - r(\mu + D)\lambda^2/(k(\mu - D))$$

(where the right-hand side of this inequality is also an increasing function of k), then by Theorem 2.3 we do not observe any limit cycles even with increasing k (see Figure 2).

In this paper, we extend a simplest spatial Rosenzweig–MacArthur predator-prey model by taking into account constant immigration of prey. One novel aspect of our model, however, is a clear formulation representing the effect of prey immigration by necessary and sufficient conditions derived for both the uniqueness of limit cycles and the global asymptotic stability of a positive equilibrium. In the context of a stabilizing mechanism, our model prediction does not violate the fact that immigration uncoupled from local dynamics is a stabilizing effect on parasitoid-host and predator-prey models (see [5]). Prey immigration introduced here stabilizes/regulates globally predator-prey populations in a simple framework, promoting equilibrium of the prey

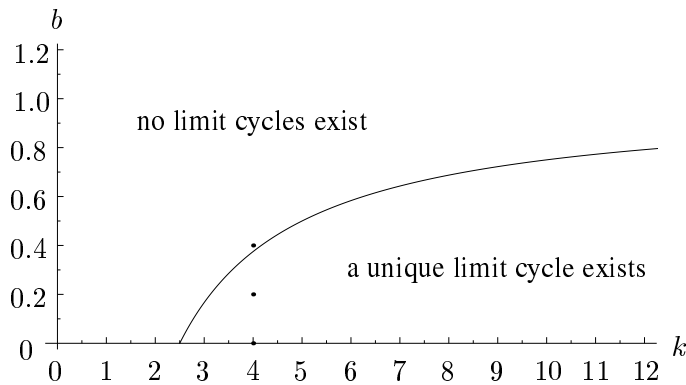


FIG. 2. Graph of the threshold $b = r D \lambda / (\mu - D) - r (\mu + D) \lambda^2 / (k (\mu - D))$. No limit cycles exist on or above the curve, while a unique limit cycle exists under the curve. Here, $r = 6$, $a = 1.5$, $\mu = 2$, $D = 0.5$, and three pairs of (b, k) (shown as dots) correspond to those of the three cases in Figure 1.

population level. The proof of these results is long but represents a standard way of transforming the system into one of Liénard theory.

The plots of the threshold in terms of k and b for the emergence of a limit cycle tell us how constant-rate prey immigration can enlarge the region in parameter space where limit cycles do not exist (see Figure 2 again). As the prey immigration rate becomes larger and larger, the region in parameter space where a limit cycle emerges becomes smaller and smaller. For the case $b \geq r D \lambda / (\mu - D)$, in particular, limit cycles never emerge even if k increases.

To expand upon this model, the next steps include the consideration of higher trophic level, more general functional responses, the roles of other spatial elements, and more general formulations for species immigration (or migration). Developing these considerations will lead to mathematically interesting difficulties that require a wider variety of techniques to resolve. Predator-prey dynamics have been extensively modeled and analyzed in the field of theoretical ecology while simultaneously having numerical considerations on various types of spatially interacting populations (for example, see [10, 16]). However, ample room remains for further exploration from the viewpoint of mathematics. Mathematically rigorous derivations of necessary and sufficient conditions on the unique existence and nonexistence of limit cycles for predator-prey populations, such as the present model, will also help to improve our understanding of predator-prey interactions as well as explore solutions to the paradox of enrichment.

4. Preliminaries.

4.1. Transformation. A general Liénard system is described by the following ordinary differential equations:

$$(4.1) \quad \begin{aligned} \frac{du}{dt} &= \psi(v) - P(u), \\ \frac{dv}{dt} &= -q(u), \end{aligned}$$

where

$$(4.2) \quad P(0) = 0 \quad \text{and} \quad u q(u) > 0 \quad \text{for} \quad u \neq 0$$

and

$$(4.3) \quad \psi(v) \text{ is increasing for } v \in \mathbb{R} \text{ and } v \psi(v) > 0 \text{ if } v \neq 0.$$

Note that the origin is the only critical point of system (4.1) under the assumptions (4.2) and (4.3). In order to transform system (P) into a Liénard-type system, we use the transformation

$$u = x - \lambda, \quad v = \log \nu - \log y, \quad d\tau = \frac{x}{a + x} dt.$$

Then system (P) is reduced to

$$\begin{aligned} \frac{du}{d\tau} &= -\nu e^{-v} + \left\{ r \left(1 - \frac{u + \lambda}{k} \right) + \frac{b}{u + \lambda} \right\} (a + u + \lambda), \\ \frac{dv}{d\tau} &= -\mu + D + \frac{aD}{u + \lambda}. \end{aligned}$$

