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ORIGINAL ARTICLE

Spreading Speed in an Integrodifference Predator–Prey System without Comparison Principle

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Abstract
In this paper, we study the spreading speed in an integrodifference system which models invasion of predators into the habitat of the prey. Without the requirement of comparison principle, we construct several auxiliary integrodifference equations and use the results of monotone scalar equations to estimate the spreading speed of the invading predators. We also present some numerical simulations to support our theoretical results and demonstrate that the integrodifference predator–prey system exhibits very complex dynamics. Our theory and numerical results imply that the invasion of predators may have a rough constant speed. Moreover, our numerical simulations indicate that the spatial contact of individuals and the overcompensatory phenomenon of the prey may be conducive to the persistence of nonmonotone biological systems and lead to instability of the predator-free state.

Keyword Integrodifference equations · Asymptotic spreading · Auxiliary equation · Noncooperative system

Mathematics Subject Classification 35C07 · 39A20 · 37C65

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1 Introduction

Discrete-time models may describe the evolutionary process of species with non-overlapping generations, and there are many well-studied difference systems modeling the interspecific and intraspecific actions among multiple species; we refer to some classical references on discrete predator–prey models by Beddington et al. (1975), Hastings (1984), Hofbauer et al. (1987), May (1974), Nicholson and Bailey (1935), a very recent paper by Weide et al. (2019) and references cited therein. Among these works, Hofbauer et al. (1987) studied the dynamics of the following coupled system

$$U_{i,n+1} = U_{i,n} \exp\left(r_i - \sum_{j=1}^{K} a_{ij} U_{j,n}\right), \quad U_{i,0} > 0, \tag{1}$$

in which $U_{i,n}$ represents the density of the ith species in the system of the nth generation, $i, j \in \{1, 2, \ldots, K\}$, $K \in \mathbb{N}$ is a constant, $n + 1 \in \mathbb{N}$ and other parameters are given to formulate the ratios of interspecific and intraspecific actions. When $K = 2$, model (1) takes the form as follows:

$$U_{1,n+1} = U_{1,n} \exp\left(r_1 - \sum_{j=1}^{2} a_{1j} U_{j,n}\right), \quad U_{2,n+1} = U_{2,n} \exp\left(r_2 - \sum_{j=1}^{2} a_{2j} U_{j,n}\right) \tag{2}$$

with $U_{1,0} > 0$, $U_{2,0} > 0$. Clearly, by selecting different parameters, model (2) may be of competitive type (if $a_{12} < 0$, $a_{21} < 0$), cooperative type (if $a_{12} > 0$, $a_{21} > 0$) or predator–prey type (if $a_{12}a_{21} < 0$). After scaling, one predator–prey system takes the following form:

$$\begin{cases} u_{n+1} = u_n e^{r_1(1-u_n-a_1 v_n)}, & n+1 \in \mathbb{N} \\ v_{n+1} = v_n e^{r_2(-1-v_n+a_2 u_n)}, & n+1 \in \mathbb{N} \\ u_0 > 0,\ v_0 > 0, \end{cases} \tag{3}$$

in which u_n and v_n are the densities of the prey and predators at the nth generation, respectively, r_1 and r_2 reflect their intrinsic growth rates, $a_1 \geq 0$ is related to the predation rate (searching efficiency, handling time, attack coefficient, etc.) of the prey by predators and $a_2 > 0$ is the conversion rate of the prey into the growth of predators.

The movement of living organisms is incredibly frequent and diverse. Different spatiotemporal models have been constructed to describe how, when and where animals, plants and microorganisms move (Nathan and Giuggioli 2013). When some species with non-overlapping generations are concerned, their evolution processes may be characterized by growth–dispersal; that is, the dispersal and the growth occur at different stages of the species. In their pioneer studies, Mollison (1977) and Weinberger (1982) investigated the growth–dispersal phenomenon and proposed discrete-time models equipping with spatial variables, which are integrodifference equations. More examples of integrodifference equations can be found in Bourgeois and LeBlanc (2017), Carrillo and Fife (2005), Jacobsen et al. (2015), Kot (1992), Kot and Schaffer (1986), Lui (1989b) and a recent book by Lutscher (2019). In particular, an integrodifference system of predator-prey interaction was proposed by Neubert et al. (1995). Equipping (3) with the effect of growth–dispersal in the spatial domain $\mathbb{R}$, we obtain the following integrodifference predator–prey model:

$$\begin{cases} u_{n+1}(x) = \int_{\mathbb{R}} u_n(y) e^{r_1(1-u_n(y)-a_1 v_n(y))} \overline{k}_1(x,y)\mathrm{d}y, & x \in \mathbb{R}, \quad n+1 \in \mathbb{N}, \\ v_{n+1}(x) = \int_{\mathbb{R}} v_n(y) e^{r_2(-1-v_n(y)+a_2 u_n(y))} \overline{k}_2(x,y)\mathrm{d}y, & x \in \mathbb{R}, \quad n+1 \in \mathbb{N}, \\ u_0(x) = u(x), \ v_0(x) = v(x), & x \in \mathbb{R}, \end{cases} \tag{4}$$

where $u_n(x)$ and $v_n(x)$, respectively, denote the densities of the prey and predators at location x of the nth generation, $\overline{k}_1(x, y)$ and $\overline{k}_2(x, y)$ formulate the spatial movement law (Carrillo and Fife 2005; Turchin 1998) and may be interpreted as probability functions to be clarified later, $u(x)$ and $v(x)$ define the initial distribution of the prey and predators, respectively.

To understand the ecological interactions in natural world, one basic topic is to explore how predators invade the habitat of the prey and how the energy transfers among different species, see some natural phenomena and mathematical models in Fagan and Bishop (2000), Murray (2003), Owen and Lewis (2001), Shigesada and Kawasaki (1997). To model the invasion process, the initial data of the system should satisfy proper conditions and we assume that

(A1) the initial function $u(x)$ is positive and uniformly continuous such that

$$0 < \liminf_{x \in \mathbb{R}} u(x) \le \limsup_{x \in \mathbb{R}} u(x) < \infty$$

and the initial function $v(x)$ is nonnegative, continuous and has a nonempty compact support.

Biologically, the assumption on the initial conditions states that the prey is the aborigine distributed uniformly in the whole space $\mathbb{R}$ while predators are invaders occupying a habitat with finite size. Besides the well-studied traveling wave solutions of predator–prey systems since Dunbar (1983), the feature of the invasion process has been recently characterized by the spreading speed that was first proposed by Aronson and Weinberger (1975) for scalar reaction-diffusion equations. In particular, Ducrot (2013, 2016) and Pan (2017) estimated the invasion speed of the predators in predator–prey systems when these systems admit the comparison principle appealing to predator–prey systems in Ye et al. (2011), and Lin et al. (2019) studied the spreading speed in an epidemic model with local monotonicity induced by nonlocal delay.

When the spatial and temporal variables are $x \in \mathbb{R}$ and $n \in \mathbb{N}$, the spreading speed of a nonnegative function is defined as follows:

Definition 1.1 Let $v_n(x)$, $n \in \mathbb{N}$, $x \in \mathbb{R}$, be nonnegative. A constant c^* is said to be the *spreading speed* of $v_n(x)$ if

(S1) $\liminf_{n\to\infty} \inf_{|x|<cn} v_n(x) > 0$ for any given $c \in (0, c^*)$;
(S2) $\limsup_{n\to\infty} \sup_{|x|>cn} v_n(x) = 0$ for any given $c > c^*$.

In population dynamics, the spreading speed describes the observed phenomenon if an observer were to move to the right or left at a fixed speed [that is, c in Definition 1.1 denotes the moving speed of the observer, see Weinberger et al. (2002)], so the speed is useful to understand the spatial expansion of individuals and is an useful index formulating population invasion (Murray 2003; Shigesada and Kawasaki 1997).

From the viewpoint of monotonicity of dynamical systems, a difference equation that is the spatially homogeneous model of the corresponding integrodifference equation may be nonmonotone and still generates complex dynamics, which often models the overcompensatory phenomenon in population dynamics [see Ali et al. (2003), May (1974, 1976), Murray (2002, Section 2.3)]. For example, fix $K = 1$ in (1) and consider

$$U_{n+1} = U_n e^{2(1-U_n)}, \quad U_0 \in (0.5, 1), \quad n+1 \in \mathbb{N},$$

then a larger U_0 leads to a smaller U_1, which is also the property of component u_n by taking $a_1 = 0$ in (3). Therefore, the above difference equation does not have the classical comparison principle in its positive invariant interval $[0, e/2]$. For the coupled system (1), it may have more complex dynamics and one may observe its plentiful dynamics in Hofbauer et al. (1987). Furthermore, it is natural to believe that (4) may admit rich spatiotemporal propagation modes. The purpose of this paper is to investigate the integrodifference system (4) by estimating the invasion speed of predators.

