

# Mathematical models of swarming and social aggregation

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**Abstract**— I survey some of the problems (both mathematical and biological) connected with aggregation of social organisms and indicate some mathematical and modelling challenges. I describe recent work with colleagues on swarming behaviour. Examples discussed include (1) a model for locust migration swarms, (2) the effect of non-local interactions on swarm shape and dynamics, and (3) an individual-based model for the spacing of neighbors in a group.

## I. Background and previous work

Many chemical and physical systems are characterized by formation of patterns, clusters and aggregates, or phenomena such as wave and pulse propagation. In biology, swarming and social aggregation form a rich and diverse collection of such phenomena. The size scale of groups ranges from microscopic cellular populations to herds, flocks, schools, and swarms of macroscopic, and sometimes enormous size. In some cases, notably swarms of locusts, these aggregates have serious impact on ecology and human activity.

These examples, and many others, have motivated studies in which both biological aspects as well as theoretical modeling and mathematical aspects of the phenomena have been investigated. Early works in the 1950's were largely descriptive biological investigations of fish schools [3] or bird flocks [4]. Some theoretical concepts for the formation of herds and groups were discussed in a classic paper by Hamilton [9]. See also [22] for simulations and a model for animal group structure. The classic book by Okubo(1980) [16] (recently modernized [18]) presented some aspects of the initial mathematical concepts applied to studying swarms. Since that time, the literature has grown substantially, with many significant contributions addressing such problems from the perspective of biology, mathematical modeling, or physics. Notable among these are [17, 19, 6, 20, 25, 7, 5, 15].

## II. Biological questions

As we will see, questions of interest to investigators from different disciplines have distinct flavor. A brief

sample of questions posed by biologists is concentrated below:

1. **Is there a functional purpose to the aggregate?** For example, plankton patches that result from hydrodynamic effects appear to have no biological purpose. Such emergent phenomena contrast with, for example, the slime mould *Dictyostelium discoideum*, whose aggregates form multicellular structures specialized to promote survival under conditions of starvation of (part of) the group as dispersed spores. Similarly, bird flocks and fish schools afford protection to members from predators, opportunities for mating, for cooperative foraging, or for safer long-range migration.
2. **How do ecological factors affect the aggregation?** Environmental factors such as availability of resources, predation pressure, temperature, light, and other factors are known to influence the behavior of individuals, as well as the tendency to aggregate.
3. Conversely, **how does aggregation affect ecological phenomena?** The density of a population is known to influence disease transmission rates, predation rates, selection pressure, and evolution of new traits. It also influences how humans exploit a resource. Schools and shoals of fish have been so efficiently exploited by fisheries, as to lead to mass extinction and collapse.

## III. Theoretical questions

### A. What causes aggregations to form?

Both intrinsic and extrinsic effects can lead to clustering and aggregation. Direct attraction and repulsion to other members of one's own kind are intrinsic to many species. Locusts, for example, have phases in which they lead a solitary life, and phases of gregarious behavior in which attraction and mutual excitation lead to swarming.

Insect swarms, some fish schools, and many other groups form as a result of attraction to some external

marker, food source, or gradient. Patchy distribution of resources in the environment can lead to clustering (and, in some cases, to active aggregation: see details about locust phase transitions described below.) Physical forces and "convergence zones" or interplay between physics of fluid and properties of the living cells have also been investigated in connection with pattern formation (e.g. by Kessler, Hill [11] and others).

### B. What causes aggregations to persist?

Some swarms serve a limited and ephemeral purpose, and disappear when this purpose no longer exists. This is the case in some mating swarms, or congregations exploiting a concentrated resource. The swarming phase of the desert locust depends on weather conditions, wind direction, state of maturity, and phase of the individuals.

### C. How do we bridge the individual and collective levels?

Can we understand the behavior of the group if we know something about the individual rules of behavior and interactions? Addressing this issue forms one of the main goals of mathematical modeling. This realm builds on experience from physical models that bridges the gap between particles and continua. Partial differential equations, stochastic differential equations, and other mathematical methods, provide useful analytical tools. These lead to insights in simpler models. Simulations help incorporate biological realism in more detailed models. However, challenges abound: One, is how to deal with the complexity of nonlinear interactions; another, is how to faithfully represent the phenomena without introducing artifacts due to the model. (See discussion below.)