Although the above system has six parameters, we pay attention to the parameters b and k particularly. For this purpose, we put

$$(4.4) \quad F(u; b, k) = \nu - \left\{ r \left(1 - \frac{u + \lambda}{k} \right) + \frac{b}{u + \lambda} \right\} (a + u + \lambda)$$

for $u > -\lambda$. We also define

$$(4.5) \quad g(u) = \mu - D - \frac{aD}{u + \lambda}$$

for $u > -\lambda$. Then we have

$$(4.6) \quad \begin{aligned} \frac{du}{d\tau} &= \nu(1 - e^{-v}) - F(u; b, k), \\ \frac{dv}{d\tau} &= -g(u). \end{aligned}$$

From (2.2) we see that

$$F(0; b, k) = \nu - \frac{\mu}{D} \left\{ r \lambda \left(1 - \frac{\lambda}{k} \right) + b \right\} = 0$$

and

$$u g(u) = aD \left(\frac{1}{\lambda} - \frac{1}{u + \lambda} \right) u > 0$$

for $u > -\lambda$ and $u \neq 0$. We therefore conclude that system (4.6) is a special case of the general Liénard system (4.1) with (4.2) and (4.3) by setting

$$\psi(v) = \nu(1 - e^{-v}), \quad P(u) = F(u; b, k), \quad q(u) = g(u).$$

Remark 4.1. Condition (2.4) is equivalent to $F'(0; b, k) < 0$, where the prime denotes d/du (for details, see subsection 4.3). It is easy to show that if $F'(0; b, k) < 0$, then the origin of (4.6) is locally repulsive. Hence, the Poincaré-Bendixson theorem guarantees that (4.6) has at least one limit cycle which is stable, because all solutions of (4.6) with the initial values in the region $\{(u, v) : u > -\lambda \text{ and } v \in \mathbb{R}\}$ are bounded in the future. Theorem 2.2 asserts that the number of limit cycles is exactly one.

4.2. Preliminary step for proving Theorem 2.1. For the sake of convenience, let

$$(4.7) \quad G(u) \stackrel{\text{def}}{=} \int_0^u g(s)ds = (\mu - D)u - aD(\log(u + \lambda) - \log \lambda).$$

Since $ug(u) > 0$ if $u \neq 0$, the function $G(u)$ is strictly decreasing for $-\lambda < u < 0$ and strictly increasing for $u > 0$. Also, we can easily check that $G(0) = 0$, $\lim_{u \rightarrow \infty} G(u) = \infty$, and $\lim_{u \rightarrow -\lambda} G(u) = \infty$.

By a simple modification of Theorem 3.1 in [21], we have the following result on the nonexistence of limit cycles.

THEOREM A. *Suppose that*

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

where $M = G(-\lambda + 0)$ and $G^{-1}(w)$ is the inverse function of $w = G(u)\text{sgn } u$. Then neither system (4.6) nor system (P) has limit cycles in Ω .

Noticing that $G^{-1}(0) = 0$ and $G^{-1}(w)$ is strictly increasing for $w \in \mathbb{R}$, we see that $G^{-1}(-w) < 0 < G^{-1}(w)$ for $w > 0$. If

$$(4.8) \quad uF(u; b, k) > 0 \quad \text{for } u > -\lambda \text{ and } u \neq 0,$$

then we have

$$F(G^{-1}(-w); b, k) < 0 < F(G^{-1}(w); b, k) \quad \text{for } 0 < w < M.$$

Hence, we can obtain the following corollary of Theorem A.

COROLLARY 4.1. *If (4.8) is satisfied, then system (P) has no limit cycles in Ω .*

4.3. Preliminary step for proving Theorem 2.2. To prove Theorem 2.2, we use alternative expressions of (2.4) and (2.5). Since $\mu > D$, we can define

$$(4.9) \quad \varphi(k) = \frac{r\lambda}{\mu - D} \left\{ D - \frac{(\mu + D)\lambda}{k} \right\}.$$

Then conditions (2.4) and (2.5) coincide with

$$b < \varphi(k) \quad \text{and} \quad b \geq \varphi(k),$$

respectively. These expressions are very convenient for examining the relation between two parameters b and k . Note that $\varphi(k)$ is strictly increasing for $k > 0$ and $\varphi(k^*) = 0$, where

$$k^* = \frac{\mu + D}{D}\lambda > \lambda,$$

and, therefore, $\varphi(k) < 0$ for $0 < k < k^*$ and $\varphi(k) > 0$ for $k > k^*$. Also, $\varphi(k)$ approaches the positive value

$$b^* = \frac{rD\lambda}{\mu - D}$$

as $k \rightarrow \infty$.

