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ORIGINAL ARTICLE

# Continuous Traveling Waves for Prey-Taxis

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**Abstract** Spatially moving predators are often considered for biological control of invasive species. The question arises as to whether introduced predators are able to stop an advancing pest or foreign population. In recent studies of reaction–diffusion models, it has been shown that the prey invasion can only be stopped if the prey dynamics observes an Allee effect.

In this paper, we include prey-taxis into the model. Prey-taxis describe the active movement of predators to regions of high prey density. This effect leads to the observation that predators are drawn away from the leading edge of a prey invasion where its density is low. This leads to counterintuitive result that prey-taxis can actually reduce the likelihood of effective biocontrol.

**Keywords** Predator–prey models · Prey-taxis · Invasion · Biocontrol

## 1. Introduction

Mathematical modeling has provided useful tools to understand biological phenomena such as disease spread, insect outbreak, animal coat patterns, wound healing, and interspecific interactions. There are three main types of interspecific interaction: predator–prey, competition, and mutualism. In a predator–prey relationship, the predator species benefits from killing and consuming the prey species, and the prey population size may be regulated as a result (Murray, 1989).

A characteristic feature of living organisms is that they respond to the environment in search for food and reproductive opportunity. One such response is movement toward or away from an external stimulus, which is called *taxis*. Taxis is facilitated by both directional behavior-change of velocity, and turning angle, and nondirectional behavior-change of speed or turning rate in response to the stimulus (Okubo and Levin, 2000). Corresponding to the type of external stimulus, various types of taxis are defined, such as aerotaxis,

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chemotaxis, geotaxis, haptotaxis, prey-taxis and others. The purposes of taxis may be numerous, including movement toward food and avoidance of enemies.

In this paper, we consider spatial predator–prey systems. In particular, we consider the foraging behavior of the predator toward high prey density and investigate the role of prey-taxis in spatial predator–prey interactions. For that, we extend the diffusion–reaction model in Owen and Lewis (2001) by incorporating the mechanism of prey-taxis into spatial predator–prey systems (Kareiva and Odell, 1987).

Predator–prey models have been studied by numerous people using different frameworks, such as discrete models (Hassell, 1978), ODE models (Wangersky, 1978; Auger et al., 2002), and diffusion–reaction models (Dunbar, 1983; Cantrell and Cosner, 1996; Owen and Lewis, 2001; Huang et al., 2003). Diffusion–reaction models describe spatial structures explicitly by means of diffusive motility of species in heterogeneous environments, and they describe temporal structures via reaction terms.

Owen and Lewis (2001) showed that when a prey species grows logistically, a predator population that catches up with an invading prey wave is in general not able to slow down the prey spread. To demonstrate this, they used diffusion–reaction systems and linearized about the leading edge of the wave (where the densities of the prey and the predator are close to zero). However, they found that for the particular prey population dynamics of Allee type, the predator can actually slow down or even reverse the prey invasion. In their model, it was assumed that the diffusion rate of the predator is much faster than the one of the prey. When the prey dynamics developed under an Allee effect, Owen and Lewis applied a singular perturbation analysis and considered the situation that the front of the predator arrives at that of the prey.

In this paper we undertake a similar analysis in the presence of prey-taxis. It turns out that the control effect of the predator is actually reduced through prey-taxis (Section 3). Effective control of a spreading prey population requires predators at the leading edge of the spreading prey population. However, the addition of prey-taxis to a model means that predators are drawn away from the leading edge by prey-taxis. This reduces the effect of the predator on controlling prey spread as compared to that from pure diffusive motion of predator.

Compared to the long history of chemotaxis (Horstmann, 2003), a prey-taxis equation was derived more recently by Kareiva and Odell (1987). Kareiva and Odell investigated the phenomenon that predators (ladybugs) tend to search for food in areas of higher prey (aphids) density, and derived the mechanism for this non-random foraging. Based on this mechanism, they studied predator aggregation in high prey density areas. (See Ferran and Dixon, 1993; Dixon, 2000 for more details of foraging behavior of ladybugs.) This inclusion of directional movement towards prey-rich environments tended to increase the chance of predator survival in a heterogeneous prey distribution (Kareiva and Odell, 1987).

The characteristic feature of prey-taxis equations is that taxis is incorporated into dispersal terms as an advection term where velocity is proportional to the gradient of the prey density. Here we obtain the model by incorporating a prey-taxis term into the reaction–diffusion model of Owen and Lewis (2001) as follows

$$v_t = \epsilon v_{xx} + vf(v) - nh(v), \tag{1}$$

$$n_t = n_{xx} - \big(\chi(v)v_x n\big)_x + \gamma n\big(h(v) - \delta\big), \tag{2}$$

where $\epsilon$, $\gamma$ and $\delta$ are positive dimensionless quantities. It is assumed that $\epsilon \ll 1$. Here $v(x,t)$ and $n(x,t)$ are prey density and predator density, respectively. The function $f(v)$ describes the prey population dynamics in absence of the predator, $h(v)$ is the functional response per predator, and $\gamma\delta$ is the mortality rate of the predator in absence of the prey. The prey-sensitivity, $\chi(v)$, is a non-negative non-increasing function of the prey density. The model (1), (2) has been derived in Lee (2006) where more details about the modeling assumptions can be found.

When applied to predator–prey models, traveling wave front solutions have shown how the predators invade an area where prey has already stabilized to its carrying capacity. Traveling wave fronts are solutions to partial differential equations (PDEs), which have a fixed shape and translate at a constant speed $c$ as time evolves. (See Murray, 1989 for a detailed discussion.)

Investigating traveling waves enables us to understand how the prey population can be controlled by the predator that is released as a biological control agent. Understanding the mechanism of the predator response to spatial prey density helps us to select a proper control agent. In addition, we may be able to diagnose the sources of failure and success in biological control campaigns. As a result, we could suggest management possibilities that are likely to be successful.

The study of traveling wave solutions falls into two groups. The first describes spread of predators into an area where prey has already stabilized to its carrying capacities. The second describes simultaneous spread of predator and prey into a new environment.

Dunbar (1983, 1984, 1986) demonstrated the existence of various traveling wave trains (traveling wave solutions which show periodic behaviors) and traveling front solutions with a range of speeds $c$ for a diffusive predator–prey system with logistic growth of the prey and a type II functional response and where only the predator moved. Huang et al. (2003) extended Dunbar's result to the case that the prey equation has a diffusion term as well. When logistic prey dynamics are replaced by a so-called Allee effect, predator–prey systems with constant diffusion terms for both species have a unique traveling wave solution with a fixed unique wave speed $c$ (Gardner, 1984). Here, the Allee effect is negative population growth at low densities due to a variety of social mechanisms such as a lower chance of finding mates, less efficient group defense, and so forth (Allee et al., 1949; Lewis and Kareiva, 1993).

In this paper, we consider the case where predator and prey spread together into a new environment. The case where only the predator moved, i.e. $\epsilon = 0$ was considered by Dunbar (1983). Owen and Lewis (2001) considered the case where prey also moved, i.e. $\epsilon > 0$. We include prey-taxis, ratio-dependent functional responses, and an Allee effect, and see results on predator control of prey.

This paper is organized as follows. In Sections 2.1, 2.2, we consider the prey population dynamics with no Allee effect growth. In particular, in Section 2.1, for standard functional responses, we study the role of prey-taxis on the prey spread and find that predators cannot slow down a prey invasion (Theorem 2.1). In Section 2.2, we investigate ratio-dependent functional responses and find that for a specific linear ratio-dependent functional response, predators can slow down a prey invasion (Theorem 2.2). An Allee effect is considered in Sections 3.2 and 3.4 with prey-taxis. A constant prey sensitivity and a non-constant prey sensitivity are considered in Sections 3.2 and 3.4, respectively, and we find that predators can stop a prey invasion (Theorems 3.1 and 3.3).

## 2. Prey dynamics with no Allee effect

In this section, we study the model (1), (2) with the case that the prey dynamics has no Allee effect. In addition, we consider standard functional responses ($h(0)=0$ and $h'(0)$ is bounded) in Section 2.1 and ratio-dependent functional responses in Section 2.2. The purpose of this section is to find if the predator with prey-taxis can stop or slow down a prey invasion. We find that when the functional response is of standard, then the presence of predators cannot slow down the prey spread, but when the functional response is of ratio-dependent type, then the presence of predators may slow down or stop the prey spread.

### 2.1. *Standard functional responses*

Here, we study the wavefront after the predators catch up with the prey invasion. In this section, we consider growth with no Allee effect ($f(0)>0$, e.g. logistic growth, $f(v)=1-v$) and a standard functional response ($h(0)=0$ and $h'(0)$) is bounded, e.g. type I–III Holling functional response. This case with no prey-taxis was considered by Owen and Lewis (2001) where it was shown that predator did not slow down spread of the prey. The traveling wave with the predator moved at the same speed as the traveling wave without the predator, namely the Fisher wave speed.

