

# Do travelling band solutions describe cohesive swarms? An investigation for migratory locusts

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**Abstract.** We explore several hypotheses for the swarming behaviour in locusts, with a goal of understanding how swarm cohesion can be maintained by the huge population of insects (up to  $10^9$  individuals) over long distances (up to thousands of miles) and long periods of time (over a week). The mathematical models that correspond to such hypotheses are generally partial differential equations that can be analysed for travelling wave solutions. The nature of a swarm (and the fact that it contains a finite number of individuals) mandates that we seek travelling band (pulse) solutions. However, most biologically reasonable models fail to produce such ideal behaviour unless unusual and unrealistic assumptions are made. The failure of such models, general difficulties encountered with similar models of other migratory phenomena, and possible approaches to alleviate these problems are described and discussed.

**Key words:** Travelling band solutions – Swarm migration – Locust swarms

## 1 Introduction

Social aggregations such as swarms, herds, schools, and flocks are known to have profound consequences for basic ecological processes such as predation, reproduction, and disease transmission. The effects of sociality, its associated evolutionary costs and benefits, and the mechanics of how social groups assemble and operate in nature are the subjects of a large body of biological

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and mathematical literature. However, social interactions are inherently difficult to approach experimentally, so our knowledge of how organisms interact in social groups is incomplete. Furthermore, from a theoretical perspective, social interactions involve highly non-linear interactions between numerous individuals. Making tractable mathematical descriptions of these behaviours raises profound and interesting theoretical challenges.

We are particularly interested in exploring the phenomenon of locust plagues. Locusts are known for their remarkable and devastating swarms, and their ability to migrate over long distances as a single coherent unit. The internal motions of the individuals in the swarm are not completely understood, but it appears that under many circumstances, there is continual interchange between locusts resting on the ground and those flying overhead. How this swarm forms, and under what conditions it can migrate are interesting problems in their own right. Here we mostly concern ourselves with the forces that hold the swarm together once it is formed. We ask what types of interactions account for a cohesive band despite the prevalence of random effects that would tend to cause dispersal. To move as a unit, without the “pressure” of a population wave sustaining migration from some source, means that both a sharp wave front and wave back must be explained. We will argue that describing this aspect of swarming is more challenging than describing the propagation of moving fronts.

## 2 Mathematical background

The bibliography for continuum models of population movement, migration, and spatial distribution and spread is a rich one. In this paper we cannot hope to survey the full extent of contributions to this vast field. However, a few preparatory words about the current status of this field are in order.

**Travelling waves** are defined as solutions to partial differential equations which have fixed shape and move at a constant speed. One of the attractive tools for finding such solutions in a system of suitably small dimension, is phase plane analysis. The equations of the model are transformed to ordinary differential equations by switching to a moving coordinate system  $z = x - ct$  where  $c$  is the wave speed, and bounded solutions with the appropriate behaviour at  $z = \pm \infty$  are sought. **Travelling fronts** are then described by heteroclinic trajectories in the appropriate phase plane. **Travelling bands**, which in this paper will be used interchangeably with **travelling pulses**, are represented by homoclinic trajectories based at the origin<sup>1</sup>. This method is described in detail in standard texts such as Edelstein-Keshet (1988) and Murray (1989), and is particularly simple when the dimension of the reduced model is 2.

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<sup>1</sup> In some cases, but not in this paper, heteroclinic trajectories which start and end on one of the two axes can also describe travelling bands, see, in particular (Odell, 1980)

Perhaps best known to mathematical biologists working on ecologically-related modelling are the “waves of invasion” that depict the geographical spread of a population. The work of Skellam (1951), based in part on Fisher (1937), fits into this category. These models describe events on the timescale of many generations of a given organism, and the dominant force leading to spatial spread is a non-zero birth rate that locally increases crowding, causing individuals to “spill over” to adjoining regions by random migration. Such models lead to travelling front solutions: the rear of the wave represents space that has already been colonized, while in front of the wave is “virgin territory”. The number of organisms in the population grows as the front propagates into new regions. It is important to note the distinction between these population invasions, in which the number of individuals is not conserved, and the migration, swarming, flocking, or schooling that takes place when a group of organisms moves from one place to another.

Perhaps one of the best understood and most frequently cited examples of a travelling wave is a solution to Fisher’s Equation, based on the work of Fisher (1937) on the spread of an advantageous gene in a population.<sup>2</sup> A review of the work on this equation, its travelling wave solutions and a good survey of spatio-temporal models and patterns can be found in Murray (1989). Akira Okubo<sup>3</sup> contributed greatly to the appreciation of diffusion and spatial variation in ecological settings (Okubo, 1980). Many other contributions in the literature have been concerned with spatially nonuniform patterns of distributions (Cohen and Murray, 1981; Bertsch et al., 1984; Bertsch, 1985). More specific treatments of the issue of migration, waves of pursuit, and spatial spread and spreading waves of infestation have also appeared (Aoki, 1987; Dunbar, 1983; Conley and Fife, 1982; Ludwig et al., 1979).

How to connect the motion of the individual with the motion of the group as a whole is a fundamental problem. Contributions by (Alt, 1980; Othmer et al., 1988; Grunbaum, 1994) describe the details of motion, and how these translate to population-level statements in partial differential equations. See also Grunbaum (1997) (in press) for a recent example of this type. On the microscopic scale, are models that link the motion of the organism to some external influence such as nutrient or food. It is important to note that the presence of an external gradient (such as nutrient, attractant, or other influence) introduces asymmetry that can have a very important effect. This is the case in models for travelling bands of chemotactic bacteria (Keller and Odell, 1975; Odell and Keller, 1976; Keller and Segel, 1971) summarized in the review by Odell (1980). It does not seem, however, to be true in the problem at hand, since locusts can continue to move as a coherent swarm in the absence of food or apparent external gradient. On the macroscopic scale, the problem of a herd grazing on grass was presented by (Gueron and Liron, 1989), in a model essentially identical to that of bacterial chemotaxis. In these cases, the

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<sup>2</sup> This paper was published at an unfortunate period in hisotry when Eugenics was in vogue

<sup>3</sup> Who, sadly, passed away in 1996 at the age of 70

timescale of interest is much shorter than the reproduction time of the organisms. Thus, the type of solutions of interest are, roughly speaking, those with a constant number of organisms. This means that, rather than fronts, one must look for travelling bands, and as we shall see, this imposes some interesting and challenging constraints on the possible behaviour.

The issue of conditions under which a population such as the nutrient-seeking bacteria (or “grass” seeking “herd”) can move as a band has been discussed at length in the above papers and others. One of the main realizations, explained elegantly by Odell (1980), is that certain effects that allow the front of the wave to propagate forward – for example random diffusive flux – must be counterbalanced at the rear of the wave to prevent broadening or “sloughing off” of tardy individuals that fall behind. Generally, in models in which organisms move up a gradient of food density, the front of the wave of migration “senses” a sizable gradient, while in the rear, where the food has been largely consumed, and where the gradient is much more shallow, some unusual and biologically suspect assumptions must be made in order to ensure that the migrating band can sustain its shape. These assumptions – for example that chemotactic sensitivity gets infinitely sharp as the food diminishes, or that food consumption drops sharply – with an infinite slope – at low food density demonstrate that it is a non-trivial process to find conditions for a traveling band to exist. The stability of such a travelling wave solution to the original system of PDE’s (Gueron and Liron, 1989; Nagai and Ikeda, 1991) is neither easy to investigate nor generally guaranteed for arbitrary perturbations. Indeed, (Nagai and Ikeda, 1991) showed that travelling waves in the Keller–Segel–Odell chemotaxis system are linearly unstable to certain “physically relevant” perturbations (decaying to zero at the front and the back of the wave).

Travelling pulse solutions occur ubiquitously in models in physiology which depict propagation of electrical signals in the heart, in nerve axons, and in other excitable tissue. A summary of some of the mathematical features of such systems is given by Ermentrout and Rinzel (1981). Since these are easily obtained in the Fitzhugh–Nagumo equation and other excitable analogues, it would seem an “easy matter” to “cook up” examples of travelling pulses in biology. However, surprisingly, this turns out not to be the case in situations in which (unlike the nerve-conduction case) the “signal” being propagated is strictly positive – as is the case with organism density.

### **3 Biological background**

#### *3.1 General information about locusts*

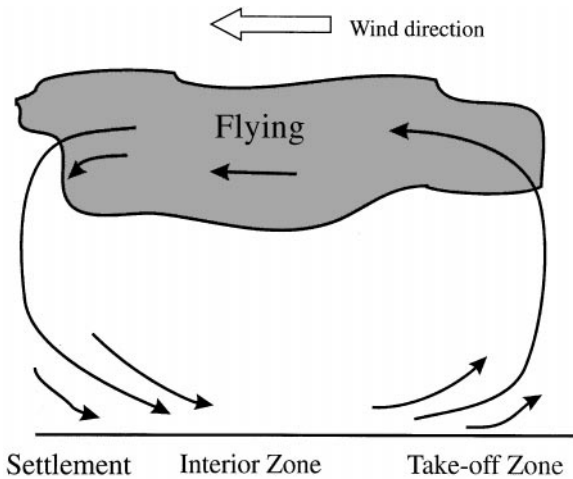
We briefly review some of what is known about African migratory locusts. These locusts have two distinct phases, solitary and gregarious. In the solitary phase, individual locusts are asocial and avoid each other. However, when a transition to gregariousness is triggered, individuals become strongly social

and form dense, long-lived migratory aggregations: “hopper bands” in non-flying juveniles; “swarms” in flying adults (Kennedy, 1951; Uvarov, 1928). Flying swarms of migratory locusts travel hundreds or thousands of kilometers, over a period of many days in a down-wind direction.

