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Effect of advection on the predator-prey dynamics with a drift-feeding predator

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Abstract

We examine a diffusive predator-prey model with a drift-feeding predator in open advective environments. Our analysis reveals key insights: (i) When predator mortality is low, the stability of the semi-trivial steady state can shift at least twice as flow speed increases, regardless of predator diffusion; (ii) For intermediate mortality and low diffusion, stability transitions occur, but beyond a critical diffusion threshold, the steady state remains stable regardless of flow speed. Using bifurcation theory and auxiliary methods, we establish the existence and uniqueness of a positive steady state. Unlike previous studies suggesting increased flow speed harms population persistence, our results show it can sometimes promote predator-prey coexistence, highlighting the complex effects of advection on ecological dynamics.

MSC: 35B32; 35B35; 35K55; 35Q92

Keywords: Predator-prey model; Flow speed; Drift-feeding predator; Stability; Bifurcation

1. Introduction

Numerous organisms inhabit environments characterized by predominantly unidirectional flow, such as streams and rivers, which provide not only a foundation for the populations living there, but also many beneficial values and services [10]. The organisms living in such an

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environment seek food and avoid being predated upon through random diffusion, while they are at risk of being swept downstream by the current and facing extinction. It was shown in [26] that the inhabitant can survive when their diffusion rate is in a certain intermediate range. Further investigations [20,29] indicate that for a single species model with logistic growth, the species can survive if and only if the flow speed is less than a critical flow speed. To explore how the joint effects of dispersal rate and flow speed alter competitive outcome for two species in advective environments, many ecologists and mathematicians have been involved, and have achieved extensively excellent works [13,27,30,36].

A great many predator-prey systems also exist in advective environments. Hilker and Lewis [10] introduced a large number of predator-prey systems in streams and rivers. For some of these models, by traveling wave speed approximations, they distinguished the following flow speed scenarios: coexistence, persistence of prey only or predator only and extinction of both populations. Studies in [22] show that the specialist predator can invade successfully if both the predator mortality rate and the advection rate are sufficiently small. In addition, their numerical results show that the random dispersals of both populations favor the invasion of the specialist predator. The findings of [18] manifest significant differences between the specialist predator-prey system and the generalist predator-prey system in advective environments, including the evolution of the critical predation rates with respect to the flow speed ratio. Numerous related works have been devoted to some of its generalizations such as general boundary conditions and response functions. We refer interested readers to [11,21,23,31,28,33–35] and some of the references therein.

Most predators mentioned above move passively by flow speed. However, some predators are not pushed by flow speed but consume prey at a specific location, namely the drift-feeding predators. For example, many stream fish are drift-feeders, i.e., they hold fixed positions in the water current and feed on invertebrates that are drifting by. How do the drift-feeding predators invade the prey and form a persistence system? What are the differences between the dynamics of the traditional predator-prey models and the predator-prey models with drift-feeding? To address these questions, Hilker and Lewis [10] proposed a predator-prey model with a drift-feeding predator, where the functional response also depends on the water speed in addition to the prey population. The model can be described by the following reaction-diffusion-advection equations:

$$
\begin{cases}
\tilde{N}_t = d_1 \tilde{N}_{xx} - v\tilde{N}_x + r\tilde{N}\Big(1 - \dfrac{\tilde{N}}{K}\Big) - 2dev\tilde{N}\tilde{P}, & 0 < x < 1, t > 0,\\
\tilde{P}_t = d_2 \tilde{P}_{xx} + (2dev\tilde{N} - \mu)\tilde{P}, & 0 < x < 1, t > 0,\\
d_1\tilde{N}_x(0,t) - v\tilde{N}(0,t) = \tilde{N}_x(1,t) = 0, & t > 0,\\
\tilde{P}_x(0,t) = \tilde{P}_x(1,t) = 0, & t > 0,\\
\tilde{N}(x,0) = \tilde{N}_0(x) \geq 0, \not\equiv 0, & 0 \leq x \leq 1,\\
\tilde{P}(x,0) = \tilde{P}_0(x) \geq 0, \not\equiv 0, & 0 \leq x \leq 1.
\end{cases}
\tag{1.1}
$$

Herein $\tilde{N} = \tilde{N}(x,t)$ and $\tilde{P} = \tilde{P}(x,t)$ account for the population densities of the predator and prey in the bounded interval [0, 1], respectively, at time t and position x, and are therefore assumed to be nonnegative with corresponding dispersal rates d_1 and d_2. The amount of prey eaten by a single predator per unit time is assumed to be $2dev\tilde{N}$, where d is the detection distance of predator per unit time, e is the capture success per prey, $v > 0$ is the velocity of drifting prey, and μ is the death rate of the predator. The prey species is assumed to satisfy Danckwert's boundary conditions, whereas the predator species is assumed to fulfill homogeneous Neumann boundary conditions.

Introduce the following changes of variable

$$N = \frac{r}{K}\tilde{N}, \quad P = 2de\tilde{P}, \quad b = 2de\frac{K}{r},$$

we obtain

$$\begin{cases} N_t = d_1 N_{xx} - vN_x + N(r-N) - vNP, & 0 < x < 1, t > 0, \\ P_t = d_2 P_{xx} + (bvN - \mu)P, & 0 < x < 1, t > 0, \\ d_1 N_x(0,t) - vN(0,t) = N_x(1,t) = 0, & t > 0, \\ P_x(0,t) = P_x(1,t) = 0, & t > 0, \\ N(x,0) = \frac{r}{K}\tilde{N}_0(x) \geq 0, \not\equiv 0, & 0 \leq x \leq 1, \\ P(x,0) = 2de\tilde{P}_0(x) \geq 0, \not\equiv 0, & 0 \leq x \leq 1. \end{cases} \tag{1.2}$$

To understand the dynamics of model (1.2), we first collect some existing consequences of the single prey species model:

$$\begin{cases} N_t = d_1 N_{xx} - vN_x + N(r-N), & 0 < x < 1, t > 0, \\ d_1 N_x(0,t) - vN(0,t) = N_x(1,t) = 0, & t > 0, \\ N(x,0) = \frac{r}{K}\tilde{N}_0(x) \geq 0, \not\equiv 0, & 0 \leq x \leq 1. \end{cases} \tag{1.3}$$

It turns out that the dynamics of (1.3) is very closely relative to the following eigenvalue problem:

$$\begin{cases} d_1 w_{xx} - vw_x + rw + \sigma w = 0, & 0 < x < 1, \\ d_1 w_x(0) - vw_x(0) = w_x(1) = 0. \end{cases} \tag{1.4}$$

It is well known (see, e.g., [4,8]) that the eigenvalue problem (1.4) admits a principal eigenvalue, denoted as σ_1. Moreover, it follows from [20, Lemma 2.2] that for fixed $d_1, r > 0$, there exists a critical value $v^* = v^*(d_1, r) \in (0, 2\sqrt{d_1 r})$ such that

$$\begin{cases} \sigma_1(d_1, v, r) < 0, & \text{if } 0 \leq v < v^*, \\ \sigma_1(d_1, v, r) = 0, & \text{if } v = v^*, \\ \sigma_1(d_1, v, r) > 0, & \text{if } v > v^*. \end{cases}$$

Therefore, for fixed $d_1 > 0$, the following single equation [16,20,29]

$$\begin{cases} d_1 N_{xx} - vN_x + N(r-N) = 0, & 0 < x < 1, \\ d_1 N_x(0) - vN(0) = 0, \quad N_x(1) = 0 \end{cases} \tag{1.5}$$

has a unique positive solution $\theta_v = \theta(x, v)$ if $0 \leq v < v^*$, and only has zero solution provided that $v \geq v^*$. We occasionally write θ_v as $\theta_v(x)$ to stress its dependence on spatial variable. Therefore, (1.2) has a semi-trivial steady state $(\theta_v, 0)$ if $0 \leq v < v^*$, and a trivial steady state $(0, 0)$ provided that $v \geq v^*$.

When the growth of the predator depends only on the prey and not on the flow speed (i.e., when the terms $2dev\tilde{N}$ are replaced by $2de\tilde{N}$), one can utilize similar arguments to that of [22, Theorem 1.2] to conclude

Lemma 1.1. *Suppose that $d_1, r > 0$ are fixed and $0 < v < v^*$. Then*

(i) *If $0 < \mu < br$, then there exists a critical value $\check{v} = \check{v}(\mu) \in (0, v^*)$ such that for every $d_2 > 0$, if $0 < v < \check{v}$, then $(\theta_v, 0)$ is unstable and (1.2) admits a unique positive steady state; while $(\theta_v, 0)$ is locally asymptotically stable provided that $\check{v} < v < v^*$.*
(ii) *If $\mu > br$, then $(\theta_v, 0)$ is locally asymptotically stable for all $d_2 > 0$ and $0 < v < v^*$.*

In sharp contrast to the case where the growth of the predator depends only on the prey, it turns out that the dynamics of (1.1) is more complicated and should be characterized more delicately. The first main consequence of this paper is how $(\theta_v, 0)$ changes its stability as d_2 and v vary, which can be stated as follows:

Theorem 1.2. *Suppose that $d_1, r > 0$ are fixed and $0 < v < v^*$. Then the following statements are true.*

(i) *If $0 < \mu < b \sup\limits_{v>0} \int_0^1 v\theta_v \mathrm{d}x$, then for every $d_2 > 0$, $(\theta_v, 0)$ changes its stability at least twice as v varies from zero to v^* (see Fig. 1.1).*
(ii) *If $b \sup\limits_{v>0} \int_0^1 v\theta_v \mathrm{d}x < \mu < b \sup\limits_{v>0} v\theta_v(1)$, then there exists a critical value $\hat{d}_2 = \hat{d}_2(\mu) > 0$ such that if $d_2 > \hat{d}_2$, then $(\theta_v, 0)$ is locally asymptotically stable for every $v \in (0, v^*)$; whereas if $0 < d_2 < \hat{d}_2$, then $(\theta_v, 0)$ changes its stability at least twice as v varies from zero to v^* (see Fig. 1.2).*
(iii) *If $\mu > b \sup\limits_{v>0} v\theta_v(1)$, then $(\theta_v, 0)$ is locally asymptotically stable for every $d_2 > 0$ and $v \in (0, v^*)$.*

Remark 1.3. Based on the stability conclusions of $(\theta_v, 0)$ derived from Theorem 1.2, we shall make some appropriate hypotheses for subsequent bifurcation analysis.

(i) If $0 < \mu < b \sup\limits_{v>0} \int_0^1 v\theta_v \mathrm{d}x$, then for every $d_2 > 0$, the stability of $(\theta_v, 0)$ changes at least twice, from stable to unstable, and thereafter from unstable to stable as v varies from small to large. Hence, we may assume that for every $d_2 > 0$, there exist exactly two constants $0 < v_1^* < v_2^* < v^*$ such that $\lambda_1(v_1^*) = \lambda_1(v_2^*) = 0$ and $\frac{\partial \lambda_1}{\partial v}(v_1^*) < 0$, $\frac{\partial \lambda_1}{\partial v}(v_2^*) > 0$, where λ_1 is the least eigenvalue of the eigenvalue problem (2.1).
(ii) If $b \sup\limits_{v>0} \int_0^1 v\theta_v \mathrm{d}x < \mu < b \sup\limits_{v>0} v\theta_v(1)$, then for every $0 < d_2 < \hat{d}_2$, the stability of $(\theta_v, 0)$ changes at least twice, from stable to unstable, and thereafter from unstable to stable as v varies from small to large. Therefore, we may assume that for every $0 < d_2 < \hat{d}_2$, there exist exactly two numbers $0 < v_3^* < v_4^* < v^*$ such that $\lambda_1(v_3^*) = \lambda_1(v_4^*) = 0$ and $\frac{\partial \lambda_1}{\partial v}(v_3^*) < 0$, $\frac{\partial \lambda_1}{\partial v}(v_4^*) > 0$.

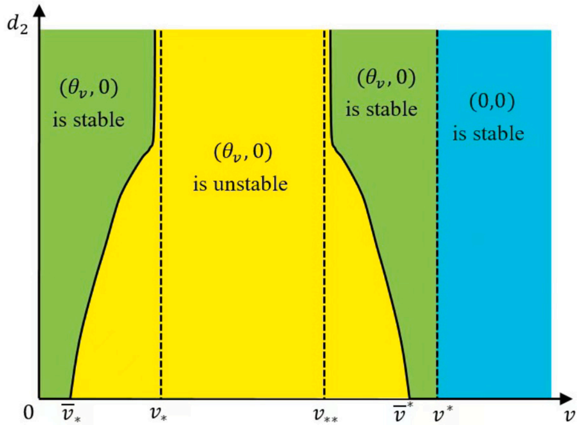

Fig. 1.1. Illustration the result of Theorem 1.2 (i), where $\bar{v}^*$ and $\bar{v}_*$ are the smallest and largest positive root of $bv\theta_v(1) = \mu$, v_* and v_{**} are the smallest and largest positive root of $b\int_0^1 v\theta_v \mathrm{d}x = \mu$, respectively.