Slow movement of the prey generates a sharp transition in prey population from the coexistence steady state on the left of the wave to zero population on the right of the wave. In Lee (2006), we derive a prey sensitivity $\chi(v)$ from a random walk approach that is fit to experimental data. From that study, we find that to leading order $\chi(v)=\frac{b}{v}$ (see also Segel, 1980), hence the case $\chi(0)=\infty$ occurs. However, it is biologically unrealistic to assume an infinite response of predators to an infinitesimal amount of prey. Additionally, the singularity at $v=0$ produces mathematical difficulties, which are not biologically relevant. Hence, in this paper we will consider some regularization, i.e. for $\tau>0$, we study $\chi(v)=\frac{b}{v+\tau}$ and $\chi(v)=\frac{b}{(v+\tau)^2}$ (see also Tyson et al., 1999).

We transform Eqs. (1), (2) using traveling wave coordinates, $z=x-ct$ (with wave speed $c$) to get

$$0=cV'+\epsilon V''+Vf(V)-Nh(V), \tag{3}$$

$$0=cN'+N''-\big(\chi(V)V'N\big)'+\gamma N\big(h(V)-\delta\big), \tag{4}$$

with $N(z)=n(x,t)$ and $V(z)=v(x,t)$. We consider the traveling wave connection between the coexistence steady state $(\tilde{v},\tilde{n})=(v_0,n_0)$ and trivial steady state $(\hat{v},\hat{n})=(0,0)$ with the conditions that $\lim_{z\to\infty}N(z)=\lim_{z\to\infty}V(z)=0$, $\lim_{z\to-\infty}N(z)=n_0$, and $\lim_{z\to-\infty}V(z)=v_0$. This describes the situation where an established prey population begins to spread along the positive direction and newly introduced predators follow the spread of the prey. Since the predator density changes via diffusion and by the local population dynamics, initially, predators may easily catch up with the prey wave. However, as soon as predators reach the front of the spreading prey, the predator spreading speed is slowed down due to the lack of prey.

We consider whether or not the traveling waves of prey slow down due to the interaction with predators. We use linear analysis for this. In a small neighborhood of a hyperbolic equilibrium $(\hat{v},\hat{u})=(0,0)$ for (3), (4), flow of the nonlinear system is topologically equivalent with that of its linearization if $(0, 0)$ is a hyperbolic steady state (Hartman, 1964). The linearized equations of Eqs. (3), (4) are,

$$0 = cV' + \epsilon V'' + \big(\hat{v} f'(\hat{v}) + f(\hat{v}) - \hat{n} h'(\hat{v})\big) V - h(\hat{v}) N, \tag{5}$$

$$0 = cN' + N'' - \big(\chi(\hat{v})\hat{n}\big) V'' + \gamma \hat{n} h'(\hat{v}) V + \gamma \big(h(\hat{v}) - \delta\big) N. \tag{6}$$

The linearized prey-taxis term can be obtained by

$$\begin{aligned}\big(\chi(v) v_x n\big)_x &= \big(\big(\chi(\hat{v}) + \chi'(\hat{v}) V\big) V_x (\hat{n} + N)\big)_x \\ &= \chi(\hat{v})\hat{n} V_{xx} + \chi'(\hat{v})\hat{n}(V V_x)_x + \chi(\hat{v})(N V_x)_x + \chi'(\hat{v})(N V V_x)_x \\ &\approx \chi(\hat{v})\hat{n} V_{xx},\end{aligned} \tag{7}$$

up to the order $V^2$ approximation.

We now look for solutions in the form

$$N, V \propto \exp(\lambda z), \tag{8}$$

where $\lambda$ is the eigenvalue. The eigenvalue $\lambda$ having negative real parts implies that the steady state $(\hat{n}, \hat{v}) = (0, 0)$ is linearly stable, since, after small perturbation, $(\hat{n}, \hat{v}) \to (0, 0)$ as $z \to \infty$. Substitution of (8) into (5), (6) gives the following condition

$$\begin{vmatrix} \epsilon\lambda^2 + c\lambda + \hat{v} f'(\hat{v}) + f(\hat{v}) - \hat{n} h'(\hat{v}) & -h(\hat{v}) \\ -\chi(\hat{v})\hat{n}\lambda^2 + \gamma \hat{n} h'(\hat{v}) & \lambda^2 + c\lambda + \gamma(h(\hat{v}) - \delta) \end{vmatrix} = 0. \tag{9}$$

Since we are interested in the predator–prey–free steady state, i.e. $(\hat{n}, \hat{v}) = (0, 0)$, (9) becomes

$$\begin{vmatrix} \epsilon\lambda^2 + c\lambda + f(0) & 0 \\ 0 & \lambda^2 + c\lambda - \gamma\delta \end{vmatrix} = 0, \tag{10}$$

which leads to the same characteristic equation as Owen and Lewis (2001) derived for the diffusion-only case. Hence, we obtain a similar result that the wave speed in a prey-taxis system is the same as that in the prey-only case. Therefore, predators cannot slow down the prey spread in the form of traveling waves. In this case, predators slow down and adjust their own spread rate to the prey's spread rate.

**Theorem 2.1.** *Consider* (1), (2) *on an unbounded domain* $-\infty < x < \infty$ *and assume*

- (i) *The functional response is zero for zero prey density* ($h(0) = 0$) *and its slope is bounded at zero density* ($h'(0)$ *bounded*), *e.g. type I*, $h(v) = v$, *or type II*, $h(v) = \frac{(\alpha+1)v}{\alpha+v}$,
- (ii) *The per capita growth rate for prey is positive for low prey densities* ($f(0) > 0$), *e.g. logistic growth of prey*, $f(v) = 1 - v$, *and*
- (iii) *Bounded prey-taxis coefficient of the form*, $\chi(v) \geq 0$, *e.g.* $\chi(v) = \frac{b}{v+\tau}$, *or* $\chi(v) = \frac{b}{(v+\tau)^2}$.

*Then the minimum traveling wave speed $c^*$ is bounded by the minimal Fisher speed*

$$c^* \geq 2\sqrt{\epsilon f(0)}.$$

*This implies that predators cannot slow down a prey invasion with speed $2\sqrt{\epsilon f(0)}$.*

This may indicate that as predators approach the tip of prey spread, they adjust their speed not to exceed the tip of the prey's spread. Through a series of simulations, it is seen that as the prey sensitivity coefficient $b$ decreases, the tip of predators catching up with prey retreats behind the tip of prey spread, so a predator free zone appears near the tip of the prey spread. A diffusion process of the predator tend to make predators smear into the tip of the prey spread, but strong prey-taxis makes predators move back. Thus, at some distance from the tip of the prey wave, the tip of the predator catching up is formed.

### 2.2. *Ratio-dependent functional responses*

Since for growth with no Allee effect, the prey-taxis term fails to have an effect on the result of the linear analysis, we now consider different functional responses, without a prey-taxis term. These cases have not been studied by Owen and Lewis (2001).

Here, we consider ratio-dependent functional responses in order to examine whether predators may slow down prey spread. Our analysis (not shown here) also indicates that prey-taxis does not play a role in stopping prey spread for the ratio-dependent case. The ratio-dependent functional responses we consider are the form of $h(v,n) = \frac{\mu v}{n+dv+\tau}$ for some positive constants $\mu$, $d$, and $\tau$ (see DeAngelis et al., 1975; Getz, 1991; Berryman et al., 1995). Here we consider four cases. The first case is of $d = \tau = 0$, the second one of $d = 0$ and $0 < \tau \ll 1$, the third one of $d > 0$ and $\tau = 0$, and the last one of $d > 0$ and $0 < \tau \ll 1$. Indeed, the first two cases are the linear ratio-dependent functional responses and the last two are the hyperbolic ratio-dependent functional responses.

We are thus interested in the following system

$$v_t = \epsilon v_{xx} + vf(v) - nh(v,n), \tag{11}$$

$$n_t = n_{xx} + \gamma n\big(h(v,n) - \delta\big). \tag{12}$$

First, we consider case 1 of a linear ratio-dependent functional response, i.e. $h(v,n) = \frac{\mu v}{n}$. When we substitute $h(v,n) = \frac{\mu v}{n}$ into Eq. (11), we have $v_t = \epsilon v_{xx} + v(f(v) - \mu)$. At $(v,n) = (0,0)$, the linear ratio-dependent functional response, $h(v,n) = \frac{\mu v}{n}$, is undefined, but the term $nh(v,n)$ is continuous at $(v,n) = (0,0)$. In this case, Eq. (11) becomes a Fisher-type equation. Thus, the condition for the wave speed is

$$c^2 \geq 4\epsilon\big(f(0) - \mu\big). \tag{13}$$

Hence, when the functional response is of the linear ratio type in case 1, then the presence of predators may slow down or stop the prey spread depending on the parameter $\mu$. In the absence of predators, the prey dynamics follow logistic growth, but the introduction of predators leads to a different prey population growth about the leading edge of the wave. The main cause for the slowing down of the prey invasion is the fact that predators are spontaneously generated by prey even at arbitrary low prey densities. As a result, the prey