Swarms are distinct and recognizable, maintaining integrity for many days, over great distances (Ellis, 1953). Movement is directed and roughly constant in speed for periods much longer than the time scales that characterize movements of individuals. These observations are reflected in the assumptions in our modeling approach, namely that we can approximate the dynamics of these aggregations as one-dimensional processes, in which individuals fall into one of two categories, moving and non-moving. Locusts undergoing sustained migratory movements typically travel in very large swarms with a “rolling” structure (Albrecht, 1967) depicted schematically in Fig. 1. While swarm structure retains an approximately constant shape and size as it moves. Individuals within the swarm actually cycle through a sequence of behaviours: (i) flying towards the leading edge of the swarm (usually downwind); (ii) settling on the ground, mostly when they reach the front of the swarm; (iii) eating and resting until overtaken by the trailing edge of the swarm; and (iv) taking off and ascending to altitude, whereupon the cycle begins again. Locusts flying overhead are thought to “excite” their counterparts on the ground and cause massive take-offs. (This scenario will lead to the first hypothesis for swarm cohesion that we explore below.) The swarm “rolls” as it moves, with individuals at altitude moving faster than the swarm as a whole and settled individuals moving little or not at all. Typically, swarming locusts are estimated to spend approximately 20–40% of their time in flight (Rainey, 1989; Ellis, 1953).

### 3.2 *Specific facts and typical parameter values*

Locust swarms are notorious for their astronomical **size**, both in their linear dimensions and in the numbers of individuals. According to Waloff (1972), rolling swarms have a length on the order of 1 km (see Fig. 1). However, large swarms (which might consist of a number of “rolling” sub-units) are frequently observed to have cross-sectional areas of 10–100 km<sup>2</sup> or more. Observations of very large swarms, for example, 6 × 5 km viewed from the side, have been recorded (Rainey, 1989). Locust **airspeed** is typically in the range of 12 km/hr with a maximum of 23 km/hr observed. Daily swarm movements and **distances covered** are often in the range of 5–50 km. However, locusts can sustain flight continuously for days on end, travelling as a swarm much as three thousand miles (when blown over the ocean, for example). This is a telling observation, for it implies that, unlike bacterial chemotaxis, or herd grazing, **the swarm can persist even when there is no nutrient gradient to provide a driving force for migration**. The wind plays a dominant role in determining the **direction of migration**. The literature contains many anecdotes: A swarm with



**Fig. 1.** A schematic diagram showing the “rolling structure” of a typical swarm of the locust *Schistocerca*. According to (Waloff, 1972), the zone of Settlement is roughly 500 m long, the Interior Zone in which sporadic take-off and landing occurs is roughly 1900 m long, and the Take-off Zone is roughly 300 m long. See also (Albrecht, 1967) for a more detailed picture, showing directions of motion in various parts of the swarm

an area of roughly  $60 \text{ km}^2$ , described by (Rainey, 1989), maintained cohesion while travelling 370 km over a period of 9 days.

The **number of individuals** in a typical swarm may be up to  $10^7 - 10^9$  (Rainey, 1989). **Densities** of airborne locusts are commonly in the range of  $0.001-0.5 \text{ locusts m}^{-3}$ , with a median of  $0.025 \text{ m}^{-3}$ . This corresponds to a spacing of roughly 2–4 m between neighbors. A typical swarm would lead to a density of  $50 \text{ locusts m}^{-2}$  for settled locusts on the ground, and as many in the column of air directly above this area (this is called the local “area density”) (Rainey, 1989).

Locust flight is subject to random dispersal effects due to atmospheric turbulence, and due to the stochasticity of the flight mechanism itself. It is of interest, particularly from the modelling standpoint, to estimate the magnitudes of such random effects. Diffusion models for insect dispersal are helpful (Okubo, 1980; Helland, 1983). However typical coefficients for diffusion are not given in these references. We can estimate the magnitude of the dispersal coefficient from indirect information. For example, atmospheric turbulence would lead to the approximate doubling of the diameter of a cloud of inert particles in a period of about 6 hrs (Rainey, 1989) if the cloud was initially the size of a typical locust swarm. This suggests that the dispersal rate of insects due to atmospheric turbulence can be of the order of  $D \approx 30 \text{ km}^2 \text{ hr}^{-1}$ . If, on the other hand, we use the basic flight speed of the locust,  $v = 15 \text{ km hr}^{-1}$  and assume that the insects make random turns roughly once per minute, we arrive at  $D \approx v^2/2\lambda \approx 2 \text{ km}^2 \text{ hr}^{-1}$  (Othmer et al., 1988). Some intermediate figure between these two is probably more accurate.

#### 4 Model 1: flying and resting locusts

Our first attempt at modelling a locust swarm was motivated by descriptions of so-called **rolling swarms** given above (Albrecht, 1967; Waloff, 1972). The

model swarm is described as a continual exchange between flying locusts and those on the ground. The idea that locusts flying overhead “excite” others to take off leads to the first hypothesis:

- Hypothesis 1: Interactions between locusts in the air and those on the ground account for the structure and cohesiveness of the swarm.

To test this hypothesis, we consider a model for the densities of flying  $F(x, t)$  and stationary  $S(x, t)$  locusts with exchange-type kinetics. In this and other models we assume a one-dimensional geometry<sup>4</sup>. We assume that the rates of landing and take-off, may depend on locust densities.

#### 4.1 Glossary of symbols

$F(x, t)$	density of flying individuals at $x, t$ ,
$S(x, t)$	density of standing individuals at $x, t$ ,
$R(S, F)$	rate of take-off,
$G(S, F)$	rate of landing,
$D$	rate of random motion of locusts while airborne,
$U$	locust flying velocity (wind drift + active flying).

#### 4.2 Equations for simple exchange between sky and ground (model 1)

Locusts have very limited mobility on the ground. Thus, it makes sense, as a first approximation, to consider ground locusts as spatially fixed compared with their flying counterparts and we later explore the consequences of including ground mobility. Consider the model

$$\frac{\partial S}{\partial t} = -R(S, F)S + G(S, F)F, \quad (1)$$

$$\frac{\partial F}{\partial t} = DF_{xx} - UF_x + R(S, F)S - G(S, F)F. \quad (2)$$

The equation for flying locusts includes random motion, drift with the wind, and active flying. We will also initially assume that flight speed and rate of random motion,  $U, D$  are constants, and only later explore the consequences of dropping this assumption. We ask whether the above model, with judicious choices of the interaction functions  $R(S, F), G(S, F)$ , can support **travelling wave solutions** moving at some speed  $c$ . By previous remarks, we are specifically interested in **travelling band solutions** for which the total number of

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<sup>4</sup> Locust swarms generally form and migrate under wind conditions. The direction of the wind determines the direction of migration, and thus essentially reduces a multi-dimensional spatial problem to 1D

individuals is finite. In the model, conditions on the density functions  $F$  and  $S$  are that they remain bounded and positive everywhere. Further, for travelling pulses, the two functions should vanish far ahead of and far behind the band of locusts, i.e.  $F, S \rightarrow 0$  for  $x \rightarrow \pm \infty$ . The functions  $R(S, F)$  and  $G(S, F)$  are at this point unspecified, except that they are nonnegative. Both carry dimensions of  $[t^{-1}]$ .

## 5 Travelling wave solutions in Model 1

We begin by transforming the two equations into the travelling wave coordinate  $z = x - ct$  where  $c$  is a constant wave speed. The dot above a variable denotes differentiation with respect to the wave variable,  $z$ . When this transformation is made we arrive at the equations

$$-c\dot{S} = -R(S, F)S + G(S, F)F, \quad (3)$$

$$-c\dot{F} = D\ddot{F} - U\dot{F} + R(S, F)S - G(S, F)F. \quad (4)$$

These equations are equivalent to a system of three first order equations, but we can reduce the dimensionality as follows: Adding the two equations leads to

$$-c(\dot{F} + \dot{S}) = D\ddot{F} - U\dot{F}. \quad (5)$$

Integrating once from  $-\infty$  to  $z$  gives

$$-c(F + S) = D(\dot{F} - \dot{F}|_{-\infty}) - U(F - F|_{-\infty}). \quad (6)$$

This implies that

$$D\dot{F} = -cS + (U - c)F + \text{Constant}, \quad (7)$$

where the constant comes from the integration step. The system of equations, in moving coordinates thus reduces to the set of two ordinary differential equations,

$$-c\dot{S} = -R(S, F)S + G(S, F)F, \quad (8)$$

$$D\dot{F} = -cS + (U - c)F + \text{Constant}. \quad (9)$$

These equations can be studied by phase-plane methods. However the details of the solutions (and the value of the arbitrary constant) will depend on auxiliary conditions which we number and explain below. We contrast the auxiliary conditions in the case of travelling front and travelling bands. The possible set of relevant **Conditions for travelling fronts/bands** include:

1.  $\lim_{z \rightarrow \infty} F, S \rightarrow 0$ ;
2.  $\lim_{z \rightarrow -\infty} F, S \rightarrow 0$ ;
3.  $F, S \geq 0$  for all  $z$ ;



The conditions above mean that: (1) there are no individuals far “ahead” of the wave, (2) there are no individuals far “behind” the wave, and (3) the densities are non-negative.

### 5.1 Necessary conditions for travelling front solutions (Model 1)

Travelling front solutions satisfy only **Conditions 1 and 3** and are thus represented by a **heteroclinic trajectory**, connecting distinct fixed points in the  $SF$  phase plane, one of which is the origin. The trajectory must be contained entirely in the positive quadrant of the  $SF$ -plane by assumption (3). For such a solution to exist,

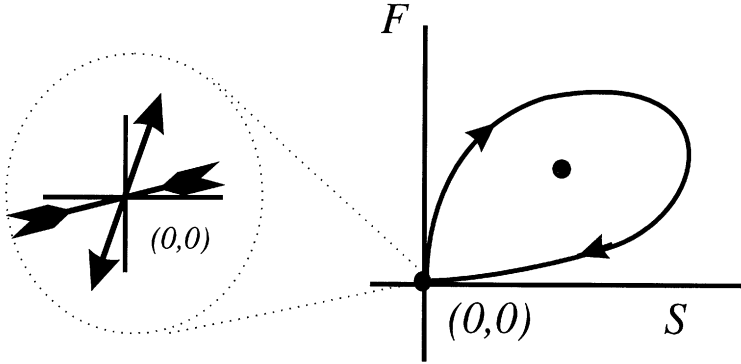
- The origin ( $F = S = 0$ ) must be either a saddle point or a stable node, i.e. it must have one negative real eigenvalue,  $\lambda^-$  to obtain the first property above.
- The eigenvector corresponding to  $\lambda^-$  must be directed into the first quadrant of the state space. (Otherwise the connection to the origin would require that  $F$  or  $S$  take on negative values, which is not permissible for population densities.)
- There must be at least one other equilibrium in the positive quadrant of the  $SF$ -plane which can be either a saddle, an unstable node, or an unstable spiral. (The location of this equilibrium essentially represents the densities of  $F, S$  far behind the wave front.)