Can we learn something about the organism behavior by studying the aggregate? This question is related to the former, but with a top-down approach. In some cases, we might wish to infer aspects of individual behavior and physiological parameters from observations of macroscopic collective phenomena. But this "inverse problem" is quite hard, since many diverse rules can lead to aggregates that look and behave quite similarly. (For example, simulations of fish schools based on very diverse sets of rules, lead to seemingly realistic dynamics [20].)

### D. What determines the shape and geometry of the swarm?

Aggregates and groups of animals occur in 1 dimension (walking along trails), 2 dimensions (in large migration herds) and 3 dimensions (flocks and schools). How does the dimensionality influence the shape of the aggregate? Sizes of groups vary from small handfuls to billions. How does group size affect the be-

haviour of the group? How does it affect the structure and the density of packing? Some swarms have well-defined sharp "fronts", others are more diffuse and ill-defined. Densities in the interior of an aggregate are often relatively constant, meaning that individuals have some preferred spacing behavior. How is this achieved? Mathematical modeling can address some of these questions. (See for example [13] where it has been argued that repulsion between individuals has to have a larger density dependence than attraction to obtain uniform density in swarms.)

## IV. A Taxonomy of models

In this section, I briefly indicate some of the common approaches used to model aggregation. While the list is presented as contrasting pairs, many modelers have combined multiple approaches to studying their system of interest

*Eulerian versus Lagrangian:* This dichotomy describes the distinction between models in which the position (velocity, state, etc) of each individual is represented, versus those that treat the density of the population over space. The dichotomy depends on our point of view: are we following a given individual to see how it is affected by its neighbors, or are we watching the herd move past us as a density wave [16]. In the classical literature, Eulerian models have tended to dominate since they lead to well-studied partial differential equations. However individual-based Lagrangian models are becoming more popular [5, 12].

*Deterministic versus stochastic:* Noise plays a dominant role at small spatial scales, and short time scales. To some extent, all biological systems have inherent variability and random effects, but in some cases, we can represent the behavior fairly well by averaging out and using a mean-field approach. In other cases, considering fluctuations is important [15].

*Local interactions versus long-ranged interactions:* Do individuals affect one another only by close-range (e.g. tactile) interactions? How do we take into account visual stimuli, or chemical signaling? Such effects can lead to attraction or repulsion at a distance. Models that incorporate such nonlocal effects generally contain integro-differential equations [10, 13].

*Analytic versus simulation models:* There is something to be gained from each approach. The former forces us to simplify the ideas and treat minimal models to the full extent possible. Many of these models are quite divorced from biological reality. This shortcoming can be addressed by more detailed simulations.

## V. Mathematical Challenges

In order to understand aggregation, we must also understand dispersal. Traditionally, random motion of a population  $p(\mathbf{x}, t)$  is represented by the simple diffu-

sion equation

$$p_t = D\Delta p.$$

This equation has the defect of predicting an infinitely fast propagation speed. (Particles concentrated at the origin at  $t = 0$  have some small but finite probability of getting arbitrarily far within an arbitrarily small time interval.) As discussed in an excellent review by Hadeller [8], this results from the feature that particles make any number of independent, uncorrelated moves per unit time. To correct such defects, some modelers consider a correlated random walk, where particles move at some fixed velocity,  $v$  and reverse direction by a Poisson process with parameter  $\mu/2$ . In 1D, this leads to the system of p.d.e.'s for the densities of individuals moving left,  $p^-(x, t)$ , and right,  $p^+(x, t)$ :

$$\begin{aligned} p_t^+ + vp_x^+ &= \frac{\mu}{2}(p^- - p^+), \\ p_t^- - vp_x^- &= \frac{\mu}{2}(p^+ - p^-). \end{aligned} \quad (1)$$

By differentiating one equation with respect to  $t$ , the other with respect to  $x$ , and eliminating cross terms  $p_{xt}$ , the above system can be rewritten in the form known as the telegraph equation,

$$\frac{1}{\mu}p_{tt} + p_t = \frac{v^2}{\mu}p_{xx}.$$

This equation can be approximated by the diffusion equation in the case that organisms move rapidly and reverse their direction of motion often, provided we assume that the ratio  $D = v^2/\mu$  approaches a constant. (The constant is the diffusion coefficient, or the random motility coefficient.) This illustrates the fact that scaling space and time appropriately is nontrivial: different scalings would, in general, lead to distinct model behavior, and possibly, to artifacts.

