Applications of functional differential equations in pest control and sand ripple modelling

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This thesis proposes dynamical models for natural phenomena. The models are investigated analytically for stability criteria and numerically to determine their evolution over time. The first phenomenon we consider is the population dynamics of predator-prey systems, although in this case the predators are small parasites rather than large carnivores. The systems are modelled using delay differential equations, but many different approaches are used within this framework, mainly focusing on the different ways of modelling man’s effect on the parasites, whether this should be done discretely or continuously in time and whether it should occur only at particular points in space or time. Secondly we look at the small scale dynamics of granular media, in the form of aeolian sand ripples. Reaction-diffusion equations are used to model the evolution of these ripples over time. We are particularly interested in creating three dimensional models which incorporate the idea of a shadow zone. A shadow zone is an area of the sand bed which is shielded from the incoming wind by a higher altitude area of the bed.

In Chapter 1 we propose stage-structured population models for species the adult members of which are subject to culling, with a view to understanding the culling regimes that are likely to result in eradication of the species. A purely time-dependent model is proposed in which culling occurs at particular discrete times, not necessarily equally spaced. Then a reaction-diffusion model is proposed for a situation in which the adults can diffuse; in this model the culling is continuous in time but occurs only at particular discrete points in space. Such a model might be appropriate for pheromone trapping of insects. For both models conditions are obtained that are sufficient for species eradication.

In Chapter 2 we propose various stage-structured population models for blowfly strike with the aim of understanding the population dynamics that result in extinction.
tion of the blowflies or co-existence of the species. The models include a purely time dependent model, a distributed delay model and a reaction-diffusion model in which the mature blowflies are allowed to move about. We also provide results of numerical simulations of some of these models which show various aspects of the model, including initial conditions for the asymptotic stability of the co-existence steady state and the existence of a threshold value of trapping, above which extinction of the blowfly species will occur.

In Chapter 3 we propose models for blowfly strike that use discrete, rather than continuous diffusion in order to simulate the blowflies travelling between a number of farms that contain independent populations of sheep. Models are proposed for both a discrete and an infinite number of farms and conditions are found for extinction of the blowflies.

Chapters 5 and 6 of this thesis focus on developing three-dimensional models of aeolian sand ripples which incorporate fully three-dimensional shadowing of the sand bed. Linear stability analyses of these models analytically determine the preferred wavenumbers and growth rates of the ripples. Numerical simulations in Chapter 7 show the evolution of ripples from a perturbed flat bed and illustrate the differences due to the presence of our shadow zone. The effect of gusting during ripple evolution is also investigated showing the instability of the ripple pattern under large changes in the angle of impact and wind direction. It is also shown that a gradual change in wind direction over time will break up an ordered ripple pattern and eventually lead to a new pattern with the crests perpendicular to the final wind direction. Continuing changes in wind direction will lead to disorder or lower amplitude ripples depending on the frequency and magnitude of the gusts.
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1.1 Introduction

Many species are subjected to some form of culling. Often this is for reasons of pest control and the aim of culling in this case might well be the localised eradication of the pest. In other situations, culling may be more to do with management of numbers to protect habitats or other species but not necessarily complete eradication.

Unlike natural mortality which one might reasonably suppose to occur continuously, the mortality attributable to culling is often more likely to take place at certain times only. Sometimes these times may be prescribed by Law, as in the case of game birds and wildfowl shooting in the UK which takes place in prescribed seasons lasting a few months only. Also, where animals such as deer (the adults of which have no natural predators in the UK or Ireland) are culled for habitat protection, culling often occurs at certain times of the year only. In the UK, badgers, which are believed to spread tuberculosis to cattle, are subjected to culling by trapping and shooting, but again there are restrictions on the timing of the culls in an attempt to reduce the problem of badger cubs being orphaned and starving to death. Crop spraying as a way to control insect pests is also a method of control likely to be happening at certain discrete times (sometimes chosen to coincide with critical stages in the insects' development).

One might also envisage situations where some form of culling takes place continuously in time but only at discrete points in space. A good example would be the trapping system used in Australia to control the blowfly *Lucilia cuprina* which is a substantial nuisance to sheep farmers. Female flies lay their eggs in a sheep's fleece. The eggs hatch into larvae which feed on the sheep's damaged skin, creating a wound that can attract other flies. The larva and pupa stages may total around 14 days [27]. One approach to controlling the fly populations is by using pesticides, but this raises concerns regarding pesticide residue on the wool as well as environ-
mental and occupational health and safety. An alternative is to trap the blowflies using specially designed translucent buckets fixed to trees at about the height at which the blowflies work. Entrance cones allow blowflies to enter but not leave the buckets, which contain a chemical attractant which smells like the blowflies food sources - rotting fleece, carcasses, urine and faeces. Manufacturers of the buckets offer advice regarding where they should be placed. The second model of the present Chapter, which we study in Section 1.3, proposes a possible model for such trapping of blowflies continuously in time but only at discrete points in a one dimensional space. The traps in our model do not have to be equally spaced apart, and neither do they all have to be equally effective.

The use of impulsive differential equations as models of pest control seems to be a relatively undeveloped application area. Liu et al [41], motivated by the topic of pest control, proposed and studied a Lotka Volterra predator prey model with impulsive effects (but no delay). Their model exhibits complex dynamics including quasiperiodicity and chaos. Models of vaccination are another obvious application area (Hui and Chen [34]). However, impulsive differential equations, as a topic in its own right, has received some attention. See, for example, Wu [66] or the book by Gopalsamy [22]. There are a number of papers giving conditions for existence of periodic solutions and oscillation properties more generally, but this is not our interest in this thesis.

Section 1.2 of this Chapter analyses a purely time dependent model for culling that occurs at particular discrete times only, while Section 1.3 analyses a reaction diffusion model incorporating culling that is continuous in time but discrete in space.

## 1.2 Culling at discrete times

In this section we propose a model for a stage structured population with two stages: immature and mature, in which births and naturally occurring deaths occur continuously but culling or trapping occurs only at certain particular times, namely at times $t_j$ with $0 < t_1 < t_2 < \cdots < t_j < \cdots$ and $t_j \to \infty$ as $j \to \infty$. At the cull which occurs at time $t_j$ a proportion $b_j$ of the adult population is culled, causing a sharp decrease in the population and consequently a discontinuity in the evolution at time $t_j$.

Let $u(t, a)$ be the density of individuals at time $t$ of age $a$, and assume that an individual becomes mature on reaching the age $\tau$. We will assume that the total
number of mature adults $u_m(t)$, defined by

$$u_m(t) = \int_{\tau}^{\infty} u(t, a) \, da$$

obeys an evolution equation of the form

$$u'_m(t) = u(t, \tau) - d(u_m(t)) - \sum_{j=1}^{\infty} b_j u_m(t-j) \delta(t - t_j), \quad (1.2.1)$$

where $u(t, \tau)$ is those of age exactly $\tau$ and therefore represents adult recruitment; See after (1.2.6) for an explanation of the other terms. It will be assumed that the immatures are governed by the standard McKendrick-von Foerster model for an age-structured population, which can be found on Page 29 of Murray (1989) [46], namely

$$\frac{\partial u}{\partial t} + \frac{\partial u}{\partial a} = -\mu u, \quad t > 0, \quad 0 < a < \tau \quad (1.2.2)$$

with $\mu > 0$ constant, the initial condition

$$u(0, a) = u_0(a) \geq 0, \quad a \geq 0, \quad (1.2.3)$$

and we also assume that the birth rate $u(t, 0)$ is a function of the total number of adults, so that

$$u(t, 0) = b(u_m(t)). \quad (1.2.4)$$

The solution of (1.2.2) subject to (1.2.3) and (1.2.4) is

$$u(t, a) = \begin{cases} u_0(a - t) \exp(-\mu t), & t < a \\ b(u_m(t - a)) \exp(-\mu a), & t > a. \end{cases} \quad (1.2.5)$$

From this expression we see that if $t > \tau$ then

$$u(t, \tau) = \exp(-\mu \tau) b(u_m(t - \tau))$$

whereas if $t < \tau$ then $u(t, \tau) = u_0(\tau - t) \exp(-\mu t)$. Insertion of these expressions for $u(t, \tau)$ into (1.2.1) yields one nonautonomous evolution equation valid for times $t \in (0, \tau)$ and another autonomous delay equation valid for all times larger than $\tau$.

It is common practice in the literature on these types of models to consider only the latter equation, but to consider it for all times $t > 0$ with prescribed initial data on $[-\tau, 0]$. This is what we shall do in this thesis (model (1.2.6) below). This practice does raise certain issues related to initial data, an issue which is discussed in detail...
in Bocharov and Hadeler [10]. Strictly speaking, the initial data is prescribed at time \( t = 0 \) only and is just the function \( u_0(a) \). One should proceed by first solving equation (1.2.1) with \( u(t, \tau) = u_0(\tau - t) \exp(-\mu t) \) for \( t \) in the interval \((0, \tau)\), and then by solving the delay equation in (1.2.6) below for times \( t > \tau \). One can understand from this procedure that only certain initial data for problem (1.2.6) below is actually related to the original problem. However, since this thesis is concerned mainly with the linearised equations, we do not feel this will be too much of a concern.

Our model thus takes the form

\[
\begin{align*}
    u'_m(t) &= e^{-\mu t}b(u_m(t - \tau)) - d(u_m(t)) - \sum_{j=1}^{\infty} b_j u_m(t_j-) \delta(t - t_j), \quad t > 0 \\
    u_m(t) &= \phi(t) \geq 0 \quad \text{for} \quad t \in [-\tau, 0); \quad u_m(0) = u^0_m > 0,
\end{align*}
\]  

(1.2.6)

where \( \mu > 0 \) represents juvenile mortality, \( u_m(t) \) is the total number of adults at time \( t \), \( u_m(t_j-) \) is the population just before the impulsive cull at time \( t_j \), \( \tau \) is the maturation time, \( b_j \) is the proportion of the mature species trapped or culled at time \( t_j \) and \( \delta \) denotes the Dirac delta function. In this model \( b(u_m(t)) \) is a function representing the birth rate of the immature species, and \( d(u_m(t)) \) represents the natural death rate of the mature species. The \( e^{-\mu t}b(u_m(t - \tau)) \) term is the rate at which immature individuals become mature, known as the maturation rate. This term incorporates the delay \( \tau \) and is essentially the birth rate \( \tau \) time units ago, corrected to allow for juvenile mortality.

In the present section we will assume the following:

\[
\begin{align*}
    0 &< t_1 < t_2 < \cdots < t_j \to \infty \quad \text{as} \quad j \to \infty, \\
    b_j &\in [0, 1] \quad \text{for all} \quad j = 1, 2, 3, \ldots, \\
    b(0) &= 0, \quad b'(0) > 0, \quad b(u_m) > 0 \quad \forall u_m > 0, \\
    d(0) &= 0, \quad d \in C^1[0, \infty), \quad d(u_m) > 0 \quad \forall u_m > 0. 
\end{align*}
\]  

(1.2.7)

Note that if we integrate the delay equation in (1.2.6) from \( t_j^- \) to \( t_j^+ \), we obtain

\[
    u_m(t_j+) = u_m(t_j-) - b_j u_m(t_j^-).
\]

As a consequence, model (1.2.6) can be reformulated as

\[
\begin{align*}
    u'_m(t) &= e^{-\mu t}b(u_m(t - \tau)) - d(u_m(t)), \quad t \neq t_j \\
    u_m(t_j+) &= (1 - b_j) u_m(t_j-) \\
    u_m(t) &= \phi(t) \geq 0 \quad \text{for} \quad t \in [-\tau, 0); \quad u_m(0) = u^0_m > 0.
\end{align*}
\]  

(1.2.8)
The two formulations (1.2.6) and (1.2.8) of the model are both useful. For most of the analysis in this section we shall be concerned only with linearised versions of these models near the zero solution. The Laplace transform provides a powerful tool for the investigation of these linearised models, but one has to take careful note of the fact that the solution \( u_m(t) \) of either (1.2.6) or the alternative formulation (1.2.8) will, in general, be discontinuous at the times \( t_j \). The well known formula

\[
\mathcal{L}\{u'(t)\} = sU - u(0)
\] (1.2.9)

for the Laplace transform of the derivative of a function, assumes the function \( u(t) \) to be continuous for all \( t > 0 \). Here, \( U \) is the Laplace transform of \( u \) and \( s \) is the transform variable. For a function \( u(t) \) which is continuous except for discontinuous jumps at the times \( t = t_j \) the corresponding formula is

\[
\mathcal{L}\{u'(t)\} = sU - u(0) + \sum_{j=1}^{\infty} e^{-st_j} (u(t_j-) - u(t_j+)).
\] (1.2.10)

Due care needs to be taken on this issue, otherwise there is a possibility of the discontinuities being taken care of twice over, and if this happens incorrect results are produced by the analysis. Even though the solution of (1.2.6) will not be continuous, in the treatment of the linearised equation the Laplace transform of the derivative term needs to be calculated using the formula (1.2.9) which assumes continuity. The discontinuities in the solution are correctly furnished by the Laplace transform analysis because of the presence of the Dirac delta function in (1.2.6). The alternative approach would be to carry out a Laplace transform analysis of the linearisation of (1.2.8). In this case the derivative term has to be dealt with using (1.2.10). It can be shown that the two approaches yield the same equation for the transformed state variable and are therefore equivalent. It must be stressed, however, that one has to stick to one approach or the other. The use of (1.2.10) in a Laplace transform analysis of the linearised version of (1.2.6) produces incorrect results.

### 1.2.1 Positivity

Next, we shall show that solutions of (1.2.6) or (1.2.8) enjoy a positivity preserving property.

**Proposition 1** Assume (1.2.7) holds, then the solution \( u_m(t) \) of (1.2.6), or the alternative formulation (1.2.8), satisfies \( u_m(t) \geq 0 \) for all \( t > 0 \).
Proof: The proof is by the method of steps and starts by establishing positivity for \( t \in (0, \tau] \). First note that positivity (in fact, strict positivity) holds if all the \( b_j \) are zero. In this case,

\[
u'_m(t) \geq -d(u_m(t)) \quad \text{when} \quad t \in (0, \tau].
\]

By comparison, \( u_m(t) \geq \hat{u}_m(t) \) where \( \hat{u}_m(t) \) is the solution of

\[
\hat{u}_m'(t) = -d(\hat{u}_m(t)), \quad t \in (0, \tau],
\]

satisfying \( \hat{u}_m(0) = u_m^0 > 0 \). From the assumptions on the function \( d \) contained within (1.2.7), it follows by Taylor’s theorem that \( d(\hat{u}_m(t)) = \hat{u}_m(t)d'(\theta(t)) \) for some function \( \theta(t) \). Therefore the above differential equation for \( \hat{u}_m(t) \) has zero as one of its solutions and is also of such a form that, given initial data, we are assured of a unique solution. With \( \hat{u}_m(0) > 0 \) it follows that \( \hat{u}_m(t) > 0 \) for all \( t > 0 \) otherwise uniqueness is violated. Therefore \( u_m(t) > 0 \) for all \( t \in (0, \tau] \) in the case when the \( b_j \) are all zero. From the method of steps it is clear that if the \( b_j \) are zero then strict positivity of \( u_m(t) \) holds for all \( t > 0 \).

The case when some or all of the \( b_j \) are non-zero does not represent a significant complication. They are all in \([0, 1]\), by (1.2.7), and so by (1.2.8) the solution is always reset from a non-negative value to a non-negative value at one of the times \( t_j \) (note, however that if one or more of the \( b_j \) is 1 then the solution is reset to zero at the corresponding time \( t_j \), so strict positivity of solutions cannot be anticipated in this case). From what we have already shown the solution is certainly strictly positive before the first impulse time \( t_1 \), and at time \( t_1 \) is reset to some non-negative value.

An argument much like that described in the previous paragraph, but with initial time \( t_1 \) rather than 0, then assures us of the non-negativity of \( u_m(t) \) until the next time \( t_2 \) at which a resetting occurs, but then the argument just described applies again until the next time \( t_3 \) and so on. The proof of Proposition 1 is complete.

1.2.2 Criteria for extinction

Linearising (1.2.6) about the steady state \( u_m = 0 \) we get

\[
u'_m(t) = e^{-\tau b' (0)} u_m(t - \tau) - d'(0) u_m(t) - \sum_{j=1}^{\infty} b_j u_m(t_j -) \delta(t - t_j). \quad (1.2.11)
\]
Integrating from $t_j-$ to $t_j+$ yields the following alternative formulation for the linearised equation:

\[ u_m'(t) = e^{-\mu t}b'(0)u_m(t) - d'(0)u_m(t), \quad t \neq t_j \]

\[ u_m(t_j+) = (1 - b_j)u_m(t_j-). \]

**Remark:** Positivity preservation, Proposition 1, also holds for the linearised problem (1.2.12).

**The case when** $e^{-\mu t}b'(0) < d'(0)$

In this subsection we will prove linear stability of the zero solution of (1.2.8) under the condition $e^{-\mu t}b'(0) < d'(0)$. The ecological interpretation of this condition is that, at low densities, adult recruitment is insufficient to outweigh naturally occurring deaths. Our result confirms that, as we would anticipate, under these circumstances the population will still go extinct when impulsive trapping or culling is introduced whatever the intensity and however frequent or infrequent the culling occurs.

**Theorem 1.2.1** Let (1.2.7) hold and assume additionally that

\[ e^{-\mu t}b'(0) < d'(0). \]

Then the solution $u_m(t)$ of the linearised problem (1.2.12) satisfies $u_m(t) \to 0$ as $t \to \infty$.

**Proof.** Applying the Laplace transform:

\[ \mathcal{L}\{u(t)\} = \int_0^\infty u(t)e^{-st}dt \]

to (1.2.12), using formula (1.2.10) to take care of the anticipated discontinuities in the solution as explained earlier, and also noting that the Laplace transform of the delay term can be written as

\[ \mathcal{L}\{e^{-\mu t}b'(0)u_m(t - \tau)\} = e^{-\mu t}b'(0) \left( \int_{-\tau}^0 u_m(\eta)e^{-s(\eta + \tau)}d\eta + e^{-s\tau}U \right) \]

where $U = U(s)$ is the Laplace transform of $u_m(t)$, equation (1.2.12) becomes

\[ [s - e^{-\mu t}b'(0)e^{-st} + d'(0)]U = u_m(0) - \sum_{j=1}^\infty e^{-st_j}(u_m(t_j-) - u_m(t_j+)) + e^{-\mu t}b'(0)\int_{-\tau}^0 u_m(\eta)e^{-s(\eta + \tau)}d\eta. \]
Using the impulse condition from (1.2.12) to substitute in for $u_m(t_j+)$ we get

\[ [s - e^{-\mu t}b'(0)e^{-st} + d'(0)]U = u_m(0) + e^{-\mu t}b'(0) \int_{-\tau}^{0} u_m(\eta)e^{-s(\eta+\tau)}d\eta - \sum_{j=1}^{\infty} e^{-st}b_j u_m(t_j-). \]  

(1.2.14)

Now define $y(t)$ by

\[ y'(t) = e^{-\mu t}b'(0)y(t-\tau) - d'(0)y(t), \quad t > 0 \]  

(1.2.15)

\[ y(t) = 0 \quad \text{for} \quad t \in [-\tau, 0); \quad y(0) = 1, \]

the continuous analogy of equation (1.2.12) without impulses. It is easy to show (similarly to the proof of Proposition 1) that $y(t) > 0$ for all $t > 0$.

Applying the Laplace transform to (1.2.15), and letting $Y = Y(s) = \mathcal{L}\{y(t)\}$, gives

\[ sY - 1 = e^{-\mu t}b'(0) \left[ \int_{-\tau}^{0} y(\xi)e^{-s(\xi+\tau)}d\xi + e^{-st}Y \right] - d'(0)Y \]

so that, since $y(t) = 0$ for $t \in [-\tau, 0)$,

\[ Y = \frac{1}{s + d'(0) - e^{-\mu t}b'(0)e^{-st}} \]  

(1.2.16)

and so

\[ y(t) = \mathcal{L}^{-1}\left\{ \frac{1}{s + d'(0) - e^{-\mu t}b'(0)e^{-st}} \right\}. \]  

(1.2.17)

From this it is easy to see that $y(t) \to 0$ as $t \to \infty$. To deduce this conclusion it suffices (by the inversion formula for Laplace transforms) to show that all the poles of the function $Y$ (i.e. the zeros of the denominator of (1.2.16)) are strictly in the left half of the complex plane. For a contradiction, assume a zero $\hat{s}$ exists satisfying $\text{Re} \hat{s} \geq 0$. Then

\[ |\hat{s} + d'(0)| = e^{-\mu t}b'(0)|e^{-s\tau}| = e^{-\mu t}b'(0)e^{-\text{Re}\hat{s}} \leq e^{-\mu t}b'(0) \]

so that $\hat{s}$ lies in the closed disk in the complex plane centred at $-d'(0)$ and of radius $e^{-\mu t}b'(0)$. But condition (1.2.13) implies that this disk is entirely within the open left half of the complex plane, and this contradicts $\text{Re} \hat{s} \geq 0$. Thus $y(t) \to 0$ as $t \to \infty$. 

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The denominator of the right hand side of (1.2.16) appears on the left hand side of (1.2.14). Dividing by this quantity and taking inverse Laplace transforms gives

\[ u_m(t) = u_m(0)y(t) + \mathcal{L}^{-1} \left\{ \frac{e^{-\mu t}b'(0) \int_0^0 u_m(\eta)e^{-s(\eta+\tau)}d\eta}{s + d'(0) - e^{-\mu t}b'(0)e^{-s\tau}} \right\} \]

\[ - \sum_{j=1}^{\infty} b_j u_m(t_j - t) \mathcal{L}^{-1} \left\{ \frac{e^{-s t_j}}{s + d'(0) - e^{-\mu t}b'(0)e^{-s\tau}} \right\} \]

\[ = u_m(0)y(t) + \mathcal{L}^{-1} \left\{ \frac{e^{-\mu t}b'(0) \int_0^0 u_m(\eta)e^{-s(\eta+\tau)}d\eta}{s + d'(0) - e^{-\mu t}b'(0)e^{-s\tau}} \right\} \]

\[ - \sum_{j=1}^{\infty} b_j u_m(t_j - t) \int_0^t y(t - s)\delta(s - t_j)ds \]

\[ = u_m(0)y(t) + \mathcal{L}^{-1} \left\{ \frac{e^{-\mu t}b'(0) \int_0^0 u_m(\eta)e^{-s(\eta+\tau)}d\eta}{s + d'(0) - e^{-\mu t}b'(0)e^{-s\tau}} \right\} \]

\[ - \sum_{j=1}^{\infty} b_j u_m(t_j - t)H(t - t_j)y(t - t_j), \quad (1.2.18) \]

where \( H(t - t_j) \) is the Heaviside function. In this calculation we have used the convolution theorem for the Laplace transform.

Our intention is to deduce from this that \( u_m(t) \to 0 \) as \( t \to \infty \) under condition (1.2.13). We already know that \( y(t) \to 0 \) under this condition. The second term in the expression (1.2.18) for \( u_m(t) \) also tends to zero as \( t \to \infty \). This is because it is the inverse Laplace transform of a ratio in which the numerator is an analytic function of \( s \) while the denominator has all of its zeros in \( \text{Re}\ s < 0 \) as has already been shown.

From non-negativity of \( u_m(t) \) for \( t > 0 \), and strict positivity of \( y(t) \), we know the sign of the last term in the expression (1.2.18) for \( u_m(t) \), and so we can write

\[ 0 \leq u_m(t) \leq u_m(0)y(t) + \mathcal{L}^{-1} \left\{ \frac{e^{-\mu t}b'(0) \int_0^0 u_m(\eta)e^{-s(\eta+\tau)}d\eta}{s + d'(0) - e^{-\mu t}b'(0)e^{-s\tau}} \right\} . \]

Hence \( u_m(t) \to 0 \) as \( t \to \infty \).

**The case when \( e^{-\mu t}b'(0) > d'(0) \)**

In this subsection we shall show that the zero solution of (1.2.8) can be asymptotically linearly stable (i.e. the population will be driven to extinction) in the case when adult recruitment outweighs deaths at low densities, if culling occurs in sufficient measure and with sufficient frequency in the sense to be described below.
Note that from the alternative formulation of the original model (1.2.8) if the \( b_i's \) are close to 1 then it means that aggressive culling is taking place and a large majority of the mature species population is wiped out at each time \( t_j \). We can also see that even if the \( b_i's \) were exactly equal to 1 and all the mature species were wiped out, this would not necessarily cause extinction, because immatures conceived at a previous time may mature at a later date. However it is reasonable to speculate that if the \( b_i's \) are close enough to 1 and culling takes place sufficiently frequently in some sense, then the population would be driven to extinction.

For reasons that will become clear later, we need to understand the properties of the function \( \phi(t) \) defined by

\[
\phi'(t) = e^{-\mu t} b'(0) \phi(t - \tau) - e^{-\mu t} b'(0) \phi(t) \\
\phi(t) = 0, \quad t \in [-\tau, 0), \quad \phi(0) = 1.
\]

**Proposition 2**

The solution \( \phi(t) \) of (1.2.19) is strictly positive for all \( t > 0 \) and satisfies

\[
\lim_{t \to \infty} \phi(t) = \frac{1}{1 + e^{-\mu t} b'(0) \tau}.
\]

Consequently, the quantity \( \phi^* := \inf_{t \geq 0} \phi(t) \) satisfies \( \phi^* > 0 \).

**Proof.** Strict positivity of \( \phi(t) \) for \( t > 0 \) follows from arguments similar to those in the first part of the proof of Proposition 1. Strict positivity together with (1.2.20) immediately yields the last statement in the Proposition, that \( \phi^* > 0 \). Therefore, it remains to prove only (1.2.20). Taking the Laplace transform of (1.2.19) and letting \( \Phi = \Phi(s) \) denote the Laplace transform of \( \phi \), we obtain

\[
s \Phi - 1 = e^{-\mu t} b'(0) \left[ \int_{-\tau}^{0} \phi(\xi) e^{-s(\xi + \tau)} d\xi + e^{-st} \Phi \right] - e^{-\mu t} b'(0) \Phi.
\]

Since \( \phi(t) = 0 \) for \( t \in [-\tau, 0) \),

\[
\Phi = \frac{1}{s - e^{-\mu t} b'(0) \tau + e^{-\mu t} b'(0)}
\]

so that

\[
\phi(t) = \mathcal{L}^{-1} \left\{ \frac{1}{s - e^{-\mu t} b'(0) \tau + e^{-\mu t} b'(0)} \right\} \\
= \frac{1}{2\pi i} \int_{\sigma - i\infty}^{\sigma + i\infty} e^{st} ds \\
= \frac{e^{\tau t}}{2\pi i} \int_{\sigma - i\infty}^{\sigma + i\infty} \frac{e^{st}}{s - e^{-\mu t} b'(0) \tau + e^{-\mu t} b'(0)}
\]
in which the integral is the standard Bromwich integral. The quantity \( \sigma \) in (1.2.21) can be taken as any real number which strictly exceeds the supremum of the real parts of the zeros of the denominator in the integrand. In this case we can take any real \( \sigma > 0 \) as we now explain. Evaluation of the integral (1.2.21) will be via Cauchy's residue theorem, which requires us to identify the poles of the integrand, i.e. the zeros of its denominator. By inspection, one of these is clearly \( s = 0 \). We claim that the equation \( s - e^{-\sigma t}e^{-\mu t}b'(0) + e^{-\mu t}b'(0) = 0 \) has no roots satisfying \( \text{Re} s \geq 0 \) other than the root \( s = 0 \). Indeed, if \( \text{Re} s \geq 0 \), then

\[
|s + e^{-\mu t}b'(0)| = e^{-\mu t}b'(0)|e^{-\sigma t}| \leq e^{-\mu t}b'(0)e^{-\text{Re} s} \leq e^{-\mu t}b'(0)
\]

so that \( s \) is in the closed disk in \( \mathbb{C} \) with centre \(-e^{-\mu t}b'(0)\) and radius \( e^{-\mu t}b'(0)\). But this disk contains no points \( s \) with \( \text{Re} s \geq 0 \) apart from \( s = 0 \). Therefore the poles of the integrand in (1.2.21) consist of the pole at \( s = 0 \) (which is easily checked to be simple) together with the remaining zeros of the integrand's denominator, all of which satisfy \( \text{Re} s < 0 \). Evaluation of (1.2.21) by Cauchy's residue theorem gives an expression of the form

\[
\phi(t) = \sum \text{res} \left\{ \frac{e^{st}}{s - e^{-\sigma t}e^{-\mu t}b'(0) + e^{-\mu t}b'(0)}, \ s \in \mathcal{P} \right\}, \quad (1.2.22)
\]

where \( \mathcal{P} \) is the set of all roots of \( s - e^{-\sigma t}e^{-\mu t}b'(0) + e^{-\mu t}b'(0) = 0 \). But we know that the roots of this equation are \( s = 0 \) together with other roots, all of which satisfy \( \text{Re} s < 0 \). It is well known that for a function \( f(s) \) of the form \( f(s) = h(s)/k(s) \) with \( h(s) \) and \( k(s) \) analytic functions of \( s \), \( h(a) \neq 0 \), \( k(a) = 0 \) and \( k'(a) \neq 0 \), that the residue of \( f(s) \) at the simple pole \( s = a \) is given by \( \text{res} \{ f(s); \ s = a \} = h(a)/k'(a) \). Applying this formula to the calculation of the residue at any \( s \in \mathcal{P} \) with \( \text{Re} s < 0 \) yields that the residue is an exponentially decaying function of \( t \). Therefore

\[
\phi(t) = \text{res} \left\{ \frac{e^{st}}{s - e^{-\sigma t}e^{-\mu t}b'(0) + e^{-\mu t}b'(0)}, \ s = 0 \right\} + \text{exponentially decaying terms in } t \\
= \frac{1}{1 + e^{-\mu t}b'(0)\tau} + \text{exponentially decaying terms in } t
\]

and so (1.2.20) holds. The proof of Proposition 2 is complete.

Remark: Although we are assured of the strict positivity of the quantity \( \phi^* \) defined in the statement of Proposition 2 we point out that \( \phi^* \) is not necessarily equal to the limit in (1.2.20). It can be shown that the convergence to the limit in (1.2.20) will be non-monotone if \( e^{-\mu t}b'(0)\tau \) is sufficiently large,
Our next main result, Theorem 1.2.2 below, presents some conditions under which extinction of the population is predicted. Even though the problem under consideration is the linearised problem (1.2.12), analysis thereof is difficult. Our method of analysis involves the use of the Euler–Maclaurin summation formula [1], a technique for converting sums to integrals or vice versa. We can only retain certain terms in the use of this formula (those that do not involve the Bernoulli numbers) and as the result the following theorem must be interpreted in an approximate sense. Nevertheless, it is quite insightful as we will discuss later. We draw the readers attention to the function $t(\cdot)$ referred to in the statement of Theorem 1.2.2 below. This function is not uniquely defined, but a sensible choice would be one that is piecewise linear but smoothed at the integers so as to be differentiable. The function $t(\cdot)$ tells us something about the spacing of the impulse times $t_i$ (for example if its derivative $t'$ is very small then the impulse times are rather close together; under these circumstances we might expect that extinction would be more likely and this is what Theorem 1.2.2 indeed predicts). Condition (1.2.23) in the theorem essentially states the impulses must occur sufficiently close together in some sense depending on the proportion of the species that is removed at each impulse and also, not surprisingly, on the per capita natural death rate and adult recruitment rate at low densities.

**Theorem 1.2.2** Let (1.2.7) hold, and let $t(\xi) : [0, \infty) \rightarrow [0, \infty)$ be a strictly monotonically increasing differentiable function with the property that $t(i) = t_i$, $i = 1, 2, 3, \ldots$ and $t(0) = 0$. If

$$e^{-\mu t}b'(0) > d'(0)$$

and

$$\inf_{j \in \mathbb{N}} \{ b_j - (e^{-\mu t}b'(0) - d'(0))t'(j) \} > 0, \quad (1.2.23)$$

then the solution $u_m(t)$ of the linearised problem (1.2.12) satisfies $u_m(t) \rightarrow 0$ as $t \rightarrow \infty$ according to an analysis based on the Euler-Maclaurin approximation (1.2.29) below.

**Proof.** It will be convenient to rewrite (1.2.12) in the form

$$u_m'(t) = e^{-\mu t}b'(0)u_m(t - \tau) - e^{-\mu t}b'(0)u_m(t) + (e^{-\mu t}b'(0) - d'(0))u_m(t), \quad t \neq t_j$$

$$u_m(t_j+) = (1 - b_j)u_m(t_j-). \quad (1.2.24)$$
Taking Laplace transforms of (1.2.24) and using formula (1.2.10) gives

\[ (s - e^{-\mu t}e^{-st}b'(0) + e^{-\mu t}b'(0))U = u_m(0) + e^{-\mu t}e^{-\mu t}b'(0) \int_{-\infty}^{0} e^{-\mu \xi} u_m(\xi) \, d\xi \]
\[ + (e^{-\mu t}b'(0) - d'(0))U - \sum_{j=1}^{\infty} b_j u_m(t_j) e^{-st_j}. \]  

(1.2.25)

Using (1.2.21) and taking inverse Laplace transforms of (1.2.25) we get

\[ u_m(t) = f(t) + \mathcal{L}^{-1} \left\{ \frac{(e^{-\mu t}b'(0) - d'(0))U}{s - e^{-\mu t}e^{-st}b'(0) + e^{-\mu t}b'(0)} \right\} \]
\[ - \sum_{j=1}^{\infty} b_j u_m(t_j -) \mathcal{L}^{-1} \left\{ \frac{e^{-st_j}}{s - e^{-\mu t}e^{-st}b'(0) + e^{-\mu t}b'(0)} \right\} \]
\[ = f(t) + (e^{-\mu t}b'(0) - d'(0)) \int_{0}^{t} \phi(t - s) u_m(s) \, ds \]
\[ - \sum_{j=1}^{\infty} b_j u_m(t_j -) \int_{0}^{t} \phi(t - s) \delta(s - t_j) \, ds \]
\[ = f(t) + (e^{-\mu t}b'(0) - d'(0)) \int_{0}^{t} \phi(t - s) u_m(s) \, ds \]
\[ - \sum_{j=1}^{\infty} b_j u_m(t_j -) \phi(t - t_j) H(t - t_j) \]  

(1.2.26)

where we recall that \( \phi(t) \) is defined by (1.2.19), and where

\[ f(t) = u_m(0) \phi(t) + \mathcal{L}^{-1} \left\{ e^{-\mu t}b'(0)e^{-st} \int_{0}^{0} e^{-\mu \xi} u_m(\xi) \, d\xi \right\} \]  

(1.2.27)

If we substitute \( t = t_i - \) into (1.2.26) and let

\[ u_i = u_m(t_i -), \quad f_i = f(t_i -) \]

we obtain, noting that \( \phi(t) \) is continuous,

\[ u_i = f_i + (e^{-\mu t}b'(0) - d'(0)) \int_{0}^{t_i} \phi(t_i - s) u_m(s) \, ds - \sum_{j=1}^{i-1} b_j u_j \phi(t_i - t_j) \]
\[ = f_i + (e^{-\mu t}b'(0) - d'(0)) \int_{0}^{t_i} \phi(t_i - t(\xi)) u_m(t(\xi)) t'(\xi) \, d\xi - \sum_{j=1}^{i-1} b_j u_j \phi(t_i - t_j), \]  

(1.2.28)

having made the substitution \( s = t(\xi) \) in the integral term.
We now convert the integral in the above expression into a sum. This will be achieved by using the Euler-Maclaurin summation formula, one version of which is

\[
\int_0^n h(k) \, dk = \sum_{k=1}^{n-1} h_k + \frac{h(0) + h(n)}{2} - \int_0^n h'(k) \left( k - [k] - \frac{1}{2} \right) \, dk,
\]

where \( h_k = h(k) \) and \([k]\) is the greatest integer \( \leq k \). This formula can be found, after some adaptation of notation, in the book by Apostol [8]. In our analysis we shall drop the integral term involving \( h'(k) \) in the right hand side of (1.2.29), but we shall discuss later the situation in which the resulting approximate formula might fail.

Applying the truncated form of (1.2.29) to (1.2.28), we get

\[
u_t = f_i + (e^{-\mu t} b'(0) - d'(0)) \left( \sum_{j=1}^{i-1} \phi(t_i - t_j) u_j + \frac{\phi(t_i) u_m(t_0) t'(0) + \phi(t_i) u_j t'(0)}{2} \right) - \sum_{j=1}^{i-1} b_j u_j \phi(t_i - t_j).
\]

We now claim that the function \( f(t) \) defined by (1.2.27) above tends to a strictly positive limit \( C > 0 \) as \( t \to \infty \) (so that also \( f_i \to C \) as \( i \to \infty \)). By Proposition 2, \( \phi(t) \) certainly approaches a strictly positive limit. The second term in the expression for \( f(t) \) does so as well, as can be shown similarly to a contour integral argument discussed earlier where the singularities were the same: a simple pole at the origin and various other poles all with strictly negative real part. By the inversion formula for Laplace transforms and Cauchy's residue theorem,

\[
\mathcal{L}^{-1} \left\{ \frac{e^{-\mu t} b'(0) e^{-st} \int_{-\tau}^{0} e^{-s\xi} u_m(\xi) \, d\xi}{s - e^{-\tau} e^{-st} b'(0) + e^{-\mu} b'(0)} \right\} = \text{res} \left\{ \frac{e^{-\mu t} b'(0) e^{-st} \int_{-\tau}^{0} e^{-s\xi} u_m(\xi) \, d\xi}{s - e^{-\tau} e^{-st} b'(0) + e^{-\mu} b'(0)}, \, s = 0 \right\} + \text{exponentially decreasing terms in } t.
\]

Thus

\[
\lim_{t \to \infty} \mathcal{L}^{-1} \left\{ \frac{e^{-\mu t} b'(0) e^{-st} \int_{-\tau}^{0} e^{-s\xi} u_m(\xi) \, d\xi}{s - e^{-\tau} e^{-st} b'(0) + e^{-\mu} b'(0)} \right\} = \frac{e^{-\mu t} b'(0) \int_{-\tau}^{0} u_m(\xi) \, d\xi}{1 + \tau e^{-\mu} b'(0)}.
\]

Hence \( f(t) \) tends to a limit as \( t \to \infty \). Writing (1.2.30) a different way, and recalling
that \( \phi(0) = 1, \)

\[
   u_i \left( 1 - \left( e^{-\mu t} b'(0) - d'(0) \right) t'(i) \right)
   \]

\[
   = \sum_{j=1}^{i-1} u_j \phi(t_i - t_j) \left[ (e^{-\mu t} b'(0) - d'(0)) t'(j) - b_j \right]

   + f_i + \frac{1}{2} (e^{-\mu t} b'(0) - d'(0)) \phi(t_i) u_m(0) t'(0).
\]

Since \( f_i \) and \( \phi(t_i) \) both approach limits as \( i \to \infty \), there exists \( C^* \) such that the totality of the last two terms in the above expression is bounded above by \( C^* \) for all \( i \). Using this fact, and also adding \( \lambda \sum_{j=1}^{i-1} u_j \) to both sides,

\[
   u_i \left( 1 - \left( e^{-\mu t} b'(0) - d'(0) \right) t'(i) \right)
   + \lambda \sum_{j=1}^{i-1} u_j

   \leq \sum_{j=1}^{i-1} u_j \left\{ \lambda + \phi(t_i - t_j) \left[ (e^{-\mu t} b'(0) - d'(0)) t'(j) - b_j \right] \right\} + C^*,
\]

with \( \lambda > 0 \) to be chosen. Recall that \( \phi(t) \geq \phi^* > 0 \), where \( \phi^* \) is defined in the statement of Proposition 2, and note also that the hypotheses of the Theorem imply that \( (e^{-\mu t} b'(0) - d'(0)) t'(j) - b_j < 0 \) for each \( j \). Hence

\[
   \lambda + \phi(t_i - t_j) \left[ (e^{-\mu t} b'(0) - d'(0)) t'(j) - b_j \right] \leq \lambda + \phi^* \left[ (e^{-\mu t} b'(0) - d'(0)) t'(j) - b_j \right]
\]

which we should like to be negative for all \( j \). Therefore we choose any \( \lambda > 0 \) such that

\[
   \lambda \leq \phi^* \inf_{j \in \mathbb{N}} \left\{ b_j - (e^{-\mu t} b'(0) - d'(0)) t'(j) \right\},
\]

which is possible because the infimum is strictly positive by hypothesis. It is easy to see that \( \lambda \) chosen like this satisfies \( \lambda < 1 \). Thus with this choice of \( \lambda \) we have

\[
   u_i \left( 1 - \left( e^{-\mu t} b'(0) - d'(0) \right) t'(i) \right)
   + \lambda \sum_{j=1}^{i-1} u_j \leq C^*.
\]

Finally note that \( (e^{-\mu t} b'(0) - d'(0)) t'(i) < b_i \leq 1 \) for each \( i \). Hence

\[
   \frac{1}{2} u_i + \lambda \sum_{j=1}^{i-1} u_j \leq u_i \left( 1 - \left( e^{-\mu t} b'(0) - d'(0) \right) t'(i) \right)

   + \lambda \sum_{j=1}^{i-1} u_j \leq C^*.
\]

Since this holds for all \( i \), and since \( u_i \geq 0 \), we can deduce that \( \sum_{j=1}^{\infty} u_j < \infty \), which implies that \( u_i \to 0 \) as \( i \to \infty \). The proof is complete.
1.3 Culling at discrete points in space

Up to now we have examined a purely time dependent model in which the culling occurs at specific times only. The present section will examine a reaction-diffusion model for the situation in which the adults (but not the juveniles) can move around in a random way and where culling occurs continuously in time but only at specific points $x_j$ in a one dimensional infinite spatial domain $x \in (-\infty, \infty)$. The equation we will analyse is

\[
\frac{\partial u_m(x, t)}{\partial t} = D \frac{\partial^2 u_m(x, t)}{\partial x^2} + e^{-\mu \tau} b(u_m(x, t - \tau)) - d(u_m(x, t)) - \sum_{j=-\infty}^{\infty} B_j u_m(x_j, t) \delta(x - x_j),
\]

\[u_m(x, t) = \phi(x, t) \geq 0 \text{ for } (x, t) \in (-\infty, \infty) \times [-\tau, 0)
\]

with $\phi(\cdot, t) \in L^2$ for each $t \in [-\tau, 0]$ and $u_m(x, 0) \neq 0$.

Model (1.3.1) is only appropriate if the juvenile members do not diffuse. This is because we are using the same derivation for the adult recruitment term $e^{-\mu \tau} b(u_m(x, t - \tau))$ as was used to derive model (1.2.6). However if the juveniles diffuse then a diffusion term would have to be added to (1.2.2) with the consequence that the solution of the latter would no longer be (1.2.5). Thus, our model (1.3.1) is strictly only for the case when the adults diffuse. Fortunately, this assumption is quite realistic in many species: For example in many insect species the juveniles are larvae and move very little or not at all. Locust larvae attach themselves to tree roots and do not move at all, whereas adult locusts can move great distances. The blowfly \textit{Lucilia cuprina} larvae live in sheep and might move a little in the sense of being carried about by their host sheep within a farm, but it is only the adults that can move great distances and thereby transfer infestations from farm to farm.

The quantities $B_j$, $j = 0, \pm1, \pm2, \ldots$ in (1.3.1) have a somewhat different ecological interpretation to the corresponding quantities $b_j$ in model (1.2.6). The quantity $B_j$ is not the proportion removed at $x_j$ but rather is a measure of the culling effort at that location (as will become clear in the next paragraph) and can be any nonnegative number. It is reasonable to anticipate that if the $B_j$ are large then the population would become extinct if either the $x_j$ are sufficiently close together or the diffusivity $D$ is sufficiently large. This is because in the limiting case when the $B_j$ are all infinite, one can imagine that the problem effectively would decompose into
ininitely many uncoupled problems each consisting of the partial differential equation in (1.3.1) on the finite domain consisting of the interval between two adjacent culling locations, subject to homogeneous Dirichlet boundary conditions.

The positioning of the delta function in (1.3.1) is such that the solution \( u_m(x, t) \) will be continuous in \( x \) but its derivative \( \partial u_m / \partial x \) will not. If we integrate (1.3.1) from \( x_j^- \) to \( x_j^+ \) the result is

\[
D \left[ \left( \frac{\partial u_m}{\partial x} \right)_{x_j^+} - \left( \frac{\partial u_m}{\partial x} \right)_{x_j^-} \right] = B_j u_m(x_j, t) \tag{1.3.2}
\]

Keeping in mind that the Laplacian representation for diffusion comes about from using the formula \( J = -D \partial u_m / \partial x \) for the flux \( J(x, t) \) (defined as the net rate at which individuals cross \( x \) in the positive \( x \) direction) then, if we imagine the domain to be broken up into subdomains defined by the culling locations, equation (1.3.2) has the interpretation that individuals that leave the subdomain \([x_j, x_{j+1}]\) at \( x_j \) do so either by being culled at \( x_j \), or by entering the adjacent subdomain \([x_{j-1}, x_j]\). The culling effort at \( x_j \) is \( B_j \) and the culling yield at this location is \( B_j u_m(x_j, t) \) per unit time, i.e. proportional to the density at \( x_j \). This leads us to expect that (1.3.1) should have a positivity preserving property, which is what we shall prove next.

For the analysis of the present section, Assumption (1.2.7) will be replaced by the following:

\[\cdots < x_{-2} < x_{-1} < x_0 < x_1 < x_2 < \cdots\]

with \( x_n \to \infty \) and \( x_{-n} \to -\infty \) as \( n \to \infty \),

\[B_j \geq 0 \quad \text{for all } j = 0, \pm 1, \pm 2, \ldots, \tag{1.3.3}\]

\[b(0) = 0, \quad b'(0) > 0, \quad b(u_m) > 0 \quad \forall u_m > 0,\]

\[d(0) = 0, \quad d \in C^1[0, \infty), \quad d'(0) > 0, \quad d(u_m) > 0 \quad \forall u_m > 0.\]

**Proposition 3** Let (1.3.3) hold. Then all solutions of (1.3.1) which decay to zero as \( |x| \to \infty \) for all \( t \geq 0 \), remain non-negative for all \( t > 0 \).

**Proof.** Let us make a \( C^1 \) extension to the definition of the death function to \( u_m < 0 \) by defining \( d(u_m) = d'(0)u_m \) when \( u_m < 0 \). Then \( d \in C^1(R) \). Let us first prove non-negativity of \( u_m(x, t) \) for \( t \in (0, \tau] \) only. The proof is by contradiction. Suppose \( u_m \) goes negative on this time interval. Since \( u_m(\pm \infty, t) = 0, u_m(x, t) \) must then attain a negative global minimum on the set \((x, t) \in (-\infty, \infty) \times (0, \tau]. \) Let us first consider the possibility that the minimum is attained at a point \((x^*, t^*)\) where \( x^* \) is
not one of the culling sites \( x_j \). Then \( x^* \) is in some open interval throughout which the delta function in (1.3.1) is inactive. Thus, \( u_m(x^*, t^*) < 0, u_{m,x}(x^*, t^*) \geq 0 \) and \( u_{m,t}(x^*, t^*) \leq 0 \) (noting that the minimum could be at a point \( t^* = \tau \)). Since \( t^* - \tau \leq 0 \) the adult recruitment term in (1.3.1) is non-negative at \((x^*, t^*)\). Using our extension of the death function to \( u_m < 0 \) it follows that

\[
\frac{\partial u_m(x^*, t^*)}{\partial t} \leq 0
\]

which is a contradiction. Now suppose that the negative global minimum is attained at a point \((x^*, t^*)\) where \( x^* \) is one of the \( x_j \). The delta function is active and the above argument fails. As a function of \( x \), the function \( u_m(x, t) \) must now show cusp like behaviour, with \( u_m(x^*, t^*) < 0, u_{m,x}(x^*, t^*) \leq 0 \) and \( u_{m,x}(x^*+, t^*) \geq 0 \) (if, for example, the second of these were violated then, for \( x \) just larger than \( x^* \), \( u_m(x, t^*) \) would be below \( u_m(x^*, t^*) \) contradicting \((x^*, t^*)\) being the global minimum). Using this information in (1.3.2) at time \( t^* \) gives

\[
D \left( \frac{\partial u_m}{\partial x} \right)_{x^*+} - D \left( \frac{\partial u_m}{\partial x} \right)_{x^*-} = B_j u_m(x^*, t^*) < 0
\]

a contradiction. Thus \( u_m(x, t) \geq 0 \) for times \( t \in (0, \tau) \). By the method of steps, \( u_m(x, t) \geq 0 \) for all \( t > 0 \) and the proof is complete.

The linearisation of (1.3.1) about the zero solution is

\[
\frac{\partial u_m}{\partial t} + \frac{\partial^2 u_m}{\partial x^2} + e^{-\mu \tau} b'(0) u_m(x, t - \tau) - d'(0) u_m(x, t) + \sum_{j=-\infty}^{\infty} B_j u_m(x, t) \delta(x - x_j).
\]

(1.3.4)

We will prove the following theorem giving conditions under which it is predicted that extinction will result. The quantity \( B_{\inf} \) embodies information on the spacing of the culling locations. The analysis uses the Euler-Maclaurin summation formula and therefore has to be interpreted in an approximate sense.

**Theorem 1.3.1** Let (1.3.3) hold. Let \( X(\xi) : \mathbb{R} \to \mathbb{R} \) be a strictly monotonically increasing differentiable function with the property that \( X(j) = x_j \) for each \( j \in \mathbb{Z} \), and let \( B(\xi) : \mathbb{R} \to [0, \infty) \) be the piecewise linear function such that \( B(j) = B_j \) for all \( j \in \mathbb{Z} \). If

\[
e^{-\mu \tau} b'(0) < d'(0) + 2B_{\inf}
\]

(1.3.5)
where

\[ B_{\text{inf}} = \inf_{y \in \mathbb{R}} \left\{ \frac{B(y)}{X'(y)} \right\}, \]

then, provided the derivative of the function \( \xi \to B(\xi)u_m^2(X(\xi), t) \) is not too high, the solution \( u_m(x, t) \) of the linearised problem (1.3.4) satisfies \( u_m(x, t) \to 0 \) in \( L^2 \) as \( t \to \infty \), according to an analysis based on the Euler-Maclaurin summation formula.

**Proof.** First note the following alternative formula for \( B_{\text{inf}} \):

\[ B_{\text{inf}} = \inf_{y \in \mathbb{R}} \left\{ B(X^{-1}(y))(X^{-1})'(y) \right\}. \tag{1.3.6} \]

We multiply (1.3.4) by \( u_m(x, t) \) and then integrate with respect to \( x \) over \((-\infty, \infty)\). The Laplacian term will be dealt with via integration by parts, but we must note carefully the effect of the discontinuities in the spatial derivative of \( u_m \). In fact

\[
D \int_{-\infty}^{\infty} \frac{\partial^2 u_m}{\partial x^2} \, dx = D \sum_{j=-\infty}^{\infty} \int_{x_{j-1}}^{x_j} \frac{\partial^2 u_m}{\partial x^2} \, dx
\]

\[
= D \sum_{j=-\infty}^{\infty} \left( u_m(x_j, t) \frac{\partial u_m}{\partial x}(x_j, t) - u_m(x_{j-1}, t) \frac{\partial u_m}{\partial x}(x_{j-1}, t) - \int_{x_{j-1}}^{x_j} \left( \frac{\partial u_m}{\partial x} \right)^2 \, dx \right)
\]

\[
= \sum_{j=-\infty}^{\infty} \left( -B_j u_m^2(x_j, t) + D u_m(x_j, t) \frac{\partial u_m}{\partial x}(x_{j+1}, t) - D u_m(x_{j-1}, t) \frac{\partial u_m}{\partial x}(x_{j-1}, t) \right)
\]

\[
- D \int_{x_{j-1}}^{x_j} \left( \frac{\partial u_m}{\partial x} \right)^2 \, dx \quad \text{using (1.3.2)}
\]

\[
= - \sum_{j=-\infty}^{\infty} B_j u_m^2(x_j, t) - D \int_{-\infty}^{\infty} \left( \frac{\partial u_m}{\partial x} \right)^2 \, dx
\]

since a telescoping series is involved. Therefore (1.3.4) becomes

\[
\frac{1}{2} \frac{d}{dt} \| u_m(t) \|^2 = -D \int_{-\infty}^{\infty} \left( \frac{\partial u_m}{\partial x} \right)^2 \, dx + e^{-\mu t} \int_{-\infty}^{\infty} u_m(x, t) u_m(x, t-\tau) \, dx
\]

\[
- d'(0) \| u_m(t) \|^2 - 2 \sum_{j=-\infty}^{\infty} B_j u_m^2(x_j, t) \tag{1.3.7}
\]

where

\[
\| u_m(t) \| = \| u_m(\cdot, t) \| = \left( \int_{-\infty}^{\infty} u_m^2(x, t) \, dx \right)^{\frac{1}{2}}.
\]
For compactness of notation, where \( u_m(x,t) \) appears under a norm we shall write it simply as \( u_m(t) \). Our aim is to show convergence of \( u_m(x,t) \) to zero in \( L^2 \), i.e. that \( \|u_m(t)\| \to 0 \) as \( t \to \infty \). From (1.3.7) it follows that
\[
\|u_m(t)\| \frac{d}{dt} \|u_m(t)\| \leq e^{-\mu t}b'(0)\|u_m(t)\|\|u_m(t-\tau)\| - d'(0)\|u_m(t)\|^2
\]
\[ - 2 \sum_{j=-\infty}^{\infty} B_j u_j^2(x_j,t), \tag{1.3.8} \]
where we used the Cauchy-Schwarz inequality on the delay term.

Euler-Maclaurin summation can be used to approximate the last term in (1.3.8) as
\[
\sum_{j=-\infty}^{\infty} B_j u_j^2(x_j,t) \approx \int_{-\infty}^{\infty} B(\xi) u_m^2(X(\xi),t) d\xi
\]
which, on making the substitution \( y = X(\xi) \), becomes
\[
\int_{-\infty}^{\infty} B(X^{-1}(y)) u_m^2(y,t) (X^{-1})'(y) dy \geq \inf_{y \in \mathbb{R}} \{ B(X^{-1}(y)) (X^{-1})'(y) \} \|u_m(t)\|^2 \tag{1.3.9}
\]
\[
= B_{\inf} \|u_m(t)\|^2 \tag{1.3.10}
\]
by the alternative formula (1.3.6) for \( B_{\inf} \). Using this estimate in (1.3.8) and dividing through by \( \|u_m(t)\| \) we get
\[
\frac{d}{dt} \|u_m(t)\| \leq e^{-\mu t}b'(0)\|u_m(t-\tau)\| - (d'(0) + 2B_{\inf}) \|u_m(t)\|. \tag{1.3.11}
\]
From this, we can conclude (using similar methods to those discussed earlier) that \( \|u_m(t)\| \to 0 \) as \( t \to \infty \) if
\[
\inf_{y \in \mathbb{R}}\{ B(X^{-1}(y)) (X^{-1})'(y) \} \geq \frac{2B_{\inf} + d'(0)}{e^{-\mu t}b'(0)} \tag{1.3.12}
\]
which holds by hypothesis. The proof is complete.

Let us discuss the situations in which the Euler-Maclaurin summation as used here might lose its ability to predict accurate results. Essentially, we are assuming that the derivative of the function \( \xi \to B(\xi) u_m^2(X(\xi),t) \) is not too high, and one situation in which this assumption might lose its validity is if the culling is aggressive but the culling sites are spaced a long way apart. Very aggressive culling would result in the population being effectively zero at the actual culling sites, but if these are a long way apart (or if there is very low diffusion) there is no reason why the
species should not survive within at least some of the (now decoupled) subdomains \( [x_j, x_{j+1}] \), essentially since individuals would be unlikely to wander into a culling site. This can be investigated by solving (1.3.4) (without the summation term) on the domain \( x \in (x_j, x_{j+1}) \) subject to homogeneous Dirichlet boundary conditions. Trial solutions of the form

\[
U_n(x, t) = e^{\lambda t} \sin \left( \frac{n\pi (x - x_j)}{x_{j+1} - x_j} \right), \quad n = 1, 2, 3, \ldots
\]

exist whenever

\[
\lambda + \frac{Dn^2\pi^2}{(x_{j+1} - x_j)^2} + d'(0) = b'(0)e^{-\mu t}e^{-\lambda t}
\]

which is another transcendental equation for \( \lambda \) that can be tackled using similar ideas to those presented earlier. Specifically it is possible to show that if

\[
e^{-\mu t}b'(0) < d'(0) + \frac{Dn^2\pi^2}{(x_{j+1} - x_j)^2}
\]

then all roots \( \lambda \) of (1.3.13) satisfy \( \text{Re} \lambda < 0 \) for every \( n = 1, 2, 3, \ldots \), giving a condition for extinction of the species inhabiting \( [x_j, x_{j+1}] \), in this case of intensive culling at sites spaced a long way apart. This condition says that, at low densities, adult recruitment is not sufficient to offset deaths together with losses at the ends of the domain where culling is occurring. If the above condition is reversed then one can show that equation (1.3.13) (with \( n = 1 \)) has a real positive root \( \lambda \), so that the species can survive in the subdomain \( [x_j, x_{j+1}] \).

