STABILITY OF TRAVELLING WAVES IN A WOLBACHIA INVASION

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Abstract. Numerous studies have examined the growth dynamics of Wolbachia within populations and the resultant rate of spatial spread. This spread is typically characterised as a travelling wave with bistable local growth dynamics due to a strong Allee effect generated from cytoplasmic incompatibility. While this rate of spread has been calculated from numerical solutions of reaction-diffusion models, none have examined the spectral stability of such travelling wave solutions. In this study we analyse the stability of a travelling wave solution generated by the reaction-diffusion model of Chan & Kim [4] by computing the essential and point spectrum of the linearised operator arising in the model. The point spectrum is computed via an Evans function using the compound matrix method, whereby we find that it has no roots with positive real part. Moreover, the essential spectrum lies strictly in the left half plane. Thus, we find that the travelling wave solution found by Chan & Kim [4] corresponding to competition between Wolbachia-infected and -uninfected mosquitoes is linearly stable. We employ a dimension counting argument to suggest that, under realistic conditions, the wavespeed corresponding to such a solution is unique.

1. Introduction. Wolbachia are common endosymbiotic bacteria that are estimated to infect up to 66% of all insect species [10]. They are primarily vertically transmitted and can induce reproductive phenotypes in its host to confer a reproductive advantage and hence improve chances of persistence. A well-studied reproductive phenotype resulting from Wolbachia infection is cytoplasmic incompatibility (CI), whereby offspring of infected males and uninfected females have an increased mortality rate. This has lead to the proposal of a deliberate Wolbachia introduction into wild mosquito populations to reduce transmission of vector-borne diseases, since particular CI-inducing Wolbachia strains have been shown to reduce proliferation of various viruses (see Brelsfoard & Dobson [3] and references therein). Two particular CI-inducing strains of Wolbachia, WMel and WMelPop, have received much attention due to evidence of these strains inhibiting dengue transmission in Aedes Aegypti mosquitoes.

Although CI has been proposed as a key mechanism for the success of Wolbachia-based strategies, fitness reducing phenotypes are also a result of certain Wolbachia

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strains. For example, both WMel and WMelPop reduce both fecundity and lifespan of infected females [16, 24, 23]. Turelli [21] first showed that the amalgamation of these Wolbachia-induced effects result in a strong Allee effect for an invasion, that is, infection is only successful if initial infection densities are above the critical Allee threshold. This threshold has been found by various modelling studies to be dependent on the fecundity cost of infection, the strength of CI in reducing offspring from infected males and uninfected females, and the probability of successful Wolbachia transmission [17, 13, 22, 8, 4].

Many studies have analysed the growth dynamics of a deliberate Wolbachia introduction via non-spatial models, but relatively few studies have studied the dynamics of the spatial spread (see Hancock & Godfray [9] and Barton & Turelli [2] for examples). This study is motivated by the reaction-diffusion model of Chan & Kim [4], who examine the spatial spread of Wolbachia in a homogeneous environment by incorporating slow and fast compartments in their model. Chan & Kim [4] numerically show that there exists a travelling wave solution corresponding to a Wolbachia invasion, that is, competition between Wolbachia-infected and -uninfected mosquitoes, and estimate the wavespeed corresponding to this solution. A simplified model which uses a weighted average of the slow and fast diffusion coefficients was found to yield similar wavespeeds. This model assumes perfect vertical transmission of Wolbachia, an increased fecundity for infected individuals, longevity reducing effects of 10% and that Wolbachia infection induces CI. Here we perform a spectral stability analysis by examining the linearised operator arising in this simplified model. We show that the essential spectrum is bounded to the left-half plane for all relevant biological parameter values and show that the point spectrum contains no elements in the right-half plane. Moreover, we show that there exists a travelling wave solution for only a unique wavespeed.

2. Problem setup. The non-dimensionalised system of partial differential equations from Chan & Kim [4] is given by

\[
\begin{align*}
    u_t &= u_{xx} - \rho u_x + u(1 - S) - \alpha \mu u, \\
    v_t &= v_{xx} - \rho v_x + Fv(1 - S)(1 - s_h A) - \mu v, 
\end{align*}
\]

where \( u \) is the density of Wolbachia-infected mosquitoes, \( v \) is the density of uninfected mosquitoes, \( S = u + v \) and \( A = u/S \). Following Chan & Kim [4], we let \( s_h = 0.45 \), \( F = 1.0526 \) and \( \mu = 0.0162 \), which correspond to parameter values for Aedes aegypti at 30°C. The parameters \( F^{-1}, \mu, \rho \) and \( s_h \) correspond to the relative fecundity of infected females to uninfected females, mortality rate, advection rate and probability of embryo death due to cytoplasmic incompatibility, respectively. Additionally, we let \( \alpha = 1.1 \), which reflects the 10% relative reduction in lifespan associated with the WMel strain of Wolbachia. These parameter values are concisely listed in Table 1. Converting to travelling wave coordinates \( z = x - (c + \rho)t \), we have that \((u(x,t), v(x,t)) = (u(z,t), v(z,t))\). This yields

\[
\begin{align*}
    u_t &= u_{zz} + cu_z + u(1 - S) - \alpha \mu u, \\
    v_t &= v_{zz} + cv_z + Fv(1 - S)(1 - s_h A) - \mu v, \\
    (u, v)(-\infty) &= e_-, \\
    (u, v)(\infty) &= e_+, \\
    (u', v')(\pm \infty) &= 0.
\end{align*}
\]
where \( e_- = (1 - \alpha \mu, 0) \) and \( e_+ = (0, 1 - \frac{\mu}{F}) \).