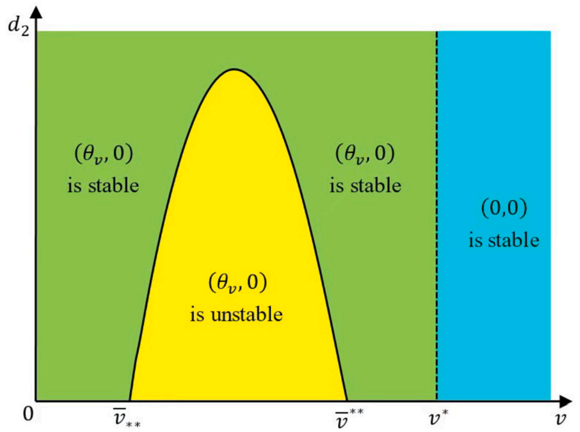

Fig. 1.2. Explanation the consequences of Theorem 1.2 (ii), where $\bar{v}_{**}$ and $\bar{v}^{**}$ are the smallest and largest positive root of $bv\theta_v(1) = \mu$, respectively.

When the flow speed is taken as a central parameter, we can establish the existence and uniqueness of the positive steady state of system (1.2) for two different ranges of the predator's death rate, respectively.

Theorem 1.4. *Suppose that $d_1, r > 0$ are fixed and $0 < v < v^*$. Then the following results are valid.*

(i) *If $0 < \mu < b \sup_{v>0} \int_0^1 v\theta_v \mathrm{d}x$, then for every $d_2 > 0$, there exist $\delta_i > 0$ $(i = 1, 2)$ such that two branches of the steady states (N_i^*, P_i^*) to (1.2) bifurcate from $(\theta_v, 0)$ at $v = v_i^*$, and they can be parameterized by v for the scopes $v \in (v_1^*, v_1^* + \delta_1) \cup (v_2^* - \delta_2, v_2^*)$, respectively. Moreover, the bifurcating solutions (N_i^*, P_i^*) are locally stable for $v \in (v_1^*, v_1^* + \delta_1) \cup (v_2^* -$*

$\delta_2, v_2^*)$. Furthermore, the branches of the steady states to (1.2) bifurcating from $(v_i^*, \theta_{v_i^*}, 0)$ are connected to each other. In addition, the bifurcation steady state to (1.2) is also unique.

(ii) *If $b \sup_{v>0} \int_0^1 v\theta_v \mathrm{d}x < \mu < b \sup_{v>0} v\theta_v(1)$, then for every $0 < d_2 < \hat{d}_2$, there exist $\delta_i > 0$ $(i = 3, 4)$ such that two branches of the steady states (N_i^*, P_i^*) to (1.2) bifurcate from $(\theta_v, 0)$ at $v = v_i^*$, and they can be parameterized by v for the scopes $v \in (v_3^*, v_3^* + \delta_3) \cup (v_4^* - \delta_4, v_4^*)$, respectively. Moreover, the bifurcating solutions (N_i^*, P_i^*) are locally stable for $v \in (v_3^*, v_3^* + \delta_3) \cup (v_4^* - \delta_4, v_4^*)$. In addition, the branches of the steady states to (1.2) bifurcating from $(v_i^*, \theta_{v_i^*}, 0)$ are connected to each other. Furthermore, the bifurcation steady state to (1.2) is unique as well.*

When the dispersal rate of the predator is regarded as a central parameter, we derive the existence and uniqueness of the positive steady state for system (1.2) under two different conditions of the predator's death rate, respectively.

Theorem 1.5. *Suppose that $d_1, r > 0$ are fixed and $0 < v < v^*$. Then the following consequences hold.*

(i) *If $0 < \mu < b \sup_{v>0} \int_0^1 v\theta_v \mathrm{d}x$, then for every $v \in \{v | b \int_0^1 v\theta_v \mathrm{d}x < \mu < bv\theta_v(1)\}$, there exists $\eta_1 > 0$ such that a branch of the steady state (N_5^*, P_5^*) to (1.2) bifurcates from $(\theta_v, 0)$ at $d_2 = d_2^*$, and it can be characterized by d_2 for the region $d_2 \in (d_2^* - \eta_1, d_2^*)$. Moreover, the bifurcating solution (N_5^*, P_5^*) is locally stable for $d_2 \in (d_2^* - \eta_1, d_2^*)$. In addition, the branch of the steady state to (1.2) bifurcating from $(d_2^*, \theta_v, 0)$ extends to be zero in d_2. Furthermore, the bifurcation steady state to (1.2) is unique.*

(ii) *If $b \sup_{v>0} \int_0^1 v\theta_v \mathrm{d}x < \mu < b \sup_{v>0} v\theta_v(1)$, then for every $v \in \{v | \mu < bv\theta_v(1)\}$, there exists $\eta_2 > 0$ such that a branch of the steady state (N_6^*, P_6^*) to (1.2) bifurcates from $(\theta_v, 0)$ at $d_2 = d_2^{**}$, and it can be described by d_2 for the range $d_2 \in (d_2^{**} - \eta_2, d_2^{**})$. Furthermore, the bifurcating solution (N_6^*, P_6^*) is locally stable for $d_2 \in (d_2^{**} - \eta_2, d_2^{**})$. Moreover, the branch of the steady state to (1.2) bifurcating from $(d_2^{**}, \theta_v, 0)$ generalizes to be zero in d_2. Additionally, the bifurcation steady state to (1.2) is also unique.*

From a biological perspective, Theorem 1.2 (i) exhibits that when the death rate of the predator is low, the predator can successfully invade the prey when rare, provided the flow speed falls within an intermediate range, regardless of whether its dispersal rate is slow or fast. However, the predator cannot invade if the flow speed is either too low or too high. This implies that within certain flow speed regimes, the availability of food resources for the predator increases with flow speed, creating favorable conditions for the predator to invade and coexist with the prey. Nevertheless, when the flow speed exceeds a critical threshold, the predator's ability to capture prey diminishes, leading to its eventual extinction. Simultaneously, the prey population is washed downstream, also resulting in extinction. Theorem 1.2 (ii) reveals that for intermediate ranges of the predator's death rate, the predator cannot invade the prey when rare if its diffusion rate exceeds a critical threshold, regardless of the flow speed. However, when the diffusion rate of the predator falls below this critical value, the dynamics shift significantly: the flow speed becomes the dominant factor, and the scenario aligns closely with the behavior described in Theorem 1.2 (i). Specifically, the predator's ability to invade and persist becomes highly sensitive to the flow speed, mirroring the conditions outlined in the earlier result. Theorem 1.2 (iii) demonstrates that when the predator's mortality rate is sufficiently high, successful invasion becomes impossible, irrespective of the flow speed or the predator's dispersal rate. This result underscores the critical role of mortality in determining the predator's ability to establish itself in the system, highlighting that under high mortality conditions, neither flow speed nor dispersal rate can facilitate successful invasion.

Theorem 1.4 (i) establishes that when the mortality rate of the predator is low, the availability of food for the predator increases with flow speed, regardless of the predator's dispersal rate. This increased availability of resources facilitates the coexistence of predator and prey populations. Theorem 1.4 (ii) further demonstrates that for intermediate predator death rates, if its diffusion rate is below a critical threshold, an increase in flow speed enables the predator to access more food, thereby promoting coexistence with the prey. Theorem 1.5 (i) implies that when the death rate of the predator is small, for some ranges of the flow speed, the predator can invade when rare and coexists with the prey if its diffusion rate is less than a critical diffusion rate. Intuitively, a lower diffusion rate is more favorable to the persistence of the predator in open advective environments. Theorem 1.5 (ii) can be interpreted in a similar manner, reinforcing the idea that limited dispersal enhances the predator's ability to establish and maintain coexistence with the prey under specific flow conditions.

In some sense, our results could be related to a harvesting problem [2,7,24]: If the harvesting rate is small, then the population steady state is large and the yield (the product of the two) is small. If the harvesting rate is large, then the population state is small and hence the yield is small again. But there is some intermediate optimum where the yield, the product of the two, is largest. In our work, the downstream flow speed acts like a harvesting term on the prey and the yield (product of flow speed and density) is what supports the predator.

The remaining of the paper is organized as follows. In Section 2, we introduce some existing results of θ_v and establish a criterion for determining the stability of $(\theta_v, 0)$. In Section 3, we separate the death rate of the predator into three distinct cases to investigate how $(\theta_v, 0)$ changes its stability as d_2 and v. Section 4 is devoted to establishing the existence and uniqueness of the bifurcation positive steady state of (1.2). Section 5 provides a comprehensive discussion and conclusion.

2. Preliminaries

In this section, we first display some existing conclusions of θ_v, and then present a criterion for determining the stability of the semi-trivial steady state $(\theta_v, 0)$ and its relevant topics.

Lemma 2.1. *Suppose that* $0 \le v < v^*$. *Then*

(i) *If* $0 < v < v^*$, *then* $0 < \theta_v < r$ *on* $[0, 1]$, *and* $0 < (\theta_v)_x < \frac{v}{d_1}\theta_v$ *in* $(0, 1)$.
(ii) θ_v *is continuously differentiable for* $v \in [0, v^*)$, *and it is decreasing pointwisely on* $[0, 1]$ *as* v *increases.*
(iii) θ_v *satisfies*

$$\lim_{v \to 0^+} \theta_v = r, \qquad \lim_{v \to v^{*-}} \theta_v = 0$$

uniformly on $[0, 1]$.

Proof. Part (i) can be proved by the maximum principle, see, e.g., [20, Lemma 3.2] and [17, Lemma 5.4 (i)]. Part (ii) follows from [17, Lemma 5.4 (ii)] and [29, Theorem 6.5]. Part (iii) is obvious. □

Lemma 2.2. *The semi-trivial steady state* $(\theta_v, 0)$ *is stable/unstable if the following eigenvalue problem, for* $(\lambda, \psi) \in \mathbb{R} \times C^2([0,1])$, *admits a positive/negative principal eigenvalue (denoted by* λ_1*):*

$$\begin{cases} d_2\psi_{xx} + (bv\theta_v - \mu)\psi + \lambda\psi = 0 & \text{in } (0,1), \\ \psi_x(0) = \psi_x(1) = 0, \quad \psi(x) > 0 & \text{on } [0,1]. \end{cases} \tag{2.1}$$

Proof. Let $X = \{(N, P) \in W^{2,p}((0,1)) \times W^{2,p}((0,1)) | d_1 N_x(0) - vN(0) = N_x(1) = 0, P_x(0) = P_x(1) = 0\}$ and $Y = L^p((0,1)) \times L^p((0,1))$ with $p > 1$. Define the operator $H(N, P) : X \to Y$ by

$$H(N, P) = \begin{pmatrix} -d_1 N_{xx} + vN_x - N(r - N) + vNP \\ -d_2 P_{xx} - (bvN - \mu)P \end{pmatrix}.$$

Then

$$D_{(N,P)}H|_{(\theta_v,0)} = \begin{pmatrix} -d_1\dfrac{\mathrm{d}^2}{\mathrm{d}x^2} + v\dfrac{\mathrm{d}}{\mathrm{d}x} - (r - 2\theta_v) & v\theta_v \\ 0 & -d_2\dfrac{\mathrm{d}^2}{\mathrm{d}x^2} - (bv\theta_v - \mu) \end{pmatrix}.$$

It follows from (1.5) and the positivity of θ_v that zero is the smallest eigenvalue of the operator $-d_1\dfrac{\mathrm{d}^2}{\mathrm{d}x^2} + v\dfrac{\mathrm{d}}{\mathrm{d}x} - (r - \theta_v)$ with Danckwert's boundary conditions. By the comparison principle for eigenvalues and the positivity of θ_v, the least eigenvalue of the operator $-d_1\dfrac{\mathrm{d}^2}{\mathrm{d}x^2} + v\dfrac{\mathrm{d}}{\mathrm{d}x} - (r - 2\theta_v)$ with Danckwert's boundary conditions is strictly positive. Therefore, to investigate the stability of semi-trivial steady state $(\theta_v, 0)$, it remains to study the sign of the least eigenvalue of (2.1). □

From [19, Lemma 14] and [32, Lemma 19], we deduce the following properties of the principal eigenvalue λ_1.

Lemma 2.3. *The principal eigenvalue* λ_1 *of the eigenvalue problem* (2.1) *depends smoothly on* d_2. *Furthermore, it possesses the following properties:*

(i) λ_1 *is strictly increasing with respect to* d_2*; Moreover,* λ_1 *is a convex function of* d_2 *as well.*
(ii) λ_1 *has the following limiting behaviors:*

$$\lim_{d_2 \to 0^+} \lambda_1 = \mu - bv\theta_v(1) \text{ and } \lim_{d_2 \to +\infty} \lambda_1 = \mu - b\int_0^1 v\theta_v \mathrm{d}x.$$

To study how the principal eigenvalue λ_1 of (2.1) changes sign as d_2 and v vary, the idea is to connect (2.1) to a relevant eigenvalue problem with indefinite weight

$$\begin{cases} \phi_{xx} + \kappa(bv\theta_v - \mu)\phi = 0, & 0 < x < 1, \\ \phi_x(0) = \phi_x(1) = 0. \end{cases} \tag{2.2}$$

Now we first collect some existing results of (2.2).

