**Mathematical Biology**

A. Mogilner · L. Edelstein-Keshet · L. Bent · A. Spiros

# Mutual interactions, potentials, and individual distance in a social aggregation

**Abstract.** We formulate a Lagrangian (individual-based) model to investigate the spacing of individuals in a social aggregate (e.g., swarm, flock, school, or herd). Mutual interactions of swarm members have been expressed as the gradient of a potential function in previous theoretical studies. In this specific case, one can construct a Lyapunov function, whose minima correspond to stable stationary states of the system. The range of repulsion ($r$) and attraction ($a$) must satisfy $r < a$ for cohesive groups (i.e., short range repulsion and long range attraction). We show quantitatively how repulsion must dominate attraction ($Rr^{d+1} > cAa^{d+1}$ where $R$, $A$ are magnitudes, $c$ is a constant of order 1, and $d$ is the space dimension) to avoid collapse of the group to a tight cluster. We also verify the existence of a well-spaced locally stable state, having a characteristic individual distance. When the number of individuals in a group increases, a dichotomy occurs between swarms in which individual distance is preserved versus those in which the physical size of the group is maintained at the expense of greater crowding.

## 1. Introduction

Social organization is one of the fundamental aspects of animal behavior. Examples of social groups appear at every size scale, from the macroscopic herds of wildebeest, flocks of birds, and schools of fish, to the smaller insect swarms, and microscopic colonies of bacteria. This paper focuses on the configuration of members of a group and the nature of mutual interactions that lead to clustering, uniform spacing, or self-avoidance of the members. The central question we address is what class of interactions result in a relatively constant **individual distance** (and consequently constant density) in the interior of the aggregate.

Mathematical modelling has addressed how social groups form, join, or split up into smaller ones, how they undergo structural organization into well-ordered

A. Mogilner: Dept. of Mathematics and Center for Genetics and Development, Univ. of California, Davis, CA, 95616, USA. e-mail: mogilner@math.ucdavis.edu

L. Edelstein-Keshet: Dept. of Mathematics, Univ. of British Columbia, Vancouver, BC V6T 1Z2, Canada. e-mail: keshet@math.ubc.ca

L. Bent: Dept. of Computer Science and Engineering, Univ. of California, San Diego, CA, 92093, USA

A. Spiros: In Silico Biosci, Portland, OR, USA.
e-mail: athan@in-silico-biosciences.com

arrays, what are ecological implications of groups, and how individual behavior, combined with environmental factors affect swarming behavior (Okubo, 1980; Grunbaum and Okubo, 1994; Parrish et al., 1997; Parrish and Edelstein-Keshet, 1999).

We here consider discrete collections of individuals, following a Lagrangian rather than Eulerian approach, in contrast to an earlier work (Mogilner and Edelstein-Keshet, 1999). We also assume that effective forces of interaction are gradient forces, an assumption that fits well in the context of much of the previous modelling work in this field. The main purpose of our paper is to exploit the special mathematical feature of classic interaction forces, i.e. their gradient character, to derive analytic insight in answering several questions: (1) What quantitative relationship between attraction and repulsion interactions keep the group from collapsing to a tight cluster? (2) What maintains a cohesive group? and (3) Under what circumstances will individuals attain a uniform average distance apart, and how does this *individual distance* depend on the attraction-repulsion forces?

### 1.1. Biological background

Ecological considerations that lead to mutual attraction between conspecifics include mating or predator avoidance: for example, see the idea of the "Selfish Herd" (Hamilton, 1971). At the same time, the competition for food and resources prevents individuals from crowding too closely together and results in an effective repulsion. One or the other of these influences may change if the environmental conditions, predation pressure, or resource availability changes. For a given set of conditions, the ultimate balance of these effects determines the structure of a group of given size.

One of the key observations for many social groups is that there is a species-specific **individual distance** (Conder, 1949; Emlen, 1952; Miller and Stephen, 1966), i.e. spacing between the individuals which characterizes a group – whether sedentary or moving – under constant environmental conditions. Emlen (1952) states that flocks of gulls are spaced one body length apart. Conder (1949) found a spacing of 2–3 body lengths in tufted ducks. Another observation is that in most flocks, this individual distance does not change as the population size of the flock increases. For example, Miller and Stephen (1966) state that sandhill cranes maintain an individual distance of about 5.8 ft, regardless of flock size. Breder (1954) followed a number of species of fish that school, and measured the individual spacing in units of the fish body length, showing that individuals are separated by 0.16–0.25 body length units. The spacing can vary with the functional significance of the aggregate. Newlands (2002) analyzed tuna shoal images, and computed different inter-individual distances for formations such as 1D "soldier" schools, 2D "surface sheets", and 3D "ball" shaped schools. Spacing can also vary with environmental conditions. For example, anchovy schools increase their separation distance at night compared to daytime (Aoki and Inagaki, 1988). Recent measurements for fiddler crabs by Viscido and Wethey (2002) illustrate the effect of a predator on this inter-individual distance.