The above system and its associated second order p.d.e. can be generalized to cases where the velocity takes values in some range (rather than a precise single value), leading to a so-called velocity jump process summarized in an integro- partial differential equation [8, 19]. There is, however, some difficulty in generalizing this framework to higher dimensions, e.g. to motion in the plane or in 3D, (a problem if we are to apply the theory to flocks or herds). Hadeller (1999) [8] notes that the generalized version of the telegraph equation

$$\tau p_{tt} + p_t = D\Delta p$$

does not preserve positivity of  $p$ , making solutions unbiological. Further, this equation (unlike the 1D version) is not derivable from a stochastic process in higher dimensions. These examples point to issues that continue to provide mathematical challenges.

## VI. Examples of Models

In this section, I summarize a number of recent models and examples based on my own interests and research. This work has been carried out over past years with the colleagues A Mogilner (UC Davis), D Grunbaum (UW), and J Watmough (UNB, Canada).

### A. Locusts

Locusts are economically devastating insect pests. The desert locust *Schistocerca gregaria* forms airborne swarms of immense size: up to billions of individuals, spread out over many kilometers, traveling at speeds of 10-15 km/hr for distances of hundreds and even thousands of kilometers. Figure 1 illustrates the structure described in [1] for a typical locust swarm: locusts take off against the wind direction at the rear of the swarm, turn to fly downwind (direction of arrow), and land towards the front to forage. (The detailed structure is hard to quantify due to the size of most swarms.)

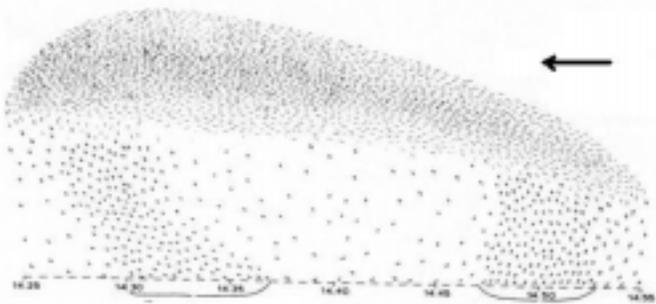


Figure 1: A rolling locust swarm; after [1]. The arrow indicates direction of motion. Shown on the bottom are the landing zone (left) and takeoff zone (right).

It is of interest to understand how swarms of this magnitude can stay together as they migrate, over periods of many days. Given their size and density, a continuum approach seemed appropriate in a model [14] described briefly below. An abstraction was to represent the swarm in 1D as a density profile along a transect parallel to the direction of motion (assumed to be in simple straight path). The variable  $x$  was thus position along the axis of the swarm, with  $x \rightarrow +\infty$  far ahead of the front and  $x \rightarrow -\infty$  far behind the back of the swarm (Reverse Fig 1).

The model we investigated considered exchange between stationary individuals on the ground  $S(x, t)$  and those flying above,  $F(x, t)$  with a basic system of equations:

$$\begin{aligned} S_t &= -R(S, F)S + G(S, F)F, \\ F_t &= DF_{xx} - UF_x + R(S, F)S - G(S, F)F \end{aligned} \quad (2)$$

Here  $R, G$  are density-dependent exchange rates between stationary and flying locusts.  $D$  is random

motion due to atmospheric turbulence and irregular flight paths of individuals,  $U$  is simple drift speed due to wind and active flight.  $D, U$  may be density dependent, i.e.  $D = D(S, F), U = U(S, F)$ , but were here assumed to be local in nature: individuals interact only with those in close proximity. The question addressed in this model was whether (and under what circumstances) such models give rise to a swarm that migrates with some fixed speed, while preserving some basic shape.

