Positive heteroclinics and traveling waves for scalar population models with a single delay

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Abstract

The existence of positive heteroclinic solutions is proven for a class of scalar population models with one discrete delay. Traveling wave solutions for scalar delayed reaction-diffusion equations are also obtained, as perturbations of heteroclinic solutions of the associated equation without diffusion. As an illustration, the results are applied to the Nicholson's blowflies equation with diffusion $\frac{\partial N}{\partial t}(t,x) = d\frac{\partial^2 N}{\partial x^2}(t,x) - \delta N(t,x) + pN(t-\tau,x)e^{-aN(t-\tau,x)}$ in the case of $p/\delta > e$, for which the nonlinearity is non-monotone.

Key words: delay differential equations, delay reaction-diffusion equations, Nicholson's blowflies equation, heteroclinic solution, traveling waves.

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1 Introduction

Delay differential equations (DDEs) have been extensively used as models in biology and other sciences, with particular emphasis in population dynamics. The present paper addresses the existence of positive heteroclinic solutions for a class of scalar ordinary DDEs with a simple discrete delay and a non-monotone nonlinearity. Such equations serve as models for the growth of a single species population, in ecology problems or in disease modelling. As a by-product, the theory in [1] allows us to obtain traveling wave solutions for scalar delayed reaction-diffusion equations, as perturbations of heteroclinic solutions connecting two hyperbolic equilibria of the associated equation without diffusion.

Although our approach applies to more general population models, this study was motivated by the well-known Nicholson's blowflies equation (see [2]),

$$N'(t) = -\delta N(t) + pN(t-\tau)e^{-aN(t-\tau)}, \qquad t \in \mathbb{R}, \tag{1}$$

where the constants τ, δ, p, a are positive. By a scaling, we may assume $a = 1$. Suppose that $p/\delta > 1$, so that (1) has two equilibria, zero and $K := \log(p/\delta)$. We write the delayed term as $g(N(t-\tau))$, where $g(x) = pxe^{-x}$, and remark that g is *monotone* on the interval $[0, K]$ if and only if $1 < p/\delta \le e$.

The diffusive version of the Nicholson's blowflies equation (with $a = 1$) is given by

$$\frac{\partial N}{\partial t}(t,x) = d\frac{\partial^2 N}{\partial x^2}(t,x) - \delta N(t,x) + pN(t-\tau,x)e^{-N(t-\tau,x)}, \; t,\, x \in \mathbb{R}, \tag{2}$$

where $d > 0$ is the diffusion rate, and has the same equilibria as (1). For $p/\delta > 1$, it is of interest to investigate the existence of traveling waves for (2), i.e., solutions $N(t,x) = \varphi(t + cx)$ (where $c > 0$) of (2), connecting the two steady states. This leads us to the problem

$$d\varphi''(t) - c\varphi'(t) - \delta\varphi(t) + \delta\beta h(\varphi(t - c\tau)) = 0, \quad t \in \mathbb{R} \tag{3}$$

$$\varphi(-\infty) = 0, \quad \varphi(\infty) = K, \tag{4}$$

where $\beta = p/\delta$, $h(x) = xe^{-x}$ for $x \ge 0$, and $K = \log\beta$ is the positive equilibrium.

Recently, a great interest has been devoted to the study of traveling waves for delayed reaction-diffusion equations, and several techniques for proving their existence have been established. Among them, the method of lower and upper solutions has proven to be a powerful tool. In his pioneering work [3], Schaaf studied the existence of traveling waves for scalar reaction-diffusion equations with a single discrete delay: assuming that the nonlinearities satisfy a *quasi-monotonicity condition*, Schaaf used upper and lower solutions, coupled with several other techniques, to established the existence of a wave front and the minimal wave speed. A remarkable generalization of the method of lower and upper solutions in [3] was recently conducted by Wu and Zou [4]. These authors not only considered n-dimensional reaction-diffusion systems with a general bounded delay, but also assumed a less restrictive *quasi-monotonicity condition*, based on the exponential ordering introduced by Smith and Thieme [5,6]. Under this quasi-monotonicity assumption, Wu and Zou used an ordered pair of upper-lower solutions, to develope a monotone iteration process converging to a wave front, so that Wu and Zou's method reduces the existence of a monotone wave front to the existence of an ordered pair of upper-lower solutions. For further theoretical results and applications of the method of upper and lower solutions, see also [7–12].