1.4 Discussion

For the purely time dependent model the most important result we have proved concerning (1.2.8), is Theorem 1.2.2 which addresses the situation when, at low densities, adult recruitment outweighs natural mortality. In this situation condition (1.2.23) essentially describes culling regimes that will result in extinction. The condition involves the proportions \( b_j \) removed at the cull times \( t_j \) and a function \( t(\xi) \) the derivative of which can be viewed as a measure of the spacing of the cull times \( t_j \).

From condition (1.2.23) one can make several inferences. If the culling effort is very small, i.e. at each cull only a small proportion \( b_j \) of the individuals are removed (which could still vary from cull to cull) then no matter how small this effort is, provided \( \inf_{j \in \mathbb{N}} b_j > 0 \) then extinction can still result if the culling occurs
sufficiently frequently in the sense that \( t'(j) \) is sufficiently small for each \( j \). A period of more aggressive culling (i.e. larger \( b_j \) for several consecutive \( j \)) can result in extinction even when the culls are less frequent. An obvious particular case is that in which the culls are equally spaced in time, i.e. \( t_j = jT \) for \( j = 1, 2, 3, \ldots \) and some constant \( T > 0 \), and the same proportion \( b^* \) removed at each cull. In this case the only obvious choice for the function \( t(\xi) \) is \( t(\xi) = T\xi \) and so condition (1.2.23) can be put in the form

\[
e^{-\mu T} b'(0) < d'(0) + \frac{b^*}{T}
\]

which says that, at low densities, the per capita death rate plus the proportion culled per unit time is too high to be compensated for by adult recruitment. Thus, the condition makes sense and is what we would expect in this particular case of a fixed proportion being culled at equally spaced culling times.

Condition (1.2.23) fails if even just one of the \( b_j \) is zero, i.e. there is a “cull”, which we might call a zero cull, at which no animals are killed. However, provided only a finite number of the \( b_j \) are zero, there will exist a time beyond which all culls are “proper” culls (i.e. culls with \( b_j > 0 \)), and one could shift the origin of time appropriately, so that in condition (1.2.23) the infimum would be taken starting at the first proper cull having no subsequent zero culls. More interesting, is the possibility of infinitely many zero culls. Mathematically, the most obvious solution is to remove them by relabelling the sequence \( t_j \) (i.e. passing to a subsequence of the original). This would, however, have the effect of changing the interpolating function \( t(\xi) \) and in particular of increasing its derivative, so that (1.2.23) would be less likely to hold. The outcome is that the population is less likely to be driven to extinction as expected.

For the model of Section 1.3, which attempts to study culling continuously in time but at discrete points in space, one can draw inferences analogous to those above for the time dependent model. The condition in Theorem 1.3.1 predicts extinction if the culling effort as described by the function \( B(y) \) is sufficiently large in a sense that also involves the spacing apart of the culling sites (as described by the function \( X(y) \)) as we would anticipate. If the culling sites are close together then \( X \) will have a small derivative and so \( B_{\text{inf}} \) is more likely to be large enough to satisfy (1.3.5).
Population dynamics of the parasitic relationship between blowflies and sheep

2.1 Introduction

A major problem for farmers in Australasia is the phenomenon of blowfly strikes, or *myiasis*. The blowfly lays its eggs on a susceptible host, usually a farmer’s sheep. They are attracted by areas of wool which are damp or dirty, specifically due to faeces. Once hatched the larvae then feed off the host causing a lesion to form. This may in turn attract other blowflies to lay their eggs on the same host. If this process is allowed to continue uncontrolled then it can be fatal to the host. Over 90 per cent of blowfly strikes on sheep are by the so-called Australian Sheep Blowfly or *Lucilia cuprina* and occur in the warmer months of the year. If susceptible sheep are present then only a small number of blowflies, around 7-10 per hectare, [31], are required for *Myiasis* to occur and be a considerable problem for the farmer. The blowflies progeny feed in damp or lumpy fleece, in or around wounds and lesions or in faeces. The female uses her enhanced sense of smell to pick out a sheep with these problems who will make a suitable host. An adult female blowfly will lay, on average, 200 eggs at a time. They have a life span of about one month and produce two or three batches of eggs in this time, although a batch from an older fly may not contain as many eggs [31]. The eggs hatch in around 12 hours and the new born larvae are about 1mm long. The larvae moult twice, once about 18 hours after hatching and then again at around 36 hours. After moulting a second time the larvae feed and grow at an increased rate for about a day until they are fully fed, which tends to be about 3-4 days after hatching, at which point they are around 12mm long. The fully grown larvae leave the host, burrow into the nearby soil and pupate. In ideal conditions they emerge as adult blowflies after about 2 weeks. Blowfly larvae are diapausal: if the temperature of the soil is not warm enough, below about 15°, [31], the larvae enter a state where development is suspended and physiological activity is diminished. This is called overwintering. During this time the larvae are
susceptible to attacks by ants and minute wasps, natural disasters such as water logging, excess cold and trampling by sheep, all of which reduce the overwintering population. When the soil temperature warms up again the overwintering larvae begin to develop until eventually, in mid to late spring, they emerge as mature blowflies.

Myiasis is not instantly fatal, but if left unattended the host has increased risk of being struck again by more blowflies. The smell produced by the larvae feeding on the sheep can attract other species such as the Green Hairy Maggot Blowfly *Chrysomya rufifacies* and the Small Green Hairy Maggot Blowfly *Chrysomya varipes*, who will also lay their eggs on the sheep [31]. The larvae of these species can go deeper into the skin of the sheep causing severe damage and even death.

There are many different ways of controlling blowfly strikes. Some involve control of the blowfly population, such as the trapping and pesticides discussed in Chapter 1 while others involve treating the sheep. Removing the wool from the sheep is one of the most effective methods as the wool can easily get soiled and start to smell thus attracting the blowflies. This can be done by shearing, crutching (the specific removal of wool from around the tail and between the rear legs) and/or mulesing. Mulesing involves removing large areas of skin from around the tail of the sheep to prevent wool growth, thus making the sheep less attractive to blowflies. However this process is very painful for the sheep and research has shown that the wound created by mulesing itself is highly susceptible to blowfly strike [15]. A combination of these methods can be very effective. Blowfly strikes are most virulent at early spring and late autumn. Shearing just before one period and crutching before the other is thought to be an effective control method [32]. Farmers can also time the birth of sheep (lambing) to occur just after shearing or crutching, to minimise the risk of soiled wool due to the birthing process [32].

Unfortunately some methods can have serious side effects. For example if the sheep are being treated by chemicals this can have an adverse effect on the wool, leaving residues [32]. Tighter environmental controls by governments in recent years has led to restrictions being placed on the marketing and processing of wool with residues.

Myiasis is also a problem in England, primarily due to the Greenbottle, *Lucilia sericata*. The life-cycle of the Greenbottle from egg to adult takes about 3-5 weeks, with 3 or 4 generations per year, [33]. Blowfly strikes affect more than 80% of English and Welsh farms and up to a million sheep are struck each year. Upland farms
are more likely to suffer and the problem is worse in the south. Myiasis is a seasonal problem. The first cases of blowfly strikes are often reported in May or June and persist until about late September. The exact times and the severity of the strikes are dependent on many factors including temperature and rainfall and thus vary every year. [33].

One of the main variables that governs the severity of a blowfly strike is the susceptibility of the host. Wall et al. [63] defined two main criteria for increased susceptibility: a) the humidity of the wool, b) the contamination of the wool with faeces. The humidity of the wool depends on the length of the wool and the amount of rain. If a sheep has been soaked to the skin it can develop fleece rot and if it happens a second time there is a risk of severe skin inflammation, which can cause serum to enter the fleece from the skin which is highly attractive to blowflies, [31].

It was found by French et al. [21] that a gravid female of the species Lucilia cuprina was three times more active in the presence of wet sheep than dry sheep. In their model Wall et al. determine that in order for eggs to survive the relative humidity of the wool must be above 65%. If it is above 80% then all the eggs survived. They determined that the probability of survival between these two values follows a linear relationship. If the host gets diarrhoea then this increases the risk of faecal contamination. Diarrhoea in sheep is often caused by parasitic nematode burdens, whose population in a host is deemed to be dependent on the faecal consistency of the host. The length of the wool is also a factor as the longer it is the more likely it is that faeces will stick to it. Wall et al. gave scores for different wool lengths between 0 and 1 (a newborn sheep having a score of 0). Thus they constructed a faecal contamination index (FCI) (wool length multiplied by level of faecal consistency) which could be calculated as a measure of the likelihood of faecal contamination.

Wall et al. then calculated the susceptibility of a host to blowfly strike by using the logistic regression equation

$$\ln(R) = \alpha + \beta_1 x_1 + \beta_2 x_2,$$  \hspace{1cm} (2.1.1)

where $\alpha$, $\beta_1$, $\beta_2$ are constants, $x_1$ represents faecal contamination and $x_2$ wool humidity. $R$ is the probability of susceptibility and is equal to the proportion of susceptible hosts over the proportion of non-susceptible hosts.

Infected sheep are more susceptible to blowfly strike, so to model this aggregation Wall et al. [63] used a negative binomial distribution generated by the parameters $m$ and $k$, where $m$ is the average number of batches of eggs laid on an individual...
host and $1/k$ is a measure of the degree of aggregation.

This data along with other factors was used by Wall et al., [63] to construct a comprehensive simulation model of blowfly strikes by *Lucilia sericata* based on previous versions [61, 62]. Their model was based on data collected on blowfly strikes on lamb and ewes on 370 farms in four regions: south-east England, south-west England, central England and Wales. They found that their model explained a significant proportion of the variance in the lamb strikes in all regions and ewe strikes in three of the four regions. The model also predicted the onset of strikes at the start of the season to within a week in three of the regions, in the fourth region the model was accurate to within three weeks. The model was thought to be useful in assessing the effectiveness of new control techniques and changes to existing practices on the frequency of blowfly strike. However the model was thought to be useful in predicting seasonal blowfly strikes pattern only if the weather projections are accurate. The model is accurate on a regional basis but was not thought to be used on a farm by farm basis especially if a particular farms methods differ from the established norm.

### 2.1.1 Delay

In many systems the evolution of a process is dependent on the past history of that process, or at least some part of it, at some previous time. The particular example we look at in this thesis is the case of the maturation of blowflies. The evolution of a population of blowflies is dependent on when their larvae mature. In a simple case you could say that larvae born at time $t$ will, if they are not killed, mature at some time $t + \tau$, where $\tau$ is the time from when an egg is laid to when the larvae emerges from its cocoon as a mature blowfly. Therefore, when working out the change in mature blowfly population at time $t$ you will need a term that is dependent on the number of eggs laid at time $t - \tau$. This is known as a time delay and occurs in some form in many systems both man made and in nature, over many different areas including physics, biology and chemistry. Other examples of systems that involve time delays are the way the body balances its levels of glucose and insulin (when this fails it leads to Diabetes), reforestation and models of immigration. It is said that any mathematical model that does not take time delays into account in these types of systems is only a first approximation to the true situation, [37]. Differential equations without delay do not accommodate this fact and so for these systems we
need to use delay differential equations (DDE's).

### 2.1.2 Previous models

There has been extensive work undertaken on modelling populations of blowflies and due to the importance of the maturation rate a lot of these involve DDE's. Many of these models are based on the experimental data of Nicholson [47]. In 1957 Nicholson gathered data on laboratory cultures of the Australian sheep blowflies *Lucilia cuprina* over a period of 2 years. In these experiments the populations were controlled by the amount of food allowed. Data was gathered in the case where the mature blowflies food was controlled and also when the food supply to the larva was controlled. He found that there was a periodic oscillation of the population of around 35-40 days. Nicholson's data showed that in each adult population cycle there were actually two peaks in reproductive activity, after an initial increase the population actually starts to die off, before a second increase is observed. This is known as a 'second burst'. Nicholson's Blowfly data has been used to derive models for blowfly populations. An early attempt to model the data by May [42], used the delayed logistic equation

\[
\frac{du_m(t)}{dt} = ru_m(t) \left(1 - \frac{u_m(t-\tau)}{K}\right),
\]

where \(u_m(t)\) is the population of blowflies, \(K\) is a constant depending on the available food, \(\tau\) the maturation delay and \(r\) the intrinsic rate of population increase. This model provided reasonable accuracy when compared to Nicholson’s data and showed that the main factor in the population dynamics was the effect of high fertility combined with long maturation rate. However it computed the delay to be 9 days while observations of the experimental data found that the delay should be 14.8±0.4 days [27]. May’s model also failed to pick up the 'second burst' phenomenon observed in Nicholson’s data.

A more sophisticated model developed in the early 1980’s by Gurney, Blythe and Nisbet, [27] did pick up the 'second burst' phenomenon. This model took the form

\[
\frac{du_m(t)}{dt} = b(u_m(t-\tau)) - du_m(t),
\]

where \(u_m(t)\) is the population of adult blowflies at time \(t\), \(\tau\) is the maturation delay, which here is the time it takes for the larvae to mature into adult blowflies, \(d\) is a positive constant to represent death rate and \(b(u_m(t-\tau))\) is a function to
represent the maturation rate. Nicholson’s data shows that when the mature blowfly population gets too high egg production effectively stops. This is because as the population of blowflies increases it becomes harder for them to find the amount of food they need. When this happens they need to use all the energy from their diminished food intake for their own maintenance and so are unable to produce any eggs. Using this observation Gurney et al. reasoned that realistically the maturation rate function needed to have the property \( b(u_m) \to 0 \) as \( u_m \) became either very large or very small. They also felt that \( b(u_m) \) should have only a single maximum value at some population that would be determined by the amount of available food. Therefore they proposed the use of the function

\[
b(u_m) = Pu_m e^{-Au_m},
\]

to model the maturation rate, where \( 1/A \) is the size of the population at which the maximum birth rate is achieved and \( P \) is a positive constant that models the maximum per capita egg production rate. Numerical simulations of this model showed a good qualitative fit to the data from [47]. Their simulations gave the 'second burst' phenomenon when the minimum population size of the adult blowflies was small in comparison with \( 1/A \). If the minimum population size was large compared to \( 1/A \) then a smooth oscillatory solution was observed. They deduced that the fluctuations observed were due to the combined effect of the long maturation rate with the single humped total reproduction curve.

More general models for a population that undergoes two life stages with a discrete time delay to represent the maturation rate have been investigated. These types of populations include mammalian and some amphibious animals as well as blowflies. One such model was proposed by Aiello and Freedman, [2]. Their model consisted of two DDE’s, one for the mature species and one for the immature

\[
\begin{align*}
\frac{du(t)}{dt} &= \alpha u_m(t) - \mu u_i(t) - \alpha e^{-\mu \tau} u_m(t - \tau) \\
\frac{du_m(t)}{dt} &= \alpha e^{-\mu \tau} u_m(t - \tau) - du_m^2(t),
\end{align*}
\]

where \( u_i(t) \) and \( u_m(t) \) are respectively the populations of the immature and mature species at time \( t \), \( \mu \) is the natural death rate of the immature species, \( \alpha \) the birth rate of the immature species and \( d \) the natural death rate of the mature species. A logistic death rate for the mature population was assumed along with a linear death
rate for the immature. The birth rate of the immatures was also assumed to be linear.

With positive initial conditions Aiello and Freedman [2] found that the positive equilibrium solution of (2.1.4), namely

\[
(u_i^*, u_m^*) = \left( \frac{\alpha^2}{d \mu} e^{-\mu T} (1 - e^{-\mu T}), \frac{\alpha}{d} e^{-\mu T} \right),
\]

(2.1.5)

would be globally asymptotically stable. It is interesting to note that this equilibrium depends on the maturation delay, \(\tau\). This is due to the fact that not all larvae will mature, as some will inevitably die, leading to a smaller than otherwise anticipated mature blowfly population. This being the case it is not uncommon for the steady state of a system to depend on the delay. They found this model did not give the periodic oscillations observed by Nicholson [47] and reproduced in the model by Gurney et al. [27]. A reaction-diffusion extension of the system (2.1.4) was later proposed by Gourley and Kuang [23]. As the immature species are now allowed to move around each individual may mature at a point in space different from where it was born. Thus the maturation rate term needed to be remodelled to account for this. Of course in some cases the immature population may not diffuse, for example if they are larvae as in the case of blowflies. To simplify their model Gourley and Kuang decided to assume that the motion of the species would be a random walk which would be modelled using Fickian diffusion. On an infinite domain their model took the form

\[
\frac{\partial u_i(x, t)}{\partial t} = D_i \Delta u_i(x, t) + \alpha u_m(x, t) - \mu u_i(x, t) - \alpha e^{-\mu T} \int_{-\infty}^{\infty} q(x - y) u_m(y, t - \tau) dy,
\]

\[
\frac{\partial u_m(x, t)}{\partial t} = D_m \Delta u_m(x, t) + \alpha e^{-\mu T} \int_{-\infty}^{\infty} q(x - y) u_m(y, t - \tau) dy - d u_m^2(x, t),
\]

(2.1.6)

where \(D_i, D_m\) are the diffusivities of the immature and mature species respectively and \(q(y)\) is the probability density function associated with the movement of the immature species. This is taken to be a Normal distribution with mean \(x\) and variance \(4D_i \tau\) and takes the form

\[
q(y) = \frac{1}{\sqrt{4\pi D_i \tau}} e^{-y^2 / 4D_i \tau}.
\]

(2.1.7)

In the limiting case when \(D_i \to 0\) we regain the maturation term in (2.1.4).

**Linear stability of the non-zero equilibrium**

Perturbing about the non-zero equilibrium by setting \(u_i(x, t) = u_i^* + \xi(x, t), u_m(x, t) = u_m^* + \nu(x, t)\), where \(u_i^*\) and \(u_m^*\) are given by (2.1.5), and linearising
(2.1.6) gives
\[
\frac{\partial \xi(x,t)}{\partial t} = D_t \Delta \xi(x,t) + \alpha v(x,t) - \mu \xi(x,t) - \alpha e^{-\mu t} \int_{-\infty}^{\infty} q(x-y) \nu(y,t-t) dy
\]
\[
\frac{\partial \nu(x,t)}{\partial t} = D_m \Delta \nu(x,t) + \alpha e^{-\mu t} \int_{-\infty}^{\infty} q(x-y) \nu(y,t-t) dy - 2du_m^* \nu(x,t).
\]
Now looking for solutions of the form \( \xi(x,t) = c_1 e^{\sigma t + ikx}, \nu(x,t) = c_2 e^{\sigma t + ikx} \) we find that we get
\[
\sigma c_1 e^{\sigma t + ikx} = -(k^2 D_t + \mu) c_1 e^{\sigma t + ikx} + \alpha c_2 e^{\sigma t + ikx} - \alpha e^{-\mu t} \int_{-\infty}^{\infty} q(x-y) c_2 e^{(t-t') + iky} dy
\]
\[
\sigma c_2 e^{\sigma t + ikx} = -k^2 D_m c_2 e^{\sigma t + ikx} + \alpha e^{-\mu t} \int_{-\infty}^{\infty} q(x-y) c_2 e^{(t-t') + iky} dy - 2du_m^* c_2 e^{\sigma t + ikx}.
\]
(2.1.8)
The main problem here is the maturation term which involves an integral, so let us look at that on its own. Using the relationship (2.1.7) we get
\[
c_2 \alpha e^{-\mu t} e^{\sigma (t-t')} \int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi D_t \tau}} e^{-(x-y)^2 / 4D_t \tau} e^{iky} dy.
\]
(2.1.9)
After some algebra (2.1.9) can be written as
\[
c_2 \alpha e^{-\mu t} e^{\sigma t + ikx} e^{-\sigma t} e^{-k^2 D_t \tau} \int_{-\infty}^{\infty} \frac{1}{\sqrt{4\pi D_t \tau}} \exp \left\{ \frac{-((x + 2ikD_t \tau) - y)^2}{4D_t \tau} \right\} dy.
\]
However the term in the integral is now a normal distribution with mean \( x + 2ikD_t \tau \) and variance \( 4D_t \tau \) and thus is equal to 1. So we are just left with \( c_2 \alpha e^{-\mu t} e^{\sigma t + ikx} e^{-\sigma t} e^{-k^2 D_t \tau}. \)
Now we can substitute this into our linearised equations, (2.1.8), and cancel the \( e^{\sigma t + ikx} \) terms to get
\[
\sigma c_1 = -k^2 D_t c_1 + \alpha c_2 - \mu c_1 - c_2 \alpha e^{-\mu t} e^{-\sigma t} e^{-k^2 D_t \tau},
\]
\[
\sigma c_2 = -k^2 D_m c_2 + c_2 \alpha e^{-\mu t} e^{-\sigma t} e^{-k^2 D_t \tau} - 2du_m^* c_2,
\]
which can be put into matrix form
\[
\begin{pmatrix}
\sigma + k^2 D_t + \mu & \alpha e^{-\mu t} e^{-\sigma t} e^{-k^2 D_t \tau} - \alpha \\
0 & \sigma + k^2 D_m + 2du_m^* - \alpha e^{-\mu t} e^{-\sigma t} e^{-k^2 D_t \tau}
\end{pmatrix}
\begin{pmatrix}
c_1 \\
c_2
\end{pmatrix}
= 0.
\]
The roots, \( \sigma \), of this dispersion relation are \( -(\mu + k^2 D_t) \) together with the roots of \( \sigma + k^2 D_m + 2du_m^* - \alpha e^{-\mu t} e^{-\sigma t} e^{-k^2 D_t \tau} = 0 \). Standard analysis (see [23]) showed that
these roots would all be in the left half of the complex plane and thus the equilibrium 
\((u^*_i, u^*_n)\) would be linearly stable, independent of the delay and diffusion.

The model (2.1.6) does not make sense on a finite domain as it does not account for interactions with the boundary. On a finite spatial domain, which in the one dimensional case can be taken to be \(0 \leq x \leq \pi\) without loss of generality, with homogeneous Neumann boundary conditions the function \(q(x-y)\) must be replaced by

\[
Q(x, y, t) = \frac{1}{\pi} + \frac{2}{\pi} \sum_{n=1}^{\infty} e^{-D_m n^2 t} \cos nx \cos ny,
\]

which is the solution to the heat equation on a finite domain

\[
\frac{\partial Q}{\partial t} = D_m \frac{\partial^2 Q}{\partial x^2}, \quad 0 < x < \pi,
\]

subject to

\[
\frac{\partial Q}{\partial x} = 0 \quad \text{at} \quad x = 0, \pi \quad \text{and} \quad Q(x, y, 0) = \delta(x - y).
\]

For the finite domain \(x \in [0, \pi]\) the second equation of (2.1.6) would be replaced by

\[
\frac{\partial u_m(x, t)}{\partial t} = D_m \frac{\partial^2 u_m(x, t)}{\partial x^2} + c e^{-\mu r} \int_0^{\pi} Q(x, y, t) u_m(y, t - \tau) dy - d u_m^2(x, t),
\]

for \(x \in [0, \pi], t > 0\), where \(Q(x, y, t)\) is given by (2.1.10), with boundary conditions

\[
\frac{\partial u_m}{\partial x}(0, t) = \frac{\partial u_m}{\partial x}(\pi, t) = 0, \quad t > 0,
\]

and initial conditions

\[
u_m(x, t) = \phi(x, t) \quad \text{for} \quad (x, t) \in [0, \pi] \times [-\tau, 0].
\]

Gourley and Kuang, [23] were able to prove that (2.1.11), subject to (2.1.12) and (2.1.13) has a unique positive solution and also that the equilibrium \(e^{-\mu r} \alpha/d\) is globally asymptotically stable if \(\alpha, d > 0, \mu, \tau \geq 0\) and the initial function \(\phi\) is Hölder continuous in \([0, \pi] \times [-\tau, 0]\), non negative and \(\phi \neq 0\), [23].

Previously we have assumed that the populations of the blowflies and the sheep will exist in the same finite area. However in reality the sheep will be confined to the field they are in while the blowflies have no such restrictions. For example consider
a farm which has five fields of sheep. Each field effectively has a different population of sheep all of which are independent of each other. However it is reasonable to assume that there would only be one population of blowflies that prey on all the fields of sheep. It is clear that if the blowflies in one field were to run out of sheep they could quite easily move to one of the other fields that has more sheep. In fact it is well known that blowflies from the surrounding area will be attracted to fields that have a large population of susceptible sheep, [33]. It may therefore be of use to construct a model for myiasis where the blowfly population can exist in a large space (e.g. a farm) but the sheep are restricted to finite areas within this larger space (e.g. fields). Other models have previously been developed using these ideas, for example Cantrell and Cosner, [14] who constructed a model for the predation of aphids living on fireweed patches by ladybirds. They assumed that the aphids would live on independent patches of fireweed. For ease of computation they decided that each patch, , would be a square with sides of length , as it was shown that any shape of patch would give results that were qualitatively similar. Instead of modelling the number of aphids they modelled the density, such that the density of aphids in a given fireweed patch was . Then they assume that a population of ladybirds exist in the air above the patches. Ladybirds can immigrate to any of the patches, with equal probability as they are capable of flying relatively long distances, to prey on the aphids and then leave again. Thus to model a system of square patches with sides of length and area , they needed state variables to denote the density of the aphids in each patch, state variables, to denote the number of ladybirds in each patch and a final state variable to denote the number of ladybirds in the air. It is important to remember that while the aphids are modelled in terms of densities the ladybirds are modelled in terms of actual numbers. So their model had the form

\[
\frac{dP_n}{dt} = I_n P_A - E_n P_n \tag{2.1.14}
\]

\[
\frac{\partial \nu_n}{\partial t} = D \Delta \nu_n + r \nu_n \left(1 - \frac{\nu_n}{K}\right) - c \nu_n \left(\frac{P_n}{\nu_n^2}\right) \tag{2.1.15}
\]

for \(x,y \in \Omega\)

\(\nu_n(x,y,t) = 0\) on \(\partial \Omega\),

where \(I_n\) represents the per capita immigration rate of ladybirds to patch \(n\), \(E_n\) the per capita emigration rate of ladybirds from patch \(n\) and \(D, r, K, c\) are positive constants. Here \(\Omega = (0, l_n) \times (0, l_n)\) and \(\partial \Omega\) is the boundary. They also constructed
more sophisticated models where they assumed a finite population of predators and also where they included the idea that ladybirds will aggregate on patches with higher aphid densities. Their results showed that it may be possible to have an inverse relationship between patch size and prey density that would be due to the presence of predators. The model also predicted maximum patch sizes, as well as minimum patch sizes, for the continued existence of the prey population, which were not found when using reaction-diffusion models for the prey alone.

2.2 A simple model of blowfly strikes

In this section we propose a model for blowfly strikes. Our model uses as a basis previous models, such as [27] and [23], to describe the relationship between immature blowflies \( u_i(t) \) and mature blowflies \( u_m(t) \) and also includes their parasitic effect on a host population, \( N(t) \). Our model takes the form

\[
\begin{align*}
\dot{u}_i(t) &= b(u_m(t))N(t) - \mu_i u_i(t) - e^{-\mu_T t} b(u_m(t - \tau))N(t - \tau) \\
\dot{u}_m(t) &= e^{-\mu_T t} b(u_m(t - \tau))N(t - \tau) - d(u_m(t)) - \mu_T u_m(t) \\
N'(t) &= rN(t)(1 - N(t)) - \gamma_s N(t)u_m(t),
\end{align*}
\]

subject to the initial conditions

\[
\begin{align*}
 u_i(0) &= u_{i,0} \geq 0, \\
 u_m(s) &= \phi_m(s) \geq 0, \\
 N(s) &= \phi_N(s) \geq 0, \\
 s &\in [-\tau, 0],
\end{align*}
\]

where \( \mu_i, \mu_T, \gamma_s, r \) are all positive constants and we define

\[
\begin{align*}
\dot{u}_i(t) &= \frac{du_i}{dt}, \\
\dot{u}_m(t) &= \frac{du_m}{dt}, \\
N'(t) &= \frac{dN}{dt}.
\end{align*}
\]

In this model \( b(u_m(t))N(t) \) represents the birth rate of blowflies, which is some function of the mature blowflies multiplied by the number of hosts, \( N(t) \) at time \( t \), so if no hosts were present then the birth rate would be zero. The \( d(u_m(t)) \) term represents the natural death rate of mature blowflies and is some increasing function.
of \( u_m(t) \). We make the following assumptions about these variables

\[
\begin{align*}
    b(0) &= 0, \quad b \in C^1[0, \infty), \quad b(u_m) > 0 \quad \text{for all} \quad u_m > 0 \\
    b(u_m) \text{ is increasing in } u_m \text{ up to a value } u_{\text{max}}, \\
    \text{with} \quad b(u_{\text{max}}) &= b_{\text{max}}, \quad \text{after which it is decreasing.} \\
    d(0) &= 0, \quad d \in C^1[0, \infty), \quad d(u_m) \text{ is strictly increasing in } u_m \\
    d(u_m) &> 0 \quad \text{for all} \quad u_m > 0.
\end{align*}
\]

We also note \( b(u_m) \) qualitatively resembles the function \( Pu_m e^{-A u_m} \), for some constants \( P \) and \( A \), see Figure 2.1 and that (2.2.5) implies that \( d(u_m) > 0 \) for all \( u_m > 0 \).

The \( \mu_t u_m(t) \) term represents the death rate of mature blowflies due to trapping. Trapping is the term used to describe man’s attempts at controlling the population. For example a farmer will lay out buckets in his field containing poisonous chemicals to attract and kill the blowflies, as described in Chapter 1. The \( \mu_t u_i(t) \) term represents the natural death rate of immature blowflies and is linear. The \( e^{-\mu t} b(u_m(t - \tau)) N(t - \tau) \) term is the rate at which immature blowflies become mature blowflies, known as the maturation rate. This term incorporates the delay, \( \tau \), because at time \( t \), only blowflies born at time \( t - \tau \) will mature. So the maturation rate at time \( t \) is related to the birth rate at time \( t - \tau \). However some of the immature blowflies will die during the larval phase and because we have a linear death rate the juvenile mortality is accounted for by the factor \( e^{-\mu t} \).

It is assumed that the host population follow a logistic growth pattern, \( r N(t) (1 - N(t)/K) \), in our model, however, the equation has been normalised to remove the carrying capacity, \( K \). The hosts death rate is modelled by the term \( \gamma_s N(t) u_m(t) \) and is taken as proportional to the number of mature blowflies and to the host population. It could be argued that this term should instead be \( \gamma_s N(t) u_i(t) \) or perhaps \( \gamma_s N(t) u_m(t - \tau) \), since it is really the larval flies that cause the sheep to die. Later we shall present some numerical simulations which investigate what happens if the sheep mortality term is taken as one of these alternative expressions. From an analytical point of view, we are concerned mainly with finding conditions which ensure the blowflies are eradicated, and our theorems on eradication can be proved even with these alternative expressions. The choice \( \gamma_s N(t) u_m(t) \) has the advantage of partially decoupling the system.

Notice that (2.2.2) and (2.2.3) do not depend at all on \( u_i(t) \) and so we can solve them independently of (2.2.1). Thus we can just look at (2.2.2) and (2.2.3) when
analysing our system.

2.2.1 Positivity and Boundedness

Proposition 4 Suppose (2.2.5) holds for the system (2.2.1, 2.2.2, 2.2.3) subject to (2.2.4) and also that $\phi_m(0), \phi_N(0) > 0$ and

$$u_i(0) = \int_{-\tau}^{0} b(u_m(s))N(s)e^{\mu s}ds,$$

(2.2.6)

then $u_i(t), u_m(t), N(t) > 0$ for all $t > 0$

Remark: Equation (2.2.6) is a compatibility condition. Such compatibility conditions on the initial data are very commonly required in stage structured models. The compatibility condition is very easy to interpret ecologically. Individuals that are mature at time 0 must have been born at some time $s \in [-\tau, 0]$. Look at a typical time interval from $s$ to $s + ds$ with $s \in [-\tau, 0]$ and $ds$ infinitesimal. Then $b(u_m(s))N(s)ds$ births will have occurred during this time interval and each such individual has to remain alive from its birth time $s < 0$ until time 0. The probability of this happening is $e^{\mu s}$.

Proof: To prove positivity of the solution to our system we first look at (2.2.3) and see that it can be written as

$$N'(t) = N(t) [r(1 - N(t)) - \gamma_s u_m(t)] = N(t)f(N(t), u_m(t)),$$

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where \( f(N(t), u_m(t)) = r(1 - N(t)) - \gamma_s u_m(t) \). We can recast this as an integral equation:

\[
\frac{N'(t)}{N(t)} = f(N(t), u_m(t))
\]

\[
\ln \left( \frac{N(t)}{N(0)} \right) = \int_0^t f(N(s), u_m(s)) ds
\]

\[
N(t) = N(0) \exp \left( \int_0^t f(N(s), u_m(s)) ds \right).
\]

Making the assumption that \( N(0) = \phi_N(0) > 0 \) we see that \( N(t) > 0 \) for all \( t > 0 \).

Now we look at (2.2.2) to prove positivity of \( u_m(t) \). Our initial conditions show that \( \phi_m(s) \geq 0 \) and \( \phi_N(s) \geq 0 \) for \( s \in [-\tau, 0] \). We shall also use the further assumption from the Proposition that \( \phi_N(0), \phi_m(0) > 0 \). First we shall prove that \( u_m(t) \) is positive for \( t \in [0, \tau] \). We see that on this interval \( u_m(t - \tau) = \phi_m(t - \tau) \geq 0 \) and \( N(t - \tau) = \phi_N(t - \tau) \geq 0 \), since \( t - \tau \in [-\tau, 0] \). So \( e^{-\mu r \tau} b(u_m(t - \tau)) N(t - \tau) \geq 0 \). Thus

\[
u_m'(t) \geq -d(u_m(t)) - \mu_T u_m(t)
\]

for all \( t \in [0, \tau] \).

Therefore we can say that \( u_m(t) \geq \bar{u}_m(t) \) where \( \bar{u}_m(t) \) is the solution of

\[
\bar{u}_m'(t) = -d(\bar{u}_m(t)) - \mu_T \bar{u}_m(t),
\]

subject to \( \bar{u}_m(s) = \phi_m(s) \geq 0 \) on \( s \in [-\tau, 0] \). We can write \( d(\bar{u}_m(t)) \) as \( d(\bar{u}_m(t)) = d(0) + \bar{u}_m(t) d'(0) + O(u^2_m) = \bar{u}_m(t) d'(0) + O(u^2_m) \), because \( d(0) = 0 \). Therefore the above equation has a factor of \( \bar{u}_m(t) \) in its right hand side. Thus by the same method as used for positivity of \( N(t) \) we conclude that \( \bar{u}_m(t) > 0 \) for all \( t \in [0, \tau] \). Because \( u_m(t) \geq \bar{u}_m(t) \) we conclude that \( u_m(t) > 0 \) for all \( t \in [0, \tau] \).

For \( t \in [\tau, 2\tau] \) we can change the origin of time to \( \tau \) and see that \( u_m(t) \) is positive by the above argument. Thus \( u_m(t) \) is positive for all \( t > 0 \), by the method of steps.

To show positivity of \( u_i(t) \) we note that the solution to (2.2.1) subject to (2.2.6) is

\[
u_i(t) = \int_{t-\tau}^t b(u_m(s)) N(s) e^{-\mu_i(t-s)} ds
\]
which, given that \( u_m(t) \) and \( N(t) \) are positive implies that \( u_i(t) \) must also be positive and thus the proof is complete.

**Proposition 5** Suppose \((2.2.5)\) holds for the system \((2.2.1,2.2.2,2.2.3)\) subject to \((2.2.4)\), then \( u_i(t), u_m(t), N(t) \) are bounded.

**Proof:** To prove that \( N(t) \) is bounded we note that, by positivity of \( N(t) \) and \( u_m(t) \),

\[
N'(t) \leq rN(t)(1 - N(t)),
\]

which implies that

\[
\limsup_{t \to \infty} N(t) \leq 1.
\]

Hence \( N(t) \) is bounded for all time.

Now we wish to show that \( u_m(t) \) is bounded. First we note that because \( d(u_m(t)) \) is an increasing function and non-negative for all values of \( u_m(t) \geq 0 \), equation \((2.2.2)\) can be written as

\[
\frac{d}{dt} u_m(t) \leq e^{-\mu_T b(u_m(t))} N(t) - \mu_T u_m(t).
\]

We know that \( b(u_m(t)) \) has a maximum value at \( b(u_{\text{max}}) \) which we will call \( b_{\text{max}} \) and we have shown that \( N(t) \) is bounded and so will have a maximum value, \( N_{\text{max}} \). Thus we get

\[
u_m'(t) \leq e^{-\mu_T b_{\text{max}} N_{\text{max}}} - \mu_T u_m(t). \tag{2.2.7}
\]

So we can say that \( u_m(t) \) is bounded above by the solution \( Y(t) \) to the equation

\[
Y'(t) + \mu_T Y(t) = e^{-\mu_T b_{\text{max}} N_{\text{max}}}, \tag{2.2.8}
\]

subject to the initial condition \( Y(0) = u_m(0) \). This equation can be solved using the integrating factor \( e^{\mu_T t} \) to give

\[
Y(t) = e^{-\mu_T b_{\text{max}} N_{\text{max}}/\mu_T} (1 - e^{-\mu_T t}) + Y(0)e^{-\mu_T t}.
\]

So because \( u_m(t) \leq Y(t) \) and \( u_m(0) = Y(0) \) we have that

\[
\begin{align*}
u_m(t) &\leq e^{-\mu_T b_{\text{max}} N_{\text{max}}/\mu_T} (1 - e^{-\mu_T t}) + u_m(0)e^{-\mu_T t} \\
&\leq e^{-\mu_T b_{\text{max}} N_{\text{max}}/\mu_T} + u_m(0)e^{-\mu_T t} \\
&\leq e^{-\mu_T b_{\text{max}} N_{\text{max}}/\mu_T} + u_m(0),
\end{align*}
\]

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and so \( u_m(t) \) is bounded.

We can now see that the equation for the immature blowflies (2.2.1) satisfies

\[
u_i'(t) \leq b_{\text{max}} N_{\text{max}} - \mu_i u_i(t),
\]

which has the same structure as (2.2.7) and so it is clear, by following the same method as for the mature blowflies, that \( u_i(t) \) is bounded and the proof is complete.

### 2.2.2 Existence of equilibrium solutions

Looking for equilibrium solutions of our system (2.2.1, 2.2.2, 2.2.3) we remember that we do not need to consider (2.2.1). Therefore we set all derivatives to zero in (2.2.2) and (2.2.3) and also set \( u_m(t-\tau) = u_m(t) \) and \( N(t-\tau) = N(t) \) to get the equations

\[
e^{-\mu \tau} b(u_m) N - d(u_m) - \mu_T u_m = 0 \tag{2.2.9}
\]

\[
r N(1 - N) - \gamma_s N u_m = 0. \tag{2.2.10}
\]

We can see by inspection that \( u_m = 0 \) is a solution of (2.2.9). Putting this into (2.2.10) we get \( r N(1 - N) = 0 \), so we have two equilibrium solutions \((u_m, N) = (0, 0), (0, 1)\).

For an equilibrium with \( u_m, N > 0 \) to exist it must satisfy

\[
e^{-\mu \tau} b(u_m) N = d(u_m) + \mu_T u_m \tag{2.2.11}
\]

\[
r(1 - N) = \gamma_s u_m. \tag{2.2.12}
\]

We can rearrange (2.2.12) to get \( N = \left(1 - \frac{\gamma_s}{r} u_m\right) \). Putting this into (2.2.11) we get

\[
e^{-\mu \tau} b(u_m) \left(1 - \frac{\gamma_s}{r} u_m\right) = d(u_m) + \mu_T u_m.
\]

Noting that \( \frac{\gamma_s}{r} u_m \geq 0 \) we can see that in order for an equilibrium solution with \( u_m > 0 \) to exist it is necessary that

\[
e^{-\mu \tau} b(u_m) \geq d(u_m) + \mu_T u_m,
\]

at the equilibrium. Thus one way to ensure that such an equilibrium does not exist is to impose the following condition

\[
e^{-\mu \tau} b(u_m) < d(u_m) + \mu_T u_m, \quad \text{for all} \quad u_m > 0. \tag{2.2.13}
\]

It is reasonable to conjecture that if the above inequality holds then the blowfly population will be eradicated and this is what we will prove later, in Theorem 8.
2.2.3 Linear Stability

We want to see if the equilibrium solutions are going to be locally stable or unstable. To do this we shall conduct a linearised stability analysis. First we perturb (2.2.2,2.2.3) about the equilibrium points \((u_m^*, N^*)\), so we set \(u_m(t) = u_m^* + \xi(t)\) and \(N(t) = N^* + \eta(t)\), where \(\xi(t)\) and \(\eta(t)\) are small. Then we Taylor expand the functions \(b\) and \(d\), linearise and rearrange the equations to give

\[
\begin{align*}
\xi'(t) &= e^{-\mu\tau} b(u_m^*) \eta(t - \tau) + \xi'(t - \tau) b'(u_m^*) - \xi(t) d'(u_m^*) - \mu \tau \xi(t) \\
\eta'(t) &= r \eta(t) (1 - 2N^*) - \gamma_s (u_m^* \eta(t) + \xi(t) N^*),
\end{align*}
\]

where at this stage \((u_m^*, N^*)\) denotes any equilibrium. Now we look for solutions of the form \(\xi(t) = c_1 e^{\sigma t}, \eta(t) = c_2 e^{\sigma t}\). Putting this into the above equations gives

\[
\begin{align*}
c_1 \sigma &= e^{-\mu \tau} (c_2 b(u_m^*) e^{-\sigma \tau} + c_1 e^{-\sigma \tau} b'(u_m^*) N^*) - c_1 d'(u_m^*) - c_1 \mu \tau \\
c_2 \sigma &= c_2 r (1 - 2N^*) - \gamma_s (c_2 u_m^* + c_1 N^*),
\end{align*}
\]

which can be put into matrix form

\[
\begin{pmatrix}
\sigma - e^{-\mu \tau} e^{-\sigma \tau} b'(u_m^*) N^* + d'(u_m^*) + \mu \tau \\
\gamma_s N^* \\
\gamma_s \sigma - \sigma (1 - 2N^*) + \gamma_s u_m^*
\end{pmatrix}
\begin{pmatrix}
c_1 \\
c_2
\end{pmatrix} = 0.
\]

(2.2.14)

For non-trivial solutions the determinant of the coefficient matrix must be zero.

**Theorem 6** Let (2.2.5) hold. Then the equilibrium solution \((u_1^*, u_m^*, N^*) = (0, 0, 0)\) of the system (2.2.1,2.2.2,2.2.3) is linearly unstable.

**Proof:** Note that if \(u_m(t) \to 0\) and \(N(t) \to \) any limit (not necessarily zero) then (2.2.1) implies \(u_1(t) \to 0\). Therefore we can focus on (2.2.2) and (2.2.3) only. For the equilibrium point \((u_m, N) = (0, 0)\), remembering that \(b(0) = d(0) = 0\) the matrix becomes

\[
\begin{pmatrix}
\sigma + d'(0) + \mu \tau & 0 \\
0 & \sigma - r
\end{pmatrix}
\begin{pmatrix}
c_1 \\
c_2
\end{pmatrix} = 0.
\]

The determinant of this matrix is

\[
(\sigma + d'(0) + \mu \tau) (\sigma - r).
\]
To be stable both roots must be in the left half of the complex plane. We see that the roots are \( \sigma = r \) and \( \sigma = -(d'(0) + \mu_T) \). However as \( r \) is positive this root will be in the right half of the complex plane and thus the equilibrium solution \((u_i^*, u_m^*, N^*) = (0, 0, 0)\) is linearly unstable.

**Theorem 7** Suppose for the system \((2.2.1, 2.2.2, 2.2.3)\) that \((2.2.5)\) holds and also that

\[
e^{-\mu_T b'(0)} < d'(0) + \mu_T,
\]

then the equilibrium point \((u_i^*, u_m^*, N^*) = (0, 0, 1)\) is asymptotically linearly stable.

**Proof:** Again note that if \( u_m(t) \to 0 \) and \( N(t) \to 1 \) then \( u_i(t) \to 0 \). So we focus on \((2.2.2)\) and \((2.2.3)\) only. For the equilibrium point \((u_m, N) = (0, 1)\) we find that \((2.2.14)\) becomes

\[
\left( \begin{array}{cc}
\gamma_0 & \sigma + r \\
\sigma - e^{-\mu_T e^{-\sigma_T}b'(0) + d'(0) + \mu_T} & 0
\end{array} \right) \left( \begin{array}{c}
c_1 \\
c_2
\end{array} \right) = 0.
\]

From this we obtain the eigenvalue equation:

\[
(\sigma - e^{-\mu_T e^{-\sigma_T}b'(0) + d'(0) + \mu_T})(\sigma + r) = 0.
\]

This time we have that one of the roots is \( \sigma = -r \), which will be in the left half of the complex plane. For this equilibrium point to be linearly stable we now need to show that the other roots will also all be in the left half of the complex plane. For a contradiction, let us assume that there exists a root \( \sigma \) such that \( \sigma > 0 \). Then

\[
|\sigma + d'(0) + \mu_T| = e^{-\mu_T b'(0)}|e^{-\delta_T}|
\]

\[
= e^{-\mu_T b'(0)}|e^{-(\Re(\delta)+\Im(\delta))})|
\]

\[
= e^{-\mu_T b'(0)}|e^{-(\Re(\delta))} e^{-i(\Im(\delta))}|
\]

\[
= e^{-\mu_T b'(0)}|e^{-(\Re(\delta))}|
\]

so that since \( \Re(\delta) \geq 0 \)

\[
|\sigma + d'(0) + \mu_T| \leq e^{-\mu_T b'(0)}.
\]

Therefore \( \sigma \) is in the disk of radius \( e^{-\mu_T b'(0)} \) centred at \(-d'(0) - \mu_T\). If we choose the radius of this disk such that the whole disk is in \( \{ \Re(\sigma) < 0 \} \) then we have a contradiction. This will be the case if

\[
e^{-\mu_T b'(0)} < d'(0) + \mu_T, \tag{2.2.15}
\]
which holds by hypothesis and so the equilibrium point \((u^*_i, u^*_m, N^*) = (0, 0, 1)\) is linearly stable.

### 2.2.4 Global Stability of the equilibrium point \((u^*_i, u^*_m, N^*) = (0, 0, 1)\)

We have shown that the equilibrium point \((u^*_i, u^*_m, N^*) = (0, 0, 1)\) is locally stable in the situation when it is the only equilibrium (other than \((0, 0, 0)\)). Let us now prove that it is globally stable under these circumstances.

**Theorem 8** Suppose for the system (2.2.1, 2.2.2, 2.2.3) that (2.2.5) holds and also that

\[
e^{-\mu_T b}(u_m) < d(u_m) + \mu_T u_m, \text{ for all } u_m > 0
\]

and that \(\phi_N(0) > 0\). Then the equilibrium point \((u^*_i, u^*_m, N^*) = (0, 0, 1)\) is globally asymptotically stable.

**Proof:** First note that if \(u_m(t) \equiv 0\) then the result is trivial. We already know that \(\limsup_{t \to \infty} N(t) \leq 1\). Let \(\epsilon > 0\) be arbitrary. Then there exists \(T > 0\) such that for \(t \geq T, N(t) < 1 + \epsilon\). So when \(t \geq T + \tau, N(t - \tau) < 1 + \epsilon\). Thus (2.2.2) becomes

\[
u'_m(t) \leq e^{-\mu_T b}(u_m(t - \tau))(1 + \epsilon) - d(u_m(t)) - \mu_T u_m(t).
\]

As we know \(b(u_m(t)) \leq b^{\text{max}}\) we get

\[
u'_m(t) \leq e^{-\mu_T b^{\text{max}}(1 + \epsilon) - d(u_m(t)) - \mu_T u_m(t).
\]

We first claim that \(u_m(t)\) is not eventually monotonically increasing. Suppose the contrary. Then since \(u_m(t)\) is bounded there exists \(\ell > 0\) with \(u_m(t) \to \ell\) as \(t \to \infty\). Letting \(t \to \infty\) and then \(\epsilon \to 0\) in (2.2.17) we get

\[
e^{-\mu_T b}(\ell) \geq d(\ell) + \mu T \ell,
\]

which, as \(\ell > 0\), contradicts inequality (2.2.16) in the hypothesis of the Theorem.

Now if we assume that \(u_m(t)\) is eventually monotonically decreasing then as we know that \(u_m(t) \geq 0\) it must eventually approach a limit, \(\ell_1\), as \(t \to \infty\). We want that limit to be 0. By the above analysis we get a contradiction if \(\ell_1 > 0\), so \(\ell_1\) must be equal to 0.

This just leaves the case where \(u_m(t)\) is neither eventually monotonically increasing nor eventually monotonically decreasing. In this case there exists a sequence of
times $t_k \to \infty$ such that $u'_m(t_k) = 0$ and $u_m(t_k) \to \ell_2$ as $k \to \infty$, where $\ell_2 = \limsup_{t \to \infty} u_m(t)$. So again we want to show that $\ell_2 = 0$ (if $\limsup_{t \to \infty} u_m(t) = 0$ then it follows that $\liminf_{t \to \infty} u_m(t) = 0$, as $u_m(t) \geq 0$, and so we have that $u_m(t) \to 0$ as $t \to \infty$). Using (2.2.17) at $t = t_k$, assuming $k$ is sufficiently large that $t_k \geq T + \tau$, we get

$$0 = u'_m(t_k) \leq e^{-\mu_T}(u_m(t_k - \tau))(1 + \epsilon) - d(u_m(t_k)) - \mu_T u_m(t_k) \quad (2.2.19)$$

$$\leq e^{-\mu_T}b_{\max}(1 + \epsilon) - d(u_m(t_k)) - \mu_T u_m(t_k). \quad (2.2.20)$$

If we let $k \to \infty$ and then let $\epsilon \to 0$ we conclude that $\ell_2$ satisfies

$$e^{-\mu_T}b_{\max} \geq d(\ell_2) + \mu_T \ell_2. \quad (2.2.21)$$

Recall that $b_{\max} = b(u_{\max})$, where $u_{\max} > 0$. We claim that $\ell_2 < u_{\max}$. For a contradiction let us assume that $\ell_2 \geq u_{\max}$. The left hand side of (2.2.21) is constant and the right hand side is increasing as a function of $\ell_2$. Therefore

$$e^{-\mu_T}b(u_{\max}) \geq d(u_{\max}) + \mu_T u_{\max}. \quad (2.2.22)$$

However since $u_{\max} > 0$ this contradicts condition (2.2.16) in our theorem. So we must have that $\ell_2 < u_{\max}$.

We have shown that $\ell_2 = \limsup_{t \to \infty} u_m(t) < u_{\max}$, we now want to show that in fact $\ell_2 = 0$. Let $\epsilon_2 > 0$ be such that $\ell_2 + \epsilon_2 \leq u_{\max}$. Then there exists a $T_2 > 0$ such that for all $t \geq T_2$ we have

$$u_m(t) \leq \ell_2 + \epsilon_2.$$

We shall in fact assume that $T_2$ is sufficiently large that additionally

$$N(t) \leq 1 + \epsilon_2.$$

Next let $k$ be sufficiently large that $t_k - \tau \geq T_2$. Then $u_m(t_k - \tau) \leq \ell_2 + \epsilon_2$ and $N(t_k - \tau) \leq 1 + \epsilon_2$. As $b(u_m)$ is increasing for all values up to $u_{\max}$ and $\ell_2 + \epsilon_2 \leq u_{\max}$ we have that when $k$ is sufficiently large such that $t_k - \tau \geq T_2$,

$$b(u_m(t_k - \tau)) \leq b(\ell_2 + \epsilon_2).$$

Therefore, putting into (2.2.2) and assuming $t_k - \tau \geq T_2$, we get

$$0 = u'_m(t_k) \leq e^{-\mu_T}b(\ell_2 + \epsilon_2)(1 + \epsilon_2) - d(u_m(t_k)) - \mu_T u_m(t_k).$$
letting $k \to \infty$

$$0 \leq e^{-\mu t}b(\ell_2 + \epsilon_2)(1 + \epsilon_2) - d(\ell_2) - \mu T \ell_2.$$

Since this holds for all sufficiently small $\epsilon_2 > 0$, we have

$$e^{-\mu t}b(\ell_2) \geq d(\ell_2) + \mu T \ell_2,$$

which contradicts the hypothesis of our theorem unless $\ell_2 = 0$. Thus we have that

$$\limsup_{t \to \infty} u_m(t) = 0,$$

i.e. $u_m(t) \to 0$ as $t \to \infty$.

We now want to show that $N(t) \to 1$ as $t \to \infty$. Let $\epsilon_3 > 0$. There exists a $T_3 > 0$

such that for $t > T_3$, $u_m(t) < \epsilon_3$. Then for $t > T_3$

$$rN(t)(1 - N(t)) - \gamma_3 \epsilon_3 N(t) \leq N'(t) \leq rN(t)(1 - N(t)). \tag{2.2.23}$$

From the right hand side of (2.2.23), $\limsup_{t \to \infty} N(t) \leq 1$ and from the left hand side $\liminf_{t \to \infty} N(t) \geq 1 - \gamma_3 \epsilon_3 / r$ (using that $N(0) = \phi_N(0) > 0$). This is true for all $\epsilon_3 > 0$, hence $\liminf_{t \to \infty} N(t) \geq 1$ and we conclude that $\lim_{t \to \infty} N(t) = 1$.

Now we look at (2.2.1) to show that $u_i(t) \to 0$ as $t \to \infty$. Let $\epsilon_4$ be arbitrary. Since $N(t) \to 1$ and $u_m(t) \to 0$,

$$b(u_m(t))N(t) - e^{-\mu t}b(u_m(t - \tau))N(t - \tau) \to 0 \quad \text{as} \quad t \to \infty.$$

Therefore there exists a $T_4 > 0$ such that when $t > T_4$

$$-\epsilon_4 \leq b(u_m(t))N(t) - e^{-\mu t}b(u_m(t - \tau))N(t - \tau) \leq \epsilon_4.$$

Therefore when $t > T_4$

$$-\epsilon_4 - \mu u_i(t) < u_i(t) < \epsilon_4 - \mu u_i(t). \tag{2.2.24}$$

From the right hand side of (2.2.24), $\limsup_{t \to \infty} u_i(t) \leq \epsilon_4 / \mu$ and from the left hand side, $\liminf_{t \to \infty} u_i(t) \geq -\epsilon_4 / \mu$. This is true for all $\epsilon_4 > 0$. Therefore

$$0 \leq \liminf_{t \to \infty} u_i(t) \leq \limsup_{t \to \infty} u_i(t) \leq 0.$$

Hence $\lim_{t \to \infty} u_i(t) = 0$.

So $u_i(t) \to 0$, $u_m(t) \to 0$ and $N(t) \to 1$ as $t \to \infty$, thus the proof is complete.