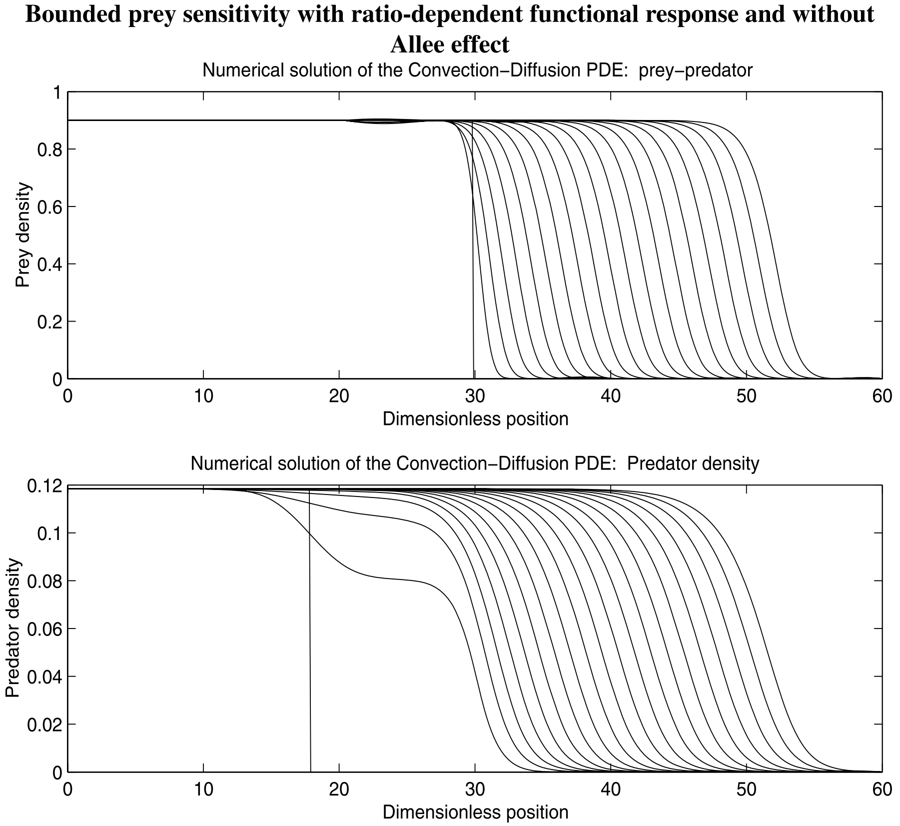

**Fig. 1** With logistic growth, $f(v) = 1 - v$, linear ratio-dependent functional response, $h(v, n) = \frac{\mu v}{n}$, and constant prey sensitivity ($\chi = 0$), introduced predators, which catch up with prey spread, and only slightly slow down the prey spread. Here $\mu = 0.1$.

intrinsic growth rate becomes smaller due to the potential interactions with predators at the leading edge of the wave, i.e. the intrinsic growth rate becomes $f(0) - \mu$. This may be biologically questionable, i.e. ratio dependence seems to break down in a biological sense at zero predator density (Abrams and Ginzburg, 2000). Figures 1 and 2 demonstrate that the prey spread with $\mu = 0.1$ and $\mu = 0.95$, respectively. Consequently, it is noted that the case of $\mu = 0.95$ shows a slower spread rate of the prey than that of $\mu = 0.1$.

We now regularize the linear ratio-dependent functional response by adding a small term $0 < \tau \ll 1$ to the denominator, i.e. $h(v, n) = \frac{\mu v}{n+\tau}$. Then at the predator–prey–free steady state, i.e. $(\hat{n}, \hat{v}) = (0, 0)$, the linearized equations of (11), (12) are

$$0 = cV' + \epsilon V'' + f(0)V, \tag{14}$$

$$0 = cN' + N'' - \gamma\delta N, \tag{15}$$

which leads to the characteristic Eq. (10). Hence predators cannot slow down the prey spread in the form of traveling waves, which is contrary to the result in case 1. This regu-

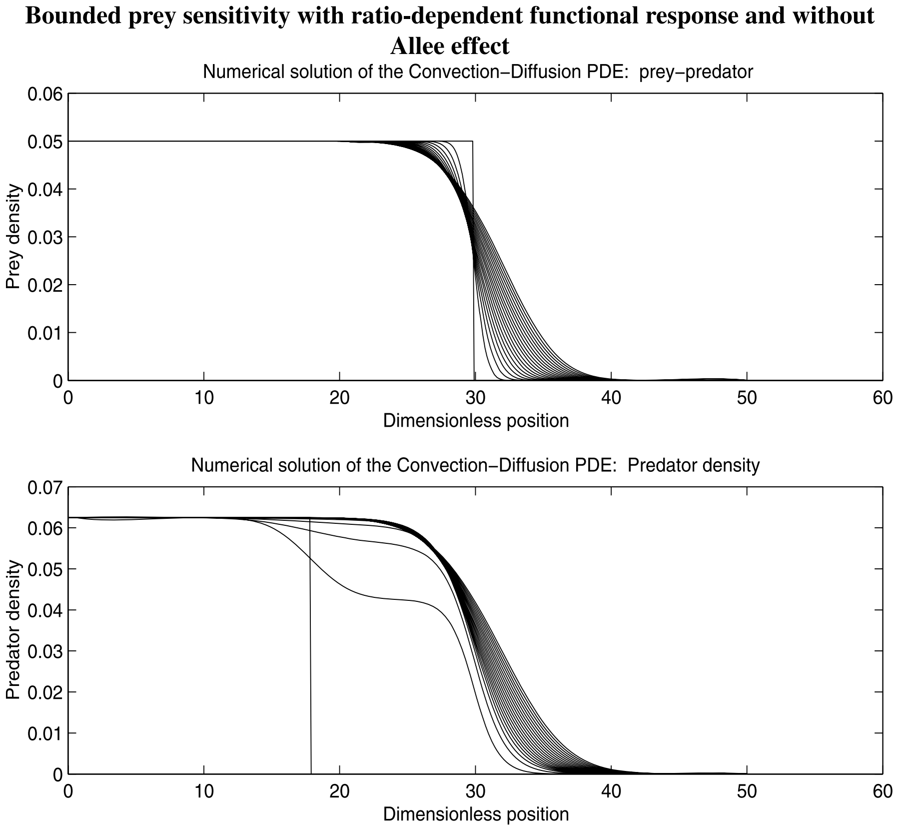

**Fig. 2** With logistic growth, $f(v) = 1 - v$, linear ratio-dependent functional response, $h(v, n) = \frac{\mu v}{n}$, and constant prey sensitivity ($\chi = 0$), introduced predators, which catch up with prey spread, and obviously slow down the prey spread. Here $\mu = 0.95$.

larization means that predators are no longer produced when the prey density approaches zero.

In case 3, a singular hyperbolic functional response, i.e. $h(v, n) = \frac{\mu v}{n+dv}$, has attracted the attention of researchers for its rich behaviors at $(v, n) = (0, 0)$ (Kuang and Beretta, 1998; Jost et al., 1999). This singular function causes a singularity for a prey and predator local dynamics, which prevents a linear stability analysis at the leading edge of a wave. For this case, other methods need to be used and we leave this case as an open problem.

Now we consider the regularized hyperbolic ratio-dependent functional response of $h(v, n) = \frac{\mu v}{n+dv+\tau}$ in (11), (12). At the predator–prey–free steady state, i.e. $(\hat{n}, \hat{v}) = (0, 0)$, the linearized equations of (11), (12) are

$$0 = cV' + \epsilon V'' + \big(f(0)\big)V, \tag{16}$$

$$0 = cN' + N'' - \gamma\delta N, \tag{17}$$

which again leads to the characteristic Eq. (10). Hence, this indicates that when the predator follow a regularized hyperbolic ratio-dependent functional response, then the predator cannot slow down the prey spread with diffusion. We summarize:

**Theorem 2.2.** *Consider* (1), (2) *with* $\chi = 0$, $f(0) > 0$, *and ratio-dependent functional response*, $h(v,n) = \frac{\mu v}{n+dv+\tau}$. *If* $d = \tau = 0$, *i.e.* $h(v,n) = \frac{\mu v}{n}$, *then the minimal traveling wave speed* $c^*$ *satisfies*

$$c^* \geq 2\sqrt{\epsilon\big(f(0) - \mu\big)}.$$

*If* $\tau > 0$, *then the minimal traveling wave speed* $c^*$ *satisfies*

$$c^* \geq 2\sqrt{\epsilon f(0)},$$

*regardless of the value of* $d \geq 0$.

*Remark.* If $d > 0$ and $\tau = 0$, i.e. $h(v,n) = \frac{\mu v}{n+dv}$, then other methods need to be used for calculating the minimal traveling wave speed $c^*$.

## 3. Prey dynamics with an Allee effect

In the previous sections, we studied logistic prey growth and used linear analysis to find the prey spread rate. However, when the prey dynamics includes an Allee effect, we cannot use linear analysis (see Lewis and Kareiva, 1993 for details) because the speed of a "pushed wave" is determined by the whole wave front. Instead of linear analysis, singular perturbation analysis of the wavefront has been used for the diffusion-only case (Owen and Lewis, 2001). In this section, we consider prey-taxis as an additional dispersal term and use singular perturbation methods to find a necessary condition for the predator to stop a prey invasion, i.e. $c = 0$. We begin this section by briefly reviewing the analysis of Owen and Lewis (2001).