Lemma 2.4. *The eigenvalue problem (2.2) has a non-zero principal eigenvalue $\kappa_1 = \kappa_1(bv\theta_v - \mu)$ if and only if $bv\theta_v - \mu$ changes sign and $\int_0^1 (bv\theta_v - \mu)\mathrm{d}x \neq 0$. More precisely,*

(i) *if $\int_0^1 (bv\theta_v - \mu)\mathrm{d}x < 0$, then $\kappa_1 > 0$;*
(ii) *if $\int_0^1 (bv\theta_v - \mu)\mathrm{d}x > 0$, then $\kappa_1 < 0$;*
(iii) *if $\int_0^1 (bv\theta_v - \mu)\mathrm{d}x = 0$, then $\kappa_1 = 0$.*

Furthermore, for $\int_0^1 (bv\theta_v - \mu)\mathrm{d}x < 0$, κ_1 is characterized by the following variational characterization:

$$\kappa_1 = \inf_{\{\phi \in H^1((0,1)) : \int_0^1 (bv\theta_v - \mu)\phi^2 \mathrm{d}x > 0\}} \frac{\int_0^1 \phi_x^2 \mathrm{d}x}{\int_0^1 (bv\theta_v - \mu)\phi^2 \mathrm{d}x}. \tag{2.3}$$

Proof. The above outcomes can be directly derived from [1,3,12]. See [14, Ch.9] for the abstract general cases. □

3. Local stability of semi-trivial steady state $(\theta_v, 0)$

In this section, we will divide the death rate of the predator into three different cases to investigate how $(\theta_v, 0)$ changes its stability as d_2 and v vary.

Lemma 3.1. *If $0 < \mu < b \sup_{v>0} \int_0^1 v\theta_v \mathrm{d}x$, then $b\int_0^1 v\theta_v \mathrm{d}x = \mu$ and $bv\theta_v(1) = \mu$ admits at least two and at most finite many positive roots, denoted as $v_1 < v_2 \leq \cdots \leq v_{2l-1} \leq v_{2l}$, and $\bar{v}_1 < \bar{v}_2 \leq \cdots \leq \bar{v}_{2k-1} \leq \bar{v}_{2k}$ with $l \geq 1$ and $k \geq 1$, respectively. Furthermore, $\int_0^1 v\theta_v \mathrm{d}x$ and $v\theta_v(1)$ satisfy*

(i) $\displaystyle\int_0^1 bv\theta_v \mathrm{d}x > \mu$ *for every $v \in \cup_{i=1}^{l} (v_{2i-1}, v_{2i})$;*
(ii) *$bv\theta_v(1) < \mu$ for every $v \in \cup_{j=0}^{k} (\bar{v}_{2j}, \bar{v}_{2j+1})$ with $\bar{v}_0 := 0$ and $\bar{v}_{2k+1} := v^*$;*
(iii) $\displaystyle\int_0^1 bv\theta_v \mathrm{d}x < \mu < bv\theta_v(1)$ *for every $v \in \cup_{0 \leq i \leq l, 1 \leq j \leq k} \{(v_{2i}, v_{2i+1}) \cap (\bar{v}_{2j-1}, \bar{v}_{2j})\}$ with $v_0 := 0$ and $v_{2l+1} := v^*$;*

(iv) $\int_0^1 bv\theta_v \mathrm{d}x = \mu$ *and* $\frac{\partial \int_0^1 bv\theta_v \mathrm{d}x}{\partial v} = 0$ *for certain points* $0 < \tilde{v}_1 \le \tilde{v}_2 \le \cdots \le \tilde{v}_M < v^*$ *with* $M \ge 1$ *(if exist).*

(v) $bv\theta_v(1) = \mu$ *and* $\frac{\partial bv\theta_v(1)}{\partial v} = 0$ *for some points* $0 < \hat{v}_1 \le \hat{v}_2 \le \cdots \le \hat{v}_N < v^*$ *with* $N \ge 1$ *(if exist).*

Proof. From Lemma 2.1 (i) and (ii), for every $x \in [0, 1]$, θ_v is uniformly bounded and strictly decreasing with respect to $v \in (0, v^*)$. Moreover, θ_v satisfies $\lim_{v\to 0^+} \theta_v = r$ and $\lim_{v\to v^*} \theta_v = 0$. Clearly, the function $\int_0^1 bv\theta_v \mathrm{d}x$ of v satisfies

$$\lim_{v\to 0^+} \int_0^1 bv\theta_v \mathrm{d}x = \lim_{v\to v^*} \int_0^1 bv\theta_v \mathrm{d}x = 0.$$

Therefore, $\int_0^1 bv\theta_v \mathrm{d}x$ admits at least one maximum point in $(0, v^*)$. Similarly, $bv\theta_v(1)$ also satisfies

$$\lim_{v\to 0^+} bv\theta_v(1) = \lim_{v\to v^*} bv\theta_v(1) = 0,$$

and has at least one maximum point in $(0, v^*)$.

In the case $0 < \mu < b \sup_{v>0} \int_0^1 v\theta_v \mathrm{d}x$, the equations $\int_0^1 bv\theta_v \mathrm{d}x = \mu$ and $bv\theta_v(1) = \mu$ admits at least two and at most finite many positive roots, denoted as $v_1 < v_2 \le \cdots \le v_{2l-1} \le v_{2l}$, and $\bar{v}_1 < \bar{v}_2 \le \cdots \le \bar{v}_{2k-1} \le \bar{v}_{2k}$ with $l, k \ge 1$, respectively. Cases (i), (ii), (iv) and (v) are obvious, it remains to prove Case (iii). Because θ_v is strictly increasing in x, we derive

$$\int_0^1 bv\theta_v \mathrm{d}x < bv\theta_v(1) \tag{3.1}$$

for every $v \in (0, v^*)$. We first display that $\bar{v}_1 < v_1 < v_2 < \bar{v}_2$. Since $\bar{v}_1 < \bar{v}_2$ and $v_1 < v_2$, we only need to prove that $\bar{v}_1 < v_1$ and $v_2 < \bar{v}_2$. If not, we may suppose that $\bar{v}_1 \ge v_1$. By Lemma 2.1 (ii) again, there exists $\eta > 0$ such that $b\int_0^1 v\theta_v \mathrm{d}x \ge bv\theta_v(1)$ for every $v \in (\bar{v}_1 - \eta, \bar{v}_1 + \eta)$, which contradicts (3.1). A similar argument can show $v_2 < \bar{v}_2$. It suffices to show that the smallest set of $\cup_{0\le i\le l, 1\le j\le k}\{(v_{2i}, v_{2i+1}) \cap (\bar{v}_{2j-1}, \bar{v}_{2j})\}$ is nonempty. When $l = k = 1$, we obtain

$$\{(0, v_1) \cap (\bar{v}_1, \bar{v}_2)\} \cup \{(v_2, v^*) \cap (\bar{v}_1, \bar{v}_2)\} = (\bar{v}_1, v_1) \cup (v_2, \bar{v}_2).$$

Here we used the fact $\bar{v}_1 < v_1 < v_2 < \bar{v}_2$. □

For five distinct situations of μ derived from Lemma 3.1, we begin to inquire about how the stability of $(\theta_v, 0)$ changes as v varies from small to large.

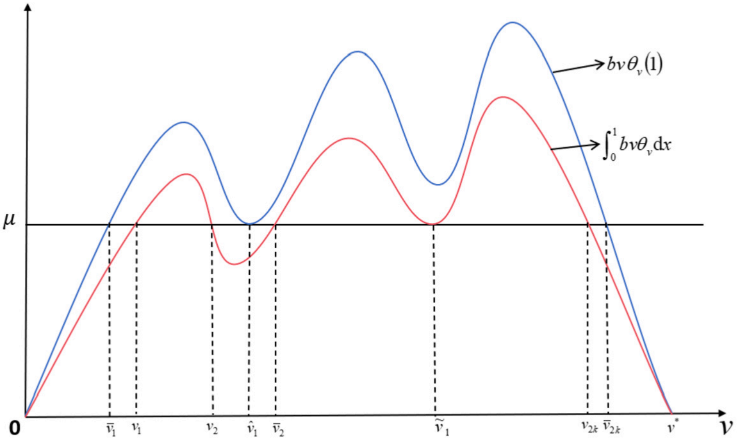

Fig. 3.1. The possible diagrams of $\int_0^1 bv\theta_v \mathrm{d}x$ and $bv\theta_v(1)$ can be utilized to illustrate the proof procedure for the case $0 < \mu < b \sup\limits_{v>0} \int_0^1 v\theta_v \mathrm{d}x$.

Lemma 3.2. *If* $0 < \mu < b \sup\limits_{v>0} \int_0^1 v\theta_v \mathrm{d}x$, *then for every* $d_2 > 0$, $(\theta_v, 0)$ *changes its stability at least twice as* v *varies from zero to* v^*.

Proof. From Lemma 2.2, the stability of $(\theta_v, 0)$ is determined by the sign of the smallest eigenvalue of the eigenvalue problem

$$\begin{cases} d_2\psi_{xx} + (bv\theta_v - \mu)\psi + \lambda\psi = 0 & \text{in } (0, 1), \\ \psi_x(0) = \psi_x(1) = 0, \quad \psi(x) > 0 & \text{on } [0, 1]. \end{cases} \tag{3.2}$$

Case (i) Dividing (3.2) by ψ, integrating by parts and reorganizing the result, we obtain

$$\lambda_1 = -d_2 \int_0^1 \frac{\psi_x^2}{\psi^2} \mathrm{d}x - \int_0^1 (bv\theta_v - \mu)\mathrm{d}x < 0$$

for any $d_2 > 0$ and $v \in \cup_{i=1}^{l} (v_{2i-1}, v_{2i})$ (see Fig. 3.1). That is, $(\theta_v, 0)$ is unstable for any $d_2 > 0$ and $v \in \cup_{i=1}^{l} (v_{2i-1}, v_{2i})$.

Case (ii) From Lemma 2.3 (ii), we derive

$$\lim_{d_2 \to 0^+} \lambda_1 = \mu - bv\theta_v(1) > 0, \lim_{d_2 \to +\infty} \lambda_1 = \mu - \int_0^1 bv\theta_v \mathrm{d}x > bv\theta_v(1) - \int_0^1 bv\theta_v \mathrm{d}x > 0$$

for every $v \in \cup_{j=0}^{k} (\bar{v}_{2j}, \bar{v}_{2j+1})$. Because λ_1 is strictly increasing with respect to d_2, $\lambda_1 > 0$ for every $d_2 > 0$ and $v \in \cup_{j=0}^{k} (\bar{v}_{2j}, \bar{v}_{2j+1})$. Hence, $(\theta_v, 0)$ is stable for every $d_2 > 0$ and $v \in \cup_{j=0}^{k} (\bar{v}_{2j}, \bar{v}_{2j+1})$.

Case (iii) In this case, for every $v \in (v_{2i}, v_{2i+1}) \cap (\bar{v}_{2j-1}, \bar{v}_{2j})$, $i = 0, 1, \cdots, l$, $j = 1, 2, \cdots, k$, it follows from Lemma 2.4 that the eigenvalue problem (2.2) has a positive principal eigenvalue, denoted by $\kappa_1^{i,j} = \kappa_1^{i,j}(bv\theta_v - \mu)$. Then there exists some $w_1^{i,j} > 0$ such that

$$\begin{cases} (w_1^{i,j})_{xx} + \kappa_1^{i,j}(bv\theta_v - \mu)w_1^{i,j} = 0, \quad 0 < x < 1, \\ (w_1^{i,j})_x(0) = (w_1^{i,j})_x(1) = 0. \end{cases}$$

Because the principal eigenvalue of (3.2) is strictly increasing in d_2 (by Lemma 2.3 (i)), we have $\lambda_1 < 0$ if $0 < d_2 < \frac{1}{\kappa_1^{i,j}}$, $\lambda_1 = 0$ at $d_2 = \frac{1}{\kappa_1^{i,j}}$ and $\lambda_1 > 0$ if $d_2 > \frac{1}{\kappa_1^{i,j}}$.

Claim 1.

$$\lim_{v \to v_{2i}^+} \kappa_1^{i,j} = \lim_{v \to v_{2i+1}^-} \kappa_1^{i,j} = 0. \tag{3.3}$$

We argue by contradiction: passing to a subsequence if necessary, we may assume that $\kappa_1^{i,j} \to \kappa_1^* > 0$ as $v \to v_{2i}^+$ and $\kappa_1^{i,j} \to \kappa_1^{**} > 0$ as $v \to v_{2i+1}^-$. From (2.3), $\kappa_1^{i,j}$ is uniformly bounded from above by some positive constant in $(v_{2i}, v_{2i+1}) \cap (\bar{v}_{2j-1}, \bar{v}_{2j})$. By elliptic regularity theory and the Sobolev embedding theorem [9], we derive $w_1^{i,j} \to w_1^* > 0$ in $C^2([0, 1])$ as $v \to v_{2i}^+$. Furthermore, w_1^* satisfies

$$\begin{cases} (w_1^*)_{xx} + \kappa_1^*[bv_{2i}\theta(x, v_{2i}) - \mu]w_1^* = 0, \quad 0 < x < 1, \\ (w_1^*)_x(0) = (w_1^*)_x(1) = 0. \end{cases} \tag{3.4}$$

Diving the above equation by w_1^*, integrating by parts and applying the boundary condition, we deduce

$$\int_0^1 \frac{(w_{1,x}^*)^2}{(w_1^*)^2}\mathrm{d}x + \kappa_1^* \int_0^1 [bv_{2i}\theta(x, v_{2i}) - \mu]\mathrm{d}x = 0.$$

Because $\int_0^1 [bv_{2i}\theta(x, v_{2i}) - \mu]\mathrm{d}x = 0$, we have $w_1^* \equiv c_1$, where $c_1 > 0$ is some constant. Plugging $w_1^* \equiv c_1$ into (3.4), since $\kappa_1^* > 0$, we obtain $bv_{2i}\theta(x, v_{2i}) - \mu = 0$. Because $\theta(x, v_{2i})$ is a function of both the variables x and v, this is a contradiction. We can use the similar arguments to conclude that $\lim_{v \to v_{2i+1}^-} \kappa_1^{i,j} = 0$.