To better present the mathematical idea, we first investigate the case when $r_1 \in (0, 1]$ such that

$$u_{n+1} = u_n e^{r_1(1-u_n)}, \quad u_0 \in [0, 1]$$

is monotone and invariant. Under the assumption, one has $u_n(x) \in [0, 1], n \in \mathbb{N}, x \in \mathbb{R}$, but the second component may be nonmonotone in v_n such that the comparison principle does not hold. Then, we study the case when $r_1 \in (1, 2)$ such that the above difference equation is not monotone, so the coupled system does not satisfy the comparison principle. Since $u_n(x) \notin [0, 1], n \in \mathbb{N}, x \in \mathbb{R}$, even the upper bound of the spreading speed of v is not evident by the deficiency of the following inequality

$$v_{n+1}(x) \geq \int_{\mathbb{R}} v_n(y) e^{r_2(a_2-1-v_n(y))} \overline{k}_2(x, y)\mathrm{d}y, \quad x \in \mathbb{R}, \quad n = 0, 1, 2, \ldots.$$

Therefore, the nonmonotonicity may be different from that in Lin et al. (2019). To overcome the difficulty arising from the deficiency of comparison principle, our technique is to construct proper auxiliary equations and extract an auxiliary equation from the coupled system. More precisely, for any given $x \in \mathbb{R}$, we try to control $u_{n+1}(x)$ by

$$v_n(y), v_{n-1}(y), \ldots, v_0(y), u_0(y), \quad y \in \mathbb{R},$$

and then, $v_{n+1}(x)$ satisfies some auxiliary inequalities of infinite delay. Although the auxiliary equations are not monotone or subhomogeneous, we still confirm the following spreading speed of predators

$$\inf_{\lambda>0} \frac{\ln(e^{r_2(a_2-1)} \int_{\mathbb{R}} e^{\lambda y}\overline{k}_2(0,y)\mathrm{d}y)}{\lambda} =: c^* \tag{5}$$

under proper conditions clarified later.

The rest of this paper is organized as follows. In Sect. 2, we recall some known results on the asymptotic spreading of scalar integrodifference equations. To focus on the mathematical idea, the case of $r_1 \in (0, 1]$ is studied in Sect. 3, and the case of $r_1 \in (1, 2)$ is further investigated in Sect. 4. We provide some numerical examples in Sect. 5 and give some discussions in Sect. 6.

2 Preliminaries

In this paper, we use the standard partial ordering in $\mathbb{R}^2$. That is, if

$$u = (u_1, u_2), \quad v = (v_1, v_2) \in \mathbb{R}^2,$$

then

$$u \le v \quad \text{if and only if} \quad u_1 \le v_1, u_2 \le v_2.$$

$C(\mathbb{R}, \mathbb{R})$ is the space of all uniformly continuous and bounded functions equipped with compact open topology. When $b > a \ge 0$, we also denote

$$C_{[a,b]} = \{u \in C : a \le u(x) \le b, x \in \mathbb{R}\},$$

and C^+ is defined by

$$C^+ = \{u \in C : u(x) \ge 0, x \in \mathbb{R}\}.$$

For the movement law, we make the following assumptions

(A2) $\overline{k}_i(x, y) = k_i(|x-y|), x, y \in \mathbb{R}$; $k_i(x) \ge 0$ a.e. $x \in \mathbb{R}$ is Lebesgue measurable and integrable such that $\int_{\mathbb{R}} k_i(x)\mathrm{d}x = 1, i = 1, 2$;
(A3) $k_2(x) > 0$ a.e. $x \in \mathbb{R}$, and there exists $\lambda > 0$ such that $\int_{\mathbb{R}} k_2(x)e^{\lambda x}\mathrm{d}x < +\infty$;
(A4) Let $\lambda' > 0$ such that

$$e^{r_2(a_2-1)} \int_{\mathbb{R}} e^{\lambda' y} k_2(y)\mathrm{d}y = e^{\lambda' c^*}$$

or

$$\inf_{\lambda>0} \frac{\ln(e^{r_2(a_2-1)} \int_{\mathbb{R}} e^{\lambda y}k_2(y)\mathrm{d}y)}{\lambda} = \frac{\ln(e^{r_2(a_2-1)} \int_{\mathbb{R}} e^{\lambda' y}k_2(y)\mathrm{d}y)}{\lambda'} = c^*,$$

then $\int_{\mathbb{R}} e^{\lambda' y} k_1(y)\mathrm{d}y < \infty$.

We now present some results from Hsu and Zhao (2008) and consider

$$\begin{cases} w_{n+1}(x) = \int_{\mathbb{R}} b(w_n(y))k(x-y)\mathrm{d}y, & x \in \mathbb{R}, \quad n = 0, 1, 2, \ldots, \\ w_0(x) = w(x), & x \in \mathbb{R}, \end{cases} \tag{6}$$

in which $w(x) \in C^+$; the movement law $k(x)$ is an even function, Lebesgue measurable and integrable such that $\int_{\mathbb{R}} k(x)\mathrm{d}x = 1$, and there exists $\lambda > 0$ such that $\int_{\mathbb{R}} k(x)e^{\lambda x}\mathrm{d}x < \infty$; and the so-called birth function $b : \mathbb{R}^+ \to \mathbb{R}^+$ satisfies the following condition:

(A5) There exists a constant $B > 0$ such that $b : [0, B] \to [0, B]$ is uniformly continuous. Moreover, $\lim_{u \to 0^+} b(u)/u := b'(0) > 1$ exists such that

$$0 < b(u) \leq b'(0)u, \quad u \in (0, B]$$

and

$$b(u) \geq b'(0)u - L'u^{1+\alpha'}, \quad u \in (0, B]$$

for some $L' > 0$ and $\alpha' > 0$.

The solution of (6) admits the following properties.

Lemma 2.1 *Suppose that (A5) is true. The initial value problem* (6) *admits a unique solution* $w_n(x) \in C_{[0,B]}, n \in \mathbb{N}$, *if* $w(x) \in C_{[0,B]}$.

(1) Assume that $b : [0, B] \to [0, B]$ *is nondecreasing. If* $\omega_{n-1}(x) \in C_{[0,B]}, n \in \mathbb{N}$, *such that*

$$\begin{cases} \omega_{n+1}(x) \geq (\leq) \int_{\mathbb{R}} b(\omega_n(y))k(x-y)\mathrm{d}y, & n+1 \in \mathbb{N}, & x \in \mathbb{R}, \\ \omega_0(x) \geq (\leq) w(x), & & x \in \mathbb{R}, \end{cases} \tag{7}$$

then $\omega_n(x) \geq (\leq) w_n(x), n \in \mathbb{N}, x \in \mathbb{R}$.

(2) If $w(x) \in C_{[0,B]}$ *admits a nonempty compact support, then*

$$\inf_{\lambda > 0} \frac{\ln(b'(0)\int_{\mathbb{R}} e^{\lambda y} k(y)\mathrm{d}y)}{\lambda} < \infty$$

is the spreading speed of $w_n(x)$.

Remark 2.2 If the inequality is $\geq (\leq)$ in (7), then $\omega_n(x)$ is **an upper (a lower) solution** of (6) when $b : [0, B] \to [0, B]$ is nondecreasing. This is the comparison principle stated by Weinberger (1982, Proposition 4.1). Moreover, if the birth function is not monotone, the spreading speed is confirmed by Hsu and Zhao (2008, Theorem 2.2).

By simple analysis, we give the following result on the existence of solutions to (4).

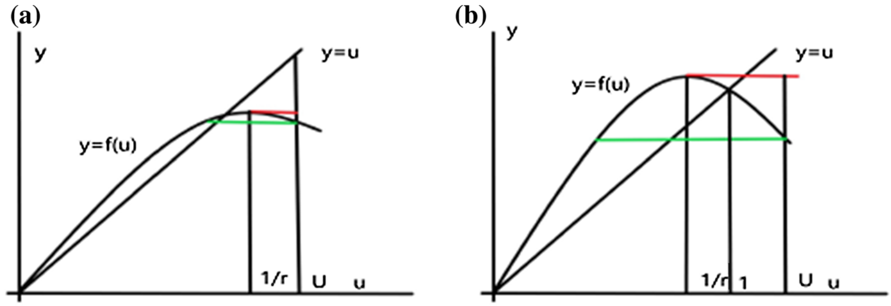

Fig. 1 The graphs of the function $f(r)$ when **a** $r \in (0, 1]$ and **b** $r > 1$ (Color figure online)

Lemma 2.3 *Assume that* (A1)*,* (A2) *hold. Then, the problem* (4) *has a unique solution* $(u_n(x), v_n(x))$*, where*

$$u_n(x) \in C^+, \quad v_n(x) \in C^+,$$

and $u_n(x), v_n(x)$ *are equicontinuous in* $n \in \mathbb{N}, x \in \mathbb{R}$*. In particular, if* (A3) *holds, then one has*

$$v_n(x) > 0, \quad n \in \mathbb{N}, \quad x \in \mathbb{R}.$$

In the rest of this paper, for some $U > 0$ and $f(u) = ue^{r(1-u)}$, we require that

$$\overline{f}(u) = \sup_{0 \le v \le u} \left[ve^{r(1-v)} \right], \quad \underline{f}(u) = \inf_{U \ge v \ge u} \left[ve^{r(1-v)} \right], \quad u \in [0, U].$$

Clearly, if $U \ge \max\{1/r, 1\}$, then there exists $\delta \in [0, 1/r]$ such that

$$\overline{f}(u) = f(u), \quad u \in [0, 1/r]; \quad \overline{f}(u) = e^{r-1}/r > f(u), \quad u \in (1/r, U]$$

and

$$\underline{f}(u) = f(u), \quad u \in [0, \delta]; \quad \overline{f}(u) < f(u), \quad u \in (\delta, U].$$

We now show these graphs in Fig. 1. When they are different, we use red line to represent $\overline{f}$ while $\underline{f}$ is in green line. These functions have been utilized in Hsu and Zhao (2008); Li et al. (2009).