From the observation above, we can choose the region in which a pair of parameters b and k satisfy condition (2.5) under the assumption (2.3). Let

$$R_1 = \{(b, k) : b \geq 0 \text{ and } \lambda < k \leq k^*\},$$

$$R_2 = \{(b, k) : b \geq \varphi(k) \text{ and } k > k^*\},$$

$$R_3 = \{(b, k) : 0 \leq b < \varphi(k) \text{ and } k > k^*\}.$$

Then we see that under the assumption (2.3), a pair of parameters b and k satisfies condition (2.5) if and only if $(b, k) \in R_1 \cup R_2$. Conversely, condition (2.4) holds if and only if $(b, k) \in R_3$.

We consider the plane curve $(F(u; b, k), G(u))$ which is parametrized by $u > -\lambda$. This curve plays an important role for nonexistence of limit cycles of system (4.6), which is equivalent to system (P). To see this, we will give another interpretation of Theorem A.

Suppose that there exists a $w_0 > 0$ such that

$$F(G^{-1}(-w_0); b, k) = F(G^{-1}(w_0); b, k).$$

Let $\alpha = -G^{-1}(-w_0) > 0$ and $\beta = G^{-1}(w_0) > 0$. Then we have

$$F(-\alpha; b, k) = F(\beta; b, k) \quad \text{and} \quad G(-\alpha) = w_0 = G(\beta).$$

This means that the curve $(F(u; b, k), G(u))$ passes through the same point at $u = -\alpha$ and $u = \beta$. Conversely, if the curve has a point of intersection with itself, then

$$F(G^{-1}(-w_0); b, k) = F(G^{-1}(w_0); b, k)$$

for some $w_0 > 0$. We therefore conclude that if the curve $(F(u; b, k), G(u))$ has no points of intersection with itself, then systems (P) and (4.6) have no limit cycles in Ω .

Since $G(u)$ is strictly decreasing for $-\lambda < u < 0$ and strictly increasing for $u > 0$, the curve $(F(u; b, k), G(u))$ continues to fall until it passes through the origin, and then it keeps rising to infinity. Hence, part of the curve for $-\lambda < u < 0$ does not cross itself. Likewise, part of the curve for $u > 0$ does not cross itself. Also, $F(u; b, k)$ satisfies

$$\lim_{u \rightarrow -\lambda} F(u; b, k) = \begin{cases} \nu - ar & \text{if } b = 0, \\ -\infty & \text{otherwise} \end{cases}$$

and $\lim_{u \rightarrow \infty} F(u; b, k) = \infty$. Hence, the curve $(F(u; b, k), G(u))$ has no points of intersection with itself if and only if

$$F(u_1; b, k) < F(u_2; b, k)$$

for arbitrary u_1 and u_2 satisfying

$$-\lambda < u_1 < 0 < u_2 \quad \text{and} \quad G(u_1) = G(u_2).$$

In Figures 3–5, the amount of u increases in the direction of the arrows.

We next consider the function

$$\Gamma(u; b, k) = \frac{F'(u; b, k)}{g(u)},$$

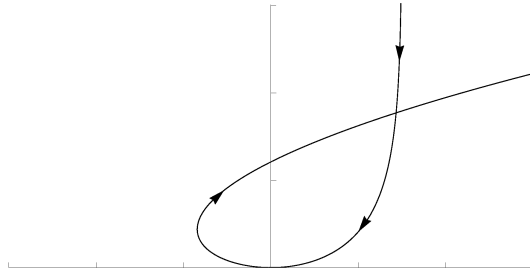


FIG. 3. The curve $(F(u; b, k), G(u))$ with $r = 6$, $k = 4$, $a = 1.5$, $\mu = 2$, $D = 0.5$, and $b = 0$.

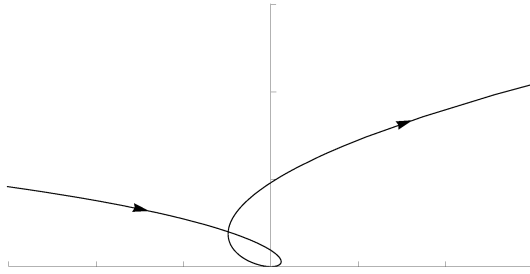


FIG. 4. The curve $(F(u; b, k), G(u))$ with $r = 6$, $k = 4$, $a = 1.5$, $\mu = 2$, $D = 0.5$, and $b = 0.2$.