### 5.2 Necessary conditions for travelling band solutions (Model 1)

Travelling band (or pulse) solutions satisfy **Conditions 1, 2 and 3** and are represented by a **homoclinic trajectory** contained entirely in the positive quadrant of the  $SF$ -plane, starting and ending at the origin. For such a solution to exist,

- The origin ( $F = S = 0$ ) must be a saddle point of the system so that the trajectory can both leave and enter this fixed point. Thus, the origin must have one positive and one negative eigenvalue (unless it is degenerate).
- The corresponding eigenvectors cannot be directed into quadrants II and IV of the state space, since we restrict our attention to non-negative solutions.
- Both the  $F$  and  $S$  nullclines must pass through quadrant I since both  $F$  and  $S$  have maxima in this quadrant.

In the next sections we demonstrate that if the first condition is satisfied, then the second condition is necessarily violated. That is, if a pulse solution exists, then it is not everywhere non-negative and will not be a biological representation of the swarm.



**Fig. 2.** For a travelling band (pulse) solution to exist, we must demonstrate a homoclinic trajectory in the  $SF$  phase plane. This implies that the origin must be a saddle point whose eigenvectors have the configuration shown in the circled inset. The  $F$  and  $S$  nullclines must pass through the first quadrant. (In the nondegenerate case, there is also an equilibrium in the first quadrant, though it is not essential to assume that this equilibrium exists.)

### 5.3 Analysis of the travelling wave equations (Model 1)

We now use the assumptions

$$\lim_{z \rightarrow -\infty} F = 0; \quad \lim_{z \rightarrow -\infty} \dot{F} = 0. \quad (10)$$

These assumptions follow from the fact that  $F$  and  $S$  are assumed to decay to zero at the back of the wave. The constant of integration is thus zero, and the system of equations, in moving coordinates is

$$-c\dot{S} = -R(S, F)S + G(S, F)F, \quad (11)$$

$$D\dot{F} = -cS + (U - c)F. \quad (12)$$

We now examine the behaviour of this system of equations with the particular aim of elucidating whether a homoclinic trajectory based at the origin can exist under any reasonable further assumptions.

Observe that the nullclines of the system consist of the curves

$$0 = -R(S, F)S + G(S, F)F, \quad (13)$$

$$0 = -cS + (U - c)F. \quad (14)$$

The  $F$  nullcline given by equation (14) must pass through the first quadrant, which implies that its slope is positive, i.e.,  $((U - c)/c) > 0$ . Assuming, without loss of generality, that  $U > 0$ , i.e. that the direction of the wind is towards the positive  $x$  axis, this constraint can be written as

$$0 < c < U.$$

**Conclusion: If a travelling wave of any type exists, its speed must be slower than the wind speed.** This follows from the fact that locusts spend time exchanging

between ground and sky, and this would makes the swarm as a whole move forward more slowly than if they were simply carried forward by the wind.

*Comment:* This has been observed and noted biologically (Albrecht, 1967).

For ease of manipulation, we can rewrite the differential equations in a dimensionless formulation. Although this is not essential, it leads to a particularly simple form of equation (22).

$$\dot{s} = \tilde{R}(s, f)s - \tilde{G}(s, f)f, \quad (15)$$

$$f = -s + f, \quad (16)$$

where

$$s = S, \quad (17)$$

$$f = \frac{U - c}{c} F, \quad (18)$$

$$\frac{\partial}{\partial \zeta} = \frac{D}{(U - c)} \frac{\partial}{\partial z}, \quad (19)$$

$$\tilde{R}(s, f) = \frac{D}{c(U - c)} R(S(s), F(f)), \quad (20)$$

$$\tilde{G}(s, f) = \frac{D}{(U - c)^2} G(S(s), F(f)). \quad (21)$$

The dot above a variable now signifies differentiation with respect to the dimensionless wave coordinate,  $\zeta$  (zeta). Linearizing the system about the fixed point  $f = s = 0$  yields

$$\begin{pmatrix} \dot{s} \\ \dot{f} \end{pmatrix} = \begin{pmatrix} \tilde{R}_0 & -\tilde{G}_0 \\ -1 & 1 \end{pmatrix} \begin{pmatrix} s \\ f \end{pmatrix} + \dots \quad (22)$$

where the parameters  $\tilde{R}_0 = \tilde{R}(0, 0) \geq 0$  and  $\tilde{G}_0 = \tilde{G}(0, 0) \geq 0$  represent the magnitudes of the interaction terms at the fixed point  $(0, 0)$ . (These are equivalent to landing and takeoff rates when the locust density is very low. They are, by definition, non-negative quantities.) The eigenvalues of this linear system are

$$\lambda^\pm = \frac{1}{2} (1 + \tilde{R}_0 \pm \sqrt{1 + \tilde{R}_0^2 - 4(\tilde{R}_0 - \tilde{G}_0)}). \quad (23)$$

Since  $\tilde{R}_0$  is positive, so is  $1 + \tilde{R}_0$ . It is clear that the situation  $\tilde{R}_0 - \tilde{G}_0 > 0$  cannot be consistent with travelling waves of any form, since then, both eigenvalues obtained with the above expression are positive, and the origin is unstable, and thus would not admit the approach of a trajectory from some other fixed point. This is inappropriate for both travelling fronts and travelling pulses, as discussed above. We must therefore assume the following **necessary condition for travelling wave solutions:**

$$\tilde{R}_0 \leq \tilde{G}_0. \quad (24)$$

If we express this condition in terms of the original (dimension-carrying) functions for take-off and landing, we find that this inequality is equivalent to

$$\left( \frac{R_0 U}{(G_0 + R_0)} \right) \leq c \quad (25)$$

This inequality has the following meaning: the quantity on the left hand side is the average velocity of the locusts in low density regions. (The ratio  $R_0/(G_0 + R_0)$  is the relative number of locusts flying with velocity  $U$ .) If this inequality is not satisfied, it means that locusts far ahead of the swarm would fly faster than the rest of the swarm. This implies that a wave of any type (front or band) would have a minimum wave speed. (Recall that, by previous results, we have already found a maximum wavespeed, i.e.  $c < U$ .)

When this condition is satisfied, we have  $(\tilde{R}_0 - \tilde{G}_0) \leq 0$  and the origin is a saddle point (or possibly degenerate). Existence of a saddle point at the origin is certainly one of the conditions for the occurrence of travelling pulse solutions, and it is consistent with travelling front solutions. However, as will be shown below, the other criteria for pulse solutions cannot be satisfied.

#### 5.4 Proof that no travelling pulse solutions can exist in Model 1

To see this, note that by the second requirement, to have a non-negative pulse solution, both eigenvectors at the origin must be directed into the first (and third) quadrants. The eigenvectors of the system are

$$\xi^\pm = \begin{pmatrix} 1 - \lambda^\pm \\ 1 \end{pmatrix}. \quad (26)$$

For the case of a saddle point,  $\lambda^+ > 1 + \tilde{R}_0 \geq 1$  and  $\lambda^- \leq 0$ . In the non-degenerate case,  $(\tilde{R}_0 \neq \tilde{G}_0)$  the stable eigenvector, corresponding to  $\lambda^-$ , points into quadrants I and III and the unstable eigenvector, corresponding to  $\lambda^+$  points into quadrants II and IV, in violation of one of the conditions of Sect. 6.2. Thus, any homoclinic trajectory with the origin as its fixed point will have to dip into a part of the phase plane where either  $F$  or  $S$  are negative. This means that we must reject any such solution as non-biological when we are considering population densities.

A few other special cases can be considered: if  $\tilde{R}_0 = \tilde{G}_0 \neq 0$  then the eigenvector corresponding to  $\lambda^+$  points into quadrant II as before, and the results are the same. If  $\tilde{R}_0 = \tilde{G}_0 = 0$  then our analysis does not rule out a homoclinic trajectory and further work is needed.

The above results demonstrate that in all but possibly the degenerate case,

- Local interactions of flying and standing locusts and simple diffusion-convection of flying locusts cannot account for a coherent swarm that migrates as a travelling band.
- Hypothesis 1, as it stands, cannot be sustained.

## 6 Model 2: motion depends on local density

With the failure of the first hypothesis, we considered the possibility that the constant diffusion and drift were oversimplifications, and this led us to explore a second hypothesis:

- Hypothesis 2: Locusts respond to local swarm density variation by changing their rate of random or directed motion. Such changes in flight speed account for the cohesion of the swarm.

To explore this hypothesis, we included aggregative terms in the original model equations. Such terms would depict tendency for locusts to cluster, tendency to adjust motion in response to crowding or thinning at the swarm edge, etc. Terms for the motion of the flyers are now functions of density. More terms are included than strictly necessary for the locust swarm: for example, flying locusts probably do not adjust motion in response to the variations of ground locust density. However, we can explore a fully general model at little further computational cost. Such a general system might have the form:

$$\frac{\partial S}{\partial t} = -R(S, F)S + G(S, F)F, \quad (27)$$

$$\frac{\partial F}{\partial t} = \frac{\partial}{\partial x} (D(S, F)F_x - E(S, F)FS_x - U(S, F)F)R(S, F)S - G(S, F)F. \quad (28)$$

$D(S, F)$  represents random motion of flying locusts in response to gradients of other flyers,  $E(S, F)$  represents a response of the flying locusts to gradients of the stationary locusts. The term  $U(F, S)$  is the locust flight speed as a function of the local densities of locusts. These terms are general enough to include a variety of possible effects, and we do not assume that they are necessarily positive for all  $S, F$  values.