3 The Case $r_1 \in (0, 1]$

In this section, we always assume that $a_2 > 1$ holds and $r_1 \in (0, 1]$ such that $ue^{r_1(1-u)}$ is monotone in $u \in [0, 1]$. $(u_n(x), v_n(x))$ is the unique solution defined by (4) and

(A1). We first define

$$R = \begin{cases} a_2 - 1, & r_2(a_2-1) \le 1, \\ e^{r_2(a_2-1)-1}/r_2, & r_2(a_2-1) > 1. \end{cases}$$

Lemma 3.1 *Assume that* (A1)–(A3) *hold and* $u(x) \in C_{[0,1]}$, $v(x) \in C_{[0,R]}$. *Then,*

$$u_n(x) \in C_{[0,1]}, \quad v_n(x) \in C_{[0,R]}, \quad n \in \mathbb{N}, \tag{8}$$

and $v_n(x)$ *satisfies*

$$\lim_{n\to\infty} \sup_{|x|>cn} v_n(x) = 0, \quad c > c^*. \tag{9}$$

Proof Under the assumption and by Lemma 2.3, we see that

$$\begin{cases} u_{n+1}(x) \le \int_{\mathbb{R}} u_n(y) e^{r_1(1-u_n(y))} k_1(x-y)\mathrm{d}y, & x \in \mathbb{R}, \quad n+1 \in \mathbb{N}, \\ u_0(x) = u(x) \in C_{[0,1]}, & x \in \mathbb{R}, \end{cases}$$

such that

$$u_n(x) \in C_{[0,1]}, \quad n \in \mathbb{N}, \quad x \in \mathbb{R}.$$

Furthermore, we have

$$\begin{cases} v_{n+1}(x) \le \int_{\mathbb{R}} v_n(y) e^{r_2(a_2-1-v_n(y))} k_2(x-y)\mathrm{d}y, & x \in \mathbb{R}, \quad n+1 \in \mathbb{N}, \\ v_0(x) = v(x), & x \in \mathbb{R}. \end{cases}$$

Clearly, $[0, R]$ is an invariant interval of the difference equation

$$v_{n+1} = v_n e^{r_2(a_2-1-v_n)}, \quad n+1 \in \mathbb{N},$$

but it may be nonmonotone in the invariant interval. Let

$$\overline{b}(v) = \max_{u\in[0,v]} \left[u e^{r_2(a_2-1-u)} \right], \quad v \in [0, R].$$

Then, $\overline{b}(v)$ is monotone such that $\overline{b}'(0) = e^{r_2(a_2-1)}$ and

$$\begin{cases} v_{n+1}(x) \le \int_{\mathbb{R}} \overline{b}(v_n(y)) k_2(x-y)\mathrm{d}y, & x \in \mathbb{R}, \quad n+1 \in \mathbb{N}, \\ v_0(x) = v(x) \in C_{[0,R]}, & x \in \mathbb{R}. \end{cases}$$

Let

$$\begin{cases} w_{n+1}(x) = \int_{\mathbb{R}} \overline{b}(w_n(y))k_2(x-y)\mathrm{d}y, & x \in \mathbb{R}, \quad n+1 \in \mathbb{N}, \\ w_0(x) = v(x) \in C_{[0,R]}, & x \in \mathbb{R}. \end{cases}$$

So Lemma 2.1 implies that

$$0 \le v_n(x) \le w_n(x) \in C_{[0,R]}, \quad n+1 \in \mathbb{N}, \quad x \in \mathbb{R},$$

and (8) is true such that

$$\lim_{n\to\infty} \sup_{|x|>cn} w_n(x) = \lim_{n\to\infty} \sup_{|x|>cn} v_n(x) = 0, \quad c > c^*.$$

The proof is complete. □

Lemma 3.2 *Define*

$$F(u,v) = ue^{r_1(1-u-a_1v)}, \quad u \in [0,2], \quad v \in [0, R+1]. \tag{10}$$

Then, there exists $a_1' > 0$ such that for each $a_1 \in (0, a_1')$, we can fix $\delta = \delta(a_1) \in (0,1)$ with

$$0 < \frac{\partial F(u,v)}{\partial u} < \delta, \quad u \in [1-a_1R, 1] \subset (0,1], \quad v \in [0,R].$$

Proof By direct calculations, we have

$$\frac{\partial F(u,v)}{\partial u} = (1-r_1u)F(u,v), \quad \left.\frac{\partial F(u,v)}{\partial u}\right|_{(u,v)=(1,0)} = 1-r_1 < 1,$$
$$\frac{\partial F(u,v)}{\partial v} = -r_1a_1F(u,v), \quad \left.\frac{\partial F(u,v)}{\partial v}\right|_{(u,v)=(1,0)} = -r_1a_1 < 0$$

and $F(1,0) = 1$. By the continuity, there exists $\underline{u} \in (0,1)$ such that

$$0 < \frac{\partial F(u,v)}{\partial u} < 1, \quad \frac{\partial F(u,v)}{\partial v} \ge -r_1a_1$$

for $u \in (\underline{u}, 1]$, $v \in [0,R]$. So there exists $a_1' > 0$ such that

$$\frac{\partial F(u,v)}{\partial u} < 1, \quad u \in [1-a_1R, 1], \quad v \in [0,R] \tag{11}$$

for any $a_1 \in [0, a_1')$. The proof is complete. □

Consider the initial value problem

$$\begin{cases} \underline{v}_{n+1}(x) = \int_{\mathbb{R}} \underline{v}_n(y) e^{r_2(-1-R)} k_2(x-y)\mathrm{d}y, & n+1 \in \mathbb{N}, \quad x \in \mathbb{R}, \\ v_0(x) = \underline{v}(x) \in C^+, & \quad x \in \mathbb{R}, \end{cases}$$

which is monotone and $\underline{v}(x)$ satisfies

$$\underline{v}(x) = \eta, \quad |x| < \sigma; \underline{v}(x) = 0, \quad |x| \geq \sigma$$

with given positive constants η, σ. Because of (A3), we further have the following conclusion by the property of continuous functions on a bounded closed interval.

Lemma 3.3 *Fix $n' \in \mathbb{N}$, then there exists $\nu = \nu(n', \eta, \sigma) > 0$ such that*

$$\underline{v}_n(x) > \nu, \quad n = 1, 2, \ldots, n', \quad |x| < 2n'(n'+1).$$

Lemma 3.4 *Assume that* (A1)–(A3) *hold. Further suppose that $v(x) \in C_{[0,R]}$, $u(x) = 1$, $x \in \mathbb{R}$, $a_1 \in [0, a_1')$, $c \in (0, c^*)$ are given. Then,*

$$\liminf_{n\to\infty} \inf_{|x|<cn} v_n(x) > 0. \tag{12}$$

Proof Firstly, we fix $\epsilon > 0$ such that

$$c < \inf_{\lambda>0} \frac{\ln(e^{r_2(a_2-1-4\epsilon)} \int_{\mathbb{R}} e^{\lambda y} k_2(y)\mathrm{d}y)}{\lambda},$$

which is evidently admissible.

By Lemma 3.1, $v_n(x) \in C_{[0,R]}$ such that

$$\begin{cases} u_{n+1}(x) \geq \int_{\mathbb{R}} u_n(y) e^{r_1(1-u_n(y)-a_1R)} k_1(x-y)\mathrm{d}y, & x \in \mathbb{R}, \quad n+1 \in \mathbb{N}, \\ u_0(x) = 1, & x \in \mathbb{R}, \end{cases}$$

which implies

$$u_n(x) \in [1 - a_1R, 1], \quad v_n(x) \in [0, R], \quad n \in \mathbb{N}, \quad x \in \mathbb{R}. \tag{13}$$

In fact, (13) is true because $xe^{r_1(1-a_1R-x)}$, $x \in [1-a_1R, 1]$, is increasing and satisfies

$$xe^{r_1(1-a_1R-x)} \leq x, \quad x \in [1 - a_1R, 1].$$

Since

$$u_n(x) - 1 \leq 0, \quad n \in \mathbb{N}, \quad x \in \mathbb{R},$$

we have

$$
\begin{aligned}
u_{n+1}(x)-1 &= \int_{\mathbb{R}} u_n(y)e^{r_1(1-u_n(y)-a_1v_n(y))}k_1(x-y)\mathrm{d}y-1\\
&= \int_{\mathbb{R}} \left[u_n(y)e^{r_1(1-u_n(y)-a_1v_n(y))}-1\right]k_1(x-y)\mathrm{d}y\\
&\geq \delta\int_{\mathbb{R}} [u_n(y)-1]\,k_1(x-y)\mathrm{d}y-r_1a_1\int_{\mathbb{R}} v_n(y)k_1(x-y)\mathrm{d}y
\end{aligned}
$$

for any $n+1\in\mathbb{N}$, $x\in\mathbb{R}$ by Lemma 3.2.