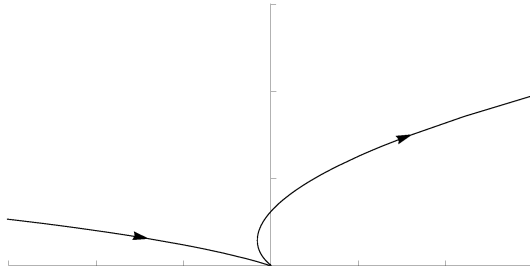


FIG. 5. The curve $(F(u; b, k), G(u))$ with $r = 6$, $k = 4$, $a = 1.5$, $\mu = 2$, $D = 0.5$, and $b = 0.4$.

which is defined for $u > -\lambda$ and $u \neq 0$. Here, $' = d/du$. Note that the reciprocal of $\Gamma(u; b, k)$ expresses the slope of the tangent line at any point on the curve $(F(u; b, k), G(u))$. By (4.4) and (4.5), we have

$$\begin{aligned}
 (4.10) \quad F'(u; b, k) &= \left\{ \frac{r}{k} + \frac{b}{(u+\lambda)^2} \right\} (a+u+\lambda) - \left\{ r \left(1 - \frac{u+\lambda}{k} \right) + \frac{b}{u+\lambda} \right\} \\
 &= \frac{r}{k} (a+u+\lambda) - r \left(1 - \frac{u+\lambda}{k} \right) + b \left\{ \frac{a}{(u+\lambda)^2} + \frac{1}{u+\lambda} \right\} \\
 &\quad - \frac{b}{u+\lambda} \\
 &= -\frac{r}{k} \{ k - 2(u+\lambda) - a \} + \frac{ab}{(u+\lambda)^2},
 \end{aligned}$$

$$(4.11) \quad F''(u; b, k) = \frac{2r}{k} - \frac{2ab}{(u + \lambda)^3},$$

and

$$(4.12) \quad g'(u) = \frac{aD}{(u + \lambda)^2}.$$

For brevity, we define

$$H(u; b, k) = F''(u; b, k)g(u) - F'(u; b, k)g'(u)$$

for $u > -\lambda$. Then

$$\Gamma'(u; b, k) = \frac{H(u; b, k)}{\{g(u)\}^2} \quad \text{for } u > -\lambda \text{ and } u \neq 0.$$

Here we examine a property of $\Gamma(u; b, k)$ in the critical case that $b = \varphi(k)$ and prove the following result, which plays an essential role in the proof of Theorem 2.2.

LEMMA 4.2. *Assume (2.3). If $k > k^*$, then the curve $(F(u; \varphi(k), k), G(u))$ has no points of intersection with itself.*

Proof. Recall that the sign of $\varphi(k)$ is determined by parameters D and μ as well as k . As seen above, the function $\varphi(k)$ is positive if $k > k^*$. From (4.4), (4.5), (4.7), (4.10), and the fact that $\mu - D = aD/\lambda$, we can easily verify that

$$F(0; \varphi(k), k) = G(0) = g(0) = 0$$

and

$$\begin{aligned} F'(0; \varphi(k), k) &= -\frac{r}{k} \left(k - 2\lambda - \frac{\mu - D}{D}\lambda \right) + \frac{(\mu - D)\varphi(k)}{D\lambda} \\ &= -\frac{r}{kD} \left\{ kD - (\mu + D)\lambda - \frac{k(\mu - D)\varphi(k)}{r\lambda} \right\} = 0. \end{aligned}$$

Hence, using L'Hospital's rule, we get

$$\lim_{u \rightarrow 0} \Gamma(u; \varphi(k), k) = \lim_{u \rightarrow 0} \frac{F''(u; \varphi(k), k)}{g'(u)}.$$

Since

$$g'(0) = \frac{\mu - D}{\lambda} > 0$$

by (4.12), we can put

$$\ell = \lim_{u \rightarrow 0} \frac{F''(u; \varphi(k), k)}{g'(u)}.$$

Let $\Gamma(0; \varphi(k), k) = \ell$. Then the function $\Gamma(u; \varphi(k), k)$ is continuous for $u > -\lambda$. If $\Gamma(u; \varphi(k), k)$ is strictly increasing for $u > -\lambda$, then the curve $(F(u; b, k), G(u))$ has no points of intersection with itself. In fact, part of the curve for $-\lambda < u < 0$ and part of the curve for $u > 0$ are separated by the straight line passing through the origin, whose slope is equal to $1/\ell$ (we interpret the straight line as the vertical axis in the case $\ell = 0$).