Constant individual distance implies that the density inside a swarm or group is fairly uniform and independent of the population size, except near the edge of a swarm – see, for example sharper density variations at the front of a wildebeest herd (Sinclair, 1977), and a locust hopper band (Uvarov, 1928). If the environment changes, then the structure of the group would also be expected to change, as would the individual distance of its members.

## 1.2. *Previous theoretical and modelling work*

Previous theoretical and modelling efforts fall into a number of categories. Many of the original ideas about group spacing were formulated qualitatively (Parr, 1927), or using simple formulae and graphs that applied to two individuals in isolation (Breder, 1954; Breder, 1951). Some recent models have been simulated with rules governing the motion of individuals and the decisions that they make about joining or leaving a group, speeding up or slowing down (Gueron et al., 1996), evading a predator (Vabo and Nottestad, 1997), or clustering when a predator approaches (Viscido and Wethey, 2002; Viscido et al., 2001). Other models use differential equations to follow aggregation dynamics using either *Eulerian* or *Lagrangian* approaches. The Eulerian approach applies nonlinear partial differential equations (PDE's) to follow the evolving swarm density (Okubo, 1980; Holmes et al., 1994). This is appealing from the analytical standpoint, since PDE's are mathematically well-studied. However, there are numerous situations where a continuous description of the swarm does not apply, (e.g., when the number of organisms in the swarm is small) and then the Lagrangian approach, following the coordinates of individuals is preferable (Turchin, 1989). These are traditionally more difficult to analyze, so most previous work is focused on simulations (Sakai, 1973; Suzuki and Sakai, 1973). Flierl et al. (1999) go further than others in deriving Eulerian equivalents of Lagrangian models. See also reviews in (Okubo, 1986; Grunbaum and Okubo, 1994).

Lagrangian models can be subdivided further into several types: (a) those in which individuals react to "forces" by accelerating, versus those in which inertial forces are neglected, (b) those in which net forces are superposition of pairwise interactions summed over the group, or some other combination. For example, reaction can depend only on the nearest neighbor (Huth and Wissel, 1992), or on a hierarchy of decisions (Gueron et al., 1996). (c) A variety of effective forces are considered in some models (Sakai, 1973; Suzuki and Sakai, 1973; Niwa, 1994; Niwa, 1996), tending to align animals and match their velocities (arrayal forces); thrust forces causing locomotion, as well as interaction forces causing attraction or repulsion from neighbors in the group. (d) Some models include stochastic forces (Niwa, 1994; Niwa, 1996) and consider fluctuations in the behaviour of individuals, whereas others are strictly deterministic. We can also subdivide the model types into those that incorporate motion in 1D (individuals following one another along a trail, a school of tuna in the "soldier formation", birds settling on a wire), 2D (herds, simplified groups of other sorts), or 3D (flocks, schools, swarms), and those that deal with heterogeneity in the individuals, e.g. their size, age, or speed.

A typical Lagrangian model is based on Newtonian mechanics equations of motion with acceleration, frictional drag, and a variety of forces causing net motion, alignment, velocity matching, as well as mutual interactions (Sakai, 1973; Suzuki and Sakai, 1973). Sakai's simulations show groups exhibiting amoebic movement, circular 'doughnut' motion, or polarized rectilinear motion in 2D. In steady state motion, fish are aligned, have the same velocity, and are spaced some distance apart from their neighbors. This spacing behavior is of interest in our model, but the detailed dynamics of formation of the group or its complex motion through a heterogeneous environment are not here addressed.

Detailed stochastic differential equation models with locomotory, arrayal, and grouping forces (similar to those used by Sakai) have been recently proposed and analyzed (Niwa, 1994; Niwa, 1996). A statistical mechanics approach, complemented with synergetics (Haken, 1983) was used to analyze transients and fluctuations in behavior of individuals in a school of fish, and derive conditions for phase transitions between amoeboid and polarized motion of the group. An important result is that fluctuations are significant for formation of the school, and that the onset time for schooling of $N$ individuals, $t_o \sim \ln(N)$, is smallest when noise is tuned to some particular level (Niwa, 1996).