Equations (28) may have weak solutions. However, since we are interested only in smooth solutions, we will not consider this possibility in detail here. It is a simple matter to investigate how the addition of these terms influences our previous conclusions, and the analysis is identical to the previous case for the first few steps. In the travelling wave coordinate system, after adding the two equations and integrating as before, we will get the new system

$$-c\dot{S} = -R(S, F)S + G(S, F)F, \quad (29)$$

$$-c(F + S) = D(S, F)\dot{F} - E(S, F)F\dot{S} - U(S, F)F. \quad (30)$$

As before, the ability to find a pulse hinges on behaviour at the origin, and we try for a saddle point at  $(0,0)$  with appropriate eigenvectors so that a homoclinic trajectory can be constructed. We find, however that linearization of the above system at the origin leads to the exact same set of ODE's with the diffusion rate  $D(0, 0)$  and speed  $u = U(0, 0)$ . The fact that  $U, D$  are functions, rather than constants is thus irrelevant. Indeed, only the behaviour of these

functions “at the low density” limit (as, for example at the back or the front of the wave) enters into the analysis here. Thus the new terms in the model do not help to eliminate the problem at the origin. The results are therefore identical, with mere redefinition of the “constants”. (Again, a possible exception exists in a degenerate case which occurs if  $D \rightarrow 0$  as  $F \rightarrow 0$ . This may be biologically interesting and deserves further work.) We make the following conclusions:

- In the simple Flying-Standing locust exchange model, taxis, non-linear drift, and non-linear diffusion of flying locusts fails to account for a coherent swarm.
- Hypothesis 2 is not supported by the analysis.

## 7 Models 2': slow motion of locusts on ground

Motion of locusts on the ground is very slight compared to that of the flying locusts, and we have ignored it in the previous model. However, a danger exists in leaving off higher derivative terms in any differential equation as the behaviour of its solutions may be corrupted (Odell, 1980). To ensure that this problem does not contaminate our results, we explored a version of the model in which the locusts on the ground are also moving, but at a much slower rate. This leads, under the travelling wave coordinates, to a higher dimensional system and we felt it wise to check if the problems constructing a travelling pulse solution could thereby be circumvented. The equations we studied were:

$$\frac{\partial S}{\partial t} = \frac{\partial}{\partial x} (A(S, F)S_x - B(S, F)SF_x) - R(S, F)S + G(S, F)F, \quad (31)$$

$$\frac{\partial F}{\partial t} = \frac{\partial}{\partial x} (D(S, F)F_x - E(S, F)FS_x - U(S, F)F) + R(S, F)S - G(S, F)F. \quad (32)$$

The motility,  $A(S, F)$ , is small, and the advection of the stationary locusts is either small or zero.

These equations can be analyzed as before, but the calculations are more tedious. We show most of these steps in the appendix to this paper. The analysis hinges on the fact that eigenvalues of a dimensionless version of this system are roots of the cubic equation

$$\varepsilon\lambda^3 + (\alpha - \varepsilon)\lambda^2 - (\alpha + \tilde{R} + \varepsilon\tilde{G})\lambda + (\tilde{R} - \alpha\tilde{G}) = 0. \quad (33)$$

Where the (dimensionless) parameters are  $\alpha = c/(U - c)$ ,  $\varepsilon = A/D$ ,  $\tilde{R} = RD/(U - c)^2$ ,  $\tilde{G} = GD/(U - c)^2$  and all functions are evaluated at  $(T, F, S) = (0, 0, 0)$ .

By investigating the forms of the eigenvectors and eigenvalues at the origin (see Appendix) we obtain a set of conditions described below: Denoting  $\lambda_1$  as the leading unstable eigenvalue, and  $\lambda_2$  as the leading stable eigenvalue, the

restrictions are

$$\begin{aligned} 0 < \lambda_1 < 1, \\ -\alpha/\varepsilon < \lambda_2 < 0. \end{aligned} \quad (34)$$

The remaining eigenvalue must be either unstable and less than  $\lambda_1$  in magnitude, or stable and greater than  $\lambda_2$  in magnitude. However, a simple renumbering can allow the conditions

$$\begin{aligned} -\alpha/\varepsilon < \lambda_2 < 0 < \lambda_1 < 1 \\ \lambda_3 < \lambda_1. \end{aligned} \quad (35)$$

In summary, necessary conditions for a travelling wave pulse are that equation (33) have three real solutions and that these solutions satisfy (35).

For  $\varepsilon = 0$ , the system reduces to the two dimensional system. Thus, for small  $\varepsilon$ , the system is a singular perturbation from the two dimensional system analyzed previously (for stationary locusts on the ground). Two of the eigenvalues are close to the eigenvalues of the 2D system, and the third eigenvalue is

$$\lambda^\infty = -\alpha/\varepsilon - \tilde{R}/\alpha + \mathcal{O}(\varepsilon). \quad (36)$$

Since  $\lambda^\infty < -\alpha/\varepsilon$ , the remaining two eigenvalues must satisfy the conditions of equation (34). However, a simple perturbation analysis of equation (33) shows that these conditions are not met if  $\varepsilon \ll 1$ . Specifically, the largest positive eigenvalue,  $\lambda_1$ , will be larger than 1 for sufficiently small  $\varepsilon$ . Hence no travelling bands will occur. Further work is necessary to determine a useful bound on  $\varepsilon$ . In conclusion, this adjustment of the model (which significantly increases the complexity of its analysis) does not change the previous predictions.

### 8 Model 3: density dependent turning

We explored a third hypothesis for the swarm cohesiveness following a suggestion in the locust literature:

- Hypothesis 3: “Swarms maintain cohesion because individuals or groups which fly out beyond their perimeter change their orientations and head back into the swarm”. (Waloff, 1962)

Waloff’s statement suggests a different approach based on the idea that locusts are continually turning back and flying into the swarm, or turning in response to local density. To explore this idea, we dropped the assumption that interactions with the ground are essential and focused on the flying locusts alone. We subdivide the flying locusts into those moving **Ahead**,  $A(x, t)$ , and those moving **Back**,  $B(x, t)$ , each moving at the same basic flight speed,  $v$ . We assumed that the turning rates  $r_{ab}, r_{ba}$  could depend on local density conditions. This idea leads to a model essentially identical to one for

*Myxobacteria* described by (Pfister 1989; Alt, 1987). The equations we explored were:

$$\frac{\partial A}{\partial t} = -(v + w) \frac{\partial A}{\partial x} - r_{ab} A + r_{ba} B, \quad (37)$$

$$\frac{\partial B}{\partial t} = (v - w) \frac{\partial B}{\partial x} - r_{ba} B + r_{ab} A. \quad (38)$$

Where  $r_{ab} = r_{ab}(A, B)$ ,  $r_{ba} = r_{ba}(A, B)$  are functions of the densities. The wind speed,  $w$  is explicitly included, and assumed constant. These equations are known to lead to the Telegrapher's equation, see for example, (Othmer et al., 1988). In a moving coordinate system, the resulting ordinary differential equations are,

$$(v + w - c) \frac{dA}{dz} = -r_{ab} A + r_{ba} B, \quad (39)$$

$$(v - w + c) \frac{dB}{dz} = -r_{ab} A + r_{ba} B. \quad (40)$$

Subtracting the two equations eliminates the kinetic terms, leading to

$$(v + w - c) \frac{dA}{dz} - (v - w + c) \frac{dB}{dz} = 0. \quad (41)$$

Integrating once and using the boundary conditions (i.e no individuals far ahead or far behind the wave) results in

$$(v + w - c) A - (v - w + c) B = 0. \quad (42)$$

which implies that the densities of individuals moving Ahead and Back are proportional everywhere. We can therefore eliminate one variable, for example  $B$ , by substituting the expression

$$B = \frac{(v + w - c)}{(v - w + c)} A \quad (43)$$

into the appropriate terms in the equation for  $A$ . This means that the system of equations reduces to a single equation, which has the basic form

$$\frac{dA}{dz} = Af(A), \quad (44)$$

where  $f(A)$  is some expression involving the original turning rates,  $r_{ab}$ ,  $r_{ba}$  but depending only on  $A$ . It is well known that such a one-dimensional equation cannot support a solution that represents a pulse because of its low dimensionality. A smooth transition between two distinct equilibria (i.e. fixed points of  $Af(A)$ ) is possible, but not a transition that starts and ends at  $A = 0$ .



A travelling front, but not a pulse could occur in such a model<sup>5</sup>. We conclude that

- Turning back and flying into the swarm might work to create a swarm front, but not a travelling band. Thus, contrary to (Waloff, 1962), this would not lead to a cohesive swarm, since it does not include a mechanism for keeping the back of the wave with the rest of the group.
- Hypothesis 3 is not supported by the analysis.

## 9 Nonlocal models

We explored a final hypothesis for the swarming behaviour,

- Hypothesis 4: The interactions that maintain swarm cohesion are not just local: locusts use visual stimuli (and other signals) to integrate and respond to swarm density over some extended distance (not just at a single point). In this way they can adjust speed to keep up with the swarm, leading to swarm cohesion.

While this hypothesis is based on biologically realistic assumptions, exploring it mathematically leads to a fundamentally different type of model which is considerably more challenging to analyse. An example of this type of model appeared in Mogilner (1995), Mogilner and Gueron (1997) to explain swarming phenomena in bacteria. In this model, the velocity of an individual was assumed to adjust itself according to some weighted average density of the swarm around the given individual. See also (Kawasaki, 1978; Alt, 1985). A typical equation for the motion of the swarmer in this type of model is

$$\frac{\partial F}{\partial t} = D \frac{\partial^2 F}{\partial x^2} - \frac{\partial}{\partial x} ((w + v)F), \quad (45)$$

where  $w$  is some superimposed drift (such as wind velocity), and where the active motion of the organisms depends on the organism density according to a convolution:

$$v = K * F = \int_{-\infty}^{\infty} K(x - x')F(x')dx'. \quad (46)$$

Both repulsive and attractive influences due to nearby organisms can be included in the kernel. A typical symmetric form for such a kernel might be

$$K = x \left( \frac{A}{a^2} e^{-(x/a)^2} - \frac{B}{b^2} e^{-(x/b)^2} \right), \quad (47)$$

<sup>5</sup> We remark that it is imple, though not biologically interesting, to get two diverging pulses, simply by setting  $r_{ab} = r_{ba} = 0$  in this system, obtaining two uncoupled “one-way” wave equations

where the magnitudes of  $A$  and  $B$  represent, respectively the induced speed per unit density caused by attraction and repulsion, and where  $a$  and  $b$  represent the spatial extent of these influence. In the original Mogilner model, an odd kernel similar to the above was used. The effect is to make front and back symmetric so that a uniform density at any level will have no effect on the swarming interactions ( $K * F = 0$  for  $F$  constant).