**Remark:** If in equation (2.2.3), $\gamma N(t)u_m(t)$ is replaced by $\gamma N(t)u_i(t)$ or $\gamma N(t)u_m(t - \tau)$ then Theorem 8 still holds, but in the proof for the case $\gamma N(t)u_i(t)$ we have to show $u_i \to 0$ and then $N(t) \to 1$, rather than vice versa.
2.3 Numerical simulations

To investigate system (2.2.1, 2.2.2, 2.2.3) further we wrote a computer programme, in Fortran, to numerically simulate the evolution of the system over time. For the simulation we needed to specify our functions, so we chose \( b(u_m) = Pu_m e^{-Au_m} \), as in [27], and \( d(u_m) = Cu_m \), for some real numbers \( A, C, P \), which we could vary as appropriate. The time stepping was carried out using the Adams-Bashforth method. The Adams-Bashforth method is an explicit linear multi-step method (i.e. it uses previous points such as \( h_{t-1}, h_{t-2}, \ldots, h_{t-n} \) to calculate \( h_{t+1} \), instead of just \( h_t \). This method can be adapted to use as many previous points as you like. We use the second order Adams-Bashforth method which just uses one previous point, \( h_{t-1} \). This has the form

\[
h_{t+1} = h_t + \frac{dt}{2} \left\{ 3 \left( \frac{\partial h}{\partial t} \right)_t - \left( \frac{\partial h}{\partial t} \right)_{t-1} \right\},
\]

(2.3.1)

where \( dt \) is the time step. A large time step can cause numerical instabilities but as our model did not involve more complicated variables such as diffusion we were able to set \( dt = 1 \). Theorem 8 showed that we would expect global stability of the equilibrium state \((u_i, u_m, N) = (0, 0, 1)\) if the condition \( e^{-\mu r} b(u_m) \leq d(u_m) + \mu r u_m \), for all \( u_m > 0 \) was satisfied. So for our initial simulation we used the values \( A = 5, C = 0.1, \mu_i = 0.01, \mu_T = 0.01, \gamma_s = 0.1, \gamma = 1, P = 0.1 \) and \( \tau = 5 \) to satisfy this condition. Setting \( \tau = 5 \) means that at iteration \( t \) of our programme, immature blowflies from iteration \( t-5 \) would mature (in this case, as \( dt = 1 \), 1 iteration corresponds to 1 day). While it is known that the maturation time of an immature blowfly of the species *Lucilia cuprina* is about 15 days [27] we envisage that our model may be applied to other species which have different maturation rates. As expected over time the populations approached the equilibrium state \((u_i, u_m, N) = (0, 0, 1)\), see Figure 2.2. The sheep population tends to 1 fairly quickly and the mature blowfly population tends to zero over time, note the scale of the immature blowfly population is very small.

Next we investigated the situation when the condition for global stability of the steady state \((0, 0, 1)\) was not initially satisfied. We found that this would be the case if we changed the value of \( P \) from 0.1 to 0.2, as seen in Figure 2.3. In this case the condition was satisfied to start off with, but not after 68 iterations, which resulted in the populations settling down to a different equilibrium \((u_i^*, u_m^*, N^*)\), where the blowflies and sheep coexist. By increasing the value of \( P \) further we started to
get oscillations in our populations. These oscillations decayed exponentially. The larger the value of \( P \) the longer it took for the oscillations to die away and when \( P = 9 \) they still have not after 1000 days, see Figure 2.3. We see that the eventual equilibrium populations of the immature and mature blowflies are proportional to \( P \). Next we set \( P = 10 \) and looked at the effect of increasing the delay, \( \tau \). Figure 2.4 shows us that for small values of \( \tau \) our system tends to an equilibrium solution with non-zero populations for all species. We see that as the delay is increased the eventual equilibrium population of the immature and mature blowflies increases. We also see that the size of the oscillations of the populations increase with \( \tau \), but still decays exponentially over time. However for \( \tau \geq 5 \) the oscillations do not appear to decay and we have a periodic solution. Looking at the graph when \( \tau = 50 \) (Figure 2.5 d) we can see that in the period before any of the immature blowflies mature, \( t < 50 \), the mature blowfly population decreases tending, to zero, and the sheep population increases, tending to 1. The immature blowfly population increases accordingly. However at the 50th iteration the immature blowflies will start to mature causing the mature blowfly population to increase and the sheep to decrease. At this point there is a sharp increase in the number of births of immature blowflies as we suddenly have more mature blowflies and lots of sheep. However the
increase of mature blowflies soon causes a decrease in the sheep population and so the birth rate of the mature blowflies decreases as does the birth rate of the immature blowflies. At iteration 100 there is a sharp increase in the mature blowflies as the immature blowflies from the 50th iteration mature. This causes a sharp decrease in the sheep population and therefore also in the immature blowfly population, which decrease to zero. Now we are back in a similar situation to what we had at the start. The mature blowflies decrease, tending to zero, the sheep increase, tending to one, and the immature blowflies increase accordingly. The whole process repeats itself in a similar manner, over and over. We see that the population of the mature blowflies have the 'second burst' feature observed in Nicholson’s blowfly data, [47] and reproduced by the model of Gurney, Blythe and Nisbet, [27]. However we see that the immature population exhibits two types of oscillation, one shorter one that shows the 'second burst' phenomenon and a larger one that only appears to have one burst.

Figure 2.6 illustrates with an example when $\tau = 90$ that for large values of $\tau$ there is a period of instability at the start of the simulation where the populations oscillate wildly. However the populations eventually settle down to a stable oscillating pattern.
Figure 2.4: Graphs to show the solution of the system settling down to equilibrium populations for small values of $\tau$ when $P = 10$ and $dt = 1$. Parameter values used are $A = 5, C = 0.1, \mu_i = 0.01, \mu_T = 0.01, \gamma_s = 0.1, r = 1$.

Figure 2.5: Graphs to show the solution of the system tending to a periodic solution for larger values of $\tau$ when $P = 10$ and $dt = 1$. Parameter values used are $A = 5, C = 0.1, \mu_i = 0.01, \mu_T = 0.01, \gamma_s = 0.1, r = 1$. 

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Figure 2.6: Graphs to show the periodic solution of the system when $\tau = 90$, $P = 10$ and $dt = 1$. Parameter values used are $A = 5$, $C = 0.1$, $\mu_i = 0.01$, $\mu_T = 0.01$, $\gamma_s = 0.1$, $r = 1$. Here the data was plotted every 10 iterations, so on the x axis, 1 corresponds to 10000 iterations.

Figure 2.7: Graphs to show the global stability of the equilibrium solution $(u^*_m, N^*)$, when using the quadratic death rate term $d(u_m) = C u_m^2$, with $P = 10$, $\tau = 5$ and $dt = 1$. Parameter values used are $A = 5$, $C = 0.1$, $\mu_i = 0.01$, $\mu_T = 0.01$, $\gamma_s = 0.1$, $r = 1$. 
Next we looked at the effect of making \( d(u_m) \) a quadratic term by setting it equal to \( Cu_m^2 \), (2.7). We saw that the quadratic death term caused the solutions to settle down to an equilibrium value more quickly.

### 2.3.1 Realistic values for Myiasis

Here we attempt to use parameter values that reflect previous observations. Much work has been done on investigating blowfly populations and it is reasonable to assume that the maturation rate of the larvae in Nicholson’s experiments with unlimited food supply, [47] will be comparable with the maturation rate of the larvae living on sheep. Gurney, Blythe and Nisbet found this delay to be \( 14.8 \pm 0.4 \) days, [27], thus it is reasonable for us to use the value of \( \tau = 15 \) days in our simulations. They also infer from Nicholson’s data that the value of \( P \) is between 7.4 and 11.4 eggs per day. However observational evidence suggests that blowflies lay eggs in batches of around 200 and lay 2 to 3 batches in their lifetime which is about a month, [31]. Even a conservative estimate of 500 eggs in 30 days gives a value of 16.667 for \( P \) which is outside the range suggested by Gurney et al.. Examination of Nicholson’s data suggests that the population of mature blowflies which maximises the number of eggs laid is very small compared to the peaks observed and thus we set \( A = 10 \). This just leaves us with the death rates of the species. Gurney et al. approximate \( Cr \) in different cases and find it to be fairly constant at around 3, [27]. They also claim that this value is in good agreement with an independent estimate. Thus as we set \( \tau = 15 \) we derive a value for \( C \) of 0.2.

As we are working on a scale of days the natural death rate of sheep will be negligible, so their death rate will be proportional to the rate of fatality of myiasis. It is well known that there is a large degree of aggregation in the laying of eggs and as a result only a few sheep in a flock would be expected to actually be infected. Wardhaugh and Dallwitz [64] collected data on the prevalence of myiasis on 25 farms around Canberra in the late 1970’s. They examined the sheep at 3 times during the year. Their data was analysed by Fenton et al., [20] who found that over the course of the 1978/79 season 0.91% of sheep were infected and in the 1979/80 season 2.16% of sheep were infected. Therefore we set the death rate of the sheep, \( \gamma_s \) to be 0.02 although it is clear that farmers will check their sheep often and remove any infestations they find thus reducing the death rate further.

Figure 2.8 shows two graphs from the same simulation. The first graph shows
Figure 2.8: difference between viewing egg populations and whole larvae populations, eggs seem to give a clearer picture. Parameter values are $\mu_1 = 0.01, \mu_T = 0, \gamma_s = 0.1, r = 1, A = 10, C = 0.2, P = 500/30, \tau dt = 15.$
Figure 2.9: shows difference in evolution depending on how the death of sheep is modelled; a) $\gamma_s N(t) u_m(t)$, b) $\gamma_s N(t) u_m(t - \tau)$, c) $\gamma_s N(t) u_l(t)$. The bold line represents the eggs, the dotted line represents mature blowflies and dashed line represents sheep. Parameter values are $\mu_i = 0.05, \mu_T = 0, \gamma_s = 0.1, \tau = 1, A = 10, C = 0.2, P = 500/30, \tau dt = 15$.

the number of eggs laid by the blowflies with the population of sheep and mature blowflies while the second graph shows the immature population with the sheep and mature blowfly population. This graph is not as illuminating as the large population of immature blowflies dwarf the other two and it is difficult to see the changes. We can see that the evolution of the mature blowflies more closely resembles the eggs laid than the evolution of the immature blowflies. It is clear to see that the 'second burst' phenomenon is more pronounced in the eggs than the larvae, where there is no significant dip in population, just an extra increase. The blowfly populations in the first graph resemble Figure 6c of the paper by Gurney et al [27] which they claim provides a satisfying qualitative fit to Nicholson's blowfly data [47]. Figure 2.9 shows that when the death rate of sheep depends on the number of mature blowflies present at time $t$ then the sheep population decreases when there are lots of mature blowflies present. However it is the immature blowflies that infect the sheep and so we would expect the sheep population to decrease more when there are many immature blowflies. Due to the maturation rate the maximum populations of immature blowflies do not coincide with the maximum population of mature blowflies and thus in the case of self sustained periodic limit cycles it does not seem
appropriate for the death rate of the sheep to depend on the mature blowflies at time $t$. The second graph in Figure 2.9 shows the evolution when the death rate depends on the number of blowflies present at time $t - \tau$, this seems more appropriate as now the sheep population decreases when there are many immature blowflies and increases when there are not. By comparing with the first graph we can see that it is similar but the sheep population rises in the second graph where it falls in the first graph and vice versa. This change in the death rate of sheep does not seem to have affected the blowfly populations. The third graph shows the evolution when the death rate of the sheep depends on the immature blowflies present at time $t$. This graph does look different as there is wider variation in the sheep population and in the blowfly populations the first 'burst' is now larger than the second 'burst'. However there is a larger population of immature blowflies than mature and so to directly compare the two cases the coefficient of the death rate of sheep $\gamma_s$ would need to be rescaled. Figure 2.10 shows the effect of changing the parameter $r$. This coefficient is a time scale that models the effectiveness of the response of the sheep population to any changes. So when $r$ is big as in the third graph the population will adapt quickly and there will be little change in the population. However when $r$ is small it takes longer for the population to adapt and we can see from the first graph that if $r$ is small enough then the periodic solution observed in the other two graphs will be destroyed and the populations will settle down to a stable equilibrium. In Figure 2.11 we see that by increasing the death rate of the larvae, $\mu_i$, we destabilise our periodic solution. A small increase removes the second burst phenomenon from the adult blowfly population. A larger increase gives a solution with exponentially decreasing oscillations over time which eventually settle down to a stable equilibrium where the species co-exist. However if $\mu_i$ is increased enough then it will cause the extinction of both the immature and mature blowflies and the sheep population will tend to the carrying capacity.

Figures 2.12 and 2.13 show the effect of an increase in trapping, $\mu_T$. Note that as we have a linear death term for the mature blowflies increasing trapping is effectively just increasing the death rate of the mature blowflies. We can see from Figure 2.12 that increasing trapping on the same scale as we increased the immature blowfly death rate does not have the same effect. It just destabilises the periodic solution causing an aperiodic complex solution similar to Figure 6d of Gurney et al. [27]. However the first graph of Figure 2.13, when $\mu_T = 1.5$, shows that this instability just occurs at the beginning of the simulation and that it eventually settles down to
Figure 2.10: difference in evolution depending on how much weight is given to logistic growth. Parameter values are $\mu_l = 0.05, \mu_T = 0, \gamma_s = 0.1, A = 10, C = 0.2, P = 500/30, \tau dt = 15$. 
Figure 2.11: shows evolution with different death rates of larvae. Parameter values are $\mu_T = 0$, $\gamma_s = 0.1$, $r = 0.4$, $A = 10$, $C = 0.2$, $P = 500/30$, $\tau dt = 15$.

Figure 2.12: shows evolution with different trapping rates. Parameter values are $\mu_i = 0$, $\gamma_s = 0.1$, $r = 1$, $A = 10$, $C = 0.2$, $P = 500/30$, $\tau dt = 15$. 
Figure 2.13: shows evolution with large trapping rates. Parameter values are $\mu_t = 0$, $\gamma_a = 0.1$, $\tau = 0.4$, $A = 10$, $C = 0.2$, $P = 500/30$, $\tau dt = 15$.

a smooth periodic solution. We can see from the second graph of Figure 2.13, when $\mu_T = 5$ that a bigger increase in trapping will cause the populations to settle down to a stable equilibrium solution. A further increase causes a return to a periodic solution but now there are extended periods where there are no adult blowflies as they have all been killed off by trapping, Figure 2.13 $\mu_T = 10$. In the end we see that if trapping is effective enough then we will get exponential decay of the blowfly population eventually wiping out the population, Figure 2.13 $\mu_T = 20$. However trapping needs to be so effective that it wipes out the recently matured blowflies before they have a chance to lay eggs, otherwise those eggs will just mature later causing another wave of blowflies.

These simulations show that focusing attention on removing the immature blowflies is a more effective way of containing blowfly strike than attempting to trap the mature blowflies, as the increase in death rate of immature blowflies needed to wipe out the population is significantly less than the increase needed in the death rate of the mature blowflies to have the same effect. However this result is for the case of a linear trapping term and would not hold if the term were a non-linear function. In our simulation we do not take into account the prospect of new blowflies coming in from outside to replace the ones that have been wiped out. However it is known that blowflies are attracted to areas where there are currently infected sheep and if the blowfly population is effectively wiped out there should not be a significant
number of infected sheep to attract outside blowflies.
2.4 A model with distributed delay

Up to now we have considered the model

\[ u'(t) = b(u_m(t))N(t) - \mu_i u_i(t) - e^{-\mu_T} b(u_m(t - \tau))N(t - \tau) \]  (2.4.1)
\[ u'_m(t) = e^{-\mu_T} b(u_m(t - \tau))N(t - \tau) - d(u_m(t)) - \mu_T u_m(t) \]  (2.4.2)
\[ N'(t) = r N(t) (1 - N(t)) - \gamma_s N(t) u_m(t), \]  (2.4.3)

where \( \mu_i, \mu_T, \gamma_s, r \) are all positive constants.

However this model only accounts for a discrete delay. So only larvae born at time \( t - \tau \) will mature at time \( t \). However it is much more likely that at each time we will have larvae born at a range of previous times maturing as one would not expect all larvae to mature at exactly the same time in their life. To incorporate this into our model we want to alter the maturation rate term, \( e^{-\mu_T} b(u_m(t - \tau))N(t - \tau) \), so that larvae born at a range of different previous times will mature at time \( t \). One way of doing this is to use a probability distribution for the time taken to mature. Let us define \( p(s) \) by saying that, for small \( ds \), \( p(s)ds \) is the probability that the maturation time is between \( s \) and \( s + ds \). Then

\[ \int_0^\infty p(s)ds = 1. \]  (2.4.4)

Note that mortality during the larval stage is accounted for by the \( e^{-\mu_s} \) term. We can multiply the maturation rate by the probability density function, \( p(s) \geq 0 \), and then integrate over all possible maturation times so the maturation rate at time \( t \) becomes

\[ \int_0^\infty e^{-\mu_s} b(u_m(t - s))N(t - s)p(s)ds. \]  (2.4.5)

Therefore the model becomes

\[ u'(t) = b(u_m(t))N(t) - \mu_i u_i(t) - \int_0^\infty e^{-\mu_s} b(u_m(t - s))N(t - s)p(s)ds \]  (2.4.6)
\[ u'_m(t) = \int_0^\infty e^{-\mu_s} b(u_m(t - s))N(t - s)p(s)ds - d(u_m(t)) - \mu_T u_m(t) \]  (2.4.7)
\[ N'(t) = r N(t) (1 - N(t)) - \gamma_s N(t) u_m(t), \]  (2.4.8)
subject to the initial conditions

\[ u_i(0) = u_{i,0} \geq 0, \quad u_m(s) = \phi_m(s) \geq 0, \quad N(s) = \phi_N(s) \geq 0, \quad \text{for all} \quad s \in [-\infty, 0], \]

(2.4.9)

where \( \mu_i, \mu_T, \gamma_s, \tau \) are all positive constants.

We would still want in this situation to have some parameter \( \tau \) measuring the mean amount of time spent in the larval stage. Some larvae will mature more quickly and some more slowly. One possibility for the probability density function, \( p(s) \), would be to use the exponential distribution with mean \( \tau \), (2.4.10), although the gamma distribution, (2.4.11), with mean defined as \( \tau = \beta/\alpha \), where \( \alpha = a/\tau, \beta = a \), with \( a \) defined in (2.4.11), might be more appropriate in this situation. These distributions are:

\[
\begin{align*}
p(s) &= \frac{1}{\tau} e^{-s/\tau}, \quad \text{(2.4.10)} \\
p(s) &= \frac{(a/\tau)^a s^{a-1} e^{-as/\tau}}{\Gamma(a)}, \quad \text{(2.4.11)}
\end{align*}
\]

where \( \Gamma \) is the gamma function. As with the discrete delay model we see that (2.4.7) and (2.4.8) do not depend on \( u_i(t) \) and can thus be solved independently of (2.4.6).

2.4.1 Positivity and Boundedness

**Proposition 9** Suppose (2.2.5) holds for the system (2.4.6, 2.4.7, 2.4.8) subject to the initial conditions (2.4.9) and a compatibility condition similar to (2.2.6) in Proposition 4. Suppose also that \( p(s) \geq 0 \), (2.4.4) holds and \( \phi_m(0), \phi_N(0) > 0 \). Then \( u_i(t), u_m(t), N(t) > 0 \) for all \( t > 0 \).

**Proof:** We see that the equation for the sheep remains the same as in (2.2.3). Therefore positivity for the sheep can be shown the same way as in Proposition 4.

We now claim that \( u_m(t) > 0 \) for all \( t > 0 \). We shall prove this by contradiction. Assume that there exists a first time \( t_0 > 0 \) at which \( u_m(t_0) = 0 \). Then we will have that \( u_m(t) > 0 \) for all \( t \in [0, t_0) \). Since \( N(t) > 0 \) for all \( t > 0 \) we see that we can...
write the integral in (2.4.7) at time $t = t_0$ as
\[
\int_0^{t_0} e^{-\mu s} b(u_m(t_0 - s)) N(t_0 - s) p(s) ds \\
= \int_0^{t_0} e^{-\mu s} b(u_m(t_0 - s)) N(t_0 - s) p(s) ds + \int_{t_0}^{\infty} e^{-\mu s} b(u_m(t_0 - s)) N(t_0 - s) p(s) ds \\
= \int_0^{t_0} e^{-\mu s} b(u_m(t_0 - s)) N(t_0 - s) p(s) ds + \int_{t_0}^{\infty} e^{-\mu s} b(u_m(t_0 - s)) N(t_0 - s) p(s) ds \\
> 0.
\]

Evaluating (2.4.7) at time $t_0$ gives
\[
u_m'(t_0) > -d(u_m(t_0)) - \mu_T u_m(t_0) = 0.
\]
However, this is a contradiction because $t_0$ is the first time at which $u_m(t)$ is zero, so we should have $\nu_m'(t_0) \leq 0$. Thus $u_m(t) > 0$ for all $t > 0$. It now remains to prove that $u_i(t) > 0$ for all $t > 0$. For this we note that the solution to (2.4.6) is
\[
u_i(t) = \int_{-\infty}^{t} \left( \int_{t-s}^{\infty} p(\xi) \ d\xi \right) b(u_m(s)) N(s) e^{-\mu(s-t)} ds,
\]
which, given that $u_m(t)$ and $N(t)$ are positive implies that $u_i(t)$ must also be positive and thus the proof is complete.

**Proposition 10** Suppose (2.2.5) holds for the system (2.4.6, 2.4.7, 2.4.8) subject to the initial conditions (2.4.9). Also suppose that $\phi_m(0), \phi_N(0) > 0$. Then $u_i(t), u_m(t), N(t)$ are bounded.

**Proof:** Again the equation for $N(t)$ is the same as (2.2.3) and so boundedness can be shown similarly to Proposition 5.

To show boundedness of $u_m(t)$ note that (2.4.7) can be written as
\[
u_m'(t) \leq b_{\text{max}} \int_0^{\infty} e^{-\mu s} N(t-s) p(s) ds - \mu_T u_m(t).
\]
Since $N(t)$ is bounded we can write
\[
u_m'(t) \leq b_{\text{max}} \sup_{s \geq 0} N(t) \int_0^{\infty} e^{-\mu s} p(s) ds - \mu_T u_m(t).
\]
Hence
\[
\lim_{t \to \infty} \sup \ u_m(t) \leq \frac{b_{\text{max}} \ N_{\text{sup}}}{\mu_T} \int_0^{\infty} e^{-\mu s} p(s) ds,
\]
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where $N^{sup} = \sup_{t \geq 0} N(t)$. Hence $u_m(t)$ is bounded.

To show boundedness of $u_i(t)$ note that (2.4.6) can be written as

$$u_i'(t) \leq b^{max} N^{sup} - \mu_i u_i(t).$$

Hence

$$\limsup_{t \to -\infty} u_i(t) \leq \frac{b^{max} N^{sup}}{\mu_i},$$

so $u_i(t)$ is bounded.

### 2.4.2 Equilibrium solutions

Looking for equilibrium solutions of (2.4.7) and (2.4.8) we find that we must satisfy

$$N \int_0^\infty e^{-\mu_i t} b(u_m)p(s)ds = d(u_m) + \mu_T u_m$$

$$r N(1 - N) = \gamma_s N u_m,$$

we can see that two such solutions are $(u_m, N) = (0, 0), (0, 1)$. We investigate the linear stability of these solutions using the same method as for the discrete delay case. We perturb and linearise the system (2.4.7) and (2.4.8) to get the matrix equation:

$$\begin{pmatrix}
\sigma - \int_0^\infty e^{-\mu_i t} e^{-\gamma s} b(u_m^*) p(s) ds + d'(u_m^*) + \mu_T - \int_0^\infty e^{-\mu_i t} e^{-\gamma s} b(u_m^*) p(s) ds \\
\gamma_s N^* - r (1 - 2N^*) + \gamma_s u_m^*
\end{pmatrix} \begin{pmatrix} c_1 \\ c_2 \end{pmatrix} = 0,$$

(2.4.12)

where $(u_m, N) = (u_m^*, N^*)$ is the equilibrium under consideration. For non-trivial solutions the determinant of this matrix must be zero.

**Theorem 11** Suppose for the system (2.4.6,2.4.7,2.4.8) that (2.2.5) holds. Then the equilibrium point $(u_m^*, u_m^*, N^*) = (0, 0, 0)$ is linearly unstable.

**Proof:** Note that if $u_m(t) \to 0$ and $N(t) \to$ any limit (not necessarily zero) then (2.4.6) implies $u_i(t) \to 0$. Therefore we can focus on (2.4.7) and (2.4.8) only. For the equilibrium point $(u_m^*, N^*) = (0, 0)$ equation (2.4.12) becomes

$$\begin{pmatrix}
\sigma + d'(0) + \mu_T & 0 \\
0 & \sigma - r
\end{pmatrix} \begin{pmatrix} c_1 \\ c_2 \end{pmatrix} = 0,$$
giving the eigenvalue equation

\[(\sigma + d'(0) + \mu_T)(\sigma - r) = 0,\]

which has a root \(\sigma = r > 0\). Thus the zero solution is linearly unstable.

**Theorem 12** Suppose for the system (2.4.6, 2.4.7, 2.4.8) that (2.2.5) holds and also that

\[b'(0) \int_0^\infty p(s) e^{-\mu_s} ds < d'(0) + \mu_T,\]

then the equilibrium point \((u_n^*, u_m^*, N^*) = (0, 0, 1)\) is linearly stable.

**Proof:** Again note that if \(u_n(t) \to 0\) and \(N(t) \to 1\) then \(u_m(t) \to 0\). So we focus on (2.4.7) and (2.4.8) only. For the equilibrium point \((u_m^*, N^*) = (0, 1)\) we find that (2.4.12) becomes

\[
\begin{pmatrix}
\sigma - \int_0^\infty e^{-\mu_s} e^{-\alpha_s b'(0)p(s)ds + d'(0) + \mu_T} & 0 \\
\gamma_s & \sigma + r
\end{pmatrix}
\begin{pmatrix}
c_1 \\ c_2
\end{pmatrix} = 0,
\]

giving the eigenvalue equation:

\[
\left(\sigma - \int_0^\infty e^{-\mu_s} e^{-\alpha_s b'(0)p(s)ds + d'(0) + \mu_T}\right)(\sigma + r) = 0.
\]

This time we have that one of the roots is \(\sigma = -r < 0\). For this equilibrium point to be linearly stable we now need to show that the other roots will also be in the left half of the complex plane. For a contradiction, let us assume that there exists a root \(\hat{\sigma}\) in the right hand side of the complex plane. Then

\[
|\hat{\sigma} + d'(0) + \mu_T| = \left| \int_0^\infty e^{-\mu_s} e^{-\alpha_s b'(0)p(s)ds} \right|
\leq b'(0) \int_0^\infty p(s) |e^{-\mu_s}||e^{-(\text{Re}(\hat{\sigma}) + i\text{Im}(\hat{\sigma}))s}| ds
\leq b'(0) \int_0^\infty p(s) e^{-\mu_s} |e^{-\text{Re}(\hat{\sigma})s}| ds
\leq b'(0) \int_0^\infty p(s) e^{-\mu_s} ds.
\]

Therefore \(\hat{\sigma}\) is in the disk of radius \(b'(0) \int_0^\infty p(s) e^{-\mu_s} ds\) centred at \(-d'(0) - \mu_T\). If we choose the radius of this disk such that the whole disk is in \{Re\(\hat{\sigma}\) < 0\} then we have a contradiction. This will be the case if

\[b'(0) \int_0^\infty p(s) e^{-\mu_s} ds < d'(0) + \mu_T,\]

(2.4.14)
which holds by hypothesis. Therefore the equilibrium point \((u^*_i, u^*_m, N^*) = (0, 0, 1)\) will be linearly stable.

**Corollary 1** Suppose for the system (2.4.6, 2.4.7, 2.4.8) that (2.2.5) holds and also that

\[
p(s) = \frac{\alpha^\beta s^{\beta-1}e^{-\beta s}}{\Gamma(\beta)}
\]

(2.4.15)

\[
\frac{\alpha^\beta b'(0)}{\alpha + \mu_i} < d'(0) + \mu_T,
\]

(2.4.16)

then the equilibrium point \((u^*_i, u^*_m, N^*) = (0, 0, 1)\) is linearly stable.

**Proof:** It is reasonable to assume that the distribution of maturation rates will follow a gamma distribution. The general form of the gamma distribution is given by (2.4.15) for some positive constants \(\alpha, \beta\). So substituting (2.4.15) into the left hand side of inequality (2.4.14) gives

\[
b'(0) \int_0^\infty s^{\beta-1}e^{-s}ds = \frac{b'(0)\alpha^\beta}{\Gamma(\beta)} \int_0^\infty s^{\beta-1}e^{-s}ds.
\]

Making the substitution \(s = (\alpha + \mu_i)s\) we get

\[
b'(0)\alpha^\beta \int_0^\infty \frac{(\alpha + \mu_i)^{\beta-1}e^{-s}}{\alpha + \mu_i}d\hat{s} = \frac{b'(0)\alpha^\beta}{\Gamma(\beta)(\alpha + \mu_i)^\beta} \int_0^\infty s^{\beta-1}e^{-s}d\hat{s}.
\]

We see that our integral is just the definition of the Gamma function: \(\Gamma(\beta) = \int_0^\infty s^{\beta-1}e^{-s}ds\). Thus inequality (2.4.14) becomes

\[
\frac{b'(0)\alpha^\beta}{\alpha + \mu_i} < d'(0) + \mu_T,
\]

(2.4.17)

which holds by hypothesis. We have shown that the equilibrium point \((u^*_i, u^*_m, N^*) = (0, 0, 1)\) is linearly stable and the proof is complete.

We can see further that if we take \(p(s)\) to be the particular Gamma distribution (2.4.11) as suggested previously, with \(a = 2\), then we get the condition

\[
\frac{4b'(0)}{(2 + \mu_T)^2} < d'(0) + \mu_T.
\]

If we chose the exponential distribution (2.4.10), which is just a special case of the gamma distribution with \(\alpha = 1/\tau, \beta = 1\), then we have

\[
\frac{b'(0)}{(1 + \mu_T)} < d'(0) + \mu_T.
\]
For sufficiently small $\mu T$, i.e., if the death rate of the immature species is small compared to the delay, we can make the approximation $(1 + \mu T) \approx e^{\mu T}$ and our inequality becomes

$$e^{-\mu T}b'(0) < d'(0) + \mu T,$$

which is the condition in Theorem 7 for linear stability in the discrete delay case.

**Theorem 13** Suppose (2.2.5) holds for the system (2.4.6,2.4.7,2.4.8) subject to the initial conditions (2.4.9) and also that $p(s) = 0$ for all $s \geq \tau$, for some $\tau > 0$. Also assume that

$$d(u_m) + \mu T u_m > b(u_m) \int_0^\tau e^{-\mu s}p(s)ds \text{ for all } u_m > 0,$$  \hspace{1cm} (2.4.18)

then the equilibrium point $(u^*_i, u^*_m, N^*) = (0, 0, 1)$ is globally asymptotically stable.

**Remark:** It is reasonable to assume that $p(s) = 0$ for all $s \geq \tau$, for some $\tau > 0$ (i.e. $p(s)$ has compact support) as we would expect there to be an upper limit on how long it takes for a larva to develop.

**Proof:** First we note that if $u_m(t) = 0$ then the result is trivial. Under the conditions in the Theorem (2.4.7) becomes

$$u'_m(t) = \int_0^\tau e^{-\mu s}b(u_m(t-s))N(t-s)p(s)ds - d(u_m(t)) - \mu T u_m(t).$$

From positivity of $N(t)$ and $u_m(t)$, $N'(t) \leq rN(t)(1 - N(t))$ and therefore $\limsup_{t \to \infty} N(t) \leq 1$. Let $\epsilon > 0$ be arbitrary. Then there exists $T > 0$ such that for $t \geq T, N(t) < 1 + \epsilon$. So when $t \geq T + \tau, N(t-s) < 1 + \epsilon$ for all $s \leq \tau$. Thus (2.4.7) becomes

$$u'_m(t) \leq \int_0^\tau e^{-\mu s}b(u_m(t-s))(1 + \epsilon)p(s)ds - d(u_m(t)) - \mu T u_m(t).$$ (2.4.19)

We first claim that $u_m(t)$ is not eventually monotonically increasing. Assume the contrary then, as we know that $u_m(t)$ is bounded there exists a $\ell > 0$ such that $u_m(t) \to \ell$ as $t \to \infty$. Thus letting $t \to \infty$ in (2.4.19) we get

$$0 \leq b(\ell)(1 + \epsilon) \int_0^\tau e^{-\mu s}p(s)ds - d(\ell) - \mu T \ell.$$

Now letting $\epsilon \to 0$ we get

$$d(\ell) + \mu T \ell \leq b(\ell) \int_0^\tau e^{-\mu s}p(s)ds,$$ \hspace{1cm} (2.4.20)
which, as \( \ell > 0 \) contradicts the hypothesis (2.4.18) in the Theorem.

Now if we assume that \( u_m(t) \) is eventually monotonically decreasing then as we know that \( u_m(t) \geq 0 \) it must eventually approach a limit, \( \ell_1 \), as \( t \to \infty \). We want that limit to be 0. By the above analysis we get a contradiction if \( \ell_1 > 0 \), so \( \ell_1 \) must be equal to 0.

This just leaves the case where \( u_m(t) \) is neither eventually monotonically increasing nor eventually monotonically decreasing. In this case there exists a sequence of times \( t_k \to \infty \) such that \( u_m'(t_k) = 0 \) and \( u_m(t_k) \to \ell_2 \) as \( k \to \infty \), where \( \ell_2 = \limsup_{t \to \infty} u_m(t) \). So again it is sufficient to show that \( \ell_2 = 0 \). Using (2.4.19) at \( t = t_k \), assuming \( k \) is sufficiently large that \( t_k \geq T + \tau \), we get

\[
0 = u_m'(t_k) \leq \int_0^T e^{-\mu s} b(u_m(t_k - s))(1 + \epsilon)p(s)ds - d(u_m(t_k)) - \mu_T u_m(t_k).
\]

\[0 \leq b^{\max}(1 + \epsilon) \int_0^T e^{-\mu s}p(s)ds - d(u_m(t_k)) - \mu_T u_m(t_k). \tag{2.4.21}
\]

If we let \( k \to \infty \) and then let \( \epsilon \to 0 \) we conclude that

\[
d(\ell_2) + \mu_T \ell_2 \leq b^{\max} \int_0^T e^{-\mu s}p(s)ds.
\]

Recall that \( b^{\max} = b(u^{\max}) \), where \( u^{\max} > 0 \). We claim that \( \ell_2 < u^{\max} \). For a contradiction let us assume that \( \ell_2 \geq u^{\max} \). The right hand side of (2.4.23) is constant and the left hand side is increasing as a function of \( \ell_2 \). Therefore

\[
d(u^{\max}) + \mu_T u^{\max} \leq b(u^{\max}) \int_0^T e^{-\mu s}p(s)ds. \tag{2.4.24}
\]

However since \( u^{\max} > 0 \) this contradicts condition (2.4.18) in our theorem. So we must have that \( \ell_2 < u^{\max} \).

We have shown that \( \ell_2 = \limsup_{t \to \infty} u_m(t) < u^{\max} \), we now want to show that in fact \( \ell_2 = 0 \). Let \( \epsilon_2 > 0 \) be such that \( \ell_2 + \epsilon_2 \leq u^{\max} \). Then there exists a \( T_2 > 0 \) such that for all \( t \geq T_2 \) we have

\[
u_m(t) \leq \ell_2 + \epsilon_2 \quad \text{and} \quad N(t) \leq 1 + \epsilon_2.
\]

Next let \( k \) be sufficiently large that \( t_k - \tau \geq T_2 \). Then \( u_m(t_k - s) \leq \ell_2 + \epsilon_2 \) and \( N(t_k - \tau) \leq 1 + \epsilon_2 \) for all \( s \leq \tau \). As \( b(u_m) \) is increasing for all values up to \( u^{\max} \) and \( \ell_2 + \epsilon_2 \leq u^{\max} \) we have that when \( k \) is sufficiently large such that \( t_k - \tau \geq T_2 \),

\[
b(u_m(t_k - s)) \leq b(\ell_2 + \epsilon_2) \quad \text{for all} \quad s \leq \tau.
\]

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Therefore, putting into (2.4.7) and assuming $t_k - \tau \geq T_2$, we get

$$0 = u_m'(t_k) \leq \int_0^T e^{-\mu_\sigma b(\ell_2 + \epsilon_2)(1 + \epsilon_2)p(s)ds - d(u_m(t_k)) - \mu_T u_m(t_k)}.$$

Letting $k \to \infty$

$$0 \leq \int_0^T e^{-\mu_\sigma b(\ell_2 + \epsilon_2)(1 + \epsilon_2)p(s)ds - d(\ell_2) - \mu_T \ell_2},$$

$$b(\ell_2 + \epsilon_2)(1 + \epsilon_2) \int_0^T e^{-\mu_\sigma p(s)ds} \geq d(\ell_2) + \mu_T \ell_2.$$ 

Since this holds for all sufficiently small $\epsilon_2 > 0$, we have

$$b(\ell_2) \int_0^T e^{-\mu_\sigma p(s)ds} \geq d(\ell_2) + \mu_T \ell_2,$$

which contradicts the hypothesis of our theorem unless $\ell_2 = 0$. Thus we have that

$$\limsup_{t \to \infty} u_m(t) = 0,$$

i.e. $u_m(t) \to 0$ as $t \to \infty$.

Proof that $N(t) \to 1$ and $u_i(t) \to 0$ now follows similar to Theorem 8. Thus we conclude that the equilibrium solution $(u^*_i, u^*_m, N^*) = (0, 0, 1)$ will be globally asymptotically stable and the proof is complete.

### 2.5 A reaction-diffusion extension

We now look at the case where we allow the individuals to move about in space. The populations $u_i(t), u_m(t), N(t)$ become population densities $u_i(x, t), u_m(x, t), N(x, t)$ respectively and we include Fickian diffusion for the species via the Laplacian terms $D_i \Delta u_i, D_m \Delta u_m, D_n \Delta u_n$ where $D_i, D_m, D_n \geq 0$ are the diffusivities associated with the larvae, the mature blowflies and the sheep respectively. It is biologically reasonable to assume that larvae do not move about, [23], and so they would not diffuse. In our case the blowflies lay their eggs on the sheep and it is well known that sheep will, in general, move about. However if we think of our domain as a continuum of fields then it would be reasonable to assume that the sheep will not leave the field they are in and thus they would have a small diffusion rate. Hence the immature blowflies will also have a small diffusion rate and thus mature in approximately the same place they were born. This allows us to use the same maturation rate as before. When they are big enough the larvae drop off the sheep and burrow into the
ground where they pupate. For this reason we do not consider the sheep and the immature blowflies to have exactly the same rate of diffusion. The mature blowflies on the other hand would travel from farm to farm and so we expect a larger rate of diffusion for them. In this case our equations (2.2.1,2.2.2,2.2.3) become

\[
\begin{align*}
\frac{\partial u_i}{\partial t}(x,t) & = D_i \Delta u_i(x,t) + b(u_m(x,t))N(x,t) - \mu_i u_i(x,t) - e^{-\mu_i \tau}b(u_m(x,t-\tau))N(x,t-\tau) \\
\frac{\partial u_m}{\partial t}(x,t) & = D_m \Delta u_m(x,t) - d(u_m(x,t)) - \mu_T u_m(x,t) + e^{-\mu_T \tau}b(u_m(x,t-\tau))N(x,t-\tau) \\
\frac{\partial N}{\partial t}(x,t) & = D_n \Delta N(x,t) + r N(x,t)(1 - N(x,t)) - \gamma N(x,t)u_m(x,t),
\end{align*}
\]

(2.5.1)

(2.5.2)

(2.5.3)

where \((x,t) \in \Omega \times (0, \infty)\). We will consider both homogeneous Dirichlet boundary conditions

\[
u_i = 0, \quad u_m = 0, \quad N = 0, \quad \text{on} \quad \Gamma = \partial \Omega \times (0, \infty)
\]

(2.5.4)

and homogeneous Neumann boundary conditions

\[
\nabla u_i \cdot \mathbf{n} = 0, \quad \nabla u_m \cdot \mathbf{n} = 0, \quad \nabla N \cdot \mathbf{n} = 0, \quad \text{on} \quad \Gamma = \partial \Omega \times (0, \infty).
\]

(2.5.5)

Note that in system (2.5.1,2.5.2,2.5.3) above the delay only appears in the variables \(u_m\) and \(N\) and not \(u_i\). Therefore the initial data takes the form

\[
\begin{align*}
u_i(x,0) & = u_{i0}(x) \geq 0 \quad x \in \bar{\Omega} \\
u_m(x,s) & = u_{m0}(x,s) \geq 0 \quad (x,s) \in \bar{\Omega} \times [-\tau,0] \\
N(x,s) & = N_0(x,s) \geq 0 \quad (x,s) \in \bar{\Omega} \times [-\tau,0],
\end{align*}
\]

where \(\Omega \subset \mathbb{R}^n (n \geq 1)\) is a bounded domain with smooth boundary \(\partial \Omega\). Here \(D_i, D_n, D_m, \mu_i, \mu_T, r, \gamma_n\) are positive constants and \(D_i, D_n\) are very small compared to \(D_m\). Existence and uniqueness results for systems of this form can be found in Wu (1996) Chapter 2 [67].

If we wish to include a larger diffusion of sheep this will affect our model because now we have a case where larvae born in one place may move around (being carried about by the sheep) and mature in a different place. So the maturation rate at position \(x\) is no longer dependent on the number of eggs laid at position \(x\) at time \(t-\tau\). Instead it will depend on the number of larvae that are at position \(x\) at time
We explain how to construct a reaction-diffusion model which properly takes this into account on an infinite and one dimensional spatial domain. The rate of egg laying at position \( y \) at time \( t - \tau \) is \( b(u_m(y, t - \tau))N(y, t - \tau) \). The number that are still alive at time \( t \) is \( e^{-\mu \tau}b(u_m(y, t - \tau))N(y, t - \tau) \). Now we assume that the movement of the larvae follows a normal distribution with mean \( y \) and variance \( 4D_\tau \). Therefore the number of larvae born at \( y \) at time \( t - \tau \) who are at \( x \) at time \( t \) will be \( q(x - y)e^{-\mu \tau}b(u_m(y, t - \tau))N(y, t - \tau) \) where \( q(y) = \exp\{-y^2/4D_\tau\}/\sqrt{4\pi D_\tau} \).

To find out how many larvae are at position \( x \) at time \( t \) we need to integrate over \( y \in (-\infty, \infty) \) to get the contributions from all parts of the domain. Thus on an infinite domain the maturation term for the case when the immatures are mobile is

\[
\int_{-\infty}^{\infty} q(x - y)e^{-\mu \tau}b(u_m(y, t - \tau))N(y, t - \tau)dy
\]

and model (2.5.1,2.5.2,2.5.3) becomes

\[
\frac{\partial u_t}{\partial t}(x, t) = D_i\Delta u_t(x, t) + b(u_m(x, t))N(x, t) - \mu u_t(x, t) - \int_{-\infty}^{\infty} q(x - y)e^{-\mu \tau}b(u_m(y, t - \tau))N(y, t - \tau)dy \tag{2.5.6}
\]

\[
\frac{\partial u_m(x, t)}{\partial t} = D_m\Delta u_m(x, t) - d(u_m(x, t)) - \mu_T u_m(x, t) + \int_{-\infty}^{\infty} q(x - y)e^{-\mu \tau}b(u_m(y, t - \tau))N(y, t - \tau)dy \tag{2.5.7}
\]

\[
\frac{\partial N}{\partial t}(x, t) = D_n\Delta N(x, t) + rN(x, t)(1 - N(x, t)) - \gamma N(x, t)u_m(x, t). \tag{2.5.8}
\]

We can extend this further for \( (x, t) \in (-\infty, \infty) \times (0, \infty) \), to include the possibility that the maturation time might be a distribution (rather than the same for every blowfly). The number of larvae that are born at position \( y \) at time \( t - s \) is proportional to the number of mature blowflies and sheep present at position \( y \) at time \( t - s \), \( b(u_m(y, t - s))N(y, t - s) \). The number still alive at time \( t \) will be \( e^{-\mu s}b(u_m(y, t - s))N(y, t - s) \). The number that will mature at time \( t \) will be the number that take time \( s \) to mature, \( e^{-\mu s}b(u_m(y, t - s))N(y, t - s)p(s) \) and the number born at \( y \) that will mature at position \( x \) at time \( t \) is \( e^{-\mu s}b(u_m(y, t - s))N(y, t - s)p(s)q(x - y) \).

Now to account for all births at all times before \( t \) at all points in space we integrate over \( y \in (-\infty, \infty) \) and \( s \in [0, \infty) \) to give

\[
\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} e^{-\mu s}b(u_m(y, t - s))N(y, t - s)p(s)q(x - y)dyds, \tag{2.5.9}
\]

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which is the rate at which larvae mature at position $x$ at time $t$. So a reaction-diffusion model which allows the mature and immature blowflies and the sheep to all move about with no restriction on the relative sizes of their diffusivities would be

$$
\frac{\partial u}{\partial t}(x, t) = D_i \frac{\partial^2 u_i}{\partial x^2}(x, t) + b(u_m(x, t))N(x, t) - \mu_i u_i(x, t) \\
- \int_0^\infty \int_{-\infty}^\infty e^{-\mu_s b(u_m(y, t-s))}N(y, t-s)p(s)q(x-y)dyds,
$$

(2.5.10)

$$
\frac{\partial u_m}{\partial t}(x, t) = D_m \frac{\partial^2 u_m}{\partial x^2}(x, t) - d(u_m(x, t)) - \mu_T u_m(x, t) \\
+ \int_0^\infty \int_{-\infty}^\infty e^{-\mu_s b(u_m(y, t-s))}N(y, t-s)p(s)q(x-y)dyds,
$$

(2.5.11)

$$
\frac{\partial N}{\partial t}(x, t) = D_n \frac{\partial^2 N}{\partial x^2}(x, t) + \gamma N(x, t)(1 - N(x, t)) - \gamma_s N(x, t)u_m(x, t),
$$

(2.5.12)

for $x \in (-\infty, \infty)$, $t > 0$.

### 2.6 Simplified reaction-diffusion model

For ease of calculation we first decided to look at the following simpler model which just models the population of the mature blowflies

$$
\frac{\partial u}{\partial t}(x, t) = D\Delta u(x, t) + e^{-\mu_T b(u(x, t - \tau))} - d(u(x, t)) - \mu_T u(x, t),
$$

(2.6.1)

for $(x, t) \in \Omega \times (0, \infty)$, with homogeneous Dirichlet boundary condition

$$
u = 0, \quad \text{on} \quad \Gamma \equiv \partial \Omega \times (0, \infty)
$$

(2.6.2)

and initial condition

$$
u(x, \theta) = u_0(x, \theta) \geq 0, \quad \text{in} \quad \overline{\Omega} \times [-\tau, 0],
$$

(2.6.3)

where $\Omega \subset \mathbb{R}^n (n \geq 1)$ is a bounded domain with smooth boundary $\partial \Omega$. Here $D, \mu_T$ are positive constants.

Note that (2.6.1) is not a particular case of any of the previous models. Rather it is an alternative model which we might view as a reasonable approximation if there

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is effectively an unlimited supply of host sheep. The steady states, φ, of (2.6.1) will be functions of x and will satisfy

\[ DΔφ(x) + e^{-μτ}b(φ(x)) - d(φ(x)) - μTφ(x) = 0, \quad \text{for } x \in Ω \]

\[ φ(x) = 0, \quad \text{for } x \in \partialΩ. \]

Clearly one solution of this is φ(x) = 0.

### 2.6.1 Linear stability of the zero solution

**Theorem 14** Let (2.2.5) hold then the zero solution of (2.6.1) subject to (2.6.2) is linearly stable when

\[ e^{-μτb'(0)} - μT - d'(0) < Dλ_1, \]

and unstable when

\[ e^{-μτb'(0)} - μT - d'(0) > Dλ_1, \]

where λ_1 is the principal eigenvalue of −Δ on homogeneous Dirichlet boundary conditions.

**Proof:** First let us linearise (2.6.1) about the zero solution. We set u(x, t) = 0 + v(x, t) where v(x, t) ≪ 1 to obtain:

\[ \frac{∂v}{∂t}(x, t) = DΔv(x, t) + e^{-μτ}b(0 + v(x, t - τ)) - d(0 + v(x, t)) - μTv(x, t). \]

Now we Taylor expand the functions b and d keeping only linear terms. Remembering that b(0) = d(0) = 0,

\[ \frac{∂v}{∂t}(x, t) = DΔv(x, t) + e^{-μτ}v(x, t - τ)b'(0) - v(x, t)d'(0) - μTv(x, t). \]

(2.6.5)

Let (λ_1, φ_1) be the eigenvalues and eigenfunctions of −Δ on homogeneous Dirichlet boundary conditions and look for trial solutions of (2.6.5) of the form v(x, t) = e^{σjτ}φ_j(x). This gives

\[ σ_jφ_j(x) = -Dλ_jφ_j(x) + e^{-μτ}e^{-σ_jτ}b'(0)φ_j(x) - d'(0)φ_j(x) - μTφ_j(x), \]

so that, since φ_j(x) ≠ 0,

\[ σ_j = -Dλ_j + e^{-μτ}e^{-σ_jτ}b'(0) - d'(0) - μT. \]
In order for the zero solution to be linearly stable we need all the roots of the above equation to be in the left half of the complex plane. For a contradiction let us assume that there exists a root, \( \hat{\sigma}_j \), in the right hand side of the complex plane. Then

\[
|\hat{\sigma}_j + d'(0) + \mu_T + D\lambda_j| = |e^{-\mu_T t}y'(0)e^{-\hat{\sigma}_j t}| \leq e^{-\mu_T t}y'(0),
\]

which is the equation of a disk with radius \( e^{-\mu_T t}y'(0) \) and centred at \(-d'(0) - \mu_T - D\lambda_j\). If we choose the radius of the disk such that the whole disk is in \( \{\text{Re}(\hat{\sigma}_j) < 0\} \) then we have a contradiction. So if we choose

\[
d'(0) + \mu_T + D\lambda_j > e^{-\mu_T t}y'(0),
\]

then the zero solution is linearly stable. As \( \lambda_j \) increases with \( j \) we see that it is sufficient to satisfy

\[
d'(0) + \mu_T + D\lambda_1 > e^{-\mu_T t}y'(0). \tag{2.6.6}
\]

Similar analysis shows that if we want the zero solution to be linearly unstable then we need

\[
d'(0) + \mu_T + D\lambda_1 < e^{-\mu_T t}y'(0). \tag{2.6.7}
\]

Indeed under the above condition it is straightforward to show that the eigenvalue equation with \( j = 1 \) has a real positive root, \( \sigma_1 \).

### 2.6.2 Global Stability of the zero solution

We have looked at local stability of the zero solution of (2.6.1) and found a condition under which it is linearly stable, namely (2.6.6). Now we wish to see if it is globally stable.

**Theorem 15** Suppose for (2.6.1) that (2.2.5) holds and let \( \lambda_1 \) be the smallest eigenvalue of \(-\Delta\) on homogeneous Dirichlet boundary conditions. Suppose also that

\[
D\lambda_1 + d'(0) + \mu_T > e^{-\mu_T t}y'(0), \tag{2.6.8}
\]

\[
d(u) \geq ud'(0), \quad \text{for all} \quad u > 0,
\]

\[
b(u) \leq ub'(0), \quad \text{for all} \quad u > 0,
\]

then solutions of (2.6.1) subject to (2.6.2) and (2.6.3) satisfy \( \|u(\cdot, t)\|_{L^2(\Omega)} \to 0 \) as \( t \to \infty \).
Remark: While the proof of the theorem relies on quite a few assumptions we do expect that, in our case, the inequalities in the theorem are likely to be satisfied.

Proof: First we shall multiply (2.6.1) by $u(x,t)$

$$u(x,t)\frac{\partial u}{\partial t}(x,t) = Du(x,t)\Delta u(x,t) + e^{-\mu \tau}u(x,t)b(u(x,t-\tau)) - u(x,t)d(u(x,t)) - \mu_T u^2(x,t).$$

Now we integrate the whole equation over $\Omega$

$$\int_{\Omega} u(x,t)\frac{\partial u}{\partial t}(x,t)dx = \int_{\Omega} Du(x,t)\Delta u(x,t)dx + \int_{\Omega} e^{-\mu \tau}u(x,t)b(u(x,t-\tau))dx - \int_{\Omega} u(x,t)d(u(x,t))dx - \mu_T \int_{\Omega} u^2(x,t)dx.$$

Using a corollary of the divergence theorem which states that $\int_{\Omega} u(x,t)\Delta u(x,t)dx = -\int_{\Omega} |\nabla u(x,t)|^2 dx$ for functions satisfying homogeneous Dirichlet boundary conditions we get

$$\frac{1}{2} \frac{d}{dt} \int_{\Omega} u^2(x,t)dx = -D \int_{\Omega} |\nabla u(x,t)|^2 dx + e^{-\mu \tau} \int_{\Omega} u(x,t)b(u(x,t-\tau))dx - \int_{\Omega} u(x,t)d(u(x,t))dx - \mu_T \int_{\Omega} u^2(x,t)dx.$$

As we assume that $d(u(x,t)) \geq d'(0)u(x,t)$ and $b(u(x,t)) \leq b'(0)u(x,t)$ in the theorem we get

$$\frac{1}{2} \frac{d}{dt} \int_{\Omega} u^2(x,t)dx \leq -D \int_{\Omega} |\nabla u(x,t)|^2 dx + e^{-\mu \tau}b'(0) \int_{\Omega} u(x,t)u(x,t-\tau)dx - d'(0) \int_{\Omega} u^2(x,t)dx - \mu_T \int_{\Omega} u^2(x,t)dx. \quad (2.6.9)$$

The Poincare inequality for functions $u \in W^1_2(\Omega)$ satisfying $u = 0$ on $\partial \Omega$ states that

$$\int_{\Omega} |\nabla u(x,t)|^2 dx \geq \lambda_1 \int_{\Omega} |u(x,t)|^2 dx,$$

where $\lambda_1$ is the smallest positive eigenvalue of $-\Delta$ on $\Omega$ ([57], page 112). Thus we get

$$\frac{1}{2} \frac{d}{dt} \int_{\Omega} u^2(x,t)dx \leq -D\lambda_1 \int_{\Omega} |u(x,t)|^2 dx + e^{-\mu \tau}b'(0) \int_{\Omega} u(x,t)u(x,t-\tau)dx - d'(0) \int_{\Omega} u^2(x,t)dx - \mu_T \int_{\Omega} u^2(x,t)dx.$$
Using the Hölder inequality

$$\int_\Omega |u(x,t)||v(x,t)|dx \leq \left( \int_\Omega |u(x,t)|^pdx \right)^{\frac{1}{p}} \left( \int_\Omega |v(x,t)|^qdx \right)^{\frac{1}{q}}$$  \hspace{1cm} (2.6.11)

where \( \frac{1}{p} + \frac{1}{q} = 1 \),

with \( p = q = 2 \) we get

$$\frac{1}{2} \frac{d}{dt} \int_\Omega |u(x,t)|^2dx \leq -D\lambda_1 \int_\Omega |u(x,t)|^2dx - d''(0) \int_\Omega |u(x,t)|^2dx - \mu_T \int_\Omega |u(x,t)|^2dx + e^{-\mu\tau}b'(0) \left( \int_\Omega |u(x,t)|^2dx \right)^{\frac{1}{2}} \left( \int_\Omega |u(x,t-\tau)|^2dx \right)^{\frac{1}{2}}.$$

The definition of the \( L^2(\Omega) \) norm is

$$\|u(\cdot,t)\| = \left( \int_\Omega |u(x,t)|^2dx \right)^{\frac{1}{2}}.$$

(2.6.12)

Using this we get

$$\frac{1}{2} \frac{d}{dt} \|u(\cdot,t)\|^2 \leq -(D\lambda_1 + d''(0) + \mu_T) \|u(\cdot,t)\|^2 + e^{-\mu\tau}b'(0) \|u(\cdot,t)\| \|u(\cdot,t-\tau)\| \|u(\cdot,t-\tau)\|^2.$$

Now we can use the argument that states that for an inequality of the form

$$\frac{d}{dt} \|y(\cdot,t)\| \leq -\alpha \|y(\cdot,t)\| + \gamma \|y(\cdot,t-\tau)\|,$$

if \( \alpha > \gamma \geq 0 \) then \( \|y(\cdot,t)\| \to 0 \) as \( t \to \infty \), (see [58] Lemma 3.1 for proof). So because inequality (2.6.8) in the Theorem must hold we can say that \( \|u(\cdot,t)\| \to 0 \) as \( t \to \infty \). Thus we have global stability of the zero solution in \( L^2 \) and the proof is complete.

Remark: Inequality (2.6.8) says that natural deaths plus trapping plus migration out of the domain exceeds adult recruitment and as expected Theorem 15 shows that in this case the blowfly population becomes extinct.