Due to the bistability in the system, and from the spatial dynamics of the PDE
\[ u_t = u_{xx} + u(1-u)(u-a) \] (essentially a reaction-diffusion equation with bistable
reaction term/strong Allee growth dynamics, see Lewis & Kareiva [15]), we expect
that there is a unique wavespeed \( c_+ \), for which there is a heteroclinic connection
between \( e_- \) and \( e_+ \) in system (2). Chan & Kim [4] use the method of lines to solve
the PDE system (1) and numerically determine the wavespeed to be approximately
0.027 for a variety of different initial functions; this suggests uniqueness of the
wavespeed. We provide a dimension counting argument to further support this
evidence in Section 5.1.

We proceed to setup the problem for computation of the essential and point
spectrum. Firstly, we linearise about the travelling wave solution \((\hat{u}(z), \hat{v}(z))\) via
the substitution
\[
\begin{pmatrix}
  u(z, t) \\
  v(z, t)
\end{pmatrix} = \begin{pmatrix}
  \hat{u}(z) \\
  \hat{v}(z)
\end{pmatrix} + \begin{pmatrix}
  p(z, t) \\
  q(z, t)
\end{pmatrix},
\]
where \( p(z, t) \) and \( q(z, t) \) are perturbations in \( H^1, \forall t \in \mathbb{R} \). Collecting first order
perturbation terms, we obtain
\[
\begin{align*}
  p_t &= p_{zz} + cp_z - \hat{u}(p+q) + p(1 - \hat{S}) - \alpha \mu p, \\
  q_t &= q_{zz} + cq_z + F\hat{v} \left( \frac{(\hat{S}^2 - \hat{u})s_h}{\hat{S}^2} - 1 \right) p + F \left( 1 - \hat{v} - \hat{S} + \frac{\hat{u}s_h(\hat{S}^2 - \hat{u})}{\hat{S}^2} \right) q - \mu q.
\end{align*}
\]
We define the linear operator \( \mathcal{L} \) by
\[
\mathcal{L} \begin{pmatrix} p \\ q \end{pmatrix} := \begin{pmatrix} p_{zz} + cp_z - \hat{u}(p+q) + p(1 - \hat{S}) - \alpha \mu p \\ q_{zz} + cq_z + F\hat{v} \left( \frac{(\hat{S}^2 - \hat{u})s_h}{\hat{S}^2} - 1 \right) p + F \left( 1 - \hat{v} - \hat{S} + \frac{\hat{u}s_h(\hat{S}^2 - \hat{u})}{\hat{S}^2} \right) q - \mu q \end{pmatrix},
\]
which has the corresponding eigenvalue problem \((\mathcal{L} - \lambda) \begin{pmatrix} p \\ q \end{pmatrix} = 0\). We introduce the
substitutions \( s = p_z \) and \( t = q_z \) to convert the eigenvalue problem into a first order
boundary value problem, and denote this equivalent operator of \((\mathcal{L} - \lambda) \begin{pmatrix} p \\ q \end{pmatrix} = 0\) by
\( \mathcal{T}(p, q, s, t)^T \), where \( \mathcal{T}(y)(z) = \left( \frac{\partial}{\partial z} - A(z, \lambda) \right) y \) and \( y = (p, q, s, t)^T \). This process yields
\[
\begin{align*}
  y'(z) &= A(z, \lambda) y(z), \\
  y(-\infty) &= (1 - \alpha \mu, 0, 0, 0)^T, \\
  y(\infty) &= (0, 1 - \frac{\mu}{F}, 0, 0)^T.
\end{align*}
\]
and
\[ A(z, \lambda) : = \begin{pmatrix} 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ \hat{u} - (1 - \hat{S}) + \alpha \mu + \lambda & \hat{u} & -c & 0 \\ F\hat{v} \left( 1 - \frac{(S^2 - v)s_h}{s^2} \right) & F \left( -1 + \hat{v} + \hat{S} - \frac{ss_h(S^2 - \hat{u})}{s^2} \right) + \mu + \lambda & 0 & -c \end{pmatrix}. \] (7)

To assess the stability of travelling wave solution \( \hat{u} \) and \( \hat{v} \) we need to locate the spectrum of the linearised operator \( L \) as an operator on \( H^1 \times H^1 \). If \( (L - \lambda)^{-1} \) does not exist or is unbounded for \( \lambda \in \mathbb{C} \), then \( \lambda \) is in the spectrum \( \sigma(L) \) of the operator \( L \). The complement of the spectrum in \( \mathbb{C} \) is the resolvent set of \( L \). Following Kapitula & Promislow [12, Section 2.2.5], we define \( \text{ind}(L) = \dim[\ker(L)] - \text{codim}[R(L)] \) as the Fredholm index of \( L \), where \( R(L) \) denotes the range of \( L \). The spectrum of a Fredholm operator \( L \) is decomposed into two sets:

(i) The essential spectrum, defined by
\[ \sigma_{\text{ess}}(L) = \{ \lambda \in \mathbb{C} | \lambda - L \text{ is not Fredholm or } \lambda - L \text{ is Fredholm, but } \text{ind}(\lambda - L) \neq 0 \}. \]

(ii) The point spectrum, defined by
\[ \sigma_{\text{pt}}(L) = \{ \lambda \in \mathbb{C} | \text{ind}(\lambda - L) = 0, \text{ but } \lambda - L \text{ is not invertible} \}. \]

We define
\[ A_{\pm}(\lambda) := \lim_{z \to \pm \infty} A(z, \lambda), \]
which are given by
\[ A_{-}(\lambda) = \begin{pmatrix} 0 & 0 & 0 & 1 \\ 0 & 0 & 0 & 1 \\ 1 - \alpha \mu + \lambda & 1 - \alpha \mu & -c & 0 \\ 0 & -F\alpha(1 - s_h) + \mu + \lambda & 0 & -c \end{pmatrix}, \] (8)
\[ A_{+}(\lambda) = \begin{pmatrix} 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 1 \\ \mu(\alpha - \frac{1}{F}) + \lambda & 0 & -c & 0 \\ F - \mu + \mu s_h & F - \mu + \lambda & 0 & -c \end{pmatrix}. \] (9)

The asymptotic operator of \( T \) is given by
\[ T_{\infty}(\lambda) \begin{pmatrix} p \\ q \\ s \\ t \end{pmatrix} := \begin{pmatrix} p \\ q \\ s \\ t \end{pmatrix}' - A_{\infty}(\lambda) \begin{pmatrix} p \\ q \\ s \\ t \end{pmatrix}, \] (10)
where \( A_{\infty} \) is the piecewise spatially constant matrix
\[ A_{\infty}(\lambda) = \begin{cases} A_{-}(\lambda) & z < 0, \\ A_{+}(\lambda) & z \geq 0. \end{cases} \] (11)

3. Essential spectrum. The PDE given in (2) is autonomous, and so the only non-constant coefficients are due to the functions \( \hat{u}(z) \) and \( \hat{v}(z) \) in the reaction terms. These are heteroclinic orbits in phase space (connecting \( e_+ = (1 - \alpha \mu, 0) \) and \( e_- = (0, 1 - \frac{s_h}{s}) \)) which decay exponentially as \( z \to \pm \infty \) as shown in Section 5. This shows that \( L \) is exponentially asymptotic. From Kapitula & Promislow [12, Theorem 3.1.11] it follows that \( L \) is a relatively compact perturbation of the asymptotic operator \( L_{\infty} \), defined as the limit of \( L \) as \( z \to \pm \infty \) and equivalent to
the operator $T_\infty(0)$. Then by Weyl’s Essential Spectrum Theorem, we have that \( \sigma_{\text{ess}}(\mathcal{L}) = \sigma_{\text{ess}}(\mathcal{L}_\infty) \), or equivalently \( \sigma_{\text{ess}}(T) = \sigma_{\text{ess}}(T_\infty) \) [12, Theorem 2.2.6].

A crucial concept behind the spectrum of an operator is the existence of an exponential dichotomy. Essentially, this states that each solution to (6) decays exponentially either in forward or backward \( z \). For spatially constant matrices, the existence of an exponential dichotomy simply means that the matrix is hyperbolic. We define the Morse index of a constant matrix \( A \) to be the dimension of the unstable subspace associated with \( A \), and let \( i_\pm(\lambda) \) denote the Morse indices of the asymptotic matrices \( A_\pm \), given by Eq. (8) and Eq. (9). It can be shown that for \( \lambda \in \mathbb{C} \) such that \( T_\infty \) is Fredholm, we have \( \text{ind}(T_\infty - \lambda) = i_-(\lambda) - i_+(\lambda) \) [12, Lemma 3.1.10]. Thus, we can characterise the essential spectrum of \( \mathcal{L}_\infty \) as

\[
\sigma_{\text{ess}}(\mathcal{L}_\infty) = \{ \lambda \in \mathbb{C} \mid i_-(\lambda) \neq i_+(\lambda) \} \cup \{ \lambda \in \mathbb{C} \mid \dim \mathbb{E}^c(A_\pm(\lambda)) \neq 0 \},
\]

where \( \mathbb{E}^c \) denotes the center subspace associated with the asymptotic linearised system.