A similar model (but with  $w = 0$  and with a different interpretation) was analyzed in detail by (Mogilner et al., 1996) with particular emphasis on peak-like behaviour of solutions when the diffusion constant,  $D$ , is very small. A result that carries over to moving coordinates  $z = x - ct$  is that in the case of small diffusion,  $D = \varepsilon$ , using a perturbation expansion, one finds peak-like behaviour which, to leading order, has the form

$$F(z) = \exp\left(-\frac{(-K'(0)N)}{2\varepsilon}z^2\right), \quad (48)$$

where

$$N = \int_{-\infty}^{\infty} F(s)ds. \quad (49)$$

Using the form for the kernel given in equation (47), the derivative  $K'(0)$  is

$$K'(0) \equiv \frac{A}{a^2} - \frac{B}{b^2}. \quad (50)$$

This means that the width of the peak, to leading order is predicted to be:

$$L = \varepsilon^{1/2} N^{-1/2} \left(\frac{B}{b^2} - \frac{A}{a^2}\right)^{-1/2}. \quad (51)$$

This result must be interpreted with caution, since it is a leading order result only. It seems to imply that a peak-like solution would exist under a moving coordinate system, and it appears that a restriction of the sort

$$\frac{A}{a^2} < \frac{B}{b^2} \quad (52)$$

has to be imposed. However, numerical simulations do not support this latter restriction, and indeed, it appears that the leading order behaviour is limited in its predictive ability. Further, the result does not lead to conclusions about the stability of the peak nor about the existence of a travelling pulse of fixed shape.

It is also possible to explore some of the consequences of the model by looking at aggregate properties such as the center of mass or the width of the swarm. This can be done to some extent directly from equation (45), and we show a few steps in this direction in an appendix to this paper. We can further use the detailed form of the kernel to draw more detailed conclusions in certain limiting cases. For example, the **small swarm approximation** holds whenever the spatial size of the swarm is small compared to the interaction distances  $a, b$ . The results in this limiting case give additional confirmation to

equation (51) (see Appendix). This suggests that formally, the effect of certain terms associated with the kernel is to counterbalance the effect of diffusion. However, because the moment equations involve higher moments yet, a definitive analysis is hampered by the possibility that infinite sums may fail to converge. Furthermore, locust swarms are generally much larger than the range of interactions of individuals, and so these results, while interesting for small swarms, may tell us very little about locusts.

While the analysis of the nonlocal equations for swarming locusts is of limited scope in this paper, we point the reader to a recent investigation by Mogilner and Edelstein-Keshet (1997) in which a simple caricature of a swarm with non-local interactions is described and analysed in much greater detail.

### 9.1 Numerical simulations: nonlocal model

We incorporated the ideas of nonlocal swarming interactions in the original version of the model to generate the system of equations shown below

The system of equations we investigated was

$$S_t = -RS + GF, \quad (53)$$

$$F_t = DF_{xx} - \frac{\partial}{\partial x} ((w + K * F)F) + RS - GF, \quad (54)$$

where  $w$  is wind speed and the swarming velocity is given by the above convolution with the slightly modified kernel,

$$K = \frac{x}{N_0} \left( \frac{A}{a^2} e^{-(x/a)^2} - \frac{B}{b^2} e^{-(x/b)^2} \right). \quad (55)$$

$N_0$  is a reference density. In this form, the parameters are more easily interpretable since now  $A, B$  have units of velocity. It is thus easier to assign values to the parameters directly. The constant  $N_0$  does not change the behaviour of the model: it simply rescales the units. This system of equations was solved numerically using the method of lines and a first order backward difference algorithm for the time-stepping. In all simulations, 240 gridpoints and a time step of  $\delta t = 0.05$  hours was used. Periodic boundary conditions were used to avoid numerical difficulties. The convolution  $K * F$  was approximated using Simpson's algorithm, and first order upwinding was used to approximate the derivative of the convection term. Centered differencing was used for the diffusion term. The resulting scheme is conservative and first order in both time and space. The domain of the system is a line segment of length  $L$ , and the total number of locusts is conserved. That is,

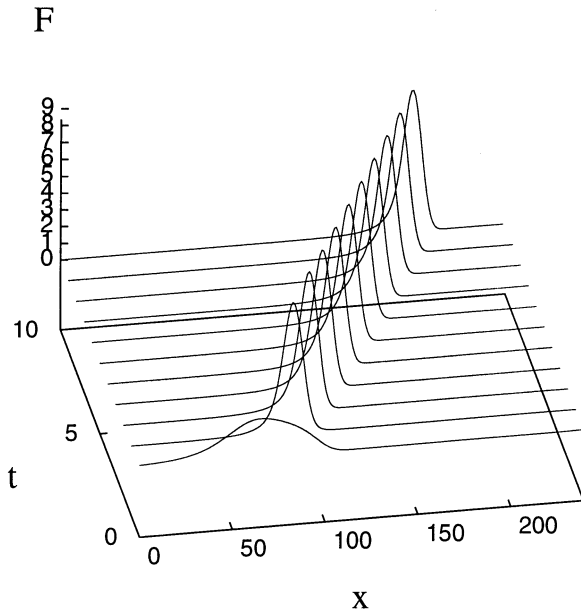
$$\int_0^L (F + S) dx = N \quad (56)$$

where  $N$  is a positive constant.  $R$  and  $G$  and the remaining parameters are constants in the simulations. The variables were all non-dimensionalized so the total density was  $F + S = 1$ .

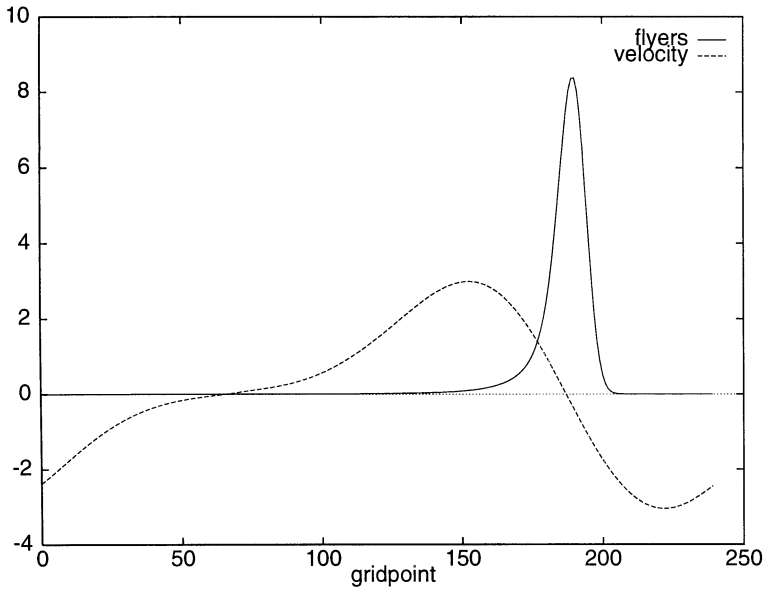
The simulation was first run without repulsion ( $B$  set to zero). Figs. 3 and 5 show how the wave develops from initial conditions. Increasing the flight speed of the locusts produced a broader band. Figures 4 and 6 show the shape of the apparent travelling band and the swarming velocity (the convolution  $v = K * F$ ) as a function of position in the swarm. Note that locusts at the front of the wave are flying back into the swarm, while the others are flying towards the front. At some distance beyond the rear of the peak, the velocity becomes negative. This is an artifact of the periodic boundary conditions: locusts are being more strongly attracted to the “swarm behind them”.

The parameter values used for the simulation runs presented here are based loosely on parameters associated with locust swarms, as described in Sect. 3.2. However, in order to get a pulse to form, we have used values for the diffusivity  $D$ , and the wind velocity  $w$  that are both an order of magnitude below realistic estimates. Although little is known about the distances over which locusts attract or repel one another in a swarm, the values chosen for  $a$  and  $b$  are thought to be reasonable, if possibly high.

The simulation run whose results are shown in Fig. 7 was designed to examine the merging of nearby swarms into one swarm. The results suggest

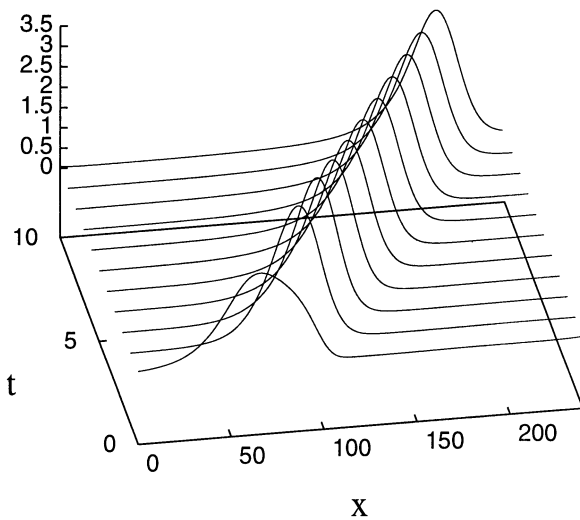


**Fig. 3.** This figure shows the formation and motion of what appears to be a travelling pulse solution to the nonlocal model with exchange kinetics. The initial distribution, the low pulse at the front of the figure, moves to the right and quickly forms a tighter peak. The parameter values used were  $N = 10^9$  locusts,  $N_0 = 4 \times 10^8$  locusts,  $L = 10$  km,  $D = 0.1$  km<sup>2</sup>/hour,  $w = 1$  km/hour,  $A = 3$  km/hour,  $B = 0$ ,  $a = 2$  km, and  $b = 1$  km. The units on the time axis are hours and the size of the domain (240 gridpoints) corresponds to 10 km