Claim 2.

$$\lim_{v \to \bar{v}_{2j-1}^+} \kappa_1^{i,j} = \lim_{v \to \bar{v}_{2j}^-} \kappa_1^{i,j} = +\infty. \tag{3.5}$$

We also argue by contradiction: passing to a subsequence if necessary, we may suppose that there exists some constant $c_2 > 0$ such that $\kappa_1^{i,j} \le c_2$ in $(v_{2i}, v_{2i+1}) \cap (\bar{v}_{2j-1}, \bar{v}_{2j})$. Furthermore, there exists some $w_1^{i,j} \in C^2([0, 1])$ such that

$$\begin{cases} (w_1^{i,j})_{xx} + \kappa_1^{i,j}(bv\theta_v - \mu)w_1^{i,j} = 0, \quad 0 < x < 1, \\ (w_1^{i,j})_x(0) = (w_1^{i,j})_x(1) = 0. \end{cases} \tag{3.6}$$

Passing to a subsequence if necessary, we may assume that $\kappa_1^{i,j} \to \kappa_1^{***} \geq 0$ and $w_1^{i,j} \to w_1^{***} > 0$ in $C^2([0,1])$ as $v \to \bar{v}_{2j-1}^+$. In addition, w_1^{***} satisfies

$$\begin{cases} (w_1^{***})_{xx} + \kappa_1^{***}[b\bar{v}_{2j-1}\theta(x,\bar{v}_{2j-1}) - \mu]w_1^{***} = 0, \quad 0 < x < 1, \\ (w_1^{***})_x(0) = (w_1^{***})_x(1) = 0. \end{cases} \tag{3.7}$$

We consider the following two subcases:

(a) $\kappa_1^{***} = 0$. Then w_1^{***} must be some positive constant. Integrating (3.6) and applying the boundary condition, we obtain $\int_0^1 (bv\theta_v - \mu)w_1^{i,j}\mathrm{d}x = 0$. By letting $v \to \bar{v}_{2j-1}^+$, we derive $\int_0^1 [b\bar{v}_{2j-1}\theta(x,\bar{v}_{2j-1}) - \mu]\mathrm{d}x = 0$. Because

$$\mu = b\bar{v}_{2j-1}\theta(1,\bar{v}_{2j-1}) > \int_0^1 b\bar{v}_{2j-1}\theta(x,\bar{v}_{2j-1})\mathrm{d}x,$$

this is a contradiction.

(b) $\kappa_1^{***} > 0$. Integrating (3.7) and applying the boundary condition, we deduce $\int_0^1 [b\bar{v}_{2j-1}\theta(x,\bar{v}_{2j-1}) - \mu]w_1^{***}\mathrm{d}x = 0$. Because

$$b\bar{v}_{2j-1}\theta(x,\bar{v}_{2j-1}) - \mu < b\bar{v}_{2j-1}\theta(1,\bar{v}_{2j-1}) - \mu = 0,$$

we also reach a contradiction. A similar argument can prove $\lim_{v \to \bar{v}_{2j}^-} \kappa_1^{i,j} = +\infty$. Then the assertion (3.5) follows.

From the assertions (3.3) and (3.5), we conclude that for every $d_2 > 0$, $d_2 - \frac{1}{\kappa_1^{i,j}}$ changes its sign at least twice as v varies in $(v_{2i}, v_{2i+1}) \cap (\bar{v}_{2j-1}, \bar{v}_{2j})$. This together with the monotonicity of λ_1 with respect to d_2 means that for every $d_2 > 0$, λ_1 changes its sign at least twice as v varies in $(v_{2i}, v_{2i+1}) \cap (\bar{v}_{2j-1}, \bar{v}_{2j})$. Here we have to exclude the possibility that $d_2 \equiv \frac{1}{\kappa_1^{i,j}}$ in some interval $[v_0, v^0] \subset (v_{2i}, v_{2i+1}) \cap (\bar{v}_{2j-1}, \bar{v}_{2j})$. If this case was true, then $\lambda_1 \equiv 0$ for every $v \in [v_0, v^0]$. Hence, we have $\lambda_1 \equiv 0$ for every $v \in (v_{2i}, v_{2i+1}) \cap (\bar{v}_{2j-1}, \bar{v}_{2j})$ as λ_1 is an analytic function with respect to v. Clearly, this is impossible. Consequently, for every $d_2 > 0$, $(\theta_v, 0)$ changes its stability at least twice as v varies in $\cup_{0 \leq i \leq l, 1 \leq j \leq k}(v_{2i}, v_{2i+1}) \cap (\bar{v}_{2j-1}, \bar{v}_{2j})$.

Case (iv) $\int_0^1 bv\theta_v\mathrm{d}x = \mu$ and $\frac{\partial \int_0^1 bv\theta_v\mathrm{d}x}{\partial v} = 0$ for certain points $0 < \tilde{v}_1 \leq \tilde{v}_2 \leq \cdots \leq \tilde{v}_M < v^*$ with $M \geq 1$ (if exist). We will divide two subcases to demonstrate that $(\theta_v, 0)$ does not change its stability at these points (if exist). Assume that $\tilde{v}_i$ is a locally minimum point of $\int_0^1 bv\theta_v\mathrm{d}x$. Then there exists $\varepsilon > 0$ such that

$$\int_0^1 (bv\theta_v - \mu)\mathrm{d}x \geq 0 \text{ in } (\tilde{v}_i - \varepsilon, \tilde{v}_i + \varepsilon).$$

From similar arguments as in Case (i), one can obtain that $\lambda_1 < 0$ for every $v \in (\tilde{v}_i - \varepsilon, \tilde{v}_i + \varepsilon)$ and $d_2 > 0$. If $\tilde{v}_i$ is a locally maximum point of $\int_0^1 bv\theta_v \mathrm{d}x$, then

$$\int_0^1 (bv\theta_v - \mu)\mathrm{d}x < 0 \text{ in } (\tilde{v}_i - \epsilon, \tilde{v}_i) \cup (\tilde{v}_i, \tilde{v}_i + \epsilon)$$

for some $\epsilon > 0$. It follows from Lemma 2.4 that (2.2) admits a positive principal eigenvalue $\kappa_1^i > 0$. Let $d_2^i = \dfrac{1}{\kappa_1^i}$. Therefore, for every $v \in (\tilde{v}_i - \epsilon, \tilde{v}_i) \cup (\tilde{v}_i, \tilde{v}_i + \epsilon)$, $\lambda_1 > 0$ if $d_2 > d_2^i$ and $\lambda_1 < 0$ if $0 < d_2 < d_2^i$. Applying the similar arguments as in Case (ii), we can conclude that $\lim_{v \to \tilde{v}_i} d_2^i = +\infty$. Thus $\lambda_1 < 0$ at $v = \tilde{v}_i$ for every $d_2 > 0$. Similar to Case (i), it is not hard to exhibit that $\lambda_1 < 0$ at $v = \tilde{v}_i$ for every $d_2 > 0$. Therefore, $(\theta_v, 0)$ does not change its stability at these points (if exist).

Case (v) $bv\theta_v(1) = \mu$ and $\dfrac{\partial bv\theta_v(1)}{\partial v} = 0$ for some points $0 < \hat{v}_1 \leq \hat{v}_2 \leq \cdots \leq \hat{v}_N < v^*$ with $N \geq 1$ (if exist). We separate two subcases to examine that $(\theta_v, 0)$ does not change its stability at these points (if exist). If $\hat{v}_j$ is a locally maximum point of $bv\theta_v(1)$, then there exists $\delta_1 > 0$ such that

$$bv\theta_v(1) - \mu \leq 0 \text{ in } (\hat{v}_j - \delta_1, \hat{v}_j + \delta_1).$$

It follows from Lemma 2.3 (ii) that

$$\lim_{d_2 \to 0^+} \lambda_1 = \mu - bv\theta_v(1) \geq 0, \lim_{d_2 \to +\infty} \lambda_1 = \mu - \int_0^1 bv\theta_v \mathrm{d}x > 0$$

for every $v \in (\hat{v}_j - \delta_1, \hat{v}_j + \delta_1)$. Because λ_1 is strictly increasing with respect to d_2, we conclude that $\lambda_1 > 0$ for every $d_2 > 0$ and $v \in (\hat{v}_j - \delta_1, \hat{v}_j + \delta_1)$.

If $\hat{v}_j$ is a locally minimum point of $bv\theta_v(1)$, then there exists $\delta_2 > 0$ such that

$$bv\theta_v(1) - \mu > 0 \text{ and } \int_0^1 (bv\theta_v - \mu)\mathrm{d}x < 0$$

for every $v \in (\hat{v}_j - \delta_2, \hat{v}_j) \cup (\hat{v}_j, \hat{v}_j + \delta_2)$. Lemma 2.4 implies that for every $v \in (\hat{v}_j - \delta_2, \hat{v}_j) \cup (\hat{v}_j, \hat{v}_j + \delta_2)$, (2.2) admits a principal eigenvalue $\kappa_1^j > 0$. Therefore, $\lambda_1 > 0$ if $d_2 > \frac{1}{\kappa_1^j}$, $\lambda_1 = 0$ if $d_2 = \frac{1}{\kappa_1^j}$ and $\lambda_1 < 0$ if $d_2 < \frac{1}{\kappa_1^j}$. Similarly, we can obtain $\lim_{v \to \hat{v}_j} \kappa_1^j = +\infty$. Hence, $\lambda_1 > 0$ at $v = \hat{v}_j$ for every $d_2 > 0$. From the above analysis, for this case, we still have $\lambda_1 > 0$ at $v = \hat{v}_j$ for every $d_2 > 0$. Therefore, $(\theta_v, 0)$ does not change its stability at these points (if exist).

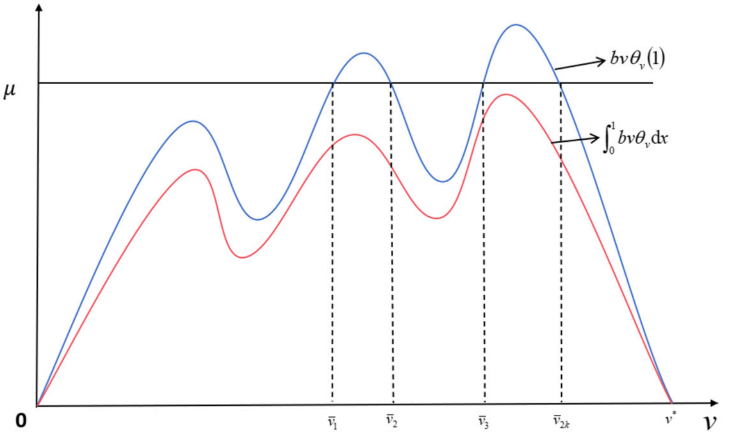

Fig. 3.2. The possible graphics of $\int_0^1 bv\theta_v \mathrm{d}x$ and $bv\theta_v(1)$ can be utilized to manifest the proof procedure for the case $b \sup\limits_{v>0} \int_0^1 v\theta_v \mathrm{d}x < \mu < b \sup\limits_{v>0} v\theta_v(1)$.

In view of Cases (i)-(v), we conclude that for every $d_2 > 0$, $(\theta_v, 0)$ changes its stability at least twice as v varies from zero to v^*. □

Lemma 3.3. *If* $b \sup\limits_{v>0} \int_0^1 v\theta_v \mathrm{d}x < \mu < b \sup\limits_{v>0} v\theta_v(1)$, *then there exists a critical value* $\hat{d}_2 = \hat{d}_2(\mu) > 0$ *such that if* $d_2 > \hat{d}_2$, *then* $(\theta_v, 0)$ *is locally asymptotically stable for every* $v \in (0, v^*)$*; whereas if* $0 < d_2 < \hat{d}_2$, *then* $(\theta_v, 0)$ *changes its stability at least twice as* v *varies from zero to* v^*.

Proof. In this case, we always have $\int_0^1 (bv\theta_v - \mu)\mathrm{d}x < 0$ for every $d_2 > 0$ and $v \in (0, v^*)$. Similar as shown in Lemma 3.1, the equation $bv\theta_v(1) = \mu$ admits at least two and at most finite many positive roots, denoted by $\bar{v}_1 < \bar{v}_2 \le \cdots \le \bar{v}_{2k-1} \le \bar{v}_{2k}$ with $k \ge 1$. Moreover, $bv\theta_v(1) > \mu$ for every $v \in \cup_{j=1}^k (\bar{v}_{2j-1}, \bar{v}_{2j})$ and $bv\theta_v(1) \le \mu$ for every $v \notin \cup_{j=1}^k (\bar{v}_{2j-1}, \bar{v}_{2j})$. Here the case $bv\theta_v(1) = \mu$ and $\dfrac{\partial bv\theta_v(1)}{\partial v} = 0$ for some points $0 < \hat{v}_1 \le \hat{v}_2 \le \cdots \le \hat{v}_N < v^*$ with $N \ge 1$ (if exist) has been excluded (see Lemma 3.2 Case (v)) and $(\theta_v, 0)$ does not change its stability at these points (if exist) (see Fig. 3.2).