Repeating the above process and utilizing $u_0(x)=1$, $x\in\mathbb{R}$, we have

$$
\begin{aligned}
&u_{n+1}(x)-1\\
&\geq \delta^2\int_{\mathbb{R}}\left[\int_{\mathbb{R}}\left[u_{n-1}(y)-1\right]k_1(x_1-y)\mathrm{d}y\right]k_1(x-x_1)\mathrm{d}x_1\\
&\quad -r_1a_1\int_{\mathbb{R}} v_n(y)k_1(x-y)\mathrm{d}y\\
&\quad -(r_1a_1)\,\delta\int_{\mathbb{R}}\left[\int_{\mathbb{R}} v_{n-1}(y)k_1(x_1-y)\mathrm{d}y\right]k_1(x-x_1)\mathrm{d}x_1\\
&\geq \delta^3\int_{\mathbb{R}}\left[\int_{\mathbb{R}}\left[\int_{\mathbb{R}}\left[u_{n-2}(y)-1\right]k_1(x_2-y)\mathrm{d}y\right]k_1(x_2-x_1)\mathrm{d}x_2\right]k_1(x-x_1)\mathrm{d}x_1\\
&\quad -r_1a_1\int_{\mathbb{R}} v_n(y)k_1(x-y)\mathrm{d}y\\
&\quad -(r_1a_1)\,\delta\int_{\mathbb{R}}\left[\int_{\mathbb{R}} v_{n-1}(y)k_1(x_1-y)\mathrm{d}y\right]k_1(x-x_1)\mathrm{d}x_1\\
&\quad -(r_1a_1)\,\delta^2\int_{\mathbb{R}}\left[\int_{\mathbb{R}}\left[\int_{\mathbb{R}} v_{n-2}(y)k_1(x_2-y)\mathrm{d}y\right]k_1(x_2-x_1)\mathrm{d}x_2\right]k_1(x-x_1)\mathrm{d}x_1\\
&\geq\cdots\\
&\geq \delta^{n+1}\int_{\mathbb{R}}\left[\cdots\left[\int_{\mathbb{R}}[u_0(y)-1]\,k_1(x_n-y)\mathrm{d}y\right]\cdots\right]k_1(x-x_1)\mathrm{d}x_1\\
&\quad -r_1a_1\int_{\mathbb{R}} v_n(y)k_1(x-y)\mathrm{d}y\\
&\quad -(r_1a_1)\,\delta\int_{\mathbb{R}}\left[\int_{\mathbb{R}} v_{n-1}(y)k_1(x_1-y)\mathrm{d}y\right]k_1(x-x_1)\mathrm{d}x_1\\
&\quad -\cdots\\
&\quad -(r_1a_1)\,\delta^n\int_{\mathbb{R}}\cdots\int_{\mathbb{R}} v_0(y)k_1(x_n-y)\mathrm{d}y\cdots k_1(x-x_1)\mathrm{d}x_1\\
&= -r_1a_1\int_{\mathbb{R}} v_n(y)k_1(x-y)\mathrm{d}y\\
&\quad -(r_1a_1)\,\delta\int_{\mathbb{R}}\left[\int_{\mathbb{R}} v_{n-1}(y)k_1(x_1-y)\mathrm{d}y\right]k_1(x-x_1)\mathrm{d}x_1\\
&\quad -\cdots
\end{aligned}
$$

$$
\begin{aligned}
&- (r_1 a_1)\, \delta^n \int_{\mathbb{R}} \cdots \int_{\mathbb{R}} v_0(y) k_1(x_n - y) \mathrm{d}y \cdots k_1(x - x_1) \mathrm{d}x_1 \\
&= -(r_1 a_1) \sum_{j=1}^{n+1} \delta^{j-1} \int_{\mathbb{R}^j} v_{n+1-j}(y) \prod_{i=1}^{j} k_1(x_{j-1} - x_j) \mathrm{d}x_{j-i+1} \\
&=: H_{n+1}(v)(x)
\end{aligned}
$$

for any $n+1 \in \mathbb{N}$, $x \in \mathbb{R}$ with $x_j = y$, $x_0 = x$. So we have

$$
\begin{aligned}
v_{n+1}(x) &= \int_{\mathbb{R}} v_n(y) e^{r_2(-1-v_n(y)+a_2 u_n(y))} k_2(x-y) \mathrm{d}y \\
&= \int_{\mathbb{R}} v_n(y) e^{r_2(a_2-1-v_n(y)+a_2(u_n(y)-1))} k_2(x-y) \mathrm{d}y \\
&\geq \int_{\mathbb{R}} v_n(y) e^{r_2(a_2-1-v_n(y)+a_2 H_n(v)(y))} k_2(x-y) \mathrm{d}y
\end{aligned} \tag{14}
$$

for any $n+1 \in \mathbb{N}$, $x \in \mathbb{R}$. According to (13),

$$
0 \geq H_{n+1}(v)(x) \geq -R r_1 a_1 \left[1 + \delta + \delta^2 + \cdots + \delta^n \right] \geq \frac{-R r_1 a_1}{1-\delta} \tag{15}
$$

for any $n+1 \in \mathbb{N}$.

By the fact that $\delta < 1$, if n is large (since we study the asymptotic spreading involving long time behavior), then there exists $N \in \mathbb{N}$ independent on n such that

$$
\begin{aligned}
H_n(v)(x) &\geq -\epsilon/a_2 - (r_1 a_1) \sum_{j=1}^{N} \delta^{j-1} \int_{[-N,N]^j} v_{n+1-j}(y) \prod_{i=1}^{j} k_1(x_{j-1} - x_j) \mathrm{d}x_{j-i+1} \\
&=: -\epsilon/a_2 + H_{n,N}(v)(x)
\end{aligned}
$$

for $x \in \mathbb{R}$, $n > N$. If $a_2 H_n(v)(y) \geq -2\epsilon$ for some $n \in \{0, 1, \ldots\}$, $x \in \mathbb{R}$, then

$$
v_n(y) e^{r_2(a_2-1-v_n(y)+a_2 H_n(v)(y))} \geq v_n(y) e^{r_2(a_2-1-2\epsilon-v_n(y))}.
$$

Otherwise, $a_2 H_n(v)(y) \leq -2\epsilon$ implies that $H_{n,N}(v)(y) \leq -\epsilon/a_2$ and

$$
(r_1 a_1) \sum_{j=1}^{N} \delta^{j-1} \int_{[-N,N]^j} v_{n+1-j}(y) \prod_{i=1}^{j} k_1(x_{j-1} - x_j) \mathrm{d}x_{j-i+1} \geq \epsilon/a_2.
$$

Since k_1 is Lebesgue integrable and $v_m(\cdot) \in C_{[0,R]}$, $m+1 \in \mathbb{N}$, there exists $\eta > 0$ depending on ϵ and some $y' \in \mathbb{R}$, $N' \leq N$, $N' \in \mathbb{N}$ such that

$$
v_{n-N'}(y') > 2\eta, \quad |y - y'| < 2N(N+1).
$$

By the equicontinuity, we may further select $\sigma > 0$ such that

$$v_{n-N'}(z) > \eta, \quad |z - y'| \leq \sigma.$$

Clearly, we have

$$\begin{aligned} v_{n+1}(x) &= \int_{\mathbb{R}} v_n(y) e^{r_2(-1-v_n(y)+a_2 u_n(y))} k_2(x-y)\mathrm{d}y \\ &\geq \int_{\mathbb{R}} v_n(y) e^{r_2(-1-R)} k_2(x-y)\mathrm{d}y \end{aligned}$$

for $n = 0, 1, \ldots, x \in \mathbb{R}$. Therefore, Lemma 3.3 and (15) imply that there exist $\mu > 0$, $M > 0$ such that $v_n(y) \geq \mu$ and $a_2 H_n(v)(y)$ satisfies

$$a_2 H_n(v)(y) \geq \frac{-Rr_1 a_1 a_2}{1-\delta} = -\frac{-Rr_1 a_1 a_2}{\mu(1-\delta)}\mu \geq -\frac{-Rr_1 a_1 a_2}{\mu(1-\delta)} v_n(y) =: -M v_n(y)$$

and

$$\begin{cases} v_{n+1}(x) \geq \int_{\mathbb{R}} v_n(y) e^{r_2(a_2-1-2\epsilon-(1+M)v_n(y))} k_2(x-y)\mathrm{d}y, \\ v_{N+1}(x) > 0 \end{cases}$$

for $x \in \mathbb{R}$, $n \geq N+1$. Further, define

$$\underline{b}(x) = \inf_{u \in [x,R]} \left[u e^{r_2(a_2-1-2\epsilon-(1+M)u)} \right],$$

then $\underline{b}(x)$, $x \in [0, R]$, is continuous and nondecreasing such that

$$\underline{b}'(0) = \lim_{x \to 0+} \frac{\underline{b}(x)}{x} = e^{r_2(a_2-1-2\epsilon)} > 1$$

and

$$\underline{b}(x) \leq \underline{b}'(0)x, \quad x \in [0, R].$$

That is, $v_n(x)$ satisfies

$$\begin{cases} v_{n+1}(x) \geq \int_{\mathbb{R}} \underline{b}(v_n(y)) k_2(x-y)\mathrm{d}y, \\ v_{N+1}(x) > 0 \end{cases}$$

for $x \in \mathbb{R}$, $n \geq N+1$. By the selection of ϵ, (12) holds due to Lemma 2.1. The proof is complete. □

Summarizing what we have done, we have the following conclusion.

Theorem 3.5 *Assume that* (A1)–(A3) *hold,* $u(x) = 1, x \in \mathbb{R}, v(x) \in C_{[0,R]}$, $u_n(x)$ *and* $v_n(x), n \in \mathbb{N}, x \in \mathbb{R}$, *are defined by* (4). *If* $a_1 > 0$ *such that*

$$\frac{\partial F(u,v)}{\partial u} < 1, \quad u \in [1 - a_1 R, 1] \subset (0,1], \quad v \in [0, R], \tag{16}$$

then c^* *defined by* (5) *is the spreading speed of* $v_n(x), n \in \mathbb{N}, x \in \mathbb{R}$.

Before ending this section, we further consider the initial value problem

$$\begin{cases} u_{n+1}(x) = \int_{\mathbb{R}} u_n(y) e^{r_1(1-u_n(y)-a_1 v_n(y))} k_1(x-y)\mathrm{d}y, & x \in \mathbb{R}, \quad n+1 \in \mathbb{N}, \\ v_{n+1}(x) = \int_{\mathbb{R}} v_n(y) e^{r_2(-1-v_n(y)+a_2 u_n(y))} k_2(x-y)\mathrm{d}y, & x \in \mathbb{R}, \quad n+1 \in \mathbb{N}, \\ u_0(x) \in C_{[1-a_1 R, 1]}, \quad v_0(x) \in C_{[0,R]}, & x \in \mathbb{R}, \end{cases} \tag{17}$$

in which $v(x)$ admits nonempty compact support and the other parameters are the same as those in the previous model.

Corollary 3.6 *Assume that* (A1)–(A3) *hold,* $u_n(x)$ *and* $v_n(x), n \in \mathbb{N}, x \in \mathbb{R}$, *are defined by* (17). *If* $a_1 > 0$ *such that* (16) *holds, then* c^* *defined by* (5) *is the spreading speed of* $v_n(x), \ n \in \mathbb{N}, x \in \mathbb{R}$.