The spatial eigenvalues of \( A_-(\lambda) \) and \( A_+(\lambda) \) are respectively given by

\[
\eta_- = \frac{1}{2} \left( -c - \sqrt{c^2 + 4(1 + \lambda - \alpha \mu)} \right), \quad \frac{1}{2} \left( -c + \sqrt{c^2 + 4(\lambda + \mu(1 - \alpha F(1 - s_h)))} \right)
\]

and

\[
\eta_+ = \frac{1}{2} \left( -c - \sqrt{c^2 + 4(F + \lambda - \mu)} \right), \quad \frac{1}{2} \left( -c + \sqrt{c^2 + 4} \left( \lambda + \mu \left( \alpha - \frac{1}{F} \right) \right) \right).
\]

These spatial eigenvalues are non-hyperbolic when \( \eta_\pm = ik \). Substituting this into Eq. (13) and (14) respectively yields the dispersion relations

\[
\lambda_{\pm}^{1,2}(k) = -1 + \alpha \mu - k^2 + ick, \quad -\mu(1 - \alpha F(1 - s_h)) - k^2 + ick,
\]

and

\[
\lambda_{\pm}^{1,2}(k) = -F + \mu - k^2 + ick, \quad \mu \left( \frac{1}{F} - \alpha \right) - k^2 + ick.
\]

These form four parabolas in the complex plane parametrised by \( k \). For \( \lambda \) in between the region bounded by \( \lambda_{\pm}^{1,2}(k) \), \( A_-(\lambda) \) has three stable eigenvalues and one unstable eigenvalue; to the left of the region \( A_-(\lambda) \) has four stable eigenvalues and to the right of the region \( A_-(\lambda) \) has two stable and two unstable eigenvalues. This is also true for \( \lambda_{\pm}^{1,2}(k) \) and \( A_+(\lambda) \). Thus the essential spectrum is given by the region bounded between \( \lambda_{1}^- \) and \( \lambda_{1}^+ \), and also between \( \lambda_{2}^- \) and \( \lambda_{2}^+ \); this is shown in Figure 1.

It will be convenient for us later on to know the location of the so-called absolute spectrum. The absolute spectrum is not spectrum per se, but its location characterises the breakdown of the analytic continuation (in terms of the spectral parameter \( \lambda \)) of the stable and unstable eigenspaces of the matrices \( A_\pm(\lambda) \). It thus follows that the absolute spectrum coincides with a branch cut of the Evans function [12, Section 3.2]. For the case at hand, the absolute spectrum can be defined [20] as the set in the complex plane where a pair of the eigenvalues of \( A_+(\lambda) \) have equal real parts. This is the set

\[
\left\{ \lambda \in \mathbb{R} \mid \lambda \leq \mu \left( \frac{1}{F} - \alpha \right) - \frac{c^2}{4} \right\}.
\]
Figure 1. The essential spectrum of $L$ is given by $\lambda$ in the shaded regions. The blue dashed and solid lines represent $\lambda_{-1}^{1,2}$ and $\lambda_{+1}^{1,2}$ respectively. The red line indicates the absolute spectrum given by Eq. (17) and the red dot at the origin represents an eigenvalue. Note that these are not drawn to scale for visualisation purposes.

We note that from Eq. (17), (15) and (16), the continuous and absolute spectrum are always bounded to the left-half plane for biologically relevant parameter constraints $F > 1, \mu > 0, s_h > 0$ and $\alpha > 1$.

4. **Point spectrum.** The existence of a travelling wave solution implies a heteroclinic connection in (4) between the equilibria $e_- = (1 - \alpha \mu, 0)$ and $e_+ = (0, 1 - \frac{\mu}{F})$. We denote the unstable subspace of the matrix $A_-$ by $U_-$ and the stable subspace of the matrix $A_+$ by $S_+$. To the right of the essential spectrum, we have that the dimension of $U_-$, which we denote by $k$, and dimension of $S_+$ sum to 4, the dimension of the entire phase space. For our case, $k = 2$.

The unstable eigenvalues of $A_-$ are given by

$$
\eta_{-1,2} = \frac{1}{2} \left( -c + \sqrt{c^2 + 4(1 + \lambda - \alpha \mu)} \right), \quad \frac{1}{2} \left( -c - \sqrt{c^2 + 4(\lambda + \mu(1 - \alpha F(1 - s_h)))} \right)
$$

and the stable eigenvalues of $A_+$ are given by

$$
\eta_{+1,2} = \frac{1}{2} \left( -c - \sqrt{c^2 + 4(F + \lambda - \mu)} \right), \quad \frac{1}{2} \left( -c + \sqrt{c^2 + 4(\lambda + \mu(\alpha - \frac{1}{F}))} \right),
$$

(18)
where we have $\eta_1^+ > \eta_2^- > 0$ and $\eta_1^- < \eta_2^+ < 0$. We denote $\zeta_{1,2}^-$ and $\zeta_{1,2}^+$ as the eigenvectors corresponding to $\eta_{1,2}$ and $\eta_{1,2}^+$ respectively.