Transforming to moving coordinate  $z = x - ct$ , we looked for traveling band, strictly nonnegative solutions in which  $F, S \rightarrow 0$  as  $z \rightarrow \pm\infty$  (no individuals far out in front of or in back of the swarm) and where the total number of individuals in the swarm is conserved. A notable lack in the literature of models for such pulse-like solutions in population migration was apparent when this work was undertaken.

Under this transformation, the system of equations (2) becomes a pair of ordinary differential equations. Conservation and boundary conditions leads to reduction of dimensionality and simplification to the system shown below [14]:

$$\begin{aligned} -cS_z &= -R(S, F)S + G(S, F)F, \\ DF_z &= -cS + (U - c)F \end{aligned} \quad (3)$$

This system can be studied in the phase plane. Specifically, biologically relevant traveling band solutions correspond to strictly nonnegative homoclinic trajectories based at the origin. It was shown in [14] that such trajectories cannot exist. The argument consisted of analysis of the eigenvectors at the origin: To obtain such homoclinic trajectories, the eigenvectors should have the configuration shown in Figure 2, but for any reasonable assumptions about  $R, G, D, U$ , this configuration cannot be obtained.

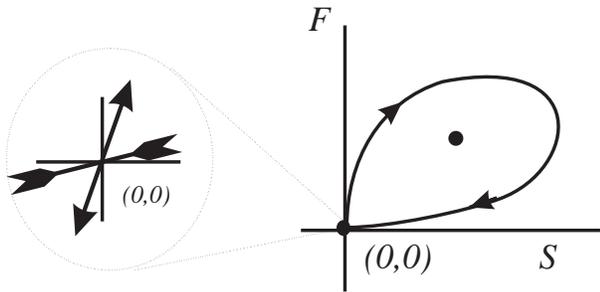


Figure 2: .

The basic reason for this non-existence result is that the model inherits problems from the random motion represented by the diffusion term. The problem, specifically, is that diffusion leads to a continual loss of individuals from the back of the swarm. Once an individual strays far behind the others, there is no

mechanism in place for returning to the group. Unfortunately, this defect cannot be cured by biologically relevant density dependent diffusion or drift, since the problems occur at low densities. (See detailed arguments in [14].) Negative results in this example motivated investigation of the effect of non-local interaction terms on swarm shape and stability. These are described in the next section.

A related problem relevant to locusts is what causes aggregation to occur in the first place. Locusts have two forms: in the 'solitary' phase, they avoid each other, whereas in the 'gregarious' phase they attract one another and swarm. Recent experimental work in the group of Simpson [21, 23, 24] has shown that a transition from solitary to a gregarious form takes place under crowded conditions. The stimulus from neighboring locusts has been identified as mechanical stimulation of the back legs. The change between states occurs over a timescale of several hours and is reversible. There is also evidence that this aspect is passed from one generation to the next, i.e. that gregarious female locusts will produce gregarious offspring. This area is ripe for further modeling.

## VII. Non-local models

To address some of the modeling issues raised in the locust swarm models [14], Mogilner and I [13] investigated a model with attraction and repulsion between organisms, and with non-local interactions. For  $p(x, t)$  population density, the model is

$$\frac{\partial p}{\partial t} = \frac{\partial}{\partial x} \left( D \frac{\partial p}{\partial x} - Vp \right)$$

where the group velocity,  $V$  is given by an expression involving convolutions

$$V(p) = cp + AK_a * p - RpK_r * p$$

with

$$K_j * p = \int K_j(x - x')p(x')dx', \quad j = a, r$$

Terms in the above integro-pde include attraction and repulsion, the latter having higher density-dependence than the former, as well as ordinary density-dependent local drift term  $cp$ .  $K_a(x), K_r(x)$  are kernels that represent the spatial extent of interactions between one individual and its neighbors a distance  $x$  away. It was found that the higher density-dependence of the repulsion term was essential to control the density of the interior of the swarm, and avoid unrealistically crowded and compact distributions.

Kernels should be odd functions to model the (anti-symmetric) effects of neighbors in front or behind an individual on its motion (either hurrying forward or lagging behind). The relative magnitudes ( $A, R$ ) and the spatial ranges of the attraction and repulsion determine how such interactions affect the swarm.