The variance of the fish distribution, an indicator of the spatial size of the group was shown to depend on some power of the number of fish in the group, $N^\eta$, with, $0 \le \eta \le 2/3$ (Niwa, 1996). For $\eta = 0$, the school size is independent of $N$, which means that individuals crowd together without limit; the value $\eta = 1/3$ corresponds to soft-core repulsion, whereas $\eta = 2/3$ arises for very strong local exclusion (hard-core repulsion) and leads to a regular geometric lattice of animals in the case of a spherical school, whose size expands with $N$ as a simple packing problem. This analysis of spacing structure of a group and the way that it scales with the number of individuals is explored in the present paper.

### 1.2.1. Mutual interaction forces

The classic literature for social interactions has many examples in which interactions between members are represented by gradient forces (Breder, 1951; Niwa, 1994; Beecham and Farnsworth, 1999). The idea of mutual attraction and repulsion between individuals in a group was proposed long ago (Parr, 1927). Parr observed herring, sprat, and mackerel groups, and noted that fish approached one another until the antagonistic stimulus (repulsion) was felt, i.e. that attraction/repulsion was distance-dependent. He observed a persistently uniform density of fish. After a disturbance in which the school underwent dynamic restructuring, its density gradually returned to normal, first near its edge, and only later in its interior.

To describe attraction of two *schools of fish* for one another, Breder (1951) used an analogy with "gravitational attraction". In a later paper, Breder (1954) considered inverse power laws for the repulsion and attraction between *individuals*, with repulsion stronger at short distances. This model was formulated in terms of a cohesiveness interaction, defined as:

$$\text{Interaction} = -\left( \frac{A}{x^m} - \frac{R}{x^n} \right) \tag{1}$$

where $A$, $R$ are magnitudes of attraction and repulsion, $x$ is the distance between individuals, and $m$, $n$ are powers that govern how quickly the interactions fall off with distance. Interpreting Breder's "cohesiveness" interaction function as a force places this model into the class of gradient force models.

A specific case considered by Breder (1954) was $m = 0, n = 2$, i.e. constant attraction and inverse square law repulsion, Interaction $= -(A - (R/x^2))$. A similar assumption was made by Niwa (1994). We will show that this assumption leads to some unrealistic aspects of group structure. Breder discussed the "point of neutrality", $x = (R/A)^{1/2}$, where attraction and repulsion are balanced and stated that this distance represents the spacing between neighboring fish in a school. Our paper challenges the accuracy of this assertion when the "group" consists of more than two individuals. We will show that when interactions with many neighbors are superimposed, the individual distance between members decreases. An analytic calculation to arrive at the group spacing behavior is one of the contributions of our paper.

A summary of empirical models used to describe attraction and repulsion between individuals in groups is presented in Table 1. Both piecewise linear, inverse-power and exponential distance dependence have been applied in the analysis of observational data (Sakai, 1973; Niwa, 1994; Beecham and Farnsworth, 1999). In some cases, the simple inverse power functions are modified to include parameters governing concavity (Warburton and Lazarus, 1991). Experimental data based on a group of eight fish (Aoki and Inagaki, 1988), were used to conclude that the mutual interaction force is analogous to harmonic-spring attraction and hard-core repulsion (Niwa, 1996). Niwa (1994) writes: "A more detailed analysis of the attraction-repulsion problem is required in order to explain the observations of packing density." Our paper is an initial step in this direction.

**Table 1.** Mutual interaction forces used in other papers

| Ref. | Attraction | Repulsion | Comments |
|---|---|---|---|
| [1] | $\dfrac{a}{x^m}$ | $\dfrac{r}{x^n}$ | gradient forces |
| [2] | $C, \quad R_o < x < R_1$ | $-c_o(R_o - x)$ | piecewise linear |
| [1],[3], | $a$ | $\dfrac{b}{x^2}$ | gradient type |
| [4] | $\dfrac{A}{x^2} \quad x \geq r_{safe}$ | $\dfrac{R}{x^3}$ | gradient type |
| [5] | $A\left[1 - \left(1 - \dfrac{x}{d}\right)^a\right]^{\frac{1}{a}}$ | $R\left[1 - \left(\dfrac{x}{d}\right)^r\right]^{\frac{1}{r}}$ | non-gradient type |

The above citations are: [1] = (Breder, 1954); [2] = (Sakai, 1973), [3] = (Niwa, 1994), [4]=(Beecham and Farnsworth, 1999), [5] = (Warburton and Lazarus, 1991)

Beecham and Farnsworth (1999) argue that foraging constraints and mutual interference effectively produce repulsion, whereas risk of predation leads to individual attraction, as in Hamilton's "selfish herd" (Hamilton, 1971). The connection of these inverse-power forces with corresponding "cost potentials" is motivated and some discussion of the effects of such interactions on animal spacing is given (Beecham and Farnsworth, 1999). An alternate set of exponential functions are also considered as candidates for depicting such cost potentials (Beecham and Farnsworth, 1999).