2.6.3 Linear stability of the positive steady state

If we assume that (2.6.7) holds then we can assume that we will have a positive steady state, \( \phi(x) \), which satisfies (2.6.4). This follows from bifurcation theory. The
function \( \phi(x) \) arises as a bifurcation (at a zero eigenvalue) from the zero solution of (2.6.1). We will assume \( \phi(x) \) is unique. If we linearise (2.6.1) about this steady state by setting \( u(x, t) = \phi(x) + v(x, t) \) with \( v(x, t) \ll 1 \) then we find that the linearised problem for \( v \) is

\[
\begin{align*}
\frac{\partial v}{\partial t}(x, t) &= D\Delta v(x, t) - v(x, t)d'(\phi(x)) - \mu_Tv(x, t) + e^{-\mu_T}v(x, t - \tau)b'(\phi(x)) \\
&\quad \text{in } \Omega \times (0, \infty) \\
v(x, t) &= 0 \quad \text{on } \Gamma.
\end{align*}
\]

(2.6.13)

Now we look for solutions of (2.6.13) of the form \( v(x, t) = \psi(x)e^{\sigma t} \) which gives the eigenvalue problem

\[
\begin{align*}
-D\Delta \psi + (\sigma + d'(\phi(x))) + \mu_T - e^{-\mu_T}e^{-\sigma \tau}b'(\phi(x)) \psi &= 0 \quad \text{in } \Omega \\
\psi &= 0 \quad \text{on } \partial \Omega.
\end{align*}
\]

(2.6.14)

An analogue of the well known one dimensional Sturm comparison theorem (which is not restricted to one dimension here) is the following

**Lemma 16** Let

\[
-D\Delta \psi + P(x)\psi = 0 \quad \text{in } \Omega
\]

\[
\psi = 0 \quad \text{on } \partial \Omega,
\]

and

\[
-D\Delta \phi + Q(x)\phi = 0 \quad \text{in } \Omega
\]

\[
\phi = 0 \quad \text{on } \partial \Omega.
\]

Suppose \( \phi > 0 \) in \( \Omega \) and \( P(x) > Q(x) \) in \( \Omega \). Then \( \psi \equiv 0 \).

(See [58] for proof).

We first use this Lemma to find conditions under which zero is not an eigenvalue of (2.6.14) and then go on to find conditions under which all eigenvalues, \( \sigma \), of (2.6.14) will have negative real part, thus proving linear stability of the positive steady state, \( \phi(x) \).

**Lemma 17** Suppose

\[
\left(d'(\phi) - \frac{d(\phi)}{\phi}\right) > e^{-\mu_T}\left(b'(\phi) - \frac{b(\phi)}{\phi}\right), \quad \text{for all } \phi > 0.
\]

Then \( \sigma = 0 \) is not an eigenvalue of (2.6.14).
Proof: To prove this Lemma we argue by contradiction. When \( \sigma = 0 \), (2.6.14) becomes

\[
-D\Delta \psi + (d'(\phi(x)) + \mu_T - e^{-\mu_T}b'(\phi(x))) \psi = 0 \quad \text{in } \Omega \\
\psi = 0 \quad \text{on } \partial \Omega,
\]

which we shall compare with the following, obtained from (2.6.4):

\[
-D\Delta \phi + \left( \frac{d(\phi)}{\phi} + \mu_T - e^{-\mu_T}b(\phi) \right) \phi = 0, \quad \text{in } \Omega \\
\phi = 0, \quad \text{on } \partial \Omega.
\]

We shall have the contradiction we need if \( \psi \equiv 0 \) and this will follow by the Sturm comparison theorem if it is true that

\[
d'(\phi) + \mu_T - e^{-\mu_T}b'(\phi) \geq \frac{d(\phi)}{\phi} + \mu_T - e^{-\mu_T}b(\phi),
\]

i.e. if

\[
\left( d'(\phi) - \frac{d(\phi)}{\phi} \right) \geq e^{-\mu_T} \left( b'(\phi) - \frac{b(\phi)}{\phi} \right),
\]

which holds by hypothesis.

Lemma 18 If all the eigenvalues, \( \lambda_n \), of a self adjoint operator \( \mathcal{L} \) are less than or equal to zero then

\[
\langle \mathcal{L}\psi, \psi \rangle \leq 0,
\]

where \( \langle \cdot, \cdot \rangle \) is the standard \( L^2 \) inner product.

Proof: Let \( (\lambda_n, \psi_n), n = 1, 2, 3, \ldots, \) be the eigenvalues/eigenfunctions of \( \mathcal{L} \) on \( \Omega \) with homogeneous Dirichlet boundary conditions. Then \( \mathcal{L}\psi_n = \lambda_n \psi_n \). Now let \( \psi \in H^1_0(\Omega) \cap H^2(\Omega) \). Then \( \psi \) can be expressed in terms of the \( \psi_n \) by an eigenfunction expansion

\[
\psi = \sum_{n=1}^{\infty} a_n \psi_n(x),
\]

so that

\[
\mathcal{L}\psi = \sum_{n=1}^{\infty} a_n \mathcal{L}\psi_n = \sum_{n=1}^{\infty} a_n \lambda_n \psi_n.
\]
(N.B, in one dimension the eigenfunctions are just sin's). We claim that the eigenfunctions $\psi_n$ are orthogonal. To see this, let $\psi_n$ and $\psi_m$ be two distinct eigenfunctions with corresponding eigenvalues $\lambda_n$ and $\lambda_m$. Then

$$\lambda_n\langle \psi_n, \psi_m \rangle = \langle \lambda_n \psi_n, \psi_m \rangle = \langle \mathcal{L} \psi_n, \psi_m \rangle = \langle \psi_n, \mathcal{L} \psi_m \rangle = \langle \psi_n, \lambda_m \psi_m \rangle = \lambda_m \langle \psi_n, \psi_m \rangle.$$ 

Therefore

$$(\lambda_n - \lambda_m) \langle \psi_n, \psi_m \rangle = 0,$$

since $\lambda_n \neq \lambda_m$ we must have $\langle \psi_n, \psi_m \rangle = 0$, i.e. eigenfunctions associated with distinct eigenvalues are orthogonal.

Since we are referring to the eigenvalues/eigenfunctions of $\mathcal{L}$ here we can drop the complex conjugate in the definition of $\mathcal{L}$, because the eigenvalues/eigenfunctions of a self-adjoint operator on homogeneous Dirichlet boundary conditions are real. Thus we find that

$$\langle \mathcal{L} \psi, \psi \rangle = \left\langle \sum_{n=1}^{\infty} a_n \lambda_n \psi_n, \sum_{n=1}^{\infty} a_n \psi_n \right\rangle$$

$$= \int_{\Omega} \left( \sum_{n=1}^{\infty} a_n \lambda_n \psi_n \right) \left( \sum_{n=1}^{\infty} a_n \psi_n \right) dx$$

$$= \sum_{n=1}^{\infty} a_n^2 \lambda_n \int_{\Omega} \psi_n^2 dx \leq 0,$$

because $\lambda_n \leq 0$ for all $n$. This completes the proof.

**Theorem 19** Suppose

$$d'(\phi(x)) + \mu_T - e^{-\mu T} b'(\phi(x)) > \frac{d(\phi(x))}{\phi(x)} + \mu_T - e^{-\mu T} \frac{b(\phi(x))}{\phi(x)} \quad \text{for all } x \in \Omega$$

$$b'(\phi(x)) \geq 0 \quad \text{for all } x \in \Omega.$$

Then all eigenvalues, $\sigma$, of (2.6.14) have negative real parts, so that the steady state $\phi(x)$ is linearly stable as a solution of (2.6.1).

**Proof:** Define $\textbf{L} = D\Delta - \mu_T - d'(\phi(x)) + e^{-\mu T} b'(\phi(x))$. As $\textbf{L}$ is self adjoint, all of its eigenvalues are real. Note that the eigenvalues, $\sigma$, of the linearisation about $\phi(x)$ are not the same as the eigenvalues, $\lambda$, of the operator $\textbf{L}$. The former may be complex but the latter are real. We claim that all the eigenvalues of $\textbf{L}$ are non-positive.

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Suppose for a contradiction that there exists a positive eigenvalue, $\lambda$, for $L$. Then there exists a non-zero function $\psi$ such that $L\psi = \lambda \psi$. Substituting in for $L$ we get

$$D \Delta \psi - \mu_T \psi - d'(\phi(x))\psi + e^{-\mu_T b'}(\phi(x))\psi = \lambda \psi,$$

$$-D \Delta \psi + (\lambda + \mu_T + d'(\phi(x)) - e^{-\mu_T b'}(\phi(x))) \psi = 0.$$  

Since $\lambda > 0$, $\lambda + d'(\phi(x)) + \mu_T - e^{-\mu_T b'}(\phi(x)) > d'(\phi(x)) + \mu_T - e^{-\mu_T b'}(\phi(x))$ for all $x \in \Omega$ and by hypothesis $d'(\phi(x)) + \mu_T - e^{-\mu_T b'}(\phi(x)) > \frac{d(\phi(x))}{\phi(x)} + \mu_T - e^{-\mu_T b'(\phi(x))}$.

Thus, as $\phi(x) > 0$, by comparing with (2.6.16) and using Lemma 16 we have that $\psi = 0$, which is a contradiction to the definition of an eigenfunction. Therefore we conclude that all eigenvalues of $L$ must be less than or equal to zero and thus from Lemma 18 we have that $\langle L\psi, \psi \rangle \leq 0$ for all functions $\psi$ such that $\psi = 0$ on $\partial \Omega$.

Let $\psi$ be a solution of (2.6.14). Multiplying (2.6.14) by $\overline{\psi}$ and integrating over $\Omega$ gives

$$0 = \int_{\Omega} (-D \Delta \psi + (\mu_T + d'(\phi(x)) - e^{-\mu_T b'}(\phi(x))) \psi) \overline{\psi}$$

$$+ \int_{\Omega} (\sigma - e^{-\mu_T}e^{-\sigma T}b'(\phi(x)) + e^{-\mu_T}b'(\phi(x))) \psi \overline{\psi}$$

$$= -\langle L\psi, \psi \rangle + \int_{\Omega} (\sigma + e^{-\mu_T}b'(\phi(x))(1 - e^{-\sigma T})) |\psi|^2.$$  

Let $\sigma = a + ib$. Taking real and imaginary parts of the previous expression, remembering that $\phi(x)$ is a function of $x$, gives

$$-\langle L\psi, \psi \rangle + \int_{\Omega} (a + e^{-\mu_T}b'(\phi(x))(1 - e^{-\sigma T}\cos(br))) |\psi|^2 dx = 0 \tag{2.6.18}$$

$$\int_{\Omega} (b + e^{-\mu_T}e^{-\sigma T}b'(\phi(x))\sin(br)) |\psi|^2 dx = 0. \tag{2.6.19}$$

As $b'(\phi(x)) \geq 0$ for all $x \in \Omega$ we find that:

If $a > 0$ then as $e^{-\mu_T}b'(\phi(x))(1 - e^{-\sigma T}\cos(br)) \geq 0$ the integral in (2.6.18) will be strictly positive. Since $-\langle L\psi, \psi \rangle \geq 0$, (2.6.18) is violated.

If $a = 0$ then $b \neq 0$ (because we have shown in Lemma 17 that zero can not be an eigenvalue) and (2.6.19) shows that $br$ can not be an integer multiple of $\pi$. Thus $|\cos(br)| < 1$ and so the integral (2.6.18) is again positive. So we have shown that if $b'(\phi(x)) \geq 0$ for all $x \in \Omega$ then all eigenvalues of (2.6.14) have strictly negative real parts and so the steady state, $\phi(x)$, is linearly stable.

The following two Theorems provide alternative sufficient conditions for stability of the steady state $\phi(x)$.
Theorem 20 Suppose (2.2.5) holds and also that
\[ \tau |b'(\phi(x))| e^{-\mu \tau} < 1 \quad \text{for all} \quad x \in \Omega, \]
then all eigenvalues, \( \sigma \), of (2.6.14) have negative real parts, so that the steady state, \( \phi(x) \) is linearly stable.

**Proof:** Let \( a \geq 0 \). Consider the integral of (2.6.19). Using the fact that \( -br \leq \sin(br) \leq br \) we get
\[
b + e^{-\mu \tau} e^{-ar} b'(\phi(x)) \sin(br) \geq b - br |b'(\phi(x))| e^{-\mu \tau} e^{-ar} \]
\[
\geq b - br |b'(\phi(x))| e^{-\mu \tau} \]
\[
> 0 \quad \text{for all} \quad x, \quad \text{by hypothesis}.
\]
Thus (2.6.19) is violated. Therefore we must have \( a < 0 \) and so the steady state \( \phi(x) \) is linearly stable.

**Remark** This theorem shows us that we can have linear stability of the steady state if \( b'(\phi(x)) \) is negative at certain points \( x \in \Omega \), but only if it is not too much negative.

Theorem 21 Suppose (2.2.5) holds and also that
\[
d'(\phi(x)) \geq \frac{d(\phi(x))}{\phi(x)}, \quad \text{for all} \quad x \in \Omega, \quad (2.6.20)
\]
\[
|b'(\phi(x))| \leq \frac{b(\phi(x))}{\phi(x)}, \quad \text{for all} \quad x \in \Omega, \quad (2.6.21)
\]
then all eigenvalues, \( \sigma \), of (2.6.14) have negative real parts, so that the steady state, \( \phi(x) \) is linearly stable.

**Proof:** The proof of this Theorem uses similar ideas to the previous two theorems, but by working with a differently defined operator \( L \) we can obtain alternative sufficient conditions for stability of \( \phi(x) \).

For this theorem we shall use the operator \( L = D\Delta - \mu T - \frac{d(\phi(x))}{\phi(x)} + e^{-\mu \tau \frac{b(\phi(x))}{\phi(x)}} \). Again \( L \) is self adjoint and therefore all of its eigenvalues are real. Using a similar argument to above we find that as \( \sigma + \mu_T + \frac{d(\phi(x))}{\phi(x)} - e^{-\mu \tau \frac{b(\phi(x))}{\phi(x)}} > \mu_T + \frac{d(\phi(x))}{\phi(x)} - e^{-\mu \tau \frac{b(\phi(x))}{\phi(x)}} \) for strictly positive \( \sigma \) all eigenvalues of \( L \) must be less than or equal to zero. Let \( \psi \) be a solution of (2.6.14). Then multiplying by \( \overline{\psi} \) and integrating over \( \Omega \) gives
\[
\int_{\Omega} \left( -D\Delta \psi + \left( \mu_T + \frac{d(\phi(x))}{\phi(x)} - e^{-\mu \tau \frac{b(\phi(x))}{\phi(x)}} \right) \psi \right) \overline{\psi} + \left( \sigma + d'(\phi(x)) - \frac{d(\phi(x))}{\phi(x)} + e^{-\mu \tau \frac{b(\phi(x))}{\phi(x)}} - e^{-\mu \tau \frac{b(\phi(x))}{\phi(x)}} \right) \overline{\psi} =
\]
\[
= -\langle L \psi, \psi \rangle + \int_{\Omega} \left( \sigma + d'(\phi(x)) - \frac{d(\phi(x))}{\phi(x)} - e^{-\mu \tau \frac{b(\phi(x))}{\phi(x)}} \right) |\psi|^2 = 0.
\]
Let \( \sigma = \alpha + i\beta \) then taking real and imaginary parts of the above equation gives

\[
\begin{align*}
- \langle L\psi, \psi \rangle & + \int_\Omega \left( \alpha + d'(\phi(x)) - \frac{d(\phi(x))}{\phi(x)} - e^{-\mu_T} \left( e^{-\alpha r} \cos(b\tau) \phi'(\phi(x)) - \frac{b(\phi(x))}{\phi(x)} \right) \right) \lvert \psi \rvert^2 = 0 \\
\int_\Omega \left( b + e^{-\mu_T} e^{-\alpha r} \sin(b\tau) \right) \lvert \psi \rvert^2 & = 0.
\end{align*}
\]

(2.6.22)

(2.6.23)

Suppose, for contradiction, that \( \alpha > 0 \). Using (2.6.20) and (2.6.21) we find that the integrand in (2.6.22) can be written as

\[
\begin{align*}
\alpha + d'(\phi(x)) - \frac{d(\phi(x))}{\phi(x)} - e^{-\mu_T} & \left( e^{-\alpha r} \cos(b\tau) \phi'(\phi(x)) - \frac{b(\phi(x))}{\phi(x)} \right) \\
\geq \alpha + d'(\phi(x)) - \frac{d(\phi(x))}{\phi(x)} - e^{-\mu_T} & \left( e^{-\alpha r} \sin(b\tau) \lvert b'(\phi(x)) \rvert \right) \\
\geq a + d'(\phi(x)) - \frac{d(\phi(x))}{\phi(x)} - e^{-\mu_T} & \left( e^{-\alpha r} \sin(b\tau) \lvert \phi'(\phi(x)) \rvert \right) \\
\geq a + d'(\phi(x)) - \frac{d(\phi(x))}{\phi(x)} & > 0
\end{align*}
\]

and so (2.6.22) is violated. If \( \alpha = 0 \) then we again have that \( b \neq 0 \), hence \( \sin(b\tau) \neq 0 \) by (2.6.23) and so \( \lvert \cos(b\tau) \rvert < 1 \). Therefore

\[
\begin{align*}
\alpha + d'(\phi(x)) - \frac{d(\phi(x))}{\phi(x)} - e^{-\mu_T} & \left( e^{-\alpha r} \sin(b\tau) \phi'(\phi(x)) - \frac{b(\phi(x))}{\phi(x)} \right) \\
\geq d'(\phi(x)) - \frac{d(\phi(x))}{\phi(x)} - e^{-\mu_T} & \frac{b(\phi(x))}{\phi(x)} \left( \lvert \cos(b\tau) \rvert - 1 \right) \\
\geq d'(\phi(x)) - \frac{d(\phi(x))}{\phi(x)} & > 0,
\end{align*}
\]

so again (2.6.22) is violated. Thus we have proved that under conditions (2.6.20) and (2.6.21) all eigenvalues of (2.6.14) must have strictly negative real parts and so the steady state, \( \phi(x) \), is linearly stable.

### 2.6.4 Global stability of the positive steady state

First we prove positivity of solutions of equation (2.6.1).
Lemma 22 Suppose for the system (2.6.1, 2.6.2, 2.6.3) that (2.2.5) holds and also that

\[ u_0(x, \theta) \neq 0 \quad \text{and} \quad u_0(x, \theta) \geq 0 \quad \text{for all} \quad x \in \Omega, \theta \in [-\tau, 0]. \]

Then \( u(x, t) > 0 \) for all \( x \in \Omega, \ t > 0. \)

**Proof:** First note that since \( u_0(x, \theta) \neq 0 \) on \( \Omega \times [-\tau, 0], \) there exists \( \theta_0 \in [-\tau, 0] \) such that \( u_0(x, \theta_0) \neq 0 \) as a function of \( x. \) Without loss of generality we can take \( \theta_0 = 0. \) Thus we assume henceforth that

\[ u_0(x, 0) \neq 0. \tag{2.6.24} \]

Let us make a \( C^1 \) extension to the definition of the death function for the case where \( u < 0. \) In this case we define \( d(u) = d'(0)u \) when \( u < 0. \) Then we have that \( d \in C^1(\mathbb{R}). \) First we shall show that \( u(x, t) \geq 0 \) for all \( t > 0 \) and all \( x \in \Omega. \) We shall first show this is true for \( t \in (0, \tau]. \) We know that \( u(x, t-\tau) \geq 0 \) on this interval as \( t-\tau \geq 0 \) and \( u_0(x, b) \geq 0. \) Therefore

\[
\frac{\partial u}{\partial t}(x, t) \geq \Delta u(x, t) - d(u(x, t)) - \mu u(x, t) \quad \text{on} \quad (x, t) \in \Omega \times (0, \tau]
\]

\[ u(x, t) = 0 \quad \text{on} \quad \partial \Omega. \tag{2.6.25} \]

To show that \( u(x, t) \geq 0 \) on \( \Omega \times (0, \tau] \) we shall assume the contrary. Suppose that there exists a \( t^* \in (0, \tau] \) and \( x^* \in \Omega \) such that \( u(x^*, t^*) < 0. \) Then \( u(x, t) \) must attain a negative global minimum on the set \( (x, t) \in \Omega \times (0, \tau]. \) However \( x^* \in \Omega \) as \( u(x, 0) \geq 0 \) on \( \partial \Omega. \) Furthermore \( u(x, 0) \geq 0 \) so the global minimum must be at a point \( u(x^*, t^*) \in \Omega \times (0, \tau]. \) As \( x^* \) is in the interior of \( \Omega \) we have that \( \Delta u(x^*, t^*) \geq 0. \) We also know that \( \partial u(x^*, t^*)/\partial t \leq 0 \) (but not necessarily equal to 0 as \( t^* \) could equal \( \tau). \) Evaluating (2.6.25) at \( (x^*, t^*) \) gives a contradiction. Thus we conclude that \( u(x, t) \geq 0 \) on \( \Omega \times [0, \tau]. \) The strong maximum principle says that for an inequality of the form

\[
\frac{\partial u}{\partial t}(x, t) \geq \Delta u(x, t) + h(x, t)u(x, t) \quad \text{on} \quad (x, t) \in \Omega \times (0, T],
\]

where \( h(x, t) \) is a bounded function, if \( u(x, 0) \geq 0 \) for all \( x \in \Omega \) and \( u(x, t) \geq 0 \) for \( x \in \partial \Omega, t > 0 \) then i) \( u(x, t) \geq 0 \) for all \( x \in \Omega, t > 0 \) and ii) either \( u(x, t) > 0 \) for all \( x \in \Omega, t > 0 \) or \( u(x, t) \equiv 0 \) for all \( x \in \Omega, t < t^*, \) for some value \( t^*. \)

However, the latter alternative violates (2.6.24), which as explained earlier can be assumed without loss of generality. Thus we conclude that \( u(x, t) > 0 \) on \( \Omega \times [0, \tau]. \)

Proof by induction then shows that \( u(x, t) > 0 \) on \( \Omega \times (0, \infty). \)
Theorem 23 Suppose the hypotheses of Lemma 22 hold and
\[ D\lambda_1 + d'(0) + \mu_T < e^{-\mu_T b'(0)} \]  
\[ b'(\phi(x)) > 0 \quad \text{for all} \ x \in \Omega, \]  
where \( \lambda_1 \) is the principal eigenvalue of \(-\Delta\) on homogeneous Dirichlet boundary conditions. Then the solutions of (2.6.1) subject to (2.6.2) and (2.6.3) converge to the unique positive steady state solution, \( \phi(x) \), satisfying (2.6.4).

Proof: Consider the eigenvalue problem
\[ D\Delta \phi(x) - d'(0)\phi(x) - \mu_T\phi(x) + e^{-\mu_T b'(0)}\phi(x) = \lambda \phi(x). \]  

We can see that by inequality (2.6.26) in the theorem, which is the condition for the zero solution of (2.6.1) to be linearly unstable, that this will have a positive solution \((\lambda^*, \phi^*)\). We claim that for sufficiently small \(\epsilon > 0, \epsilon \phi^*\) is a lower solution of
\[ D\Delta \phi(x) + e^{-\mu_T b(\phi(x))} - d(\phi(x)) - \mu_T \phi(x) = 0. \]  

To see this note that
\[ D\Delta (\epsilon \phi^*) + e^{-\mu_T b(\epsilon \phi^*)} - d(\epsilon \phi^*) - \mu_T \epsilon \phi^* \]
\[ = D\Delta (\epsilon \phi^*) - d'(0)\epsilon \phi^* - \mu_T \epsilon \phi^* + e^{-\mu_T b'(0)}(\epsilon \phi^*)^2 + \epsilon^{-\mu_T b(\epsilon \phi^*)} - d(\epsilon \phi^*) \]
\[ = \lambda^* \epsilon \phi^* + e^{-\mu_T b(\epsilon \phi^*)} - d(\epsilon \phi^*) \]
\[ = (\lambda^* + d'(0) - e^{-\mu_T b'(0)} + e^{-\mu_T b(\epsilon \phi^*)} - d(\epsilon \phi^*) - d(\epsilon \phi^*)/\epsilon \phi^*) \epsilon \phi^*, \]

since \(\lambda^* > 0\) we can choose \(\epsilon\) sufficiently small that
\[ \lambda^* + d'(0) - e^{-\mu_T b'(0)} + e^{-\mu_T b(\epsilon \phi^*)} - d(\epsilon \phi^*)/\epsilon \phi^* > 0, \]

which is possible because the left hand side \(\rightarrow \lambda^*\) as \(\epsilon \rightarrow 0\). Thus for \(\epsilon\) small enough, \(\epsilon \phi^*\) is a lower solution of (2.6.4). We know from (2.6.27) that there is an upper solution \(\bar{\phi} = \phi_{\text{max}}\) which is the value at which the function \(b\) attains its maximum. Let \(u(x, t)\) be the solution of (2.6.1) with initial data \(\epsilon \phi^*\). We claim that \(\partial u(x, t)/\partial t \geq 0\). Consider \(S = \{t \geq 0 : \partial u(x, t)/\partial t \geq 0, \text{ for all } x \in \Omega\}\). Clearly \(0 \in S\) since
\[ \lim_{t \to 0^+} \frac{\partial u}{\partial t}(x, t) = D\Delta(\epsilon \phi^*) - \mu_T(\epsilon \phi^*) - d(\epsilon \phi^*) + e^{-\mu_T b(\epsilon \phi^*)} > 0, \]
because $\epsilon \phi^*$ is a lower solution. We will now show $(0, \tau) \subset S$. For $t \in (0, \tau)$, let $w_h(x, t) = u(x, t + h) - u(x, t)$, where $h$ is sufficiently small such that $t + h \in (0, \tau]$ and $u(x, h) - u(x, 0) \geq 0$. Thus, as $u(x, t) = u_0(x, t) = \epsilon \phi^*$ for all $x \in \Omega$, $t \leq 0$ we get

$$\frac{\partial w_h}{\partial t}(x, t) = \frac{\partial u}{\partial t}(x, t + h) - \frac{\partial u}{\partial t}(x, t)$$

$$= D \Delta w_h - \mu_T w_h - (d(u(x, t + h) - d(u(x, t)))$$

$$+ e^{-\mu_T} (b(u(x, t + h - \tau) - b(u(x, t - \tau)))$$

$$= D \Delta w_h - \mu_T w_h - (d(u(x, t + h) - d(u(x, t))) + e^{-\mu_T} (b(\epsilon \phi^*) - b(\epsilon \phi^*))$$

$$= D \Delta w_h - \mu_T w_h - (u(x, t + h) - u(x, t))d'(\bar{w}_h(x, t))$$

$$= D \Delta w_h - \mu_T w_h - (\mu_T + d'(\bar{w}_h(x, t)))w_h,$$

by the mean value theorem. We also see that $w_h(x, 0) = u(x, h) - u(x, 0) \geq 0$. Thus the maximum principle implies that $w_h(x, t) \geq 0$ and hence, letting $h \to 0$ we get $\partial u(x, t) / \partial t \geq 0$. Therefore $(0, \tau) \subset S$. As $S$ is a closed set we know that $[0, \tau] \subset S$ will also hold.

Now we show that $(\tau, 2\tau) \subset S$. For $t \in (\tau, 2\tau)$ let $w_h(x, t) = u(x, t + h) - u(x, t)$, where $h$ is sufficiently small such that $t + h \in (\tau, 2\tau]$ and $u(x, t + h) - u(x, t) \geq 0$. We are assuming that the values of $\phi(x)$, $x \in \Omega$ are always in the interval of values for which $b(\cdot)$ is increasing, so that $b'(\phi(x)) \geq 0$ for all $x \in \Omega$. Thus for $t \in (\tau, 2\tau)$ we get

$$\frac{\partial w_h}{\partial t}(x, t) = \frac{\partial u}{\partial t}(x, t + h) - \frac{\partial u}{\partial t}(x, t)$$

$$= D \Delta w_h - \mu_T w_h - (u(x, t + h) - u(x, t))d'(\bar{w}_h(x, t))$$

$$+ e^{-\mu_T} (b(u(x, t + h - \tau) - b(u(x, t - \tau)))$$

$$= D \Delta w_h - \mu_T w_h - (u(x, t + h) - u(x, t))d'(\bar{w}_h(x, t))$$

$$= D \Delta w_h - \mu_T w_h - (\mu_T + d'(\bar{w}_h(x, t)))w_h + e^{-\mu_T} w_h(x, t - \tau)b'(\bar{w}_h(x, t - \tau)).$$

Because $t - \tau \in (0, \tau)$ we know that $w_h(x, t - \tau) \geq 0$ and thus we conclude that $e^{-\mu_T} w_h(x, t - \tau)b'(\bar{w}_h(x, t - \tau)) \geq 0$. Therefore

$$\frac{\partial w_h}{\partial t}(x, t) \geq D \Delta w_h - (\mu_T + d'(\bar{w}_h(x, t)))w_h,$$

so, as above, we can conclude that $w_h(x, t) \geq 0$ for $t \in (\tau, 2\tau)$ and consequently that $[\tau, 2\tau] \subset S$. Thus by induction we get that $[0, n] \subset S$ for any integer $n \geq 0$. Hence $[0, \infty) = S$, i.e. $\partial u(x, t) / \partial t \geq 0$ for all $t \geq 0$. So we have that $u(x, t) \to \phi(x)$ as $t \to \infty$. 

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We can then do the same with the upper solution, but show that \( \frac{\partial u(x, t)}{\partial t} \leq 0 \), where \( \frac{\partial u(x, t)}{\partial t} \) is the solution of (2.6.4) with initial data \( \phi \). Thus we have that our solution will tend to the positive steady state \( \phi(x) \).
2.7 Extension to reaction diffusion model

We now attempt to extend the ideas of the previous section to the reaction diffusion model (2.5.1, 2.5.2, 2.5.3). Notice that (2.5.2) and (2.5.3) do not depend at all on \( u_i(x, t) \) and so we can solve them independently of (2.5.1). Thus we can just look at (2.5.2) and (2.5.3) when analysing the system. The steady states, \( \phi_m(x), \phi_n(x) \), of (2.5.2, 2.5.3) satisfy

\[
D_m \Delta \phi_m(x) + e^{-\mu_T}b(\phi_m(x))\phi_n(x) - d(\phi_m(x)) - \mu_T \phi_m(x) = 0, \quad \text{for } x \in \Omega
\]

\[
D_n \Delta \phi_n(x) + r\phi_n(x)(1 - \phi_n(x)) - \gamma_s \phi_n(x)\phi_m(x) = 0, \quad \text{for } x \in \Omega
\]

\[
\phi_m(x) = 0, \quad \text{for } x \in \partial \Omega
\]

\[
\phi_n(x) = 0, \quad \text{for } x \in \partial \Omega
\]

(2.7.1)

for the homogeneous Dirichlet problem. We shall in fact, also look at the spatially uniform steady states of the homogeneous Neumann problem.

2.7.1 Equilibrium solutions

Disregarding boundary conditions for the moment let us linearise (2.5.2, 2.5.3) about the steady state, \( (\phi_m(x), \phi_n(x)) \) (where \( \phi_m \) and \( \phi_n \) may in fact be constants) by setting \( u_m(x, t) = v(x, t) + \phi_m(x), N(x, t) = n(x, t) + \phi_n(x) \). We obtain

\[
\frac{\partial v(x, t)}{\partial t} = D_m \Delta v(x, t) + \phi_m + e^{-\mu_T}b(\phi_m + v(x, t - \tau)) (\phi_n + n(x, t - \tau))
\]

\[-d(\phi_m + v(x, t)) - \mu_T (\phi_m + v(x, t))
\]

\[
\frac{\partial n(x, t)}{\partial t} = D_n \Delta n(x, t) + \phi_n + r(\phi_n + n(x, t)) (1 - (\phi_n + n(x, t)))
\]

\[-\gamma_s (\phi_m + v(x, t)) (\phi_n + n(x, t))
\]

Now we can Taylor expand the functions \( b \) and \( d \), linearise and rearrange the equations to give

\[
\frac{\partial v(x, t)}{\partial t} = D_m \Delta v(x, t) + e^{-\mu_T}b(\phi_m)n(x, t - \tau) + e^{-\mu_T}b'(\phi_m)\phi_nv(x, t - \tau)
\]

\[-v(x, t)d'(\phi_m) - \muTv(x, t)
\]

(2.7.2)

\[
\frac{\partial n(x, t)}{\partial t} = D_n \Delta n(x, t) + rn(x, t) (1 - 2\phi_n) - \gamma_s (\phi_m n(x, t) + v(x, t)\phi_n).
\]
Ignoring boundary conditions for the moment, system (2.5.2,2.5.3) has spatially uniform steady states, \((\phi_m^*, \phi_n^*) = (0,0), (0,1)\). However \((0,1)\) will not be a solution of the whole system on Dirichlet boundary conditions as \(N(x,t) = 1\) for all \(x \in \Omega, t > 0\) does not satisfy the boundary condition \(N(x,t) = 0\) on \(\partial\Omega\). However if we were to use Neumann boundary conditions then it would be satisfied and \((0,1)\) would be a steady state. In principle we could even imagine using mixed boundary conditions where we have for example Dirichlet boundary conditions for the blowflies and Neumann for the sheep.

### 2.7.2 Linear stability of the zero solution

**Theorem 24** Suppose that (2.2.5) holds for the system (2.5.1,2.5.2,2.5.3) on homogeneous Dirichlet boundary conditions and also that

\[
\tau < D_n\lambda_1,
\]

where \(\lambda_1\) is the principal eigenvalue of \(-\Delta\) on homogeneous Dirichlet boundary conditions. Then the zero solution is linearly stable.

**Remark:** The zero solution can be stable under homogeneous Dirichlet boundary conditions because the individuals can leave the domain.

**Proof:** Note that if \(u_n(t) \to 0\) and \(N(t) \to 0\) then \(u(t) \to 0\). So we focus on (2.5.2) and (2.5.3) only. The linearised equations (2.7.2) about the zero solution become

\[
\begin{align*}
\frac{\partial v(x,t)}{\partial t} &= D_m\Delta v(x,t) - v(x,t)d'(0) - \mu_T v(x,t) \\
\frac{\partial n(x,t)}{\partial t} &= D_n\Delta n(x,t) + r n(x,t).
\end{align*}
\]

(2.7.3)

Let \((\lambda_i, \phi_i), i = 1, 2, 3, \ldots\) be the eigenvalues and eigenfunctions of \(-\Delta\) on homogeneous Dirichlet boundary conditions and look for trial solutions of the form

\[
\begin{pmatrix}
v(x,t) \\
n(x,t)
\end{pmatrix} = \begin{pmatrix} c_1 \\ c_2 \end{pmatrix} e^{\sigma t}\phi_i(x).
\]

Substituting into (2.7.3) gives

\[
\begin{align*}
\sigma_i \phi_i(x)c_1 &= -D_m\lambda_i \phi_i(x)c_1 - d'(0)\phi_i(x)c_1 - \mu_T \phi_i(x)c_1 \\
\sigma_i \phi_i(x)c_2 &= -D_n\lambda_i \phi_i(x)c_2 + r \phi_i(x)c_2,
\end{align*}
\]
which can be put into matrix form
\[
\begin{pmatrix}
\sigma_i + d'(0) + \mu_T + D_m \lambda_i & 0 \\
0 & \sigma_i - r + D_n \lambda_i
\end{pmatrix}
\begin{pmatrix}
c_1 \\
c_2
\end{pmatrix} = 0.
\]

For non-trivial solutions the determinant of this matrix must be zero. Hence
\[
(\sigma_i + d'(0) + \mu_T + D_m \lambda_i)(\sigma_i + D_n \lambda_i - r) = 0.
\]

To be stable both roots, \(\sigma_i\), must be in the left half of the complex plane for every \(i\). We see that the roots are \(\sigma_i = r - D_n \lambda_i\) and \(\sigma_i = -(d'(0) + \mu_T + D_m \lambda_i)\). Thus for the equilibrium point \((0, 0)\) to be stable we must satisfy the condition \(r < D_n \lambda_i\), for all \(i\). As \(\lambda_i\) increases with \(i\) we conclude that if this inequality holds for \(\lambda_1\) it will hold for all \(\lambda_i\). Thus the zero solution will be linearly stable if
\[
r < D_n \lambda_1,
\]
which holds by hypothesis.

### 2.7.3 Linear stability of the steady state \((\phi_m^*, \phi_n^*) = (0, 1)\) on Neumann boundary conditions

**Theorem 25** Suppose that (2.2.5) holds for the system (2.5.1,2.5.2,2.5.3) on homogeneous Neumann boundary conditions and also that
\[
e^{-\mu\tau}b'(0) < d'(0) + \mu_T,
\]
then the steady state \((u_m, u_n, N) = (0, 0, 1)\) is linearly stable.

**Proof:** Again note that if \(u_m(t) \to 0\) and \(N(t) \to 1\) then \(u_i(t) \to 0\). So we focus on (2.5.2) and (2.5.3) only. The linearised system (2.7.2) about the equilibrium \((u_m, N) = (0, 1)\) is
\[
\begin{align*}
\frac{\partial v(x, t)}{\partial t} &= D_m \Delta v(x, t) + e^{-\mu\tau}b'(0)v(x, t - r) - d'(0)v(x, t) - \mu_T v(x, t) \\
\frac{\partial n(x, t)}{\partial t} &= D_n \Delta n(x, t) - \gamma s v(x, t) - \gamma n(x, t).
\end{align*}
\]

(2.7.4)

Let \((\lambda_i, \phi_i), i = 0, 1, 2, 3, \ldots\) be the eigenvalues and eigenfunctions of \(-\Delta\) on homogeneous Neumann boundary conditions (note that \(\lambda_0 = 0\) with \(\phi_0\) a constant) and look for trial solutions of the form
\[
\begin{pmatrix}
v(x, t) \\
n(x, t)
\end{pmatrix} =
\begin{pmatrix}
c_1 \\
c_2
\end{pmatrix} e^{\alpha t} \phi_i(x).
\]

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Substituting into (2.7.4) gives
\[
\begin{align*}
\sigma_i \phi_i(x) c_1 &= -D_m \lambda_i \phi_i(x) c_1 + e^{-\mu \tau} b'(0) \phi_i(x) e^{-\sigma \tau} c_1 - d'(0) \phi_i(x) c_1 - \mu_T \phi_i(x) c_1 \\
\sigma_i \phi_i(x) c_2 &= -D_n \lambda_i \phi_i(x) c_2 - r \phi_i(x) c_2 - \gamma_s \phi_i(x) c_1.
\end{align*}
\]

This can be put in matrix form
\[
\begin{pmatrix}
\sigma_i - e^{-\mu \tau} e^{-\sigma \tau} b'(0) + d'(0) + \mu_T + D_m \lambda_i \\
\gamma_s + r + D_n \lambda_i
\end{pmatrix}
\begin{pmatrix}
c_1 \\
c_2
\end{pmatrix}
= 0.
\]

For non-trivial solutions the determinant of this matrix must be zero.

\[
\left( \sigma_i + D_m \lambda_i + d'(0) + \mu_T - e^{-\mu \tau} e^{-\sigma \tau} b'(0) \right) (\sigma_i + r + D_n \lambda_i) = 0.
\]

This time we have that one root of the equation is \( \sigma_i = -(r + D_n \lambda_i) < 0 \). For the equilibrium \((u_m, N) = (0, 1)\) to be linearly stable we now need to show that the other roots will also be in the left half of the complex plane. For a contradiction, let us assume that there exists a root \( \sigma_i \) in the right hand side of the complex plane. Then

\[
|\sigma_i + d'(0) + \mu_T + D_m \lambda_i| = e^{-\mu \tau} b'(0) |e^{-\sigma \tau}| = e^{-\mu \tau} b'(0) e^{-(\Re \sigma_i) \tau},
\]

so that

\[
|\sigma_i + d'(0) + \mu_T + D_m \lambda_i| \leq e^{-\mu \tau} b'(0).
\]

Therefore \( \sigma_i \) is in the disk of radius \( e^{-\mu \tau} b'(0) \) centred at \( -d'(0) - \mu_T - D_m \lambda_i \). So if we choose the radius of our disk such that the whole disk is in \( \{Re \sigma_i < 0\} \) then we have a contradiction. So we choose

\[
e^{-\mu \tau} b'(0) < d'(0) + \mu_T + D_m \lambda_i. \tag{2.7.5}
\]

Again this has to hold for all \( i \). Note that \( \lambda_i \) increases with \( i \), so if we satisfy the condition for \( \lambda_0 \) it will hold for all \( \lambda_i \). However on Neumann boundary conditions \( \lambda_0 = 0 \), so if

\[
e^{-\mu \tau} b'(0) < d'(0) + \mu_T, \tag{2.7.6}
\]

holds then we can conclude that the equilibrium point \((u_i, u_m, N) = (0, 0, 1)\) of system (2.5.1,2.5.2,2.5.3) is linearly stable.
2.7.4 Positivity of solutions to (2.5.1,2.5.2,2.5.3)

Positivity of solutions can be proved similarly to the proof of Proposition 4 and the Laplacian terms are handled using comparison theorems related to the maximum principle for parabolic operators (see Protter and Weinberg (1967) [52] or Smith (1995) [56]).

2.7.5 Global stability of the steady state \((\phi_m^*, \phi_n^*) = (0, 1)\) on Neumann boundary conditions

Theorem 26 Suppose that (2.2.5) holds for system (2.5.1,2.5.2,2.5.3) on homogeneous Neumann boundary conditions and also that

\[ e^{-\mu t}b(u) < d(u) + \mu r u \quad \text{for all } u > 0 \]

and that

\[ N(x, s) \geq 0, \quad u_i(x, 0) \geq 0, \quad u_m(x, s) \geq 0, \quad s \in [-\tau, 0], \]

with \(N(x, 0) \neq 0\). Then the steady state \((u_i, u_m, N) = (0, 0, 1)\) is globally asymptotically stable.

Remark: The strategy of proof we adopt here is different from that used for the proof of Theorem 15. Note that the Poincare inequality, in the form used in the proof of Theorem 15, does not hold on homogeneous Neumann boundary conditions.

Proof: From (2.5.1,2.5.2,2.5.3) we get

\[ \frac{\partial N}{\partial t} \leq D_n \Delta N + rN(1 - N). \]

By comparison, \(N(x, t) \leq \tilde{N}(x, t)\) where \(\tilde{N}(x, t)\) is the solution of

\[ \frac{\partial \tilde{N}}{\partial t} = D_n \Delta \tilde{N} + r\tilde{N}(1 - \tilde{N}) \]

\[ \frac{\partial \tilde{N}}{\partial n} = 0 \quad \text{on } \partial \Omega \]

\[ \tilde{N}(x, 0) = N(x, 0), \quad x \in \bar{\Omega}. \]

It is known, [13], that, since \(N(x, 0) \neq 0\) by hypothesis, \(\tilde{N}(x, t) \to 1\) as \(t \to \infty\), uniformly in \(x\). This means that

\[ \lim_{t \to \infty} \sup_{x \in \Omega} N(x, t) \leq 1. \]
Let $\epsilon > 0$ be arbitrary. Then there exists $T > 0$ such that, for all $t \geq T$ and all $x \in \overline{\Omega}, \ N(x, t) \leq 1 + \epsilon$. Then for all $t \geq T + \tau$,

$$\frac{\partial u_m}{\partial t} \leq D_m \Delta u_m(x, t) - d(u_m(x, t)) - \mu_T u_m(x, t) + e^{-\mu_T \tau} b(u_m(x, t - \tau))(1 + \epsilon). \quad (2.7.7)$$

Next we make the claim that

$$\ell_2 := \limsup_{t \to \infty} \max_{x \in \overline{\Omega}} u_m(x, t) < u^\text{max}$$

where we recall that $u^\text{max}$ is defined by (2.2.5). Suppose the contrary, i.e. that $\ell_2 \geq u^\text{max}$. There exists a sequence of times $t_k$, and for each such time a corresponding spatial point $x_k \in \overline{\Omega}$ at which $\max_{x \in \overline{\Omega}} u_m(x, t_k)$ is attained, such that $u_m(x_k, t_k) \to \ell_2$ as $k \to \infty$ and also such that either $\partial u_m(x_k, t_k)/\partial t = 0$ for each $k$ or $\partial u_m(x_k, t_k)/\partial t \to 0$ as $k \to \infty$. Note also that $\Delta u_m(x_k, t_k) \leq 0$ for each $k$; this is because $x_k$ is the point at which the maximum is attained (in fact $\Delta u_m(x_k, t_k) \leq 0$ even if $x_k$ is on the boundary of $\Omega$ because the boundary conditions are homogeneous Neumann). Assuming that $k$ is so large that $t_k \geq T + \tau$, evaluating (2.7.7) at $(x_k, t_k)$ and using

$$\frac{\partial u_m}{\partial t}(x_k, t_k) \leq -d(u_m(x_k, t_k)) - \mu_T u_m(x_k, t_k) + e^{-\mu_T \tau} b(u_m(x_k, t_k - \tau))(1 + \epsilon). \quad (2.7.8)$$

Letting $k \to \infty$ in (2.7.8) and using the upper bound $b^\text{max}$ gives

$$0 \leq -d(\ell_2) - \mu_T \ell_2 + e^{-\mu_T \tau} b^\text{max}(1 + \epsilon).$$

This is true for all $\epsilon > 0$, hence

$$e^{-\mu_T \tau} b^\text{max} \geq d(\ell_2) + \mu_T \ell_2,$$

which can be written

$$e^{-\mu_T \tau} b(\ell_2^\text{max}) \geq d(\ell_2) + \mu_T \ell_2.$$

Since we are supposing $\ell_2 \geq u^\text{max}$, and since the death function is monotone, it follows from the above that

$$e^{-\mu_T \tau} b(u^\text{max}) \geq d(u^\text{max}) + \mu_T u^\text{max},$$

which, since $u^\text{max} > 0$, is contrary to the hypothesis of the Theorem. Thus $\ell_2 < u^\text{max}$.
Let \( \epsilon_2 > 0 \) be sufficiently small that \( \ell_2 + \epsilon_2 \leq u^{\max} \). Then there exists \( T_2 > 0 \) such that, for all \( t \geq T_2 \) and all \( x \in \overline{\Omega} \) the inequalities:

\[
\ell_2 + \epsilon_2 \leq u_m(x, t) \leq u^{\max}
\]

and

\[
N(x, t) \leq 1 + \epsilon_2,
\]

both hold. Note that for all times \( t \) exceeding \( T_2 \), \( u_m(x, t) \) is confined to the interval of values of \( u_m \) in which \( b(u_m) \) is increasing. This means that, when \( k \) is sufficiently large that \( t_k - \tau > T_2 \),

\[
b(u_m(x_k, t_k - \tau)) \leq b(\ell_2 + \epsilon_2),
\]

so that if we evaluate \((2.5.2)\) at \((x_k, t_k)\) and use the above bound and the inequality \( N(x, t) \leq 1 + \epsilon_2 \), and recall also that \( \Delta u_m(x_k, t_k) \leq 0 \), we get

\[
\frac{\partial u_m}{\partial t}(x_k, t_k) \leq -d(u_m(x_k, t_k)) - \mu_2 u_m(x_k, t_k) + e^{-\mu_2 \tau} b(\ell_2 + \epsilon_2)(1 + \epsilon_2). \quad (2.7.9)
\]

Letting \( k \to \infty \),

\[
0 \leq -d(\ell_2) - \mu_2 \ell_2 + e^{-\mu_2 \tau} b(\ell_2 + \epsilon_2)(1 + \epsilon_2).
\]

This is true for all sufficiently small \( \epsilon_2 > 0 \), hence

\[
e^{-\mu_2 \tau} b(\ell_2) \geq d(\ell_2) + \mu_2 \ell_2.
\]

If \( \ell_2 > 0 \) this is contrary to the hypothesis of the theorem. Hence \( \ell_2 = 0 \), i.e.

\[
\limsup_{t \to \infty} \max_{x \in \overline{\Omega}} u_m(x, t) = 0.
\]

Hence \( u_m(x, t) \to 0 \) as \( t \to \infty \), uniformly for \( x \in \overline{\Omega} \).

We now wish to show that \( N(x, t) \) tends uniformly to \( 1 \) as \( t \to \infty \). We have already shown that \( \limsup_{t \to \infty} \max_{x \in \Omega} N(x, t) \leq 1 \). Therefore it is now sufficient to show that

\[
\liminf_{t \to \infty} \min_{x \in \overline{\Omega}} N(x, t) \geq 1. \quad (2.7.10)
\]

Let \( \epsilon_3 > 0 \) be arbitrary. Then there exists \( T_3 > 0 \) such that, for all \( t > T_3 \) and all \( x \in \overline{\Omega} \),

\[
0 \leq u_m(x, t) < \epsilon_3.
\]
Therefore, when \( t > T_3 \),
\[
\frac{\partial N}{\partial t}(x, t) \geq D_n \Delta N(x, t) + r N(x, t)(1 - N(x, t)) - \gamma_0 \epsilon_3 N(x, t).
\]

So, by comparison, \( N(x, t) \geq \hat{N}(x, t) \), where \( \hat{N}(x, t) \) satisfies
\[
\begin{align*}
\frac{\partial \hat{N}}{\partial t} &= D_n \Delta \hat{N} + r \hat{N}(1 - \hat{N}) - \gamma_0 \epsilon_3 \hat{N}, \\
\frac{\partial \hat{N}}{\partial n} &= 0 \quad \text{on } \partial \Omega \\
\hat{N}(x, T_3) &= N(x, T_3), \quad x \in \overline{\Omega},
\end{align*}
\]

which is an initial value problem starting at time \( T_3 \) rather than 0. Since \( N(x, 0) \neq 0 \), \( N(x, t) > 0 \) for all \( t > 0 \), \( x \in \overline{\Omega} \) by the strong maximum principle, and thus in particular \( N(x, T_3) > 0 \) for all \( x \in \overline{\Omega} \). Therefore it is known, [13], that we have
\[
\hat{N}(x, t) \to 1 - \frac{\gamma_0 \epsilon_3}{r},
\]
as \( t \to \infty \), uniformly for \( x \in \overline{\Omega} \). Hence
\[
\liminf_{t \to \infty} \min_{x \in \overline{\Omega}} N(x, t) \geq 1 - \frac{\gamma_0 \epsilon_3}{r}.
\]

Since this holds for arbitrarily small \( \epsilon_3 \), we conclude that (2.7.10) holds.

The proof that \( u_i(x, t) \) tends uniformly to 0 is similar.

### 2.8 Travelling waves in a reaction-diffusion model for myiasis

Consider the reaction-diffusion system
\[
\begin{align*}
\frac{\partial u_i}{\partial t} &= D_i \frac{\partial^2 u_i}{\partial x^2} + b(u_m(x, t)) N(x, t) - \mu u_i(x, t) - e^{-\mu \tau} b(u_m(x, t - \tau)) N(x, t - \tau), \\
\frac{\partial u_m}{\partial t} &= D_m \frac{\partial^2 u_m}{\partial x^2} + e^{-\mu \tau} b(u_m(x, t - \tau)) N(x, t - \tau) - d(u_m(x, t)) - \mu_r u_m(x, t), \\
\frac{\partial N}{\partial t} &= D_n \frac{\partial^2 N}{\partial x^2} + r N(x, t)(1 - N(x, t)) - \gamma N(x, t) u_m(x, t),
\end{align*}
\]
for \( x \in (-\infty, \infty) \), where \( D_i \) and \( D_n \) are very small.

We can see that one steady state that exists is \((u_i^*, u_m^*, N^*) = (0, 0, 1)\) and that another steady state, if it exists, \((u_i^*, u_m^*, N^*) = (\phi_i, \phi_m, \phi_n)\) at which the blowflies and sheep coexist must satisfy

\[
D_m \Delta \phi_m(x) + e^{-\mu_T b} \phi_m(x) \phi_n(x) - d(\phi_m(x)) - \mu_T \phi_m(x) = 0, \quad \text{for } x \in (-\infty, \infty)
\]

\[
D_n \Delta \phi_n(x) + \phi_n(x)(1 - \phi_n(x)) - \gamma \phi_n(x) \phi_m(x) = 0, \quad \text{for } x \in (-\infty, \infty).
\]

We wish to look for a travelling-front solution to our system as travelling waves are an appropriate type of solution to look for when studying the invasion of a blowfly population into a domain. We seek a travelling wave that will move to the left with speed \( c \). So to convert (2.8.1,2.8.2,2.8.3) to travelling wave form we set \( u_i(x, t) = I(z), u_m(x, t) = U(z), N(x, t) = V(z) \) where \( z = x + ct \) and without loss of generality \( c > 0 \). Thus system (2.8.1, 2.8.2,2.8.3) becomes

\[
cI'(z) = D_i I''(z) + b(U(z))V(z) - \mu I(z) - e^{-\mu_T b}(U(z - ct))V(z - ct)
\]

(2.8.4)

\[
cU'(z) = D_m U''(z) + e^{-\mu_T b}(U(z - ct))V(z - ct) - d(U(z)) - \mu_T U(z),
\]

(2.8.5)

\[
cV'(z) = D_n V''(z) + \tau V(z)(1 - V(z)) - \gamma V(z)U(z),
\]

(2.8.6)

where \( ' \) represents differentiation with respect to \( z \). We can see that (2.8.5) and (2.8.6) are independent of \( I(z) \) and so we can just look at these two equations when analysing system (2.8.4, 2.8.5,2.8.6).

If we start at the steady state \((0, 0, 1)\) and introduce some blowflies to the system we would expect that, at least initially, the blowfly populations would increase and the sheep population would decrease. We anticipate a solution such that ahead of the front we have \( I(-\infty) = 0, U(-\infty) = 0, V(-\infty) = 1 \) and behind the front we have \( I(\infty) = \phi_i, U(\infty) = \phi_m, V(\infty) = \phi_n \). To approximate the solution as \( z \to -\infty \) we set \( I = \tilde{I}, U = \tilde{U}, V = 1 + \tilde{V}, \) where \( \tilde{I}, \tilde{U}, \tilde{V} \) are small. Dropping the tilde's and applying to equations (2.8.5) and (2.8.6) we get

\[
cU'(z) = D_m U''(z) + e^{-\mu_T b}(U(z - ct))(1 + V(z - ct)) - d(U(z)) - \mu_T U(z),
\]

(2.8.7)

\[
cV'(z) = D_n V''(z) - \tau(1 + V(z))V(z) - \gamma(1 + V(z))U(z).
\]

(2.8.8)
Taylor expanding the birth and death functions and linearising the equations we get

\[ cU'(z) = D_m U''(z) + e^{-\mu_T b'(0)}U(z - cr) - d'(0)U(z) - \mu_T U(z), \quad (2.8.9) \]
\[ cV'(z) = D_n V''(z) - rV(z) - \gamma U(z). \quad (2.8.10) \]

Looking for solutions of the form \((U, V) = (k_1, k_2)e^{\lambda z}\) we get

\[ k_1(c\lambda - D_m \lambda^2 - e^{-\mu_T b'(0)}e^{-\lambda cr} + d'(0) + \mu_T) = 0, \quad (2.8.11) \]
\[ c\lambda k_2 - D_n \lambda^2 k_2 + r k_2 + \gamma k_1 = 0. \quad (2.8.12) \]

Looking at equation (2.8.11) we see that we have

\[ c\lambda - D_m \lambda^2 = e^{-\mu_T b'(0)}e^{-\lambda cr} - d'(0) - \mu_T. \quad (2.8.13) \]

We assume henceforth that \(e^{-\mu_T b'(0)} > d'(0) + \mu_T\) because instability of the \(u_m = 0\) state is clearly a necessary condition for a travelling wave of invasion to form. The graphs of the right hand side and left hand side of (2.8.13) as functions of \(\lambda\) either have zero, one or two intersections. In order for the front to have \(U(z) \to 0\) as \(z \to -\infty\) \textit{without oscillating} it is necessary for (2.8.13) to have at least one real positive root. The absence of any such roots indicates that \(U(z)\) would approach 0 as \(z \to \infty\) in an oscillatory manner and this would mean that the blowfly population is going negative which is biologically infeasible. It is clear that we can go from the situation where (2.8.13) has no real, positive roots to a situation where it does have such roots by varying certain parameters. This can be seen by sketching the graphs of the left and right hand sides of (2.8.13) as functions of \(\lambda\), for various different values of \(c\). We can determine the minimum wave speed by finding the situation in which the two curves touch so that (2.8.13) has exactly one real repeated root. This will happen when

\[ c\lambda^* - D_m (\lambda^*)^2 = e^{-\mu_T b'(0)}e^{-\lambda^* cr} - d'(0) - \mu_T, \quad (2.8.14) \]
\[ c - 2D_m \lambda^* = -cr e^{-\mu_T b'(0)}e^{-\lambda^* cr}. \quad (2.8.15) \]

where \(\lambda^* > 0\) is the repeated root. We can multiply (2.8.14) by \(cr\) and then add (2.8.14) to remove the exponential term, giving the following quadratic equation in \(\lambda^*:\)

\[ cr D_m (\lambda^*)^2 - (c^2 \tau - 2D_m)\lambda^* - c - cr (d'(0) + \mu_T) = 0, \quad (2.8.16) \]
which can be solved to give
\[ \lambda^* = \frac{1}{2cT D_m} \left( c^2 \tau - 2D_m \pm \sqrt{c^4 \tau^2 + 4D_m^2 + 4D_m c^2 \tau^2 (d'(0) + \mu_T)} \right). \]  
(2.8.17)

As all terms in the square root are positive it can be seen that \( \sqrt{c^4 \tau^2 + 4D_m^2 + 4D_m c^2 \tau^2 (d'(0) + \mu_T)} > c^2 \tau \) and so the value of \( \lambda^* \) which subtracts the square root will be negative. Therefore \( \lambda^* \) is given by (2.8.17) taking the positive square root. Substituting this value of \( \lambda^* \) into (2.8.15) gives the following equation for the minimum speed \( c \):
\[
\frac{1}{cT} \left( 2D_m - \sqrt{c^4 \tau^2 + 4D_m^2 + 4D_m c^2 \tau^2 (d'(0) + \mu_T)} \right) = -cT b'(0) \exp \left\{ -\mu_T - \frac{1}{2D_m} \left( c^2 \tau - 2D_m + \sqrt{c^4 \tau^2 + 4D_m^2 + 4D_m c^2 \tau^2 (d'(0) + \mu_T)} \right) \right\} 
\]  
(2.8.18)

The maximum of the left hand side of (2.8.13) as a function of \( \lambda \) is
\[ \frac{c^2}{4D_m}. \]

In the case of the repeated root when the two graphs are just touching simple graphical considerations show that this maximum value must be below the right hand side of (2.8.13) at \( \lambda = 0 \) which is \( b'(0)e^{-\mu_T} - d'(0) - \mu_T \). Therefore we get the inequality
\[ \frac{c^2}{4D_m} < b'(0)e^{-\mu_T} - d'(0) - \mu_T \]
which gives us the following inequality for the minimum wavespeed \( c \)
\[ c < 2\sqrt{D_m (b'(0)e^{-\mu_T} - d'(0) - \mu_T)} \]  
(2.8.19)

Recall we assumed \( e^{-\mu_T} b'(0) > d'(0) + \mu_T \). One conclusion to be drawn from (2.8.19) is that the blowflies will invade at a slower speed if their maturation delay \( \tau \) or juvenile mortality \( \mu \) increases. The same applies if there is an increase in trapping, \( \mu_T \), or adult mortality, \( d'(0) \). Conversely we can see that if the amount that the mature blowflies diffuse, \( D_m \), increases then they will invade at a faster speed.