We initialise Eq. (6) at $z = -\infty$ with $\zeta_1^-$, $\zeta_2^-$ and at $z = \infty$ with $\zeta_1^+$, $\zeta_2^+$, and solve the system towards a matching point, which we pick to be $z = 0$. We denote the solutions of the former by $w_1^-(0, \lambda)$, $w_2^-(0, \lambda)$ and the latter by $w_1^+(0, \lambda)$, $w_2^+(0, \lambda)$, where $w_i^-(z, \lambda)$ satisfy

$$
\begin{align*}
\frac{d}{dz}w_i^-(z, \lambda) &= A(z, \lambda)w_i^-(z, \lambda), \\
w_i^-(z, \lambda) &\sim \exp(\eta_i^-z)\zeta_i^- \quad \text{for } z \ll 0
\end{align*}
$$

and $w_i^+(z, \lambda)$ satisfy

$$
\begin{align*}
\frac{d}{dz}w_i^+(z, \lambda) &= A(z, \lambda)w_i^+(z, \lambda), \\
w_i^+(z, \lambda) &\sim \exp(\eta_i^+z)\zeta_i^+ \quad \text{for } z \gg 0.
\end{align*}
$$

The Evans function is defined by

$$D(\lambda) = \det \left[w_1^-(0, \lambda), w_2^-(0, \lambda), w_1^+(0, \lambda), w_2^+(0, \lambda)\right],$$

which has the property that $D(\lambda) = 0$ if and only if $\lambda$ is in the point spectrum of the operator $L$. Roots of the Evans function correspond to solutions of the boundary value problem defined by Eq. (6), which decay appropriately as $z \to \pm \infty$.

4.1. Compound matrix method. The Evans function is numerically difficult to compute due to the stiffness of the problem stemming from the difficulty of resolving different modes of growth and decay. For example, since we have that $\eta_1^+ > \eta_2^-$, any numerical errors occurring when solving for $w_2^-(0, \lambda)$ will grow at a rate proportionate to $\exp(\eta_1^-z)$. Thus, although the solutions $w_1^-(z, \lambda)$, $w_2^-(z, \lambda)$ are linearly independent at $z = -\infty$, they quickly become numerically linearly dependent. Several methods have been proposed to overcome this issue such as the method of continuous orthogonalisation, the compound matrix method, Magnus methods and Grassmanian spectral shooting [6, 7, 18, 19, 14]. Following Allen & Bridges [1], we employ the compound matrix method which converts the problem into the six-dimensional wedge product space $\Lambda^2(\mathbb{C}^4)$, with basis $B = \{e_1 \wedge e_2, e_1 \wedge e_3, e_1 \wedge e_4, e_2 \wedge e_3, e_2 \wedge e_4, e_3 \wedge e_4\}$, where $\{e_1, e_2, e_3, e_4\}$ is the standard basis for $\mathbb{C}^4$. The numerical advantage of this approach is that the evolution of $w_1^-$, $w_2^-$ and $w_1^+, w_2^+$ are incorporated into a single trajectory given by $w_1^\pm \wedge w_2^\pm$ and $w_1^\pm \wedge w_2^\pm$ respectively. The coordinate vector of $w_1^- \wedge w_2^-$ relative to the basis $B$ is given by

$$[w_1^- \wedge w_2^-]_B := \phi^- = (\phi_1^-, \phi_2^-, \phi_3^-, \phi_4^-, \phi_5^-, \phi_6^-),$$

$$w_1^\pm = \begin{bmatrix} w_{1,1}^- \wedge w_{2,1}^- \\ w_{1,2}^- \wedge w_{2,2}^- \\ w_{1,3}^- \wedge w_{2,3}^- \end{bmatrix}, \quad w_2^\pm = \begin{bmatrix} w_{1,2}^- \wedge w_{2,1}^- \\ w_{1,3}^- \wedge w_{2,2}^- \\ w_{1,4}^- \wedge w_{2,3}^- \end{bmatrix},$$

$$\phi_1^- = \begin{bmatrix} w_{1,1}^- \wedge w_{2,1}^- \\ w_{1,2}^- \wedge w_{2,2}^- \\ w_{1,3}^- \wedge w_{2,3}^- \end{bmatrix}, \quad \phi_2^- = \begin{bmatrix} w_{1,1}^- \wedge w_{2,1}^- \\ w_{1,2}^- \wedge w_{2,2}^- \\ w_{1,3}^- \wedge w_{2,3}^- \end{bmatrix},$$

and the second subscript in $w_{i,j}$ denotes the $j$th element within the vector $w_i^-$. Similarly, $[w_1^\pm \wedge w_2^\pm]_B := \phi^+$ is given by Eq. (23) with $w_{i,j}^-$ replaced by $w_{i,j}^+$. 


It can be shown (see Allen & Bridges [1]) that $\phi(z) = \phi^-(z), \phi^+(z)$ satisfy the equation
\[ \phi' = \tilde{A}(z, \lambda)\phi, \tag{24} \]
where $\tilde{A}$ is the induced matrix given by
\[
\tilde{A} = \begin{pmatrix}
A_{11} + A_{22} & A_{23} & A_{24} & -A_{13} & -A_{14} & 0 \\
0 & A_{11} + A_{33} & A_{34} & A_{12} & 0 & -A_{14} \\
A_{42} & A_{43} & A_{11} + A_{44} & 0 & A_{12} & A_{13} \\
0 & A_{21} & 0 & A_{22} + A_{33} & A_{34} & -A_{24} \\
-A_{41} & A_{31} & A_{43} & A_{22} + A_{44} & A_{23} & 0 \\
0 & -A_{41} & A_{31} & A_{32} & A_{33} + A_{44} & 0
\end{pmatrix},
\tag{25}
\]
with $A_{ij}$ given by Eq. (7).