To prove that $\Gamma(u; \varphi(k), k)$ is strictly increasing for $u > -\lambda$, it is enough to show that $H(u; \varphi(k), k) > 0$ for $u > -\lambda$ and $u \neq 0$. By (4.5) and (4.10)–(4.12), we have

$$F'(u; \varphi(k), k)g'(u) = -\frac{arD}{k} \left\{ \frac{k}{(u+\lambda)^2} - \frac{2}{u+\lambda} - \frac{a}{(u+\lambda)^2} \right\} + \frac{a^2 D \varphi(k)}{(u+\lambda)^4}$$

and

$$F''(u; \varphi(k), k)g(u) = \frac{arD}{k} \left\{ \frac{2}{\lambda} - \frac{2}{u+\lambda} \right\} - 2a^2 D \varphi(k) \left\{ \frac{1}{\lambda(u+\lambda)^3} - \frac{1}{(u+\lambda)^4} \right\}.$$

Hence, we get

$$\begin{aligned} H(u; \varphi(k), k) &= \frac{arD}{k} \left\{ -\frac{a}{(u+\lambda)^2} + \frac{k}{(u+\lambda)^2} - \frac{4}{u+\lambda} + \frac{2}{\lambda} \right\} \\ &\quad + \frac{a^2 D \varphi(k)}{\lambda} \left\{ \frac{\lambda}{(u+\lambda)^4} - \frac{2}{(u+\lambda)^3} \right\} \\ &= \frac{arD}{k} \left\{ -\frac{a}{(u+\lambda)^2} + \frac{(\mu+D)\lambda}{D(u+\lambda)^2} - \frac{4}{u+\lambda} + \frac{2}{\lambda} + \frac{k(\mu-D)\varphi(k)}{rD\lambda(u+\lambda)^2} \right\} \\ &\quad + \frac{a^2 D \varphi(k)}{\lambda} \left\{ \frac{\lambda}{(u+\lambda)^4} - \frac{2}{(u+\lambda)^3} \right\} \\ &= \frac{arD}{k} \left\{ -\frac{a}{(u+\lambda)^2} + \frac{(\mu+D)\lambda}{D(u+\lambda)^2} - \frac{4}{u+\lambda} + \frac{2}{\lambda} \right\} \\ &\quad + \frac{a(\mu-D)\varphi(k)}{\lambda(u+\lambda)^2} + a(\mu-D)\varphi(k) \left\{ \frac{\lambda}{(u+\lambda)^4} - \frac{2}{(u+\lambda)^3} \right\} \\ &= \frac{2arDu^2}{k\lambda(u+\lambda)^2} + \frac{a(\mu-D)\varphi(k)u^2}{\lambda(u+\lambda)^4}. \end{aligned}$$

From (2.3), we see that $H(u; \varphi(k), k)$ is positive for $u > -\lambda$ and $u \neq 0$ and, therefore, $\Gamma(u; \varphi(k), k)$ is strictly increasing for $u > -\lambda$. \square

5. Proof of Theorem 2.1. We prove Theorem 2.1 by using Corollary 4.1.

Proof of Theorem 2.1. In the case $k \leq r\lambda^2/(r\lambda + b)$, system (P) has no positive equilibrium. It naturally has no limit cycles in Ω . Hence, we consider only the case that

$$(5.1) \quad \frac{r\lambda^2}{r\lambda + b} < k \leq \lambda.$$

Let

$$h_1(u) = \frac{a}{u+\lambda} + 1$$

and

$$h_2(u; b, k) = r(u+\lambda) \left(1 - \frac{u+\lambda}{k} \right) + b$$

for $u > -\lambda$. Then

$$(5.2) \quad F(u; b, k) = \nu - h_1(u)h_2(u; b, k).$$

It is clear that

$$(5.3) \quad h_1(u) \geq 1$$

and

$$(5.4) \quad h_1'(u) = -\frac{a}{(u+\lambda)^2} < 0$$

for $u > -\lambda$. Since

$$h_2(u; b, k) = -\frac{r}{k} \left(u + \lambda - \frac{k}{2}\right)^2 + b + \frac{kr}{4},$$