## A. Onset of aggregation

One case considered was that of normalized kernels

$$K_j(x) = -\frac{x}{2a_j^2} e^{-x^2/2a_j^2} \quad a_j = a, r.$$

Here  $a_j$  governs the spatial extent of the given effect. A similar odd kernel was used in a model by Kawasaki [10]. To investigate the onset of aggregation, we determined whether perturbing a uniform steady state density  $P$ , with small perturbations (wavenumber  $q$ )

$$p(x, t) = P + \epsilon \exp \lambda t \exp iqx$$

lead to growth or decay. (Growth signifies that the original homogeneous distribution is breaking up into aggregates). This question can be investigated by simple linear stability analysis. As in many integro-pde models, the expressions that determine the sign of the (real part of the) eigenvalues involves Fourier transforms of the kernels, which, in this case, are

$$\hat{K}_j(q) = iqa_j \exp(-q^2 a_j^2/2) \quad a_j = a, r$$

It was shown in [13] that swarming will occur when

$$P \left( Aae^{(-q^2 a^2/2)} - RrPe^{(-q^2 r^2/2)} \right) - D > 0$$

This basically says that attraction is stronger (in some sense) than combined effects of repulsion and random motion. Moreover, the most unstable wavenumber has the property that

$$q^2 = 2 \frac{\ln(Aa^3) - \ln(RPr^3)}{a^2 - r^2}.$$

This result can be interpreted: it means that either attraction has longer range ( $r < a$ ) and is stronger ( $RP < A$ ), a case that pertains to organisms that seek each other's company, but avoid close contact or *both* inequalities are reversed, which would mean that organisms avoid one another unless in close proximity, and only then attract. (The latter is less relevant to most biological aggregations.)

## B. Swarm shape

A simpler set of interaction kernels (odd step functions with spatial extent  $a = r$  and normalized height) were used to investigate the shape and cohesion of the swarms in this model. These kernels account for a finite range of attraction and repulsion between organisms, but the interaction is simplified as roughly constant over that range.

The following results were obtained (by analysis and, for purposes of comparison, by numerical simulation).

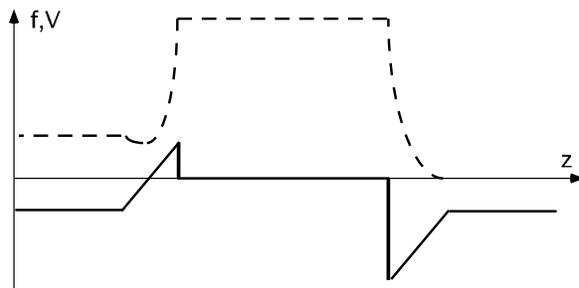


Figure 3: Idealized shape of swarm obtained with non-local model (dotted lines) and velocity of individuals (solid line). In simulations, the flat top is actually pointed at the front and somewhat rounded towards the rear of the swarm.

- The density of the interior of the swarm depends on the relative strengths of attraction and repulsion: higher attraction leads to more crowded, smaller diameter swarms. Figure 3 shows an idealized version of such a shape.)
- Repulsion (in particular, the fact that density dependence of repulsion is higher) leads to a relatively constant density away from the swarm edges. Repulsion keeps the swarm from collapsing to a tight cluster.
- The non-local nature of the model leads to relatively sharp front and back edges. Individuals too far forward tend to move back into the swarm, whereas those falling behind tend to move forward faster to catch up. (See solid curve in Figure 3.) However, there is some continual loss of individuals that get left behind unless random motion is absent ( $D = 0$ ). This loss eventually leads to dissipation of the swarm.
- The lifetime of a swarm of diameter  $L$  is exponentially large, with the following parameter dependence:

$$T = \frac{LR}{cA} \exp \left[ \frac{A^2 r}{4RD} \left( 1 - \frac{4c}{A} \right) \right]$$

This shows that repulsion and random motion accelerate breakup (since  $RD$  appears in the denominator in the exponential), but also that it is important to have non-local attraction stronger than simple local drift to preserve the swarm over a long time.

- If random motion is density dependent so that  $D \rightarrow 0$  as the density of the population decreases, there is a locally stable true traveling band solution. However, this solution is not globally stable.