For Eq. (2) with $1 < \beta \le e$, So and Zou [11] proved the existence of a traveling wave front with speed c, for $c > c_*$, where the minimal speed c_* is explicitely given. Their result is based on the monotone iteration scheme developed by Wu and Zou [4], which can be used if $1 < \beta \le e$, since in this case the function $h(x) = xe^{-x}$ is increasing on $[0, 1] \supset [0, K]$, thus $\phi \mapsto -\delta\phi(0) + \delta\beta h(\phi(-\tau))$ satisfies the quasimonotonicity condition in [4]. Hence, for $1 < \beta \le e$ the existence of traveling waves proven in [11] follows immediately by [4], after the authors proved the existence of an ordered pair of upper-lower solutions — which actually had already been considered by Diekmann [13, Theorem 6.1] and Schaaf [3, Theorem 2.10] in other settings. We also remark that, although the stronger quasimonotonicity condition in Schaaf [3] holds for (3) with $1 < \beta \le e$, Schaaf's positivity requirement fails, and hence his results cannot be invoked. For the case $\beta > e$, clearly h is not monotone on $[0, K]$, and neither Shaaf nor Wu and Zou's methods are applicable.

The alternative approach presented in [1], and used here to study Eq. (2) with $\beta > e$, exploits the natural connection between the existence of a traveling wave solution for a delayed reaction-diffusion equation, and the existence of a heteroclinic solution for its corresponding delayed ordinary differential equation.

Motivated by the case $\beta > e$ in (1) and its diffusive version (2), we address here the situation of scalar DDEs that can be written in the form

$$x'(t) = -\delta x(t) + g(x(t-\tau)), \quad t \in \mathbb{R}, \tag{5}$$

where $\delta > 0$ and g is a continuous function, as well as the correspondent reaction-diffusion equations with a spatial variable and diffusion,

$$\frac{\partial N}{\partial t}(t,x) = d\frac{\partial^2 N}{\partial x^2}(t,x) - \delta N(t,x) + g(N(t-\tau,x)), \qquad t, x \in \mathbb{R}, \tag{6}$$

with $d > 0$. For (5) written as $x'(t) = f(x(t), x(t-\tau))$, we suppose that the function $f(x, y) = -\delta x + g(y)$ may not satisfy the quasimonotonicity condition in [4]. To be more precise, the following assumptions on g will be assumed:

A1: $g : \mathbb{R} \to \mathbb{R}$ is continuous and C^1 in a neighborhood of zero, $g(0) = 0$, $g(x) > 0$ for $x > 0$, $\lim_{x\to\infty} g(x) = 0$; there is $x_M > 0$ such that $g(x)$ is strictly increasing on $(0, x_M)$ and strictly decreasing on (x_M, ∞);
A2: there is a unique positive root K of the equation $g(x) = \delta x$, and $K > x_M$;
A3: $g'(0) > \delta$ and $g(x) \le g'(0)x$ for x in a neighborhood $[0, \nu]$ of zero in $\mathbb{R}_+$.

We note that hypothesis (A3) was already chosen by Diekmann [13] for the study of traveling solutions of an integral equation. In (A3), the convexity condition $g(x) \le g'(0)x$ for $x > 0$ small is clearly satisfied if there exists $g''(0) < 0$. For the particular case of the Nicholson's equation, $g(x) = \delta\beta x e^{-x}$, we have $x_M = 1$, and $K > x_M$ corresponds to the case $\beta > e$ under our study.

In this paper, we look for positive heteroclinic orbits of (5) connecting the equilibria $x = 0$ to $x = K$, as t goes from $-\infty$ to ∞, and apply the results in [1] to conclude also the existence of traveling waves for (6), i.e., solutions of

$$d\varphi''(t) - c\varphi'(t) - \delta\varphi(t) + g(\varphi(t - c\tau)) = 0, \quad t \in \mathbb{R},$$

such that $\varphi(-\infty) = 0, \varphi(\infty) = K$. The following theorem is an immediate consequence of Theorem 1.1 in [1], applied to the particular situation of scalar models (6):

Theorem 1 *Consider Eq. (5) where g is C^2 and satisfies (A1-A3), and assume that:*

H1: the equilibrium K of (5) is asymptotically stable (i.e., all eigenvalues of the linearized equation for (5) about $x = K$ have negative real parts);
H2: the trivial equilibrium of (5) is hyperbolic, and the unstable manifold at zero is M-dimensional, with $M \ge 1$ (i.e., all eigenvalues of the linearized equation for (5) about $x = K$ have non-zero real parts and there are $M \ge 1$ eigenvalues with positive real parts);
H3: there is a heteroclinic solution $u : \mathbb{R} \to \mathbb{R}$ for (5) connecting $x = 0$ to $x = K$.