Proof Evidently, (13) still holds. Note that

$$\left| \delta^{n+1} \int_{\mathbb{R}} \left[\cdots \left[\int_{\mathbb{R}} [u_0(y) - 1] k_1(x_n - y)\mathrm{d}y \right] \cdots \right] k_1(x - x_1)\mathrm{d}x_1 \right|$$
$$\le \delta^{n+1} \to 0, \quad n \to \infty,$$

and the convergence is uniform in x. Therefore, we have

$$u_{n+1}(x) - 1 \ge -\delta^{n+1} + H_{n+1}(v)(x)$$

for any $n+1 \in \mathbb{N}, x \in \mathbb{R}$, and

$$v_{n+1}(x) \ge \int_{\mathbb{R}} v_n(y) e^{r_2(a_2 - 1 - v_n(y) - a_2\delta^n + a_2 H_n(v)(y))} k_2(x-y)\mathrm{d}y$$

for any $n+1 \in \mathbb{N}, x \in \mathbb{R}$. By the fact that $\delta < 1$, if n is large, we know that there exists $N \in \mathbb{N}$ independent on n such that $\delta^n < \epsilon/a_2$ and

$$-\delta^n + H_n(v)(x) \ge -2\epsilon/a_2 + H_{n,N}(v)(x), \quad n > N.$$

If $-a_2\delta^n + a_2 H_n(v)(y) \ge -3\epsilon$, then

$$v_n(y) e^{r_2(a_2 - 1 - v_n(y) + a_2 H_n(v)(y))} \ge v_n(y) e^{r_2(a_2 - 1 - 3\epsilon - v_n(y))}.$$

Otherwise, $-a_2\delta^n + a_2 H_n(v)(y) \le -3\epsilon$ implies $H_{n,N}(v)(y) \le -\epsilon/a_2$. Combining these with a discussion similar to that after (15), we obtain

$$\begin{cases} v_{n+1}(x) \ge \int_{\mathbb{R}} v_n(y) e^{r_2(a_2-1-3\epsilon-(1+M)v_n(y))} k_2(x-y)\mathrm{d}y, \\ v_{N+1}(x) > 0 \end{cases}$$

for $x \in \mathbb{R}$, $n \ge N+1$. The proof is complete. □

4 The Case $r_1 \in (1, 2)$

In this section, we always assume that (A1)–(A4) are satisfied and $a_2 > 1$ holds. To state our main result, we first introduce some constants as follows. Define

$$D = e^{r_2(a_2-1)-1}/r_2, \quad R_1 = \frac{e^{r_1-1}}{r_1} = \sup_{x>0}\left(xe^{r_1(1-x)}\right)$$

and

$$R_2 = \sup_{x\in[0,a_2R_1-1]}\left(xe^{r_2(a_2R_1-1-x)}\right) = \begin{cases} a_2R_1-1, & r_2(a_2R_1-1) \le 1, \\ \frac{e^{r_2(a_2R_1-1)-1}}{r_2}, & r_2(a_2R_1-1) > 1. \end{cases}$$

Consider the following initial value problem

$$\begin{cases} u_{n+1} = u_n e^{r_1(1-u_n-a_1v_n)}, & n+1 \in \mathbb{N}, \\ v_{n+1} = v_n e^{r_2(-1-v_n+a_2u_n)}, & n+1 \in \mathbb{N}, \\ u_0 > 0, \ v_0 > 0. \end{cases} \tag{18}$$

Then, it is clear that

$$u_n \in (0, R_1], \quad v_n \in (0, R_2], \quad n \in \mathbb{N}$$

if $u_0 \in (0, R_1]$, $v_0 \in (0, R_2]$.

Since

$$u_{n+1} \ge u_n e^{r_1(1-u_n-a_1R_2)}, \quad n+1 \in \mathbb{N},$$

it follows that there exists $\underline{R} > 0$ such that

$$u_n \ge \underline{R}, \quad n \in \mathbb{N} \tag{19}$$

if $1 - a_1R_2 > 0, \ u_0 \ge \underline{R}$. In fact, let

$$\underline{b}(u) = \inf_{x\in[u,R_1]}\left(xe^{r_1(1-x-a_1R_2)}\right), \quad u \in [0, R_1],$$

then $\underline{\underline{b}}(u)$, $u \in [0, R_1]$, is monotone and there exists $\underline{R} \in (0, R_1]$ such that

$$\underline{\underline{b}}(u) = \underline{R}, \quad u \in [\underline{R}, R_1]; \quad \underline{\underline{b}}(u) < \underline{R}, \quad u \in [0, \underline{R}).$$

In summary, we see that

$$[\underline{R}, R_1] \times [0, R_2]$$

is a positively invariant region of (18), which further implies the following invariance result.

Lemma 4.1 *Assume that* $1 - a_1 R_2 > 0$, $u(x) \in C_{[\underline{R}, R_1]}$, $v(x) \in C_{[0, R_2]}$. *Then*

$$u_n(x) \in C_{[\underline{R}, R_1]}, \quad v_n(x) \in C_{[0, R_2]}. \tag{20}$$

Consider

$$F(u, v) = ue^{r_1(1-u-a_1 v)}, \quad u \in [\underline{R}, R_1], \quad v \in [0, R_2],$$

we have the following conclusion similar to Lemma 3.2.

Lemma 4.2 *There exists* $a_1' > 0$ *such that for each* $a_1 \in (0, a_1')$, *we can fix* $\delta = \delta(a_1) \in (0, 1)$, $L = L(a_1) > 0$, $\overline{V} > D$ *with*

(1) $|F(u_1, v_1) - F(u_2, v_2)| \le \delta|u_1 - u_2| + L|v_1 - v_2|$, $(u_i, v_i) \in [\underline{R}, R_1] \times [0, R_2]$;
(2) *they satisfy*

$$r_2 L\overline{V} < 1 - \delta, \quad \overline{V} \ge De^{\frac{r_2 a_2 L\overline{V}}{1-\delta}}; \tag{21}$$

(3) *denote* $\int_{\mathbb{R}} e^{\lambda' x} k_1(x) \mathrm{d}y = e^{\lambda' b}$, *then* $\delta e^{\lambda'(b-c^*)} < 1$, $a_2 Le^{\lambda'(b-c^*)} \le 1 - \delta e^{\lambda'(b-c^*)}$.

Remark 4.3 Regarding $\underline{R}$ and R_1 as functions of r_1 and a_1, we have

$$\lim_{r_1 \to 1, a_1 \to 0} \underline{R} = \lim_{r_1 \to 1, a_1 \to 0} R_1 = 1.$$

Then, we obtain the existence of δ at least for $r_1 - 1 > 0$, $a_1 \ge 0$ being small enough. In particular, if $r_1 - 1 \to 0$, $a_1 \to 0$, then $\delta \to 0$, $L \to 0$. Since a_1 represents the predation rates of predators, the condition implies that the capture ratio is small when predators appear, which means a small perturbation of the prey around the predator-free steady state 1.

Lemma 4.4 *Assume that* $1 - a_1 R_2 > 0$, $u(x) = 1$, $x \in \mathbb{R}$, $v(x) \in C_{[0, R_2]}$. *Then, there exists* $a_1' > 0$ *such that* $a_1 \in [0, a_1')$ *implies*

$$\liminf_{n \to \infty} \inf_{|x| < cn} v_n(x) > 0, \quad c \in (0, c^*).$$

Proof We prove the result by fixing $c \in (0, c^*)$. By direct calculation, we obtain

$$\begin{aligned}
|u_{n+1}(x) - 1| &= \left| \int_{\mathbb{R}} u_n(y) e^{r_1(1-u_n(y)-a_1 v_n(y))} k_1(x-y)\mathrm{d}y - 1 \right| \\
&\le \int_{\mathbb{R}} \left| u_n(y) e^{r_1(1-u_n(y)-a_1 v_n(y))} - 1 \right| k_1(x-y)\mathrm{d}y \\
&\le \delta \int_{\mathbb{R}} |u_n(y) - 1|\, k_1(x-y)\mathrm{d}y + L \int_{\mathbb{R}} v_n(y) k_1(x-y)\mathrm{d}y
\end{aligned}$$

for any $n+1 \in \mathbb{N}$, $x \in \mathbb{R}$. Thus, we have

$$\begin{aligned}
&|u_{n+1}(x) - 1| \\
&\quad \le \delta^2 \int_{\mathbb{R}} |u_{n-1}(y) - 1|\, k_1(x-y)\mathrm{d}y + L \int_{\mathbb{R}} v_n(y) k_1(x-y)\mathrm{d}y \\
&\qquad + L\delta \int_{\mathbb{R}} \left[\int_{\mathbb{R}} v_{n-1}(y) k_1(x_1 - y)\mathrm{d}y \right] k_1(x - x_1)\mathrm{d}x_1 \\
&\quad \le \cdots \\
&\quad \le \delta^{n+1} \int_{\mathbb{R}} |u_0(y) - 1|\, k_1(x-y)\mathrm{d}y + L \int_{\mathbb{R}} v_n(y) k_1(x-y)\mathrm{d}y \\
&\qquad + L\delta \int_{\mathbb{R}} \left[\int_{\mathbb{R}} v_{n-1}(y) k_1(x_1 - y)\mathrm{d}y \right] k_1(x - x_1)\mathrm{d}x_1 \\
&\qquad + \cdots \\
&\qquad + L\delta^n \int_{\mathbb{R}} \cdots \int_{\mathbb{R}} v_0(y) k_1(x_n - y)\mathrm{d}y \cdots k_1(x - x_1)\mathrm{d}x_1 \\
&\quad = L \sum_{j=1}^{n+1} \delta^{j-1} \int_{\mathbb{R}^j} v_{n+1-j}(y) \prod_{i=1}^{j} k_1(x_{j-1} - x_j)\mathrm{d}x_{j-i+1} \\
&\quad =: \mathcal{H}_{n+1}(v)(x)
\end{aligned}$$

for any $n+1 \in \mathbb{N}$, $x \in \mathbb{R}$ with $x_j = y$, $x_0 = x$, which further leads to

$$\begin{aligned}
v_{n+1}(x) &= \int_{\mathbb{R}} v_n(y) e^{r_2(-1-v_n(y)+a_2 u_n(y))} k_2(x-y)\mathrm{d}y \\
&= \int_{\mathbb{R}} v_n(y) e^{r_2(a_2-1-v_n(y)+a_2(u_n(y)-1))} k_2(x-y)\mathrm{d}y \\
&\ge \int_{\mathbb{R}} v_n(y) e^{r_2(a_2-1-v_n(y)-a_2\mathcal{H}_n(v)(y))} k_2(x-y)\mathrm{d}y
\end{aligned}$$

for any $n+1 \in \mathbb{N}$, $x \in \mathbb{R}$. Because $\delta \in (0, 1)$, $\mathcal{H}_n(x)$ is finite for any $x \in \mathbb{R}$, $n \in \mathbb{N}$. Similar to the discussion after (14) in Sect. 3, we complete the proof. □