### 2.9 Numerical simulations of reaction-diffusion model for Myiasis

To investigate our reaction-diffusion model (2.5.1,2.5.2,2.5.3) further we wrote a computer programme, in Fortran, to numerically simulate the evolution of the system over time on the one dimensional space \( x = [0, 40] \). For this programme we
chose \( b(u_m) = Pu_m e^{-A u_m} \) and \( d(u_m) = Cu_m \), for some real numbers \( A, C, P \), which we could vary as appropriate. The time stepping was carried out using the Adams-Bashforth method where, \( dt \) is the time step. Initially we set the population of the immature blowflies to zero and the populations of the mature blowflies and the sheep to follow normal distributions over the spatial domain with the mean at 20, the centre of our space, and variance 4, so that the populations are effectively zero on the boundary. First we ran a simulation on homogeneous Dirichlet boundary conditions where we kept the parameters fixed at \( P = 25, \tau = 100, dt = 0.01, A = 1, C = 0.9, \mu_i = 1, \mu_T = 0.01, \gamma_s = 1, r = 1, D_i = 0.01, D_m = 0.01, D_n = 0.01 \) and looked at the evolution over time, Figure 2.14. Note that in this case the time to maturation of the immature blowflies is one day. While it is known that the maturation time of an immature blowfly of the species \( Lucilia cuprina \) is about 15 days we envisage that our model may be applied to other species which have different maturation rates. We can see from Figure 2.14 that the populations start off oscillating but end up settling down to equilibrium values where we have existence of both the blowflies and the sheep.

We then decided to look at the effect of varying \( P \) but keeping \( \tau = 100 \). Figure 2.15 shows the populations at the spatial position \( x = 20 \) against time, which is measured in days. The graphs show that the populations oscillate with decreasing amplitude over time until eventually reaching an equilibrium population. As \( P \) increases the frequency and amplitude of the oscillations also increase, but the amplitude of the oscillations still decrease over time until eventually reaching an equilibrium population. We can also see that as \( P \) increases the equilibrium population for the blowflies gets larger while the sheep gets smaller. Indeed working to two decimal places the populations of the species after 1000 days when \( P = 5 \) are \((u_i, u_m, N) = (0.50, 0.32, 0.68)\), but when \( P = 140 \) the populations are \((u_i, u_m, N) = (1.49, 0.95, 0.05)\).

We then looked at the effects of varying \( \tau \) while keeping \( P = 70 \). We found that increasing the delay initially caused an increase in the equilibrium solution of the population of immature blowflies but once \( \tau \) passed a threshold value it caused the eventual extinction of the blowfly population as can be seen from the final graph in Figure 2.16. This is due to the fact that the gestation period of the mature blowflies is so long compared to the death rate that most of the mature blowflies die before the immature ones mature and so the maturation does not cause a significant enough
Figure 2.14: Graphs to show the evolution over time of our system on homogeneous Dirichlet boundary conditions, when $P = 25$, $\tau = 100$ and $dt = 0.01$. Parameter values used are $A = 1$, $C = 0.9$, $\mu_i = 1$, $\mu_T = 0.01$, $\gamma_s = 1$, $r = 1$, $D_i = 0.01$, $D_m = 0.01$, $D_n = 0.01$. 
Figure 2.15: Graphs of different values of $P$ over time when, $\tau = 100$ and $dt = 0.01$. Parameter values used are $A = 1, C = 0.9, \mu_i = 1, \mu_T = 0.01, \gamma_s = 1, r = 1, D_i = 0.01, D_m = 0.01, D_n = 0.01$. 
increase in the population to stop the mature blowflies eventually dying out. Once the mature blowflies have died out it follows that no more immatures will be born and thus the sheep population is free to reach its maximum population.

We then attempted to increase the amount of diffusion of the immature blowflies in our model. As we are thinking of our domain as a continuum of fields we will not have larger diffusion of either the sheep or the immature blowflies. If we did wish to incorporate larger diffusion of either of these species we would need to change the maturation term to accommodate distributed delay. We also note that as the blowflies live on the sheep it is perhaps not biologically reasonable to say that they would diffuse at different rates, especially as once they have dropped off the sheep they burrow into the ground and generally do not travel a significant horizontal distance. When increasing the diffusion we had to be careful to avoid the problem of grid scale instability, which can occur if the time step is too big. Therefore we needed to modify our time step so that it depended on the diffusivity, $dt = 0.1dx^2/D_m$. While this solved the problem of grid scale instability it meant that for large diffusion our time step became much smaller than before and thus we needed to run the simulation for longer in order to evolve the system over the same time period as before.
Figure 2.17 show that with no diffusion all three populations appear to have reached a spatially uniform equilibrium (except directly on the boundary). However the incorporation of diffusion removes the spatial uniformity as the effect of the boundary conditions start to spread into the domain. We see that by increasing $D_m$ the mature blowfly population now tends to zero on the boundaries from a greater distance, at a shallower gradient. This effects both the other species as well. In the top two graphs of Figure 2.17 all species obey homogeneous Dirichlet boundary conditions. In the bottom two graphs the mature blowflies still obey homogeneous Dirichlet boundary conditions but the sheep and the immature blowflies obey homogeneous Neumann boundary conditions, which we consider to be more realistic. However we can see that the different choices of boundary conditions have little effect in this case. The main difference is that under homogeneous Neumann boundary conditions the sheep can exist on the boundary and actually achieve a higher population as there are no parasites to feed off and possibly kill them here. There are no immature blowflies at the boundary even when they obey homogeneous Neumann boundary conditions. This is because there are no mature blowflies at the boundary and therefore no chance for immature blowflies to be born there. Therefore the only way for immature blowflies to exist on the boundary would be if they had come from another point in space, which will not happen in our model.

In Theorem 25 we showed that under homogeneous Neumann boundary conditions the steady state $(u_m, u_n, N) = (0, 0, 1)$ would be linearly stable if $e^{-\mu_T}y'(0) < d'(0) + \mu_T$. For the functions used in our numerical simulations this inequality becomes $e^{-\mu_T dt}P < C + \mu_T$. We can show this condition numerically. By fixing $\mu_i = 0.5, \tau dt = 1, C = 0.9, \mu_T = 0.01$ we get a condition dependent on $P$; $e^{-0.5P} < 0.91$, which gives a critical value of $P = 1.5$. We can see from the first two graphs of Figure 2.18, taken after 100 days, that when we set $P = 1$ we get the equilibrium $(0, 0, 1)$, but when $P = 2$ we get an equilibrium with existence of both species. A linear stability analysis on mixed boundary conditions, where the mature blowflies obey homogeneous Dirichlet boundary conditions but the immature blowflies and the sheep obey homogeneous Neumann boundary conditions, includes the term $D_m \lambda_1$ which suggests that for parameter values which do not give stability of the steady state a sufficient increase of the diffusion parameter $D_m$ should lead to stability. Indeed we can see from the third graph of Figure 2.18, taken after 16 days, that the co-existence equilibrium from when $P = 2$ and $D_m = 1$ is changed to the $(0, 0, 1)$ steady state when $D_m = 100$. 

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Figure 2.17: Graphs to show the effects of changing $D_m$ on the populations after 30 days. In the top two graphs all species obey homogeneous Dirichlet boundary conditions but in the bottom two graphs the sheep and the immature blowflies obey homogeneous Neumann boundary conditions. Parameter values used are $P = 25$, $\tau dt = 1$, $A = 1$, $C = 0.9$, $\mu_i = 1$, $\mu_T = 0.01$, $\gamma_b = 1$, $r = 1$, $D_i = 0$, $D_n = 0$. 
Figure 2.18: Graphs to show the stability conditions of the steady state $(u_m, u_n, N) = (0, 0, 1)$ on mixed boundary conditions at $t = 100,000dt$. Parameter values used are $\tau dt = 1, A = 1, C = 0.9, \mu_i = 0.5, \mu_T = 0.01, \gamma_s = 1, r = 1, D_i = 0.01, D_n = 0.01$. 
To investigate how much effect our initial conditions had we tried out different sorts of distributions for our initial conditions. Figure 2.19 shows three different initial populations and the evolutions of the species after 1000 days, when the populations had reached equilibrium. The first two graphs are from an initial normal distribution, as used in Figure 2.14. We then tried an exponential distribution which had the mean on the left hand side of the space and a relative long tail over the rest of the space. Finally we choose random initial conditions, where we used a random number function $\chi(t)$ to generate a random number between 0 and 1 for every point in the space. Figure 2.19 shows that all three different initial conditions end up with the same equilibrium population.

2.9.1 Spatially dependent trapping

We think of our spatial domain as a continuum of fields, with the mature blowflies able to travel among the fields while the sheep are restricted. Thus the diffusivity of the sheep, and consequently the immature blowflies are very small, while the
diffusivity of the mature blowflies could be much bigger. One area of interest is to investigate what would happen if the trapping intensity varied over the space, for example if some farms had a more effective trapping policy than others. We simulated this scenario by letting the trapping coefficient, \( \mu_T \) be a different value for \( x \in [35, 65] \) than in the rest of the spatial domain. We can see the results in Figure 2.20. These graphs show the evolution of the number of eggs laid over time at specific points in space, \( x = 50, x = 40, x = 30, x = 20, x = 10 \) and \( x = 1 \). We started our simulation off with the populations constant in space, we set the sheep population equal to one, the mature blowflies equal to 0.1 and the immature blowflies equal to zero. The first graph in Figure 2.20 shows the evolution with no trapping and diffusion of mature blowflies. We see that in this case it settles down to a periodic solution that behaves exactly the same over the whole domain. The second graph shows what happens if we allow diffusion of the mature blowflies, by setting \( D_m = 10 \). Now we see that the system does not behave in the same way over the whole domain. After some initial noise up to \( t = 45 \) we see that it does settle down to a periodic solution. The frequency of eggs laid is higher near the edge of the domain at \( x = 10 \) and does not oscillate so much. In the third graph we allow a large amount of trapping, by setting \( \mu_T = 5 \). Here we see that we have a small amount of eggs laid to begin with, but the number laid decrease exponentially over time and eventually die out causing the extinction of both immature and mature blowflies. Next we investigated what would happen if we allowed this amount of trapping in just a small portion of the domain, for \( x \in [35, 65] \) but did not allow diffusion. As might be expected we can see from the fourth graph of Figure 2.20 that in this case the solution behaves like the third graph for \( x \in [35, 65] \) and, after an initial settling down period, like the first graph outside this interval, as we do not allow movement of species over space. Thus it seemed like it would be more interesting to allow diffusion so we set \( D_m = 10 \). The result can be seen in graph five. Here we can clearly see a difference in behaviour, the evolution no longer looks similar to the first or third graphs. In fact we no longer have a periodic solution. The introduction of diffusion has smoothed out our solution so that the number of eggs laid settle down to an equilibrium solution, which is different at different points in space. We can see that solution is lowest in the middle of our interval where we have a high amount of trapping, \( x = 50 \). Closer to the edge however, at \( x = 40 \) the frequency is much higher and only just lower than at \( x = 20 \) where there is no trapping. We then investigated what would happen if we reversed our trapping so
that there was a high amount of trapping over most of the space but a small area where no trapping occurred, \( x \in [35, 65] \). We can see from the last graph of Figure 2.20 that again a non periodic equilibrium solution is reached. The places where there is no trapping reach a higher equilibrium value and we can see that the further away we get from this interval the lower is the equilibrium solution. We also see that the highest population does not occur at the center of the interval, \( x = 50 \), but rather nearer the edge.

Figure 2.20: shows evolution with different trapping rates over space. Parameter values are \( \mu_i = 0.1, \gamma_s = 0.1, r = 0.1, D_i = 0, D_n = 0, A = 10, C = 0.2, P = 500/30, \tau dt = 15. \)
2.9.2 A simulation to show overwintering

It is well documented that when the weather gets cold enough the immature blowflies will overwinter. This means that instead of being in their pupa for just over a week they will stay in this state until the weather gets warmer. Our model does not account for this phenomenon. Thus we adapted our computer programme to show this. This involved creating a new variable to model the overwintering blowflies, \( u_h(t) \). We introduced a variable to keep track of the months, where month 1 was October and month 12 September. We claim that between October and March, Australian summertime, the system will evolve according to our original model but between April and September any immature blowflies that would mature in the summer would instead overwinter. At the beginning of October overwintering blowflies will start to become mature blowflies. It is also known that overwintering blowflies may be susceptible to being eaten or dying of natural causes, so a death term must be included. Thus our model for the evolution of overwintering flies is

\[
\frac{\partial U_h}{\partial t}(x, t) = e^{-\mu_h t}b(u_m(x, t - \tau))N(x, t - \tau) - \mu_h u_h(x, t) \quad \text{if} \quad m \in [1, 6],
\]

\[
\frac{\partial U_h}{\partial t}(x, t) = -T u_h(x, t) \quad \text{if} \quad m \in [7, 12],
\]

(2.9.1)

where \( \mu_h \) is the death rate of overwintering blowflies, \( T \) is the conversion rate from overwintering to mature blowflies and \( m \) is the month of the year as described above. We did not include diffusion in this model as we wanted the time step to be quite large so we could observe the evolution over long periods of time. The equations for the other species are similar to (2.5.1, 2.5.2, 2.5.3) except that we set the diffusion coefficients to zero and when \( m \in [1, 6] \) the mature blowfly equation will have the additional term \( Tu_h(x, t) \) to model the overwintering blowflies maturing. This set up showed that the evolution over time of our model took a similar form to previously during the summer months but in the winter we see that the mature and immature blowflies die out. During this time there is a high population of overwintering flies which do not feed on the sheep and so the sheep population reach their carrying capacity. At the beginning of the next summer we see that the overwintering flies become mature blowflies and our model evolves again. Figure 2.21 shows a simulation over 3 years at the point \( x = 50 \). We see that we get oscillations of the populations over the summer before reaching the winter where the blowflies die. We can see that the population of mature blowflies at the onset
of winter determines the population of overwintering flies.

![Graph showing evolution of species over 2 years with rate of conversion of overwintering to mature](image)

Figure 2.21: Graphs to show evolution over time of the overwintering model Parameter values used are $\tau dt = 12, A = 1, C = 0.3, \mu_i = 0.01, \mu_T = 0.01, \gamma_s = 1, r = 1, P = 500/30, \mu_h = 0.01, T = 0.9, dt = 0.1.$
3.1 Discrete diffusion model

In this section we attempt to construct a model for blowfly strike (or *Myiasis*) using discrete diffusion. In this case we envisage that there exist a series of patches and the blowflies are able to travel between them but can only travel to an adjacent patch during one time step. We define \( u = \) immature blowflies, \( U = \) mature blowflies and \( V = \) sheep. We also include a linear death term for the mature blowflies that includes natural death rate, \( d \) and death rate due to trapping, \( T_n \). Thus our model will take the form

\[
\begin{align*}
\frac{du_n}{dt} & = b(U_n(t))V_n(t) - \mu u_n(t) - e^{-\mu \tau} b(U_n(t - \tau)) V_n(t - \tau) \\
\frac{dU_n}{dt} & = e^{-\mu \tau} b(U_n(t - \tau)) V_n(t - \tau) - (d + T_n) U_n + D(U_{n+1}(t) + U_{n-1}(t) - 2U_n(t)) \\
\frac{dV_n}{dt} & = rV_n(t)(1 - V_n(t)) - \gamma V_n(t) U_n(t),
\end{align*}
\]

for \( n \in \mathbb{Z} : = \{0, \pm 1, \pm 2, \ldots\} \),

where \( D, d, T_n, \gamma, \mu, r \) and \( \tau \) are positive constants and with initial conditions

\[
\begin{align*}
u_n(0) & = \phi_n^u(0) \geq 0, \quad n \in \mathbb{Z}, \\
U_n(s) & = \phi_n^U(s) \geq 0, \quad n \in \mathbb{Z}, \quad s \in [-\tau, 0] \\
V_n(s) & = \phi_n^V(s) \geq 0, \quad n \in \mathbb{Z}, \quad s \in [-\tau, 0].
\end{align*}
\]

These patches could be in a long line or, perhaps more realistically, in a ring. We shall first consider the case of an infinite number of patches in a line.
3.1.1 Positivity and boundedness

We can see that (3.1.2) and (3.1.3) do not depend on $u_n(t)$ so we do not need to look at (3.1.1) when analysing our system. We wish to prove positivity of $U_n(t)$.

**Proposition 27** Suppose for the system (3.1.1, 3.1.2, 3.1.3) subject to (3.1.4) and a compatibility condition similar to (2.2.6) in Proposition 4 that $T_{\text{sup}} < \infty, V_{\text{sup}}^0 < \infty$

where

$$
T_{\text{sup}} = \sup_{n \in \mathbb{Z}} T_n, \\
V_{\text{sup}}^0 = \sup_{n \in \mathbb{Z}} V_n(0),
$$

then $u_n(t), U_n(t), V_n(t) \geq 0$ for all $n \in \mathbb{Z}, t > 0$.

First we shall show that $U_n(t)$ is positive for $t \in (0, \tau]$. On this interval we have that $t - \tau \in [-\tau, 0]$ and thus the delayed term in (3.1.2) involves the initial data $\phi_n^U(s)$ and $\phi_n^V(s)$ which is positive by hypothesis. Thus we have

$$
\frac{dU_n}{dt} \geq -(d + T_{\text{sup}})U_n(t) + D(U_{n+1}(t) + U_{n-1}(t) - 2U_n(t)).
$$

Therefore $U_n(t) \geq \bar{U}_n(t)$ where $\bar{U}_n$ satisfies

$$
\frac{d\bar{U}_n}{dt} = -(d + T_{\text{sup}})\bar{U}_n(t) + D(\bar{U}_{n+1}(t) + \bar{U}_{n-1}(t) - 2\bar{U}_n(t)),
$$

subject to $\bar{U}_n(s) = U_n(s) \geq 0, \ s \in [-\tau, 0]$.

To solve (3.1.5) we shall need to use the discrete Fourier transform

$$
F^*(t, \omega) = \frac{1}{\sqrt{2\pi}} \sum_{n=-\infty}^{\infty} e^{-in\omega} F_n(t)
$$

and the inverse discrete Fourier transform

$$
F_n(t) = \frac{1}{\sqrt{2\pi}} \int_{-\pi}^{\pi} e^{in\omega} F^*(t, \omega) d\omega.
$$

From now on we shall denote $\sum_{n=-\infty}^{\infty}$ by $\sum_n$. First we multiply both sides of (3.1.5) by $e^{-in\omega}/\sqrt{2\pi}$ and then sum over $n$ to give

$$
\frac{1}{\sqrt{2\pi}} \sum_n \frac{d\bar{U}_n}{dt} e^{-in\omega} = -\frac{1}{\sqrt{2\pi}} (d + T_{\text{sup}}) \sum_n \bar{U}_n(t) e^{-in\omega} + \frac{D}{\sqrt{2\pi}} \sum_n \bar{U}_{n+1}(t) e^{-in\omega} + \frac{D}{\sqrt{2\pi}} \sum_n \bar{U}_{n-1}(t) e^{-in\omega} - \frac{2D}{\sqrt{2\pi}} \sum_n \bar{U}_n(t) e^{-in\omega}.
$$

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Noting that we can write \( \sum_{n=-\infty}^{\infty} \tilde{U}_{n+1}(t)e^{-in\omega} = \sum_{m=-\infty}^{\infty} \tilde{U}_m(t)e^{-im(m-1)\omega} \) and \( \sum_{n=-\infty}^{\infty} \tilde{U}_{n-1}(t)e^{-in\omega} = \sum_{m=-\infty}^{\infty} \tilde{U}_m(t)e^{-im(m+1)\omega} \) we apply the discrete Fourier transform to (3.1.5) to get

\[
\frac{d}{dt} \tilde{U}^*(t, \omega) = -(d + T_{\text{sup}}) \tilde{U}^*(t, \omega) + De^{i\omega} \tilde{U}^*(t, \omega) + De^{-i\omega} \tilde{U}^*(t, \omega) - 2D \tilde{U}^*(t, \omega)
\]

which can be easily solved by separation of variables to give

\[
\tilde{U}^*(t, \omega) = \tilde{U}^*(0, \omega) \exp \left\{ -(d + T_{\text{sup}}) + D(2 \cos \omega - 2) \right\} t.
\]

Also note that

\[
\tilde{U}^*(0, \omega) = \frac{1}{\sqrt{2\pi}} \sum_{n=-\infty}^{\infty} e^{-in\omega} \tilde{U}_n(0),
\]

hence using the inverse formula for the discrete Fourier transform, we obtain

\[
\tilde{U}_n(t) = \frac{1}{\sqrt{2\pi}} \int_{-\pi}^{\pi} e^{in\omega} \tilde{U}^*(0, \omega) e^{-(d + T_{sup}) + D(2 \cos \omega - 2)t} \, d\omega
\]

\[
= \frac{1}{\sqrt{2\pi}} \int_{-\pi}^{\pi} e^{-in\omega} e^{-(d + T_{\text{sup}})t} e^{2Dt(\cos \omega - 1)} \left\{ \frac{1}{\sqrt{2\pi}} \sum_{m=-\infty}^{\infty} e^{-im\omega} \tilde{U}_m(0) \right\} \, d\omega
\]

\[
= \frac{1}{2\pi} e^{-(d + T_{\text{sup}})t} \sum_{m=-\infty}^{\infty} \tilde{U}_m(0) \int_{-\pi}^{\pi} e^{i(n-m)\omega} e^{2Dt(\cos \omega - 1)} \, d\omega
\]

\[
= \frac{1}{2\pi} e^{-(d + T_{\text{sup}})t} \sum_{m=-\infty}^{\infty} \tilde{U}_m(0) \int_{-\pi}^{\pi} 2 \cos(n-m)\omega e^{2Dt(\cos \omega - 1)} \, d\omega
\]

Now we define

\[
\beta_\alpha(t) = 2e^{-2\alpha} \int_{0}^{\pi} \cos(t\omega)e^{2\alpha \cos \omega} \, d\omega.
\]

It has been shown in the paper by Weng et. al. [65] that \( \beta_\alpha(t) \geq 0 \) and hence

\[
\tilde{U}_n(t) = \frac{1}{2\pi} e^{-(d + T_{\text{sup}})t} \sum_{m=-\infty}^{\infty} \tilde{U}_m(0) \beta_D(n-m) > 0 \quad \text{on} \quad t \in (0, \tau).
\]  

(3.1.6)

Therefore \( \tilde{U}_n(t) \geq 0 \) (and hence \( U_n(t) \geq 0 \)) on \( t \in (0, \tau] \). We can prove positivity for \( t \in (\tau, 2\tau] \) by following a similar method and so on to prove that \( U_n(t) \geq 0 \) for
all \( t > 0 \) by the method of steps.

Next we prove positivity and boundedness of \( V_n(t) \) for \( t > 0 \). We see that (3.1.3) can be written as

\[
\frac{dV_n}{dt} = V_n(t) \left[ r(1 - V_n(t)) - \gamma U_n(t) \right].
\]

As we assume \( V_n(0) \geq 0 \) we have \( V_n(t) \geq 0 \) for all \( n \) and all \( t > 0 \). Also since \( U_n(t) \geq 0 \),

\[
\frac{dV_n}{dt} \leq r V_n(t)(1 - V_n(t)).
\]

Thus

\[
V_n(t) \leq \frac{e^{rt}V_n(0)}{1 + V_n(0)(e^{rt} - 1)} = \frac{e^{rt}}{\frac{1}{V_n(0)} + e^{rt} - 1}.
\]

By hypothesis in the proposition \( V_n(0) \leq V_0^{sup} \), where \( V_0^{sup} \) is some value independent of \( n \), which we would take to be \( \sup_{n \in \mathbb{Z}} \{ V_n^0(s) \}, \ s \in [-\tau, 0] \). Thus we have

\[
\sup_{n \in \mathbb{Z}} V_n(t) \leq \frac{e^{rt}}{V_0^{sup} + e^{rt} - 1}
\]

and therefore

\[
\lim_{t \to \infty} \sup_{n \in \mathbb{Z}} \left\{ \sup_{n \in \mathbb{Z}} V_n(t) \right\} \leq 1. \tag{3.1.7}
\]

To show positivity of \( u_n(t) \) we note that the solution to (3.1.1), subject to a suitable compatibility condition is

\[
u_n(t) = \int_{t-\tau}^{t} b(U_n(s))V_n(s)e^{-\mu(t-s)} ds,
\]

which, given that \( U_n(t) \) and \( V_n(t) \) are positive implies that \( u_n(t) \) must also be positive. The proof of Proposition 27 is complete.

### 3.2 Linear stability of model

For this section we shall treat the trapping term as constant in space, so we set \( T_n = T \) in equation (3.1.1). Looking for spatially uniform equilibrium solutions to the system (3.1.2,3.1.3) we find

\[
0 = e^{-\mu t} b(U^*) V^* - (d + T) U^*
\]

\[
0 = r V^*(1 - V^*) - \gamma V^* U^*.
\]
We can see by inspection that \((U^*, V^*) = (0, 0), (0, 1)\) satisfy the above equations. Let us investigate the possibility of an equilibrium with \(U^* > 0\) and \(V^* > 0\). Solving the second equation for \(V^*\) we get \(1 - \gamma U^*/r = V^*\). Then \(U^*\) is determined by:

\[
e^{-\mu r} b(U^*) \left(1 - \frac{\gamma}{r} U^*\right) = (d + T) U^* \tag{3.2.1}
\]

and the corresponding value for \(V^*\) is found from \(V^* = 1 - \gamma U^*/r\), provided (3.2.1) has a root \(U^* \in (0, r/\gamma)\). The natural condition for an equilibrium with \(U^* > 0\) to exist is that:

\[
e^{-\mu r} b(U) > (d + T) U \quad \text{for small} \quad U, \tag{3.2.2}
\]

\[
e^{-\mu r} b(U) < (d + T) U \quad \text{for large} \quad U. \tag{3.2.3}
\]

We now perturb our equations about a steady state \((U^*, V^*)\) by setting \(U_n(t) = U^* + \xi_n(t), V_n(t) = V^* + \eta_n(t)\), where \(\xi_n(t), \eta_n(t)\) are small. Substituting into equations (3.1.2,3.1.3) we get:

\[
\frac{d\xi_n}{dt} = e^{-\mu r} b(U^*) \eta_n(t - \tau) + \xi_n(t - \tau) b'(U^*) V^* - (d + T) \xi_n(t) + D (\xi_{n+1}(t) + \xi_{n-1}(t) - 2 \xi_n(t))
\]

\[
\frac{d\eta_n}{dt} = r \eta_n(t)(1 - 2V^*) - \gamma (V^* \xi_n(t) + \eta_n(t) U^*).
\]

Now we look for solutions of the form \(\xi_n(t) = c_1 e^{\sigma t} e^{i\theta}, \eta_n(t) = c_2 e^{\sigma t} e^{i\theta}\). After cancellation this gives:

\[
\sigma c_1 = e^{-\mu r} (b(U^*) e^{-\sigma \tau} + c_1 e^{-\sigma \tau} b(U^*) V^*) - (d + T) c_1 + D c_1(e^{i\theta} + e^{-i\theta} - 2)
\]

\[
\sigma c_2 = r c_2(1 - 2V^*) - \gamma (V^* c_1 + c_2 U^*).
\]

Noting that \(e^{i\theta} + e^{-i\theta} - 2 = 2 \cos \theta - 2 = -4 \sin^2(\theta/2)\) we put these equations into matrix form:

\[
\begin{pmatrix}
\sigma - e^{-\mu r} e^{-\sigma \tau} b(U^*) V^* + d + T + 4D \sin^2(\theta/2) & -e^{-\mu r} e^{-\sigma \tau} b(U^*) \\
\gamma V^* & \sigma - r(1 - 2V^*) + \gamma U^*
\end{pmatrix}
\begin{pmatrix}
c_1 \\
c_2
\end{pmatrix} = 0.
\]

For non-trivial solutions the determinant of this matrix must be zero.

**Theorem 28** Suppose that \(b(0) = 0\) and \(b(U) \geq 0\) for all \(U \geq 0\) holds in system (3.1.1,3.1.2,3.1.3). Suppose also that \(T_n = T,\) independent of \(n,\) then the equilibrium point \((u^*, U^*, V^*) = (0, 0, 0)\) is linearly unstable.
Proof: For the equilibrium point \((u^*, U^*, V^*) = (0, 0, 0)\), since \(b(0) = 0\) (3.2.4) becomes
\[
\begin{pmatrix}
\sigma + d + T + 4D\sin^2(\theta/2) & 0 \\
0 & \sigma - r
\end{pmatrix}
\begin{pmatrix}
c_1 \\
c_2
\end{pmatrix} = 0.
\]
Thus one eigenvalue is \(\sigma = r > 0\), hence \((0, 0, 0)\) is linearly unstable.

**Theorem 29** Suppose that \(b(0) = 0, b(U) \geq 0\) for all \(U \geq 0\) and \(b(U)\) is differentiable in system (3.1.1, 3.1.2, 3.1.3). Suppose also that \(T_n = T\), independent of \(n\) and that
\[
e^{-\mu r}b'(0) < d + T,
\]
then the equilibrium point \((u^*, U^*, V^*) = (0, 0, 1)\) is linearly stable.

Proof: For the equilibrium point \((u^*, U^*, V^*) = (0, 0, 1)\) we find that (3.2.4) becomes
\[
\begin{pmatrix}
\sigma - e^{-\mu r}e^{-\sigma r}b'(0) + d + T + 4D\sin^2(\theta/2) & 0 \\
\gamma & \sigma + r
\end{pmatrix}
\begin{pmatrix}
c_1 \\
c_2
\end{pmatrix} = 0.
\]
giving the eigenvalue equation
\[
(\sigma - e^{-\mu r}e^{-\sigma r}b'(0) + d + T + 4D\sin^2(\theta/2)) (\sigma + r) = 0.
\]
One eigenvalue is \(\sigma = -r < 0\). For \((0, 0, 1)\) to be linearly stable we now need to show that the eigenvalues attributable to the other factor are also in the left half of the complex plane. For a contradiction, let us assume that there exists an eigenvalue \(\hat{\sigma}\) in the right hand side of the complex plane. Then
\[
|\hat{\sigma} + d + T + 4D\sin^2(\theta/2)| = e^{-\mu r}b'(0)|e^{-\hat{\sigma} r}| = e^{-\mu r}b'(0)e^{-(Ra(\theta))r},
\]
so that
\[
|\hat{\sigma} + d + T + 4D\sin^2(\theta/2)| \leq e^{-\mu r}b'(0).
\]
Thus if
\[
e^{-\mu r}b'(0) < d + T + 4D\sin^2(\theta/2),
\]
then a contradiction is reached. If this holds for \(\theta = 0\) it will hold for all \(\theta\). So if
\[
e^{-\mu r}b'(0) < d + T,
\]
holds then the equilibrium point \((u^*, U^*, V^*) = (0, 0, 1)\) is linearly stable.
3.3 Global stability of the steady state $(u^*, U^*, V^*) = (0, 0, 1)$ on an infinite lattice

To prove global stability we follow a similar idea to that in the paper by Gourley & Wu [25]. Note that we do not require $T_n$ to be independent of $n$ here. We define $U(t) = \{U_n(t)\}_{n=-\infty}^{\infty}$. We use the following result from the book by K. Deimling [17]

**Lemma 30** Let $X$ be a Banach space over $\mathbb{R}$ or $\mathbb{C}$. Assume that $f : [0, \infty) \times X \to X$ is continuous and that there exists a constant $L \geq 0$ such that

$$|f(t, x) - f(t, y)| \leq L|x - y|.$$ 

Then for any given $x^0 \in X$ there exists a unique continuously differentiable function $x : [0, \infty) \to X$ such that $x(t) = f(t, x(t))$ for $t \in [0, \infty)$ and $x(0) = x^0$.

We shall take $X = \ell^2$ where we define $\ell^2$ to be the Hilbert space of sequences $(U_n)_{n=-\infty}^{\infty}$ such that $\sum_{n=-\infty}^{\infty} U_n^2 < \infty$, with the norm

$$\|U\|_{\ell^2} = \left( \sum_{n=-\infty}^{\infty} U_n^2 \right)^{1/2}.$$ 

**Theorem 31** Let the initial data for (3.1.2,3.1.3) $\phi^U, \phi^V : [-\tau, 0] \to \ell^2$ be continuous and $\phi^U_n(s), \phi^V_n(s) \geq 0$ for each $s \in [-\tau, 0]$ and each $n \in \mathbb{Z}$. Assume that $b(0) = 0, b(U) \geq 0$ for all $U > 0$ and further that

$$\sup_{U \geq 0} \frac{e^{-\mu r} b(U)}{(d + T_{\text{inf}})U} < 1 \quad (3.3.7)$$

$$V_0 := \sup_{n \in \mathbb{Z}} V_n(0) < \infty \quad (3.3.8)$$

$$T_{\text{inf}} := \inf_{n \in \mathbb{Z}} T_n > 0 \quad (3.3.9)$$

then

$$\sup_{n \in \mathbb{Z}} U_n(t) \to 0 \quad \text{as} \quad t \to \infty. \quad (3.3.10)$$

**Remark:** We would intuitively expect as a necessary condition for survival that adult recruitment rate of blowflies should be sufficient to offset the combined effects of natural death and trapping, on at least one of the patches. If adult recruitment is insufficient to offset this even with minimum trapping then we expect the species to have no chance of survival. Thus condition (3.3.7) is the natural condition to impose.
**Proof:** If we apply Lemma 30 to the coupled system (3.1.2,3.1.3) on consecutive intervals \([nr,(n+1)r], n = 0, 1, 2, \ldots\), we conclude that a solution of (3.1.2,3.1.3) exists such that \(\{U_n(t)\}_{n=-\infty}^{\infty}, \{V_n(t)\}_{n=-\infty}^{\infty} \in \ell^2\) for each \(t > 0\). We see that if the supremum in (3.3.7) is attained at \(U = 0\) then (3.3.7) becomes \(e^{-\mu t}v(0) < d + T_{inj}\) which is the type of condition we would expect to get from a linearised stability analysis. It is an elementary property of real numbers that if \(\alpha < 1\) and \(\epsilon\) is small enough then \(\alpha(1 + \epsilon) \leq 1\). Therefore there exists an \(\epsilon > 0\) such that

\[
(1 + \epsilon) \sup_{U \geq 0} \left( \frac{e^{-\mu t}b(U)}{(d + T_{inj})U} \right) \leq 1
\]

and so

\[
e^{-\mu t}b(U)(1 + \epsilon) \leq (d + T_{inj})U, \quad \text{for all} \quad U \geq 0. \tag{3.3.11}
\]

We already know from (3.1.7) that

\[
\lim_{t \to \infty} \sup_{n \in \mathbb{Z}} \{\sup_{t \in \mathbb{Z}} V_n(t)\} \leq 1.
\]

With \(\epsilon > 0\) chosen as above there exists \(T > 0\) such that for \(t \geq T\), \(\sup_{n \in \mathbb{Z}} V_n(t) < 1 + \epsilon\) and so for each fixed \(n\), \(V_n(t) < 1 + \epsilon\). So when \(n \in \mathbb{Z}\) and \(t \geq T + \tau\), \(V_n(t-\tau) < 1 + \epsilon\). Thus (3.1.2) becomes, for \(t > T + \tau\)

\[
\frac{dU_n}{dt} \leq e^{-\mu t}b(U_n(t-\tau))(1 + \epsilon) - (d + T_n)U_n + D(U_{n+1}(t) + U_{n-1}(t) - 2U_n(t)). \tag{3.3.12}
\]

We multiply (3.3.12) by \(U_n(t)\) and sum over \(n \in \mathbb{Z}\) to give

\[
\sum_n \frac{dU_n(t)}{dt} U_n(t) \leq \sum_n e^{-\mu t}b(U_n(t-\tau))(1 + \epsilon)U_n(t) - \sum_n (d + T_n)U_n^2(t)
\]

\[
+ D \sum_n U_n(t)(U_{n+1}(t) + U_{n-1}(t) - 2U_n(t))
\]

\[
= \sum_n e^{-\mu t}b(U_n(t-\tau))(1 + \epsilon)U_n(t)
\]

\[
- \sum_n (d + T_n)U_n^2(t) - D \sum_n (U_n(t) - U_{n-1}(t))^2
\]

\[
+ D \sum_n [U_n(t)(U_{n+1}(t) - U_n(t)) - U_{n-1}(t)(U_n(t) - U_{n-1}(t))],
\]

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where $\sum_n = \sum_{n=-\infty}^{\infty}$. However we can see that the last term on the right hand side will sum to zero because $U_n(t) \to 0$ as $|n| \to \infty$. So we have

$$\frac{1}{2} \frac{d}{dt} \sum_n U_n^2(t) + D \sum_n (U_n(t) - U_{n-1}(t))^2 \leq \sum_n e^{-\nu \tau} b(U_n(t - \tau))(1 + \epsilon) U_n(t) - \sum_n (d + T_n) U_n^2(t).$$

Using (3.3.11) and noting that $T_n \geq T_{inf}$, for all $n \in \mathbb{Z}$ we get

$$\frac{1}{2} \frac{d}{dt} \sum_n U_n^2(t) + D \sum_n (U_n(t) - U_{n-1}(t))^2 \leq (d + T_{inf}) \sum_n U_n(t) - \sum_n (d + T_{inf}) U_n^2(t) \leq \frac{d + T_{inf}}{2} \left( \sum_n U_n^2(t - \tau) + \sum_n U_n^2(t) \right) - (d + T_{inf}) \sum_n U_n^2(t) = \frac{d + T_{inf}}{2} \left( \sum_n U_n^2(t - \tau) - \sum_n U_n^2(t) \right).$$

Integrating with respect to time from 0 to $t$ we get

$$\frac{1}{2} \left( \|U(t)\|_2^2 - \|U(0)\|_2^2 \right) + \int_0^t D \sum_n (U_n(s) - U_{n-1}(s))^2 ds \leq \frac{d + T_{inf}}{2} \int_0^t \|U(s - \tau)\|_2^2 ds - \frac{d + T_{inf}}{2} \int_0^t \|U(s)\|_2^2 ds,$$

which can be rearranged to give

$$\|U(t)\|_2^2 - \|U(0)\|_2^2 + (d + T_{inf}) \int_0^t \|U(s)\|_2^2 ds + 2D \int_0^t \sum_n (U_n(s) - U_{n-1}(s))^2 ds \leq (d + T_{inf}) \int_0^t \|U(s - \tau)\|_2^2 ds = (d + T_{inf}) \int_{-\tau}^0 \|U(s)\|_2^2 ds$$

$$\leq (d + T_{inf}) \int_{-\tau}^t \|U(s)\|_2^2 ds = (d + T_{inf}) \int_{-\tau}^0 \|U(s)\|_2^2 ds + (d + T_{inf}) \int_0^t \|U(s)\|_2^2 ds.$$

Thus we have the inequality

$$\|U(t)\|_2^2 + 2D \int_0^t \sum_n \bar{U}_n^2(s) ds \leq \|U(0)\|_2^2 + (d + T_{inf}) \int_{-\tau}^0 \|U(s)\|_2^2 ds, \quad (3.3.13)$$

where we define

$$\bar{U}_n(t) = U_n(t) - U_{n-1}(t), \quad \bar{U} = \{\bar{U}_n(t)\}_{n=-\infty}^{\infty}. \quad (3.3.14)$$
From (3.3.13) we see that $||U(t)||_2$ remains bounded as $t \to \infty$ and also that

$$\int_0^\infty \left( \sum_n \bar{U}_n^2(s) \right) ds < \infty.$$

Assuming that the latter implies $\sum_n \bar{U}_n^2(t) \to 0$ as $t \to \infty$, then we have

$$\sum_n (U_n(t) - U_{n-1}(t))^2 \to 0 \quad \text{as} \quad t \to \infty.$$

It is also known, [25], that sequences $\{\omega_n\}_{n=-\infty}^{\infty} \in \ell^2$ satisfy the inequality

$$\sup_{n \in \mathbb{Z}} |\omega_n| \leq \sqrt{2} \left( \sum_n \omega_n^2 \right)^{1/4} \left( \sum_n (\omega_n - \omega_{n-1})^2 \right)^{1/4}.$$

So by letting $\omega_n = U_n(t) \geq 0$ we get

$$\sup_{n \in \mathbb{Z}} U_n(t) \leq \sqrt{2} ||U(t)||_2^{1/2} \left( \sum_n (U_n(t) - U_{n-1}(t))^2 \right)^{1/4},$$

which tends to zero as $t \to \infty$ because $||U(t)||_2$ is bounded independently of $t$ and $\sum_n (U_n(t) - U_{n-1}(t))^2 \to 0$ as $t \to \infty$. Thus the proof is complete.

### 3.4 Global stability of the steady state

$(u^*, U^*, V^*) = (0, 0, 1)$ on a finite lattice

The above analysis will not work on a finite lattice, primarily because we can not use the fact that the sequence $D \sum_n [U_n(t)(U_{n+1}(t) - U_n(t)) - U_{n-1}(t)(U_n(t) - U_{n-1}(t))]$ will sum to zero. However the analysis up to this point will still hold. We shall look at the case where our system obeys the discrete analogy of the homogeneous Neumann problem. Thus we need to rewrite the system (3.1.1,3.1.2,3.1.3) as

$$\frac{du_n}{dt} = b(U_n(t))V_n(t) - \mu u_n(t) - e^{-\mu \tau} b(U_n(t-\tau))V_n(t-\tau) \quad (3.4.15)$$

$$\frac{dU_n}{dt} = e^{-\mu \tau} b(U_n(t-\tau))V_n(t-\tau) - (d + T_n)U_n + D(AU)_n \quad (3.4.16)$$

$$\frac{dV_n}{dt} = rV_n(t)(1 - V_n(t)) - \gamma V_n(t)U_n(t) \quad (3.4.17)$$

for $n \in \mathbb{Z} := \{1, 2, \ldots, N\}$,
for \( t > 0 \), subject to the initial conditions

\[
\begin{align*}
\mathbf{u}_n(0) &= u_n^0 \geq 0, \\
\mathbf{U}_n(s) &= U_n^0(s) \geq 0, \\
\mathbf{V}_n(s) &= V_n^0(s) \geq 0, \quad n = 1, 2, \ldots, N, \quad s \in [-\tau, 0],
\end{align*}
\]

(3.4.18)

where \((\mathbf{A}\mathbf{U})_n\) means the \(n\)th component of the vector \(\mathbf{A}\mathbf{U}\) with:

\[
\mathbf{U} = \begin{pmatrix} U_1 \\ U_2 \\ \vdots \\ U_N \end{pmatrix}, \quad \mathbf{A} = \begin{pmatrix} -1 & 1 & 0 & \cdots & 0 & 0 \\ 1 & -2 & 1 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & -2 & 1 \\ 0 & 0 & 0 & \cdots & 1 & -1 \end{pmatrix}.
\]

(3.4.19)

It is explained in detail in Kyrychko, Gourley & Bartuccelli [38] why this is the discrete analogy of the homogeneous Neumann problem.

**Theorem 32** Suppose in system (3.4.15, 3.4.16, 3.4.17) subject to (3.4.18) that \(V_n^0(0) > 0\) for each \(n\), \(b(0) = 0\), \(b(U) > 0\) for all \(U > 0\) and that

\[
T_{\inf} = \min(T_1, T_2, \ldots, T_n),
\]

\[
\sup_{U > 0} \left( \frac{e^{-\mu T} b(U)}{(d + T_{\inf}) U} \right) < 1.
\]

Suppose also that \(\epsilon > 0\) and that \(\mathbf{U}_n(t)\) is any solution to the equation

\[
\frac{d\mathbf{U}_n}{dt} = e^{-\mu T} b(\mathbf{U}_n(t - \tau))(1 + \epsilon) - (d + T_{\inf})\mathbf{U}_n + D(\mathbf{A}\mathbf{U})_n,
\]

(3.4.20)

satisfying

\[
\mathbf{U}_n(s) \geq \mathbf{u}_n(s), \quad \text{for all} \quad s \in [-\tau, 0], n \in \mathcal{N},
\]

then \(\mathbf{U}_n(t) \leq \mathbf{U}_n(t)\) for all \(t \in (0, \infty)\), \(n \in \mathcal{N}\) and furthermore the equilibrium solution \((\mathbf{u}_*, \mathbf{U}_*, \mathbf{V}_*) = (0, 0, 1)\) is globally asymptotically stable.

**Proof:** The proof is divided into two parts:

*Case A:* \(b(U)\) is increasing for all \(U > 0\).
We see that there exists an $\epsilon > 0$ such that
\[
(1 + \epsilon) \sup_{U \geq 0} \left( \frac{e^{-\mu r} b(U)}{(d + T_{inf}) U} \right) < 1
\]
and so with this $\epsilon$ we have
\[
e^{-\mu r} b(U) (1 + \epsilon) < (d + T_{inf}) U, \quad \text{for all } U > 0. \quad (3.4.21)
\]
From (3.4.17) we see that, for each $n$, \( \limsup_{t \to \infty} V_n(t) \leq 1 \). With $\epsilon$ defined as above there exists $T > 0$ (which can be taken independent of $n$ since the lattice is finite here) such that for all $t \geq T$ and all $n \in \hat{Z}$, $V_n(t) < 1 + \epsilon$. Therefore when $n \in \hat{Z}$ and $t \geq T + \tau$, $V_n(t - \tau) < 1 + \epsilon$ and (3.4.16) becomes
\[
\frac{dU_n}{dt} \leq e^{-\mu r} b(U_n(t - \tau))(1 + \epsilon) - (d + T_{inf}) U_n + D(AU)_n, \quad \text{for all } t > T + \tau.
\]
(3.4.22)

We see by comparing (3.4.20) and (3.4.22) that we get
\[
\frac{dU_n}{dt} - e^{-\mu r} b(U_n(t - \tau))(1 + \epsilon) + (d + T_{inf}) U_n - D(AU)_n
\leq
\frac{d\hat{U}_n}{dt} - e^{-\mu r} b(\hat{U}_n(t - \tau))(1 + \epsilon) + (d + T_{inf}) \hat{U}_n - D(A\hat{U})_n,
\]
and we want to conclude from this that $U_n(t) \leq \hat{U}_n(t)$. Letting $\eta_n(t) = \hat{U}_n(t) - U_n(t)$, the above inequality becomes
\[
\frac{d\eta_n}{dt} - e^{-\mu r} \left[ b(\hat{U}_n(t - \tau)) - b(U_n(t - \tau)) \right] (1 + \epsilon) + (d + T_{inf}) \eta_n - D(A\eta)_n \geq 0,
\]
where $\eta = (\eta_1, \eta_2, \cdots, \eta_n)^T$. We want to show $\eta_n(t) \geq 0$ for all $t \geq 0$. We shall first establish this for $t \in (0, \tau]$. Looking on the interval $t \in (0, \tau]$ we see that $t - \tau \in (-\tau, 0]$ and so the above inequality becomes
\[
\frac{d\eta_n}{dt} - e^{-\mu r} \left[ b(\hat{U}_n(s)) - b(U_n(s)) \right] (1 + \epsilon) + (d + T_{inf}) \eta_n - D(A\eta)_n \geq 0,
\]
with $s = t - \tau \in [-\tau, 0]$.

By hypothesis we know that $U_n(s) \leq \hat{U}_n(s)$ in $[-\tau, 0]$ Applying the mean value theorem to the square bracketed term, we obtain
\[
\frac{d\eta_n}{dt} - e^{-\mu r} b'(\theta(s)) \eta_n(s)(1 + \epsilon) + (d + T_{inf}) \eta_n - D(A\eta)_n \geq 0, \quad (3.4.23)
\]
with \( s = t - \tau \in [-\tau, 0] \), where \( \theta(s) \) is such that \( U_n(s) \leq \theta(s) \leq \hat{U}_n(s) \). Since the birth function is increasing, \( \theta'(\theta(s)) \geq 0 \). We wish to show that \( \eta_n(t) \geq 0 \) for all \( n \in \mathbb{Z}, t \in (0, \tau] \). For a contradiction let us assume this is not the case. Then \( \eta_n(t) \) must attain a negative minimum at some node \( n^* \) and some time \( t^* \) in the set \( \{(n, t) \in \{1, 2, \ldots, N\} \times [0, \tau] \} \). We know that \( \eta_n(0) \geq 0 \), for each \( n \) and so \( t^* > 0 \) (but \( t^* \) could equal \( \tau \)). This implies that \( \eta_n(t^*) \leq 0 \). Looking at the \( n^* \)th component of \( A\eta \) at time \( t^* \), we see that it will either be \( \eta_{n^*-1}(t^*) + \eta_{n^*+1}(t^*) - 2\eta_{n^*}(t^*) \) or, if \( n^* = 1 \), it will be \( -\eta_1(t^*) + \eta_2(t^*) \) or, if \( n^* = N \), it will be \( \eta_{N-1}(t^*) - \eta_N(t^*) \).

All these expressions must be non negative since \( \eta_{n^*}(t^*) \) is the minimum. As we know that \( \eta_{n^*}(t^*) < 0 \) and is the minimum point we see that (3.4.23) can not be satisfied (evaluating (3.4.23) at \( n = n^* \) and \( t = t^* \) shows this), therefore we must have that \( \eta_n(t) \geq 0 \) for all \( n \in \mathbb{Z}, t \in [0, \tau] \) which implies that \( U_n(t) \leq \hat{U}_n(t) \) for all \( t \in (0, \tau] \). We can conduct the same analysis on the interval \( t \in (\tau, 2\tau] \) to achieve the same result. This analysis continues and from the method of steps it follows that \( U_n(t) \leq \hat{U}_n(t) \) for all \( t \in (0, \infty) \) as required.

Exploiting the fact that \( \hat{U}_n(t) \) can be any solution of (3.4.20) subject to \( \hat{U}_n(s) \geq U_n(s), \quad s \in [-\tau, 0], n \in \mathbb{Z}, \) we shall now take \( \hat{U}_n(t) = \omega(t) \), where \( \omega(t) \) is independent of \( n \) and is the solution of

\[
\begin{align*}
\frac{d\omega(t)}{dt} &= e^{-\mu_T}b(\omega(t) - \tau))(1 + \epsilon) - (d + T_{in})\omega(t) \quad (3.4.24) \\
\omega(s) &= \max_{n \in \mathbb{Z}} U_n(s), \quad s \in [-\tau, 0]. \quad (3.4.25)
\end{align*}
\]

We want to show that \( \omega(t) \to 0 \) as \( t \to \infty \). However, we showed earlier that all solutions of the differential equation (2.2.17) approach zero, subject to the condition \( e^{-\mu_T}b(u_m) < d(u_m) + \mu_T u_m \). As (3.4.24) is a particular case of (2.2.17) with appropriate choice for the function \( d(u_m(t)) \) in the latter we conclude that \( \omega(t) \to 0 \) as \( t \to \infty \) subject to the condition \( e^{-\mu_T}b(\omega)(1 + \epsilon) < (d + T_{in})\omega \), for all \( \omega > 0 \), which holds because of (3.4.21).

Positivity of \( U_n(t) \) implies that

\[
0 \leq U_n(t) \leq \omega(t),
\]

but \( \omega(t) \to 0 \) as \( t \to \infty \) so we have that \( U_n(t) \to 0 \) as \( t \to \infty \).

We have shown that \( U_n(t) \to 0 \) as \( t \to \infty \) for each \( n \), and we now want to show that \( V_n(t) \to 1 \) as \( t \to \infty \) for each \( n \). Let \( \epsilon_3 \in (0, r/\gamma) \) be arbitrary. Since \( U_n(t) \to 0 \) for each \( n \) and since there are finitely many \( n \), there exists a \( T_3 \) for each \( n \).
such that for \( t > T_3 \) and all \( n \), \( U_n(t) < \epsilon_3 \). Then for \( t > T_3 \)
\[
\frac{dV_n(t)}{dt} \geq rV_n(t)(1 - V_n(t)) - \gamma \epsilon_3 V_n(t)
\]
and so, since \( \epsilon_3 \gamma < r \) and since \( V_n(0) > 0 \) for each \( n \) by hypothesis
\[
\liminf_{t \to \infty} V_n(t) \geq 1 - \frac{\gamma \epsilon_3}{r}.
\]
This holds for all sufficiently small \( \epsilon_3 \), therefore
\[
\liminf_{t \to \infty} V_n(t) \geq 1.
\]
Also since both \( V_n(t) \) and \( U_n(t) \) are positive
\[
\frac{dV_n(t)}{dt} \leq rV_n(t)(1 - V_n(t)),
\]
so \( \limsup_{t \to \infty} V_n(t) \leq 1 \). Hence \( \lim_{t \to \infty} V_n(t) = 1 \) for each \( n \).

Now we look at (3.4.15) to show that \( u_n(t) \to 0 \) as \( t \to \infty \). Let \( \epsilon_4 > 0 \) be arbitrary. Since \( U_n \to 0 \) and \( V_n \to 1 \) and since there are finitely many \( n \), there exists a \( T_4 \) such that for all \( t > T_4 \) and all \( n \)
\[
-\epsilon_4 < b(U_n(t))V_n(t) - e^{-\tau} b(U_n(t - \tau))V_n(t - \tau) < \epsilon_4.
\]
Hence for \( t > T_4 \) and all \( n \),
\[
\frac{du_n(t)}{dt} < \epsilon_4 - \mu u_n(t)
\]
and thus \( \limsup_{t \to \infty} u_n(t) \leq \epsilon_4/\mu \). Since this is for all \( \epsilon_4 > 0 \) we can conclude
\[
\limsup_{t \to \infty} u_n(t) \leq 0.
\]
Similarly \( \liminf_{t \to \infty} u_n(t) \geq 0 \) and so \( u_n(t) \to 0 \) as \( t \to \infty \) for each \( n \). So \( u_n(t) \to 0, U_n(t) \to 0 \) and \( V_n(t) \to 1 \) as \( t \to \infty \), for each \( n \), thus the proof is complete, for the case when the birth function is increasing.