On a smaller size scale, e.g. slime molds, bacteria, or other types of cells, aggregation also occurs, but mechanisms for grouping are based on chemical, rather than visual or tactile information. Diffusible chemical signals, and chemotaxis provide a well-known mechanism underlying aggregation (Keller and Segel, 1970). In a separate analysis (Lee et al., 2001), it has been shown that chemical signaling between chemotactic cells leads to an "effective interaction force" with components

$$F(x) = -A \exp\left(-\frac{x}{a}\right).$$ (2)

where $x$ is distance between cells, $A$ is related to magnitude of chemotactic effect and $a$ is the spatial range of the chemoattractant ($a \sim \sqrt{D/b}$ with $D$ a diffusion coefficient, and $b$ a decay rate of the chemotactic chemical). The effective force is negative at $x > 0$ corresponding to attraction: when one individual is at $x = 0$, and a second is at $x > 0$, then the effective force (2) on the second individual leads to convergence. Positive values of the force at $x > 0$ corresponds to repulsion. The underlying assumption is that the motion of the individual cells is slow on the timescale of diffusion and decay of signaling chemicals. When both attractants and repellents are secreted, the generalized attraction-repulsion force has the form:

$$F(x) = R \exp\left(-\frac{x}{r}\right) - A \exp\left(-\frac{x}{a}\right).$$ (3)

This form of distance dependence can also be applied to the grouping of individuals under the effect of mutual interactions.

Short-ranged repulsion and long-ranged attraction are needed for realistic spacing behavior and cohesion in a group. The distance at which attraction and repulsion between a pair of neighbors exactly balance will be denoted the **comfortable distance**. (See also the "safe distance", $r_{safe}$, in Beecham and Farnsworth (1999)). For a group of two, the comfortable distance is identical to the actual spacing, but we show that this distance is *not the same* as the equilibrium spacing in a larger group with additive mutual interactions.

### 1.2.2. Additivity assumptions
In a group with $N > 2$ individuals, mutual interactions occur with numerous neighbors. Simple additivity of forces over members of the school is considered by Niwa (1994) in a nonlinear Langevin equation model. Other models use a weighted additive superposition or assume interactions occur only with immediate neighbors (Huth and Wissel, 1992). The additivity assumption was recently questioned by Gueron et al. (1996) who assumed that repulsion was induced by neighbors in a

"stress zone", attraction induced by others further away in an "attraction zone", and no influence was made by individuals in some intermediate "neutral zone".

The idea that animals compute some average or superposition over the entire swarm or herd may be biologically unrealistic. However, our interaction forces are represented by functions that drop off rapidly with distance. This means that neighbors further than the typical spatial range of the force have negligible interaction effect, in any case. Thus any local sum over immediate neighbors is very well approximated by an infinite series.

## 2. Formulation of the model

### 2.1. Definitions and equations

**Notation**

| | |
|---|---|
| $N$ | Number of individuals in the group |
| $\mathbf{x}(t)$ | Position vector (a list of positions of each of $N$ individuals) |
| $x_i(t)$ | Position of $i^{th}$ organism at time $t$ |
| $\mathbf{V}$ | Velocity vector (a list of velocities of each of $N$ individuals) |
| $\mathbf{F}$ | Vector of forces on the individuals at time $t$ |
| $x, z$ | Distance of an individual to some other individual in the group |
| $\mathbf{V}(x)$ | Component of the velocity of an individual which stems from interactions with another individual at distance $x$ away |
| $\mathbf{F}^r(x)$ | Repulsion-based part of $F(x)$ |
| $\mathbf{F}^a(x)$ | Attraction-based part of $F(x)$ |
| $s$ | Comfortable distance (See definition below) |
| $\delta$ | Individual distance (See definition below) |
| $R, r$ | Magnitude, respectively range of repulsion |
| $A, a$ | Magnitude, respectively range of attraction |
| $C$ | Dimensionless constant, $C = R/A$ |
| $l$ | Dimensionless constant, $l = a/r$ |
| $P(x)$ | Scalar potential function, negative integral of $F(x)$ |
| $P^{a,r}(x)$ | Scalar potential functions for the attraction, respectively repulsion |
| $W(\mathbf{x})$ | Lyapunov function. (Reduces to $P(x)$ for two individuals) |
| $\bar{W}(\mathbf{x})$ | Lyapunov function restricted to manifold of groups with equidistant individuals |

The following terminology is used to avoid confusion.