Lemma 4.5 *Assume that* $u(x) = 1$, $x \in \mathbb{R}$, $v(x) \in C_{[0,R_2]}$, *and* $a_1 \in (0, a_1')$ *such that Lemma 4.2 holds. Then,*

$$\limsup_{n\to\infty} \sup_{|x|>cn} v_n(x) = 0, \quad c > c^* \tag{22}$$

Proof By the estimation of $\mathcal{H}_n$ in the proof of Lemma 4.4, we see that

$$\begin{aligned} v_{n+1}(x) &= \int_{\mathbb{R}} v_n(y) e^{r_2(-1-v_n(y)+a_2u_n(y))} k_2(x-y)\mathrm{d}y \\ &\le \int_{\mathbb{R}} v_n(y) e^{r_2(a_2-1-v_n(y)+a_2\mathcal{H}_n(v)(y))} k_2(x-y)\mathrm{d}y \\ &\le \int_{\mathbb{R}} F(v_n(y)) e^{r_2a_2\mathcal{H}_n(v)(y)} k_2(x-y)\mathrm{d}y, \end{aligned}$$

in which

$$F(v) = \sup_{x\le v}\left[xe^{r_2(a_2-1-x)}\right], \quad v \ge 0.$$

Evidently, we see that

$$F(v) = \begin{cases} ve^{r_2(a_2-1-v)}, & v \in [0, 1/r_2], \\ D, & v \ge 1/r_2. \end{cases}$$

Since F is nondecreasing and $\mathcal{H}_n$ is monotone increasing, then

$$\mathcal{V}_{n+1}(x) = \int_{\mathbb{R}} F(\mathcal{V}_n(y)) e^{r_2a_2\mathcal{H}_n(\mathcal{V})(y)} k_2(x-y)\mathrm{d}y \tag{23}$$

is monotone, and $v_n(x)$ is the lower solution of the above equation if

$$\mathcal{V}_0(x) \ge v(x), \quad x \in \mathbb{R}.$$

Therefore, if

$$\limsup_{n\to\infty} \sup_{|x|>cn} \mathcal{V}_n(x) = 0, \quad c > c^*,$$

then (22) holds. To study the spreading speed of (23), the main difficulty is that (23) is not subhomogeneous. For the complexity of the propagation threshold of an equation that is not subhomogeneous, see examples by Hadeler and Rothe (1975), Weinberger et al. (2007).

Again by the monotonicity, it suffices to construct $V_n(x)$ such that

$$V_{n+1}(x) \ge \int_{\mathbb{R}} F(V_n(y)) e^{r_2a_2H_n(V)(y)} k_2(x-y)\mathrm{d}y, \quad n+1 \in \mathbb{N}, \quad x \in \mathbb{R}$$

with

$$\limsup_{n\to\infty}\sup_{|x|>cn} V_n(x)=0,\quad V_0(x)\geq v(x),\quad x\in\mathbb{R},\quad c>c^*.$$

Further, define a continuous function

$$V_n(x)=\min\{e^{\lambda'(x+c^*n)+P}, e^{\lambda'(-x+c^*n)+P}, \overline{V}\},\quad n+1\in\mathbb{N},$$

where $P>0$ such that

$$V_0(x)\geq v(x),\quad x\in\mathbb{R}.$$

By (21), the result is clear if $V_{n+1}(x)=\overline{V}$ for some $n\in\mathbb{N}$, $x\in\mathbb{R}$ since

$$r_2a_2\mathcal{H}_{n-1}(V)(y)\leq r_2a_2L\overline{V}[1+\delta+\cdots+\delta^{n-1}]\leq\frac{r_2a_2L\overline{V}}{1-\delta}.$$

When $V_{n+1}(x)=e^{\lambda'(x+c^*n+c^*+P)}$, then $V_n(y)\leq e^{\lambda'(y+c^*n+P)}$ such that

$$\begin{aligned}\mathcal{H}_{n+1}(v)(x)&\leq Le^{\lambda'(x+c^*n-c^*+P)}e^{\lambda'b}+L\delta e^{\lambda'(x+c^*n-2c^*+P)}e^{2\lambda'b}+\cdots\\&\leq\frac{Le^{\lambda'(x+c^*n-c^*+P)}e^{\lambda'b}}{1-\delta e^{\lambda'(b-c^*)}}\end{aligned}\tag{24}$$

by (3) of Lemma 4.2. If $V_n(y)=e^{\lambda'(y+c^*n+P)}\leq 1/r_2$, then (3) of Lemma 4.2 implies that

$$F(V_n(y))e^{r_2a_2\mathcal{H}_n(V)(y)}\leq V_n(y)e^{r_2(a_2-1-V_n(y)+a_2\mathcal{H}_n(V)(y))}\leq V_n(y)e^{r_2(a_2-1)}$$

since

$$\begin{aligned}-V_n(y)+a_2\mathcal{H}_n(V)(y)&\leq -e^{\lambda'(y+c^*n+P)}+\frac{a_2Le^{\lambda'(y+c^*n-c^*+P)}e^{\lambda'b}}{1-\delta e^{\lambda'(b-c)}}\\&=e^{\lambda'(y+c^*n+P)}\left[-1+\frac{a_2Le^{\lambda'(b-c^*)}}{1-\delta e^{\lambda'(b-c^*)}}\right].\end{aligned}\tag{25}$$

Otherwise, $V_n(y)\geq 1/r_2$ such that

$$\begin{aligned}F(V_n(y))e^{r_2a_2\mathcal{H}_n(V)(y)}&=De^{r_2a_2\mathcal{H}_n(V)(y)}\\&=V_n(y)e^{r_2(a_2-1)}\frac{De^{r_2a_2\mathcal{H}_n(V)(y)}}{V_n(y)e^{r_2(a_2-1)}}\\&\leq V_n(y)e^{r_2(a_2-1)}\\&\leq e^{\lambda'(y+c^*n+P)}e^{r_2(a_2-1)}\end{aligned}$$

if

$$De^{r_2 a_2 \mathcal{H}_n(V)(y)} \le V_n(y) e^{r_2(a_2-1)}.$$

Since $V_n(y) \ge 1/r_2$, the above inequality holds if

$$De^{\frac{r_2 L \overline{V}}{1-\delta}} \le e^{r_2(a_2-1)}/r_2 = De$$

by (2) of Lemma 4.2. From the definition of λ', we see that

$$e^{\lambda'(x+c^*n+c^*+P)} = e^{r_2(a_2-1)} \int_{\mathbb{R}} e^{\lambda'(y+c^*n+P)} k_2(x-y)\mathrm{d}y$$

and confirm (22). We now complete the proof. □

Summarizing the above discussions, we obtain the following conclusion.

Theorem 4.6 *Assume that $u(x) = 1, v(x) \in C_{[0,R_2]}, x \in \mathbb{R}$, and $u_n(x), v_n(x), n \in \mathbb{N}, x \in \mathbb{R}$, are defined by (4). If $a_1 > 0$ such that Lemma 4.2 holds, then c^* is the spreading speed of $v_n(x), n \in \mathbb{N}, x \in \mathbb{R}$.*

When $u(x) \in C_{[\underline{R},R_1]}$, we may come to a similar conclusion motivated by Sect. 3. Since the process and the result are similar to that in Sect. 3, we omit them. Note that (21) involves several parameters, we may further simplify the condition under proper assumptions. For example, we make the following assumption.

(2') $r_2(a_2-1) + \frac{a_2 L}{1-\delta} \le 1$.

Corollary 4.7 *Theorem 4.6 remains true if* (2) *of Lemma 4.2 is replaced by* (2').