### VIII. Individual-based models

Recent work [12] explores the Lagrangian-based approach in which *spacing between neighbors* in a group is of primary interest. Positions of individuals relative to the group centroid,  $\mathbf{x}_i(t), i = 1..N$  are defined. It is assumed that rearrangement occurs through mutual attraction and repulsion. Typically, we consider

$$\frac{d\mathbf{x}}{dt} = \mathbf{V},$$

where  $\mathbf{V} = \{V_i\}_{i=1}^N$  is a vector of individual velocities. We neglect inertial motion, and assume that velocities are proportional to forces in steady state motion

$$\mathbf{V} = \mathbf{F}^r - \mathbf{F}^a,$$

where  $\mathbf{F}^a, \mathbf{F}^r$ , are attraction and repulsion. Specific forms considered for the distance dependence of these interaction forces in 1D include inverse powers

$$F^a(x) = \frac{A}{x^m}, \quad F^r(x) = \frac{R}{x^n}, \quad (4)$$

and exponentials

$$F^a(x) = A \operatorname{sign}(x) e^{-\frac{|x|}{a}},$$

(Similarly for  $F^r(x)$ ). Here  $A, R$  are magnitudes of attraction, repulsion, and  $a, r$  are parameters governing the decay over distance of the effects.

An attractive feature of these forms of interaction functions, used throughout the biological literature to represent attraction and repulsion, e.g. between fish in a school [3] or between individuals in a herd or other social aggregation [2] is that they are expressible as the gradient of some potential function. This means that there is a *Lyapunov function*, whose minima correspond to stable stationary states of the system. (For these forces, this function is easily constructed.) This fact has been mentioned [2] but has not been exploited in previous analysis of individual spacing distances.

The potential function corresponding to exponential interactions is

$$P(x) = Rr \exp(-|x|/r) - Aa \exp(-|x|/a).$$

and the Lyapunov function is formed by superimposing such potentials:

$$W(\mathbf{x}) = \frac{1}{2} \sum_{i,j=1}^N P(x_i - x_j).$$

where the sum is taken over individuals.

In the case of exponential interactions, with strong short-ranged repulsion and long-ranged attraction

( $R > A, a > r$ ) two organisms would prefer to stay a distance  $s$  apart given by:

$$s = \frac{a}{((a/r) - 1)} \ln(R/A).$$

However, when the group is larger, due to interactions with non-nearest neighbors, we showed that the actual individual distance shrinks. It is found that if repulsion is not sufficiently strong, the group will collapse into a tight cluster. Under the appropriate conditions, the finite distance between neighbors in a large group with equidistant neighbors can be estimated: This is done by finding the minimum of the Lyapunov function. The result is that the **individual distance** in a large group is

$$\delta \simeq \sqrt{12 \frac{Rr^2 - Aa^2}{R - A}}.$$

This distance is smaller than the distance maintained between an isolated pair ( $\delta < s$ ). The form of the expression reveals precise conditions on the attraction and repulsion to avoid collapse of the swarm to an infinitely tight cluster, namely, it must be true that

$$Rr^2 > Aa^2, R > A.$$

The reversed inequality pair is also possible theoretically, but of lesser biological relevance.

Simulations exploring such attraction-repulsion interactions (see Figure 4) have been used to investigate such interactions in groups moving in 2D.

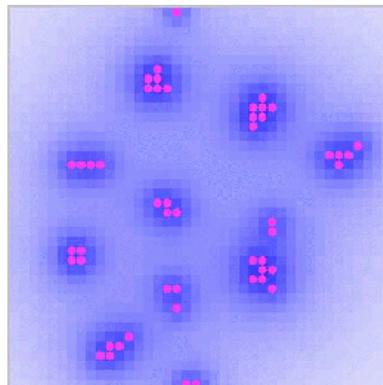


Figure 4: Cellular automata simulations written by Athan Spiros: a group of fifty individuals with inverse-power attraction and repulsion; eq. 4 with  $A = 14, R = 9.5, a = 2.0, r = 3.0$ . Groups are still merging and collapsing. Available interactively online at [www.math.ubc.ca/~ais/chemosim](http://www.math.ubc.ca/~ais/chemosim)

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