it has the maximum value at $u = -\lambda + k/2 < 0$. From (5.1) it follows that

$$h_2(0; b, k) = r\lambda \left(1 - \frac{\lambda}{k}\right) + b > 0.$$

Hence, it turns out that

$$(5.5) \quad \begin{aligned} h_2(u; b, k) &> 0 && \text{for } -\lambda < u < \hat{u}, \\ h_2(u; b, k) &\leq 0 && \text{for } u \geq \hat{u} \end{aligned}$$

for some $\hat{u} > 0$, and

$$(5.6) \quad h_2'(u; b, k) < 0 \quad \text{for } u > -\lambda + \frac{k}{2}.$$

By (5.2)–(5.6), we have

$$F'(u; b, k) = -h_1'(u)h_2(u; b, k) - h_1(u)h_2'(u; b, k) > 0$$

for $0 \leq u < \hat{u}$. Hence, using (2.2), we obtain

$$(5.7) \quad \begin{aligned} F(u; b, k) &> F(0; b, k) = \nu - h_1(0)h_2(0; b, k) \\ &= \nu - \frac{\mu}{D} \left\{ r\lambda \left(1 - \frac{\lambda}{k}\right) + b \right\} = 0 \end{aligned}$$

for $0 < u < \hat{u}$. By (5.2), (5.3), and (5.5), we also have

$$(5.8) \quad F(u; b, k) \geq \nu \quad \text{for } u \geq \hat{u}.$$

Here we define the function

$$\tilde{h}_2(u; b, k) = r(u + \lambda) \left(1 - \frac{\lambda}{k}\right) + b$$

for $u > -\lambda$. Then we get

$$\lim_{u \rightarrow -\lambda} \tilde{h}_2(u; b, k) = b = \lim_{u \rightarrow -\lambda} h_2(u; b, k)$$

and

$$\tilde{h}_2(0; b, k) = r\lambda \left(1 - \frac{\lambda}{k}\right) + b = h_2(0; b, k).$$

Since $h_2(u; b, k)$ is upwards convex and $\tilde{h}_2(u; b, k)$ is linear, we have

$$(5.9) \quad h_2(u; b, k) > \tilde{h}_2(u; b, k) > 0$$

for $-\lambda < u < 0$. From (5.1) we see that

$$(5.10) \quad \tilde{h}_2'(u; b, k) = r \left(1 - \frac{\lambda}{k} \right) \leq 0$$

for $u > -\lambda$.

Let

$$\tilde{F}(u; b, k) = \nu - h_1(u)\tilde{h}_2(u; b, k).$$

Then, using (5.3), (5.4), (5.9), and (5.10), we obtain

$$\tilde{F}'(u; b, k) = -h_1'(u)\tilde{h}_2(u; b, k) - h_1(u)\tilde{h}_2'(u; b, k) > 0$$

for $-\lambda < u < 0$. Hence, by (2.2) again, we have

$$\begin{aligned} \tilde{F}(u; b, k) &< \tilde{F}(0; b, k) = \nu - h_1(0)\tilde{h}_2(0; b, k) \\ &= \nu - \frac{\mu}{D} \left\{ r\lambda \left(1 - \frac{\lambda}{k} \right) + b \right\} = 0 \end{aligned}$$

for $-\lambda < u < 0$. By (5.2), (5.3), and (5.9), we get

$$(5.11) \quad F(u; b, k) < \tilde{F}(u; b, k) < 0$$

for $-\lambda < u < 0$.

From (5.7), (5.8), and (5.11) we conclude that

$$uF(u; b, k) > 0 \quad \text{for } u > -\lambda \text{ and } u \neq 0,$$

namely, (4.8). Thus, by Corollary 4.1, system (P) has no limit cycles in Ω . □

6. Proof of Theorem 2.2. There are two components in Theorem 2.2. We can divide Theorem 2.2 into the following two propositions.

PROPOSITION 6.1. *If (2.3) and (2.5) are satisfied, then system (P) has no limit cycles in Ω .*

PROPOSITION 6.2. *If (2.3) and (2.4) are satisfied, then system (P) has a unique limit cycle in Ω .*

6.1. Nonexistence of limit cycles. In a series of papers [20, 22, 23, 24], Sugie and coworkers studied a more general predator-prey system than system (P) with $b = 0$:

$$(6.1) \quad \begin{aligned} \frac{dx}{dt} &= r x \left(1 - \frac{x}{k} \right) - \frac{x^p y}{a + x^p}, \\ \frac{dy}{dt} &= y \left(\frac{\mu x^p}{a + x^p} - D \right), \end{aligned}$$

where p is an arbitrary positive number. We can describe the following theorems by combining their results.