Proof Since (2) of Lemma 4.2 only appears in the study of (23), we define a new monotone equation

$$\mathcal{V}_{n+1}(x) = \int_{\mathbb{R}} \mathcal{V}_n(y) e^{r_2(a_2-1-\mathcal{V}_n(y)+a_2\mathcal{H}_n(\mathcal{V})(y))} k_2(x-y)\mathrm{d}y \tag{26}$$

with

$$0 \le \mathcal{V}_n(x) \le 1/r_1, \mathcal{V}_0(x) \ge v(x), \quad x \in \mathbb{R}, \quad n = 0, 1, 2, \ldots.$$

Further, define

$$V_n(x) = \min\{e^{\lambda'(x+c^*n)+P}, e^{\lambda'(-x+c^*n)+P}, 1/r_2\}, \quad n+1 \in \mathbb{N}.$$

We prove that $V_n(x)$ is an upper solution of (26) when $V_0(x) \ge v(x), x \in \mathbb{R}$. In fact, when $V_{n+1}(x) = \frac{1}{r_2}$, since $V_i(y) \le 1/r_2, i \in \{0, 1, \ldots, n\}, y \in \mathbb{R}$, we have

$$r_2 a_2 \mathcal{H}_{n-1}(V)(y) \le r_2 a_2 L[1 + \delta + \cdots + \delta^{n-1}]/r_2 \le \frac{a_2 L}{1-\delta}$$

and the monotonicity implies that

$$\begin{aligned}
&\int_{\mathbb{R}} V_n(y) e^{r_2(a_2-1-V_n(y)+a_2\mathcal{H}_n(V)(y))} k_2(x-y)\mathrm{d}y \\
&\quad \le \int_{\mathbb{R}} \frac{1}{r_2} e^{r_2(a_2-1-1/r_2+a_2\mathcal{H}_n(V)(y))} k_2(x-y)\mathrm{d}y \\
&\quad \le \int_{\mathbb{R}} \frac{1}{r_2} e^{r_2(a_2-1-1/r_2)+a_2L/(1-\delta)} k_2(x-y)\mathrm{d}y \\
&\quad \le \frac{1}{r_2} = V_{n+1}(x).
\end{aligned}$$

At the same time, if

$$V_{n+1}(x) = e^{\lambda'(x+c^*n+c^*)+P} < 1/r_2$$

such that

$$-V_n(y) + a_2\mathcal{H}_n(V)(y) \le 0, \quad y \in \mathbb{R}, \quad n+1 \in \mathbb{N}, \tag{27}$$

then

$$\begin{aligned}
&\int_{\mathbb{R}} V_n(y) e^{r_2(a_2-1-V_n(y)+a_2\mathcal{H}_n(V)(y))} k_2(x-y)\mathrm{d}y \\
&\quad \le \int_{\mathbb{R}} V_n(y) e^{r_2(a_2-1)} k_2(x-y)\mathrm{d}y \\
&\quad \le \int_{\mathbb{R}} e^{r_2(a_2-1)+\lambda'(y+c^*n)+P} k_2(x-y)\mathrm{d}y \\
&\quad = e^{\lambda'(y+c^*n+c^*)+P},
\end{aligned}$$

and it suffices to verify (27). Because the proof of (27) is similar to (25), we omit the details and complete the proof. □

5 Numerical Simulations

In this section, we present some numerical results on the asymptotic spreading of the predator–prey system by using MATLAB. By taking the Gaussian type kernel, we simulate several different cases. Firstly, we have

$$\inf_{\lambda>0} \frac{\ln\left(e^r \int_{\mathbb{R}} e^{\lambda y} e^{\frac{-y^2}{D}} \mathrm{d}y/\sqrt{\pi D}\right)}{\lambda} = \sqrt{Dr}, r > 0, \quad D > 0.$$

To characterize the invasion process, the level sets of unknown functions are useful to characterize the changes of habitat. If $U_n(x)$ is the unknown function, $\lambda \in \mathbb{R}$, we denote the level sets

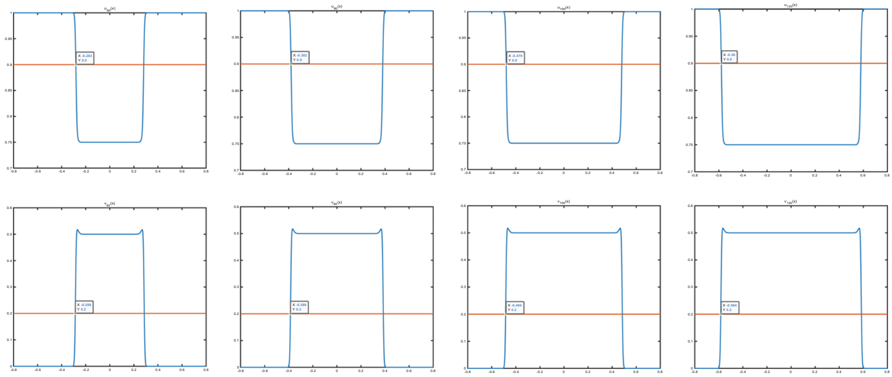

Fig. 2 Snapshots of the solution $(u_n(x), v_n(x))$ of model (28) (Color figure online)

Table 1 Approximate level sets in (28)

Time	60	80	100	120
$L\Gamma_n^u(0.9)$	-0.283	-0.382	-0.479	-0.58
$L\Gamma_n^v(0.2)$	-0.289	-0.388	-0.484	-0.584

$$\Gamma_n^U(\lambda) = \{x : U_n(x) = \lambda\}$$

and

$$L\Gamma_n^U(\lambda) = \inf_{x\in\mathbb{R}} \{x : U_n(x) = \lambda\}.$$

Then, for some $\lambda > 0$, the movement of $L\Gamma_n^v(\lambda)$ may reflect the expansion of the predators on the left side while the movement of $L\Gamma_n^u(\lambda)$ may reflect the atrophy of the prey on the left side.

Example 5.1 Firstly, we consider the following model

$$\begin{cases} u_{n+1}(x) = \frac{1}{\sqrt{0.0004\pi}} \int_{\mathbb{R}} e^{-\frac{(x-y)^2}{0.0004}} u_n(y) e^{(1-u_n(y)-0.5v_n(y))} \mathrm{d}y, \\ v_{n+1}(x) = \frac{1}{\sqrt{0.000025\pi}} \int_{\mathbb{R}} e^{-\frac{(x-y)^2}{0.000025}} v_n(y) e^{(-1-v_n(y)+2u_n(y))} \mathrm{d}y. \end{cases} \tag{28}$$

By (5), we have

$$c^* = \sqrt{0.000025} = 0.005,$$

and it has a positive steady state $(0.75, 0.5)$. We now present the snapshots of solutions $u_n(x)$ and $v_n(x)$ in Fig. 2 and some approximate level sets in Table 1.

From Fig. 2 and Table 1, we see that predators $v_n(x)$ invade the habitat of the prey $u_n(x)$ almost at a constant speed 0.005, which coincides with our analytical results.

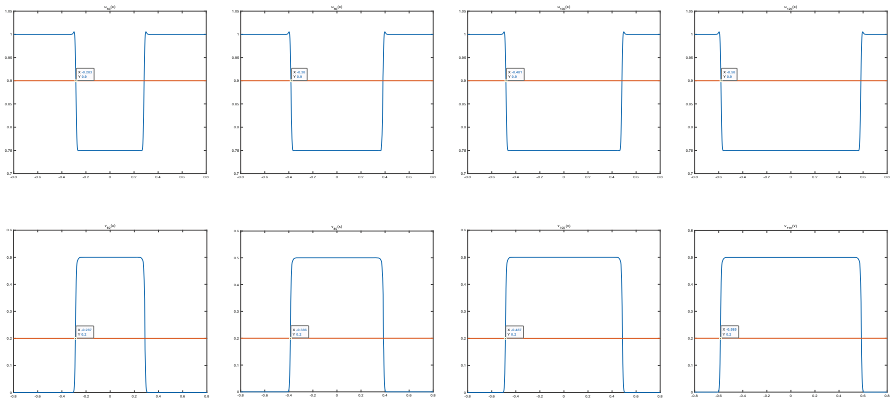

Fig. 3 Snapshots of the solution $(u_n(x), v_n(x))$ of model (29) (Color figure online)

Table 2 Approximate level sets in (29)

Time	60	80	100	120
$L\Gamma_n^u(0.9)$	-0.283	-0.38	-0.481	-0.58
$L\Gamma_n^v(0.2)$	-0.287	-0.386	-0.487	-0.585

Note that (28) is monotone, the solution rapidly converges to its constant steady state on any compact interval of the habitat.

Example 5.2 We consider the case $r_1 \in (1, 2)$ in the following system

$$\begin{cases} u_{n+1}(x) = \frac{1}{\sqrt{0.0004\pi}} \int_{\mathbb{R}} e^{-\frac{(x-y)^2}{0.0004}} u_n(y) e^{1.5(1-u_n(y)-0.5v_n(y))} \mathrm{d}y, \\ v_{n+1}(x) = \frac{1}{\sqrt{0.000025\pi}} \int_{\mathbb{R}} e^{-\frac{(x-y)^2}{0.000025}} v_n(y) e^{(-1-v_n(y)+2u_n(y))} \mathrm{d}y. \end{cases} \tag{29}$$

Then, (5) implies that

$$c^* = \sqrt{0.000025} = 0.005,$$

and the system has a positive steady state $(0.75, 0.5)$. We now present the graphs of $u_n(x)$ and $v_n(x)$ in Fig. 3 and some approximate level sets in Table 2, by which we see that the predators v_n invade the habitat of the prey u_n almost at a constant speed 0.005. Note that the steady state 1 is stable in $u_{n+1} = u_n e^{1.5(1-u_n)}$, $u_0 > 0$, but the oscillation of u_n is possible. In Fig. 3, a slight oscillation of $u_n(x)$ occurs compared with that in Fig. 2.