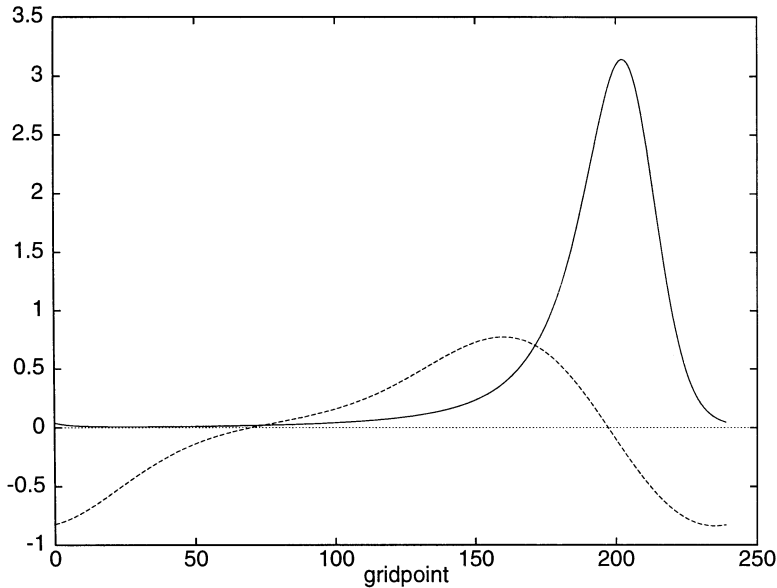


**Fig. 4.** This figure shows the shape of the pulse at the end of the simulation of Fig. 3. The (dimensionless) density of flying locusts and the (dimensionless) magnitude of their swarming velocity  $v = K * F$  are shown. Periodic boundary conditions result in the fact that locusts distributed over the first 50 gridpoints seem to be flying back towards the swarm “behind them”

F



**Fig. 5.** The travelling pulse in this figure is much broader than the pulse of Fig. 3. The parameter values used to produce this figure were identical to Fig. 3 except that a value of  $A = 1$  km/hour was used here. The time units and spatial scale is identical to that of Fig. 3



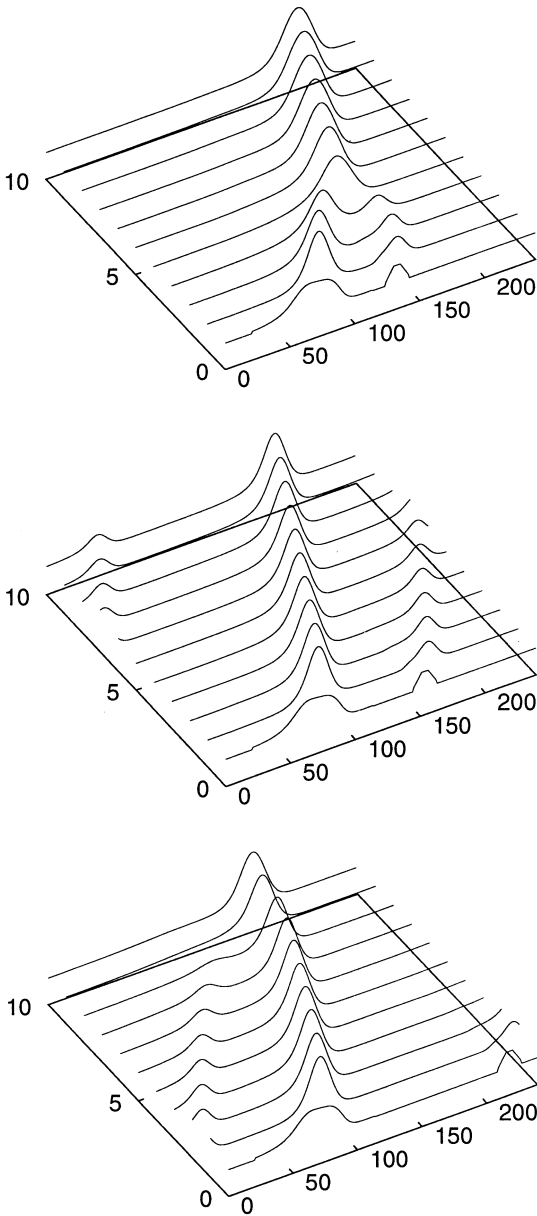
**Fig. 6.** This figure shows the last timestep of the travelling pulse of Fig. 5. The higher curve is the density and the lower curve shows the velocity at different points in the swarm. Note that the velocities in this case are much lower than for the peaked wave. However, the wave itself is faster

that smaller swarms travel faster than larger ones. Thus a small and a large swarm will merge if the small swarm is to the rear of the large swarm. However, as the upper plot of Fig. 7 shows, if the smaller swarm is ahead of, but sufficiently close to the larger swarm, it will be slowed and the two will merge.

The simulation shown in Fig. 8 shows a swarm forming from stationary locusts. Other than wind velocity and diffusivity, the parameter values are in a realistic range for locusts. The distribution of flying locusts quickly forms two pulses from the initial data and these gradually merge into a single pulse over a time equivalent to a single day.

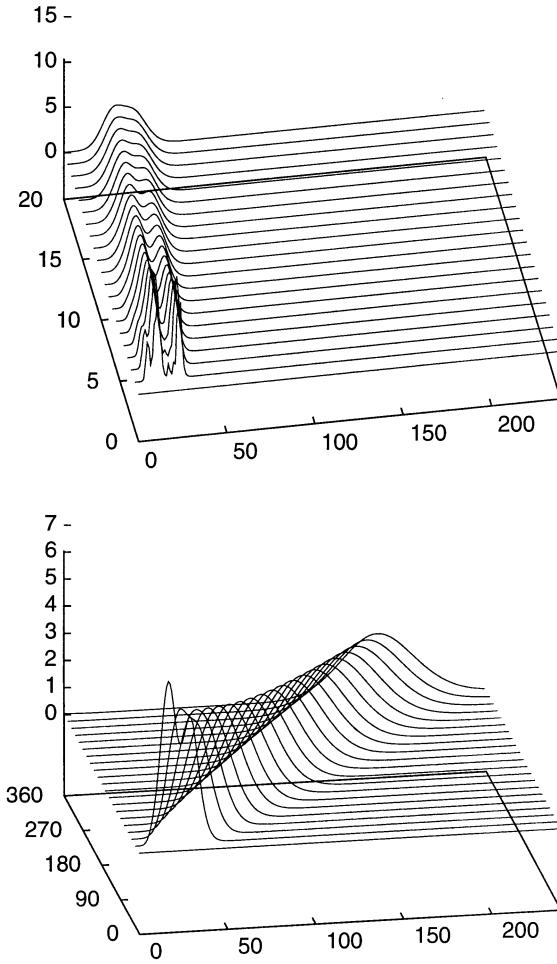
Simulation runs with higher wind speeds or diffusivities produced pulses that looked qualitatively like sinusoids with a period equal to that of the domain length. Since such functions are eigenvalues of the diffusion operator, this suggests that the diffusion of locusts dominates over the integral term at higher wind speeds. As these observations have not yet been explored by analysis, the possibility exists that some of these conclusions may be associated with numerical artifacts.

Although the model described here is able to form a peak-like propagating solution, running the model for longer times reveals that the peak tends to broaden out eventually. This is shown in Fig. 8. We find that although the effect of the swarming term is to cause clustering and lead to formation of



**Fig. 7.** The above figures show different velocities of large and small waves. The parameter values used in all three figures were  $N = 10^9$  locusts,  $N_o = 4 \times 10^8$  locusts,  $L = 10$  km,  $D = 0.1$  km<sup>2</sup>/hour,  $w = 1$  km/hour,  $A = 4$  km/hour,  $B = 0$ ,  $a = 1$  km, and  $b = 1$  km. The only differences between the figures are the initial conditions. In each successive figure, the smaller pulse was moved further ahead of the larger pulse. Note that the smaller pulse moves faster than the larger pulse. In the top figure, the smaller pulse is slowed, and merges with the larger pulse. Whereas, in the second figure, the simulation starts with the smaller pulse farther ahead of the larger pulse and the two pulses do not merge. In the final figure, the smaller pulse catches up with the larger pulse and the two merge. Time and distance units are identical to those of Fig. 3.

a pulse, it does not appear to result in a true travelling pulse in the classical sense of this term. In general, true stable pulses were not observed in our simulations. Further, the only possible candidates for reasonable propagating solutions in the form of gradually widening pulses were found for low values of both wind speed and diffusivity. (However, we have by no means fully



**Fig. 8.** These figures show simulations of the model with replusion included in the integral term. The initial conditions were a random distribution of stationary locusts in the first tenth of the domain. The parameter values used were  $N = 10^9$  locusts,  $N_o = 4 \times 10^8$  locusts,  $L = 100$  km,  $D = 0.1$  km<sup>2</sup>/hour,  $w = 0.75$  km/hour,  $A = 12$  km/hour,  $B = 0.3$  km/hour,  $a = 200$  m, and  $b = 100$  m. The size of the domain (240 grid-points) corresponds to 100 km. In the first figure, the simulation represents 20 hours of interactions. In the second figure, the simulation is over 360 hours of interactions. We see from the second of these that the locust swarm migrates down the domain, but that it does broaden, i.e. it is not a true travelling pulse

explored parameter space. The range for the parameters  $B$ ,  $b$ , and  $a$  of the kernel are not well known. Nor are the exchange rates  $R$  and  $G$ . We have chosen values that seem reasonable. Further experimentation, both *in numero* and *in vivo* may be called for.)

## 9.2 General comments about the nonlocal model

The theoretical analysis and the numerical simulations of models of this type are at the infancy stages, and we can at best draw some preliminary conclusions. More work is required to understand the behaviour of such models under various assumptions about the types of interaction terms. Results to



date with one specific model are not promising for the following reasons:

1. The shape of the swarm obtained numerically is that of a very dense and localized peak, unlike the shape of a locust swarm (rather uniformly dense and wide in size).
2. Parameter values specific to locusts do not give a good fit to the numerical model. There is difficulty in obtaining the appropriate behaviour with the given values of wind speed and diffusivity.
3. Preliminary analysis, though tentative, suggests that the width of the peak decreases as the number of individuals in the swarm increases (a greater inward pull). This, like (1) is unrealistic.