Then, there is $c^* > 0$ such that, for each $c > c^*$, the set of all traveling wave solutions of (6) connecting zero to K and propagating at speed c forms a C^1-smooth M-dimensional manifold in some $C_b(\mathbb{R}, \mathbb{R})$-neighbourhood of the heteroclinic solution u in (H3). (Here, $C_b(\mathbb{R}, \mathbb{R})$ is the space of bounded continuous functions equipped with the sup norm.)

In Section 2 of the present paper, we shall prove the existence of a *positive* heteroclinic orbit for (5) from zero to K, with asymptotic exponential behaviour as $t \to -\infty$. For this, we shall use a positive lower solution of the *ordinary* DDE (5) as a lower bound of the heteroclinic solution to be found, and prove its existence by using a fixed-point argument. In order to be able to apply Schauder's fixed-point theorem, and to compensate for the fact that g is not increasing in a neighbourhood of the positive equilibrium K, we shall require that K is a global attractor of all positive solutions of Eq. (5), i.e., all positive solutions of (5) go to K as $t \to \infty$. Although this seems a rather restrictive setting, if (H1) holds it is quite natural to assume also that K is globally attracting. In fact, since the *Wright's conjecture* for the delayed logistic equation was presented in [14], for several other scalar ordinary DDEs, such as the Nicholson's equation (see e.g. Smith [15]), it has been conjectured that the asymptotic stability of the positive equilibrium implies its global attractivity (in the set of all positive solutions). We also recall that it is well-known that the positive equilibrium K of Nicholson's equation (1) is globally attractive in the case $1 < \beta \leq e$ studied by So and Zou [11].

In Section 3, we use the results in Section 2 and Theorem 1 to conclude the existence of traveling waves for the reaction-diffusion equation (6). As an illustration, we address the existence of traveling wave solutions for the diffusive Nicholson's equation (2) in the case of $p/\delta > e$, i.e., when the delayed term is given by a non-monotone function, improving the criterion in [1].

2 Positive heteroclinic solutions

Throughout this section, we assume that g in (5) satisfies (A1-A3). In order to simplify the notation, let

$$g(x) = \delta\beta h(x), \qquad x \in \mathbb{R},$$

where $\beta := g'(0)/\delta > 1$, so that $h'(0) = 1$. We observe that $\beta h(x) > x$ for $x \in (0, K)$ and $\beta h(x) < x$ for $x > K$, and $\max_{x \geq 0} h(x) = h(x_M)$ with $\beta h(x_M) > K > x_M$.

For (5), define the differential operator L,

$$L\phi(t) = \phi'(t) + \delta\phi(t) - \delta\beta h(\phi(t-\tau)), \quad t \in \mathbb{R}. \tag{7}$$

For the linearized equation of (5) about zero,

$$x'(t) = -\delta x(t) + \delta\beta x(t-\tau)\,,$$

the characteristic equation is

$$\Delta(\lambda) = 0, \quad \text{where} \quad \Delta(\lambda) = \lambda + \delta - \delta\beta e^{-\lambda\tau}\,. \tag{8}$$

Lemma 2 *Let $\lambda_1 > 0$ be the unique real root of (8) and consider $\varepsilon \in (0, \lambda_1)$ sufficiently small.*

(i) For $M = M(\varepsilon) > 0$ sufficiently large, the function

$$\phi_*(t) = \begin{cases} (1 - Me^{\varepsilon t})e^{\lambda_1 t}, & t \leq t_1, \\ 0, & t > t_1, \end{cases} \tag{9}$$

with $t_1 = -(\log M)/\varepsilon$, is a lower solution *of (5), i.e., $\phi_* : \mathbb{R} \to \mathbb{R}$ is continuous, differentiable almost everywhere on $\mathbb{R}$, and satisfies*

$$L\phi_* \leq 0, \quad \text{a.e. } t \in \mathbb{R}.$$

(ii) Moreover,

$$\max_{t \in \mathbb{R}} \phi_*(t) \leq K_0, \tag{10}$$

where $K_0 \in (0, x_M)$ is defined by $h(K_0) = h(\beta h(x_M))$.

PROOF. Let $M \geq 1$. For $t > t_1$, we have $L\phi_*(t) = -\delta\beta h(\phi_*(t-\tau)) \leq 0$. Consider now $t < t_1$. Since $h'(0) = 1$, for some $a > 0$ we have $h(x) \geq x(1 - ax)$ for $x \geq 0$ small. For $\max_{t\in\mathbb{R}} \phi_*(t)$ small, we obtain