- By a **cohesive** group we mean a group in which the distances between individuals are bounded from above (members of a cohesive group tend to stay together, and avoid dispersing).
- A **well-spaced** group is a group which does not collapse into a tight cluster, i.e. where some minimal bin size exists such that each bin contains at most one individual. Moreover, the size of such a bin is independent of the number of individuals in the group.
- An **equidistant** or **uniformly spaced** group is defined as an aggregate in which all nearest neighbors have identical distances of separation.

- The **comfortable distance**, $s$, is the spacing between two individuals (interacting in isolation) at which attraction and repulsion balance.
- The **individual distance**, $\delta$, is the separation distance between nearest neighbors in a group. (For a group consisting of two members, the two above definitions coincide; for a larger group, we will show that $\delta < s$.)

*Remarks.* Well-spaced groups need not be uniformly spaced and visa versa. Further, no finite group can be uniformly spaced throughout, as edge effects will lead to distinct spacing close to the exterior.

*The model*

We consider a swarm of $N$ identical individuals, viewed in a coordinate system moving with the velocity of the swarm's centroid. This means that we are only modelling relative rearrangements of the individuals, not the motion of the swarm as a whole. The model applies to both sedentary and moving groups, where net motion may be determined in relation to other intrinsic/extrinsic factors.

The positions of individuals relative to the group centroid, $\mathbf{x}_i(t), i = 1 \ldots N$ can change through rearrangement due to mutual interactions. Let

$$\frac{d\mathbf{x}}{dt} = \mathbf{V}, \tag{4}$$

where $\mathbf{V} = \{V_i\}_{i=1}^{N}$ is the vector of velocities of the individuals relative to the swarm centroid.

In general, a law of motion is given mathematically by an equation of the form

$$k_1(d^2\mathbf{x}_i/dt^2) = k_2\mathbf{F}_i(\mathbf{x}) + k_3\mathbf{F}_{res}.$$

Here, the acceleration (left hand side) is proportional to total force (right hand side), e.g. the sum of attraction and repulsion (first term, RHS) and an effective resistance force (second term, RHS).

In the simplest situation, a viscous-like resistance force is proportional to the velocity,

$$\mathbf{F}_{res} = -k_3 V.$$

This is particularly relevant when the motion is slow. It often happens that $k_1$ is small, and then the acceleration term is only transiently significant, over a short period of time. In that case, $d^2\mathbf{x}_i/dt^2 \sim 0$, and

$$\mathbf{V} = k\mathbf{F},$$

where $\mathbf{F}$ is a vector of mutual interaction forces. The constant $k$ has units of velocity per force, and may depend on resistance, drag, or viscosity. To avoid carrying this constant, we select units so that $k = 1$ from here on. This approach is essentially one in which we are neglecting inertial forces. (In the case of cell aggregation, this is justified by the low Reynolds number regime.) Position, velocity, and forces are treated as vectorial quantities unless otherwise indicated.

With both attraction and repulsion, velocity is expressed as

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

where $\mathbf{F}^a$, $\mathbf{F}^r$, are effective attractive, respectively repulsive forces, each depending on distance between the interacting individuals. For two individuals in isolation, at positions $x_i$ and $x_j$, mutual forces would depend on the magnitude and direction of the vector $(x_i - x_j)$. If the simplest additive superposition is used to describe the effect of group members on a given individual, $i$, at position $x_i$, then the expression for the velocity of the $i^{th}$ individual is:

$$\mathbf{V}_i = \sum_{j \neq i} \left( \mathbf{F}^r (x_i - x_j) - \mathbf{F}^a (x_i - x_j) \right), \tag{5}$$

where the sum is taken over all other individuals $j = 1, \ldots, N, \ j \neq i$. The superposition is a sum of pairwise interactions between a given individual, $i$, and all other swarm members, but remains essentially local since we assume that forces fall off rapidly with distance.