We initialise the problem at $z = -\infty$ with $\phi^-(-\infty)$ and at $z = \infty$ with $\phi^+(\infty)$ and solve towards the matching point $z = 0$. The Evans function is then defined to be
\[
D(\lambda) = w_1^- \wedge w_2^- \wedge w_1^+ \wedge w_2^+, \tag{26}
\]
\[
= \phi_0^- \phi_0^+ + \phi_1^- \phi_1^+ + \phi_2^- \phi_2^+ + \phi_3^- \phi_3^+ + \phi_4^- \phi_4^+ + \phi_5^- \phi_5^+.
\]
For numerical stability, we scale the solution according to its exponential growth and decay rates by letting
\[
\begin{align*}
\phi^- (z) &= \psi^- (z) e^{-(\eta_1^- + \eta_2^-)z}, \\
\phi^+ (z) &= \psi^+ (z) e^{-(\eta_1^+ + \eta_2^+)z},
\end{align*}
\tag{27}
\]
which leads to
\[
\begin{align*}
\frac{d\psi^-(z)}{dz} &= (\tilde{A} - (\eta_1^- + \eta_2^-)I)\psi^-(z) \quad \text{for} \quad z < 0, \\
\frac{d\psi^+(z)}{dz} &= (\tilde{A} - (\eta_1^+ + \eta_2^+)I)\psi^+(z) \quad \text{for} \quad z > 0,
\end{align*}
\tag{28}
\]
where the Evans function is equivalent to Eq. (26) except with $\phi$ replaced with $\psi$.

Since the Evans function is analytic to the right of the essential spectrum, we have via the Argument Principle that
\[
\frac{1}{2\pi i} \oint_C \frac{D'(\lambda)}{D(\lambda)} \, d\lambda = N, \tag{29}
\]
where $N$ is the number of zeroes in the interior of the region enclosed by $C$.

To check for eigenvalues of $\mathcal{L}$ with positive real part, we set up a closed semicircle contour $C$ excluding the origin, as shown below in Figure 2. We let $r_s$ and $r_b$ denote the radius of the smaller and larger circular arc respectively.

We compute the image of $C$ under $D(\lambda)$, which we denote as $D[C]$, and show $D[C]$ in Figure 3-4 for $(r_s, r_b) = (0.1, 10)$ and $(0.001, 500)$. By the Argument Principle, the number of times $D[C]$ winds around the origin is equal to the number of zeroes of $D(\lambda)$ in the interior of the region enclosed by $C$. Figures 3-5 show that the winding number of $D[C]$ around the origin is zero and thus there are no zeroes of the Evans function in the right-half of the complex plane.
Figure 2. The contour $C$.

Figure 3. The image of $C$ under $D(\lambda)$, where $r_s = 0.1$ and $r_b = 10$. 
Figure 4. The image of $C$ under $D(\lambda)$, where $r_s = 0.001$ and $r_b = 500$.

Figure 5. Plots (a) and (b) show the change in argument for $D[C]$ corresponding to Figures 3 and 4 respectively.

Figure 6b and 6a show the Evans function computed on the real line for $\lambda \in [0, 200]$ and $\lambda \in [-0.002607, 0.001]$ respectively. The only roots of the Evans function are at $\lambda = 0$ and $\lambda \approx -0.0026075$, the latter being the edge of the absolute spectrum, which we denote by $\gamma_A$. The former is due to translational invariance of the travelling wave solution $(\hat{u}, \hat{v})$, while the latter is due to $\gamma_A$ being a branch point of $D(\lambda)$. We note that the root at $\lambda = 0$ is simple, and because of translational invariance must persist throughout all nearby parameter regimes. We have already shown that the root of the Evans function at the branch point is in the left half plane and thus we conclude that no new eigenvalues can be introduced by perturbation.

Since system (1) has no spectrum in the right half plane, the solution given by $\hat{u}$ and $\hat{v}$ is spectrally stable. Moreover, as the linearised operator $L$ is an exponentially asymptotic operator, we have that it is also a sectorial operator [12, 5, see Chapter XVII, §6, Proposition 3 in the former and Example 4.1.8 in the latter]. Thus,
spectral stability of the travelling wave solution \( \hat{u} \) and \( \hat{v} \) also implies linear stability. We refer the reader to Section 5 for details on computing \( \hat{u} \) and \( \hat{v} \).

We note that for parameter values such that \( \gamma_A \) lies closer to the origin, for example \( \alpha = 1 \) (corresponding to \( \gamma_A \approx -0.001435 \)), the method described above fails to detect a zero for the Evans function evaluated at \( \gamma_A \), although the qualitative behaviour in the right-half plane remains the same. We show this in Figure 6.