### *3.1. Singular perturbation method for standing waves*

Here, we briefly sketch the singular perturbation for standing waves. Owen and Lewis (2001) study models (1), (2) without prey-taxis ($\chi = 0$). Due to the sharp transition layer for small $\epsilon$, a singular perturbation approach is used to find two conditions

$$\int_0^{v_0} vf(v) - g(v_0)h(v)\,dv = 0, \tag{18}$$

$$\int_{v_0}^{v_s} vf(v)g'(v)\,dv = \frac{1}{2}\delta g(v_s)^2, \tag{19}$$

(See Owen and Lewis, 2001 and Lee, 2006 for more details.)

A singular perturbation analysis of the wavefront consists of two steps. The first step is to consider a stationary wave in a transition layer and the result appears in (19). The second step is to match the right- and left-outer solutions and the result is in (18). To

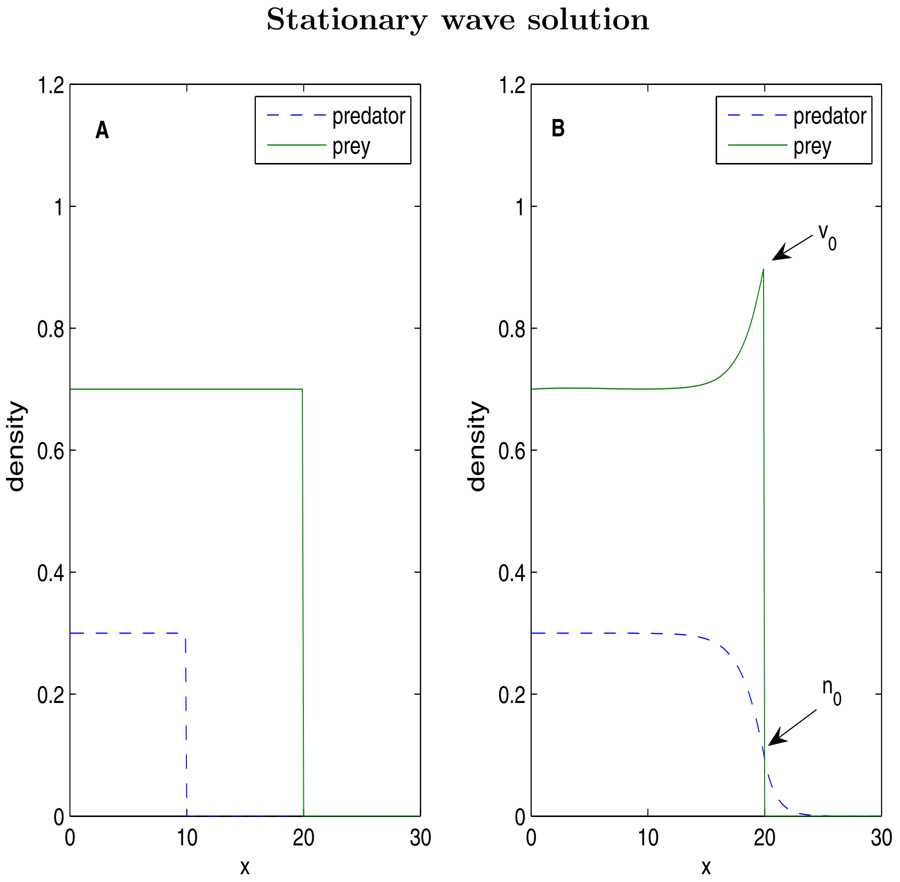

**Fig. 3** Stationary wave solution to Eqs. (1) and (2) with logistic growth, $f(v) = 1 - v$, type I functional response and $h(v) = v$. Here $\delta = 0.7$, $\epsilon = 0$, and $\gamma = 1$. In A, dashed and solid lines show initial predator and prey distribution, respectively. In B, dashed and solid lines show predator and prey distribution, respectively, at $t = 500$.

describe a standing prey wave ($c = 0$) with sharp transition, we begin with a predator–prey model for a completely immobile prey (Hastings et al., 1997). We assume that the distribution of prey reached a steady state (Fig. 3A shows the initial distributions of the predator and prey density). Introduced predators initially move forward and stop at the prey front to reach a steady state (Fig. 3B shows the distributions of the predator and prey density after 500 time units).

In the second step, we allow the prey to move with a small diffusion rate. When prey move slowly compared to their predators, a transition layer appears at the wave front (see Fig. 4B). In the transition layer, the predator density remains about constant $n = n_0$ to leading order and the corresponding prey density is $v_0$.

It is noted that when we apply these two conditions (18), (19) from Owen and Lewis (2001) to the situation where the prey population growth is logistic or shows an Allee

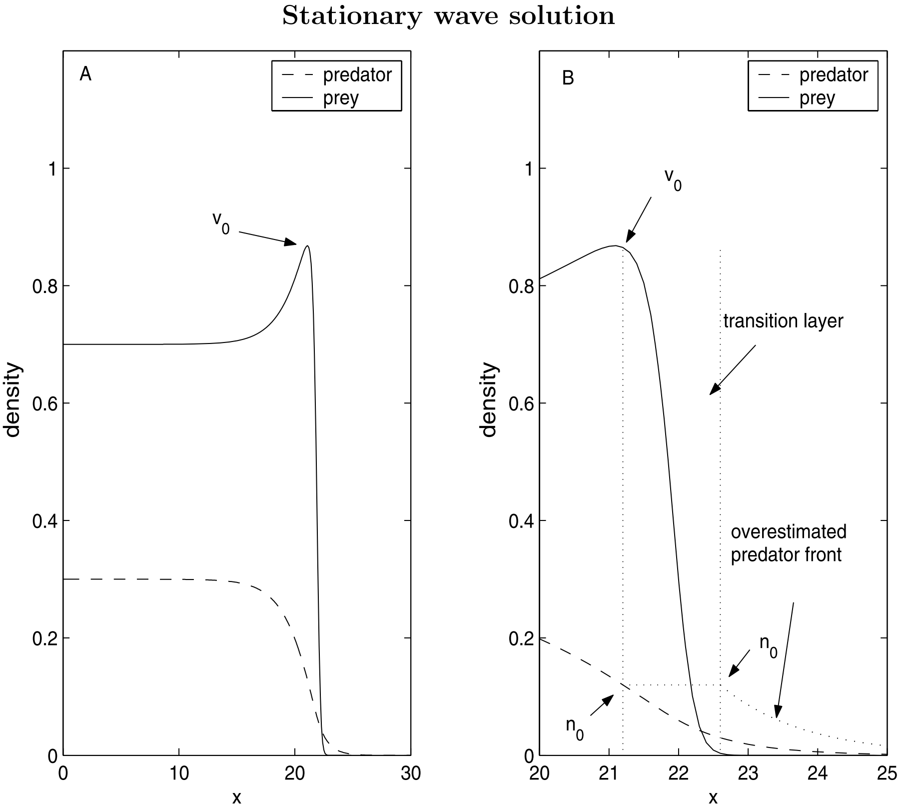

**Fig. 4** Stationary wave solution to Eqs. (1) and (2) with logistic growth, $f(v) = 1 - v$, type I functional response and $h(v) = v$. Here $\delta = 0.7$, $\epsilon = 0.01$, and $\gamma = 1$. In A, dashed and solid lines show initial predator and prey distribution, respectively. In B, dashed and solid lines show predator and prey distribution, respectively, at $t = 10$.

effect, the predator density is slightly overestimated in the transition area (see Fig. 4B). With logistic growth, the overestimated predators fail to stop the prey spread. Therefore, the predators from the exact solution cannot stop the prey spread. In contrast, with an Allee effect, the overestimated predators stop the prey spread, however, it does not guarantee that the predators from the exact solution may stop the prey spread. As the prey diffusion rate $\epsilon$ increases, this error increases. Thus, the parameter $a$ shown in the Allee effect would have to increase for predators to stop the prey spread as $\epsilon$ increases.

The same method can be used for non-zero wave speeds. Before we derive a necessary condition for stopping prey in the predator–prey model with prey-taxis, we also note that a singular perturbation analysis of the wavefront can be applied for the case with logistic growth as well. As a result, singular perturbation gives an idea that the appearance of the predator can stop or slow down the prey spread but that method may not give an idea how much the prey slow down due to the predator.

### *3.2. Constant prey sensitivity*

We now resume finding the stopping conditions for the case of prey-taxis. Recall that a key difference between our model and the model of Owen and Lewis is that prey-taxis is added in our model. To find a spread rate, we study the wavefront after the predators catch up with the prey and the coexistence is observed. Slow movement of the prey generates a sharp transition that connects the coexistence steady state on the left to the zero population on the right.