THEOREM B. *Suppose that (2.3) holds. Then system (6.1) has exactly one limit cycle in Ω if and only if*

$$(pD - (p - 2)\mu)\lambda < (pD - (p - 1)\mu)k.$$

To be exact, if

$$(6.2) \quad (pD - (p-2)\mu)\lambda \geq (pD - (p-1)\mu)k,$$

then system (6.1) has no limit cycles in Ω . As a matter of fact, the “only if” part of Theorem B is proved by the use of Theorem A. In the special case that $p = 1$, condition (6.2) coincides with $k^* \geq k$. If $\lambda < k \leq k^*$, then

$$(6.3) \quad F(u_1; 0, k) < F(u_2; 0, k)$$

holds for arbitrary u_1 and u_2 satisfying

$$-\lambda < u_1 < 0 < u_2 \quad \text{and} \quad G(u_1) = G(u_2)$$

(for details, see [20, 22, 23, 24]). Using this fact and Lemma 4.2, we give the proof of Proposition 6.1.

Proof of Proposition 6.1. Recall that condition (2.5) holds if and only if $(b, k) \in R_1 \cup R_2$ under the assumption (2.3) (see subsection 4.3).

Suppose that $(b, k) \in R_1$. Then, $\lambda < k \leq k^*$. Partially differentiate $F(u; b, k)$ with respect to b to obtain

$$\frac{\partial}{\partial b} F(u; b, k) = \frac{\mu}{D} - \frac{a}{u + \lambda} - 1 = \frac{a u}{\lambda(u + \lambda)}$$

so that

$$(6.4) \quad \begin{aligned} \frac{\partial}{\partial b} F(u; b, k) &< 0 \quad \text{for} \quad -\lambda < u < 0, \\ \frac{\partial}{\partial b} F(u; b, k) &> 0 \quad \text{for} \quad u > 0. \end{aligned}$$

Hence, using (6.3), we have

$$F(u_1; b, k) \leq F(u_1; 0, k) < F(u_2; 0, k) \leq F(u_2; b, k)$$

for arbitrary u_1 and u_2 satisfying $-\lambda < u_1 < 0 < u_2$ and $G(u_1) = G(u_2)$. This estimation shows that the curve $(F(u; b, k), G(u))$ has no points of intersection with itself. Consequently, it follows from Theorem A that system (P) has no limit cycles in Ω .

Suppose that $(b, k) \in R_2$. Then, $b \geq \varphi(k)$. Hence, from (6.4) it turns out that

$$F(u_1; b, k) \leq F(u_1; \varphi(k), k) \quad \text{and} \quad F(u_2; \varphi(k), k) \leq F(u_2; b, k),$$

where $-\lambda < u_1 < 0 < u_2$. Since $(b, k) \in R_2$, it follows that $k > k^*$. Hence, by means of Lemma 4.2, we see that the curve $(F(u; \varphi(k), k), G(u))$ has no points of intersection with itself and, therefore,

$$F(u_1; \varphi(k), k) < F(u_2; \varphi(k), k),$$

where $G(u_1) = G(u_2)$. Hence, we obtain

$$F(u_1; b, k) < F(u_2; b, k)$$

for arbitrary u_1 and u_2 satisfying

$$-\lambda < u_1 < 0 < u_2 \quad \text{and} \quad G(u_1) = G(u_2),$$

which implies that the curve $(F(u; b, k), G(u))$ also has no points of intersection with itself. Using Theorem A again, we see that system (P) has no limit cycles in Ω . \square

6.2. Uniqueness of limit cycles. Recall that system (P) is equivalent to the general Liénard system (4.1) with

$$(6.5) \quad \psi(v) = \nu(1 - e^{-v}), \quad P(u) = F(u; b, k), \quad q(u) = g(u),$$

and that $\psi(v)$, $P(u)$, and $q(u)$ given by (6.5) satisfy the assumptions (4.2) and (4.3) (see subsection 4.1). As described in Remark 4.1, if condition (2.4) is satisfied, then system (4.1) with (6.5) has at least one stable limit cycles, and so does system (P). Hence, to prove Proposition 6.2, we have only to show that system (P) has at most one limit cycle.