5. **Wave profile.** To compute \( A(z, \lambda) \) explicitly at any \( z \) requires either a numerical or exact solution for \( \hat{u}(z) \) and \( \hat{v}(z) \) satisfying Eq. (1). We use MATLAB’s `bvp4c` solver to find a numerical solution corresponding to the case where the populations represented by \( \hat{u} \) and \( \hat{v} \) are in competition. The boundary conditions listed in (6) are not sufficient for `bvp4c` to find a unique solution. We note that since the linearisation of (2) as \( z \to \pm \infty \) is given by \( y' = A_\infty(0)y \), we have

\[
\begin{align*}
\begin{cases} 
    u' &\sim \eta_2^- (u - (1 - \alpha \mu)) \quad \text{as } z \to -\infty, \\
    v' &\sim \eta_2^- v
\end{cases}
\end{align*}
\]

\[
\begin{align*}
\begin{cases} 
    u' &\sim \eta_2^+ (u - \left(1 - \frac{\mu}{F}\right)) \quad \text{as } z \to \infty, \\
    v' &\sim \eta_2^+ v
\end{cases}
\end{align*}
\]

with \( \eta_2^\pm \) as defined in Eq. (18)-(19), but with \( \lambda = 0 \). To ensure uniqueness of the solution, we include this information on the derivatives in the boundary conditions by setting
\[
\begin{align*}
    u'(L) &= \eta^+_2 u(L), \\
    v'(L) &= \eta^+_2 \left( v(L) - \left(1 - \frac{\mu}{F} \right) \right), \\
    v'(-L) &= \eta^-_2 v(-L),
\end{align*}
\]
where \( L \) is a large number chosen to represent numerical infinity (chosen to be \( L = 200 \) in Figure 7). The numerical solution of the wave profiles \( \hat{u} \) and \( \hat{v} \) are shown in Figure 7.

**Figure 7.** Solution to the boundary value problem (6). Figure (a) shows the wave profile of \( \hat{u}(z) \) and \( \hat{v}(z) \), represented by solid and dashed lines respectively. Figure (b) shows the heteroclinic connection between equilibrium states \( e^- = (1 - \alpha \mu, 0) \) and \( e^+ = (0, 1 - \mu_F) \), where the solid and dashed line represent the solution in \( u - u' \) and \( v - v' \) space respectively.

5.1. **Local uniqueness of the wave speed.** To show local uniqueness of the wave speed, we use a dimension counting argument, similar to what is applied in [11].

The travelling wave \( (\hat{u}, \hat{v}) \), will be a \( t \)-independent solution of (2). Introducing the variables \( w := u_z \) and \( y := v_z \) we can write (2) out as a 4-dimensional first order system of equations:

\[
\begin{align*}
    u_z &= w, \\
    v_z &= y, \\
    w_z - cw - u(1 - S) - \alpha \mu u, \\
    y_z &= -cy - Fv(1 - S)(1 - s_h A) - \mu v.
\end{align*}
\]

We have that the wave around which we are linearising \( (\hat{u}, \hat{v}, \hat{w}, \hat{y}) \), will be a heteroclinic orbit in the nonlinear ODE (33), connecting the fixed points \( (1 - \alpha \mu, 0, 0, 0) \) and \( (0, 1 - \frac{\mu}{F}, 0, 0) \). For brevity we will denote these fixed points by \( \hat{e}_- \) and \( \hat{e}_+ \), respectively. We denote the unstable manifold of \( \hat{e}_- \) in the full nonlinear system (33) by \( W^u(\hat{e}_-) \), and the stable manifold of \( \hat{e}_+ \), by \( W^s(\hat{e}_+) \). We observe that the existence of a travelling wave for speed \( c_\ast \) implies at least a one dimensional intersection between the 2-dimensional manifolds \( W^u(\hat{e}_-) \) and \( W^s(\hat{e}_+) \) in the ambient 4-dimensional phase space.
We next extend (33) by the equation \( c_z = 0 \) to produce the 5-dimensional system

\[
\begin{align*}
  u_z &= w, \\
  v_z &= y, \\
  w_z - cw - u(1 - S) - \alpha \mu u, \\
  y_z &= -cy - F v(1 - S) (1 - s_h A) - \mu v, \\
  c_z &= 0.
\end{align*}
\]

(34)

Now we have that \((1 - \alpha \mu, 0, 0, 0, c)\) and \((0, 1 - \frac{\mu}{F}, 0, 0, c)\) will be fixed points in this extended system, for any value of \(c\). We choose a small interval around \(c^*\), say \(C_\varepsilon := (c^* - \varepsilon, c^* + \varepsilon)\), and we consider the 3 dimensional manifolds \(W^s(\tilde{e}_-) \times C_\varepsilon\), and \(W^s(\tilde{e}_+) \times C_\varepsilon\). These three dimensional manifolds will correspond to the centre-unstable, and centre-stable manifolds of the fixed points \((1 - \alpha \mu, 0, 0, 0, c)\), and \((0, 1 - \frac{\mu}{F}, 0, 0, c)\) in the larger system (34).

We assume that these manifolds intersect transversally in the the 5 dimensional phase space. Such an assumption is biologically realistic. Given that these manifolds intersect transversally, they must do so in a manifold of dimension 1. But we already have such an intersection, namely the heteroclinic connection for \(c = c^*\) between \((1 - \alpha \mu, 0, 0, 0, c^*)\) and \((0, 1 - \frac{\mu}{F}, 0, 0, c^*)\). This shows that the wave speed is at least locally unique. Figure 8 provides a schematic of this argument.