We want to find out whether predators with a prey-taxis strategy can stop prey spread, i.e. if $c = 0$ is possible. Here, we consider a constant prey sensitivity, i.e. $\chi(v) = \chi$. We use the singular perturbation method of Owen and Lewis (2001), which needs a critical modification due to the prey-taxis term. Due to the zero wave speed we consider the temporal steady state of the following system

$$v_t = \epsilon v_{xx} + vf(v) - nh(v), \tag{20}$$

$$n_t = n_{xx} - (\chi v_x n)_x + \gamma n\big(h(v) - \delta\big), \tag{21}$$

where the constant $\chi$ is the prey sensitivity of the predator and $\epsilon$, $\gamma$, and $\delta$ positive dimensionless parameters. We consider Allee dynamics, $f(v) = (1 - v)(v - a)$ and a type I functional response, $h(v) = v$ (later we will consider various forms of $f(v)$, and $h(v)$). The stationary system is as follows

$$0 = \epsilon v_{xx} + vf(v) - nh(v), \tag{22}$$

$$0 = n_{xx} - (\chi v_x n)_x + \gamma n\big(h(v) - \delta\big). \tag{23}$$

*Transition layer.* Rescaling the spatial coordinate to $\xi = \frac{x}{\sqrt{\epsilon}}$, Eqs. (22), (23) are written as

$$0 = v_{\xi\xi} + vf(v) - nh(v), \tag{24}$$

$$0 = n_{\xi\xi} - (\chi v_\xi n)_\xi + \epsilon\gamma n\big(h(v) - \delta\big). \tag{25}$$

The boundary conditions of the transition layer are: $\lim_{\xi\to\pm\infty} v_\xi(\xi) = 0$, $\lim_{\xi\to\infty} v(\xi) = 0$, and $\lim_{\xi\to-\infty} v(\xi) = v_0$. As $\epsilon \to 0$, $n$ follows $n_{\xi\xi} - (\chi v_\xi n)_\xi = 0$. Integrating this equation, we have $n_\xi - \chi v_\xi n = C_0$. As $\xi \to \pm\infty$, $n_\xi \to C_0$, since $v_\xi \to 0$. For large $|\xi|$, $n_\xi \approx C_0$. Integrating one more time, then for large $|\xi|$ we have $n \approx C_0\xi + C_1$ where $C_0$ and $C_1$ are integral constants. However, for any non-zero constant $C_0$, a different sign of $\xi$ generates a negative population for the predators for $|\xi| \gg 1$, i.e. if $C_0 > 0$, then for negative large $\xi$, $n$ becomes negative. Thus, $C_0$ must be zero. We now have $n_\xi - \chi v_\xi n = 0$ for all $\xi$ and $n_\xi = 0$ for large $|\xi|$. Isolating $n$ on the left side and $v$ on the right side, we have

$$\frac{1}{n} n_\xi = \chi v_\xi. \tag{26}$$

This can be integrated directly with respect to $\xi$ so that

$$\ln\big(n(\xi)\big) - \ln\big(n(-\infty)\big) = \int_{-\infty}^{\xi} \chi v_\xi \, d\xi = \chi\big(v(\xi) - v(-\infty)\big). \tag{27}$$

Since $n(-\infty) = n_0$, a constant to be determined, we have

$$n(\xi) = n_0 \exp\bigl(\chi\bigl(v(\xi) - v_0\bigr)\bigr). \tag{28}$$

In contrast to the case studied by Owen and Lewis (2001), the predator density is not constant in the transition layer, but rather given by (28). Note that $n(-\infty) = n_0$ and $n(\infty) = n_1 = n_0 \exp(-\chi v_0)$. We substitute relation (28) for $n$ into (24), and then we have a single equation for $v$, namely

$$v_{\xi\xi} + vf(v) - n_0 \exp\bigl(\chi\bigl(v(\xi) - v_0\bigr)\bigr)h(v) = 0, \tag{29}$$

where the boundary conditions are: $\lim_{\xi\to\pm\infty} v_\xi(\xi) = 0$, $\lim_{\xi\to\infty} v(\xi) = 0$, and $\lim_{\xi\to-\infty} v(\xi) = g^{-1}(n_0) = v_0$, where $g(v) = \frac{vf(v)}{h(v)}$ (the transformation in Eq. (29) has also been used by Nanjundiah, 1973). Multiplying Eq. (29) by $dv/d\xi$, and integrating with respect to $\xi$ from $-\infty$ to $\infty$ gives

$$\int_{-\infty}^{\infty} \left\{ \frac{d^2v}{d\xi^2} + vf(v) - n_0 \exp\bigl(\chi\bigl(v(\xi) - v_0\bigr)\bigr)h(v) \right\} \frac{dv}{d\xi}\, d\xi = 0. \tag{30}$$

The first term is integrated directly and the second term is done by using a change of variables from $\xi$ to $v$, to get

$$\frac{1}{2}\left(\frac{dv}{d\xi}\right)^2 \Bigg|_{-\infty}^{\infty} + \int_0^{v_0} vf(v) - n_0 \exp\bigl(\chi(v - v_0)\bigr)h(v)\, dv = 0. \tag{31}$$

Applying the boundary conditions and $n_0 = g(v_0)$ yields

$$\int_0^{v_0} vf(v) - g(v_0) \exp\bigl(\chi(v - v_0)\bigr)h(v)\, dv = 0, \tag{32}$$

which determines $v_0$ consistent with a stationary solution.

*Right-hand outer solutions.* We now consider Eqs. (22), (23) setting $\epsilon = 0$ and $z = x$ so that $v$ and $n$ satisfy

$$0 = vf(v) - nh(v), \tag{33}$$

$$0 = n_{zz} - (\chi v_z n)_z + \gamma n\bigl(h(v) - \delta\bigr). \tag{34}$$

From Eq. (33), $v = 0$ or $n = g(v) = \frac{vf(v)}{h(v)}$. Since we are looking for the right-hand outer solutions, we here focus on $v = 0$ so that in Eq. (34) $v_z$ becomes zero and we get

$$n_{zz} - \gamma\delta n = 0, \tag{35}$$

with boundary conditions: $\lim_{z\to\infty} n(z) = 0$ and $n(0) = n_1 = n_0 \exp(-\chi v_0)$. Therefore, after applying boundary conditions to (35), we get

$$n(z) = n_1 \exp\bigl(-\sqrt{\gamma\delta}z\bigr), \quad \text{and subsequently} \quad \frac{dn}{dz}(0) = -n_0 \exp(-\chi v_0)\sqrt{\gamma\delta}. \tag{36}$$

*Left-hand outer solutions.* We now consider the other outer layer. Recall that without prey-taxis, in the transition layer $n(\xi)$ was constant so that Eq. (36) played the role of a boundary condition to find left-hand outer solutions. (See Owen and Lewis, 2001 for details.) However, the prey-taxis term makes the procedure of matching the solutions more complicated. Here, we consider the conserved flux in the transition layer so that $(\frac{dn}{dx} - \chi n \frac{dv}{dx})|_{x=0} = (\frac{dn}{d\xi} - \chi n \frac{dv}{d\xi})|_{\xi=\infty} = (\frac{dn}{dz})|_{z=0} = -n_0 \exp(-\chi v_0)\sqrt{\gamma\delta}$. The last equality comes from matching the inner solution and the outer solution of the transition layer and the right hand outer solution. $n = g(v)$ is put into Eq. (23) to get

$$n_{xx} - (\chi v_x n)_x + \gamma n\big(h\big(g^{-1}(n)\big) - \delta\big) = 0, \tag{37}$$

with boundary conditions: $n(0) = n_0$, $\lim_{x\to-\infty} n(x) = n_s$, $(\frac{dn}{dx} - \chi n \frac{dv}{dx})|_{x=0} = -n_0 \exp(-\chi v_0)\sqrt{\gamma\delta}$, and $\frac{dn}{dx}(-\infty) = 0$, which satisfy the conservation of flux in the transition layer.