To understand what this implies, we first consider pairwise interactions and then investigate how these scale for the size of an entire group. Consider, first, the positions of two individuals in 1D, $x_1(t)$, $x_2(t)$, with forces depending only on the separation distance $x = x_1 - x_2$. Then

$$\frac{dx_i}{dt} = V = F(x_i - x_j), \quad i = 1, 2, \ j \neq i. \tag{6}$$

We assume forces have the following properties:

1. The magnitude of the interactions decreases as the distance between individuals grows. (As $x \to \infty$, $F \to 0$.)
2. $F(x)$ is an odd function: $F(-x) = -F(x)$. Symmetry follows from the fact that the individuals are identical so if individual 1 is attracted to 2, then 2 is also attracted to 1. The sign of the motion (positive or negative) depends on whether the neighbor is ahead or behind, accounting for the fact that $F$ is odd.
3. For repulsion, $F(x) > 0$ at $x > 0$ and for attraction $F(x) < 0$ at $x > 0$. In repulsion, the spacing $x$ increases whereas in attraction $x$ decreases.

In the case of two isolated individuals, by symmetry of $F$, equations (6) imply that the center of mass, $(x_1 + x_2)/2$, does not change, and the inter-individual spacing, $x = (x_1 - x_2)$, satisfies

$$\frac{dx}{dt} = 2F(x). \tag{7}$$

**The case of gradient forces**

For the specific case of *gradient forces* and an arbitrary number $N$ of individuals, the system of equations of motion (4) has the form:

$$\frac{d\mathbf{x}}{dt} = -\nabla W, \quad \text{or} \quad \frac{d\mathbf{x_i}}{dt} = -\nabla_i W, \quad i = 1 \ldots N \tag{8}$$

In a 1D array, $dx_i/dt = -dW/dx_i$, $i = 1 \ldots N$. The resulting system of equations has a gradient character (Cross and Hohenberg, 1993). Local and global minima of

the minimization functional, i.e. the **Lyapunov function**, $W$, correspond to locally and globally stable stationary states of the system. One can predict stable configurations of the swarm by identifying such minima. In what follows, we consider the 1D system. All formulae can be easily generalized to higher dimensions when the forces are radially symmetric.

In the simple case of two individuals ($N = 2$), with distance of separation $x$ and mutual interaction force $F(x)$, we define a scalar potential function:

$$P(x) = -\int_{-\infty}^{x} F(y)\, dy.$$

The attraction and repulsion **potential functions** are then:

$$P^{r,a}(x) = -\int_{-\infty}^{x} F^{r,a}(y)\, dy, \quad P(x) = P^r(x) - P^a(x). \tag{9}$$

The lower limit of integration is arbitrary, here chosen so that $P(\pm\infty) = 0$. $P(x)$ is the **Lyapunov function** whose minima are stable equilibria for a pair of individuals (7).

*The Lyapunov function for the swarm*

In a 1D swarm with more than two individuals, we can re-write equation (5) for the velocity of the $i^{th}$ individual in the form:

$$V_i = \sum_{j=1, j\neq i}^{N} \left(F^r(x_i - x_j) - F^a(x_i - x_j)\right) \quad i = 1 \ldots N \tag{10}$$

The corresponding Lyapunov function for the gradient equations of motion (8) for a group of $N$ individuals is a linear superposition of all interactions:

$$W(\mathbf{x}) = W^r(\mathbf{x}) - W^a(\mathbf{x}) = \frac{1}{2} \sum_{i,j=1, i\neq j}^{N} (P^r(x_i - x_j) - P^a(x_i - x_j)). \tag{11}$$

The factor $1/2$ is needed so that every pair of individuals will be counted once, rather than twice. Note that for $N = 2$, the function reduces to $W(x) = P(x)$.

The Lyapunov function can be identified as an energy potential function in physical systems. It plays a role analogous to a "fitness landscape" in biology: a minimum on this "landscape" is a locally stable state, and corresponds to a favored configuration. The lowest, most "energetically favored" minimum would be the state with the highest probability of occurrence in observations of nature. We use the Lyapunov function as an analytic tool for identifying the configurations of animal groups that would be stable under a given set of interaction forces.

## 3. Specific examples of gradient forces

As indicated in the Introduction, many of the forces used traditionally (including those of (Breder, 1954)) are gradients of the appropriate potential function. We have chosen here to take as illustrative example the case of exponential forces, where parameters are interpretable in an elegant, biologically relevant way. Results for the inverse power forces are presented in the Appendix.