$$\begin{aligned} L\phi_*(t) &\leq e^{\lambda_1 t}\Big\{(\lambda_1 + \delta) - M(\lambda_1 + \varepsilon + \delta)e^{\varepsilon t} \\ &-\delta\beta e^{-\lambda_1\tau}(1 - Me^{\varepsilon(t-\tau)})[1 - a(1 - Me^{\varepsilon(t-\tau)})e^{\lambda_1(t-\tau)}]\Big\} \\ &= e^{\lambda_1 t}\Big\{ - Me^{\varepsilon t}[(\lambda_1 + \varepsilon + \delta) - \delta\beta e^{-(\lambda_1+\varepsilon)\tau}] + a(1 - Me^{\varepsilon(t-\tau)})^2\delta\beta e^{-2\lambda_1\tau}e^{\lambda_1 t}\Big\} \\ &= e^{\lambda_1 t}\Big[- Me^{\varepsilon t}\Delta(\lambda_1 + \varepsilon) + a(1 - Me^{\varepsilon(t-\tau)})^2\delta\beta e^{-2\lambda_1\tau}e^{\lambda_1 t}\Big]. \end{aligned}$$

Since $0 < \varepsilon < \lambda_1$ and $t < t_1 \leq 0$, we have $e^{\lambda_1 t} \leq e^{\varepsilon t}$, and

$$L\phi_*(t) \leq e^{(\lambda_1+\varepsilon)t}\Big[- M\Delta(\lambda_1 + \varepsilon) + a(1 - Me^{\varepsilon(t-\tau)})^2\delta\beta e^{-2\lambda_1\tau}\Big].$$

Note that $\Delta(\lambda_1 + \varepsilon) > 0$. Since $0 < 1 - Me^{\varepsilon(t-\tau)} < 1$, we obtain

$$L\phi_*(t) \leq e^{(\lambda_1+\varepsilon)t}\Big[- M\Delta(\lambda_1 + \varepsilon) + a\delta\beta e^{-2\lambda_1\tau}\Big],$$

hence $L\phi_*(t) \leq 0$ if $M = M(\varepsilon)$ is chosen so that $M \geq 1$ and

$$M \geq \Delta(\lambda_1 + \varepsilon)^{-1}a\delta\beta e^{-2\lambda_1\tau}.$$

This proves (i), for any fixed $\varepsilon \in (0, \lambda_1)$, provided $\max_{t\in\mathbb{R}} \phi_*(t)$ is sufficiently small.

Let t_0 be such

$$\max_{t\in\mathbb{R}} \phi_*(t) = \phi_*(t_0).$$

Since $\phi_*'(t_0) = 0$, we have $\lambda_1 = M(\varepsilon + \lambda_1)e^{\varepsilon t_0}$, and therefore for $0 < \varepsilon << 1$,

$$\phi_*(t_0) = \Big(1 - \frac{\lambda_1}{\varepsilon + \lambda_1}\Big)e^{\varepsilon t_0} < \frac{\varepsilon}{\varepsilon + \lambda_1},$$

hence $\max_{t\in\mathbb{R}} \phi_*(t)$ is arbitrarily small as $\varepsilon \to 0^+$, in particular, $\max_{t\in\mathbb{R}} \phi_*(t) \le K_0$. ■

Remark 3 *In the case of the Nicholson's equation with diffusion and $1 < \beta \le e$, for c large, So and Zou [11] proved that the function ϕ_* defined by (9), with λ_1 being the first positive real root of the characteristic equation for the linearized equation for (3) at zero, is a lower solution for (3). We note that the pair of lower-upper solutions in [11] had already been given by Diekmann [13] for an integral equation (see also Atkinson and Reuter [16]), and has since been used by other authors [3,7,11].*

We now consider the space $C(\mathbb{R},\mathbb{R})$ of continuous real functions on $\mathbb{R}$, and the operator $T : C(\mathbb{R},\mathbb{R}) \to C(\mathbb{R},\mathbb{R})$ defined by

$$T\varphi(t) = \delta\beta \int_{-\infty}^{t} e^{-\delta(t-s)}h(\varphi(s-\tau))ds, \quad t \in \mathbb{R}, \tag{11}$$

whose domain contains the set of all non-negative continuous functions. Clearly, a positive function $\varphi(t)$ is a global bounded solution of (5) if and only if $\varphi(t) = T\varphi(t),\ t \in \mathbb{R}$. Our goal now is to show that T is completely continuous on a suitable convex, closed set of a Banach space, and invoke Schauder's fixed-point theorem to find a fixed-point φ of T satisfying

$$\varphi(-\infty) = 0, \quad \varphi(\infty) = K.$$

In what follows, let $x_0 > 0$ and $h(x) \le x$ on $[0, x_0]$ (see (A3)), and define $t_0 = (\log x_0)/\lambda_1$.