**Case B: \( b(U) \) is a non-monotone function.**

It is assumed here that \( b(U) \) qualitatively resembles \( PUE^{-AU} \). Here we wish to show that for each \( n \in \hat{Z} \), \( \limsup_{t \to \infty} U_n(t) < U_{\max} \), where \( U_{\max} \) is the value of \( U \) that maximises the birth function.
Let $\epsilon$ be defined as in case A, together with the corresponding $T$ with the property that $n \in \hat{Z}$ and $t \geq T + \tau$ implies $V_n(t - \tau) < 1 + \epsilon$. Then for $t \geq T + \tau$

$$\frac{dU_n}{dt} \leq e^{-\mu r} b(U_n(t - \tau))(1 + \epsilon) - (d + T_{inf})U_n + D(AU)_n$$

$$\leq e^{-\mu r} b(U_{max})(1 + \epsilon) - (d + T_{inf})U_n + D(AU)_n.$$ 

Let $\omega_2(t)$ be the solution of

$$\frac{d\omega_2}{dt} = e^{-\mu r} b(U_{max})(1 + \epsilon) - (d + T_{inf})\omega_2,$$

such that

$$\omega_2(T + \tau) = \max_{n \in \hat{Z}} U_n(T + \tau).$$

We can show that $U_n(t) \leq \omega_2(t)$, for all $t \geq T + \tau$. Thus we have that

$$\limsup_{t \to \infty} U_n(t) \leq \lim_{t \to \infty} \omega_2(t) = \frac{e^{-\mu r} b(U_{max})(1 + \epsilon)}{d + T_{inf}}.$$ 

This is true for all sufficiently small $\epsilon > 0$. Hence, for each $n \in \hat{Z}$,

$$\limsup_{t \to \infty} U_n(t) \leq \frac{e^{-\mu r} b(U_{max})}{d + T_{inf}}.$$ 

From Figure 3.1 we can see that

$$\frac{e^{-\mu r} b(U_{max})}{d + T_{inf}} < U_{max},$$

so for each $n$, $\limsup_{t \to \infty} U_n(t) < U_{max}$. Note that this is a strict inequality and there are only finitely many $n$. So there exists $T_4 > 0$ independent of $n$ such that for $t \geq \max\{T_4, T + \tau\}$, and all $n$,

$$U_n(t) \leq U_{max}.$$ 

Hence for $t$ sufficiently large $U_n(t)$ is confined to the interval of values for which the function $b(U)$ is monotone increasing and the proof proceeds as for case A.
Figure 3.1: Graph to show that $\frac{e^{\mu b(U_{\text{max}})}}{(d + T_{\text{inj}})} < U_{\text{max}}$. 
4

Introduction to Dynamics of aeolian sand ripples

4.1 History

While looking at pictures of deserts you may have noticed that the sand tends to be in the form of a series of small propagating waves. They are only a few centimeters in wavelength and their heights are only about one fifteenth of this. Their crests lie perpendicular to the wind. These waves are known as aeolian sand ripples. They get their name from the fact that they are formed by the action of the wind on the sand bed. As well as in the desert aeolian sand ripples can also be found on beaches, by the sea and have even been noticed on Mars [26].

![Diagram of a typical sand ripple (after Hoyle and Woods [28]), showing the hopping process and labelling the angle, $\alpha$, between the horizontal and the sand bed, the angle, $\beta$, between the incoming saltation flux and the horizontal and various zones of the ripple.]

Figure 4.1: Diagram of a typical sand ripple (after Hoyle and Woods [28]), showing the hopping process and labelling the angle, $\alpha$, between the horizontal and the sand bed, the angle, $\beta$, between the incoming saltation flux and the horizontal and various zones of the ripple.

Interest in aeolian sand ripples began in the early part of the 20th century and one of the most influential studies was The Physics of Blown Sand and Desert Dunes by R.A. Bagnold in 1941 [9]. One of the most important ideas to come out of this
study was the notion that *saltation* (derived from the Latin word *saltare* meaning to dance or to jump) played an important part in the formation of the ripples. When the wind is strong enough it can start to pick up grains from the sand bed and carry them for a relatively long distance. By this point the grains have a large amount of energy and so when they finally drop back to the sand bed they do so at high speed (up to about 1 m/s [6]). Having hit the sand bed these grains will rebound and are often caught up by the wind again, doomed to repeat this process over and over. This process is known as saltation. The impact of these high energy, or ‘saltating’, grains cause other grains in the neighbourhood of the impact point to be removed from the sand bed. These grains will have a much lower energy than the saltating grains as they are not carried along by the wind, only by the force of the impact and so they will not travel as far (generally no more than one ripple wavelength). This process was named *surface creep* by Bagnold [9] but later the more scientific term *reptation* (derived from the Latin for ‘to crawl’) was suggested by P.K. Haff [4] and is more commonly used today. These processes are illustrated in Figure 1 along with a typical aeolian sand ripple and some common terms associated with it.

It has been observed that the saltating grains impact the sand bed at a roughly constant angle of between 10° - 16° [9]. Experiments have been undertaken to investigate the effect of the saltating grains on the bed, for example Mitha et al. [45], who used steel pellets to investigate the effect of a single grain impacting a bed made up of similar grains. They noticed that a single impact by a high-energy pellet caused, on average, 10 pellets from the bed to be ejected, as well as rebounding itself. The ejected pellets are equivalent to the reptating grains and have much less energy and lower speeds than the incoming pellet, or saltating grain. Most of the energy caused by the impact is used up by the rebounding grain. It was noticed that the ejected grains came from an area roughly 10 grain diameters wide, whose centre was slightly ahead of the impact point. The incoming grain rebounded at an angle significantly higher than it came in at, which is important for the grain to sustain itself in saltation. As summarised in [16], it has been found that decreasing the angle of incidence increases the ratio of the rebound to impact vertical speeds. For angles around 10°, as in saltation, this ratio is greater than one and so the rebounding saltating grain can rise to the same height as it was before it started its previous descent. In this case the grains are able to continue in saltation indefinitely. Changing the impact angle has little effect on the reptating grains but increasing the impact speed causes an increase in the number of grains entering into reptation.
from a single impact [45].

Bagnold [9] predicted that a large population of grains would be caught up in saltation, travelling from one ripple to another, thus creating consecutive areas of high and low impact intensity, which gives rise to the motion of surface grains. He noticed a connection between his predicted saltation path lengths and the observed wavelengths of the ripples and thus suggested that the 'characteristic path length' had an important effect on the ripple spacing.

Bagnold's work has been hugely influential, however his concept of the origin of ripple spacing has been challenged over the years. Sharp [55] said that because ripples begin as small amplitude short-wavelength forms and grow to their eventual steady-state dimensions, Bagnold's concept is at least suspect. Sharp's argument was qualitatively based on the geometrical grounds that the ripple wavelength should depend on the ripple amplitude and the angle between the sand bed and incoming saltating grains, both of which are controlled by the particle size and air velocity. Later experimental work backed this up [54]. Sharp's study based on measurements taken in the Kelso Dunes also showed that under different wind velocities, aeolian sand ripples would travel between 0.35 and 3.2 inches per minute [55]. While he concedes that the relationship is approximate due in part to the difficulty in measuring velocities of winds that constantly fluctuate in speed, sometimes increasing from low speeds up to 30mph within seconds, he did find that there was an approximate linear relationship between wind velocity and velocity of ripple movement

\[ V_{rm} = \frac{V_w - 15.5}{7}, \]

where \( V_{rm} \) is velocity of ripple movement and \( V_w \) is wind velocity in miles per hour. According to this model ripples would not move below a wind velocity of 15.5mph. This was considered reasonable as the threshold velocity for noticeable movement of ripples in the Kelso Dunes was between 11 and 13mph. It was also acknowledged that the actual relationship may not be a straight line as it may flatten out at velocities above 30mph, but a lack of observations at these velocities prevented accurate results. Sharp also observed that ripples that move 1 wavelength in 1 minute will be able to quickly adjust to changes in wind regime.

Bagnold's work on sand ripple formation has subsequently been developed and modified by many people, for example [28, 4, 11, 69, 51], compared with field observations, for example [55, 7], and inspired numerical experiments such as [48, 49].
4.2 Analytical Models

4.2.1 One-species models

Anderson

Anderson [4] produced one of the most important analytical models of aeolian saltation. He deduced that reptation was actually a more important factor than saltation and disputed Bagnold’s proposed model by arguing that such short saltation trajectories as Bagnold proposed would not land with enough energy to produce significant reptation transport. Anderson’s model, based on the relation between the rate of change of bed elevation and the divergence of sediment flux, or the ‘erosion equation’, took the form

\[
\frac{\partial h}{\partial t} = -\frac{1}{\rho_b} \left( \frac{\partial Q}{\partial x} + \rho_p \frac{\partial V_s}{\partial t} \right),
\]

(4.2.1)

where \( h \) is the height of the bed at time \( t \), \( V_s \) is the total volume of sand in transport per unit area of the bed, \( \rho_p \) is the particle density and \( \rho_b = \rho_p (1 - \eta) \) is the bulk density of the sediment in the bed where \( \eta \) = porosity of the bed. The porosity of a substance is the proportion of the non-solid volume to the total volume of material, in this case it is generally thought to be about 0.35. \( Q \) is the horizontal mass flux of sand per unit width of flow. However Anderson assumed, as did many other people trying to model sand ripples, that the amount of sand in transport is roughly constant over time. This meant that the derivative of \( V_s \) with respect to time vanishes in the above equation, leaving us with

\[
\frac{\partial h}{\partial t} = -\frac{1}{\rho_b} \frac{\partial Q}{\partial x}.
\]

(4.2.2)

Thus the height of the bed is inversely proportional to the horizontal mass flux. To make the following equations easier to read we define

\[
h_{x^n} = \frac{\partial^n h}{\partial x^n}, \quad h_y = \frac{\partial h}{\partial y}, \quad h_t = \frac{\partial h}{\partial t},
\]

\[
\rho_{x^n} = \frac{\partial^n \rho}{\partial x^n}, \quad \rho_y = \frac{\partial \rho}{\partial y}, \quad \rho_t = \frac{\partial \rho}{\partial t}.
\]

The horizontal mass flux is given by

\[
Q(x) = Q_s + m_p \int_{x-a}^{x} N_{ij}(x) dx,
\]

(4.2.3)
where $Q_s$ is the flux due to grains in saltation, $m_p$ is the mass of a sand grain, $a$ is the reptation length and $N_{ej}(x)$ is the number of grains ejected from the bed per unit time per unit surface length, at position $x$. $N_{ej}(x) = n_t N_{im}(x)$, where $n_t$ is the number of grains sent into reptation by one saltating grain impacting the bed and $N_{im}(x)$ is the number of particles in saltation that hit the bed per unit area per unit time, or the 'impact rate'. Anderson defined this to be

$$N_{im}(x) = N_0 \left[ 1 + \frac{\tan \alpha}{\tan \beta} \right] \cos \alpha,$$

(4.2.4)

where $\alpha$ and $\beta$ are as defined in Figure 1 and $N_0$ is the impact rate on a flat surface ($\alpha = 0$). As $\tan \alpha = h_x$ and $\cos \alpha \simeq 1$ for small $\alpha$ we get

$$Q(x) = Q_s + m_p \int_{x-a}^{x} n_t N_0 (1 + h_x \cot \beta) dx.$$

(4.2.5)

This leads to the following expression for the mass flux

$$Q(x) = Q_0 + q_{ej} \cot \beta [h(x) - h(x - a)],$$

(4.2.6)

where $Q_0 = Q_s + q_{ej}a$ and $q_{ej} = m_p n_t N_0$. $Q_0$ is the expected mass flux due to saltation and reptation and $q_{ej}$ is the 'mass ejection rate' from a flat bed. Thus the continuity equation (4.2.2) becomes

$$\frac{\partial h(x)}{\partial t} = -\beta^* \left[ \frac{\partial h(x)}{\partial x} - \frac{\partial h(x - a)}{\partial x} \right],$$

(4.2.7)

where $\beta^* = (q_{ej} \cot \beta)(\rho_b)^{-1}$. This version of Anderson's model chooses the probability distribution of reptation lengths to be uniform which corresponds to the probability density being a delta function, $p(a) = \delta(a - \bar{a})$ with $\bar{a}$ being the mean reptation length. However this is not a realistic distribution for the reptation lengths and so Anderson decided to include the probability density function, $p(a)$, as a variable. Thus (4.2.6) becomes

$$Q(x) = Q_0 + q_{ej} \cot \beta \int_{0}^{\infty} [h(x) - h(x - a)]p(a) da.$$

(4.2.8)

Anderson found equations for the growth rate and translation speeds of bed perturbations of various wavelengths by trying the solution $h = h_0 e^{i(k(x - ct)}$ in (4.2.7), where $h_0$ is half the initial height from the trough to the crest of the ripple, $k$ is the
wavenumber and $c$ is the phase speed. This gave an equation in terms of the phase speed

$$c = \beta^* \left(1 - e^{-ika}\right). \quad (4.2.9)$$

Splitting into real and imaginary parts $c = c_r + c_i$ we get

$$c_r = \beta^*(1 - \cos(ka)), \quad c_i = \beta^* \sin(ka), \quad (4.2.10)$$

where $c_r$ is the translation speed and $c_i/\beta^*$ is the growth rate. He found a maximum in the growth rate at the point $ka = \pi/2$ which gave the length of the ripple equal to four reptation lengths. Unfortunately he also found maxima at every $ka$ multiple of $2\pi$ (giving rise to successively shorter ripples of two reptation lengths, one reptation length, half a reptation length, etc...). This was due to the unrealistic growth of ripples caused by reptation happening on ripples upwind. He found that this behaviour was due to the assumption of uniform reptation lengths and that including a range of different lengths would damp the growth of these shorter ripples. This is because the distribution in lengths allows reptations starting at the same point to land with similar probability on either side of the upwind ripples. This reduces the associated difference in size of the mass flux between the crest and the trough of these ripples. Indeed using (4.2.8) and choosing $p(a)$ to be the probability density function of a gamma distribution, Anderson found his phase speed equations to be

$$c_r = \beta^* \left(\frac{(k\alpha)^4 + 12(k\alpha)^2}{4 + (k\alpha)^2}\right), \quad c_i = \beta^* \frac{16k\alpha}{4 + (k\alpha)^2}. \quad (4.2.11)$$

These equations produced a single maximum in the growth rate giving the length of the ripple equal to six reptation lengths, having successfully damped the shorter wavelengths. An exponential distribution, which is a specific case of a gamma distribution, was also tried with similar results.

Since the publication of Anderson's paper [4] it has since been suggested, [16] [28], that, as in aeolian sand ripples the reptation length is generally smaller than the ripple wavelength, you could treat ripple formation as a local process and therefore Taylor expand the $h(x - a)$ term in (4.2.6). Using this method Csahtok et al [16] found they could rewrite (4.2.6) in the form

$$Q(x) = Q_0 + q_{aj} \cot \beta \left[ ah_{xx} - \frac{a^2}{2} h_{xxx} - \frac{a^3}{6} h_{xxxx}\right]. \quad (4.2.12)$$

Putting this into (4.2.7) gave

$$h_t = -\beta^* ah_{xx} - \beta^* \frac{a^2}{2} h_{xxx} - \beta^* \frac{a^3}{6} h_{xxxx}. \quad (4.2.13)$$

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The first term on the right hand side is responsible for the ripple instability. This is equivalent to the term that Anderson had in his model (4.2.9). However there are now two more terms, the second term, which represents drift and the last term, which is a hyperdiffusion term, that will dampen very short scales (terms with a big wavenumber). These higher derivative terms have the same effect on the growth rate as introducing a probability distribution and in fact the preferred growth rate is the same as the one Anderson found from (4.2.11).

**Hoyle & Woods**

In 1997 an analytical model of propagating sand ripples was developed by Hoyle and Woods [28], which extended Anderson’s model [4]. As well as reptation this model included the effects of rolling and avalanching. Their governing equation was similar to (4.2.2) but took the form

\[
\frac{\partial h}{\partial t} = -\frac{1}{\rho_b} \left( \frac{\partial Q_{\text{hop}}}{\partial x} + \frac{\partial Q_{\text{roll}}}{\partial x} \right),
\]

(4.2.14)

where \(Q_{\text{hop}}\) represents the hopping grains and \(Q_{\text{roll}}\) the rolling or avalanching grains. The \(Q_{\text{hop}}\) term took the form

\[
\frac{\partial Q_{\text{hop}}}{\partial x} = -a_p \int_{-\infty}^{\infty} p(a)[N_{ej}(x, t) - N_{ej}(x - a, t)]da,
\]

(4.2.15)

where \(a_p\) is the average cross sectional area of a grain. The evolution of the surface, at position \((x, y)\), is proportional to the difference between the number of sand grains ejected from the bed, at position \((x, y)\), and the number of sand grains entering the bed, at position \((x, y)\). After Taylor expanding the \(N_{ej}(x - a, t)\) term to first order the equation became

\[
\frac{\partial Q_{\text{hop}}}{\partial x} = -a_p \bar{a} \frac{\partial N_{ej}(x)}{\partial x},
\]

(4.2.16)

where \(\bar{a}\) is the mean reptation length. The gradient of the hopping grains is inversely proportional to the gradient of the ejected grains. Hoyle and Woods defined

\[
N_{ej}(x) = J \cos \beta \frac{h_x + \tan \beta}{(1 + h_x^2)^{1/2}},
\]

(4.2.17)

where \(J\) is a constant of proportionality. So their hopping term became

\[
\frac{\partial Q_{\text{hop}}}{\partial x} = \beta_i h_x \frac{[1 + h_x \cot \beta]}{[1 + (h_x)^2]^{3/2}},
\]

(4.2.18)
where $\beta^*_i = -J \alpha \cos \beta$.

When a stationary sand bed is tilted at an angle, grains near the surface of the bed may become unstuck and roll down the slope, due to a balance between gravity and friction [9]. Over time this will have the effect of making the surface smoother. Thus the rolling term took the form

$$Q_{roll} = -F \frac{g}{r} \sin \alpha \cos \alpha = \frac{F g h_x}{r (1 + (h_x)^2)}, \quad (4.2.19)$$

where $g$ represents gravity, $r$ friction and $F$ is a constant of proportionality. If the sand bed is tilted too far then the number of rolling grains increases dramatically so that in effect the angle of the slope will not get any higher. The angle at which this happens is called the angle of repose, $\alpha_r$, and the increased number of rolling grains is known as an avalanche. However sand ripples are not stationary and Hoyle and Woods hypothesised that for a moving ripple there would be a different angle, less than or equal to the angle of repose, at which avalanching would occur. They called this the dynamic angle of repose, $\gamma$. This tied in with the previous observation that the top of the lee slope, near the crest, is roughly inclined at the angle of repose [55]. Consequently the rolling term (4.2.19) became

$$Q_{roll} = -F \frac{g}{r} \tan^2 \gamma \frac{h_x}{(1 + h_x^2)(\tan^2 \gamma - (h_x)^2)^{1/2}}. \quad (4.2.20)$$

Equation (4.2.20) shows that when the gradient of the slope approaches the dynamic angle of repose $$(\tan^2 \gamma - (h_x)^2) \to 0$$ and so the flux of rolling grains becomes very large. Conversely if the bed is flat then this term will disappear. Substituting the derivative of (4.2.20) and (4.2.18) into (4.2.14) gives

$$\frac{\partial h}{\partial t} = \left( \beta^*_i \frac{1 + h_x \cot \beta}{[1 + h_x^2]^{3/2}} + \tilde{D} \right) \frac{\partial^2 h}{\partial x^2}, \quad (4.2.21)$$

where $\tilde{D}$ represents the evolution due to rolling and is given by

$$\tilde{D} = Fa_p \tan^2 \gamma \frac{g}{r} \frac{2(h_x)^4 + [1 - (h_x)^2] \tan^2 \gamma}{[1 + (h_x)^2]^2 [\tan^2 \gamma - (h_x)^2]^{3/2}}.$$

This model also incorporated the concept of a shadow zone which was developed by Sharp [55]. Because the incoming saltating grains all arrive in a straight line at roughly the same angle there will be an area on the lee slope that will be shielded from them by the sand bed itself. Consequently there is no saltation here and so hopping will not occur. This area is known as the shadow zone (see Figure 1) and
here the ripple evolves according to the equation
\[
\frac{\partial h}{\partial t} = \tilde{D} \frac{\partial^2 h}{\partial x^2}.
\] (4.2.22)

There is no contribution from the hopping term here and the ripple evolves due to rolling grains alone. This shadow zone controls the wavelength of the ripple. After a certain distance the incoming saltating grains will be able to hit the sand ripple again (see Figure 1). The model determines this point as the beginning of the stoss slope of the following ripple. From here on the ripple again evolves according to (4.2.21), until the next shadow zone. Hoyle and Woods found that they could simplify their model by making the assumption that \( |h_x| \leq \tan \gamma \sim \tan 30^\circ \) and consequently \((h_x)^2 \ll 1\). This led to the following equation for (4.2.21), which neglects terms of \(O(h_x)^2\) and higher, except \([\tan^2 \gamma - (h_x)^2]\), because both terms are of the same order of magnitude
\[
\frac{\partial h}{\partial t} = \left( \beta^*_1 \cos \beta + \frac{D \tan^2 \gamma}{[\tan^2 \gamma - (h_x)^2]^{3/2}} \right) \frac{\partial^2 h}{\partial x^2},
\] (4.2.23)

where \( D = F a_p \tan^2 \gamma (g/r) \). Equation (4.2.22) is similarly modified with \((D \tan^2 \gamma)(\tan^2 \gamma - (h_x)^2)^{-3/2}\) replacing \(\tilde{D}\).

Hoyle and Woods’ model could predict qualitative features shown by sand ripples, such as a threshold value of saltation flux intensity below which ripples will not evolve. It also shows that at low saltation fluxes the lee slope is smooth but above a critical value a slip face develops near the crest, in accordance with observations, [9] and also with numerical simulations [5, 39]. A slip face is an area at the top of the lee slope that is maintained at a constant angle, roughly equal to the angle of repose, by avalanching. It is inclined at a steeper angle than the rest of the lee slope. A decrease in speed of propagation of the ripple, proportional to the size of the ripple, is predicted, consistent with observations that smaller ripples catch up to and merge with larger ones [55].

### 4.2.2 Two-species models

#### A sandpile model

In 1991 Mehta et al. [43] came up with the idea of using two parameters instead of just one to describe the evolution of sand piles. They used a system of coupled Langevin equations based on two coordinates representing the motion of independent particles (the macroscopic angle of tilt) and clusters (a variable which represents...
the average extent to which clusters of particles protrude from the surface). Subsequently [44] Mehta et al. chose the two variables to represent the local density of immobile grains (or 'height'), \( h(x, t) \) and the rolling grain density, \( \rho(x, t) \). This 'two-species' model uses the idea that a ripple is actually made up of two layers of grains: a thin layer of flowing grains on top of the much thicker layer of relatively stationary grains that make up the rest of the sand bed. Mehta's model was for deviations from \( h_x = \tan(\alpha_x) \) and now consisted of two partial differential equations that took the form 

\[
\begin{align*}
\frac{\partial h}{\partial t} &= D_h \frac{\partial^2 h}{\partial x^2} - T(h, \rho) + \eta_h(x, t) \\
\frac{\partial \rho}{\partial t} &= D_\rho \frac{\partial^2 \rho}{\partial x^2} + \chi(\rho(h_x)_-) + T(h, \rho) + \eta_\rho(x, t),
\end{align*}
\]

(4.2.24)

where \( \chi \) represents the mobility of the sand grains, \( D_h \) and \( D_\rho \) are diffusivities and \( \eta_h(x, t) \) and \( \eta_\rho(x, t) \) are source terms which were taken to be independent normal random variables (although it was acknowledged that the exact structure of these terms would depend on the physical situation). The term \((h_x)_-\) was defined such that it would only be effective in the case where the gradient of the slope was greater than the angle of repose, so if this was true then \((h_x)_- = h_x\) otherwise \((h_x)_- = 0\). The term \((h_x)_+\) was also defined, to be effective if the slope was less than the angle of repose, in which case \((h_x)_+ = h_x\), otherwise \((h_x)_+ = 0\). The first terms of (4.2.24) represent diffusion. In this model the diffusion terms represent the rearrangement of clusters (in the sand bed equation) and the relaxation of the flowing grains (in the flowing layer equation) which represents the collisions between the grains. The \( \chi(\rho(h_x)_-) \) term represents flux-divergence (the variation in \( \rho \) due to non uniformity in the current of flowing grains), this only happens when the gradient of the slope is greater than the angle of repose.

The \( T(h, \rho) \) term that appears in both equations is a transfer term that models the exchange of grains between the sand bed and the flowing layer, it takes the form

\[
T(h, \rho) = -\kappa \rho h_{xx} - \lambda h_x(h_x)_+ - \nu \rho h_x - \nu (h_x)_-.
\]

(4.2.25)

In (4.2.25) the term \( \kappa \rho h_{xx} \) only contributes in the presence of flowing grains and it is independent of the slope. The purpose of this term is to model the smoothing effect of the grains rolling down the slope. If \( h_{xx} > 0 \) then there is a dip in the ripple and this term models the effect of the flowing grains in filling this in. Conversely if \( h_{xx} < 0 \) then there is a bump in the ripple and this term models the effect of
smoothing it out. The larger $\rho$ is the more grains there are moving over the ripple and so the more effect this term will have.

The $v\phi h_x^-$ term smooths out deviations from the critical slope rather than changes in the curvature of the bed. If $h_x < 0$ then the slope is steeper than the angle of repose and this term models the effect of grains from the flowing layer sticking onto the sand bed. If $h_x > 0$ then the slope is shallower than the angle of repose and so grains from the sand bed are tipped out into the flowing layer. The larger $\rho$ is the more grains there are moving over the ripple and so the more effect this term will have.

The $v(h_x)^-$ term models the effect of tilting a static sand pile, it is relevant even in the case where there are no flowing grains. Without this term a tilted static sand pile would not generate flowing grains. It only comes into effect when the gradient of the sandpile is greater than the angle of repose and models the effect of removing grains from the sand bed and tipping them into the flowing layer, reducing the gradient. This is because this term will be positive in the transfer term and so will decrease $h_t$ and increase $\rho_t$.

The term $\lambda \rho(h_x)^+$ limits the number of grains transferred from the sand bed to the flowing layer when tilting occurs. It only comes into effect when the gradient of the sandpile is less than the angle of repose and models the effect of grains from the flowing layer sticking onto the sand bed. This is because this term will be negative in the transfer term and so will increase $h_t$ and decrease $\rho_t$. The larger $\rho$ is the more grains will stick onto the sand bed. This is effectively an artificially imposed restriction required for accurate numerical simulations, as it prevents any grains not at the border of the sand bed and the flowing layer from transferring between the layers.

The $v\phi h_x^-$ term has a similar effect to a combination of the last two terms and was removed when the model was refined by Hoyle & Mehta [30]. The main difference was that the tipping out of grains from the sand bed was allowed in the absence of any flowing grains. This was the main difference between Mehta's model and the hydrodynamic model proposed by Bouchaud et al [11]

**A hydrodynamic model**

The hydrodynamic model developed by Bouchaud et al. in 1995 [11] used the same variables, $h$ and $\rho$, as [44], as they believed them to be more directly related to the physics of the problem. This model has become known as the BCRE model, after
its authors. The governing equations of their system take the form

$$
\frac{\partial h}{\partial t} = -T(h, \rho) \tag{4.2.26}
$$

$$
\frac{\partial \rho}{\partial t} = D \rho \frac{\partial^2 \rho}{\partial x^2} - \nu \rho - \nu_x + T(h, \rho), \tag{4.2.27}
$$

where $\nu$ represents drift velocity and

$$
T(h, \rho) = -\rho (c \rho_x + \kappa \rho_{xx}), \tag{4.2.28}
$$

where $c, \kappa > 0$. This transfer term has four properties: a) a static grain will not move unless dislodged by an already moving grain, b) grains will not be dislodged unless the slope of the sand pile exceeds a critical angle associated with the angle of repose, $\alpha_c$, as this model is for deviations from a slope at the angle of repose, so no angles are required in the formula, c) if the slope does not exceed $\alpha_c$ then grains currently in motion will tend to come to rest on the bed, becoming static, d) if $h_x = \alpha_c$ but $h_{xx} \neq 0$ then smoothing of the surface takes place, at a rate proportional to $\rho$. Unlike [44] a static sand pile will not generate flowing grains. When a static sand pile is perturbed slightly, it will evolve for a short period before all the grains come to rest and the sand pile returns to a static state (although in a new configuration). This effect is common in powders and is important in the context of this model. Numerical simulations showed that a static sand pile with a constant flowing grain density $\rho_0$ on a flat bed would move uphill with velocity $v_h = c\rho_0$.

### 4.2.3 Two-Species models for aeolian sand ripples

**Hoyle & Mehta**

The models by Bouchaud and Mehta were not designed specifically for the case of aeolian sand ripples, but since the publication of these papers many two-species models for aeolian sand ripples have been suggested such as in Mehta's own work with Hoyle, [29, 30]. This model combines their previous work, [44, 28], to produce a two-species continuum model for aeolian sand ripples. It extends [28] to include transfer terms similar to those in [44] and uses the same two-species structure. Their second model, [30], was deemed to be the most parsimonious model and took the form

$$
\frac{\partial h}{\partial t} = D_h \frac{\partial h_{xx}}{\partial x} - T(h, \rho) + f(x, t) \tag{4.2.29}
$$

$$
\frac{\partial \rho}{\partial t} = D_\rho \frac{\partial^2 \rho}{\partial x^2} + \chi (\rho h_x) + T(h, \rho) + \int_a \rho(a) f(x - a, t) \, da, \tag{4.2.30}
$$
where \( \chi > 0 \) and \( f(x, t) = a_p J \cos \beta (h_x + \tan \beta) \). The \( f(x, t) \) is equivalent to equation (4.2.17) from [28], but without the bottom half of the fraction i.e. neglecting terms of \( O(h_x^2) \). The \( \chi (\rho h_x)_x \) term represents flux divergence and is similar to the term in [44], but it is valid whatever the gradient of the slope is. The transfer term is given by

\[
T(h, \rho) = \begin{cases} 
\lambda \rho(|h_x| - \tan \alpha_r) & \text{if } 0 \leq |h_x| \leq \tan \alpha_r \\
\nu(|h_x| - \tan \alpha_r)(\tan^2 \gamma - (h_x)^2)^{-1/2} & \text{if } \tan \alpha_r \leq |h_x| \leq \tan \gamma 
\end{cases}
\]

(4.2.31)

with \( \lambda, \nu \) positive constants. This is similar to the transfer term in [44]. If the gradient of the sand bed is less than the angle of repose then the transfer term acts like the \( \lambda \rho (h_x)_+ \) term in [44] by modelling the effect of grains from the flowing layer sticking onto the sand bed. In this case the transfer term will be negative as \( |h_x| < \tan \alpha_r \) and so it will reduce \( \rho_t \) and increase \( h_t \). If the gradient is greater than the angle of repose, but less than the dynamic angle of repose, then the transfer term acts like the \( \nu (h_x)_- \) term in [44] by modelling the effect of tipping grains out of the sand bed into the flowing layer. In this case the transfer term will be positive as \( |h_x| > \tan \alpha_r \) and so it will reduce \( h_t \) and increase \( \rho_t \). However in this model this term also includes the effect of avalanching by dividing by \( (\tan^2 \gamma - (h_x)^2)^{1/2} \), so that as the gradient of the slope approaches the dynamic angle of repose the transfer term will tend to infinity. In their first model, [29], Hoyle & Mehta also included \( -\kappa \rho h_x \) in the transfer term in comparison with [44], but later, after carrying out numerical simulations, decided that this term did not have a significant effect on the evolution of the ripples.

The model was then non-dimensionalised using

\[
x \to x_0 \tilde{x}, \quad t \to t_0 \tilde{t}, \quad a \to a_0 \tilde{a}, \quad \rho \to \rho_0 \tilde{\rho}, \quad h \to h_0 \tilde{h},
\]

where

\[
x_0 = \frac{D_h}{a_p J \cos \beta}, \quad t_0 = \frac{D_h}{(a_p J \cos \beta)^2}, \quad h_0 = \frac{D_h \tan \gamma}{a_p J \cos \beta}, \quad \rho_0 = \frac{a_p J \sin \beta}{\lambda \tan \alpha_r}.
\]
Thus dropping the tildes the model equations (4.2.29, 4.2.30) became

\[ h_t = h_{xx} - \hat{f}(x, t) \]

\[ \begin{aligned}
&= \rho \cot \alpha_r \tan \beta (|h_x| - \cot \gamma \tan \alpha_r) \quad \text{if } 0 \leq |h_x| \leq \cot \gamma \tan \alpha_r \\
&= \nu^*(|h_x| - \cot \gamma \tan \alpha_r)(1 - (h_x)^2)^{-1/2} \quad \text{if } \cot \gamma \tan \alpha_r \leq |h_x| \leq 1.
\end{aligned} \] (4.2.32)

\[ \rho_t = \frac{D_p}{D_h} \rho_{xx} + \chi^*(\rho h_x)_x + \frac{h_0}{\rho_0} \int p(a) f(x - a) da \]

\[ + \frac{h_0}{\rho_0} \begin{aligned}
&= \rho \cot \alpha_r \tan \beta (|h_x| - \cot \gamma \tan \alpha_r) \quad \text{if } 0 \leq |h_x| \leq \cot \gamma \tan \alpha_r \\
&= \nu^*(|h_x| - \cot \gamma \tan \alpha_r)(1 - (h_x)^2)^{-1/2} \quad \text{if } \cot \gamma \tan \alpha_r \leq |h_x| \leq 1.
\end{aligned} \] (4.2.33)

where

\[ \hat{f}(x, t) = h_x + \cot \gamma \tan \beta, \quad \nu^* = \frac{\nu h_0}{h_0}, \quad \chi^* = \frac{\chi h_0}{D_h}. \]

From these equations it can be seen that a steady state exists when \( \rho = 1 \) and \( h = h_0 \), where \( h_0 \) is any real constant.

Perturbing the equations by setting \( \rho = 1 + \rho^* e^{\sigma t + i k x}, h = h_0 + h^* e^{\sigma t + i k x} \) and linearising they found two growth rates

\[ \sigma = -h_0 \tan \beta \cot \gamma, \] (4.2.34)

\[ \sigma = \left( \bar{a} - \frac{\rho_0}{h_0} \chi^* - 1 \right) k^2. \] (4.2.35)

Thus they deduced that in order to see ripples evolve from a flat bed they needed to satisfy the condition \( \bar{a} > \rho_0 h_0^{-1} \chi^* + 1 \). In dimensional units this is equivalent to

\[ \bar{a} \alpha_p J \cos \beta > D_h + \chi \alpha_p J \frac{\sin \beta}{\lambda \tan \alpha_r}. \]

This gave a strength of saltation flux at which ripples will evolve

\[ J_e > \frac{D_h \lambda \tan \alpha_r}{\bar{a} \alpha_p \cos \beta \lambda \tan \alpha_r - \chi \alpha_p \sin \beta}, \] (4.2.36)

which corresponds to the value found in [28]. This model is able to predict the ripple wavelength and speed. Numerical simulations were then undertaken using this model and they showed the evolution of realistic ripple profiles from a perturbed flat bed. The simulations showed that, after a short period, where the initial perturbations
decayed away, ripples began to form on the surface. Over time the shorter ripples 'caught up' to and merged with the larger ones until eventually there was only one ripple left. Also it was noticed that the stoss slope was longer and shallower than the lee slope. However they noticed that if their avalanching term was left out (by setting $\nu = 0$ in their equations) then this was not the case. Instead the ripples looked more symmetrical and the lee slope was shallower than the stoss slope, which does not agree with observations [55], suggesting that avalanching is important for the development of realistic ripple profiles.

**Prigozhin**

At the same time similar work was being undertaken by Prigozhin [51]. He developed a deterministic continuous model in order to describe better the essential physics. His model, which left out diffusion terms, took the form

$$h_t = T(h, \rho) - f_2(x, t),$$

$$\rho_t = -j_x - T(h, \rho) + Q(x, t),$$

where $j = -\chi \rho h_x$, $Q(x, t) = \int_y f_2(y, t)p(y, x)dy$, $f_2(x, t) = f_0 \sin \alpha (\sin \beta)^{-1}$, $f_0$ being the rate of erosion for a flat surface, and where $p(y, x)$ is the probability density function of the hop lengths, which Prigozhin approximated by a normal distribution, $p(x, y) \sim N(x_0 + m, \sigma_r^2)$, where $x_0$ is the ejection point, $m$ is the mean reptation length and $\sigma_r^2$ is the variance of the reptation length. The transfer term is given by

$$T(h, \rho) = \kappa_0 \rho \left(1 - \frac{|h_x|^2}{\tan^2 \alpha_r}\right).$$

This is similar to the transfer term of [30] in the case where the gradient of the slope is less than the angle of repose, but here the gradient term is squared. This makes mathematical analysis easier. So when the gradient of the sand bed is less than the angle of repose the transfer term is positive and so this has the effect of increasing $h_t$ and decreasing $\rho_t$ (grains from the flowing layer stick to the sand bed). If the gradient of the sand bed is greater than the angle of repose then the transfer term is negative and so $h_t$ is decreased and $\rho_t$ is increased (grains are tilted out of the sand bed into the flowing layer). This model does not account for the case of a dynamic angle of repose, but considers that rolling grains will not stop at all if the gradient of the slope exceeds $\alpha_r$. Prigozhin also accounts for the shadow zone by
setting \( f_2(x,t) = 0 \) where the bed is shielded from the incoming saltation flux.

The model was non-dimensionalised using

\[
\tilde{t} = \frac{f_0}{L} t, \quad \tilde{x} = \frac{1}{L} x, \quad \tilde{h} = \frac{1}{L} h, \quad \tilde{\rho} = \frac{\kappa_0}{f_0} \rho, \quad \tilde{f} = \frac{1}{f_0} f, \quad \tilde{j} = \frac{1}{f_0 L} j, \quad \tilde{T} = \frac{1}{f_0} T.
\]

Dropping the tildes this gave

\[
j = -\nu \rho h_x, \quad T(h, \rho) = \rho \left( 1 - \frac{|h_x|^2}{\tan^2 \alpha} \right), \quad \frac{f_0}{\kappa_0 L} \rho_t = -j_x + Q - T.
\]

However \( f_0/(\kappa_0 L) \ll 1 \) and so the small term was neglected giving

\[
j_x = Q - T. \quad (4.2.40)
\]

Linearising the equations gave \( T(h, \rho) = \rho, \ f_2 = 1 + \cot \beta h_x \). Thus putting these linearised terms into (4.2.37) gave an equation for \( \rho \)

\[
\rho = 1 + h_x + \cot \beta h_x. \quad (4.2.41)
\]

By setting \( m = 1 - \dot{m} h_x \) and expanding the probability distribution in terms of \( p_0(x) \), the density of the standard normal distribution \( N(1, \sigma^2) \), to give \( p(x,y) = p_0(y-x) + \dot{m} p_0'(y-x) h_x \), \( Q \) can be linearised to give

\[
Q = 1 + \cot \beta p_0 * h_x + \dot{m} p_0' * h_x. \quad (4.2.42)
\]

where \( * \) is the operator of convolution. Putting these values for \( j, Q \) and \( T \) into (4.2.43) and linearising gave

\[
h_t = \nu h_x x + \cot \beta (p_0 * h_x - h_x) + \dot{m} p_0 * h_x. \quad (4.2.43)
\]

This allowed Prigozhin to find the growth rate for his model, by substituting in the solution \( h = e^{\sigma t + ikx} \) to get

\[
\sigma = -\nu k^2 + \cot \beta ik (\tilde{p}_0 - 1) - \dot{m} k^2 \tilde{p}_0, \quad (4.2.44)
\]

where \( \tilde{p}_0 = \exp(-k^2 \sigma^2/2 - ik) \) is the Fourier transform of \( p_0 \). He noted that this was the same as Anderson's growth rate in the case where \( \nu = \dot{m} = 0 \). Prigozhin found that initially, the ripple wavelength would be \( 2\pi/k_0 \) where \( k_0 \) is the wavenumber
which gives a positive maximum for the real part of (4.2.47). He found that this maximum existed and that ripples would form if

$$\cot \beta > \bar{n} + \nu.$$  \hspace{1cm} (4.2.48)

Numerical simulations showed that Prigozhin’s model also produced the skewed ripple shape (the stoss slopes being less steep than the lee slopes) and the ripple merger effect seen in [28]. When a small ripple merges with a larger one it was found that, if the small ripple was sufficiently big, then instead of just merging an even smaller ripple would emerge from the front of the larger ripple, which itself had gained in mass. It was felt that this interaction may explain the similar phenomenon of small secondary ripples appearing during wind tunnel experiments [54], instead of the suggestion put forward by that paper that it was due to the backward eddy flow behind a ripple. Prigozhin felt that this was a doubtful explanation due to the shallowness of sand ripples producing negligible amounts of backwards eddies that could not cause sand grains to saltate against the direction of the wind and thus could not create sand ripples.

A two-species model with wind

In 1998 Bouchaud along with Terzidis and Claudin extended his model [11] to account for the effect of an external wind acting to dislodge particles from the static bed [59]. Their governing equations take the same form as (4.2.26), the difference is in the form of the transfer term, which they define as $T(h, \rho) = T_{ej} + T_{dep}$, where $T_{ej}$ represents the ejection process of grains (either in saltation or reptation, the model uses an averaged quantity of the two) and $T_{dep}$ the deposition process. The ejection process depends on wind velocity and is given by

$$T_{ej} = \alpha_0 + \alpha_1 h_x - \alpha_2 h_{xx},$$ \hspace{1cm} (4.2.49)

where the $\alpha_i$ depend on wind velocity. They note that $\alpha_0$ will only be non-zero if the wind velocity is strong enough, greater than some value $v^*$. This form allows for sand grains to be ejected from the bed, even if there are no flowing grains. The minus sign in front of the second derivative models the fact that grains are more likely to be ejected at the crest of a ripple than in a trough. The deposition process, which will include the effect of the incoming saltating grains and the reptating grains coming to rest, is dependent on the wind velocity and the slope of the ripple, it takes
the form

\[ T_{dep} = \rho(\gamma_0 + \gamma_1 h_x - \gamma_2 h_{xx}) - \beta_1 \rho^2, \]  

(4.2.50)

where \( \gamma_0 \) is negative for small wind velocities, less than \( v^* \) and positive for wind velocities greater than \( v^* \). The \( \gamma_1 \) term is positive as it models the case that more grains are ejected by saltation than come to rest. Similar to \( \alpha_2 \), \( \gamma_2 \) is positive as it again models the case that grains are more likely to move at crests than troughs. The \( \beta_1 \rho^2 \) term describes the non-linear effects associated with the deposition process such as the collision between grains in motion leading to dissipation and thus reducing the effectiveness of the impacts on the sand bed, or the fact that the flowing layer will screen the hydrodynamical flow thus reducing the transfer of energy between the wind and the saltating grains. Thus the transfer term can be written as

\[ T(h, \rho) = (\rho \gamma_0 + \alpha_0) - \beta_1 \rho^2 + (\rho \gamma_1 + \alpha_1) h_x - (\rho \gamma_2 + \alpha_2) h_{xx}. \]  

(4.2.51)

**Valance & Rioual**

Subsequently a new interpretation of this model was proposed by Valance and Rioual [60]. Their model was similar to [59], but they decided to make the distinction between saltation and reptation. They considered that as the number of saltating grains remains approximately constant, they can be treated as such. Their only purpose is to provide energy for the system. There is no transfer of grains between saltation and reptation, only between static grains on the sand bed and the grains in reptation. The governing equations are again the BCRE equations, (4.2.26), but without the diffusion term, \( D_{\rho \rho_{xx}} \), which they deemed unnecessary. The transfer term has a similar setup to that of [59], \( T(h, \rho) = T_{ej} + T_{dep} \), but they split the ejection process up further, \( T_{ej} = T_{ej}^a + T_{ej}^w \), where \( T_{ej}^a \) represents grains ejected due to the impact of the saltating grains and \( T_{ej}^w \) represents grains ejected due to the wind force. They define these, in general, to be

\[ T_{ej}^a = \alpha_0(1 + \alpha_1 h_x - \alpha_2 h_{xx}), \quad T_{ej}^w = \beta_0(1 + \beta_1 h_x - \beta_2 h_{xx}), \]  

(4.2.52)

similar to [59], where the \( \alpha_i \) and \( \beta_i \) are positive constants. Using the formula for the number of ejected grains

\[ N_{ej}(x) = n_i N_{im}(x) = n_i d^3 J \tan \beta (1 + \cot \beta h_x), \]  

(4.2.53)

where \( n_i \) is the number of grains sent into reptation by one saltating grain impacting the bed and \( d \) is the grain diameter, they decided that \( \alpha_0 = n_i d^3 J \tan \beta \) and \( \alpha_1 = \)
While simulations have shown that dislodgement of grains by the wind is relatively unimportant, [4], they felt that at the crests of ripples there would be a significant effect. They felt that even if the wind was not very strong it would still have some sort of smoothing effect and thus decided to include the second derivative term $T_{w}^{ij} = -\beta_{0}^{2}h_{xx}$. The deposition process is given by

$$T_{dep} = -\rho\gamma_{0}(1 - \gamma_{1}h_{x} + \gamma_{2}h_{xx}) = -\rho\gamma^{*}$$

(4.2.54)

where this equation defines $\gamma^{*}$ and $(\gamma^{*})^{-1}$ represents the time a sand grain is moving in reptation. The reptation length can be defined as $\bar{a} = \overline{V}/\gamma_{0}$, where $\overline{V}$ is the mean speed of reptating grains. The first derivative term shows that the reptation length on the stoss slope will be longer than on the lee slope. The second derivative term shows that the reptation length of a grain at the crest of a ripple will be longer than a grain at the trough. The $\gamma^{-1}$ term represents the time a grain is in motion on a flat bed. Putting this together, the equation for the transfer term is

$$T(h, \rho) = n_{d}d^{3}J\tan\beta(1 + \cot\beta h_{x} + \alpha_{2}h_{xx}) + \beta_{0}^{2}h_{xx} - \rho\gamma_{0}(1 - \gamma_{1}h_{x} + \gamma_{2}h_{xx}).$$

(4.2.55)

Linearising their system around $h = h_{0}$ (representing a flat bed) they found the steady-state $\rho_{0} = \alpha_{0}/\gamma_{0}$. By setting $h = h_{0} + h^{*}e^{(\sigma + ikx)}$ and $\rho = \rho_{0} + \rho^{*}e^{(\sigma + ikx)}$ they found an equation for the growth rate of their system

$$\sigma = -\gamma_{0}l_{0}\frac{\alpha_{0}(\alpha_{1} + \gamma_{1})l_{0}k^{2} - \alpha_{1}(\alpha_{2} + \gamma_{2})l_{0}k^{2} - (\beta_{0}^{2}l_{0}k^{2})^{2}}{1 + l_{0}k}$$

(4.2.56)

where $l_{0} = \overline{V}/\gamma_{0}$. They found that modes of long wavelength, relative to the reptation length, will dominate. Therefore it can be expected that these modes will dominate the nonlinear dynamics near the ripple formation threshold. Thus the growth rate can be written as

$$\frac{\sigma}{\gamma_{0}} = \epsilon(\alpha_{1} + \gamma_{1})l_{0}^{2}k^{2} - \epsilon l_{0}^{2}(\alpha_{2} + \gamma_{2}) + (\alpha_{1} + \gamma_{1})l_{0}(ik^{3} + l_{0}k^{4}) - l_{0}(\beta_{0}^{2}/\gamma_{0})(ik^{3} + l_{0}k^{4})$$

(4.2.57)

where $\epsilon = \alpha_{0}/\overline{V}$. Close to the point where ripples start forming $\epsilon \ll 1$ (as it corresponds to $\alpha_{0} \ll \overline{V}$ which implies that the wind is not strong enough to sustain saltation) and it is found that

$$Re(\sigma) \sim \gamma_{0}\epsilon(\alpha_{1} + \gamma_{1})l_{0}^{2}k^{2} - \epsilon l_{0}^{2}l_{0}k^{4},$$

(4.2.58)

$$Im(\sigma) \sim \gamma_{0}l_{0}^{2}l_{0}k^{3},$$

(4.2.59)

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where \( l_0 = \beta_0 \beta_2 / V \). They found that the fastest growing wavelength was

\[
\frac{2\pi}{k} = 2\pi \sqrt{\frac{2l_0 l_c}{c(\alpha_1 + \gamma_1)}}. \tag{4.2.60}
\]

In 2000 Valance and Rioual, together with Csahók and Misbah produced a paper extending their ideas of the hydrodynamic model \([16]\). They believed that while the Anderson model \([4]\) is good for modelling the start of the ripple instability it should not be used to predict the following non-linear behaviour of the sand bed, which they attempted to consider in their model. Here, instead of defining \( n_t \) to be constant, as Anderson did \([4]\), they decided that it would depend on the curvature of the sand bed. Thus they defined the number of grains ejected per impact to be \( n = n_t (1 - c\kappa) \) where \( \kappa \) represents the bed curvature and \( c \) is a constant of proportionality. So

\[
T_{ej} = d^3 n_t (1 - c\kappa) N_{imp} = d^3 n_t N_0 \left( 1 - c \frac{h_{aw}}{(1 + h_x^2)^{3/2}} \right) \frac{(1 + h_x \cot \beta)}{(1 + h_x^2)^{1/2}}. \tag{4.2.61}
\]

Which can be written in a form similar to before

\[
T_{ej} = \alpha_0 (1 + \alpha_1 h_x - \alpha_2 h_{xx}) - \alpha_0 (\alpha_3 h_x^2 + \alpha_4 (h_x^2)_x) + O(h_x^3), \tag{4.2.62}
\]

where \( \alpha_0 = d^3 n_t N_0, \alpha_1 = \cot \beta, \alpha_2 = c, \alpha_3 = 1/2, \alpha_4 = c \cot \beta \). In this paper they also define two situations. The first situation is where there is only a slight wind, where the equations remain the same as in \([60]\) (with the new \( T_{ej} \) term) and the second is when there is a strong wind, in which case they feel that the incoming saltation flux will be dense enough to dampen the effect of the wind near the sand bed. In this case they omit the \( T_{ej} \) term.

### 4.3 Numerical Models

Not all research has concentrated on producing analytical models, many numerical models have also been suggested. While the analytical models are mathematically more interesting because they allow for prediction of terms such as the ripple wavelength and growth rate, it is difficult to use them to generate simulations of ripples. The numerical models are generally designed specifically with the idea of creating a computer programme to simulate ripple evolution over time while analytical models generally have to be discretised in order to produce a working computer programme,
in effect converting them to numerical models. Thus it is inevitable that some of the accuracy of the analytical models will be lost in this conversion. It is also worth noticing that numerical models tend to produce more stable and realistic simulations than analytical models. However this is mostly due to the fact that the stability is artificially built into the system.

**An aeolian sand ripple model**

One of the most important numerical models was produced by Nishimori and Ouchi, [48]. This model is a discrete model in both space and time and is a kind of *coupled map lattice model*, as it has a continuous variable representing the averaged surface height at each site. This model incorporates both saltation and reptation. The saltation step is defined as

\[
\begin{align*}
h_{n'}(x, y) &= h_n(x, y) - q, \\
h_{n'}(x + L(h_n(x, y)), y) &= h_n(x + L(h_n(x, y)), y) + q,
\end{align*}
\]

where \( h(x, y) \) is the height of the sand bed at position \((x, y)\) and \( q \) is the amount of sand transferred from position \((x, y)\) to \((x + L, y)\). In this model a full time step from \( n \) to \( n + 1 \) consists of both the saltation and reptation steps, hence after the saltation step we are at a time \( n' \) between \( n \) and \( n + 1 \). Contrary to most of the analytical models they do not treat the saltation flux as constant. In fact they assume that the saltation length, \( L(h(x, y)) \) is dependent on the take-off position of the grain, they use the following approximation

\[
L = L_0 + bh_n(x, y),
\]

where \( x \) is the take-off position, \( L_0 \) represents the force of the wind and \( b \) is related to the average wind velocity a grain experiences in flight, this is treated as a constant, due to problems associated with calculating it. This equation basically shows that the higher the grain is at take-off, the further it will travel in saltation. Their reptation equation takes the form

\[
h_{n+1}(x, y) = h_{n'}(x, y) + D_r \left[ \frac{1}{6} \sum_{NN} h_{n'}(x, y) + \frac{1}{12} \sum_{NNN} h_{n'}(x, y) - h_{n'}(x, y) \right],
\]

where \( \sum_{NN} h(x, y) \) is the sum over the nearest neighboring sites of \((x, y)\) and \( \sum_{NNN} h(x, y) \) is the sum over the second nearest neighboring sites (on a two dimensional lattice the nearest neighboring sites are the eight squares surrounding the \((x, y)\) square.
and the second nearest neighboring sites are the sixteen squares surrounding them). This equation relaxes the local height of the ripple at a speed dependent on the convexity of the sand surface, \( D_r \) being the rate of relaxation. This form of the equations makes it easier to conduct numerical simulations to observe the evolution of the ripples over time. They ran many simulations from a perturbed flat bed, while varying the parameters \( L_0 \) and \( D_r \). They found that the system evolved into ripples when they set \( D_r = 1.5 \) and \( L_0 = 5.0 \). When they fixed \( D_r = 1.5 \) and varied \( L_0 \) they found that there was a threshold value of \( L_0 \) below which ripples did not form. Above this there was a practically linear relationship between \( L_0 \) and the wavelength of the ripples. Varying both parameters they found that there was a threshold value of \( D_r \), which depended on \( L_0 \), above which ripples would not develop, but that ripples would appear if \( L_0 \) was big enough. To investigate these results Nishimori and Ouchi actually turned their discrete system into a continuous one

\[
\frac{\partial h}{\partial t} = D_r h_{xx} + A \left[ N(\eta) \frac{\partial \eta}{\partial x} - N(x) \right], \tag{4.3.5}
\]

where \( N \) is the outgoing sand flux, \( \eta \) is the \( x \) coordinate of the take-off point of sand grains which land at \( x \) and \( A \) is a constant of proportionality. Using the solution \( h = \exp(\sigma t + ikx) \) and the fact that \( \eta_x = (1 + \eta)^{-1} \sim 1 - \eta \) they got the following formula for the growth rate

\[
Re(\sigma) = -AN(x)bk \sin(kL_0) - D_r k^2. \tag{4.3.6}
\]

Looking for a positive growth rate, they found that there was a critical value of \( L_0 \), that depended on \( D_r \), at which the two graphs \( y = AN(x)bk \sin(kL_0) \) and \( y = D_r k \) intersected. This is the threshold value for ripple formation. At higher values of \( L_0 \) you get multiple intersections. They hypothesised that the wavelength corresponding to the maximum growth rate increases in proportion to \( L_0 \), which would be consistent with Bagnold's observations [9]. Thus for their model the ripple wavelength was determined by the saltation length, whereas in the Anderson model [4] and most other analytical models the wavelength is determined by the reptation length. Also the ripple wavelength is of the same order of magnitude as the saltation length which is contradictory to previous work.

Csahók et al [16] say that the way of describing the saltation in this model should be seriously questioned. They argue that it is a problem that this model does not deem the ejection of grains due to saltation important enough to include, despite
evidence to the contrary [9], and also that the variation in saltation lengths due to
the take-off position has never been verified by experiments, so should not be used.

Csahók et al., [16] wrote Nishimori and Ouchi’s equations in the form
\[
\frac{\partial h}{\partial t} = -\frac{1}{\rho_s} \left( \frac{\partial Q_s}{\partial x} + \frac{\partial Q_{rep}}{\partial x} \right) = -d^3(N_s(x) - \frac{\partial \eta}{\partial x} N_s(\eta)) + D_r \frac{\partial^2 h}{\partial x^2}, \tag{4.3.7}
\]
where \(N_s\) is the saltating grain flux. To leading order, where \(N_s\) is constant this
gave
\[
\frac{\partial h}{\partial x} = -bN_s \frac{\partial h}{\partial x} + D_r \frac{\partial^2 h}{\partial x^2}. \tag{4.3.8}
\]
Thus they found the growth rate to be
\[
\sigma = -bd^3 N_s ike^{-ikL_0} - D_r k^2 \tag{4.3.9}
\]
and the critical value of \(L_0\) to be \(L_c = 3\pi D_r/(2bd^3 N_s)\).

In 1997 Nishimori produced a simple computational model for sand dunes [50],
showing the evolution of dunes and the different types that were produced depending
on the direction of the wind and whether this changed during the simulation.