### 3.1. Exponential forces

Following (Lee et al., 2001), we consider an example where effective force is made up of exponential terms representing repulsion and attraction,

$$F^a(x) = A \exp(-x/a), \quad F^r(x) = R \exp(-x/r), \quad x > 0$$

where $x$ is distance between an interacting pair. The functions are extended to negative values of $x$ as odd functions. Formally,

$$V(x) = F^r(x) - F^a(x) = \text{sign}(x) \left( R \, \exp\left(-\frac{|x|}{r}\right) - A \, \exp\left(-\frac{|x|}{a}\right)\right). \quad (12)$$

The parameters $R, A > 0$ are magnitudes and $r, a > 0$ are the spatial ranges of the repulsion and attraction. Four cases result:

*Case 1.* If $R > A$ and $r > a$, repulsion extends further radially, and has greater magnitude than attraction. Repulsion dominates, so individuals are repelled from one another at all distances. (In this case, a social aggregate would not exist.)

*Case 2.* If $A > R$ and $a > r$, attraction is always stronger than repulsion, and individuals always get closer to each other. We expect the equilibrium state to be a tight cluster.

*Case 3.* $R < A$ and $r > a$. In this case, attraction dominates close to the origin, and repulsion dominates at large distances. This means that the individuals would either flee away from each other or collapse to a point. This is unbiological.

*Case 4.* $R > A$ and $a > r$. This is the short-ranged repulsion and long-ranged attraction case, and is the most interesting and biologically relevant: In this case, for a pair of individuals in isolation, there is a comfortable distance, $s$:

$$s = \frac{a}{((a/r) - 1)} \ln(R/A). \quad (13)$$

We rescale the spatial variable in units of the range of repulsion, $r$, and velocity in units of the strength of attraction, $A$. In terms of such dimensionless units, this spacing is then:

$$s' = \frac{l}{(l - 1)} \ln(C). \quad (14)$$

The shape of the function $V(x)$ given by equation (12) depends on the relative magnitudes of the exponential terms (Figure 1), and, in particular, on the dimensionless ratios $C = R/A$ and $l = a/r$ as shown in the $Cl$ parameter plane of Figure 2.
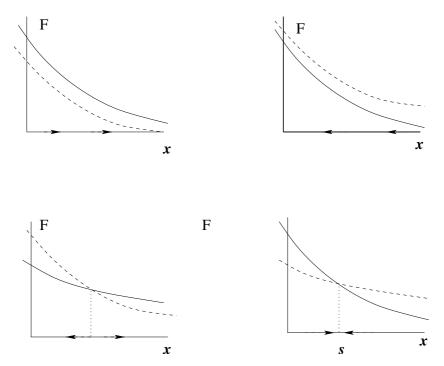
**Fig. 1.** The four basic qualitative cases discussed in Section 3 are shown here (top to bottom and left to right). Solid line: repulsive force (velocity), dotted line: attractive force (velocity). Case 1: Repulsion dominates everywhere. Case 2: Attraction dominates everywhere. Case 3. Short range attraction and long range repulsion: this case shows unstable spacing and Case 4: Short range repulsion and long range attraction. In the last case, a stable "comfortable distance", $s$ between 2 individuals would occur. The cases are qualitatively similar for the inverse-power and exponential forces, except for the behavior at very small distances.

*The corresponding potentials and Lyapunov functions*

The force in equation (12) is a gradient force with potential function

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

except for a singularity at $x = 0$ which stems from the discontinuity in $F(x)$. The shapes of $V(x)$ and $P(x)$ in the four basic cases above are shown as insets in Figure 2. Note that the forces of mutual interactions are odd functions of $x$, so the potential functions are even.

For a pair in isolation, short-ranged repulsion and long-ranged attraction (Case 4) result in the potential $P(x)$ having a minimum at the comfortable distance, $x = \pm s$. (The conditions $V(x) > 0$ at $x < s$, $V(x) < 0$ at $x > s$, $V(x) = 0$ at $x = s$ are equivalent to conditions that minimize $P(x)$ at $x = s$.)