For every $v \in (\bar{v}_{2j-1}, \bar{v}_{2j})$, it follows from Lemma 2.4 that (2.2) admits a principal eigenvalue $\kappa_1^j > 0$. Because λ_1 is strictly increasing with respect to d_2 (by Lemma 2.3 (i)), we have $\lambda_1 > 0$ if $d_2 > \frac{1}{\kappa_1^j}$, $\lambda_1 = 0$ if $d_2 = \frac{1}{\kappa_1^j}$, and $\lambda_1 < 0$ if $d_2 < \frac{1}{\kappa_1^j}$. Applying the similar arguments as in the proof of (3.5), we conclude

$$\lim_{v \to \bar{v}_{2j-1}^+} \kappa_1^j = \lim_{v \to \bar{v}_{2j}^-} \kappa_1^j = +\infty. \tag{3.8}$$

Define

$$\hat{d}_2 := \max_{1 \le j \le k} \frac{1}{\inf_{v \in (\bar{v}_{2j-1}, \bar{v}_{2j})} \kappa_1^j}.$$

In fact, for every $v \in (\bar{v}_{2j-1}, \bar{v}_{2j})$, we have $\int_0^1 (bv\theta_v - \mu)\mathrm{d}x < 0$ for every $d_2 > 0$ and $bv\theta_v(1) > \mu$. Lemma 2.4 implies that the eigenvalue problem (2.2) has a positive principal eigenvalue κ_1^j for every $v \in (\bar{v}_{2j-1}, \bar{v}_{2j})$. This together with (3.8) indicates that $\inf_{v\in(\bar{v}_{2j-1},\bar{v}_{2j})} \kappa_1^j$ must be positive.

We shall inquire about the following two cases:

(i) $d_2 > \hat{d}_2$. In this case, we obtain $d_2 > \frac{1}{\kappa_1^j}$ for any j and $v \in (\bar{v}_{2j-1}, \bar{v}_{2j})$. Because λ_1 is strictly increasing in d_2, we conclude $\lambda_1 > 0$ for every $v \in (\bar{v}_{2j-1}, \bar{v}_{2j})$. Hence, $\lambda_1 > 0$ for every $v \in \cup_{j=1}^k (\bar{v}_{2j-1}, \bar{v}_{2j})$. On the other hand, for every $v \notin \cup_{j=1}^k (\bar{v}_{2j-1}, \bar{v}_{2j})$, we have $bv\theta_v(1) \le \mu$. From Lemma 2.3 (ii), we find

$$\lim_{d_2\to 0^+} \lambda_1 = \mu - bv\theta_v(1) \ge 0, \lim_{d_2\to+\infty} \lambda_1 = \mu - \int_0^1 bv\theta_v \mathrm{d}x > 0.$$

Therefore, $\lambda_1 > 0$ for every $d_2 > 0$ and $v \notin \cup_{j=1}^k (\bar{v}_{2j-1}, \bar{v}_{2j})$. Consequently, $\lambda_1 > 0$ for every $d_2 > \hat{d}_2$ and $v \in (0, v^*)$. That is, if $d_2 > \hat{d}_2$, then $(\theta_v, 0)$ is stable for every $v \in (0, v^*)$.

(ii) $d_2 < \hat{d}_2$. In this case, there must exists some j such that $d_2 < \frac{1}{\inf_{v\in(\bar{v}_{2j-1},\bar{v}_{2j})} \kappa_1^j}$. Thus $\frac{1}{d_2} > \inf_{v\in(\bar{v}_{2j-1},\bar{v}_{2j})} \kappa_1^j$. This together with (3.8) implies that $\frac{1}{d_2} - \kappa_1^j$ changes its sign at least twice as v varies in $(\bar{v}_{2j-1}, \bar{v}_{2j})$. Hence, λ_1 changes its sign at least twice as v varies in $(\bar{v}_{2j-1}, \bar{v}_{2j})$. Here it remains to exclude the possibility that $\frac{1}{d_2} \equiv \kappa_1^j$ in some interval $[\bar{v}_0, \bar{v}^0] \subset (\bar{v}_{2j-1}, \bar{v}_{2j})$. If this case was true, then $\lambda_1 \equiv 0$ for every $v \in [\bar{v}_0, \bar{v}^0]$. Because λ_1 is an analytic function with respect to v, we obtain $\lambda_1 \equiv 0$ for every $v \in (\bar{v}_{2j-1}, \bar{v}_{2j})$. Obviously, this is a contradiction. From the above analysis, $\lambda_1 > 0$ for every $d_2 > 0$ and $v \notin \cup_{j=1}^k (\bar{v}_{2j-1}, \bar{v}_{2j})$. Therefore, if $0 < d_2 < \hat{d}_2$, then λ_1 changes its sign at least twice as v varies from zero to v^*. In other words, if $0 < d_2 < \hat{d}_2$, then $(\theta_v, 0)$ changes its stability at least twice as v varies from zero to v^*. $\square$

It remains to mention the proof of Theorem 1.2. Part (i) and (ii) follows from Lemmas 3.2 and 3.3, respectively. The proof of (iii) is trivial, we omit it here.

4. Bifurcation analysis of positive steady state to system (1.1)

In this section, we shall utilize bifurcation theories [5,6] to investigate positive steady state of (1.2). To this end, we first make some preparations. The steady state system of (1.2) can be written as

$$\begin{cases} d_1 N_{xx} - vN_x + N(r - N) - vNP = 0, & 0 < x < 1, \\ d_2 P_{xx} + (bvN - \mu)P = 0, & 0 < x < 1, \\ d_1 N_x(0) - vN(0) = N_x(1) = 0, \\ P_x(0) = P_x(1) = 0. \end{cases} \tag{4.1}$$

Set $X = \{(N, P) \in W^{2,p}((0,1)) \times W^{2,p}((0,1)) | d_1 N_x(0) - vN(0) = N_x(1) = 0, P_x(0) = P_x(1) = 0\}$ and $Y = L^p((0,1)) \times L^p((0,1))$ with $p > 1$. Denote the operator $F(v, N, P) : \mathbb{R}_+ \times X \to Y$ by

$$F(v, N, P) = \begin{pmatrix} d_1 N_{xx} - vN_x + N(r-N) - vNP \\ d_2 P_{xx} + (bvN - \mu)P \end{pmatrix}.$$

It is obvious to see that $F(v, \theta_v, 0) = 0$. Moreover, it is not difficult to verify that the derivatives $D_v F(v, N, P)$, $D_{(N,P)} F(v, N, P)$, $D_v D_{(N,P)} F(v, N, P)$ exist and are all continuous in the neighborhood of $(v, \theta_v, 0)$.

4.1. The advection rate is treated as a bifurcation parameter

Lemma 4.1. *If* $0 < \mu < b \sup\limits_{v>0} \int_0^1 v\theta_v \mathrm{d}x$, *then for every* $d_2 > 0$, *there exist some* $\delta > 0$ *and some functions* $v_i(s) \in C^2((-\delta, \delta))$ *with* $v_i(0) = v_i^*$ $(i = 1, 2)$ *such that all nonnegative steady states of* (1.2) *in the neighborhood of* $(v_i^*, \theta(x, v_i^*), 0)$ *can be described by*

$$(v, N_i^*, P_i^*) = (v_i(s), \theta(x, v_i(s)) + s\varphi_i^* + s^2\zeta_i^*, s\psi_i^* + s^2\xi_i^*), 0 < s < \delta, \tag{4.2}$$

where (φ_i^*, ψ_i^*) *is determined by* (4.4) *and* (4.3), *and* (ζ_i^*, ξ_i^*) *lies in the complement of the kernel of* $D_{(N,P)}F|_{(v_i^*, \theta(x,v_i^*),0)}$ *in* X. *Furthermore, the bifurcation direction of the solution* $(v_i^*, \theta(x, v_i^*), 0)$ *can be parameterized by* $v_1'(0) > 0$ *and* $v_2'(0) < 0$, *respectively.*

Proof. It follows from Remark 1.3 (i) that for every $d_2 > 0$, there exist two constants $0 < v_1^* < v_2^* < v^*$ such that $\lambda_1(v_1^*) = \lambda_1(v_2^*) = 0$ and $\frac{\partial \lambda_1}{\partial v}(v_1^*) < 0$, $\frac{\partial \lambda_1}{\partial v}(v_2^*) > 0$. By Lemma 2.2, there exists $\psi_i^* \in C^2([0, 1])$ with $\psi_i^* > 0$ $(i = 1, 2)$ such that

$$\begin{cases} d_2(\psi_i^*)_{xx} + (bv_i^*\theta(x, v_i^*) - \mu)\psi_i^* + \lambda_1(v_i^*)\psi_i^* = 0, & 0 < x < 1, \\ (\psi_i^*)_x(0) = (\psi_i^*)_x(1) = 0. \end{cases} \tag{4.3}$$

Through some calculations, we obtain

$$D_{(N,P)}F|_{(v_i^*, \theta(x,v_i^*),0)} = \begin{pmatrix} d_1 \frac{\mathrm{d}^2}{\mathrm{d}x^2} - v_i^* \frac{\mathrm{d}}{\mathrm{d}x} + (r - 2\theta(x, v_i^*)) & -v_i^*\theta(x, v_i^*) \\ 0 & d_2 \frac{\mathrm{d}^2}{\mathrm{d}x^2} + (bv_i^*\theta(x, v_i^*) - \mu) \end{pmatrix}$$

and

$$D_v D_{(N,P)}F|_{(v_i^*, \theta(x,v_i^*),0)} = \begin{pmatrix} -\frac{\mathrm{d}}{\mathrm{d}x} - 2\theta'(x, v_i^*) & -\theta(x, v_i^*) - v_i^*\theta'(x, v_i^*) \\ 0 & bv_i^*\theta'(x, v_i^*) + b\theta(x, v_i^*) \end{pmatrix},$$

where $'$ denotes the derivative with respect to v. Consequently, the kernel space of $D_{(N,P)}F|_{(v_i^*, \theta(x,v_i^*),0)}$ is spanned by (φ_i^*, ψ_i^*) and $\dim \mathcal{N}(D_{(N,P)}F|_{(v_i^*, \theta(x,v_i^*),0)}) = 1$, where ψ_i^* is the associated eigenfunction of (4.3) and φ_i^* is determined by

$$\begin{cases} d_1(\varphi_i^*)_{xx} - v_i^*(\varphi_i^*)_x + (r - 2\theta(x, v_i^*))\varphi_i^* = v_i^*\theta(x, v_i^*)\psi_i^*, & 0 < x < 1, \\ d_1(\varphi_i^*)_x(0) - v_i^*\varphi_i^*(0) = (\varphi_i^*)_x(1) = 0. \end{cases} \tag{4.4}$$

Indeed, from (1.5) and the positivity of $\theta(x, v_i^*)$, zero is the least eigenvalue of the operator $-d_1\frac{\mathrm{d}^2}{\mathrm{d}x^2} + v_i^*\frac{\mathrm{d}}{\mathrm{d}x} - (r - \theta(x, v_i^*))$ with Danckwert's boundary conditions. Then the least eigenvalue of the operator $-d_1\frac{\mathrm{d}^2}{\mathrm{d}x^2} + v_i^*\frac{\mathrm{d}}{\mathrm{d}x} - (r - 2\theta(x, v_i^*))$ with Danckwert's boundary conditions is strictly positive. Moreover, there holds

$$\varphi_i^* = \Big[-d_1\frac{\mathrm{d}^2}{\mathrm{d}x^2} + v_i^*\frac{\mathrm{d}}{\mathrm{d}x} - (r - 2\theta(x, v_i^*))\Big]^{-1}[-v_i^*\theta(x, v_i^*)\psi_i^*] < 0.$$

In addition, it follows from the Fredholm alternative that $\operatorname{codim}\mathcal{R}(D_{(N,P)}F|_{(v_i^*,\theta(x,v_i^*),0)}) = 1$.

For the eigenvalue problem (2.1), let ψ_1 be an associated eigenfunction of the principal eigenvalue λ_1. We normalize ψ_1 such that $\int_0^1 \psi_1 \mathrm{d}x = 1$. It can be shown that both λ_1 and ψ_1 are smooth functions of v [4,8]. Differentiating (2.1) with respect to v yields

$$\begin{cases} d_2\psi'_{1,xx} + (b\theta(x,v) + bv\theta'(x,v))\psi_1 + (bv\theta(x,v) - \mu)\psi'_1 + \dfrac{\partial\lambda_1}{\partial v}\psi_1 + \lambda_1\psi'_1 = 0, 0 < x < 1, \\ \psi'_{1,x}(0) = \psi'_{1,x}(1) = 0. \end{cases} \tag{4.5}$$

Multiplying (4.5) by ψ_1, integrating by parts and applying the boundary conditions, we derive

$$\int_0^1 (b\theta(x,v) + bv\theta'(x,v))\psi_1^2 \mathrm{d}x = -\frac{\partial\lambda_1}{\partial v}\int_0^1 \psi_1^2 \mathrm{d}x.$$

From elliptic regularity theory and the Sobolev embedding theorem [9], we see that $\psi_1 \to \psi_i^*$ in $C^2([0,1])$ as $v \to v_i^*$. Thus

$$\int_0^1 (b\theta(x,v_i^*) + bv_i^*\theta'(x,v_i^*))(\psi_i^*)^2 \mathrm{d}x = -\frac{\partial\lambda_1}{\partial v}(v_i^*)\int_0^1 (\psi_i^*)^2 \mathrm{d}x \neq 0 \tag{4.6}$$

as $\frac{\partial\lambda_1}{\partial v}(v_1^*) < 0$ and $\frac{\partial\lambda_1}{\partial v}(v_2^*) > 0$. Therefore, the equation $d_2\psi_{xx} + (bv_i^*\theta(x,v_i^*) - \mu)\psi = (b\theta(x,v_i^*) + bv_i^*\theta'(x,v_i^*))\psi_i^*$ is not solvable. Thus the transversality condition

$$\begin{aligned} &D_v D_{(N,P)}F|_{(v_i^*,\theta(x,v_i^*),0)}\begin{pmatrix}\varphi_i^* \\ \psi_i^*\end{pmatrix} \\ &= \begin{pmatrix} -(\varphi_i^*)_x - 2\theta'(x,v_i^*)\varphi_i^* - \theta(x,v_i^*)\psi_i^* - v_i^*\theta'(x,v_i^*)\psi_i^* \\ (b\theta(x,v_i^*) + bv_i^*\theta'(x,v_i^*))\psi_i^* \end{pmatrix} \notin \mathcal{R}(D_{(N,P)}F|_{(v_i^*,\theta(x,v_i^*),0)}) \end{aligned}$$

holds.