Multiplying Eq. (37) by $(dn/dx - \chi n\, dv/dx)$, and integrating with respect to $x$ from $-\infty$ to 0 we find

$$\int_{-\infty}^{0} \big\{n_{xx} - (\chi n v_x)_x + \gamma n\big(h\big(g^{-1}(n)\big) - \delta\big)\big\}\left(\frac{dn}{dx} - \chi n \frac{dv}{dx}\right) dx = 0. \tag{38}$$

As we did for the analysis in the transition layer, the first term is integrated directly and the second term is done by using a change of variables from $\xi$ to $n$, to get

$$\frac{1}{2}\left(\frac{dn}{dx} - \chi n \frac{dv}{dx}\right)^2\Bigg|_{-\infty}^{0} + \int_{n_s}^{n_0} \gamma n\big(h\big(g^{-1}(n)\big) - \delta\big)\left(1 - \chi \frac{n}{g'(g^{-1}(n))}\right) dn = 0. \tag{39}$$

Using $n = g(v)$ in some parts of the above expression, we can write the integral as into

$$\int_{v_s}^{v_0} \gamma g(v)\big(h(v)g'(v) - h(v)\chi g(v) + \delta\chi g(v)\big)\, dv - \int_{n_s}^{n_0} \gamma\delta n\, dn. \tag{40}$$

Applying the boundary conditions to Eq. (39) and $n_0 = g(v_0)$ yields

$$\begin{aligned}
&\gamma \int_{v_0}^{v_s} g(v)h(v)g'(v)\, dv + \gamma\chi \int_{v_0}^{v_s} g^2(v)\big(\delta - h(v)\big)\, dv \\
&\quad = -\gamma\delta \frac{(n_0^2 - n_s^2)}{2} + \frac{1}{2}\left(\frac{dn}{dx} - \chi n \frac{dv}{dx}\right)^2\Bigg|_{x=0} \\
&\quad = \gamma\delta \frac{(g^2(v_s) - g^2(v_0))}{2} + \frac{1}{2} g^2(v_0)\exp(-2\chi v_0)\gamma\delta,
\end{aligned}$$

which gives a condition that the left- and right-hand outer solutions satisfy a flux-balanced matching if and only if the following matching condition is satisfied

$$\begin{aligned}
&\int_{v_0}^{v_s} v f(v) g'(v)\, dv + \chi \int_{v_0}^{v_s} g^2(v)\big(\delta - h(v)\big)\, dv \\
&\quad = \delta \frac{(g^2(v_s) - g^2(v_0))}{2} + \frac{1}{2} g^2(v_0)\exp(-2\chi v_0)\delta.
\end{aligned}$$

**Theorem 3.1.** *Consider* (1), (2) *with* $\chi(v) = \chi$, $f(v) = k(v - a)(1 - v)$, *and type I functional response*, $h(v) = v$. *Then we have a unique coexistence steady state* $(v_s, n_s) = (\delta, k(\delta - a)(1 - \delta))$ *for* $0 < a < \delta < 1$ *and we have the following two conditions in order for zero wave speed solutions. Those conditions restrict the values of* $v_0$, $\delta$, *and* $\chi$

$$\int_0^{v_0} vf(v) - g(v_0)\exp\bigl(\chi(v - v_0)\bigr)h(v)\,dv = 0, \tag{41}$$

$$\int_{v_0}^{v_s} vf(v)g'(v)\,dv + \chi\int_{v_0}^{v_s} g^2(v)\bigl(\delta - h(v)\bigr)\,dv = \delta\frac{(g^2(v_s) - g^2(v_0))}{2} + \frac{1}{2}g^2(v_0)\exp(-2\chi v_0)\delta. \tag{42}$$

*For given* $\delta$ *and* $\chi$, *we can find the critical Allee threshold* $a_0 = a(\delta, \chi)$ *for prey stopping.*

### *3.3. Critical Allee threshold*

If $\chi$ is zero, then conditions (41), (41) reduce to conditions (18), (19). In this section, we consider the relationships of the critical Allee thresholds for the cases of prey-only, diffusion-only in a predator–prey system, and prey-taxis. We denote the critical Allee threshold for prey stopping for the diffusion only case by $a^*(\delta)$. It is noted that for the diffusion-only case the predator density is constant in the transition layer, but including prey-taxis allows the predator density to vary in the transition layer. Therefore, when we match the right-hand and left-hand outer solutions we need some adjustments. Note that we have an additional constraint;

$$v_s \le v_0. \tag{43}$$

(See Owen and Lewis, 2001 for details.) In addition, it is seen that $a < v_0 < 1$.

Owen and Lewis (2001) found that without taxis the critical Allee threshold $a^*(\delta)$ for prey stopping becomes smaller due to presence of predator. Here, we consider the relationship between $a_0$ and $\chi$, which is obtained from (41) and (41). Setting $\bar{a}$ as the critical Allee threshold of the prey only case, i.e. $v_t = \epsilon v_{xx} + vf(v)$ then, in the following three Lemmas, we will show that $a^*(\delta) \le a_0(\delta, \chi) \le \bar{a}$. For that, we will show that the critical Allee threshold $a_0(\delta, \chi)$ is an increasing function with respect to $\chi$. Then we will show that $v_0$ approaches $v_s$ as $\chi \to \infty$. Finally, we will show that $\lim_{\chi\to\infty} a_0(\delta, \chi) \le \bar{a}$.

**Lemma 3.1.** *Assume* $f(v) = k(1 - v)(v - a)$ *and* $h(v) = v$. *For a given* $\delta$ *we assume that* $\chi$ *and* $a_0(\chi)$ *satisfy condition* (41). *Then the critical Allee threshold* $a_0(\chi)$ *is monotonically increasing with respect to* $\chi$.

*Proof:* For fixed $\delta$ we consider $a_0$ as a function of $\chi$ and $v_0$ as a constant. Given $g(v_0) = f(v_0)$, we differentiate Eq. (41) with respect to $\chi$ and isolate $\frac{da_0}{d\chi}$

$$\frac{da}{d\chi} = \frac{6(1 - v_0)(v_0 - a_0)}{\chi}\frac{F_1}{F_2}, \tag{44}$$

where $F_1 = -2 + 2\exp(-\chi v_0) + \chi v_0 \exp(-\chi v_0) + \chi v_0$ and $F_2 = -2\chi^2 v_0^3 - 6\chi v_0 - 6v_0 - 6\exp(-\chi v_0) + 3\chi^2 v_0^2 + 6\chi v_0^2 + 6v_0 \exp(-\chi v_0) + 6$.

From Theorem 3.1, we have $a < v_s = \delta < 1$, which combined with condition (43) leads to $a_0(\chi) < v_s \le v_0$. Moreover, for given $h(v)$ and $f(v)$, we have $n = g(v) = f(v)$. A biologically relevant $n_0 > 0$ indicates that $v_0 < 1$, otherwise $n_0$ would be negative. As a result $a_0(\chi) < v_s \le v_0 < 1$ guarantees $\frac{6(1-v_0)(v_0-a_0)}{\chi} > 0$. Now we move on to find the sign of $F_1$. The derivative and the second derivative of $F_1$ with respect to $\chi$ are

$$\frac{dF_1}{d\chi} = -v_0\bigl(-1 + \exp(-\chi v_0) + \chi v_0 \exp(-\chi v_0)\bigr), \tag{45}$$

and

$$\frac{d^2 F_1}{d\chi^2} = v_0^3 \chi \exp(-\chi v_0) > 0, \tag{46}$$

respectively. Since $\frac{d^2 F_1}{d\chi^2} > 0$, $\frac{dF_1}{d\chi}$ is increasing function with respect to $\chi$. At $\chi = 0$, $\frac{dF_1}{d\chi} = 0$. Thus for $\chi > 0$, $\frac{dF_1}{d\chi}$ is positive, which implies that $F_1$ is increasing function with respect to $\chi$. At $\chi = 0$, we obtain $F_1 = 0$. Therefore, we have positive $F_1$ for positive $\chi$.

The derivative, the second derivative, and the third derivative of $F_2$ with respect to $\chi$ are

$$\frac{dF_2}{d\chi} = -2v_0\bigl(2\chi v_0^2 + 3 - 3\exp(-\chi v_0) - 3\chi v_0 - 3v_0 + 3v_0 \exp(-\chi v_0)\bigr), \tag{47}$$

$$\frac{d^2 F_2}{d\chi^2} = 2v_0^2\bigl(-2v_0 - 3\exp(-\chi v_0) + 3 + 3v_0 \exp(-\chi v_0)\bigr), \tag{48}$$

and

$$\frac{d^3 F_2}{d\chi^3} = 6v_0^3 \exp(-\chi v_0)(1 - v_0), \tag{49}$$

respectively. Since $0 < v_0 < 1$, $\frac{d^3 F_2}{d\chi^3}$ is positive, which implies that $\frac{d^2 F_2}{d\chi^2}$ is increasing with respect to $\chi$. At $\chi = 0$, $\frac{d^2 F_2}{d\chi^2} = 2v_0^3 > 0$. Thus $\frac{d^2 F_2}{d\chi^2} > 0$ for $\chi \ge 0$. Thus $\frac{dF_2}{d\chi}$ is increasing function with respect to $\chi$. At $\chi = 0$, $\frac{dF_2}{d\chi} = 0$. Thus for $\chi > 0$, $\frac{dF_2}{d\chi}$ is positive, which implies that $F_2$ is increasing function with respect to $\chi$. At $\chi = 0$, $F_2 = 0$. Hence, we have positive $F_2$.

Therefore from (44), $\frac{da_0}{d\chi}$ is shown to be positive for positive $\chi$. Hence, $a_0(\chi)$ is increasing as $\chi$ increases. □

We showed that the critical Allee threshold $a_0(\chi)$ is an increasing function with respect to $\chi$. Now we will show that $a_0(\chi)$ is bounded by $\bar{a}$ from the prey-only case. For that we will show that $v_0$ approaches $v_s$ as $\chi \to \infty$.