Many studies have been made on the existence of at most one limit cycle of (4.1) under the assumptions (4.2) and (4.3) (for example, see [25, 26, 27] and references therein). Here we present a modification of Zhang’s theorem in [26] without proof (Kuang and Freedman [11] also modified the same theorem).

THEOREM C. *Assume (4.2) and (4.3). If $P'(0) < 0$, and if $P'(u)/q(u)$ is nondecreasing for $u \neq 0$, then system (4.1) has at most one limit cycle.*

Note that $P'(0) = F'(0; b, k) < 0$ if and only if (2.4) holds. Taking the relation (6.5) into account and applying Theorem C to system (4.6), we have the following result.

LEMMA 6.3. *Suppose that (2.3) and (2.4) hold. If $\Gamma(u; b, k)$ is nondecreasing for $u > -\lambda$ and $u \neq 0$, then system (4.6) has at most one limit cycle, and so does system (P).*

We prove Proposition 6.2 by using Lemma 6.3.

Proof of Proposition 6.2. We will show that $\Gamma(u; b, k)$ is nondecreasing for $u > -\lambda$ and $u \neq 0$. To see this, it is enough to show that $H(u; b, k) > 0$ for $u > -\lambda$ and $u \neq 0$.

By (4.5) and (4.10)–(4.12), we have

$$\begin{aligned} H(u; b, k) &= F''(u; b, k)g(u) - F'(u; b, k)g'(u) \\ &= \frac{arD}{k} \left\{ -\frac{a}{(u + \lambda)^2} + \frac{k}{(u + \lambda)^2} - \frac{4}{u + \lambda} + \frac{2}{\lambda} \right\} \\ &\quad + \frac{a^2bD}{\lambda} \left\{ \frac{\lambda}{(u + \lambda)^4} - \frac{2}{(u + \lambda)^3} \right\}. \end{aligned}$$

Partially differentiating $H(u; b, k)$ with respect to b , we obtain

$$\frac{\partial}{\partial b} H(u; b, k) = -\frac{a^2D}{\lambda(u + \lambda)^4}(\lambda + 2u)$$

and, therefore,

$$\begin{aligned} \frac{\partial}{\partial b} H(u; b, k) &> 0 \quad \text{for } -\lambda < u < -\frac{\lambda}{2}, \\ \frac{\partial}{\partial b} H(u; b, k) &\leq 0 \quad \text{for } u \geq -\frac{\lambda}{2}. \end{aligned}$$

As mentioned in subsection 4.3, condition (2.4) holds if and only if $(b, k) \in R_3$, namely, $b < \varphi(k)$ and $k > k^*$. Since $b < \varphi(k)$, we see that

$$(6.6) \quad H(u; b, k) \geq H(u; \varphi(k), k) \quad \text{for } u \geq -\frac{\lambda}{2} \text{ and } u \neq 0.$$

Since $k > k^*$, we can use Lemma 4.2. As shown in the proof of Lemma 4.2, $H(u; \varphi(k), k)$ is positive for $u > -\lambda$ and $u \neq 0$. Hence, by (6.6), we obtain

$$H(u; b, k) > 0 \quad \text{for } u \geq -\frac{\lambda}{2} \text{ and } u \neq 0.$$

On the other hand, we have

$$(6.7) \quad H(u; b, k) \geq H(u; 0, k) \quad \text{for } -\lambda < u < -\frac{\lambda}{2}.$$

Using the fact that $\mu - D = aD/\lambda$ and $k > k^* = (\mu + D)\lambda/D$, we get

$$\begin{aligned} H(u; 0, k) &= \frac{arD}{k} \left\{ -\frac{a}{(u+\lambda)^2} + \frac{k}{(u+\lambda)^2} - \frac{4}{u+\lambda} + \frac{2}{\lambda} \right\} \\ &> \frac{arD}{k} \left\{ -\frac{a}{(u+\lambda)^2} + \frac{(\mu+D)\lambda}{D(u+\lambda)^2} - \frac{4}{u+\lambda} + \frac{2}{\lambda} \right\} \\ &= \frac{2arDu^2}{k\lambda(u+\lambda)^2} > 0 \end{aligned}$$

for $u > -\lambda$ and $u \neq 0$. Hence, from (6.7) we see that

$$H(u; b, k) > 0 \quad \text{for } -\lambda < u < -\frac{\lambda}{2}.$$

We therefore conclude that $H(u; b, k) > 0$ for $u > -\lambda$ and $u \neq 0$. \square

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