A model for particle size segregation

Two years later Nishimori & Ouchi proposed a second model [49] in which they
investigated particle size segregation, the phenomenon where heavier sand grains
gather at the crest of a ripple while the lighter ones gather in the trough [53]. To do
this they used cellular automata (CAs). Cellular automata are dynamical systems
in which state, time and space are all discrete. They split the area you are looking
at into many ‘cells’. Each cell has different states it can be in (e.g dead or alive,
child or teenager or adult) and there exist a set of rules that govern the transition
from one state to another. At each time step the state of a cell will depend on its
closest neighbours. They have been used for studying many physical and chemical
phenomena. For the specific case of sand ripples Nishimori and Ouchi decided
that each cell could be in one of three states, to represent grain size: \(\psi_0\), which
represents the cell just containing air, \(\psi_1\), which represents light sand grains and \(\psi_2\)
which represents heavy sand grains. They wrote
\[
S_{t,i,j}^t = \psi_0, \psi_1, \psi_2, \tag{4.3.10}
\]

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where $S_{i,j}^t$ represents the state of the cell at position $(i,j)$ at time $t$, $i$ being the horizontal index and $j$ being the vertical index. They use two rules to determine the change in state of the cells: saltation and reptation. The first rule is very similar to their saltation length from their previous paper (4.3.3), namely

$$L = L_0 + b' h(i),$$

(4.3.11)

where $b' = b/m_{i,j}$ and where $m_{i,j} = \psi_0^3$ represents the mass of a grain. This alteration accounts for the fact that the saltation length of a light grain will be longer than the saltation length of a heavy grain. Also for this paper they set $L_0 = 0$ and defined

$$h(i) = \sum_{j=1}^{h_{\text{max}}} \sigma S_{i,j}^t,$$

(4.3.12)

where $h_{\text{max}}$ is the vertical system size and

$$\sigma = \begin{cases} 
0, & S_{i,j}^t = \psi_0 \\
1/S_{i,j}^t, & S_{i,j}^t = \psi_1, \psi_2.
\end{cases}$$

(4.3.13)

Thus the change of state due to saltation is given by

$$S_{i,h(i)}^t = \psi_0, \quad S_{i,h(i)+1}^t = S_{i,h(i)}^t;$$

$$h(i) = h(i) - 1, \quad h(i + L) = h(i + L) + 1,$$

(4.3.14)

with $t'$ being between $t$ and $t+1$. They assume that every grain on the surface of the sand bed will be drawn into saltation at each time step. To define surface reptation they use

$$h(i) - h(i + 1) \equiv \theta,$$

(4.3.15)

the height gradient. If $\theta$ exceeds a critical value $\theta_c$ then the upper grain falls to an adjacent site. Thus $\theta$ is like the maximum angle of repose, but for a single grain. Again they only consider the rolling motion of reptation and not the hopping, although the length scale of their saltation flux is comparable to a hop length. The change of state due to reptation is given by

$$S_{\text{out},h(k_{\text{out}})}^{t+1} = \psi_0, \quad S_{\text{out},h(k_{\text{in}})+1}^{t+1} = S_{\text{out},h(k_{\text{out}})}^{t};$$

$$h(k_{\text{out}}) = h(k_{\text{out}}) - 1, \quad h(k_{\text{in}}) = h(k_{\text{in}}) + 1,$$

(4.3.16)
\[ i_{out} = \begin{cases} 
  i, & \theta > 0 \\
  i + 1, & \theta < 0 
\end{cases}, \quad i_{in} = \begin{cases} 
  i + 1, & \theta > 0 \\
  i, & \theta < 0 
\end{cases} \]

There are different values of \( \theta_c \) depending on the size of the grain

\[ \theta_c = \begin{cases} 
  \theta_{1c} & \text{if } S_{i_{out}, h(i_{out})} = \psi_1 \\
  \theta_{2c} & \text{if } S_{i_{out}, h(i_{out})} = \psi_2 
\end{cases} \]  

(4.3.17)

As heavy grains would generally be harder to dislodge than lighter grains they set \( \theta_{2c} > \theta_{1c} \). They used the total potential energy (TPE) to measure the extent of particle size segregation. If heavy grains end up at higher positions than where they started then the TPE will increase. It is also a measure of the 'roughness' of the ripple. TPE is the sum of the potential energy of every grain in the system

\[ TPE = \sum_i \sum_j m_{ij} g j, \]  

(4.3.18)

where \( g \) is acceleration due to gravity. It can also be written continuously

\[ TPE = \int_0^N \int_0^h x \rho(x,z) gz dz dx, \]  

(4.3.19)

where \( \rho \) is the mass density of the ripple and \( x \) is the horizontal position on the ripple, which goes from 0 to \( N \). They assume that \( \rho \) is constant which gives

\[ TPE = \frac{1}{2} \rho g \int_0^N h^2(x) dx. \]  

(4.3.20)

The height, \( h(x) \), was split into the average height, \( \bar{h} \) and the deviation, \( \delta h(x) \) giving \( h(x) = \bar{h} + \delta h(x) \). Thus by assuming mass conservation (integral of deviation = 0), they found that the variation of the TPE between a rough and flat surface was

\[ \delta(TPE) = TPE_{\text{rough}} - TPE_{\text{flat}} \]  

(4.3.21)

\[ = \frac{1}{2} \rho g \left[ \int_0^N (\bar{h} + \delta h(x))^2(x) dx - \int_0^N \bar{h}^2 dx \right] \]  

(4.3.22)

\[ = \frac{1}{2} \rho g \int_0^N (\delta h(x))^2(x) dx \geq 0. \]  

(4.3.23)

However if \( \rho \) is not constant then it is possible for the TPE to become lower than the TPE of a flat surface, despite an increase in the roughness of the system. Using
\( \bar{\rho} \) as an average value of the heavy and light grains they use \( \Delta TPE_{seg} = TPE(\rho) - TPE(\bar{\rho}) \) as an index for particle size segregation.

They started simulations with a perturbed flat bed \( h = h_0 + \delta \) and a ratio of heavy to light grains of 2 : 8 which are randomly distributed. They noticed that there were four types of dynamics that their CA model could be classified into, corresponding to whether there was a difference between heavy and light grains in i) the saltation and the reptation dynamics, ii) the reptation dynamics only, iii) the saltation dynamics only or iv) no change in the dynamics of either. They ran simulations for all four types to see which ones had the greatest effect on particle size segregation. They found that ii), the difference in creep dynamics, was the best at splitting up the heavy and light grains. As the crest of the ripple is the most unstable place they deduced that this is where segregation takes place, with the heavier grains being able to stay at the crest of the ripple longer than the lighter grains.

4.4  Locality vs nonlocality

One of the most controversial questions in this field is the question of locality vs nonlocality, or whether the dynamics of a given region depend on that of a region that is located at a distance which is significantly further away than the wavelength of the ripple. If this is true then it can be said that the sand surface dynamics are nonlocal. Opinion is divided on this question and more specifically on how much influence the saltation process has on the ripple dynamics. It is not disputed that the saltation length is much larger than the ripple wavelength and as such information is being passed between two quite distant points, suggesting the importance of nonlocality. However it has been shown [4] that reptation is the driving force behind ripple evolution and these grains move on a much shorter scale, generally several times smaller than the ripple wavelength. There are two major arguments against nonlocality as summarised in [16]: 1) the saltating grain population hits the sand bed at roughly the same angle everywhere along the bed [9], thus when they impact on a region there is no way to distinguish two grains that come from two different areas of the sand surface; 2) when a grain is extracted from the bed, thus becoming a saltating grain, it is transported by a turbulent flow where at such a high Reynolds number the length at which two particles stay together is so small that during saltation the grains 'lose the memory of where they came from'. Using these two facts it is argued that it is difficult to believe that saltating grains provide
any effective interaction between the topography of two distant regions on the surface and thus it is difficult to be in favour of nonlocality [16]. Thus the argument against nonlocality is effectively that saltating grains serve merely to bring energy into the system, as they exchange very few grains with the reptating population, and so ripple formation depends basically on the local topography of the surface and the information is propagated only by the reptating grains. However, [51] argues that introducing the concept of a shadow zone into the model (the area on the lee slope that saltating grains cannot hit) introduces nonlocality. Also in models such as [29] the inclusion of the term that is an integral over the hop lengths taking the form $f(x - a)$, thus incorporating information from a large part of the sand bed, also introduces nonlocality. Although it can be argued that a Taylor expansion of this integral will give an adequate description, provided that the average hop lengths are small. This would give a local equation.
A three dimensional analytical model of propagating sand ripples

5.1 Introduction

Here we attempt to extend Hoyle & Woods analytical model of sand ripples [28] to three dimensions. We now include two horizontal axes, $x$ and $y$ as well as a vertical $z$ axis. We are effectively treating the sand bed as a plane.

5.2 Hopping

The number, $N(x, y, t)$, of sand grains ejected per unit time, per unit surface area, from the surface at position $(x, y)$ on the sand bed, at time $t$, is proportional to the flux of saltating grains perpendicular to the surface at that point, $I_h$:

$$N(x, y, t) = J I_h = -\vec{J} \cdot \vec{n}, \quad (5.2.1)$$

where $\vec{n}$ is the unit upward normal vector to the ripple surface $z = h(x, y, t)$, $\vec{I}$ is the incoming saltation flux, $(I_x, I_y, I_z)$ and $\vec{J}$ is a constant of proportionality. To work out $I_h$ we first need to find $\vec{I} \cdot \vec{n}$. The normal to the surface is

$$\vec{n} = \frac{\nabla(z - h(x, y, t))}{|\nabla(z - h(x, y, t))|},$$

and so

$$-\vec{I} \cdot \vec{n} = \frac{I_x(-h_x) + I_y(-h_y) + I_z}{(1 + h_x^2 + h_y^2)^{1/2}}.$$

Therefore the equation for the number of sand grains ejected is

$$N(x, y, t) = \frac{\vec{J} I_x h_x + I_y h_y - I_z}{(1 + h_x^2 + h_y^2)^{1/2}}. \quad (5.2.2)$$
Figure 5.1: The incoming saltation flux, showing the impact angles, $\beta$ and $\theta$.

From Figure 5.1 we see that we can rewrite (5.2.2) as

$$N(x, y, t) = I \frac{h_x \cos \beta \cos \theta + h_y \cos \beta \sin \theta + \sin \beta}{(1 + h_x^2 + h_y^2)^{1/2}},$$

$$= \frac{J h_x \cos \theta + h_y \sin \theta + \tan \beta}{(1 + h_x^2 + h_y^2)^{1/2}},$$

(5.2.3)

where $J = I \bar{J} \cos \beta$. Assume each sand grain hops a distance $a$ in the $x$ direction and a distance $b$ in the $y$ direction, with the joint probability density function $p(a,b)$, where

$$\int_a \int_b p(a,b) \, da \, db = 1.$$  
(5.2.4)

Define

$$\bar{a} = \int_a a p(a) \, da \quad \text{and} \quad \bar{b} = \int_b b p(b) \, db$$

(5.2.5)

to be the mean hop lengths in the $x$ and $y$ directions respectively. Also remember that the marginal distributions of $a$ and $b$ are

$$p(a) = \int_b p(a,b) \, db \quad \text{and} \quad p(b) = \int_a p(a,b) \, da.$$  
(5.2.6)
The net number, \( \delta n(x, y, t) \), of sand grains arriving in the area between \( (x, y), (x + \delta x, y) \), \( (x, y + \delta y) \) and \( (x + \delta x, y + \delta y) \), in time \( \delta t \), is the difference between the number hopping in and the number hopping out

\[
\delta n(x, y, t) = \left\{ -\int_a^b \int p(a, b)[N(x, y, t) - N(x - a, y - b, t)] \, da \, db \right\} \delta x \delta y \delta t. \tag{5.2.7}
\]

The change in surface elevation \( \delta h(x, y, t) \) in time \( \delta t \) is given by

\[
\delta x \delta y \delta h(x, y, t) = a_v \delta n(x, y, t), \tag{5.2.8}
\]

where \( a_v \) is the average volume occupied by a sand grain in the ripple. Combining equations (5.2.7) and (5.2.8) gives

\[
\frac{\partial h}{\partial t}(x, y, t) = -a_v \int_a^b \int p(a, b)[N(x, y, t) - N(x - a, y - b, t)] \, da \, db. \tag{5.2.9}
\]

We can now expand the integrand in equation (5.2.9) as a Taylor series in \( a \) and \( b \). We may truncate this Taylor series at first order, as we assume that the gradient \( N(x, y, t) \) varies slowly, except at the troughs and crests, \( \left( |\nabla N| << 1/a, 1/b \right) \) thus higher order terms are negligible. Applying this to equation (5.2.9) gives

\[
\frac{\partial h}{\partial t}(x, y, t) = -a_v \left\{ \int_a^b \int p(a, b) \frac{\partial N}{\partial x}(x, y, t) \, da \, db + \int_b^a \int p(a, b) \frac{\partial N}{\partial y}(x, y, t) \, da \, db \right\}
\]

\[
= -a_v \left\{ \frac{\partial N}{\partial x}(x, y, t) \int_a^b p(a, b) \, da + \frac{\partial N}{\partial y}(x, y, t) \int_b^a p(a, b) \, da \right\}.
\]

To leading order and using (5.2.6) we get

\[
\frac{\partial h}{\partial t}(x, y, t) = -a_v \left\{ \frac{\partial N}{\partial x}(x, y, t) \int_a p(a) \, da + \frac{\partial N}{\partial y}(x, y, t) \int_b p(b) \, db \right\}.
\]

Then using (5.2.5) we get

\[
\frac{\partial h}{\partial t}(x, y, t) = -a_v \left\{ a \frac{\partial N}{\partial x}(x, y, t) + b \frac{\partial N}{\partial y}(x, y, t) \right\}. \tag{5.2.10}
\]

Now we need to work out the partial derivatives of \( N(x, y, t) \). We get these from equation (5.2.2). Let us define

\[
U = I_x^x h_x + I_y^y h_y - I^x \tag{5.2.11}
\]

\[
V = 1 + h_x^2 + h_y^2. \tag{5.2.12}
\]

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Then
\[
\frac{\partial N}{\partial x} = \frac{\ddot{J}(I^x h_{xx} + I^y h_{yx})V^\frac{1}{2} - \dot{J}UV^{-\frac{1}{2}}(h_x h_{xx} + h_y h_{yx})}{V}.
\]

\[
= \frac{\ddot{J}}{V^{\frac{1}{2}}} \left\{ (I^x h_{xx} + I^y h_{yx})V^{\frac{1}{2}} - UV^{-\frac{1}{2}}(h_x h_{xx} + h_y h_{yx}) \right\}
\]

\[
= \frac{\ddot{J}}{V^{\frac{1}{2}}} \left\{ (I^x h_{xx} + I^y h_{yx})V - U(h_x h_{xx} + h_y h_{yx}) \right\}
\]

\[
= \frac{\ddot{J}}{V^{\frac{1}{2}}} \left\{ (I^x h_{xx}(1 + h_x^2 + h_y^2) + I^y h_{yx}(1 + h_x^2 + h_y^2)) - h_x h_{xx}(I^x(h_x) + I^y(h_y) - I^z)
\]

\[-h_y h_{yx}(I^y(h_x) + I^y(h_y) - I^z) \right\}.
\]

Noting that the $I^x h_{xx} h_x^2$ and $I^y h_{yx} h_y^2$ terms cancel and rearranging we arrive at the

\[
\frac{\partial N}{\partial x} = \frac{\ddot{J}}{V^{\frac{1}{2}}} \left\{ h_{xx}[I^x(1 + h_x^2) - h_x(I^y h_y - I^z)] + h_{yx}[I^y(1 + h_y^2) - h_y(I^x h_x - I^z)] \right\}.
\]

\[
(5.2.13)
\]

Similarly we find the partial derivative of $N(x, y, t)$ with respect to $y$ to be

\[
\frac{\partial N}{\partial y} = \frac{\ddot{J}}{V^{\frac{1}{2}}} \left\{ h_{yy}[I^y(1 + h_y^2) - h_y(I^x h_x - I^z)] + h_{yx}[I^x(1 + h_x^2) - h_x(I^y h_y - I^z)] \right\}.
\]

\[
(5.2.14)
\]

Substituting equations (5.2.13) and (5.2.14) into equation (5.2.10) and rearranging

we get

\[
\frac{\partial h}{\partial t} = -\frac{a_v \ddot{J}}{V^\frac{1}{2}} \left\{ (I^x(1 + h_x^2) - h_x(I^y h_y - I^z)) (\ddot{h}_{xx} + \ddot{h}_{xy})
\]

\[-(I^y(1 + h_y^2) - h_y(I^x h_x - I^z)) (\ddot{h}_{yx} + \ddot{h}_{yy}) \right\}.
\]

\[
(5.2.15)
\]

We can write (5.2.15) as

\[
\frac{\partial h}{\partial t} = -C_1 \ddot{h}_{xx} - C_2 \ddot{h}_{yy} - h_{xy} \{ \ddot{b}C_1 - \ddot{a}C_2 \},
\]

\[
(5.2.16)
\]

where

\[
C_1 = \frac{a_v \ddot{J}}{V^\frac{1}{2}} (\cos \theta(1 + h_y^2) - h_y (h_x \sin \theta + \tan \beta)),
\]

\[
C_2 = \frac{a_v \ddot{J}}{V^\frac{1}{2}} (\sin \theta(1 + h_x^2) - h_x (h_y \cos \theta + \tan \beta)).
\]

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Figure 5.2: A grain rolling on the sand surface, inclined at an angle $\alpha$, under the influence of gravity, $g$, and friction, $ru$, where $r$ is the friction coefficient and $u$ is the velocity of the grain.

5.3 Rolling

We now incorporate the effect of rolling of the sand grains under the influence of gravity, $g$, and friction, where the friction coefficient is $r$. We get an equation for the speed the grains roll along the surface

$$ru = g - (g \cdot n)n,$$

where $g = (0, 0, -g)^T$ and $n = (-h_x, -h_y, 1)/(1 + h_x^2 + h_y^2)^{1/2}$. To simplify matters we set $r$ to be constant, instead of a function of the size and compactness of the sand grains. Substituting in these values we get

$$ru = (0, 0, -g) - \left\{ (0, 0, -g) \cdot \frac{(-h_x, -h_y, 1)}{(1 + h_x^2 + h_y^2)^{1/2}} \right\} \frac{(-h_x, -h_y, 1)}{(1 + h_x^2 + h_y^2)^{1/2}}$$

$$= (0, 0, -g) - \frac{g(h_x, h_y, -1)}{1 + h_x^2 + h_y^2}$$

$$= \frac{-g}{1 + h_x^2 + h_y^2} (h_x, h_y, h_x^2 + h_y^2).$$

We assume that the horizontal number flux, $Q(x, y, t)$, of sand grains is proportional to the horizontal speed of rolling and so we have

$$Q(x, y, t) = \frac{Fg}{r} \frac{(h_x, h_y, 0)}{(1 + h_x^2 + h_y^2)},$$

where $F$ is a constant of proportionality.

For a static sand pile there exists a maximum angle of the surface slope, $\alpha_r$, beyond which the sand can no longer be supported and avalanching occurs. This angle is
known as the angle of repose and depends on how tightly the grains are packed together. For sand this angle is about 30°. For travelling sand ripples, as in our case, it has been proposed [28] that there is a maximum angle, \( \gamma \), of the lee slope, no greater than \( \alpha_r \), at which a slip face will develop where sand will avalanche rather than roll. This angle is called the dynamic angle of repose [28]. This process is in accord with Bagnold's [9] observations that a slip face will develop on the lee slope of sand dunes over a certain height. The slip face is an area on the lee slope that starts at the crest and that is kept at a constant angle \( \gamma \) by avalanching. Thus if the angle of the lee slope attempts to exceed \( \gamma \), the sand flux down the slope becomes very large. We adjust our model so that equation (5.3.2) becomes

\[
Q(x, y, t) = \frac{F g}{r} \tan^2 \gamma \frac{(h_x, h_y, 0)}{(1 + h_x^2 + h_y^2)(\tan^2 \gamma - h_x^2 - h_y^2)^{1/2}}. \tag{5.3.3}
\]

The evolution of the surface profile depends on the surface sand flux according to the equation

\[
\frac{\partial h}{\partial t} = -a_v \nabla \cdot Q. \tag{5.3.4}
\]

Now we need to work out the divergence of \( Q \). Let us define

\[
W = \tan^2 \gamma - h_x^2 - h_y^2. \tag{5.3.5}
\]

Then we find

\[
\frac{\partial Q_x}{\partial x} = \frac{D}{V^2 W^{1/2}} \left\{ h_{xx} VW - h_x (h_{xx} h_x + h_{xy} h_y)(2W - V) \right\}, \tag{5.3.6}
\]

where \( D = -F g \tan^2 \gamma / r \) and \( V \) is defined by (5.2.12). Similarly the partial derivative of \( Q_y \) with respect to \( y \) is

\[
\frac{\partial Q_y}{\partial y} = \frac{D}{V^2 W^{1/2}} \left\{ h_{yy} VW - h_y (h_{yy} h_x + h_{yx} h_y)(2W - V) \right\}. \tag{5.3.7}
\]

Thus, substituting into equation (5.3.4) we see that the variation in elevation at any point \((x, y)\) on the ripple, due to the process of rolling, is given by

\[
\frac{\partial h}{\partial t} = D \left\{ VW (h_{xx} + h_{yy}) - (2W - V) (h_x [h_{xx} h_x + h_{xy} h_y] + h_y [h_{xy} h_x + h_{yx} h_y]) \right\}, \tag{5.3.8}
\]

where \( D = (a_v F g \tan^2 \gamma) / (r V^2 W^{3/2}) \). After some algebra this gives

\[
\frac{\partial h}{\partial t} = D \left\{ h_{xx} ((\tan^2 \gamma - h_y^2)(1 + h_y^2 - h_x^2) + 2h_y^2) + h_{yy} ((\tan^2 \gamma - h_x^2)(1 + h_x^2 - h_y^2) + 2h_x^2) + 2h_x h_y h_{xy} (3h_x^2 + 3h_y^2 + 1 - 2\tan^2 \gamma) \right\},
\]

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which can be written as
\[
\frac{\partial h}{\partial t} = D_1 h_{xx} + D_2 h_{yy} + 2D_3 h_{xy},
\]
(5.3.9)
where
\[
D_1 = \frac{\alpha_v F g \tan \gamma \left\{ (\tan^2 \gamma - h_y^2)(1 + h_y^2 - h_x^2) + 2h_x^4 \right\} }{rV^2W^{\frac{3}{2}}},
\]
\[
D_2 = \frac{\alpha_v F g \tan \gamma \left\{ (\tan^2 \gamma - h_x^2)(1 + h_x^2 - h_y^2) + 2h_y^4 \right\} }{rV^2W^{\frac{3}{2}}},
\]
\[
D_3 = \frac{\alpha_v F g \tan \gamma h_y h_x \left\{ 3h_x^2 + 3h_y^2 + 1 - 2 \tan^2 \gamma \right\} }{rV^2W^{\frac{3}{2}}},
\]
We also include a hyperdiffusion term to regularise the model, damping the growth of large wavenumbers. Heuristically this term models a noise-induced cut-off, where randomness in the surface roughness and collisions between reptating grains prevent the growth of structures on very short length scales. The term we need to add in is
\[
Z = \zeta \nabla^4 h = \zeta \left\{ h_{xxxx} + 2h_{xxyy} + h_{yyyy} \right\},
\]
(5.3.10)
where \( \zeta \) is a constant.

5.4 Combined model

Combining the effects of hopping (5.2.15), rolling (5.3.9) and hyperdiffusion (5.3.10) gives a phenomenological equation governing the evolution of the surface of the ripple, \( h(x, y, t) \):
\[
\frac{\partial h}{\partial t} = h_{xx} \{ D_1 - \bar{a} C_1 \} + h_{yy} \{ D_2 - \bar{b} C_2 \} + h_{xy} \{ 2D_3 - \bar{b} C_1 - \bar{a} C_2 \} - \zeta \nabla^4 h,
\]
(5.4.1)
where
\[
C_1 = \frac{\alpha_v J}{V^{\frac{3}{2}}} \left( \cos \theta (1 + h_y^2) - h_x (h_y \sin \theta + \tan \beta) \right),
\]
\[
C_2 = \frac{\alpha_v J}{V^{\frac{3}{2}}} \left( \sin \theta (1 + h_x^2) - h_y (h_x \cos \theta + \tan \beta) \right),
\]
\[
D_1 = \frac{\alpha_v F g \tan \gamma \left\{ (\tan^2 \gamma - h_y^2)(1 + h_y^2 - h_x^2) + 2h_x^4 \right\} }{rV^2W^{\frac{3}{2}}},
\]
\[
D_2 = \frac{\alpha_v F g \tan \gamma \left\{ (\tan^2 \gamma - h_x^2)(1 + h_x^2 - h_y^2) + 2h_y^4 \right\} }{rV^2W^{\frac{3}{2}}},
\]
\[
D_3 = \frac{\alpha_v F g \tan \gamma h_y h_x \left\{ 3h_x^2 + 3h_y^2 + 1 - 2 \tan^2 \gamma \right\} }{rV^2W^{\frac{3}{2}}},
\]
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No hopping occurs on areas of the sand bed that are in shadow, since they are shielded from the saltation flux. In those regions the modified equation

\[ \frac{\partial h}{\partial t} = h_{xx} D_1 + h_{yy} D_2 + 2h_{xy} D_3 - \zeta \nabla^4 h, \]

holds.


5.5 Stability analysis for the one-species model

In this section we investigate the stability of our model (5.4.1). We want our model to be unstable to small perturbations so that we will see ripples develop from a flat bed subject to some initial random noise component. In the early stages of ripple evolution from a flat bed there are no shadow zones as \(|\nabla h| < \tan \beta\) everywhere and so equation (5.4.2) is not relevant. We can therefore use equation (5.4.1) only to determine the initial growth rate of sand ripples and their preferred wavelength.

First we need to find the steady states. Looking for spatially uniform steady states, where we would set all derivatives to zero, we see that our equation (5.4.1) reduces to zero on both sides. So any constant value of \(h\) would be acceptable: we call this \(h_c\). Thus we can set \(h = h_c + \tilde{h}(x, y, t)\) and then drop the tildes to give

\[
\frac{\partial h}{\partial t} = h_{xx}\{D_1 - \bar{a}C_1\} + h_{yy}\{D_2 - \bar{b}C_2\} + h_{xy}\{2D_3 - \bar{b}C_1 - \bar{a}C_2\} - \zeta \nabla^4 h.
\]

We now linearise our equation, by removing all terms of order \(|\nabla h|^2\) and above. Note that we are dividing by \(V\) and \(W\), as defined by (5.2.12, 5.3.5), in certain places but by Taylor expanding \(V^a\) to first order in \(|\nabla h|^2\) we get that

\[
(1 + h_x + h_y^2)^a = 1 + a(h_x^2 + h_y^2) + O(h_x^4, h_y^4) = 1,
\]

for all \(a \in \mathbb{N}\). We also note that \(W^{3/2} = (\tan^2 \gamma - h_x^2 - h_y^2)^{3/2}\) and so if we are ignoring terms of order \(h_x^2\) and \(h_y^2\) then

\[
W^{3/2} = (\tan^2 \gamma)^{3/2} = \tan^3 \gamma.
\]

With these simplifications we can linearise our coefficients to give

\[
C_1 = a_x J (\cos \theta - h_x \tan \beta),
C_2 = a_y J (\sin \theta - h_y \tan \beta),
D_1 = \frac{a_x F g \tan \gamma}{r},
D_2 = \frac{a_y F g \tan \gamma}{r},
D_3 = 0.
\]

However these are all diffusion coefficients and so will be multiplied by a second derivative term. Thus any \(h_x\) or \(h_y\) terms will contribute only at second order in the
derivatives, so we can remove them as well. Thus we get the linearised equation
\[
\frac{\partial h}{\partial t} = \left\{ \frac{a_v F g \tan \gamma}{r} - \bar{a}_u \bar{J} \cos \theta \right\} h_{xx} + \left\{ \frac{a_v F g \tan \gamma}{r} - \bar{b}_u \bar{J} \sin \theta \right\} h_{yy} \\
- \left\{ \bar{b}_u \bar{J} \cos \theta + \bar{a}_u \bar{J} \sin \theta \right\} h_{xy} - \zeta \left\{ h_{axxx} + 2h_{xxyy} + h_{yyyy} \right\}.
\] (5.5.2)

Now we set
\[
h(x, y, t) = h_0 e^{\sigma t + iqx + ipy},
\]
where \( \sigma \) is the growth rate of a Fourier mode with wavevector \((q, p)\) and \(h_0\) is a constant. Substituting into equation (5.5.2) gives
\[
\sigma = \left( \bar{a}_u \bar{J} \cos \theta - \frac{a_v F g \tan \gamma}{r} \right) q^2 + a_v \bar{J} (\bar{b} \cos \theta + \bar{a} \sin \theta) pq + \\
\left( \bar{b}_u \bar{J} \sin \theta - \frac{a_v F g \tan \gamma}{r} \right) p^2 - \zeta (p^2 + q^2)^2.
\] (5.5.3)

This can be written in the form
\[
\sigma = a_v \bar{J} (q \bar{a} + p \bar{b}) (q \cos \theta + p \sin \theta) - \frac{a_v F g \tan \gamma}{r} (q^2 + p^2) - \zeta (p^2 + q^2)^2,
\]
which factorises to give
\[
\sigma = a_v \bar{J} (q \bar{a} + p \bar{b}) (q \cos \theta + p \sin \theta) - \frac{a_v F g \tan \gamma}{r} (q^2 + p^2) - \zeta (p^2 + q^2)^2.
\] (5.5.4)

As we are looking at the stability of a flat bed we would like the bed to become unstable so that we will see some ripples forming (if it were stable then the bed would remain flat). Therefore we require \( \sigma > 0 \). As all the terms in (5.5.4) are positive we see that, to second order, \( \sigma > 0 \) if and only if
\[
a_v \bar{J} (q \bar{a} + p \bar{b}) (q \cos \theta + p \sin \theta) > \frac{a_v F g \tan \gamma}{r} (q^2 + p^2),
\]
which gives us the inequality
\[
J > \frac{F g \tan \gamma (q^2 + p^2)}{r (q \bar{a} + p \bar{b}) (q \cos \theta + p \sin \theta)}.
\] (5.5.5)

So for our model to be unstable we must choose \( J \) so that it satisfies (5.5.5).
5.5.1 Fastest growing wavelengths

Equation (5.5.3) gives us an expression for the growth rate in terms of the wavelengths $p$ and $q$. The fastest growing wavelengths will be the values of $p$ and $q$ which give us the maximum value of $\sigma$. To find this maximum we need to calculate the partial derivatives of $\sigma$ with respect to $p$ and $q$. We can simplify the calculations by setting the wind to be in the $x$ direction. Therefore $\theta$, the angle of the saltation flux in the $y$ direction, will be zero, as will the average reptation length in the $y$ direction, $\tilde{b}$. Thus we see that (5.5.3) reduces to

$$\sigma = \left(\bar{a}a_w J - \frac{a_w F\gamma \tan \gamma}{r}\right) q^2 - \frac{a_w F\gamma \tan \gamma}{r} p^2 - \zeta \left(p^2 + q^2\right)^2,$$

which we can write in the form

$$\sigma = Aq^2 + Bp^2 - \zeta \left(p^2 + q^2\right)^2,$$

where

$$A = \bar{a}a_w J - \frac{a_w F\gamma \tan \gamma}{r}, \quad B = -\frac{a_w F\gamma \tan \gamma}{r}.$$

So the partial derivatives of $\sigma$ are

$$\frac{\partial \sigma}{\partial p} = 2Bp - 4\zeta (p^2 + q^2)p, \quad \frac{\partial \sigma}{\partial q} = 2Aq - 4\zeta (p^2 + q^2)q,$$

$$\frac{\partial^2 \sigma}{\partial p^2} = 2B - 12\zeta p^2 - 4\zeta q^2, \quad \frac{\partial^2 \sigma}{\partial q^2} = 2A - 12\zeta q^2 - 4\zeta p^2, \quad \frac{\partial^2 \sigma}{\partial p \partial q} = -8\zeta pq.$$

We will have a stationary point when the first derivatives are zero. It will be a maximum if

(a) $\frac{\partial^2 \sigma}{\partial p^2} = 2B - 12\zeta p^2 - 4\zeta q^2 < 0$, \hspace{1cm} (5.5.8)

(b) $\frac{\partial^2 \sigma}{\partial q^2} = 2A - 12\zeta q^2 - 4\zeta p^2 < 0$, \hspace{1cm} (5.5.9)

(c) $\frac{\partial^2 \sigma}{\partial p^2} \frac{\partial^2 \sigma}{\partial q^2} - \left(\frac{\partial^2 \sigma}{\partial p \partial q}\right)^2 = \left(2B - 12\zeta p^2 - 4\zeta q^2\right) \left(2A - 12\zeta q^2 - 4\zeta p^2\right) - (-8\zeta pq)^2 > 0$. \hspace{1cm} (5.5.10)

This extrema occurs at values $(q, p)$ where

$$\left\{2B - 4\zeta (p^2 + q^2)\right\} p = 0,$$ \hspace{1cm} (5.5.11)
\[
\left\{ 2A - 4\zeta(p^2 + q^2) \right\} q = 0. \quad (5.5.12)
\]

From (5.5.11) we see that either \( p = 0 \), or
\[
2B - 4\zeta(p^2 + q^2) = 0 \quad \Rightarrow \quad (p^2 + q^2) = \frac{B}{2\zeta}. \quad (5.5.13)
\]

If \( p = 0 \), then substituting into (5.5.12) we get that
\[
\left\{ 2A - 4\zeta q^2 \right\} q = 0 \quad \Rightarrow \quad q = 0 \quad \text{or} \quad q^2 = \frac{A}{2\zeta}. \quad (5.5.14)
\]

If \( (p^2 + q^2) = B/(2\zeta) \), then substituting into (5.5.12) we get that
\[
\left\{ 2A - 2B \right\} q = 0 \quad \Rightarrow \quad q = 0 \quad \text{or} \quad A = B.
\]

As we do not expect that \( A = B \) in general, we are left with the fact that \( q = 0 \) which means that \( p^2 = B/(2\zeta) \).

Thus we have three stationary points
\[
(q^2, p^2) = (0, 0), \quad (5.5.15)
\]
\[
(q^2, p^2) = \left( 0, \frac{B}{2\zeta} \right), \quad (5.5.16)
\]
\[
(q^2, p^2) = \left( \frac{A}{2\zeta}, 0 \right). \quad (5.5.17)
\]

Now we want to know if our solutions are maxima or not. For solution (5.5.15) the conditions (5.5.8) give
\[
2B < 0, \quad 2A < 0, \quad AB > 0.
\]

From this we see that we need both \( A \) and \( B \) to be negative. Because \( B = -(a_u F g \tan \gamma)(r)^{-1} \) it will always be negative, as \( a_u, F, g, \tan \gamma \) and \( r \) are all positive. So the only condition we have for solution (5.5.15) to be a maximum is
\[
J < \frac{F g \tan \gamma}{ar} \equiv J_c. \quad (5.5.18)
\]

For solution (5.5.16), we have conditions from (5.5.8)
\[
(a_1) \quad 2B < 12\zeta \left( \frac{B}{2\zeta} \right) \quad \Rightarrow \quad -4B < 0 \quad \Rightarrow \quad B > 0
\]
\[
(b_1) \quad 2A - 4\zeta \left( \frac{B}{2\zeta} \right) < 0 \quad \Rightarrow \quad 2(A - B) < 0 \quad \Rightarrow \quad B > A
\]
\[
(c_1) \quad -8B(A - B) > 0.
\]
We can see that if \((a_1)\) and \((b_1)\) are true then \((c_1)\) will also be true, but \(B\) is negative so this solution will never be a maximum. For our solution \((5.5.17)\) we get that

\[
\begin{align*}
(a_2) \quad & 2B - 4\zeta \left( \frac{A}{2\zeta} \right) < 0 \implies 2(B - A) < 0 \implies A > B \\
(b_2) \quad & 2A - 12\zeta \left( \frac{A}{2\zeta} \right) < 0 \implies -4A < 0 \implies A > 0 \\
(c_2) \quad & 2(B - A)(-4A) > 0.
\end{align*}
\]

Again we see that \((c_2)\) will hold if \((a_2)\) and \((b_2)\) do. As \(B\) is always negative condition \((a_2)\) will hold if \((b_2)\) does. Thus we just need \(A > 0\) for this solution to be a maximum. This gives us the condition

\[
\overline{a}_\nu J - \frac{a_\nu F g \tan \gamma}{r} > 0 \implies J > \frac{F g \tan \gamma}{\overline{a}_\nu} \equiv J_c.
\]

Thus aeolian sand ripples will grow if the scaled saltation flux intensity, \(J\), exceeds the threshold value, \(J_c\). So if \(J > J_c\) the maximum growth rate occurs at \((q^2, p^2) = \left( \frac{A}{2\zeta}, 0 \right)\). As we are working in radians we find the length of the fastest growing wave is

\[
L = \frac{2\pi}{q} = 2\pi \sqrt{\frac{2\zeta}{A}} = 2\pi \sqrt{\frac{2\zeta}{\overline{a}_\nu(J - J_c)}}. \tag{5.5.19}
\]

If \(J < J_c\) we have \(\sigma \leq 0\) and the flat bed is stable.
A three-dimensional two-species continuum model for aeolian sand ripples

6.1 Introduction

Following on from the three-dimensional analytical model we now extend this one-species model to two species in order to obtain more realistic ripple profiles. Our modelling approach follows in a similar vein to previous work on two-dimensional two-species models, such as [43, 30]. We split the ripple up into a thin layer of flowing grains, with density $\rho(x, y, t)$, on top of a relatively stationary sand bed, $h(x, y, t)$, with $x$ and $y$ the horizontal coordinates and $t$ time. The evolution of the ripple depends on the impact of the saltating grains causing other grains to hop out of the sand bed and land in the flowing layer, and the smoothing effects which are a result of the rolling and avalanching terms.

6.2 Hopping

From our previous model we have a constant incoming saltation flux, $I = (I_x, I_y, I_z)$, which we expect to dislodge grains in the sand bed sending them into reptation. These reptating grains will eventually land in the flowing layer. The saltating grains will continue in saltation after rebounding from the sand bed due to their high energy. The number of sand grains, $N(x, y, t)$, ejected per unit time per unit surface area, from the surface at position $(x, y)$ on the sand bed, at time $t$ is given by

$$N(x, y, t) = \frac{J h_x \cos \theta + h_y \sin \theta + \tan \beta}{(1 + h_x^2 + h_y^2)^{1/2}}.$$  \hspace{1cm} (6.2.1)

The probability distribution of the reptation lengths are as defined for the one species model, (5.2.5, 5.2.6). The number, $\delta n_0(x, y, t)$, of sand grains leaving the surface in the area between $(x, y), (x + \delta x, y), (x, y + \delta y)$ and $(x + \delta x, y + \delta y)$, in time $\delta t$, is given by $\delta n_0(x, y, t) = N(x, y, t)\delta x \delta y \delta t$. The change $\delta h$ in the surface height satisfies

$$\delta x \delta y \delta h(x, y, t) = -a_v \delta n_0(x, y, t) = -a_v N(x, y, t) \delta x \delta y \delta t,$$  \hspace{1cm} (6.2.2)
where $a_v$ is the average volume of the sand grain. In the limit we find that the contribution to the evolution equation for $h(x, y, t)$ from hopping alone is

$$
\eta_h(x, y, t) = -a_v J \frac{h_x \cos \theta + h_y \sin \theta + \tan \beta}{(1 + h_x^2 + h_y^2)^{1/2}}.
$$

(6.2.3)

The number $\delta n_t(x, y, t)$ of sand grains arriving on the layer of flowing grains in the area between $(x, y), (x + \delta x, y), (x, y + \delta y)$ and $(x + \delta x, y + \delta y)$, in time $\delta t$ is given by

$$
\delta n_t(x, y, t) = \left\{ \int_a^b \int_p(a, b) N(x - a, y - b, t) \, da \, db \right\} \delta x \delta y \delta t.
$$

(6.2.4)

The change in depth of the flowing layer satisfies

$$
\delta x \delta y \delta \rho(x, y, t) = a_v \delta n_t(x, y, t) = a_v \left\{ \int_a^b \int_p(a, b) N(x - a, y - b, t) \, da \, db \right\} \delta x \delta y \delta t
$$

(6.2.5)

and hence the contribution to the evolution equation for the flowing layer depth from hopping alone is

$$
\eta_p(x, y, t) = \int_a^b \int_p(a, b) N(x - a, y - b, t) \, da \, db
$$

$$
= a_v J \int_a^b \int_p(a, b) \frac{h_x(x - a, y - b, t) \cos \theta + h_y(x - a, y - b, t) \sin \theta + \tan \beta}{\left\{ 1 + h_x^2(x - a, y - b, t) + h_y^2(x - a, y - b, t) \right\}^{1/2}} \, da \, db.
$$

(6.2.6)

We can expand the integrand in (6.2.6) as a Taylor series in $a$ and $b$. We may also truncate this at first order, as we assume that the gradient $N(x, y, t)$ varies slowly, except at the troughs and crests. Now equation (6.2.6) becomes

$$
\eta_p(x, y, t) = \int_a^b \int_p(a, b) \left\{ p(a, b) N(x, y, t) - p(a, b) a \frac{\partial N}{\partial x}(x, y, t) - p(a, b) b \frac{\partial N}{\partial y}(x, y, t) \right\} \, da \, db,
$$

which using probability arguments (5.2.6) gives

$$
\eta_p(x, y, t) = \int_a^b \int_p(a, b) N(x, y, t) \, da \, db - \int_a^b a p(a) \frac{\partial N}{\partial x}(x, y, t) \, da - \int_b p(b) \frac{\partial N}{\partial y}(x, y, t) \, db,
$$

and using equation (5.2.5) gives

$$
\eta_p(x, y, t) = N(x, y, t) - a \frac{\partial N}{\partial x}(x, y, t) - b \frac{\partial N}{\partial y}(x, y, t).
$$

(6.2.7)
We include diffusion terms as well as terms for the transfer of grains between the flowing layer and the sand bed, leading to the equations

\[ h_t = D_h \nabla^2 h - T(x, y, t) + \eta_h(x, y, t) \tag{6.2.8} \]
\[ \rho_t = D_{\rho} \nabla^2 \rho - \nabla \cdot j + T(x, y, t) + \eta_{\rho}(x, y, t), \tag{6.2.9} \]

where \( \nabla \cdot j \) is the divergence of the flux of flowing grains due to gravity and is defined as

\[
\nabla \cdot j = -\nabla \cdot (\chi \rho \nabla h) = -\chi \left\{ (\rho h_x)_x + (\rho h_y)_y \right\}
\]

and so we have

\[ \rho_t = D_{\rho} \nabla^2 \rho + \chi \left\{ (\rho h_x)_x + (\rho h_y)_y \right\} + T(x, y, t) + \eta_{\rho}, \tag{6.2.10} \]

where \( D_h, D_{\rho} \) and \( \chi \) are positive constants. The term \( D_h \nabla^2 h \) represents the diffusion of the sand bed due to the rearrangement of clusters while the term \( D_{\rho} \nabla^2 \rho \) represents diffusion due to the relaxation of the flowing grains. These diffusion terms are strictly intracluster motions. The intercluster motions are governed by \( T(x, y, t) \), the transfer term. It represents the interaction between the sand bed, \( h(x, y, t) \), and the flowing grains, \( \rho(x, y, t) \). It is given by

\[ T(x, y, t) = \lambda \rho(|\nabla h|^2 - \tan^2 \alpha) \quad \text{for} \quad 0 \leq |\nabla h|^2 \leq \tan^2 \alpha \tag{6.2.11} \]

and

\[ T(x, y, t) = \nu \rho \left( (|\nabla h|^2 - \tan^2 \alpha) \left( \tan^2 \gamma - |\nabla h|^2 \right)^{-1} \right) \quad \text{for} \quad \tan^2 \alpha \leq |\nabla h|^2 \leq \tan^2 \gamma \tag{6.2.12} \]

where \( \lambda \) and \( \nu \) are positive constants and \( \alpha \) is the angle of repose. Within a given range above the angle of repose a sandpile can be either static or flowing. The maximum angle of stability, \( \gamma \), gives the upper bound of this region. For slopes greater than \( \tan^2 \gamma \) the sandpile will avalanche. Thus we have two different forms of the transfer term for the two regimes when different mechanisms apply. For slopes less than the angle of repose, \( \tan^2 \alpha \), the term \( \lambda \rho(|\nabla h|^2 - \tan^2 \alpha) \) represents the tendency of grains in the flowing layer to lose momentum and thus stick to the sand bed. For slopes greater than \( \tan^2 \alpha \) this is replaced by \( (|\nabla h|^2 - \tan^2 \alpha)(\tan^2 \gamma - |\nabla h|^2)^{-1} \), which models the tendency of stable grains in the sand bed to be shed.
into the flowing layer due to the increasing angle of the lee slope. This process only begins once the slope has exceed the angle of repose. As the slope approaches \( \gamma \) the rate of shedding of grains becomes very large: avalanching occurs. Therefore our governing equations take the form

\[
\begin{align*}
  h_t &= D_h \nabla^2 h - \left\{ \begin{array}{ll}
  \lambda \rho (|\nabla h|^2 - \tan^2 \alpha) & \text{for } 0 \leq |\nabla h|^2 \leq \tan^2 \alpha \\
  - J (h_x \cos \theta + \sin \theta h_y + \tan \beta)
  \end{array} \right. \\
  \rho_t &= D_p \nabla^2 \rho + \chi [(\rho h_x)_x + (\rho h_y)_y] \\
  &+ \left\{ \begin{array}{ll}
  \lambda \rho (|\nabla h|^2 - \tan^2 \alpha) & \text{for } 0 \leq |\nabla h|^2 \leq \tan^2 \alpha \\
  \nu (|\nabla h|^2 - \tan^2 \alpha) (\tan^2 \gamma - |\nabla h|^2)^{-1} & \text{for } \tan^2 \alpha \leq |\nabla h|^2 \leq \tan^2 \gamma \\
  + \int_a^b p(a, b) J (h_x (x - a, y - b, t) \cos \theta + h_y (x - a, y - b, t) \sin \theta + \tan \beta) \, da \, db.
  \end{array} \right.
\end{align*}
\]

(6.2.13)

6.3 Nondimensionalising the two-species model

We have many parameters in our model which can make mathematical analysis tricky. However we can reduce the number of parameters by nondimensionalising our model to get a simpler system of equations. To do this we must first set:

\[
h = h_0 \tilde{h}, \quad \rho = \rho_0 \tilde{\rho}, \quad x = x_0 \tilde{x}, \quad y = y_0 \tilde{y}, \quad t = t_0 \tilde{t}, \quad \alpha = \alpha_0 \tilde{\alpha}, \quad \beta = \beta_0 \tilde{\beta},
\]

where

\[
\begin{align*}
  t_0 &= \frac{D_h}{(J)^2}, \quad x_0 = y_0 = \frac{D_h}{J}, \quad h_0 = \frac{D_h \tan \gamma}{J}, \quad \rho_0 = \frac{J}{\lambda \tan \gamma}.
\end{align*}
\]

We find

\[
\begin{align*}
  \frac{t_0}{x_0} = \frac{t_0}{y_0} = \frac{1}{J}, \quad \frac{t_0}{x_0^2} = \frac{t_0}{y_0^2} = 1/D_h, \quad \frac{t_0}{h_0} = \frac{1}{\tan \gamma J}, \quad \frac{h_0}{x_0} = \frac{h_0}{y_0} = \tan \gamma, \quad \frac{t_0 \rho_0}{h_0} = \frac{1}{\lambda \tan^2 \gamma}.
\end{align*}
\]
Dropping the tilde's and substituting this into equations (6.2.13) and (6.2.14) gives us:

\[
\begin{align*}
\dot{h}_t &= D_h \left( \frac{t_0}{x_0} h_{xx} + \frac{t_0}{y_0} h_{yy} \right) - J \left( \frac{t_0}{x_0} h_x \cos \theta + \frac{t_0}{y_0} h_y \sin \theta + \frac{t_0}{h_0} \tan \beta \right) \\
&\quad + \begin{cases} \\
\frac{\lambda t_0}{h_0} \rho \left( \frac{h_0}{x_0} h_x \right)^2 + \left( \frac{h_0}{y_0} h_y \right)^2 - \tan^2 \alpha \\
\mathrm{for} \ |\nabla h|^2 \leq \tan^2 \alpha
\end{cases} \\
&\quad - \begin{cases} \\
\nu \left( \frac{h_0}{x_0} h_x \right)^2 + \left( \frac{h_0}{y_0} h_y \right)^2 - \tan^2 \alpha \left( \tan^2 \gamma - \left( \frac{h_0}{x_0} h_x \right)^2 - \left( \frac{h_0}{y_0} h_y \right)^2 \right)^{-1} \\
\mathrm{for} \ \tan^2 \alpha \leq |\nabla h|^2 \leq \tan^2 \gamma
\end{cases}
\end{align*}
\]

(6.3.1)

\[
\begin{align*}
\rho_t &= D_\rho \left( \frac{t_0}{x_0} h_{xx} + \frac{t_0}{y_0} h_{yy} \right) + \chi h_0 \left( \frac{t_0}{x_0^2} (\rho h_x)_{xx} + \frac{t_0}{y_0^2} (\rho h_y)_{yy} \right) + \frac{t_0}{\rho_0} \int_a \int_b p(a, b) J \\
&\quad \left( \frac{h_0}{x_0} h_x(x-a, y-b, t) \cos \theta + \frac{h_0}{y_0} h_y(x-a, y-b, t) \sin \theta + \tan \beta \right) x_0 da y_0 db \\
&\quad + \begin{cases} \\
\lambda t_0 \rho \left( \frac{h_0}{x_0} h_x \right)^2 + \left( \frac{h_0}{y_0} h_y \right)^2 - \tan^2 \alpha \\
\mathrm{for} \ |\nabla h|^2 \leq \tan^2 \alpha
\end{cases} \\
&\quad - \begin{cases} \\
\frac{\rho_0}{h_0} \nu \left( \frac{h_0}{x_0} h_x \right)^2 + \left( \frac{h_0}{y_0} h_y \right)^2 - \tan^2 \alpha \left( \tan^2 \gamma - \left( \frac{h_0}{x_0} h_x \right)^2 - \left( \frac{h_0}{y_0} h_y \right)^2 \right)^{-1} \\
\mathrm{for} \ \tan^2 \alpha \leq |\nabla h|^2 \leq \tan^2 \gamma
\end{cases}
\end{align*}
\]

(6.3.2)

which we can write as
\[ h_t = \nabla^2 h_x - \left( h_x \cos \theta + h_y \sin \theta + \frac{\tan \beta}{\tan \gamma} \right) \delta \left\{ \begin{array}{ll}
\rho(\sqrt{h^2} - \frac{\tan^2 \alpha}{\tan^2 \gamma}) & \text{for } |\nabla h|^2 \leq \tan^2 \alpha \\
\nu^* (|\nabla h|^2 - \frac{\tan^2 \alpha}{\tan^2 \gamma})(1 - h_x^2 - h_y^2)^{-1} & \text{for } \tan^2 \alpha \leq |\nabla h|^2 \leq \tan^2 \gamma 
\end{array} \right. 
\]

\[ \rho_t = \frac{D_p}{D_h} \nabla^2 \rho + \chi^* \left( (\rho h_x)_x + (\rho h_y)_y \right) + \delta \left\{ \begin{array}{ll}
\frac{\rho h_0}{\rho_0} \rho(\sqrt{h^2} - \frac{\tan^2 \alpha}{\tan^2 \gamma}) & \text{for } |\nabla h|^2 \leq \tan^2 \alpha \\
\frac{\rho h_0}{\rho_0} \nu^* (|\nabla h|^2 - \frac{\tan^2 \alpha}{\tan^2 \gamma})(1 - h_x^2 - h_y^2)^{-1} & \text{for } \tan^2 \alpha \leq |\nabla h|^2 \leq \tan^2 \gamma 
\end{array} \right. 
\]

\[ + x_0^2 \frac{D_h}{\chi} \int_a \int_b p(a, b) J \left( h_x(x - a, y - b, t) \cos \theta + h_y(x - a, y - b, t) \sin \theta + \frac{\tan \beta}{\tan \gamma} \right) \mathrm{d}a \mathrm{d}b, \]

where

\[ \nu^* = \nu \frac{\eta_0}{h_0} = \frac{\nu}{J \tan \gamma}, \]

\[ \chi^* = \chi \frac{\eta_0 \eta_0}{x_0^2} = \frac{\chi \tan \gamma}{J}. \]
6.4 Probability Distributions

While deriving models it is often unnecessary to define the probability density function, \( p(a, b) \), used in the splash function. This is the case in [28] where Taylor-expanding the integral to second order means that only the mean of the hop lengths is needed, which are given by previous experiments [45]. However in some two-species model e.g. [30], it is unreasonable to Taylor expand the integral to second order only as we would lose information from the higher order derivatives that is not insignificant in this case. It is particularly important to include these higher order times in stability analysis. The inclusion of these terms means that we now need to know more than just the means of the distribution. We will also need to know higher moments. In order to evaluate these expectations we will need to define the probability distribution. It has been suggested before that the actual distribution of the hop lengths makes little difference to the accuracy of the results [4]. Anderson tried three different distributions. First he chose the probability distribution of reptation lengths to be uniform, this corresponded to the probability density being a delta function. Then he tried two distributions that were more representative of the actual reptation lengths, the gamma distribution and the exponential distribution. He found that these more realistic cases damped the growth of the shorter wavelengths and gave rise to a single fastest growing wavenumber which was of the order of six times the mean reptation length. However he noticed that the fastest growth rate was not much affected by the choice of distribution.