Some of these difficulties may be overcome by suitable alterations to this basic model (for example, to prevent the buildup of densities above certain levels). A problem which is less easily corrected is the loss of individuals from the back of the wave. Analysis of related models which include nonlinear density dependence (Mogilner and Edelstein-Keshet, 1997) suggests that non-local models with interactions in a more general class, fail to produce exact travelling pulses that are globally stable to loss of individuals, but succeed in producing quasi-stable swarms. It stands to reason that biological organisms have a finite sensing distance and that interactions with others can at best occur within a limited distance. This argues for the fact that all nonlocal models will contain kernels that have either compact support or that decay rapidly beyond a finite distance. That in turn implies that swarming terms can work to keep group members together only within a limited distance of the swarm edge. If we believe that diffusion-like motion persists beyond this range, it follows that some members of the group may always fall behind and get lost. The analysis to make these informal remarks more rigorous is continuing.

This leads to the conclusion that:

- While long-ranged interactions can contribute to group cohesion, these have limited ability to prevent the loss of individuals from a group. Preliminary investigation of one such model suggests that such terms cannot account for pure travelling pulse solutions.
- Hypothesis 4, though still to be explored in fuller detail, does not appear at this stage, to be supported by numerical results or preliminary analysis.

## 10 Discussion

The models for spatially propagating population phenomena have been, thus far, of a relatively restricted set of classes. In one class are those models in which an invasion takes place, and concomitant population growth feeds it. All models related to the Fisher equation are of this type. In another class are those models in which a band of organisms climbs a gradient of some substance, such as a chemoattractant. The Keller–Segel models are of this

latter type. It is surprising to discover that comparisons between migratory phenomena *per se* and waves of invasion have rarely been made in the literature and that discussions of travelling bands in the context of population movement models are hard to find. The Keller–Segel models and associated chemotactic variants were the only models of this type that we have found. Classification of realistic population movement models that support travelling band solutions (with other mechanisms, higher dimensionality, etc) seems to be an interesting and challenging *mathematical* problem which merits attention.

In this paper, we have shown that hypotheses that seemed biologically reasonable, even those suggested by the biological experts, when incorporated in a set of representative models, failed to produce the ideal behaviour of a travelling band solution. These included nonlinear local as well as long-ranged interactions, variations in the flight speed to respond to density changes, and turning back at the edge of the swarm. It is important to note that the presence of an external gradient (such as nutrient, attractant, or other influence) would introduce an important asymmetry between the front and the back of the wave, making it easier to “cook up” a model with travelling band solutions. Even when a nutrient gradient is biologically reasonable, elaborate and unrealistic assumptions about chemotactic sensitivity and food consumption are needed to prevent organisms from being left behind in the wake of the wave (Odell, 1980).

An important difference in many swarms or flocks of animals that move as cohesive units is that a food source or an external gradient of some type is neither necessary biologically, nor observable in many cases. For example, fish schools and bird flocks maintain a tight formation as they move over considerable distances, without necessarily relying on gradients or forces other than their mutual interactions. Evidence suggests that locusts can sustain swarm cohesion in the absence of such gradients. Explaining such phenomena with mathematical models proves to be a challenging undertaking, because, while interactions coupled with some random and group motion can explain the forward propagation of a front, they are seldom enough to also explain the “catching up” that occurs at the back of the wave.

The failure of our model hypotheses to describe travelling bands appears to hinge strongly on the trailing-edge dispersion that results from the advection-diffusion PDE formalism. In contrast to our difficulties in generating a mathematical description of the coherent, rolling-swarm phenomenon, it is easy to postulate a simple physical model that accounts for cohesion in, say, a water droplet falling through the atmosphere or moving under some other external wind shear. This, too, is a system composed of many units (molecules) that diffuse and interact. But a physical model takes into account a distinct behaviour at the surface of the drop: one assumes discontinuous physical properties, with the interactions between individual molecules reflected at the population level as surface tension at the interface. Even in such systems, evaporation, absent only when the temperature is absolute zero, would tend to lead to loss of particles.

Although continuum models have been used often in modeling spatial distributions of populations, one reason for their failure, in this case is that scaling assumptions implicit in the advection-diffusion approximation are inappropriate. Specifically, advection-diffusion equations are usually derived from random-walk behaviours by assuming that the characteristic time- and space-scales of individual movements are small (“local”) compared to the “global” scales characterizing the variation in the statistical properties of those movements (e.g., average “run” length changes significantly only over a distance of many run lengths). Typically, movement statistics change slowly because individual behaviour is determined by responses to environmental factors (attractants, density of conspecifics, etc.) that themselves vary slowly. We note that in the physical model of rolling swarm dynamics, these relative scalings are reversed: the density of water molecules changes quickly relative to the mean free path of an individual molecule at the edge of the droplet. It is not clear how to derive a behavioural analog of the conservative physical forces underlying surface tension approximations (Cohen and Murray, 1981; Ochoa, 1984). However, it seems likely to us that novel generalizations of surface-tension type physical models will be highly informative, as has been the case in advection-diffusion equations for biological random walks.

An interesting philosophical point is whether one really expects to see in nature anything like the ideal mathematical travelling pulses that have eluded our attempts in this paper. Do we expect to find a perfect pulse or band of locust density whose shape is fixed as it propagates? When our investigation of locust swarms was in its initial stages, we assumed that such behaviour would occur in a suitably derived or adapted model. However, the many guesses and biologically motivated hypotheses proved that this optimism was unfounded.

Interestingly, stemming from the difficulties encountered by in the Keller–Segel–Odell analysis of bacterial chemotaxis, similar philosophical issues were raised. In the case of bacterial chemotaxis, it was remarked experimentally that, on close inspection, what had been seen as a band of bacteria does undergo subtle change, and slows down as it moves. This led to the suggestion that exact travelling waves can be dispensed with, and that gradually slowing or broadening bands can represent the behaviour. An example of this type of analysis with more realistic assumptions on the chemotaxis and nutrient consumption is given in (Novick-Cohen and Segel, 1984).

In the case of locusts, the search for travelling band solutions was fuelled by biological statements that the swarms are cohesive over many days as they sweep through hundreds of kilometers. However, due to the gigantic size of such swarms, good pictures (other than hand-drawn sketches) are hard to find. One aerial photograph of a locust swarm is given on the opening pages of Okubo’s classic (1980) book. From this photograph it appears that the shape of a locust swarm is nowhere near as perfect as we initially surmised. Indeed, its trailing edge is wispy and cloud-like and it is likely that many locusts are left behind as the swarm moves. This means that we should expand the class of

models and solutions considered to include those that broaden, as done in the bacterial chemotaxis model.

With the difficulties of explaining migratory bands using such mathematical formalism, we have come to appreciate that new approaches are required. For the case of locusts, the exact nature of their interactions are still not known biologically, and the problem of modelling them accurately remains an open one. For other aggregations such as fish schools or bird flocks where the aggregate consists of a smaller group, we may need to reject the standard continuum formulation (where all densities are smooth functions) in favour of other approaches.

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## Appendix

### A.1 Analysis of equations (32)

The system of equations (32) is translated into travelling wave coordinates, the two equations are added, and the result integrated to obtain

$$-c(S + F) = AS_z - BSF_z + DF_z - EFS_z - UF. \quad (57)$$

A second equation can be obtained by summing  $DS_z + BSF_z$ . This produces an equation which is linear in  $S_{zz}$  and independent of  $F_{zz}$ .

$$\begin{aligned} -c(DS_z + BSF_z) &= D(AS_z)_z - DF_z(BS)_z + D_zBSF_z \\ &\quad - BS(EFS_z - UF)_z - (D - BS)(RS - GF). \end{aligned} \quad (58)$$

Introducing the variable  $T = S_z$  and linearizing the two previous equations about  $(T, F, S) = (0, 0, 0)$  obtains the system

$$\begin{pmatrix} \dot{T} \\ \dot{F} \\ \dot{S} \end{pmatrix} = \begin{pmatrix} -c/A & -G/A & R/A \\ -A/D & (U-c)/D & -c/D \\ 1 & 0 & 0 \end{pmatrix} \begin{pmatrix} T \\ F \\ S \end{pmatrix} + \mathcal{O}((T + F + S)^2), \quad (59)$$

where the elements of the matrix are evaluated at  $(T, F, S) = (0, 0, 0)$ . Introducing the dimensionless coordinates

$$\zeta = \frac{(U-c)}{D} z, \quad (60)$$

$$s' = \frac{D}{U-c} T, \quad (61)$$

$$f = \frac{U - c}{D} F, \quad (62)$$

$$s = S, \quad (63)$$

and neglecting second and higher order terms, the system becomes

$$\begin{pmatrix} \dot{s}' \\ \dot{f} \\ \dot{s} \end{pmatrix} = \begin{pmatrix} -\alpha/\varepsilon & -\alpha\tilde{G}/\varepsilon & \tilde{R}/\varepsilon \\ -\varepsilon/\alpha & 1 & -1 \\ 1 & 0 & 0 \end{pmatrix} \begin{pmatrix} s' \\ f \\ s \end{pmatrix}. \quad (64)$$

The dimensionless parameters are

$$\alpha = c/(U - c), \quad (65)$$

$$\varepsilon = A/D, \quad (66)$$

$$\tilde{R} = RD/(U - c)^2, \quad (67)$$

$$\tilde{G} = GD/(U - c)^2, \quad (68)$$

where the right hand sides are evaluated at  $(T, F, S) = (0, 0, 0)$ .

The eigenvalues of the system are the roots of the cubic equation

$$\varepsilon\lambda^3 + (\alpha - \varepsilon)\lambda^2 - (\alpha + \tilde{R} + \varepsilon\tilde{G})\lambda + (\tilde{R} - \alpha\tilde{G}) = 0. \quad (69)$$

Although the solutions can be written out explicitly, they are complex, and fail to illuminate the situation. However, if we assume that the eigenvalues are real, which is a minimal requirement for the existence of a pulse solution, then the eigenvectors are of the form

$$\xi = \begin{pmatrix} \lambda \\ (1 + \varepsilon\lambda/\alpha)/(1 - \lambda) \\ 1 \end{pmatrix}. \quad (70)$$

For a pulse solution, the leading stable eigenvector (pulse back) should be in the positive octant, whereas the leading unstable eigenvector (pulse front) should be in the octant where  $s' < 0$ ,  $f > 0$ , and  $s > 0$ . The term '**leading**' indicates the eigenvalues with the largest (signed) value.