**Lemma 3.2.** *Assume $f(v) = (1 - v)(v - a)$ and $h(v) = v$. Then as $\chi \to \infty$, $v_0$ approaches $v_s$.*

*Proof:* We rearrange Eq. (42)

$$\int_{v_0}^{v_s} g^2(v)\big(\delta - h(v)\big)\,dv$$

$$= \frac{\delta\frac{(g^2(v_s)-g^2(v_0))}{2} + \frac{1}{2}g^2(v_0)\delta\exp(-2\chi v_0) - \int_{v_0}^{v_s} vf(v)g'(v)\,dv}{\chi}, \tag{50}$$

$$\left|\int_{v_0}^{v_s} g^2(v)\big(\delta - h(v)\big)\,dv\right|$$

$$\le \frac{|\delta\frac{(g^2(v_s)-g^2(v_0))}{2}| + \frac{1}{2}g^2(v_0)\delta\exp(-2\chi v_0) + |\int_{v_0}^{v_s} vf(v)g'(v)\,dv|}{\chi}. \tag{51}$$

From the assumption that $f(v) = (1-v)(v-a)$ and $h(v) = v$, it is easily seen that $f, h \in L_2[v_s, v_0]$. Thus there exists positive $C_1$ such that $|\int_{v_0}^{v_s} vf(v)g'(v)dvt| \le C_1$, which leads to

$$\left|\int_{v_0}^{v_s} g^2(v)\big(\delta - h(v)\big)\,dv\right| \le \frac{C_1 + \delta(\frac{g^2(v_s)+2g^2(v_0)}{2})}{\chi}, \tag{52}$$

where the right-hand side of the equation approaches zero as $\chi \to \infty$. Thus, we have $\int_{v_0}^{v_s} g^2(v)(\delta - h(v))\,dv = 0$. However, $g^2(v) > 0$ and $\delta - h(v) < 0$ for $v \in [v_s = \delta, v_0]$ give $\int_{v_0}^{v_s} g^2(v)(\delta - h(v))\,dv > 0$ unless $v_0 = v_s$. Therefore, as $\chi \to \infty$, $v_0 \to v_s$. □

Now we will show that $a_0(\chi)$ is bounded by $\bar{a}$.

**Lemma 3.3.** *Assume $f(v) = (1-v)(v-a)$ and $h(v) = v$. Then as $\chi \to \infty$, the critical Allee threshold $a_0(\chi)$ is bounded by the Allee threshold $\bar{a}$ for prey-only case.*

*Proof:* We rearrange Eq. (41) and obtain

$$\int_0^{v_0} vf(v)\,dv = \int_0^{v_0} g(v_0)\exp\big(\chi(v-v_0)\big)h(v)\,dv, \tag{53}$$

$$\left|\int_0^{v_0} vf(v)\,dv\right| = \left|\int_0^{v_0} g(v_0)\exp\big(\chi(v-v_0)\big)h(v)\,dv\right|$$

$$\le \max_{v\in[0,v_0]}\big|g(v)\big|\left(\int_0^{v_0}\big|h(v)\big|^2 dv\right)^{1/2}\left(\int_0^{v_0}\exp\big(2\chi(v-v_0)\big)\,dv\right)^{1/2}$$

$$\le \max_{v\in[0,v_0]}\big|g(v)\big|\left(\int_0^{v_0}\big|h(v)\big|^2 dv\right)^{1/2}\left(\frac{1-\exp(-2\chi v_0)}{2\chi}\right)^{1/2}. \tag{54}$$

As $\chi \to \infty$, for positive $v_0$ we have $(\frac{1-\exp(-2\chi v_0)}{2\chi}) \to 0$. In addition from the Lemma 3.2, we know that $v_0 \to v_s$. Thus the critical Allee threshold $a_0(\infty)$ satisfies

$$\int_0^{v_s} vf(v)\,dv = 0, \tag{55}$$

which can be integrated. With $v_s = \delta$, we have

$$0 = \frac{\delta^2}{12}\big(3\delta^2 - 4\delta a_0(\infty) - 4\delta + 6a_0(\infty)\big). \tag{56}$$

Thus

$$a_0(\infty) = \frac{\delta(3\delta - 4)}{2(2\delta - 3)}, \tag{57}$$

from which it is easily seen that $a_0(\infty)$ is an increasing function with respect to $\delta$. In case of $\delta = 1$, we have $a_0(\infty) = \bar{a}$ and for $\delta < 1$ we find $a_0(\infty) < \bar{a}$. ☐

We summarize the results

**Theorem 3.2.** *Let $\delta > 0$, $\epsilon > 0$, and $k > 0$ be given. Let $a_0(\chi)$ denote the critical Allee threshold that corresponds to a standing wave ($c = 0$) and satisfies conditions* (41), (42). *Let $a^*$ denote the corresponding critical Allee threshold for the diffusion only model of* Owen and Lewis (2001) ($\chi = 0$) *and let $\bar{a}$ denote the critical Allee threshold for the prey-only model. Then $a_0(\chi)$ is strictly monotonically increasing for positive $\chi$ and*

$$a^* < a_0(\chi) \le \bar{a}. \tag{58}$$

For $\chi > 0$ the predator effect on the prey is reduced as compared to the case of $\chi = 0$. For instance, if the prey growth rate is described by an Allee effect, $f(v) = k(v - a)(1 - v)$, and $a = a^*$ (the critical Allee threshold from a predator–prey model with diffusion only), then depending on the model used, we have three scenarios. (1) Without any interaction with predators, the prey population will invade with a certain positive speed. (2) The prey may continue invasion with a speed slowed down due to interaction with predators when diffusion and prey-taxis is included in the predator model. (3) Since $a = a^*$, the diffusion only model will predict that the prey invasion stops. In the following section, we will take a non-constant prey sensitivity into account.

### *3.4. Non-constant prey sensitivity*

For the case of non-constant prey sensitivity, we have similar results for prey stopping with a constant prey sensitivity. We follow the similar analysis as in Section 3.2. (See Appendix A for details.) As a result, we have the following theorem.

**Theorem 3.3.** *Consider* (1), (2) *with $\chi(v) = \frac{b}{v+\tau}$, $f(v) = k(v - a)(1 - v)$, and type I functional response, $h(v) = v$. Then we have a unique coexistence steady state $(v_s, n_s) = (\delta, k(\delta - a)(1 - \delta))$ for $0 < a < \delta < 1$ and we have the following two conditions in order for zero wave speed solutions. Those conditions restrict the values of $v_0$, $\delta$, and $b$.*

$$\int_0^{v_0} vf(v) - g(v_0)h(v)\left(\frac{v+\tau}{v_0+\tau}\right)^b dv = 0, \tag{59}$$

$$\int_{v_0}^{v_s} vf(v)g'(v)\,dv + b\int_{v_0}^{v_s} \frac{g^2(v)}{v+\tau}\big(\delta - h(v)\big)\,dv = \delta\frac{(g^2(v_s) - g^2(v_0))}{2}. \tag{60}$$

*For given $\delta$ and $b$, we can find the critical Allee threshold $a_0 = a(\delta, b)$ for prey stopping.*

We now consider the relationship between $a_0$ and $b$. We will follow the steps in Section 3.2 to show that $a^*(\delta) < a_0(\delta, b) \leq \bar{a}$.

**Lemma 3.4.** *Assume* $f(v) = (1 - v)(v - a)$ *and* $h(v) = v$. *For a given* $\delta$ *we assume that* $b$ *and* $a_0(b)$ *satisfy condition* (59). *Then there is a* $\tau^*$ *such that for* $0 \leq \tau \leq \tau^*$ *the critical Allee threshold* $a_0(b)$ *is monotonically increasing with respect to* $b$.

*Proof:* See Appendix B. ☐

It is noted by simulations that when $\tau$ is big, the function $a_0(b)$ is not monotonically increasing with respect to $b$.

Now we will show that $a_0(b)$ is bounded by $\bar{a}$ from the prey-only case. For that we will show that $v_0$ approaches $v_s$ as $b \to \infty$.

**Lemma 3.5.** *Assume* $f(v) = (1 - v)(v - a)$ *and* $h(v) = v$. *Then as* $b \to \infty$, $v_0$ *approaches* $v_s$.

*Proof:* The proof is similar to the proof of Lemma 3.2. We just omit the exponential term and replace $\chi$ by $b$. ☐

Now we will show that $a_0(b)$ is bounded by $\bar{a}$.

**Lemma 3.6.** *Assume* $f(v) = (1 - v)(v - a)$ *and* $h(v) = v$. *Then as* $b \to \infty$, *the critical Allee threshold* $a_0(b)$ *is bounded by the Allee threshold* $\bar{a}$ *for prey-only case.*

*Proof:* See Appendix B. ☐

We summarize the results

**Theorem 3.4.** *Let* $\delta > 0$, $\epsilon > 0$, *and* $k > 0$ *be given. Let* $a_0(b)$ *denote the critical Allee threshold that corresponds to a standing wave* ($c = 0$) *and satisfies conditions* (59), (60). *Let* $a^*$ *denote the corresponding critical Allee threshold for the diffusion only model of* Owen and Lewis (2001) ($b = 0$) *and let* $\bar{a}$ *denote the critical Allee threshold for the prey-only model. Then there is a* $\tau^*$ *such that for* $0 \leq \tau \leq \tau^*$, $a_0(b)$ *is strictly monotonically increasing for positive* $b$ *and*

$$a^* < a_0(b) \leq \bar{a}. \tag{61}$$

For $b > 0$ the predator effect is also not as strong as for $b = 0$. Or, it dilutes the predator effect at the wave front. It was noted that prey-taxis inhibits predators from stopping the prey spread. (See Theorem 3.4 for details.)