Substituting (4.2) into the second equation of (4.1), dividing by s^2, integrating by parts and applying (4.3), we conclude

$$\frac{b[v_i(s)\theta(x,v_i(s))-v_i^*\theta(x,v_i^*)]}{s}\psi_i^*+bv_i(s)\varphi_i^*\psi_i^*+d_2(\xi_i)_{xx}+[bv_i(s)\theta(x,v_i(s))-\mu](\xi_i)_x$$
$$=-[bv_i(s)\zeta_i\psi_i^*+bv_i(s)\varphi_i^*\xi_i]s+o(s).$$

Multiplying both sides of the above equality by ψ_i^*, integrating by parts and taking the limit, we obtain

$$v_i'(0)\int_0^1[\theta(x,v_i^*)+v_i^*\theta'(x,v_i^*)](\psi_i^*)^2\mathrm{d}x=-\int_0^1 v_i^*\varphi_i^*(\psi_i^*)^2\mathrm{d}x.$$

This together with the negativity of φ_i^* and (4.6) implies that $v_1'(0)>0$ and $v_2'(0)<0$. □

Lemma 4.2. *$(N_i^*,P_i^*)\to(\theta(x,v_i^*),0)$, $P_i^*/\|P_i^*\|_{L^\infty((0,1))}\to\psi_i^*,\psi\to\psi_i^*$ and $\varphi\to\varphi_i^*$ in $C^1([0,1])$ as $s\to 0$, where $\psi>0$ is the corresponding eigenfunction of the least eigenvalue λ_1 of (2.1) with $\|\psi\|_{L^\infty((0,1))}=1$.*

Proof. From (4.2), it can be seen that $(N_i^*,P_i^*)\to(\theta(x,v_i^*),0)$ in $C^1([0,1])$ as $s\to 0$. Let $\vartheta_i=P_i^*/\|P_i^*\|_{L^\infty(0,1)}$. By elliptic regularity theory and Sobolev embedding theorem [9], we may assume that $\vartheta_i\to\vartheta_i^*$ in $C^1([0,1])$ as $s\to 0$, where $\vartheta_i^*\geq 0$ satisfies $\|\vartheta_i^*\|_{L^\infty((0,1))}=1$ and

$$\begin{cases} d_2(\vartheta_i^*)_{xx}+(bv_i^*\theta(x,v_i^*)-\mu)\vartheta_i^*=0, & 0<x<1,\\ (\vartheta_i^*)_x(0)=(\vartheta_i^*)_x(1)=0. \end{cases}$$

Thus $\vartheta_i^*\equiv\psi_i^*$ on $[0,1]$. In other words, $P_i^*/\|P_i^*\|_{L^\infty(0,1)}\to\psi_i^*$ in $C^1([0,1])$ as $s\to 0$. We can use the similar arguments to conclude that $\lambda_1\to 0$, $\psi\to\psi_i^*$ and $\varphi\to\varphi_i^*$ in $C^1([0,1])$ as $s\to 0$. □

After some preparations, we now begin to inquire about the local stability of the bifurcation solutions (N_i^*,P_i^*) for small $s>0$.

Lemma 4.3. *The bifurcation solution $(v,N_i^*,P_i^*)=(v_i(s),\theta(x,v_i(s))+s\varphi_i^*+s^2\zeta_i^*,s\psi_i^*+s^2\xi_i^*)$ is linearly stable for small $s>0$.*

Proof. Linearizing the equation (4.1) at (N_i^*,P_i^*), we have

$$\begin{cases} d_1\varphi_{xx}-v_i(s)v\varphi_x+(r-2N_i^*-v_i(s)P_i^*)\varphi-v_i(s)N_i^*\psi+\lambda\varphi=0, & 0<x<1,\\ d_2\psi_{xx}+(bv_i(s)N_i^*-\mu)\psi+bv_i(s)P_i^*\varphi+\lambda\psi=0, & 0<x<1,\\ d_1\varphi_x(0)-v_i(s)\varphi(0)=0,\quad \varphi_x(1)=0,\\ \psi_x(0)=\psi_x(1)=0. \end{cases}\tag{4.7}$$

Denote operators Π_s and $\Pi_0: X\to Y$ by

$$\Pi_s\begin{pmatrix}\varphi\\ \psi\end{pmatrix}=\begin{pmatrix} d_1\varphi_{xx}-v_i(s)\varphi_x+(r-2N_i^*-v_i(s)P_i^*)\varphi-v_i(s)N_i^*\psi\\ d_2\psi_{xx}+(bv_i(s)N_i^*-\mu)\psi+bv_i(s)P_i^*\varphi\end{pmatrix},$$

and

$$\Pi_0\begin{pmatrix}\varphi\\ \psi\end{pmatrix}=\begin{pmatrix}d_1\varphi_{xx}-v_i^*\varphi_x+(r-2\theta(x,v_i^*))\varphi-v_i^*\theta(x,v_i^*)\psi\\ d_2\psi_{xx}+(bv_i^*\theta(x,v_i^*)-\mu)\psi\end{pmatrix},$$

respectively. Because $(N_i^*,P_i^*)\to(\theta(x,v_i^*),0)$ in $C^1([0,1])$ as $s\to 0$ (by Lemma 4.2), the operator Π_s uniformly converges to Π_0 in operator norm as $s\to 0$. Moreover, it follows from Lemma 4.1 that the kernel of Π_0 is spanned by (φ_i^*,ψ_i^*), and zero is a K-simple eigenvalue of Π_0 (where the operator K is the canonical injection from X to Y). Therefore, there exists a unique K-simple eigenvalue $\chi=\chi(s)$ of Π_s with $\chi\to 0$ as $s\to 0$. Suppose that χ is an eigenvalue of (4.7) and (φ,ψ) is its associated eigenfunction. Obviously, we have $\chi=-\lambda$.

The remaining proof will be divided into two distinct cases:

(i) $\psi\neq 0$ on $[0,1]$. We normalize ψ such that $\|\psi\|_{L^\infty((0,1))}=1$. Since $(N_i^*,P_i^*)\to(\theta(x,v_i^*),0)$ in $C^1([0,1])$ as $s\to 0$, we can apply similar argument as in Lemma 4.2 to conclude that $(\varphi,\psi)\to(\varphi_i^*,\psi_i^*)$ in $C^1([0,1])$ as $s\to 0$. Multiplying the equation of ψ by P_i^*, the equation of P_i^* by ψ and applying integration by parts and the boundary conditions, we derive

$$\chi\int_0^1 P_i^*\psi\mathrm{d}x=\int_0^1 bv_i(s)P_i^2\varphi\mathrm{d}x.$$

Dividing both sides of the above equality by $\|P_i^*\|^2_{L^\infty((0,1))}$ and applying the consequences $P_i^*/\|P_i^*\|_{L^\infty((0,1))}\to\psi_i^*$, $\varphi\to\varphi_i^*$ and $\psi\to\psi_i^*$ in $C^1([0,1])$ as $s\to 0$, we deduce

$$\lim_{s\to 0}\frac{\chi}{\|P_i^*\|_{L^\infty((0,1))}}=\frac{\int_0^1 bv_i^*\varphi_i^*\psi_i^*\mathrm{d}x}{\int_0^1\psi_i^*\mathrm{d}x}.$$

In view of the positivity of ψ_i^* and $\varphi_i^*<0$, we have $\chi<0$ for small $s>0$.

(ii) $\psi\equiv 0$ on $[0,1]$. Therefore, $\varphi\not\equiv 0$ and satisfies

$$\begin{cases}d_1\varphi_{xx}-v_i(s)\varphi_x+(r-2N_i^*-v_i(s)P_i^*)\varphi=\chi\varphi, & 0<x<1,\\ d_1\varphi_x(0)-v_i(s)\varphi(0)=0,\quad \varphi_x(1)=0.\end{cases}$$

Because $(N_i^*,P_i^*)\to(\theta(x,v_i^*),0)$ in $C^1([0,1])$ as $s\to 0$ and the smallest eigenvalue of the operator $-d_1\dfrac{\mathrm{d}^2}{\mathrm{d}x^2}+v_i^*\dfrac{\mathrm{d}}{\mathrm{d}x}-(r-2\theta(x,v_i^*))$ with Danckwert's boundary conditions is strictly positive, we obtain $\chi<0$ for small $s>0$. That is, all eigenvalues of (4.7) must have positive real part, i.e., (N_i^*,P_i^*) is linearly stable for small $s>0$. □

Lemma 4.4. *Suppose that* $0<v<v^*$ *and* $d_2>0$. *Let* (N,P) *be a positive solution of* (4.1).

(i) *There exists* $\eta>0$ *such that if* $d_2>\eta$, *then*

$$0<N<r \text{ and } 0<P<C_1,$$

where $C_1>0$ *is some constant depending on* η,b,r,μ *and* v^*.

(ii) *If* $v \notin (0, v^*)$, *then* (4.1) *admits no positive solution.*

Proof. (i) It follows from the maximum principle that $N < r$ for every $x \in [0, 1]$. Integrating the first and second equation of (4.1), applying the boundary conditions and reorganizing the results, we obtain

$$bvN(1) + \mu \int_0^1 P\mathrm{d}x = b \int_0^1 N(r - N)\mathrm{d}x.$$

Hence,

$$\int_0^1 P\mathrm{d}x < \frac{b}{\mu} \int_0^1 N(r - N)\mathrm{d}x \le \frac{br^2}{4\mu}.$$

By applying Harnack inequality to the second equation of (4.1), there exists some $\eta > 0$ such that if $d_2 > \eta$, then $\max_{x\in[0,1]} P \le \tilde{C}_1 \min_{x\in[0,1]} P$ for some positive constant $\tilde{C}_1$ relying on η, b, r, μ and v^*. Then the conclusions of (i) follow immediately.

(ii) Integrating the second equation of (4.1) and applying the boundary condition, we have

$$\int_0^1 (bvN - \mu)P\mathrm{d}x = 0.$$

If $v \le 0$, then $P \equiv 0$. It can be seen from (4.1) that

$$0 = d_1 N_{xx} - vN_x + N(r - N) - vNP \le d_1 N_{xx} - vN_x + N(r - N).$$

That is, θ_v is a supersolution of the first equation of (4.1) and satisfies $N \le \theta_v$. Because $\theta_v = 0$ for $v \ge v^*$, we conclude that $N = 0$ and $P = 0$ for $v \ge v^*$. Therefore, (4.1) has no positive solution for $v \notin (0, v^*)$. □

Proof of Theorem 1.4. The proof of part (ii) is similar to that of part (i), here we only present the proof of part (i). The local bifurcation result and the stability of the bifurcation steady state can be found in Lemmas 4.1 and 4.3, respectively. Now it suffices to generalize the local bifurcation result to a global one and display the uniqueness of the bifurcation positive steady state.

Step 1. Global bifurcation. Denote $\mathcal{S}^+$ by

$$\mathcal{S}^+ := \left\{(v_1(s), N_1^*(s), P_1^*(s)) : 0 < s < \delta\right\},$$

where $(v_1(s), N_1^*(s), P_1^*(s))$ satisfies (4.2). Define

$$Z := \left\{(N_1, P_1) \in X : \int_0^1 P_1 \psi_1^* \mathrm{d}x = 0\right\}.$$

Then $\operatorname{span}\{(\varphi_1^*, \psi_1^*)\} \oplus Z = X$. We extend the local bifurcation $\mathcal{S}^+$ to a global one by application of the global bifurcation consequences for Fredholm operators [15, Theorems 1.1 and 1.2] or [25, Theorems 4.3 and 4.4]. It follows from [15, Theorems 4.2 and 4.5] or [25, Theorem 3.3] that for any $(v, N, P) \in \mathbb{R}_+ \times X$, the Fréchet derivative $D_{(N,P)}F(v, N, P)$ is a Fredholm operator with index zero, and $F : \mathbb{R}_+ \times X \to Y$ is C^1 smooth. Moreover, we can apply [15, Theorem 1.1] or [25, Theorem 4.3] to obtain a connected component Λ of the set

$$\mathcal{S} := \{(v, N, P) \in \mathbb{R}_+ \times X : F(v, N, P) = 0, (N, P) \neq (\theta_v, 0)\}$$

emanating from $(v, N, P) = (v_1^*, \theta_{v_1^*}, 0)$. Similarly, we can show the existence of a connected component of $\mathcal{S}$ emanating from $(v, N, P) = (v_2^*, \theta_{v_2^*}, 0)$. In addition, either Λ is not compact in $\mathbb{R}_+ \times X$, or Λ contains a point $(v, \theta_v, 0)$ with $v \neq v_1^*$. Note that $\mathcal{S}^+ \subset \Lambda$. Let $X_+ = \{(N, P) \in X : N > 0, P > 0 \text{ on } [0, 1]\}$. Then $\Lambda \cap (\mathbb{R}_+ \times X_+) \neq \emptyset$.