Denoting  $\lambda_1$  as the leading unstable eigenvalue, and  $\lambda_2$  as the leading stable eigenvalue, the restrictions are

$$\begin{aligned} 0 < \lambda_1 < 1, \\ -\alpha/\varepsilon < \lambda_2 < 0. \end{aligned} \quad (71)$$

The remaining eigenvalue must be either stable and less than  $\lambda_1$  in magnitude, or unstable and greater than  $\lambda_2$  in magnitude. However, a simple renumbering can allow the conditions

$$\begin{aligned} -\alpha/\varepsilon < \lambda_2 < 0 < \lambda_1 < 1 \\ \lambda_3 < \lambda_1. \end{aligned} \quad (72)$$

### A.2 Moments of the distribution, nonlocal model

We consider the model given by equation (45) with velocity composed of the wind drift,  $u$ , and the swarming velocity  $v$  as given in equation (46). We define the following **Moments** of the distribution:

$$F_0(t) = \int_{-\infty}^{\infty} F(x, t) dx, \quad (73)$$

$$F_1(t) = \int_{-\infty}^{\infty} xF(x, t) dx, \quad (74)$$

$$F_2(t) = \int_{-\infty}^{\infty} x^2 F(x, t) dx. \quad (75)$$

Then note that the **total number of individuals** is  $N = F_0(t)$ , and the **center of mass** of the swarm is  $\bar{X}(t) = F_1/N$ . The **variance of the distribution** is given by

$$V(t) = \frac{1}{N} \int_{-\infty}^{\infty} (x - \bar{X})^2 F(x, t) dx. \quad (76)$$

It can be shown that the relationship between second moment and variance is

$$F_2 = N(V + \bar{X}^2). \quad (77)$$

We can find the appropriate moments of the distribution directly from equation (45), as follows:

**Total number of individuals:** It is simple to show that the total number of individuals is conserved by integrating both sides of equation (45) over space, and showing that terms on the right hand side are zero (after integrating by parts and making the appropriate assumptions about behaviour at  $\pm \infty$ ). We omit the details. Thus

$$\frac{dF_0}{dt} = 0 \quad (78)$$

so that  $F_0$ , and thus also  $N$  is constant. This is clear from the fact that equation (45) includes no source-sink terms, only terms for redistribution over space. Thus the total number of individuals throughout the (unbounded) region is constant.

**Center of mass:** Multiply both sides of equation (4) by  $x$  and integrate to obtain:

$$\frac{\partial}{\partial t} \int_{-\infty}^{\infty} xF dx = \int_{-\infty}^{\infty} x \left( D \frac{\partial^2 F}{\partial x^2} - \frac{\partial}{\partial x} ((w + v)F) \right) dx. \quad (79)$$

Integrating by parts on the right hand side leads to

$$\begin{aligned} \frac{\partial}{\partial t} \int_{-\infty}^{\infty} x F dx &= \left[ x \left( D \frac{\partial F}{\partial x} - (w + v) F \right) \right]_{-\infty}^{\infty} \\ &\quad - \int_{-\infty}^{\infty} \left( D \frac{\partial F}{\partial x} - (w + v) F \right) dx . \end{aligned} \quad (80)$$

Appropriate assumptions about the kernel  $K$  will guarantee that the velocities  $(w + v)$  remain bounded at  $\pm \infty$ . If we assume that at  $x \rightarrow \pm \infty$  the swarm density, and its derivative, go to zero (faster than a power of  $1/x$ ) we obtain (after a second integration by parts that removes the term  $D\partial F/\partial x$  from the remaining integral):

$$\frac{dF_1}{dt} = \int_{-\infty}^{\infty} (w + v) F dx = wN + \int_{-\infty}^{\infty} (K * F) F dx . \quad (81)$$

Thus

$$\frac{d\bar{X}}{dt} = w + \frac{1}{N} \int_{-\infty}^{\infty} (K * F) F dx . \quad (82)$$

Thus the center of mass moves with a velocity that consists of (a) the wind drift and (b) a swarming terms that is superimposed on this drift. However, it will be seen further that when  $K$  is odd, the swarming terms make no contribution to the velocity of the center of mass.

**Variance of the distribution:** We multiply both sides of equation (45) by  $(x - \bar{X})^2$  and integrate to obtain:

$$\frac{\partial}{\partial t} \int_{-\infty}^{\infty} (x - \bar{X})^2 F dx = \int_{-\infty}^{\infty} (x - \bar{X})^2 \left( D \frac{\partial^2 F}{\partial x^2} - \frac{\partial}{\partial x} [(w + v) F] \right) dx . \quad (83)$$

We integrate by parts as before, and assume that  $F(x, t)$  and its derivative go to zero at  $\pm \infty$  faster than  $1/(x - \bar{X})^2$ , to arrive at the following:

$$\frac{dNV(t)}{dt} = 2D \int_{-\infty}^{\infty} F dx + 2 \int_{-\infty}^{\infty} (x - \bar{X}) (w + v) F dx . \quad (84)$$

We use the definitions of  $N$  and  $v$  and the fact that  $N$  is constant to simplify this to

$$\frac{dV(t)}{dt} = 2D + \frac{2}{N} \int_{-\infty}^{\infty} (x - \bar{X}) (w + K * F) F dx . \quad (85)$$

Since the wind velocity,  $w$  is assumed to be constant, it is easy to show that it leads to a term that drops out of the expression, resulting in

$$\frac{dV(t)}{dt} = 2D + \frac{2}{N} \int_{-\infty}^{\infty} (x - \bar{X}) (K * F) F dx . \quad (86)$$

This result shows that diffusion tends to increase the variance at a constant rate, and it is up to swarming term in the integral to reverse this effect, if at all.

**Width of the swarm:** The width of the swarm,  $W$  is related to its variance by  $W = \sqrt{V}$ . Thus, once the variance is known, so is the width.

### A.3 Small swarm approximation

If the swarm is small enough that the interaction distances are larger than the size of the swarm, then the kernel can be approximated locally fairly well by a few term in its Taylor series:

$$K(x) = x \left( \frac{A}{a^2} e^{-(x/a)^2} - \frac{B}{b^2} e^{-(x/b)^2} \right) \quad (87)$$

$$= x \left[ \frac{A}{a^2} \left( 1 - \frac{x^2}{a^2} + \frac{1}{2} \frac{x^4}{a^4} - \frac{1}{3!} \frac{x^6}{a^6} + \dots \right) - \frac{B}{b^2} \left( 1 - \frac{x^2}{b^2} + \frac{1}{2} \frac{x^4}{b^4} - \frac{1}{3!} \frac{x^6}{b^6} + \dots \right) \right] \quad (88)$$

$$= \left[ \frac{A}{a^2} - \frac{B}{b^2} \right] x - \left[ \frac{A}{a^4} - \frac{B}{b^4} \right] x^3 + \frac{1}{2} \left[ \frac{A}{a^6} - \frac{B}{b^6} \right] x^5 + \dots \quad (89)$$

In this case, we can also calculate the first few terms in the swarming-induced velocity term  $v = K * F$  as follows:

$$v = K * F = \int_{-\infty}^{\infty} K(x - x') F(x') dx' \quad (90)$$

$$= \left[ \frac{A}{a^2} - \frac{B}{b^2} \right] \int_{-\infty}^{\infty} (x - x') F(x') dx' - \left[ \frac{A}{a^4} - \frac{B}{b^4} \right] \int_{-\infty}^{\infty} (x - x')^3 F(x') dx' \quad (91)$$

$$+ \frac{1}{2} \left[ \frac{A}{a^6} - \frac{B}{b^6} \right] \int_{-\infty}^{\infty} (x - x')^5 F(x') dx' + \dots \quad (92)$$

$$\approx \left[ \frac{A}{a^2} - \frac{B}{b^2} \right] (x - \bar{X}) N - \left[ \frac{A}{a^4} - \frac{B}{b^4} \right] \left( x^3 - 3x^2 \bar{X} + 3x(V + \bar{X}^2) - \frac{F_3}{N} \right) N \quad (93)$$

where  $F_3$  and higher moments of the distribution appear. For the small swarm approximation, the higher moments should be small, and can be neglected, but this is not true for large swarms. Applying this approximation to the aggregate swarm properties described in the previous section gives the following leading order behaviour:

**Center of mass:**

$$\frac{d\bar{X}}{dt} = w \quad (94)$$



The center of mass just moves with the wind speed. It can be shown that the higher order terms vanish when the kernel is odd. The swarming term in that case does not contribute to group motion, only to internal motion in the swarm. This is not the case if the kernel is an even function (Mogilner and Edelstein-Keshet, 1997).

#### Variance of the distribution:

$$\frac{dV(t)}{dt} = 2D + 2 \left[ \frac{A}{a^2} - \frac{B}{b^2} \right] \int_{-\infty}^{\infty} (x - \bar{X})^2 F dx + \dots \quad (95)$$

This can then be simplified to

$$\frac{dV(t)}{dt} = 2D - 2 \left[ \frac{B}{b^2} - \frac{A}{a^2} \right] NV + \dots \quad (96)$$

The leading term in the expansion suggests that a possibility arises (when the term in square brackets is positive) that the effect of the swarming kernel to leading order is to reverse the widening effect of the diffusion in the model. When this happens, we expect that the variance would stabilize (but only to leading order) at the approximate value

$$V = \frac{D}{\left[ \frac{B}{b^2} - \frac{A}{a^2} \right] N} \quad (97)$$

This result also suggests that the width of the swarm, according to a leading order estimate has the form

$$W = \sqrt{V} \approx D^{1/2} \left[ \frac{B}{b^2} - \frac{A}{a^2} \right]^{-1/2} N^{-1/2} \quad (98)$$

which agrees with a result obtained by a perturbation expansion in the case of small diffusion  $D = \varepsilon$ . However, as noted in the text, this approximation has neglected the effects of higher order terms and may be misleading. In particular, for swarms that are not small, this approximation may be meaningless.

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