Lemma 4 *For all $\varphi \in C(\mathbb{R},\mathbb{R})$, φ non-negative, then $T\varphi$ is bounded and differentiable, with*

$$0 \le T\varphi(t) \le \beta h(x_M), \qquad |(T\varphi)'(t)| \le \delta\beta h(x_M)\ , \quad t \in \mathbb{R}. \tag{12}$$

Moreover, if $\varphi \in C(\mathbb{R},\mathbb{R})$ with $0 \le \varphi(t) \le e^{\lambda_1 t},\ t \le t_0$, then $0 \le T\varphi(t) \le e^{\lambda_1 t},\ t \le t_0$, where λ_1 is the positive real root of (8).

PROOF. Recall that $0 \le h(x) \le h(x_M)$, $x \ge 0$. Consider any non-negative $\varphi \in C(\mathbb{R}, \mathbb{R})$. Then, for $t \in \mathbb{R}$,

$$0 \le T\varphi(t) \le \delta\beta e^{-\delta t} h(x_M) \int\limits_{-\infty}^{t} e^{\delta s}\, ds = \beta h(x_M)\,,$$

and $(T\varphi)'(t) = -\delta T\varphi(t) + \delta\beta h(\varphi(t-\tau))$, with $0 \le T\varphi(t), \beta h(\varphi(t-\tau)) \le \beta h(x_M)$, implying that

$$|(T\varphi)'(t)| \le \delta\beta h(x_M).$$

This proves (12). Now, assume also that $\varphi(t) \le e^{\lambda_1 t},\ t \le t_0$. Since $h(x) \le x$, $x \in [0, x_0]$, we have

$$\begin{aligned} T\varphi(t) &\le \delta\beta e^{-\delta t} \int\limits_{-\infty}^{t} e^{\delta s} \varphi(s-\tau) ds \\ &\le \delta\beta e^{-\delta t} \int\limits_{-\infty}^{t} e^{\delta s} e^{\lambda_1 (s-\tau)} ds = \frac{\delta\beta e^{-\lambda_1 \tau}}{\delta + \lambda_1} e^{\lambda_1 t} = e^{\lambda_1 t}\,, \quad t \le t_0. \end{aligned}$$

■

In the sequel, ϕ_* is as in (9), with $\varepsilon > 0$ and $M \ge 1$ chosen so that ϕ_* is a lower solution of (5) for which (10) holds.

Lemma 5 *We have*

(i) $T\phi_*(t) \ge \phi_*(t)$, *for all* $t \in \mathbb{R}$;
(ii) for $\varphi \in C(\mathbb{R}, \mathbb{R})$ *satisfying* $\phi_*(t) \le \varphi(t) \le \beta h(x_M),\ t \in \mathbb{R}$, *then* $\phi_*(t) \le T\varphi(t),\ t \in \mathbb{R}$.

PROOF. For $\phi_1 := T\phi_*$, we have

$$\phi_1'(t) + \delta\phi_1(t) - \delta\beta h(\phi_*(t-\tau)) = 0, \quad t \in \mathbb{R}\,. \tag{13}$$

Define $w(t) = \phi_1(t) - \phi_*(t)$. From (13) and the fact that ϕ_* is a lower solution of (5), it follows that

$$r(t) := w'(t) + \delta w(t) \ge 0, \quad t \in \mathbb{R}\,,$$

with $r(t)$ is continuous, and bounded from Lemma 4. We get

$$w(t) = ce^{-\delta t} + \int\limits_{-\infty}^{t} e^{-\delta(t-s)} r(s)\, ds$$

for some constant $c \in \mathbb{R}$. On the other hand, $w(t)$ is bounded on $\mathbb{R}$, implying that $c = 0$. Hence $w(t) \geq 0$ for $t \in \mathbb{R}$, and the proof of (i) is complete.

Now, consider $\varphi \in C(\mathbb{R}, \mathbb{R})$, with $\phi_*(t) \leq \varphi(t) \leq \beta h(x_M)$, $t \in \mathbb{R}$. Since $\phi_*(t) \leq K_0$, $t \in \mathbb{R}$, then

$$h(\varphi(t)) \geq h(\phi_*(t)) \quad \text{if} \quad \varphi(t) \leq K_0$$

because h is increasing in $[0, K_0]$, and

$$h(\varphi(t)) \geq h(K_0) = h(\beta h(x_M)),\ h(\phi_*(t)) \leq h(K_0) \quad \text{if} \quad \varphi(t) \geq K_0,$$

by (10) and the definition of K_0. For $t \in \mathbb{R}$, we get

$$h(\varphi(t)) \geq h(\phi_*(t)),$$

therefore $T\varphi(t) \geq T\phi_*(t)$, and (ii) follows now from (i). ■

Define

$$S = \{\varphi \in C(\mathbb{R}, \mathbb{R}) : \phi_*(t) \leq \varphi(t) \leq \beta h(x_M) \text{ for } t \in \mathbb{R},\ \varphi(t) \leq e^{\lambda_1 t} \text{ for } t \leq t_0\}. \quad (14)$$

We now use an exponential weighting. Inspired on the work of Ma [10], we consider the space $C(\mathbb{R}, \mathbb{R})$ equipped with the norm

$$\|\varphi\|_\rho = \sup_{t \in \mathbb{R}} |\varphi(t)| e^{-\rho|t|}$$

where $\rho \in (0, \min\{\lambda_1, \delta\})$. Note that $(C(\mathbb{R}, \mathbb{R}), \|\cdot\|_\rho)$ is a Banach space.