The easiest choice of probability distribution would be the bivariate normal distribution. This is simply the equivalent of the normal distribution but for two variables (the hop lengths in the \( x \) and \( y \) direction in our case). The bivariate normal distribution has probability density function

\[
p(a, b) = \frac{1}{2\pi\sigma_a\sigma_b\sqrt{1-p^2}} \exp \left\{ -\frac{1}{2(1-p^2)} \left[ \left( \frac{a-\mu_a}{\sigma_a} \right)^2 - 2p \left( \frac{a-\mu_a}{\sigma_a} \right) \left( \frac{b-\mu_b}{\sigma_b} \right) + \left( \frac{b-\mu_b}{\sigma_b} \right)^2 \right] \right\},
\]

where \(-\infty < \mu_a, \mu_b < +\infty\) are the mean reptation lengths in the \( x \) and \( y \) directions respectively, \( \sigma_a, \sigma_b > 0 \) are the standard deviations of the reptation lengths and \(-1 < p < 1\) is the covariance. We can find the expectations we want by using the
joint moment generating function. This is defined as
\[ M_{a,b}(\theta_1, \theta_2) = E(e^{a \theta_1 + b \theta_2}) = \int_a \int_b e^{a \theta_1 + b \theta_2} p(a,b) \, da \, db. \] (6.4.2)

We then find our required expectations by the relation
\[ \left[ \frac{\delta^{t+x} M_{a,b}(\theta_1, \theta_2)}{\delta \theta_1 \theta_2} \right]_{\theta_1=\theta_2=0} = E(a^t b^s). \] (6.4.3)

It can be shown that the joint moment generating function for the bivariate gamma distribution is
\[ M_{a,b}(\theta_1, \theta_2) = \exp \{ (\theta_1 \mu_a + \theta_2 \mu_b) + 0.5(\theta_1^2 \sigma_a^2 + 2 \theta_1 \theta_2 \rho \sigma_a \sigma_b + \theta_2^2 \sigma_b^2) \}. \] (6.4.4)

This distribution would seem a logical choice as many papers have previously used the normal distribution for their two dimensional models, e.g., [4], [30], [51]. However, many consider a gamma distribution more realistic [4]. While we would expect the distribution of hop lengths in the \( y \) direction to be normal (on average you would get the same number of grains hopping either side of the incoming saltation flux), it is not so obvious that the hop lengths in the \( x \) direction should be normal. In fact, evidence shows that the grains that hop backwards from the impact point will not travel nearly as far as those hopping forwards [45]. This suggests that our distribution in the \( x \) direction will be positively skewed and thus will not be normal. A more obvious choice would be the gamma distribution. We therefore would like a bivariate distribution which acts like the gamma distribution in the \( x \) direction and the normal distribution in the \( y \) direction. Such a distribution exists and it is called the univariate normal/gamma distribution. This is defined as follows:

First let the random variable \( X \) represent the probability distribution of hop lengths in the \( x \) direction and \( Y \) represent the probability of hop lengths in the \( y \) direction. If we let the distribution of \( X \) be gamma such that: \( X \sim G[n/2, d/2] \) for any \( n > 0 \) and \( d > 0 \) and suppose that the conditional distribution of \( Y \) given \( X \) is normal \( Y|X \sim N[m, CX^{-1}] \), for some \( m \) and \( C \), then the joint distribution of \( X \) and \( Y \) is called (univariate) normal/gamma

\[ p(Y, X) = \left( \frac{X}{2\pi C} \right)^{\frac{3}{2}} \exp \left[ -\frac{X(Y - m)^2}{2C} \right] \frac{d^{\frac{3}{2}}}{2^{\frac{3}{2}} \Gamma(\frac{3}{2})} X^{\frac{3}{2} - 1} \exp \left[ -\frac{Xd}{2} \right]. \] (6.4.5)

If we simplify the calculations by setting the wind to be in the \( x \) direction, as in our stability analysis, then the hop lengths in the \( y \) direction are centered around the \( x \)
axis and thus we know that our average hop length, $m$, will be zero. Using this and with some tidying up we can use (6.4.5) to derive a formula for the function $p(a, b)$ in our model

$$p(a, b) = \frac{a^{n-1} d^\frac{n}{2}}{2^n \Gamma(\frac{n}{2})(\pi C)^{\frac{n}{2}}} \exp \left[ -\frac{a}{2} \left( \frac{b^2}{C} + d \right) \right]. \quad (6.4.6)$$

6.5 Stability analysis of the two-species model

Here we perform a stability analysis of our two-species model. We want the flat bed to be unstable to small perturbations so that we see ripples develop. As we are only interested in the beginning stages of the ripple evolution with small perturbations, we are only interested in the regime where $0 < |\nabla h|^2 < \tan^2 \alpha$ so we only need look at the $\lambda \rho (|\nabla h|^2 - \tan^2 \alpha) \left( \frac{\tan^2 \gamma}{|\nabla h|^2} \right)^{-1}$ and the $\kappa \nabla^2 h$ (which smoothes the surface by filling in hollows and 'eroding' bumps) part of the transfer term. Thus our model equations are

$$h_t = D_h \nabla^2 h - \frac{\lambda \rho (|\nabla h|^2 - \tan^2 \alpha)}{\sqrt{\tan^2 \gamma - |\nabla h|^2}} + \kappa \nabla^2 h - N(x, y, t) \quad (6.5.1)$$

$$\rho_t = D_\rho \nabla^2 \rho + \chi \left\{ \rho h_x + (\rho h_y)_y \right\} + \frac{\lambda \rho (|\nabla h|^2 - \tan^2 \alpha)}{\sqrt{\tan^2 \gamma - |\nabla h|^2}} - \kappa \nabla^2 h$$

$$+ \int_a \int_b p(a, b) N(x - a, y - b, t) \, da \, db, \quad (6.5.2)$$

where

$$N(x, y, t) = \frac{J h_x \cos \theta + h_y \sin \theta + \tan \beta}{(1 + h_x^2 + h_y^2)^{1/2}} \quad (6.5.3)$$

and where $J = a_y I \bar{J} \cos \beta$. We can find spatially uniform steady states by setting all derivatives to zero. This gives, from both equations,

$$\lambda \rho \frac{\tan^2 \alpha}{\tan \gamma} - J \tan \beta = 0 \quad \Rightarrow \quad \rho = \frac{J \tan \beta \tan \gamma}{\lambda \tan^2 \alpha} = \rho_c$$

and $h$ can be any constant, which we define as $h_c$. We now perturb the steady states by setting

$$h = h_c + \tilde{h}, \quad \rho = \rho_c + \tilde{\rho}.$$

To simplify the model we expand out the bottom half of (6.5.3). Dropping the tildes and linearising in $h$ and $\rho$ gives

$$(1 + h_x^2 + h_y^2)^{1/2} = 1 + O(h_x^2, h_y^2) = 1.$$
Thus

\[ N(x, y, t) = J \left( h_x \cos \theta + h_y \sin \theta + \tan \beta \right). \]

Taylor expanding the integrand in (6.5.2) to third order gives us

\[
\int_a^b \int_b^a p(a, b) N(x - a, y - b, t) \, da \, db = - N(x, y, t) \int_a^b \int_b^a \frac{\partial N}{\partial x} (x, y, t) \, da \, db + \frac{1}{2} \left\{ \frac{\partial^2 N}{\partial x^2} (x, y, t) \int_a^b \int_b^a a^2 p(a, b) \, da \, db \right\} \\
- 2 \frac{\partial^2 N}{\partial x \partial y} (x, y, t) \int_a^b \int_b^a a b p(a, b) \, da \, db \int_b^a \int_b^a b^2 p(a, b) \, da \, db \right\} \\
- \frac{1}{6} \left\{ \frac{\partial^3 N}{\partial x^3} (x, y, t) \int_a^b \int_b^a a^3 p(a, b) \, da \, db + 3 \frac{\partial^3 N}{\partial x^2 \partial y} (x, y, t) \int_a^b \int_b^a a^2 b p(a, b) \, da \, db \right\} \\
+ 3 \frac{\partial^3 N}{\partial x \partial y^2} (x, y, t) \int_a^b \int_b^a a b^2 p(a, b) \, da \, db \right\} \\
+ \frac{\partial^3 N}{\partial y^3} (x, y, t) \int_a^b \int_b^a b^3 p(a, b) \, da \, db \right\},
\]

which from the definitions of probability distributions (5.2.5) and (5.2.6) gives

\[
\int_a^b \int_b^a p(a, b) N(x - a, y - b, t) \, da \, db = - \frac{1}{6} \left\{ \frac{\partial^3 N}{\partial x^3} + 3 \frac{\partial^2 N}{\partial x \partial y^2} + 3 \frac{\partial^2 N}{\partial y^2} + \frac{\partial^3 N}{\partial y^3} \right\} N(x, y, t).
\]

We can simplify the calculations by setting the wind to be in the \( x \) direction. Therefore \( \theta = 0 \) and consequently \( \tan(\theta) = 0 \). Also we will expect the number of grains hopping to one side of the \( x \) axis to equal the number hopping to the other side, as we have no bias towards one side or the other. So we expect the average reptation length in the \( y \) direction to be zero, i.e. \( \bar{b} = 0 \). Consequently we expect all expectations containing odd powers of \( b \) (\( ab \), \( a^2 \bar{b} \) and \( \bar{b}^3 \)) to be zero as well. Taking this into account and substituting for \( N \) from equation (6.5.3) gives us

\[
\int_a^b \int_b^a p(a, b) N(x - a, y - b, t) \, da \, db = \frac{1}{2} \left\{ \frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} + \frac{\partial^3 N}{\partial x^3} + 3 \frac{\partial^2 N}{\partial x \partial y} + 3 \frac{\partial^2 N}{\partial y^2} + \frac{\partial^3 N}{\partial y^3} \right\} N(x, y, t).
\]

If we were to define the probability density function \( p(a, b) \) by (6.4.6) then we could use this to work out the expectations.
From equation (6.5.1) we find

$$h_t = D_h \nabla^2 h - \lambda (\rho_c + \rho) \frac{|\nabla h|^2 - \tan^2 \alpha}{\sqrt{\tan^2 \gamma - |\nabla h|^2}} + \kappa (\rho_c + \rho) \nabla^2 h - J (h_x + \tan \beta),$$

By setting $\tilde{\lambda} = \lambda (\tan \gamma)^{-1}$, dropping the tilde and linearising we get

$$h_t = D_h \nabla^2 h + \lambda \rho \tan^2 \alpha + \kappa \rho_c \nabla^2 h - J h_x. \quad (6.5.5)$$

From equation (6.5.2) we have

$$\rho_t = D_\rho \nabla^2 \rho + \chi \{ (\rho_c + \rho) (h_{xx} + h_{yy}) + (\rho_c + \rho) \rho h_x + (\rho_c + \rho) \rho h_y \}$$

$$+ \lambda (\rho_c + \rho) \frac{|\nabla h|^2 - \tan^2 \alpha}{\sqrt{\tan^2 \gamma - |\nabla h|^2}} - \kappa (\rho_c + \rho) \nabla^2 h + N^*(h),$$

which after linearising and cancelling terms gives

$$\rho_t = D_\rho \nabla^2 \rho + \chi \rho_c \{ h_{xx} + h_{yy} \} - \lambda \rho \tan^2 \alpha - \kappa \rho_c \nabla^2 h + N^*(h). \quad (6.5.6)$$

Now we try solutions of the form

$$h = h^* e^{\sigma t + ikx + ily}, \quad \rho = \rho^* e^{\sigma t + ikx + ily},$$

where $\sigma$ is the growth rate and $(k, l)$ is the wavevector. From equations (6.5.1) and (6.5.2) we find

$$\sigma h^* = -D_h (k^2 + l^2) h^* + \lambda \tan^2 \alpha \rho^* - \kappa \rho_c (k^2 + l^2) h^* - Jkh^*$$

$$\sigma \rho^* = -D_\rho (k^2 + l^2) \rho^* - \chi \rho_c (k^2 + l^2) h^* - \lambda \tan^2 \alpha \rho^* + \kappa \rho_c (k^2 + l^2) h^*$$

$$+ J \left\{ ikh^* + \bar{a}k h^* + \frac{1}{2} \left( -\bar{a}^3 ik^3 h^* - \bar{b}^2 ikl^2 h^* \right) + \frac{1}{6} \left( \bar{a}^3 k^4 h^* + \bar{a} \bar{b}^2 k^2 l^2 h^* \right) \right\},$$

where we have cancelled a factor of $e^{\sigma t + ikx + ily}$. Rearranging gives

$$\sigma h^* = -(D_h + \kappa \rho_c) (k^2 + l^2) h^* - Jkh^* + \lambda \rho^* \tan^2 \alpha \quad (6.5.7)$$

$$\sigma \rho^* = -(D_\rho \rho^* + (\chi - \kappa) \rho_c h^*) (k^2 + l^2) - \lambda \rho^* \tan^2 \alpha + N^*(h^*), \quad (6.5.8)$$

where

$$N^*(h^*) = J k \left( i + \bar{a}k - \frac{\bar{a}^2 k^2}{2} i - \frac{\bar{b}^2 l^2}{2} i - \frac{\bar{a}^3 k^3}{6} - \frac{\bar{a} \bar{b}^2 k^2 l^2}{2} \right) h^*. $$

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Equations (6.5.7) and (6.5.8) can be put into matrix form

\[
\begin{pmatrix}
\sigma + Jk \iota + (D_h + \kappa \rho_c)(k^2 + l^2) & -\lambda \tan^2 \alpha \\
(\chi - \kappa)\rho_c(k^2 + l^2) - N^*(h^*) & \sigma + \lambda \tan^2 \alpha + D_p(k^2 + l^2)
\end{pmatrix}
\begin{pmatrix}
h^* \\
\rho^*
\end{pmatrix}
= 0.
\]

(6.5.9)

For non-trivial solutions the determinant of this matrix must be zero. We find that the determinant of (6.5.9) is

\[
\left(\sigma + Jk \iota + (D_h + \kappa \rho_c)(k^2 + l^2)\right)\left(\sigma + \lambda \tan^2 \alpha + D_p(k^2 + l^2)\right) + \lambda \tan^2 \alpha
\]

\[
= 0.
\]

(6.5.10)

We are clearly going to have an imaginary part to our eigenvalues. Thus we will have a travelling wave solution. We want this solution to be unstable, so that we see growing waves. Thus we want the real part of \( \sigma \) to be greater than zero. Assuming \(|k|, |l| \ll 1\), then to order one we have a growth rate eigenvalue associated with the relaxation of the flowing grain density \( \rho \) to its equilibrium value. Thus (6.5.10) reduces to \( \sigma(\sigma + \lambda \tan^2 \alpha) \) and so \( \sigma = -\lambda \tan^2 \alpha \) for a nonzero solution. To find the second eigenvalue we first take \( \sigma \) to be \( O(k^2) \) in (6.5.10) and extract all the terms of order \( k^2 \) or \( l^2 \) and solve for \( \sigma \), which gives us

\[
\sigma_0 = (J\bar{a} - D_h - \chi \rho_c)k^2 - (D_h + \chi \rho_c)l^2.
\]

We then set \( \sigma = \sigma_0 + \tilde{\sigma} \) where \( \tilde{\sigma} \) is \( O(k^3) \), extract all the terms of order \( k^3 \) or \( l^3 \) and solve for \( \tilde{\sigma} \), which gives us

\[
\sigma_1 = -\left(\frac{J(J\bar{a} + D_p - D_h - \chi \rho_c)}{\lambda (\tan(\alpha))^2} + \frac{J\bar{a}^2}{2}\right)ik^3 - \left(\frac{J(D_p - D_h - \chi \rho_c)}{\lambda (\tan(\alpha))^2} + \frac{Jb^2}{2}\right)ik^2.
\]

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Then we set $\sigma = \sigma_0 + \sigma_1 + \tilde{\sigma}$ where $\tilde{\sigma}$ is $O(k^4)$, extract all the terms of order $k^4$ or $l^4$ and solve for $\tilde{\sigma}$, to give

$$
\sigma_2 = -\left(\frac{J\alpha^3}{6}\right)k^4 + \left\{\frac{J^2(D_h + \chi \rho_c - D_p - J\alpha)}{\lambda^2 (\tan(\alpha))^4} - \frac{(D_h + \chi \rho_c - D_p)(\chi - \kappa)\rho_c - J\alpha(D_h + (2\chi - \kappa)\rho_c - D_p) + J^2\alpha^2 + \frac{1}{2}J^2\alpha^2}{\lambda(\tan(\alpha))^2} + \frac{J^2(D_h + \chi \rho_c - D_p)}{\lambda^2 (\tan(\alpha))^4} + 2\frac{(D_h + \chi \rho_c - D_p)(\chi - \kappa)\rho_c - J\alpha(D_h + (2\chi - \kappa)\rho_c - D_p) + \frac{1}{2}J^2\alpha^2}{\lambda(\tan(\alpha))^2} - \frac{J\alpha\beta}{2}\right\}k^4 l^2
$$

Thus the expression for our growth rate is the sum of the above three expressions, $\sigma = \sigma_0 + \sigma_1 + \sigma_2$. However we are only interested in the real part so it reduces to

$$
\sigma = (J\alpha - D_h - \chi \rho_c)k^2 - (D_h + \chi \rho_c)l^2 - \frac{J\alpha^3}{6}k^4 + \left\{\frac{J^2(D_h + \chi \rho_c - D_p - J\alpha)}{\lambda^2 (\tan(\alpha))^4} - \frac{(D_h + \chi \rho_c - D_p)(\chi - \kappa)\rho_c - J\alpha(D_h + (2\chi - \kappa)\rho_c - D_p) + J^2\alpha^2 + \frac{1}{2}J^2\alpha^2}{\lambda(\tan(\alpha))^2} + \frac{J^2(D_h + \chi \rho_c - D_p)}{\lambda^2 (\tan(\alpha))^4} + 2\frac{(D_h + \chi \rho_c - D_p)(\chi - \kappa)\rho_c - J\alpha(D_h + (2\chi - \kappa)\rho_c - D_p) + \frac{1}{2}J^2\alpha^2}{\lambda(\tan(\alpha))^2} - \frac{J\alpha\beta}{2}\right\}k^4 l^2
$$

which we can write as

$$
\text{Re}(\sigma) = A_2k^2 + B_2l^2 + C_2k^4 + D_2k^2l^2 + E_2l^4,
$$

(6.5.11)
where

\[ A_2 = \frac{J\bar{a} - D_h - \chi \rho_c}{\lambda (\tan(\alpha))^2}, \quad (6.5.12) \]

\[ B_2 = -\frac{(D_h + \chi \rho_c)}{\lambda (\tan(\alpha))^2}, \quad (6.5.13) \]

\[ C_2 = \frac{(D_h + \chi \rho_c - D_p)(\chi - \kappa) \rho_c - J\bar{a}(D_h + (2\chi - \kappa)\rho_c - D_p) + \frac{1}{2} J^2 a^2}{\lambda (\tan(\alpha))^2} \]

\[ + \frac{J^2 (D_h + \chi \rho_c - D_p - J\bar{a}) - \frac{Ja^3}{6}}{\lambda^2 (\tan(\alpha))^4}, \quad (6.5.14) \]

\[ D_2 = \frac{2(D_h + \chi \rho_c - D_p)(\chi - \kappa) \rho_c - J\bar{a}(D_h + 2\chi \rho_c - \kappa \rho_c - D_p) + \frac{1}{2} J^2 b^2}{\lambda (\tan(\alpha))^2} \]

\[ + \frac{J^2 (D_h + \chi \rho_c - D_p) - \frac{Ja b^2}{2}}{\lambda^2 (\tan(\alpha))^4}, \quad (6.5.15) \]

\[ E_2 = \frac{(D_h + \chi \rho_c - D_p)(\chi - \kappa) \rho_c}{\lambda (\tan(\alpha))^2}, \quad (6.5.16) \]

where all terms are positive. To find the fastest growing mode we maximise the real part of (6.5.11) over \( k \) and \( l \)

\[ \frac{\partial \sigma}{\partial k} = 2k(A_2 + 2C_2 k^2 + D_2 l^2) = 0, \quad (6.5.17) \]

\[ \frac{\partial \sigma}{\partial l} = 2l(B_2 + D_2 k^2 + 2E_2 l^2) = 0. \quad (6.5.18) \]

We must have that our wavenumbers are positive \((k, l > 0)\). From these equations we can see that we have four possible types of solution, i) \( k = l = 0 \), ii) \( k = 0, l \neq 0 \), iii) \( k \neq 0, l = 0 \), iv) \( k \neq 0, l \neq 0 \). In order for our solutions to be a maximum they must satisfy the following criteria

\[ \frac{\partial^2 \sigma}{\partial k^2} = 12C_2 k^2 + 2A_2 + 2l^2 D_2 < 0, \quad (6.5.19) \]

\[ \frac{\partial^2 \sigma}{\partial l^2} = 12E_2 l^2 + 2B_2 + 2D_2 k^2 < 0, \quad (6.5.20) \]

\[ \frac{\partial^2 \sigma}{\partial k^2} \frac{\partial^2 \sigma}{\partial l^2} - \left( \frac{\partial^2 \sigma}{\partial k \partial l} \right)^2 = (12C_2 k^2 + 2A_2 + 2l^2 D_2)(12E_2 l^2 + 2B_2 + 2D_2 k^2) \]

\[ -16D_2 k^2 l^2 > 0. \quad (6.5.21) \]

Case i) is straightforward and gives a zero growth rate. Looking at the maximum conditions \((6.5.19, 6.5.20, 6.5.21)\) for i), we see that they reduce to

\[ 2A_2 < 0, \quad (6.5.22) \]

\[ 2B_2 < 0, \quad (6.5.23) \]

\[ 4A_2 B_2 > 0. \quad (6.5.24) \]
From (6.5.13) we can see that $B_2$ will always be negative and so (6.5.23) is satisfied. Now if $A_2$ is negative it automatically follows that (6.5.24) will be satisfied and if it is positive then it will not be. Thus the only condition we need to consider is (6.5.22). Therefore the solution $k = l = 0$ will be a maximum if and only if

$$J\tilde{a} < D_h + \chi \rho_c,$$

(6.5.25)

which gives us a threshold value below which no ripples will form. For case ii), we know that $k = 0$, so we can put this into (6.5.18) to get

$$4E_2l^3 + 2B_2l = 0 \implies l = 0, \pm \sqrt{-\frac{B_2}{2E_2}}.$$

If $k = 0$ and $l = 0$ we get solution i). $B_2$ is negative so if $E_2$ is negative then the square root will be negative and thus both solutions will be imaginary and thus invalid. If $E_2$ is positive then we must have solution ii). However looking at the maximum conditions for ii) we see that they reduce to

$$2A_2 - \frac{B_2D_2}{E_2} < 0,$$

(6.5.26)

$$-4A_2 < 0,$$

(6.5.27)

$$-\left(2A_2 - \frac{B_2D_2}{E_2}\right)4B_2 > 0$$

(6.5.28)

and as we know that $B_2$ is negative (6.5.27) must be positive and so ii) can not be a maximum.

For iii) we know that $l = 0$ and so we can put this into (6.5.17) to get

$$0 = 4C_2k^3 + 2A_2k \implies k = 0, \pm \sqrt{-\frac{A_2}{2C_2}}.$$

If $l = 0$ and $k = 0$ we get solution i). Looking at the maximum conditions for iii) we see that

$$-4A_2 < 0,$$

(6.5.29)

$$2B_2 - \frac{D_2A_2}{C_2} < 0,$$

(6.5.30)

$$-4A_2 \left(2B_2 - \frac{D_2A_2}{C_2}\right) > 0.$$  

(6.5.31)

Note that (6.5.31) will be satisfied if (6.5.29) and (6.5.30) are. We can see from (6.5.29) that $A_2 > 0$. This means that $C_2$ must be negative for $k$ to be a real
positive wavenumber. We also know that \( B_2 \) is negative and so for (6.5.30) to hold we must satisfy the inequality
\[
D_3 < \frac{2B_2C_2}{A_2}.
\] (6.5.32)

For iv) we know that both \( k \) and \( l \) do not equal zero. Therefore the terms in the brackets of (6.5.18) and (6.5.17) must equal zero
\[
(A_2 + 2C_2k^2 + D_2l^2) = 0 \\
(B_2 + D_2k^2 + 2E_2l^2) = 0.
\]

Solving these two equations simultaneously we get that
\[
k^2 = \frac{D_2B_2 - 2E_2A_2}{4C_2E_2 - D_2^2} > 0 \quad \text{(6.5.33)}
\]
\[
l^2 = \frac{A_2D_2 - 2C_2B_2}{4C_2E_2 - D_2^2} > 0 \quad \text{(6.5.34)}
\]
So we have four solutions for \( k \) and \( l \), as we are looking for nonnegative solutions only, we will only want the positive roots of \( k \) and \( l \).

Looking at the maximum conditions, (6.5.19,6.5.20,6.5.21), we see that we can rewrite them as
\[
2(2C_2k^2 + A_2 + D_2l^2) + 8C_2k^3 < 0, \quad \text{(6.5.35)}
\]
\[
2(D_2k^2 + B_2 + 2E_2l^2) + 8E_2l^2 < 0, \quad \text{(6.5.36)}
\]
\[
(2(2C_2k^2 + A_2 + D_2l^2) + 8C_2k^3)(2(D_2k^2 + B_2 + 2E_2l^2) + 8E_2l^2) - 16D_2k^2l^2 > 0. \quad \text{(6.5.37)}
\]

The brackets in (6.5.35) and (6.5.36) are the same as the brackets in (6.5.17) and (6.5.18) and we know that for case iv) these brackets must equal zero. Therefore the maximum conditions (6.5.19,6.5.20,6.5.21) reduce to
\[
C_2k^2 < 0, \quad \text{(6.5.38)}
\]
\[
E_2k^2 < 0, \quad \text{(6.5.39)}
\]
\[
(4C_2E_2 - D_2^2)k^2l^2 > 0. \quad \text{(6.5.40)}
\]
Thus we see that for (6.5.38) to be negative we need \( C_2 < 0 \) and for (6.5.39) to be negative we need \( E_2 < 0 \). This gives us the condition
\[
\frac{(D_h + \chi \rho_c - D_p)(\chi - \kappa) \rho_c}{\lambda (\tan (\alpha))^2} < 0.
\]
As we expect \( D_h + \chi \rho_c > D_p \) this tells us that \( \chi > \kappa \). For the Jacobian, (6.5.40), to be positive we need to satisfy the condition
\[
D_2^2 < 4C_2E_2 \tag{6.5.41}
\]
Note that \( 4C_2E_2 - D_2^2 \) is the denominator of both wavenumbers in (6.5.33). As this is positive it means that the numerators must also be positive. Therefore, assuming \( A_2 > 0 \), we must also satisfy
\[
\begin{align*}
D_2B_2 - 2E_2A_2 &> 0 \implies D_2 < \frac{2E_2A_2}{B_2} \\
A_2D_2 - 2C_2B_2 &> 0 \implies D_2 > \frac{2C_2B_2}{A_2}
\end{align*}
\]
in order for \( k^2, l^2 > 0 \). This second condition is interesting as it is the reverse inequality of (6.5.32) which was a condition needed for case iii) to be the maximum growth rate. Thus we have the following bounds on \( D_2 \)
\[
\frac{2C_2B_2}{A_2} < D_2 < \frac{2E_2A_2}{B_2} \tag{6.5.42}
\]
We have shown that there exists a threshold value of saltation flux
\[
\frac{D_h + \chi \rho_c}{\bar{a}} = J_c.
\]
If the scaled saltation flux intensity, \( J \), is less than this value then sand ripples will not form from a perturbed flat bed.
If \( J > J_c, C_2 < 0 \) and \( D_2 < D_c \) then sand ripples will form and the maximum growth rate will occur at
\[
(k, l) = \left( \sqrt{-\frac{A_2}{2C_2}}, 0 \right)
\]
and the length of the fastest growing wave is
\[
L = \frac{2\pi}{k} = 2\pi \sqrt{-\frac{2C_2}{A_2}}. \tag{6.5.43}
\]
If \( J > J_c, C_2 < 0, \chi < \kappa \) and (6.5.42) is satisfied then sand ripples will form and the maximum growth rate will occur at
\[
(k, l) = \left( \sqrt{\frac{D_2B_2 - 2E_2A_2}{4C_2E_2 - D_2^2}}, \sqrt{\frac{A_2D_2 - 2C_2B_2}{4C_2E_2 - D_2^2}} \right)
\]
and the length of the fastest growing wave is
\[
L = \frac{2\pi}{\sqrt{k^2 + l^2}} = \frac{2\pi \sqrt{2C_2E_2 - D_2^2}}{\sqrt{A_2(2E_2 - D_2) + B_2(2C_2 - D_2)}}. \tag{6.5.44}
\]
Equations (5.4.1) and (5.4.2) were integrated using a compact finite difference code, [35] with second-order Adams-Bashforth time-stepping and periodic boundary conditions on a $200 \times 200$ grid. All simulations were started from the same perturbed flat bed.

It is necessary to work out which parts of the sand bed are in shadow, as the governing equations for these points differ from those for points not in shadow. A point $(i,j)$ on the sand bed is deemed to be in the shadow zone if a line from this point backwards along the direction of the saltation flux intersects the sand bed. In effect this shows that there is an obstacle between the sand bed at $(i,j)$ and the incoming saltation flux, so that the saltating grain will hit the obstacle and not the point $(i,j)$. If the point $(i,j)$ is deemed to be in the shadow zone then the term $N(i,j)$ representing the number of sand grains ejected per unit time is set to zero, as are the derivatives of $N(i,j)$. The height of the sand bed at points along the line of the saltation flux is calculated using linear interpolation.

A typical simulation is shown in Figure 7.1. The parameters are chosen such that we are above the threshold for ripple growth. Only certain combinations of parameters are important as we can scale space and time. Parameter values are $\theta = 0^\circ, \beta = 10^\circ, J = 5, \alpha = 0.2, \delta = 0, F = 0.1$. The equations are integrated from $t = 0$ to $t = 250,000\Delta t$, where $\Delta t = 7.29 \times 10^{-6}$, starting from a perturbed flat bed with the wind in the $x$ direction. Coarsening occurs through ripple merger, so the ripple wavelength increases over time. We calculate the maximum and minimum height of the sand bed over each ripple. From these values we find the average maximum and average minimum over the whole bed. The average amplitude is then taken to be the difference between these two values. The average maximum is calculated by taking a cross-section of the sand bed along the $x$ axis and finding all the ripple peaks in that cross-section. We then find the mean of these peak heights. This is done for every point $j$ on the $y$ axis to create a vector of 200 mean...
peak heights. Finally we calculate the average of the mean peak heights to get our average maximum over the whole sand bed. We find the average minimum in a similar way and then calculate the average amplitude from these values. For the simulation shown in Figure 7.1 the average amplitude at \( t = 250,000 \Delta t \) is 0.496.

The simulation in Figure 7.1 uses our three-dimensional shadow zone. Figure 7.2 shows a graphical representation of the areas of the sand bed that are in shadow at \( t = 250,000 \Delta t \) and compares it with the areas that would be in shadow if we were to use local shadowing, where the bed is deemed to be in shadow if \( \mathbf{e} \cdot \nabla h < - \tan \beta \). It is clear that the three-dimensional calculation of the shadow zone leads to a significant difference from local shadowing. Our shadow zone covers more of the sand bed, including areas of positive slope, which local shadowing always excludes.

A simulation with the same parameter values but without a shadow zone can be seen in Figure 7.3. We can see that in this simulation the ripples are less broken-up. In this case the average amplitude of the ripples is 0.954 after 250,000\( \Delta t \) which is considerably larger than when we have a shadow zone.

Next we look at simulations where we change the angle of impact, \( \beta \), gradually over time (Figure 7.4). First we change \( \beta \) from 10° to 5°, setting

\[
\beta(t) = 10 - \frac{5t}{t_{\text{max}}},
\]

where \( t \) is time and \( t_{\text{max}} \) is the time it takes for the angle of impact to change fully, which in this simulation we take to be 250,000\( \Delta t \). This results in larger areas of the sand bed being in shadow. Simulations where we change the impact angle from 10° to 8° and from 10° to 1° can also be seen in Figure 7.4. This series shows that as \( \beta \) is decreased the ripple pattern becomes less well defined. Sand ripples are formed because the hopping of sand grains overcomes rolling, thus as no hopping is allowed to occur in the shadow zone we would expect a model with a larger shadow zone to evolve more slowly. Clearly as the angle of impact is decreased more of the sand bed will be likely to be in shadow and so we would expect slower evolution. Indeed looking at the average amplitude of ripples in the simulations we find that it decreases from 0.496 when the final angle of impact, \( \beta_f \), is 10° to 0.379 when \( \beta_f = 8° \), 0.273 when \( \beta_f = 5° \) and finally to 0.126 when \( \beta_f = 1° \).

If simulations are run with \( \beta \) constant, we find the average amplitude of the ripples is 0.0645 at \( \beta = 1° \), 0.252 at \( \beta = 5° \), 0.373 at \( \beta = 8° \) and of course 0.496 at \( \beta = 10° \). As expected the shallower the angle of impact, the lower is the amplitude of the ripples. Comparing with the simulations shown in Figure 7.4 we also see
that when the angle of impact changes over time by a relatively small amount
the resulting ripples tend to be similar in amplitude to ripples that evolve with
$\beta$ constant at the final angle of impact. As the magnitude of the change impact
angle increases the average amplitude becomes increasingly larger than that for the
corresponding simulation with constant $\beta$.

Next we look at the effect of gusts of wind where the angle of impact, $\beta(t)$, is
changed randomly at regular intervals:

$$\beta(t) = \omega_1 \chi(t),$$

where $\chi(t)$ is a real number generated at random from the interval $[0, 1]$ and $\omega_1$ is the
maximum possible angle of impact. Figure 7.5 shows that when the impact angle
of saltating grains is varied randomly to a value between $0^\circ$ and $90^\circ$ every $100\Delta t$
the ripples have much lower amplitude than those in Figure 7.1. Indeed the average
amplitude of the ripples in this case is only 0.0141 which is very small compared
with the amplitude of 0.496 from our first simulation when the angle of impact is
constant at $\beta = 10^\circ$. The ripples are also not as well defined and we can see that
some of the ripples appear to merge together and others peter out. Because the
ripples never reach a sufficiently high amplitude the shadow zone never comes into
effect.

A series of simulations undertaken where $\beta$ gusts between $0^\circ$ and various max-
imum angles is shown in Figure 7.6. From this we can see that in the first two
graphs, where $\omega_1$ is $70^\circ$ and $50^\circ$, the ripples are again quite broken-up but the last
two graphs, where $\omega_1$ is $30^\circ$ and $10^\circ$, show a far more ordered ripple pattern. The
average amplitudes of the ripples in these graphs are 0.0595, 0.227, 0.406 and 0.241
when $\omega_1 = 70^\circ, 50^\circ, 30^\circ$ and $10^\circ$ respectively, which are all lower than the amplitude
for ripples in Figure 7.1, in which the impact angle is constant at $10^\circ$. We can also
see that for large values of $\omega_1$, the amplitude increases as $\omega_1$ decreases. For the
last graph however, when $\omega_1 = 10^\circ$, the average amplitude is 0.241 which is smaller
than the amplitude for $\omega_1 = 30^\circ$. This is because decreasing $\beta$ increases the effect-
tiveness of the saltation flux but also puts more of the surface into shadow. These
two effects are opposing and at shallower angles of impact the shadow zone has the
greater effect, causing the amplitude of the ripples to decrease.

Finally, we compare the case when $\omega_1 = 30^\circ$ with a simulation where $\beta$ is kept
constant at $15^\circ$, the same average value as when $\omega_1 = 30^\circ$. The average amplitude
in the constant case is 0.584 which is larger than that for the gusting simulation
with $\omega_1 = 30^\circ$ suggesting that varying the angle of impact decreases the amplitude of the ripples.

Looking at Figure 7.7 we can see that varying the time interval between changes in $\beta$ has an effect on the resulting ripple pattern. When changing the time interval from $100\Delta t$ to $10,000\Delta t$ we see that both when $\omega_1 = 90^\circ$ and when $\omega_1 = 30^\circ$ the ripples are less well defined when the interval between changes is longer. This effect is more pronounced when $\omega_1 = 90^\circ$ where we can see that when the time between changes is $10,000\Delta t$ the wavelength of the ripples has increased, due to ripple merger, although the average amplitude of the ripples is smaller at 0.00477, as opposed to 0.0141 when the interval is $100\Delta t$. For $\omega_1 = 30^\circ$ with changes every $10,000\Delta t$ the average amplitude is 0.297 which is also smaller than the amplitude of 0.406 when the interval is $100\Delta t$.

Another effect of gusts of wind is to change the wind direction, $\theta(t)$, so we investigate to see what will happen if $\theta(t)$ is changed from $0^\circ$ by some random amount at regular intervals:

$$\theta(t) = 2\omega_2 (\chi(t) - 0.5),$$

where $\chi(t)$ is a real number generated at random from the interval $[0, 1]$ and $\omega_2$ is a constant that corresponds to the maximum deviation of $\theta$ from $0^\circ$. We start off by looking at potentially large gusts of wind, where we vary $\theta$ by some random amount between $\pm 90^\circ$. In this case we notice that when the wind direction is changed at intervals of $100\Delta t$ ripples do not form properly. Figure 7.8 shows that bumps can be distinguished but they are of low amplitude and do not form a coherent ripple across the space. The average amplitude is only 0.00713.

A series of simulations where the wind direction varies through different maximum angles (Figure 7.9), shows that the smaller the change in wind direction the more coherent the ripples appear and the more the simulations look like Figure 7.1, where the wind direction is constant at $\theta = 0^\circ$. The amplitude of the ripples increases as the magnitude of the change of wind direction decreases. The average amplitude for a change of $\pm 70^\circ$ is 0.0156, for $\pm 50^\circ$ it is 0.0714, for $\pm 30^\circ$ it is 0.343 and for $\pm 10^\circ$ it is 0.439, which is close to the average amplitude of 0.496 of the ripple pattern observed under constant wind direction. This shows that small changes in wind direction of around $\pm 10^\circ$ will not affect the ripple pattern too greatly, but in the case of larger fluctuations the ripples can be all but destroyed.

Looking at Figure 7.10 we see that for large changes in wind direction of $\pm 90^\circ$
increasing the interval between changes in wind direction from $100\Delta t$ to $10,000\Delta t$ allows a more noticeable ripple pattern to form although still pretty broken up and of low amplitude: the average amplitude for an interval of $10,000\Delta t$ is 0.0113. Not all the ripples are necessarily lined up with their crests in the current direction of the wind, showing the susceptibility of the ripples to adapt as the direction of the wind changes. This effect is also seen for smaller changes of $\pm 30^\circ$ where when the interval is $10,000\Delta t$ we see that the ripples are inclined at a slight angle to the average direction of the wind. This is because the most recent deviation from this average direction has persisted long enough to turn the ripples round. This is not the case when the interval is $100\Delta t$. The change in time interval does not have a great effect on the average ripple amplitude which is 0.344.

Next we look at the effect of changing the wind direction, $\theta(t)$, from $0^\circ$ to $20^\circ$ gradually over time,

$$\theta(t) = \frac{20t}{t_{\text{max}},}$$

where $t$ is time and $t_{\text{max}}$ is the time it takes for the wind to fully change direction, which in this simulation (Figure 7.11) we take to be 250,000$\Delta t$. The idea behind this is to simulate typical changes experienced in the field during the course of an observation. As expected we find that the ripples evolve with their crests perpendicular to the wind direction but as the wind direction is changing over the period of the simulation the ripples have to keep adapting. We find that the average amplitude of the ripples in this simulation is only 0.437, which is smaller than the value of 0.496 from the simulation in Figure 7.1 where the wind direction is fixed.

We then look at the combined effect of this systematic change of wind direction together with gusting where the saltation flux direction changes randomly. We continue to set the wind direction going from $0^\circ$ to $20^\circ$ over a period of 250,000$\Delta t$, but superimpose changes by some random angle between $\pm 30^\circ$ at intervals of $100\Delta t$, (Figure 7.12). In this case we set the wind direction, $\theta(t)$, to be

$$\theta(t) = \theta_2(t) + \frac{20t}{t_{\text{max}},}$$

where $\theta_2(t) = 40(\chi(t) - 0.5)\chi(t)$ is a real number generated at random from the interval [0, 1]. We find that the random gusts of wind reduce the area of the sand bed that is in shadow at any given time. The average amplitude of the ripples is 0.407, which is greater than that for wind gusting between $\pm 30^\circ$ without a systematic trend, but less than that achieved with the systematic variation alone. The frequency of
the gusts appears to have little effect, however: simulations which change the wind direction every iteration, every 10 iterations, every 100 iterations and every 1000 iterations, all give similar results.

Simulations where we let the ripples evolve for \( t = 250,000 \Delta t \) with the wind set at 0° before then gradually changing the direction of the wind to 20° over the next 250,000 iterations (Figure 7.13) have a noticeably different effect to when we change the wind from the beginning. In this case the ripples start off at the beginning of the wind change with their crests perpendicular to the \( x \) direction and end up rotated and with many defects. This is due to the fact that the ripples need to be broken up before they can start moving round by 20°. Consequently many of the ripples are still perpendicular to the \( x \) direction and are more fragmented. It seems that initially while the ripples are still forming a change in wind direction will quickly have an effect, but once the ripples have formed they are more resistant to change. Also we can see that the areas of the shadow zone are larger and more fragmented in this simulation as the ripples are not perpendicular to the direction of the wind.

Simulations were also conducted where we varied the strength of the saltation flux, \( J \). We found that increasing \( J \) caused the sand ripples to develop faster and the wavelength to shorten (Figure 7.14). However if \( J \) became too big numerical instabilities were introduced. A simulation with \( J = 8 \) only ran until 3,000\( \Delta t \) before numerical instabilities terminated the programme. The average amplitudes taken at 250,000\( \Delta t \) were 0.00161 when \( J = 3 \), 0.0136 when \( J = 4 \), 0.496 when \( J = 5 \) and 0.775 when \( J = 6 \), showing that increasing the saltation flux increases the ripple amplitude. These simulations also showed that if \( J \) was reduced to below the threshold value for saltation flux, \( J_c \) in equation (5.5.18), then ripples would not form.

We have developed a three-dimensional model for aeolian sand ripples largely based on the models by Anderson [4] and Hoyle & Woods [28]. Our model includes a shadow zone that will be effective on positive as well as negative slopes. We have shown analytically that there exists a threshold value, \( J_c \), for the scaled saltation flux above which ripples will develop. Numerical simulations show that for certain parameter values ripples will evolve from a flat bed and given long enough their crests will align perpendicular to the wind direction, in keeping with observations [55]. The presence of a shadow zone causes the ripples to evolve more slowly, since a simulation without a shadow zone run for the same length of time from the same initial conditions results in ripples with higher amplitude. The resulting ripple
Figure 7.1: The simulated sand bed at $t = 2.5 \times 10^5 \Delta t$, where $\Delta t = 7.29 \times 10^{-6}$ with the wind set in the $x$ direction blowing from left to right. Parameter values are $\theta = 0^\circ$, $\beta = 10^\circ$, $J = 5$, $\bar{a} = 0.2$, $\bar{b} = 0$, $F = 0.1$. 
Figure 7.2: Graphical representation of our shadow zone (top) and the shadow zone under local shadowing (bottom) for the simulation in Figure 7.1 at $t = 2.5 \times 10^5 \Delta t$, where $\Delta t = 7.29 \times 10^{-6}$. The pictures are shown at $t = (2.5 \times 10^5 + 1) \Delta t$. Areas in shadow are shaded light grey. The remaining parameter values are, $\theta = 0^\circ$, $J = 5$, $\bar{a} = 0.2$, $\bar{b} = 0$ and $F = 0.1$. 
Figure 7.3: Comparison between a simulation run without a shadow zone (top) and a simulation run with our shadow zone (bottom) at $t = 2.5 \times 10^5 \Delta t$, where $\Delta t = 7.29 \times 10^{-6}$. Parameter values are $\theta = 0^\circ, \beta = 10^\circ, J = 5, \bar{a} = 0.2, \bar{b} = 0, F = 0.1$. 
Figure 7.4: The simulated sand bed at $t = 2.5 \times 10^5 \Delta t$, where $\Delta t = 7.29 \times 10^{-6}$, with $\beta$ changing over time from $10^\circ$ to: a) $\beta$ does not change, b) $8^\circ$, c) $5^\circ$ and d) $1^\circ$ by $t = 2.5 \times 10^5 \Delta t$. The remaining parameter values are $\theta = 0^\circ$, $\alpha = 0.2$, $\beta = 0$, $J = 5$ and $F = 0.1$. 
Figure 7.5: The simulated sand bed at $t = 2.5 \times 10^5 \Delta t$, where $\Delta t = 7.29 \times 10^{-6}$, with $\beta$ randomly varying to angles between $0^\circ$ and $90^\circ$ at intervals of $100\Delta t$. The remaining parameter values are $\bar{a} = 0.2, \bar{b} = 0, J = 5, F = 0.1$. 
Figure 7.6: The simulated sand bed at \( t = 2.5 \times 10^5 \Delta t \), where \( \Delta t = 7.29 \times 10^{-6} \), with \( \beta \) randomly varying at intervals of 100\( \Delta t \) between: a) 0° and 70°, b) 0° and 50°, c) 0° and 30° and d) 0° and 10°. The remaining parameter values are \( a = 0.2, b = 0, J = 5, F = 0.1 \).
Figure 7.7: The simulated sand bed at $t = 2.5 \times 10^5 \Delta t$, where $\Delta t = 7.29 \times 10^{-6}$, with $\beta$ randomly varying between: a) $0^\circ$ and $90^\circ$ at intervals of $100\Delta t$, b) $0^\circ$ and $90^\circ$ at intervals of $10,000\Delta t$, c) $0^\circ$ and $30^\circ$ at intervals of $100\Delta t$ and d) $0^\circ$ and $30^\circ$ at intervals of $10,000\Delta t$. The remaining parameter values are $\bar{a} = 0.2, \bar{b} = 0, J = 5, F = 0.1$. 
Figure 7.8: The simulated sand bed at $t = 2.5 \times 10^5 \Delta t$, where $\Delta t = 7.29 \times 10^{-6}$, with the wind direction varying by $\pm 90^\circ$ at intervals of $100\Delta t$. The average hop lengths in the $x$ and $y$ directions are given by $\bar{a} = \frac{1}{5} \cos(\theta)$ and $\bar{b} = \frac{1}{5} \sin(\theta)$, as $\theta$ varied. The remaining parameter values are $J = 5, F = 0.1$. 
Figure 7.9: The simulated sand bed at $t = 2.5 \times 10^5 \Delta t$, where $\Delta t = 7.29 \times 10^{-6}$, with the wind direction randomly varying at intervals of $100 \Delta t$ between: a) $\pm 70^\circ$, b) $\pm 50^\circ$, c) $\pm 30^\circ$ and d) $\pm 10^\circ$. The average hop lengths in the $x$ and $y$ directions are given by $\bar{a} = \frac{1}{5} \cos(\theta)$ and $\bar{b} = \frac{1}{5} \sin(\theta)$, as $\theta$ varied. The remaining parameter values are $J = 5, F = 0.1$. 
Figure 7.10: The simulated sand bed at $t = 2.5 \times 10^5 \Delta t$, where $\Delta t = 7.29 \times 10^{-6}$, with the wind direction varying between: a) $\pm 90^\circ$ at intervals of $100\Delta t$, b) $\pm 90^\circ$ at intervals of $10,000\Delta t$, c) $\pm 30^\circ$ at intervals of $100\Delta t$ and d) $\pm 30^\circ$ at intervals of $10,000\Delta t$. The average hop lengths in the $x$ and $y$ directions are given by $\bar{a} = \frac{1}{5} \cos(\theta)$ and $\bar{b} = \frac{1}{5} \sin(\theta)$, as $\theta$ varied. The remaining parameter values are $J = 5, F = 0.1$. 
Figure 7.11: The simulated sand bed at $t = 2.5 \times 10^5 \Delta t$, where $\Delta t = 7.29 \times 10^{-6}$, with the wind direction changing from $0^\circ$ to $20^\circ$, over the period $0 \leq t \leq t_{\text{max}}$ where $t_{\text{max}} = 2.5 \times 10^5 \Delta t$. The average hop lengths in the $x$ and $y$ directions are given by $\bar{a} = \frac{1}{5} \cos(\theta)$ and $\bar{b} = \frac{1}{5} \sin(\theta)$, as $\theta$ varied. The remaining parameter values are $J = 5, F = 0.1$. 

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Figure 7.12: The simulated sand bed at $t = 2.5 \times 10^5 \Delta t$, where $\Delta t = 7.29 \times 10^{-6}$, with the wind direction changing from $0^\circ$ to $20^\circ$ at $t = 2.5 \times 10^5 \Delta t$ and random wind changes to angles between $\pm 30^\circ$ at intervals of $100 \Delta t$. The average hop lengths in the $x$ and $y$ directions are given by $\bar{a} = \frac{1}{5} \cos(\theta)$ and $\bar{b} = \frac{1}{5} \sin(\theta)$, as $\theta$ varied. The remaining parameter values are $J = 5$, $\bar{a} = \frac{1}{5} \cos(\theta)$, $\bar{b} = \frac{1}{5} \cos(\theta)$, $F = 0.1$. 
Figure 7.13: The simulated sand bed at $t = 5 \times 10^5 \Delta t$, where $\Delta t = 7.29 \times 10^{-6}$, with the wind direction changing from $0^\circ$ to $20^\circ$ after $t = 2.5 \times 10^5 \Delta t$ for $t = 2.5 \times 10^5 \Delta t$. The average hop lengths in the $x$ and $y$ directions are given by $\bar{a} = \frac{1}{2} \cos(\theta)$ and $\bar{b} = \frac{1}{5} \sin(\theta)$, as $\theta$ varied. The remaining parameter values are $J = 5, \bar{a} = \frac{1}{5} \cos(\theta), \bar{b} = \frac{1}{5} \cos(\theta), F = 0.1$. 
Figure 7.14: Pictures of the sand bed at \( t = 2.5 \times 10^5 \Delta t \), where \( \Delta t = 7.29 \times 10^{-6} \) with varying saltation flux intensities. The values of saltation flux are a) \( J = 3 \), b) \( J = 4 \), c) \( J = 5 \), d) \( J = 6 \). The remaining parameter values were \( \theta = 0^\circ, \beta = 10^\circ, a = 0.2, b = 0, F = 0.1 \).
pattern when the shadow zone is incorporated is also more broken-up. We see that the shadow zone in our model will extend past the lee slope if need be, which is useful for modelling the effect of changes in the wind direction as observed in the field. Our simulations show that such changes will disturb the evolution of ripples and lead to a more disordered pattern. The extent of the disorder will depend on the magnitude and frequency of changes in wind direction. A gradual change in the direction of the wind will break up an ordered ripple pattern and eventually lead to a new pattern with the crests perpendicular to the final wind direction. Continuing changes in wind direction will lead to disorder or lower amplitude ripples depending on the frequency and magnitude of the change. We also observed a similar disorder with variation of the angle of impact. We plan to develop our model further to consider megaripples, made up of two different sizes of grains, which can extend to wavelengths of 20m with heights of tens of centimeters. Megaripples are highly irregular and the effect of fully three-dimensional shadowing is likely to be important in developing accurate models.
In this thesis we have investigated ways of modelling the phenomenon of blowfly strikes through the use of various delay differential equations generally with the aim of finding conditions for the extinction of the blowfly species, which would be beneficial to farmers. We have found through linear and global stability analysis of these models that extinction can often be achieved by effective trapping. How effective the trapping must be depends on the conditions we have established, which often depend on the birth and death rates of the species. However our models are by no means exhaustive and it may be beneficial to adapt them in various ways. For example in the system (2.2.1,2.2.2,2.2.3) it may be useful to model the death rate of the sheep by the term $\gamma_s u_s(t)N(t)$ instead of $\gamma_s u_m(t)N(t)$. Also the assumption that the birth rate is proportional to $N$ is itself a questionable assumption if $N$ is very large, but the birth rate could be of the form $b(u_m(t))B(N(t))$ for a function $B(N(t))$ that tends to a constant for large $N$. Another way to address this would be to restrict the initial conditions for $N$ from (2.2.4) to be no greater than the carrying capacity, which in our case 1 as the model has been nondimensionalised. Thus we have that $\phi_N(s) \in (0,1), \ s \in [-\tau,0]$. Therefore $N$ will never exceed the carrying capacity and so the formula for the birth rate will hold.

Our models were not dependent on temperature, but it has been observed [31] that blowfly strikes are less likely in mid summer as the hot dry conditions can dessiccate eggs and flies reducing the risk of a strike, suggesting that climatic conditions could be an important factor in the prevalence of blowfly strikes. It may also be interesting to look at the effect of including a non-linear trapping term as there are many different ways used to control blowfly strikes and while many are effective some have serious side effects, such as the use of chemicals leaving residues in the wool [32]. Also it has been observed that a combination of preventative measures can be more effective, for example mulesing, shearing and crutching [32]. Thus a multiple regression model, such as equation (2.1.1), used by Wall et. al. may be
used to model the combined effect of different methods.

Another preventative measure that is not discussed in this thesis is the idea of 'Sterile Male Blowfly Release'. This involves releasing sterile male blowflies into the population with the aim that the females, who only mate a few times in their short life, will mate with these sterile males and thus not produce any eggs. This process has a history of success, for example the screwworm was removed from North America and the tsetse fly from Zanzibar. The sterile release method can be modelled mathematically by reducing the birth function by a factor of $f/(f + n)$, where $f$ and $n$ are the numbers of fertile and sterile individuals, respectively [18]. However [18] warn that, according to their model, which is not specifically for blowfly strikes, it may be unwise to use the sterile release method if predation is virulent as the number of sterile insects needed to be released to control the population increases with the level of predation.

Another area of interest would be to carry out more extensive numerical simulations. We have looked at simple two dimensional simulations of the systems (2.2.1, 2.2.2, 2.2.3) and (2.5.1, 2.5.2, 2.5.3), but these could be extended to more realistic three dimensional models. Also simulations of a model with distributed delay would be interesting, where the sheep and immature blowflies would be allowed to diffuse.

It may also be useful to address the diffusion more realistically. In this thesis we have only allowed for Fickian diffusion, which says that the species diffuse in the form of a random walk, i.e. with no real thought. However it is more likely in reality that the species will move with a purpose. For example the mature blowflies are more likely to move to areas where there are more sheep. This is particularly relevant in the case where the mature blowflies obey homogeneous Dirichlet boundary conditions and can not exist on the boundary of the domain but the sheep obey homogeneous Neumann boundary conditions and can. In this case it is unlikely that sheep existing on the boundary will voluntarily decide to move back to an area when they are in danger and thus will aggregate on the boundary even when allowed to diffuse.

Further work could also be carried out in the area of travelling wave solutions, which can model a wave of invasion of the blowfly across an entire country or continent. An individual blowfly typically only flies a few miles in its life, but it only has to lay eggs somewhere other than where it matures in order to initiate a wave of invasion which might move relatively slowly but could easily cover an entire continent in the full-
ness of time. We have not rigorously proved the existence of such a wave of invasion in this thesis, but we have done some linearised analysis to determine the possible speeds of invasion, based on the criteria that the travelling front must be positive everywhere (2.8.1,2.8.2,2.8.3). Such a linearised analysis yields a semi-infinite interval of possible invasion speeds, and we are acting on the assumption that ecologically realistic initial data would evolve to a wave travelling at the minimum speed. We have not proved rigorously in this thesis that this is what actually happens. We have, however, determined an upper bound on the minimum speed (2.8.19) which offers us some insight into its dependence on the ecological parameters such as the maturation delay. A rigorous proof of the existence of a wave-front solution along with an analytical calculation of its stability properties could be an area for future research, although investigations of this kind can be very difficult even for reaction-diffusion models without delay. Even in Fisher’s equation $u_t = D u_{xx} + u(1 - u)$ it is quite difficult to rigorously prove the stability properties of the travelling wave fronts though it is known that, in this equation, evolution to anything other than the minimum speed $c_{min} = 2 \sqrt{D}$ requires severe restrictions on the initial data.

Another aspect we have not considered in this thesis is advection of the mature blowfly population. This is likely to be relevant as mature blowflies are generally quite small and their movement could easily be influenced by sudden gusts of relatively strong wind. This could be modelled by a first derivative term coupled with a coefficient to measure the speed of the advection.

Another area for future work would be to extend system (2.2.1,2.2.2,2.2.3) to include state-dependent time delay, so that $\tau$ is an increasing function of the total population of both the immature and mature blowflies $\tau(u)$, $u = u_i + u_m$. This modification will mean that the maturation time will depend on $u$, the total population of blowflies, such that the larger $u$ becomes the longer the larva take to mature. This seems like a likely scenario as the larva must feed off the sheep to grow and eventually mature. If there is a large number of individuals competing for the same food source it will take them longer to get enough and thus their maturation time would increase. The more mature blowflies there are, the more likely it is that there will be a large number of competing larva.

It might also be interesting to categorise the sheep as to whether they are susceptible or not. It is well known [63] that a clean healthy sheep is less likely to be infected than one that is not, for example the smell of an open wound or faeces will attract the mature blowfly. These sheep will then become less susceptible again if
they are treated by the farmer. Therefore it might be appropriate to model treated, susceptible and infected sheep by separate equations, as is done for epidemic models such as those used to model rabid foxes or the spread of tuberculosis. This method could also incorporate the idea of vaccinating the sheep against blowfly strike [12].

Overwintering is another aspect we have not looked at much in this thesis. We produced one numerical simulation, Figure 2.21, and equation (2.9.1) suggested a very simple way that this might be modelled. The length of the overwintering phase is dependent on soil temperature [31] which perhaps should be the defining factor in the length of the overwintering phase, as if there are climatic differences over the domain then the overwintering flies will emerge at different times at different points in space. Also no analytical work was done to see how this may effect the extinction criteria.

In our work on aeolian sand ripples we are interested in the behaviour of the system above the threshold value of saltation flux, when sand ripples will develop from an initially perturbed flat bed, and the effects of our three dimensional shadow zone on the evolution of ripples. In this instance we do not expect the exact form of the smoothing terms to be critical to the behaviour of the system. However below threshold it is acknowledged that they may have more of an effect as in the case where there is no reptation our model predicts a flattening of any surface when actually there should be no change in surface elevation. Thus it may be useful to modify the way we model the rolling grains in (5.4.1), to include dependence on wind drag.

In the derivation of our model (5.4.1,5.4.2) we use a Taylor expansion truncated at first order which inevitably means that we lose some information about the system, in this case some nonlocal effects of hopping. While we consider that these effects are minimal it might be interesting to see what would happen if we retained them. We also note that the hyperdiffusion term (5.3.10) that we include to model small scale cut-off induced by phenomena such as surface roughness and intergrain collisions ends up influencing the maximum growth rate and corresponding wavelength, (5.5.19). While we consider that nonlinear effects such as coarsening will rapidly become more important such that the short scale cut-off will not influence the long term development of ripples, it would be interesting to investigate whether the choice of cut-off affects ripple characteristics and if so how.

We have produced numerical simulations of our one species model of aeolian sand ripples (5.4.1,5.4.2) which show the evolution of ripples from a perturbed flat bed
and have investigated the effect of varying certain parameters. However it would also be interesting to investigate numerically our three dimensional two-species model of aeolian sand ripples (6.2.13). Furthermore, the connection between coarsening and shadowing is the subject of much debate and a satisfactory resolution of the issue requires further detailed study in future works.

We plan to develop our models for aeolian sand ripples (5.4.1, 5.4.2), (6.2.13) further to consider megaripples, made up of two different sizes of grains, which can extend to wavelengths of 20m with heights of tens of centimeters. Megaripples are highly irregular and the effect of fully three-dimensional shadowing is likely to be important in developing accurate models.
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