Let $\Gamma = \Lambda \cap (\mathbb{R}_+ \times X_+)$. Then Γ consists of the local positive solution branch $\mathcal{S}^+$ near the bifurcation point $(v_1^*, \theta_{v_1^*}, 0)$. Let Λ^+ be the connected component of $\Lambda \backslash \{(v_1(s), N(s), P(s)) : -\delta < s < 0\}$. Thus $\Gamma \subset \Lambda^+$. It follows from [15, Theorem 1.2] or [25, Theorem 4.4] that one of the following alternatives holds:

(i) Λ^+ is not compact in $\mathbb{R}_+ \times X$;
(ii) There exists $\hat{v} \neq v_1^*$ such that $(\hat{v}, \theta_{\hat{v}}, 0) \in \Lambda^+$;
(iii) There exists $(v, \theta_v + N, P)$ with $(N, P) \in Z \backslash \{0\}$.

Suppose (iii) holds. For every $(v, N, P) \in \Gamma$, we have $P > 0$ on $[0, 1]$. Therefore,

$$\int_0^1 P\psi_1^* \mathrm{d}x > 0,$$

which contradicts the definition of Z.

For case (i), Lemma 4.4 (i) indicates that any positive solution of (4.1) is uniformly bounded for every $v \in (0, v^*)$. Integrating the first equation of (4.1) from 0 to x and applying the boundary condition, we conclude that N_x is uniformly bounded in $(0, 1)$. It follows from (4.1) that N_{xx} and P_{xx} are also uniformly bounded in $(0, 1)$. Therefore, positive solutions of (4.1) must be bounded in X. Hence case (i) implies that $\Gamma \backslash \{(v_1^*, \theta_{v_1^*}, 0)\} \not\subset \mathbb{R}_+ \times X_+$. Thus there exists $(\hat{v}, \hat{N}, \hat{P}) \in (\Gamma \backslash \{(v_1^*, \theta_{v_1^*}, 0)\}) \cap \partial(\mathbb{R}_+ \times X_+)$, which is the limit of a sequence of $\{(v_n, N_n, P_n)\} \subset \Gamma \cap (\mathbb{R}_+ \times X_+)$ with $N_n, P_n > 0$ on $[0, 1]$. Then $(\hat{v}, \hat{N}, \hat{P}) \in \partial(\mathbb{R}_+ \times X_+)$ means that (a) $\hat{N} \geq 0$, $\hat{N}(x^*) = 0$ for some point $x^* \in [0, 1]$; or (b) $\hat{P} \geq 0$, $\hat{P}(x_*) = 0$ for some point $x_* \in [0, 1]$; or (c) $\hat{v} \to 0$; or (d) $\hat{v} \to +\infty$.

If $\hat{N} \geq 0$, $\hat{N}(x^*) = 0$ for some point $x^* \in [0, 1]$, then it follows from the strong maximum principle that $\hat{N}(x^*) \equiv 0$ on $[0, 1]$. Similarly, we obtain $\hat{P}(x_*) \equiv 0$ on $[0, 1]$ for case (b). Therefore, we have the following two alternatives: (1) $(\hat{N}, \hat{P}) \equiv (0, 0)$; (2) $(\hat{N}, \hat{P}) \equiv (\theta_{\hat{v}}, 0)$.

Suppose that $(\hat{N}, \hat{P}) \equiv (0, 0)$ holds. Then there exists $(v_n, N_n, P_n) \in X$ such that $v_n \to \hat{v}$ and $(N_n, P_n) \to (0, 0)$ as $n \to +\infty$. By the equation of N in (4.1), we have $\lambda_1(bv_nN_n - \mu) = 0$. By letting $n \to +\infty$, we derive $\lambda_1(-\mu) = 0$. Because $\lambda_1(-\mu) = \mu > 0$, this is impossible.

Assume that $(\hat{N}, \hat{P}) \equiv (\theta_{\hat{v}}, 0)$ holds. Then there exists $(v_n, N_n, P_n) \in X$ such that $v_n \to \hat{v}$ and $(N_n, P_n) \to (\theta_{\hat{v}}, 0)$ as $n \to +\infty$. It follows from the equation of N in (4.1) that $\lambda_1(bv_nN_n - \mu) =$

0. Taking $n \to +\infty$, we can conclude $\lambda_1(b\hat{v}\theta_{\hat{v}} - \mu) = 0$. Note that $\hat{v} = v_1^*$ is the only point on Γ where positive solutions bifurcate. This is a contradiction.

It is obvious that cases (c) $\hat{v} \to 0$ and (d) $\hat{v} \to +\infty$ can be excluded by Lemma 4.4 (ii). Therefore, the remaining possibility is case (ii). Namely, $(\hat{v}, \hat{N}, \hat{P}) = (v_2^*, \theta_{v_2^*}, 0)$, the only possible point on the other connected component of $\mathcal{S}$ where positive solutions bifurcate.

Step 2. Uniqueness. The uniqueness of the bifurcation positive solution of (4.1) can be proved by the maximum principle. Suppose (4.1) admits two positive solutions (N_1, P_1) and (N_2, P_2). Let $\tilde{N} = N_1 - N_2$ and $\tilde{P} = P_1 - P_2$. Then $(\tilde{N}, \tilde{P})$ satisfies

$$\begin{cases} d_1\tilde{N}_{xx} - v\tilde{N}_x + (r - N_1 - N_2 - vP_1)\tilde{N} = vN_2\tilde{P}, & 0 < x < 1, \\ d_2\tilde{P}_{xx} + (bvN_1 - \mu)\tilde{P} = -bvP_2\tilde{N}, & 0 < x < 1, \\ d_1\tilde{N}_x(0) - v\tilde{N}(0) = \tilde{N}_x(1) = 0, \\ \tilde{P}_x(0) = \tilde{P}_x(1) = 0. \end{cases} \tag{4.8}$$

Set

$$\mathcal{L}_1 = d_1\frac{\mathrm{d}^2}{\mathrm{d}x^2} - v\frac{\mathrm{d}}{\mathrm{d}x} + (r - N_1 - N_2 - vP_1) \text{ and } \mathcal{L}_2 = d_2\frac{\mathrm{d}^2}{\mathrm{d}x^2} + (bvN_1 - \mu).$$

Then (4.8) is equivalent to

$$\begin{cases} \mathcal{L}_1\tilde{N} = vN_2\tilde{P}, & 0 < x < 1, \\ \mathcal{L}_2\tilde{P} = -bvP_2\tilde{N}, & 0 < x < 1, \\ d_1\tilde{N}_x(0) - v\tilde{N}(0) = \tilde{N}_x(1) = 0, \\ \tilde{P}_x(0) = \tilde{P}_x(1) = 0. \end{cases} \tag{4.9}$$

Because (N_1, P_1) is a positive solution of (4.1), we can conclude that the principal eigenvalues

$$\lambda_1(\mathcal{L}_1) < \lambda_1(r - N_1 - vP_1) = 0 \text{ and } \lambda_1(\mathcal{L}_2) = \lambda_1(bvN_1 - \mu) = 0.$$

We first claim that both $\tilde{N}$ and $\tilde{P}$ must change sign in $(0, 1)$. Without loss of generality, we may suppose that $\tilde{P} > 0$ in $(0, 1)$. It follows from the first equation of (4.9) that $\mathcal{L}_1\tilde{N} > 0$ in $(0, 1)$. By the strong maximum principle, we have $\tilde{N} < 0$ on $[0, 1]$. Multiplying the second equation of (4.1) by $\tilde{P}$ and (4.8) by P_1, integrating by parts and applying the boundary conditions, we obtain

$$bv\int_0^1 \tilde{N}P_1P_2\mathrm{d}x = 0,$$

which contradicts the fact that $bv\int_0^1 \tilde{N}P_1P_2\mathrm{d}x < 0$. Suppose $\tilde{N} > 0$ in $(0, 1)$. A similar argument as above can show $bv\int_0^1 \tilde{N}P_1P_2\mathrm{d}x = 0$, a contradiction. Hence, both $\tilde{N}$ and $\tilde{P}$ must change sign in $(0, 1)$.

Second, we claim that $\tilde{N}$ and $\tilde{P}$ have at most finitely many zeros in $(0, 1)$ where they change sign. Suppose $\tilde{N}(x_k) = 0$ for an infinite sequence of distinct points $\{x_k\} \subset [0, 1]$ where $\tilde{N}$ changes sign. By compactness, we may assume that there exists $x_0 \in [0, 1]$ such that $x_k \to x_0$ as

$k \to +\infty$ (passing to a subsequence if necessary). It follows from the mean value theorem that $\tilde{N}(x_0) = 0$, $\tilde{N}_x(x_0) = 0$ and $\tilde{N}_{xx}(x_0) = 0$. By the first equation of (4.9), we have $\tilde{P}(x_0) = 0$. We can apply the maximum principle to the second equation of (4.9) to conclude that $\tilde{P}$ must change sign in any neighborhood of x_0. Hence, $\tilde{P}_x(x_0) = 0$. By the uniqueness of the Cauchy problem associated with (4.9), we derive $(\tilde{N}, \tilde{P}) = (0, 0)$, which is a contradiction to $(\tilde{N}, \tilde{P}) \neq (0, 0)$. The same assertion holds for the zeros where $\tilde{P}$ changes sign.

It is not difficult to obtain $\tilde{N}(0) \neq 0$ or $\tilde{P}(0) \neq 0$. Otherwise, $\tilde{N}(0) = 0$ and $\tilde{P}(0) = 0$. By the uniqueness of the Cauchy problem associated with (4.9), we obtain $(\tilde{N}, \tilde{P}) = (0, 0)$, a contradiction. Thus we may suppose that $\tilde{N}(0) > 0$ and $0 < x_1 < x_2 < \cdots < x_q < 1$ are the finite sequence of zeros of $\tilde{N}$ in $(0, 1)$ where it changes sign. Moreover, $\tilde{N}(x) > 0$ in $(0, x_1)$. We claim that

$$(-1)^i \tilde{P}(x_i) > 0 \text{ for } i \in \{1, 2, \cdots, q\}.$$

We first argue by contradiction to show $\tilde{P}(x_1) < 0$. If $\tilde{P}(x_1) \geq 0$, then

$$\mathcal{L}_2 \tilde{P} = -bvP_2\tilde{N} < 0, \; 0 < x < x_1, \quad \tilde{P}_x(0) = 0, \; \tilde{P}(x_1) \geq 0,$$

and $\mathcal{L}_2 P = 0$ in $(0, x_1)$. The general maximum principle says that $\tilde{P}/P$ cannot reach its non-positive minimum in $(0, x_1)$. If $\min_{x \in [0, x_1]} \tilde{P}/P = \tilde{P}(0)/P(0) \leq 0$, then $(\tilde{P}/P)_x|_{x=0} > 0$ by the general maximum principle, which contradicts $(\tilde{P}/P)_x|_{x=0} = [\tilde{P}_x(0)P(0) - \tilde{P}(0)P_x(0)]/P^2(0) = 0$. Therefore, we may suppose that $\min_{x \in [0, x_1]} \tilde{P}/P = \tilde{P}(x_1)/P(x_1) \leq 0$. In view of $\tilde{P}(x_1) \geq 0$, we have $\tilde{P}(x_1) = 0$ and $\tilde{P}(x) > 0$ in $(0, x_1)$. Consequently,

$$\mathcal{L}_1 \tilde{N} = vN_2\tilde{P} > 0, \; 0 < x < x_1, \quad \tilde{N}_x(0) = 0, \; \tilde{N}(x_1) = 0.$$

By the strong maximum principle, we obtain $\tilde{N}(x) < 0$ in $(0, x_1)$, which contradicts $\tilde{N}(x) > 0$ in $(0, x_1)$. Hence $\tilde{P}(x_1) < 0$.