Lemma 6 *The set S is $\|\cdot\|_\rho$-closed, bounded, convex and non-empty.*

PROOF. From (9), (10), we have $\phi_*(t) \leq e^{\lambda_1 t}$ and $\phi_*(t) \leq K_0$, $t \in \mathbb{R}$, thus in particular $\phi_* \in S$. It is clear that S is convex and $\|\varphi\|_\rho \leq \beta h(x_M)$ for $\varphi \in S$. Since the $\|\cdot\|_\rho$-convergence implies the uniform convergence in any compact set of $\mathbb{R}$, it follows that S is $\|\cdot\|_\rho$-closed. ■

Lemma 7 *Consider the space $C(\mathbb{R}, \mathbb{R})$, equipped with the norm $\|\cdot\|_\rho$. Then, $T : S \to C(\mathbb{R}, \mathbb{R})$ is (Lipschitz) continuous.*

PROOF. Recall that h is Lipschitz continuous on $[0, \beta h(x_M)]$; let ℓ be a Lipschitz constant on $[0, \beta h(x_M)]$. Consider $\varphi, \psi \in S$. For $t \leq \tau$,

$$|T\varphi(t) - T\psi(t)| \leq \delta\beta\ell e^{-\delta t} \int_{-\infty}^{t} e^{\delta s} |\varphi(s-\tau) - \psi(s-\tau)|\, ds$$

$$\leq \delta\beta\ell e^{-\delta t} e^{\rho\tau} \|\varphi - \psi\|_\rho \int_{-\infty}^{t} e^{(\delta-\rho)s}\, ds\,,$$

hence

$$\begin{cases} |T\varphi(t) - T\psi(t)|e^{\rho t} \le K_1 \|\varphi - \psi\|_\rho, & \text{if } t \le 0, \\ |T\varphi(t) - T\psi(t)|e^{-\rho t} \le K_1 e^{-2\rho t}\|\varphi - \psi\|_\rho \le K_1\|\varphi - \psi\|_\rho, & \text{if } 0 \le t \le \tau, \end{cases} \tag{15}$$

where $K_1 = \delta\beta\ell e^{\rho\tau}/(\delta - \rho)$. For $t > \tau$,

$$\begin{aligned} &|T\varphi(t) - T\psi(t)| \\ &\le \delta\beta\ell e^{-\delta t}\Big\{\int_{-\infty}^{\tau} e^{\delta s}|\varphi(s-\tau) - \psi(s-\tau)|ds + \int_{\tau}^{t} e^{\delta s}|\varphi(s-\tau) - \psi(s-\tau)|ds\Big\} \\ &\le \delta\beta\ell e^{-\delta t}\|\varphi - \psi\|_\rho\Big\{\int_{-\infty}^{\tau} e^{\delta s}e^{\rho(\tau - s)}\,ds + \int_{\tau}^{t} e^{\delta s}e^{\rho(s-\tau)}\,ds\Big\} \\ &\le \delta\beta\ell\|\varphi - \psi\|_\rho\Big[\frac{e^{-\delta(t-\tau)}}{\delta - \rho} + \frac{e^{\rho(t-\tau)} - e^{-\delta(t-\tau)}}{\delta + \rho}\Big] = \|\varphi - \psi\|_\rho(K_2e^{-\delta t} + K_3e^{\rho t}), \end{aligned}$$

where $K_2 = \delta\beta\ell(\frac{1}{\delta-\rho} - \frac{1}{\delta+\rho})e^{\delta\tau}$ and $K_3 = \delta\beta\ell\frac{e^{-\rho\tau}}{\delta+\rho}$, implying that

$$|T\varphi(t) - T\psi(t)|e^{-\rho t} \le \|\varphi - \psi\|_\rho(K_2e^{-(\delta+\rho)t} + K_3) \le (K_2 + K_3)\|\varphi - \psi\|_\rho\,. \tag{16}$$

From (15) and (16), we conclude that

$$\|T\varphi - T\psi\|_\rho \le \max\{K_1, K_2 + K_3\}\|\,\varphi - \psi\|_\rho\,.$$ ■