## 4. Conclusion

In this paper, we studied the role of prey-taxis in controlling prey invasion. Hence, we considered traveling wave solutions to the prey-taxis model

$$v_t = \epsilon v_{xx} + v f(v) - n h(v), \tag{62}$$

$$n_t = n_{xx} - \big(\chi(v)v_x n\big)_x + \gamma n\big(h(v) - \delta\big), \tag{63}$$

where $\epsilon \ll 1$.

When the predator interact spatially with the prey by means of a diffusion process, predators may not slow down prey spread without an Allee effect in the prey dynamics (Owen and Lewis, 2001). In Sections 2.1, 2.2, we considered growth without an Allee effect, with standard functional responses, and ratio-dependent functional responses. We used linear analysis to investigate whether the predator may slow down and stop the prey spread. It was shown that without an Allee effect, the predator with any type of standard functional response cannot stop the prey spread. However, it was seen that the predator with a linear ratio-dependent functional response of $h(v,n) = \frac{\mu v}{n}$ can slow down the prey spread while a linear ratio-dependent functional response of $h(v,n) = \frac{\mu v}{n+\tau}$ cannot slow down the prey spread. We found that in the case of growth with no Allee effect, the prey-taxis term does not slow the wave.

In Sections 3.2 and 3.4, we considered an Allee effect in the prey growth term and derived the conditions for stopping the prey spread with prey taxis. For the case of constant and non-constant prey sensitivities, we found prey-taxis inhibits predators from stopping the prey spread. (See Lemmas 3.1–3.3 for a constant prey sensitivity and see Lemmas 3.4–3.6 for a non-constant prey sensitivity.)

An invading species may stop due to an Allee effect (see Lewis and Kareiva, 1993). When the species interacts with its predator with a much faster diffusion rate, the invading species may stop at a smaller critical Allee threshold $a^*$ than the critical Allee threshold $\bar{a}$ of the prey-only case (see Owen and Lewis, 2001). Here, we incorporated prey-taxis into predator dispersal and investigated the role of the prey-taxis term for stopping the prey spread. Prey-taxis was seen to play an opposite role in stopping the prey spread with respect to a diffusion only model of predators. That is, prey-taxis dilutes the diffusion dispersal of predators at the front of prey spread so that invading prey have more chance to survive due to less predators as the prey sensitivity is biggest.

Natural enemies have been considered as biological control agents (Crawley, 1992; Shigesada and Kawasaki, 1997). In some cases, natural enemies have worked well for suppressing the outbreak of a pest, but it does not work well in many other cases (Dixon, 2000). For predators, there has been a dichotomy between a generalist and a specialist, which are correlated with type II or type III functional responses (Turchin, 2003). However, in this research, we found that the dispersal behaviors (diffusion or prey-taxis) of the predators are more important for the biological control than the type of functional responses for prey stopping. Thus it is noted that further research on the dispersal behavior of predators interacting with spatially distributed prey is needed to understand some predators as proper and efficient control agents. Not including prey-taxis might overestimate the success of a control agent.

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## Appendix A: Derivation of stopping conditions for non-constant prey sensitivity

Here, we consider $\chi(v) = \frac{b}{v+\tau}$ for $\tau > 0$ and derive the corresponding stopping conditions. Then from the transition layer analysis, we have

$$\int_0^{v_0} vf(v) - g(v_0)h(v)\left(\frac{v+\tau}{v_0+\tau}\right)^b dv = 0. \tag{A.1}$$

In the transition layer, the predator–prey relationship is

$$n = n_0\left(\frac{v+\tau}{v_0+\tau}\right)^b, \tag{A.2}$$

and as $v \to 0$, we have $n \to 0$. Thus the right-hand outer solution is

$$n(x) = 0, \quad \text{and subsequently} \quad \frac{dn}{dx}(0) = 0. \tag{A.3}$$

For the left-hand outer solution, we can follow similar steps as before. Conservation of flux across $n = n_0$ gives $\frac{dn}{dx} - \frac{b}{v+\tau}\frac{dv}{dx}n|_{(v_0,n_0)} = \frac{dn}{dx} - \frac{b}{v+\tau}\frac{dv}{dx}n|_{(0,0)} = 0$. Then a flux-balanced matching condition gives

$$\int_{v_0}^{v_s} vf(v)g'(v)\,dv + b\int_{v_0}^{v_s} \frac{g^2(v)}{v+\tau}\big(\delta - h(v)\big)\,dv = \delta\frac{(g^2(v_s) - g^2(v_0))}{2}. \tag{A.4}$$

## Appendix B: Proof of Lemmas

*Proof of Lemma 3.4:* Given $\tau \geq 0$ we consider $a_0$ as a function of $b$ and $v_0$ as a constant. Given $g(v_0) = f(v_0)$, we can compute (59) explicitly (by using Maple). Even though the result is long and complicated, we can isolate $a$, which is denoted by $a_0$, and compute

$$\frac{da_0}{db} = 3v_0^3(v_0+\tau)^b(1-v_0)(2-v_0)\frac{A}{B^2}, \tag{B.1}$$

with $B = -6\tau^{2+b}(1-v_0) - (v_0+\tau)^b(2v_0^3b^2 - 3b^2v_0^2 - 3bv_0^2 + 6v_0\tau^2 - 6\tau^2 - 2v_0^3 + 6\tau bv_0 - 6\tau bv_0^2)$ and $A = \tau^{2+b}(2+b)(1+b)\ln(\frac{v_0+\tau}{\tau}) + (3+2b)\tau^{2+b} + (v_0+\tau)^b({}_v0 + \tau)(-3\tau - 2\tau b + v_0 + v_0b^2 + 2v_0b)$.

The derivative of $a_0$ with respect to $b$ is seen to be continuous for all $\tau \geq 0$. In addition, at $\tau = 0$, the derivative is

$$\left.\frac{da_0}{db}\right|_{\tau=0} = \frac{(1-v_0)(2-v_0)v_0}{(2v_0b - 2v_0 - 3b)^2} > 0, \tag{B.2}$$

for $v_0 < 1$ and $b > 0$. Therefore, $\frac{da_0}{db}$ is shown to be positive at $\tau = 0$. Let

$$A = \left\{y : y \in [0,\infty) \text{ and } \left.\frac{da_0}{db}\right|_{\tau=y} \geq 0\right\}. \tag{B.3}$$

Then, we consider a connected subset of $A$, which includes $\tau = 0$ and is denoted by $A_0$. Then $A_0$ is non-empty set since $\tau = 0 \in A_0$. If $A_0$ is unbounded, that is for all $y \geq 0$, $\frac{da_0}{db}|_{\tau=y} \geq 0$, then we can choose any number bigger than zero as a value $\tau^*$. If $A_0$ is bounded, let $\tau^* = \sup A_0$. Then for $\tau \leq \tau^*$, we obtain $\frac{da_0}{db}|_\tau \geq 0$. Hence, there exists a $\tau^* \geq 0$ such that for $\tau \leq \tau^*$, the critical Allee threshold $a_0$ is increasing as $b$ increases. □

*Proof of Lemma 3.6:* We rearrange Eq. (59) and obtain

$$\int_0^{v_0} v f(v)\, dv = \int_0^{v_0} g(v_0) h(v) \left(\frac{v+\tau}{v_0+\tau}\right)^b dv, \tag{B.4}$$

$$\begin{aligned}\left|\int_0^{v_0} v f(v)\, dv\right| &= \left|\int_0^{v_0} g(v_0) h(v) \left(\frac{v+\tau}{v_0+\tau}\right)^b dv\right| \\ &\leq \max_{v\in[0,v_0]} \left|g(v)\right| \left(\int_0^{v_0} \left|h(v)\right|^2 dv\right)^{1/2} \left(\int_0^{v_0} \left(\frac{v+\tau}{v_0+\tau}\right)^{2b}\right)^{1/2} \\ &\leq \max_{v\in[0,v_0]} \left|g(v)\right| \left(\int_0^{v_0} \left|h(v)\right|^2 dv\right)^{1/2} \left(\frac{v_0+\tau}{2b+1}\right)^{1/2}.\end{aligned} \tag{B.5}$$

As $b \to \infty$, for positive $v_0$ we have $(\frac{v_0+\tau}{2b+1}) \to 0$. In addition, from the Lemma 3.5, we know that $v_0 \to v_s$. Thus the Allee threshold $a_0(\infty)$ satisfies

$$\int_0^{v_s} v f(v)\, dv = 0. \tag{B.6}$$

Here we can use the same argument as in Lemma 3.3 to show that in the case of $\delta = 1$, we have $a_0(\infty) = \bar{a}$ and for $\delta < 1$ we find $a_0(\infty) < \bar{a}$. □

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