Now it suffices to show that $\tilde{P}(x_i)\tilde{P}(x_{i+1}) < 0$ for $i \in \{1, 2, \cdots, q-1\}$. Without loss of generality, we may suppose that $\tilde{P}(x_i) < 0$ and $\tilde{N}(x) < 0$ in (x_i, x_{i+1}). We will display $\tilde{P}(x_{i+1}) > 0$ by an indirect argument. Otherwise, we assume $\tilde{P}(x_{i+1}) \leq 0$. Note that

$$\mathcal{L}_2 \tilde{P} = -bvP_2\tilde{N} > 0 \text{ and } \mathcal{L}_2 P = 0, \quad x_i < x < x_{i+1}.$$

By the general maximum principle, $\tilde{P}/P$ cannot arrive at its nonnegative maximum in (x_i, x_{i+1}). In view of $\tilde{P}(x_i) < 0$, one can obtain that $\tilde{P}/P$ cannot reach its nonnegative maximum at x_i. Suppose that $\max_{x \in [x_i, x_{i+1}]} \tilde{P}/P = \tilde{P}(x_{i+1})/P(x_{i+1}) \geq 0$. Because $\tilde{P}(x_{i+1}) \leq 0$, we have $\tilde{P}(x_{i+1}) = 0$ and $\tilde{P}/P < 0$ in (x_i, x_{i+1}). Therefore,

$$\mathcal{L}_1 \tilde{N} = vN_2\tilde{P} < 0, \; \tilde{N}(x_i) = \tilde{N}(x_{i+1}) = 0, \quad x_i < x < x_{i+1}.$$

It follows from the strong maximum principle that $\tilde{N}(x) > 0$ in (x_i, x_{i+1}), a contradiction to $\tilde{N}(x) < 0$ in (x_i, x_{i+1}). Hence, $\tilde{P}(x_{i+1}) > 0$. A similar argument can show that if $\tilde{P}(x_i) > 0$ and $\tilde{N} > 0$ in (x_i, x_{i+1}), then $\tilde{P}(x_{i+1}) < 0$. Therefore, $(-1)^i \tilde{P}(x_i) > 0$ for $i \in \{1, 2, \cdots, q\}$.

Finally, we discuss the last interval by contradiction again. In this case, there are two cases: (a) $\tilde{N} > 0$ in $(x_q, 1)$; (b) $\tilde{N} < 0$ in $(x_q, 1)$.

(a) In this case, from the above analysis, we have $\tilde{P}(x_q) > 0$. Note that

$$\mathcal{L}_2\tilde{P} = -bvP_2\tilde{N} < 0 \text{ and } \mathcal{L}_2 P = 0, \quad x_q < x < 1.$$

The general maximum principle implies that $\tilde{P}/P$ cannot arrive at its non-positive minimum in $(x_q, 1)$. By virtue of $\tilde{P}(x_q) > 0$, we can conclude that $\tilde{P}/P$ cannot reach its non-positive minimum at x_q. Then $\min_{x\in[x_q,1]} \tilde{P}/P = \tilde{P}(1)/P(1) \le 0$. It follows from the general maximum principle that $(\tilde{P}/P)_x|_{x=1} < 0$. On the other hand, $(\tilde{P}/P)_x|_{x=1} = [\tilde{P}_x(1)P(1) - \tilde{P}(1)P_x(1)]/P^2(1) = 0$, a contradiction.

(b) In this case, from the above analysis, we have $\tilde{P}(x_q) < 0$. Note that

$$\mathcal{L}_2\tilde{P} = -bvP_2\tilde{N} > 0 \text{ and } \mathcal{L}_2 P = 0, \quad x_q < x < 1.$$

The general maximum principle indicates that $\tilde{P}/P$ cannot arrive at its nonnegative maximum in $(x_q, 1)$. In view of $\tilde{P}(x_q) < 0$, we can conclude that $\tilde{P}/P$ cannot reach its nonnegative maximum at x_q. Then $\max_{x\in[x_q,1]} \tilde{P}/P = \tilde{P}(1)/P(1) \ge 0$. From the general maximum principle, we have $(\tilde{P}/P)_x|_{x=1} > 0$. On the other hand, $(\tilde{P}/P)_x|_{x=1} = [\tilde{P}_x(1)P(1) - \tilde{P}(1)P_x(1)]/P^2(1) = 0$, a contradiction. Therefore, we obtain $(\tilde{N}, \tilde{P}) \equiv (0, 0)$. This completes the proof.

4.2. The dispersal rate of the predator is regarded as a bifurcation parameter

Denote the operator $G(d_2, N, P) : \mathbb{R}_+ \times X \to Y$ by

$$G(d_2, N, P) = \begin{pmatrix} d_1 N_{xx} - vN_x + N(r - N) - vNP \\ d_2 P_{xx} + (bvN - \mu)P \end{pmatrix}.$$

Note that $G(d_2, \theta_v, 0) = 0$. Moreover, it can be verified that the derivatives $D_{d_2}G(d_2, N, P)$, $D_{(N,P)}G(d_2, N, P)$, $D_{d_2}D_{(N,P)}G(d_2, N, P)$ exist and are all continuous in the neighborhood of $(d_2, \theta_v, 0)$.

Lemma 4.5. *If $0 < \mu < b \sup_{v>0} \int_0^1 v\theta_v \mathrm{d}x$, then for every $v \in \{v | b\int_0^1 v\theta_v \mathrm{d}x < \mu < bv\theta_v(1)\}$, there exist $\eta > 0$ and $d_2(s) \in C^2((-\eta, \eta))$ with $d_2(0) = d_2^*$ such that all nonnegative steady state of (1.2) in the neighborhood of $(d_2^*, \theta_v, 0)$ can be described as*

$$(d_2, N_5^*, P_5^*) = (d_2(s), \theta_v + s\varphi^{**} + s^2\chi^{**}, s\psi^{**} + s^2\omega^{**}), \quad 0 < s < \eta, \tag{4.10}$$

where $(\varphi^{**}, \psi^{**})$ is defined as (4.12) and (4.11), and (χ^{**}, ω^{**}) lies in the complement of the kernel of $D_{(N,P)}G|_{(d_2^*,\theta_v,0)}$ in X. Furthermore, the bifurcation direction of the solution $(d_2^*, \theta_v, 0)$ can be characterized by $d_2'(0) < 0$.

Proof. For every $v \in \{v | b\int_0^1 v\theta_v \mathrm{d}x < \mu < bv\theta_v(1)\}$, from Lemma 2.3 (ii), we find

$$\lim_{d_2\to 0^+} \lambda_1 = \mu - bv\theta_v(1) < 0 \text{ and } \lim_{d_2\to+\infty} \lambda_1 = \mu - b\int_0^1 v\theta_v \mathrm{d}x > 0.$$

Because λ_1 is strictly increasing in d_2, there exists a unique $d_2^* = d_2^*(v) > 0$ such that if $0 < d_2 < d_2^*$, then $\lambda_1 < 0$, $\lambda_1 = 0$ at $d_2 = d_2^*$ and $\lambda_1 > 0$ if $d_2 > d_2^*$. By elliptic regularity and the Sobolev embedding theorem, there exists $\psi \to \psi^{**} \in C^2([0,1])$ as $d_2 \to d_2^*$. Moreover, $\psi^{**} > 0$ satisfies

$$d_2^*\psi_{xx}^{**} + (bv\theta_v - \mu)\psi^{**} = 0 \text{ in } (0,1), \quad \psi_x^{**}(0) = \psi_x^{**}(1) = 0. \tag{4.11}$$

In other words, $\lambda_1 = 0$ is the principal eigenvalue of the eigenvalue problem (2.1) with $d_2 = d_2^*$ and $\psi = \psi^{**}$.

Through some simple computations, we arrive at

$$D_{(N,P)}G|_{(d_2^*,\theta_v,0)}\begin{pmatrix}\varphi\\ \psi\end{pmatrix} = \begin{pmatrix} d_1\varphi_{xx} - v\varphi_x + (r-2\theta_v)\varphi - v\theta_v\psi \\ d_2^*\psi_{xx} + (bv\theta_v - \mu)\psi\end{pmatrix}.$$

Thus the kernel space of $D_{(N,P)}G|_{(d_2^*,\theta_v,0)}$ is spanned by $(\varphi^{**}, \psi^{**})$ and $\dim\mathcal{N}(D_{(N,P)}G|_{(d_2^*,\theta_v,0)}) = 1$, where ψ^{**} is the unique positive solution of (4.11) (up to a constant multiplier), and φ^{**} is uniquely determined by

$$d_1\varphi_{xx}^{**} - v\varphi_x^{**} + (r-2\theta_v)\varphi^{**} - v\theta_v\psi^{**} = 0 \text{ in } (0,1), \quad \varphi_x^{**}(0) = \varphi_x^{**}(1) = 0.$$

It follows from (1.5) and the positivity of θ_v that zero is the smallest eigenvalue of the operator $-d_1\dfrac{\mathrm{d}^2}{\mathrm{d}x^2} + v\dfrac{\mathrm{d}}{\mathrm{d}x} - (r-\theta_v)$ with Danckwert's boundary conditions. By the comparison principle for eigenvalues and the positivity of θ_v, the least eigenvalue of the operator $-d_1\dfrac{\mathrm{d}^2}{\mathrm{d}x^2} + v\dfrac{\mathrm{d}}{\mathrm{d}x} - (r-2\theta_v)$ with Danckwert's boundary conditions is strictly positive. Therefore,

$$\varphi^{**} = \Big[-d_1\frac{\mathrm{d}^2}{\mathrm{d}x^2} + v\frac{\mathrm{d}}{\mathrm{d}x} - (r-2\theta_v)\Big]^{-1}(-v\theta_v\psi^{**}) < 0. \tag{4.12}$$

The Fredholm alternative indicates that $\mathrm{codim}\mathcal{R}(D_{(N,P)}G|_{(d_2^*,\theta_v,0)}) = 1$. It remains to examine the transversality condition. Since $\int_0^1 (\psi_x^{**})^2\mathrm{d}x \neq 0$, the equation $d_2^*\psi_{xx} + (bv\theta_v - \mu)\psi = \psi_{xx}^{**}$ is not solvable. Hence,

$$D_{d_2}D_{(N,P)}G|_{(d_2^*,\theta_v,0)}\begin{pmatrix}\varphi^{**}\\ \psi^{**}\end{pmatrix} = \begin{pmatrix}0\\ \psi_{xx}^{**}\end{pmatrix} \notin \mathcal{R}(D_{(N,P)}G|_{(d_2^*,\theta_v,0)}).$$

Plugging (4.10) into the equation of v in (4.1) and dividing both sides by s yields

$$\begin{aligned}&\frac{d_2(s) - d_2^*}{s}\psi_{xx}^{**} + d_2(s)\omega_{xx}^{**} + (bv\theta_v - \mu)\omega^{**}\\ &= -bv\varphi^{**}\psi^{**} - (bv\psi^{**}\chi^{**} + bv\varphi^{**}\omega^{**})s + o(s).\end{aligned} \tag{4.13}$$

Multiplying both sides of (4.13) by ψ^{**}, integrating by parts, applying the boundary condition and taking the limit, we obtain

$$d_2'(0)\int_0^1 (\psi_x^{**})^2 \mathrm{d}x = \int_0^1 bv\varphi^{**}(\psi^{**})^2 \mathrm{d}x < 0.$$

This finishes the proof. □

Proof of Theorem 1.5. We here only prove part (i), the proof of part (ii) is similar. The local bifurcation conclusion immediately follows from Lemma 4.5. The stability of the bifurcation steady state can be examined by similar argument as in Lemma 4.3. The rest of proof can be achieved by similar argument to that of Theorem 1.4, we skip it here.

5. Discussion

We examined a predator-prey model with a drift-feeding predator in advective environments. In contrast to the predator-prey models without drift-feeding predators, the dynamics of this model is more complicated. For instance, for some ranges of the immorality rate and diffusion rate of the predator, the semi-trivial steady state of this model can change its stability at least twice (from stable to unstable, and then from unstable to stable) as the flow speed increases from small to large. Based on the stability results of the semi-trivial steady state, we derived the existence and uniqueness of positive steady state via bifurcation theories and the maximum principle. These findings imply that an appropriate increase in the flow speed will be beneficial for the invasion of the predator, which is in sharp contrast to the previous belief that increasing the flow speed has an exclusively negative impact on the persistence of both predator and prey species.

In comparison with traditional predator-prey models studied in previous studies [19,22,32], the drift-feeding model exhibits novel insights: (i) The predator does not move according to the flow speed; however, the growth of the predator depends on both the prey population and the flow speed; (ii) It was shown in [19,32] that when considering the corresponding eigenvalue problem that determines the stability of the semi-trivial steady state, the monotonicity of $v\theta_v(1)$ plays a critical role in understanding its principal eigenvalue. In sharp contrast, in this paper, $v\theta_v(1)$ has no monotonicity with respect to v; (iii) Previous investigation [22, Theorem 1.2] indicates that for some regions of the death rate of the predator, there exists a unique critical flow speed such that the predator can invade if and only if the flow speed is less than the critical flow speed, while the predator cannot invade when the flow speed is larger than the critical flow speed. However, our studies exhibit that there exist at least two critical flow speeds that separate the range of flow speed into three distinct areas: non-invasive area, invasive area and non-invasive area.

There are at least three remaining questions for further investigation: (i) How to precisely describe $v\theta_v(1)$ and $\int_0^1 v\theta_v \mathrm{d}x$ change as v increases (monotonicity or first increase and then decrease) because they play a vital role in inquiring about the dynamics of the predator-prey model; (ii) The asymptotic profiles of the positive steady state of (1.2) when one of the dispersal rates tends to zero or infinity, while the other one is fixed; (iii) What would be the dynamics of model (1.2) when the boundary conditions are changed to more general boundary conditions? for instance,

$$d_1 N_x(0,t) - vN(0,t) = 0, \quad d_1 N_x(1,t) - vN(1,t) = -qvN(1,t), \quad q \geq 0,$$
$$P_x(0,t) = P_x(1,t) = 0, \quad t > 0.$$

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Data availability

No data was used for the research described in the article.

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