Lemma 8 *For S defined as in (14), the set $T(S)$ is relatively compact in $(C(\mathbb{R},\mathbb{R}), \|\cdot\|_\rho)$.*

PROOF. Let $\psi_n = T\varphi_n$, with $\varphi_n \in S$. From Lemma 4, (ψ_n) is uniformly bounded on $\mathbb{R}$ and equicontinuous. By Ascoli-Arzelà theorem, for each compact interval $I \subset \mathbb{R}$ there is a subsequence of (ψ_n) which converges uniformly on I to some $\psi_I \in C(I,\mathbb{R})$. For $I_k = [-k,k],\ k \in \mathbb{N}$, we construct subsequences $(\psi_{\alpha_k(n)})$, with $\alpha_k : \mathbb{N} \to \mathbb{N}$ increasing, such that $(\psi_{\alpha_1(n)})$ is a subsequence of (ψ_n), $(\psi_{\alpha_{k+1}(n)})$ is a subsequence of $(\psi_{\alpha_k(n)}),\ k \in \mathbb{N}$, and $\psi_{\alpha_k(n)} \to \psi^k$ uniformly on $I_k,\ k \in \mathbb{N}$. Clearly $\psi^{k+1}|_{I_k} = \psi^k$ for $k \ge 1$. Define $\phi \in C(\mathbb{R},\mathbb{R})$ by $\phi(t) = \psi^k(t), \quad \text{if } |t| \le k, \quad t \in \mathbb{R}$.

Consider now the "diagonal" subsequence $(\psi_{\alpha_n(n)})$. Let $\epsilon > 0$ be given. Choose $n_0 \in \mathbb{N}$ such that $e^{-\rho n_0}\beta h(x_M) \le \epsilon$. By Lemma 4, $0 \le \psi_{\alpha_n(n)}(t), \phi(t) \le \beta h(x_M)$, thus if $|t| \ge n_0$ we have

$$|\psi_{\alpha_n(n)}(t) - \phi(t)|e^{-\rho|t|} \le e^{-\rho n_0}\beta h(x_M) \le \epsilon\,, \quad n \in \mathbb{N}.$$

On the other hand, $\psi_{\alpha_n(n)} \to \phi$ uniformly on $[-n_0, n_0]$. Consequently, there exists $n_1 \geq n_0$ such that

$$|\psi_{\alpha_n(n)}(t) - \phi(t)|e^{-\rho|t|} \leq |\psi_{\alpha_n(n)}(t) - \phi(t)| \leq \epsilon$$

for $n \geq n_1$ and $|t| \leq n_0$. This proves that $\|\psi_{\alpha_n(n)} - \phi\|_\rho \to 0$. ∎

We are now in the position to state the main result of this section.

Theorem 9 *Consider Eq. (5) with conditions (A1-A3), and assume that the positive equilibrium K is globally attractive (in the set of all positive solutions). Then, there is a positive heteroclinic solution of (5) connecting $x = 0$ to $x = K$; i.e., there is a positive solution $u(t)$ of (5), defined on $\mathbb{R}$ and satisfying*

$$u(-\infty) = 0, \quad u(\infty) = K.$$

Furthermore, $u(t) = O(e^{\lambda_1 t})$ as $t \to -\infty$, where λ_1 is the positive root of (8).

PROOF. Consider S as in (14). From Lemmas 4 and 5, $T(S) \subset S$. From Lemmas 7 and 8, $T : S \to S$ is $\|\cdot\|_\rho$-completely continuous. Lemma 6 allows us to use the Schauder's fixed-point theorem to conclude that there is $u \in S$ such that $Tu = u$. Thus, $u(t)$ is a positive global solution of (5) satisfying $\phi_*(t) \leq u(t) \leq e^{\lambda_1 t}$ for $t \leq t_0$. Since K is globally attractive, it follows that $u(\infty) = K$. ∎

Corollary 10 *Consider the Nicholson's equation (1) with $\beta = p/\delta > 1$ (and $a = 1$). If the equilibrium $x = \log\beta$ is globally attractive (in the set of all positive solutions), then there is a positive heteroclinic solution connecting the equilibria $x = 0$ to $x = \log\beta$.*

Remark 11 *For Eq. (1), we note that the positive equilibrium K is globally attractive on $(0, \infty)$ for all values of the delay τ if $\beta \leq e^2$; if $\beta > e^2$, then K is a global attractor of all positive solutions if the delay τ is small, and several criteria have been established in the literature (see [15,17,18] and references therein).*

3 Existence of traveling waves

As an immediate consequence of Theorems 1 and 9, we state some results on the existence of traveling waves for scalar reaction-diffusion equations.