![Figure 8](image)

Figure 8. A diagram showing the uniqueness of \(c^*\) by dimension counting, where \(\tilde{e}_-, \tilde{e}_+\) denote the equilibria at the end points of the heteroclinic orbit in (33). In the illustration, \(W^u(\tilde{e}_-) \times C_\varepsilon\) are shown as 2-dimensional manifolds which intersect transversally in 3-dimensional space. The one dimensional intersection corresponds to the heteroclinic connection between \(\tilde{e}_-\) and \(\tilde{e}_+\) at \(c^*\).

6. Discussion. In this study we have shown the linear stability of a travelling wave solution to a model for Wolbachia spread. This is achieved by computing the essential, point and absolute spectrum of the linearised operator and showing the absence of spectrum in the right-half plane. We prove that the essential and absolute spectrum is bounded to the left-half plane for all biologically relevant parameter settings. Due to the numerical nature of locating the point spectrum, we
only show that there is no point spectrum in the right-half plane for fixed parameter values. In addition to the parameter values in Table 1, we show that this is true for other parameter values in Section 6. Our results suggest that although Wolbachia may be difficult to establish in a local area due to a CI-induced strong Allee effect in the growth dynamics, once it is established the spread of infection is a stable phenomenon.

In addition to our study being an investigation of Wolbachia spread dynamics, we present our study as an example of a dynamical systems approach to determining stability of travelling wave solutions in a system of PDEs. Models demonstrating such solutions are ubiquitous, particularly as mathematical modelling is becoming increasingly integrated with the scientific method. The dynamical systems tools we have used in this study can be applied to a wide variety of models currently used in mathematical biology; we believe that their application will improve understanding of the dynamics generated by a model and motivate research in more complicated biological models.

One of the key obstacles impeding the wider use of the tools in this study is the difficulty in computing the point spectrum via the Evans function. There are two key difficulties regarding this. Firstly, numerical methods for evaluating the Evans function sometimes fail, due to the evaluation requiring the solution to a stiff problem. Although in this study we have successfully used the compound matrix method, it is not guaranteed to work for all cases. Secondly, evaluating the Evans function requires the solution whose stability we are interested in. While obtaining such a solution is straightforward when the system of PDEs is exactly solvable, in many cases it is not exactly solvable and instead one must rely on a numerical solution obtained through solving a boundary value problem (see Section 5). Depending on the dimensionality of the problem and the dimensions of the stable and unstable subspaces at the equilibria, this can be a non-trivial numerical problem.

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**Appendix.** In this section we provide simulations for the wave profile and Evans function for parameter values differing to those used in the main text. For each set of parameter values, Figure (a) shows the wave profile of $\hat{u}(z)$ and $\hat{v}(z)$, represented by solid and dashed lines respectively. Figure (b) shows the heteroclinic connection between equilibrium states $e_-(1 - \alpha \mu, 0)$ and $e_+(0, 1 - \frac{\mu}{F})$, where the solid and dashed line represent the solution in $u-u'$ and $v-v'$ space respectively. Figures (c) and (d) show the image of $C$ (see Figure 2) under $D(\lambda)$, where $r_s = 0.001$ and $r_b = 500$. Figure (e) shows the change in argument for $D(C)$. The wave profiles for parameter sets one to four were produced with wavespeeds $c = 0.05133$, 0.04266, 0.06966 and 0.03133 respectively. These wavespeeds were obtained via numerically solving the PDE system (1) as in [4].
Table 2. Parameter set one

| Symbol | Definition                                  | Value |
|--------|---------------------------------------------|-------|
| $F$    | Relative fecundity of uninfected to infected females | 1.05  |
| $s_h$  | Probability of embryo death due to CI       | 0.7   |
| $\mu$  | Mortality rate                              | 0.03  |
| $\alpha$ | Reduction in lifespan due to infection    | 1.2   |

Table 3. Parameter set two

| Symbol | Definition                                  | Value |
|--------|---------------------------------------------|-------|
| $F$    | Relative fecundity of uninfected to infected females | 1.1   |
| $s_h$  | Probability of embryo death due to CI       | 0.9   |
| $\mu$  | Mortality rate                              | 0.02  |
| $\alpha$ | Reduction in lifespan due to infection    | 1.3   |

Table 4. Parameter set three

| Symbol | Definition                                  | Value |
|--------|---------------------------------------------|-------|
| $F$    | Relative fecundity of uninfected to infected females | 1.1   |
| $s_h$  | Probability of embryo death due to CI       | 0.8   |
| $\mu$  | Mortality rate                              | 0.05  |
| $\alpha$ | Reduction in lifespan due to infection    | 1.2   |

Table 5. Parameter set four

| Symbol | Definition                                  | Value |
|--------|---------------------------------------------|-------|
| $F$    | Relative fecundity of uninfected to infected females | 1.4   |
| $s_h$  | Probability of embryo death due to CI       | 0.9   |
| $\mu$  | Mortality rate                              | 0.1   |
| $\alpha$ | Reduction in lifespan due to infection    | 1.2   |
Figure 9. Simulations corresponding to parameter set one, listed in Table 2.
Figure 10. Simulations corresponding to parameter set two, listed in Table 3.
Figure 11. Simulations corresponding to parameter set three, listed in Table 4.
Figure 12. Simulations corresponding to parameter set four, listed in Table 5.