Example 5.3 We consider the case that cannot be studied by the results in Sects. 3, 4

$$\begin{cases} u_{n+1}(x) = \frac{1}{\sqrt{0.0004\pi}} \int_{\mathbb{R}} e^{-\frac{(x-y)^2}{0.0004}} u_n(y) e^{2.5(1-u_n(y)-0.5v_n(y))} \mathrm{d}y, \\ v_{n+1}(x) = \frac{1}{\sqrt{0.000025\pi}} \int_{\mathbb{R}} e^{-\frac{(x-y)^2}{0.000025}} v_n(y) e^{(-1-v_n(y)+3u_n(y))} \mathrm{d}y. \end{cases} \tag{30}$$

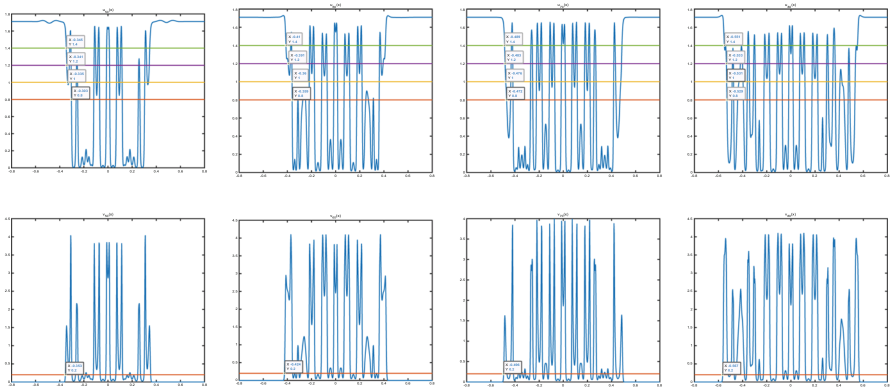

Fig. 4 Snapshots of the solution $(u_n(x), v_n(x))$ of model (30) (Color figure online)

Table 3 Approximate level sets in (30)

Time	50	60	70	80
$L\Gamma_n^u(1.4)$	-0.345	-0.41	-0.489	-0.551
$L\Gamma_n^u(1.2)$	-0.341	-0.391	-0.483	-0.533
$L\Gamma_n^u(1.0)$	-0.335	-0.36	-0.476	-0.531
$L\Gamma_n^u(0.8)$	-0.303	-0.359	-0.472	-0.529
$L\Gamma_n^v(0.2)$	-0.353	-0.424	-0.496	-0.567

We now give the graphs of $u_n(x)$ and $v_n(x)$ in Fig. 4 and level sets in Table 3. Here the spreading speed is almost 0.007, which is close to the speed determined by (5) or the equation

$$v_{n+1}(x) = \frac{1}{\sqrt{0.000025\pi}} \int_{\mathbb{R}} e^{-\frac{(x-y)^2}{0.000025}} v_n(y) e^{(2-v_n(y))} \mathrm{d}y.$$

The numerical results are similar to those in Sects. 3, 4, but this could not be determined by the conclusions in Sects. 3, 4. Note that the steady state 1 is unstable in $u_{n+1} = u_n e^{2.5(1-u_n)}, u_0 > 0$, and we may observe spatial oscillation in Fig. 4, which is different from that in Figs. 2, 3. To formulate the oscillation, we use several different level sets in Table 3, which do not move synchronously. But the average speeds of moving level sets are very close.

Example 5.4 Finally, we consider

$$\begin{cases} u_{n+1}(x) = \frac{1}{\sqrt{0.0004\pi}} \int_{\mathbb{R}} e^{-\frac{(x-y)^2}{0.0004}} u_n(y) e^{4.5(1-u_n(y)-0.5v_n(y))} \mathrm{d}y, \\ v_{n+1}(x) = \frac{1}{\sqrt{0.000025\pi}} \int_{\mathbb{R}} e^{-\frac{(x-y)^2}{0.000025}} v_n(y) e^{(-1-v_n(y)+0.95u_n(y))} \mathrm{d}y. \end{cases} \tag{31}$$

We simulate the case in Fig. 5, from which the invasion is also successful for large r_1 although $a_2 < 1$. However, the corresponding difference system does not admit such a persistence dynamics, see Fig. 6.

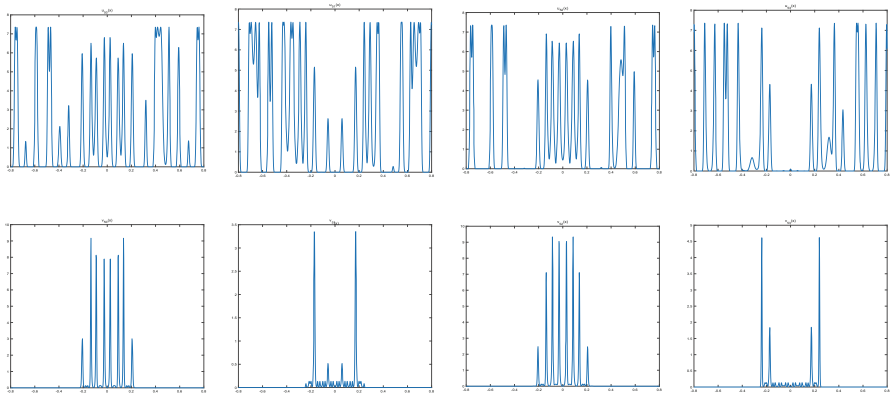

Fig. 5 Snapshots of the solution $(u_n(x), v_n(x))$ of model (31) (Color figure online)

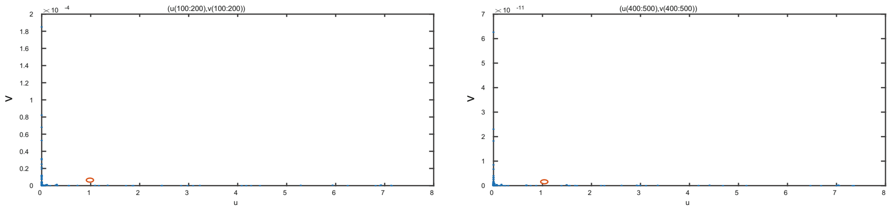

Fig. 6 Snapshots of the solutions $u_{n+1} = u_n e^{4.5(1-u_n-0.5v_n)}$, $v_{n+1} = v_n e^{-1-v_n+0.95u_n}$ with $u_0 = 1$, $v_0 = 0.2$. In the left (right) graph, we plot from (u_{100}, v_{100}) to (u_{200}, v_{200}) ((u_{400}, v_{400}) to (u_{500}, v_{500})), and the red cycle denotes the mean from (u_{100}, v_{100}) to (u_{200}, v_{200}) ((u_{400}, v_{400}) to (u_{500}, v_{500})) (Color figure online)

6 Discussion

Spreading speeds of monotone semiflows have been widely studied by Fang and Zhao (2014), Liang and Zhao (2007), Lui (1989a) and Weinberger et al. (2002). Note that the overcompensatory is universal in population dynamics, there are many mathematical models involving nonmonotone or local monotone birth functions. If a system is locally monotone such that it can be controlled by two systems generating monotone semiflows and admitting the same spreading speed, then some results on spatial propagation were established by Bourgeois et al. (2018), Hsu and Zhao (2008), Li et al. (2009), Wang and Castillo-Chavez (2012) and Yi et al. (2013). Moreover, the interspecific action leads to many coupled systems that do not generate monotone semiflows, and the predator–prey systems and competitive systems are typical nonmonotone systems. When a competitive system admitting comparison principle is concerned, we refer to Lin et al. (2011). In this paper, we studied a predator–prey system without comparison principle. The difficulty in studying (4) is that it does not satisfy comparison principle and cannot be controlled by two monotone semiflows admitting the same spreading speeds. We hope our method can be generalized to analyze other coupled systems including epidemic models.

Define

$$E=(e_1,e_2):=\left(\frac{1+a_1}{1+a_1a_2},\frac{a_2-1}{1+a_1a_2}\right),$$

which is the unique spatial homogeneous positive steady state of (4) if $a_2>1$. From some numerical examples, we observed the convergence of $u_n(x)$ and $v_n(x)$ in any compact domain. When the system is monotone, the convergence is evident by the dominated convergence theorem or Fatou lemma. We also want to know the convergence in any compact interval when the system is not monotone. In particular, very likely (4) admits nontrivial periodic solutions, is it possible to find the relationship between the long time behavior of $u_n(x)$ and $v_n(x)$ and the nonconstant periodic solutions of (4) if $x\in\mathbb{R}$ lies in any given bounded interval? For the topic, we refer to Bourgeois et al. (2018) for some results on scalar equations.

If $a_1=0, u_0(x)=1, x\in\mathbb{R}$, in (4), then $u_n(x)=1, n\in\mathbb{N}, x\in\mathbb{R}$. So $v_n(x)$ satisfies

$$\begin{cases} v_{n+1}(x)=\int_{\mathbb{R}} v_n(y)e^{r_2(a_2-1-v_n(y))}k_2(x-y)\mathrm{d}y, & x\in\mathbb{R},\quad n+1\in\mathbb{N},\\ v_0(x)=v(x), & x\in\mathbb{R}.\end{cases}$$

Evidently, we have

$$\lim_{n\to\infty}\sup_{x\in\mathbb{R}} v_n(x)=0 \ \text{ if } \ a_2\in(0,1). \tag{32}$$

However, our numerical result implies that $a_1>0, a_2\in(0,1)$ may lead to the persistence of predators $v_n(x)$. That is, the consumption of the prey leads to the nonhomogeneous of spatial distribution of individuals, which further leads to the persistence of the predators. But in the corresponding nonmonotone difference system, we did not observe similar persistence phenomena. Moreover, in the monotone case of the prey component ($r_1\in(0,1)$), the extinction of predators or (32) is also clear when $a_1>0, a_2\in(0,1)$. So, we conjecture that instability of the predator-free steady state and persistence of system is the coupled effect of spatial dispersal and overcompensating that happen at different stages. More precisely, because of the overcompensation, the local consumption of the prey leads to its relative small density at the current generation and its relative large density in the next generation. Then, the spatial contact leads to relative more resource for the nearby predators, and this makes the system persistent. Therefore, this may imply dispersal-driven instability of the predator-free state, and we refer to Neubert et al. (1995, Section 4) for the dispersal-driven instability of the positive steady state. Evidently, if a threshold on asymptotic spreading exists, this threshold cannot be given by (5). These are challenging questions and deserve further consideration.

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