Theorem 12 *Assume (A1-A3) with g a C^2-function. Assume also that*

(i) the positive equilibrium K of (5) is globally attractive (in the set of all positive solutions) and locally exponentially stable;
(ii) the trivial equilibrium of (5) is hyperbolic.

Then for $c > 0$ sufficiently large, (6) has a traveling wave solution of speed c, connecting the trivial equilibrium to the positive equilibrium K.

We finally consider Nicholson's equation with diffusion.

Theorem 13 *Consider Eq. (2) with $a = 1$ and $\Lambda := \log\beta - 1 > 0$, and assume that:*

(i) either $\beta \le e^2$, or $\beta > e^2$ and $\tau < \tau^*$ where

$$e^{\delta\tau^*}\Lambda\log\Big(\frac{\Lambda^2+\Lambda}{\Lambda^2+1}\Big) = 1; \tag{17}$$

(ii) $\tau \neq \tau_n$, where

$$\tau_n = \frac{2n\pi - \arccos(1/\beta)}{\delta\sqrt{\beta^2-1}}, \quad n \in \mathbb{N}. \tag{18}$$

Then for $c > 0$ sufficiently large, there is a solution of the problem (3)-(4), i.e., (2) has a traveling wave solution of speed c, connecting the trivial equilibrium to the positive equilibrium K.

PROOF. Condition $\beta \le e^2$ implies that the positive equilibrium K is locally asymptotically stable and attracts all positive solutions (see [1,17,18]). Now let $\beta > e^2$. From [18, Theorem 2.1], condition $\tau < \tau^*$ for τ^* as in (17) implies that K is globally attractive, and locally asymptotically stable. On the other hand, (ii) implies that $x = 0$ is a hyperbolic equilibrium of (1) [1]. Recall that for all $\tau > 0$ there is always a root $\lambda_1 > 0$ of the characteristic equation (8), hence the local unstable manifold for (5) at $x = 0$ is at least one-dimensional. The conclusion follows now from Theorems 1 and 9. ■

Remark 14 *For $\tau < \hat{\tau}$, where*

$$\hat{\tau} = \frac{\pi - \arccos(1/\Lambda)}{\delta\sqrt{\Lambda^2-1}}, \tag{19}$$

the positive equilibrium K of the Nicholson's equation is locally asymptotically stable (see e.g. [1]). We note that τ^* is a good approximation for $\hat{\tau}$ [18]. In accordance with Smith conjecture [15, p. 116], we conjecture that the local asymptotical stability of the positive steady state of the scalar Nicholson's equation implies the existence of traveling waves with speed c, for sufficiently large c.

Remark 15 *Theorem 13 strongly improves the result in [1, Theorem 6.5]. We recall that in [1] the authors used the exponential ordering theory of Smith and Thieme [5,6], to deduce that the semiflow of (1) is strictly monotone (with respect to the exponential ordering), and hence conclude the existence of a* *heteroclinic for (1) connecting the trivial to the positive equilibria under the hypothesis* $\tau < \tau_0$ *if* $\beta \le e^2$ *and* $\tau < \min\{\tau_0, \hat{\tau}\}$ *if* $\beta > e^2$*, where* $\tau_0, \hat{\tau}$ *are defined respectively by (18), (19), and the additional assumption*

$$\tau < \tilde{\tau}\,, \tag{20}$$

where $\tilde{\tau} > 0$ *is the unique solution of*

$$\delta\beta\tau e^{\delta\tau+1}|h'_{min}| = 1, \text{ where } h'_{min} = \min_{x\in[0,K]} h'(x) = \begin{cases} (1-\log\beta)/\beta, & \text{if } \beta \le e^2, \\ -e^{-2}, & \text{if } \beta > e^2. \end{cases}$$

In our Theorem 13, condition (20) is not required if $\beta \le e^2$*. For the situation* $\beta > e^2$*, condition (20) reads as*

$$\delta\beta\tau e^{\delta\tau-1} < 1 \tag{21}$$

and is replaced in Theorem 13 by condition

$$e^{\delta\tau^*}\Lambda\log\Big(\frac{\Lambda^2+\Lambda}{\Lambda^2+1}\Big) < 1,$$

which is strictly weaker than the restriction (21).

Due to the biological interpretation of model (2), as well as other population models written in the form (6), it is of great interest to prove the existence of *positive* traveling wave solutions. Unfortunately, this cannot be concluded from Theorems 12 and 13 by the above procedure, and remains an open question. The study of the positivity and uniqueness (up to a shift in time) of traveling waves for (6) have been pursued by the authors; we refer the reader to [19], where further results can be found.

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