We now seek conditions that guarantee well-spaced behavior in the case of the swarm ($N \gg 2$). In order to explicitly calculate how individual distance depends on the parameters governing the interactions, we use a simplified setting: a 1-D
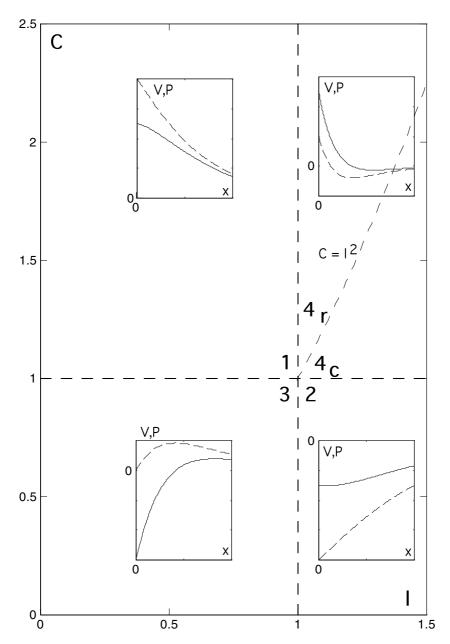
**Fig. 2.** The $Cl$ parameter plane shown here is subdivided into distinct regions. In each, the forms of the functions for velocity, $V(x)$, (solid line) and for the potential, $P(x)$ (dashed line) given by our exponential repulsion and attraction (15) are displayed. The numbering scheme for these regions corresponds to the four qualitatively different cases described in Section 3. Region 4 is subdivided by the parabola $C = l^2$ into regions $4_c$ where the group collapses versus $4_r$ where the group is well-spaced.

array of individuals, a very large group size ($N \to \infty$), and thus negligible edge effects. Further, we assume a pre-existing uniform spacing and ask how the individual distance, $\delta$, depends on parameters associated with the forces. (We find that this spacing does not coincide with the pairwise comfortable distance, $s$, due to the superposition of interactions of numerous individuals.) The individual distance can be found in closed form, given our simplifying assumptions and geometry. The minimum of the Lyapunov function is taken over equidistant distributions of individuals, not over the wider class of all possible distributions. In a later section, we show how such results can be generalized to other geometries and group sizes.

We consider the rescaled variables, using the range of repulsion, $r$, as the distance scale, and the magnitude of the attraction, $A$, as the velocity scale (and thus $r/A$ as the time scale). Then,

$$V(x') = Ce^{-x'} - e^{-x'/l}, \quad P(x') = Ce^{-x'} - le^{-x'/l}, \tag{15}$$

where $x' = x/r$ is a dimensionless distance, $l = a/r$ is the ratio of the range of attraction to the range of repulsion, and $C = R/A$ is the ratio of the magnitudes of these effects. (In what follows, we will drop the primes, and use the notation $x$ for the dimensionless coordinate $x'$.)

The above results can be used to infer the following conclusions about groups of $N \gg 1$ organisms. (Refer to Figure 2 for regions in the parameter plane where each of these parameter ranges occur, with the corresponding potential, $P$ and velocity $V$ as insets.)

*Case 1.* If $C > 1$ and $l < 1$, neither potential, nor Lyapunov functions have local minima at a finite inter-individual distance. This is a case of net repulsion which does not lead to cohesive group structure, and is not relevant to biological groups.

*Case 2.* If $C < 1$ and $l > 1$, both the potential and the Lyapunov functions are not bounded from below when the mutual distances between individuals all tend to zero. There are no other local minima of the Lyapunov function. This case also fails to lead to an aggregate with a well-defined individual distance.

*Case 3.* $C < 1, l < 1$. The spacing distance is unstable. The organisms collapse to a point if all mutual distances are closer than a certain distance, and move apart if all mutual distances are greater than some other given distance.

*Case 4.* $C > 1$ and $l > 1$. For a pair of interacting individuals ($N = 2$), the comfortable distance, $s$, is the global minimum. For $N > 2$, suppose that an equilibrium spacing exists, and call that spacing $\delta$. The net potential *per organism* is then,

$$\bar{W} = 2 \sum_{j=1}^{\infty} W_j = 2 \sum_{j=1}^{\infty} P(j\delta) = 2 \left[ \frac{-l}{e^{\delta/l} - 1} + \frac{C}{e^{\delta} - 1} \right]. \tag{16}$$

Here $W_j = P(j\delta)$ is the potential corresponding to the interaction of a given organism with a neighbor at a distance $\pm j\delta$ in the group. The factor of 2 accounts for both leftward and rightward interactions. The series is geometric and its sum, shown in (16) is readily computed.

We now consider the implications of Case 4 in detail. The following observations can be made from the asymptotic behavior of the net potential given by equation (16).

In the asymptotic limit $\delta \gg l$, when the spacing is larger than the range of attraction, the first term in equation (16) dominates and so $\bar{W}$ is approximated by:

$$\bar{W} = -2le^{-\delta/l} + O(e^{-\delta}), \quad \delta \gg l.$$

Thus, at large spacing $\delta$, the net potential approaches zero asymptotically from below. This implies that it is "energetically unfavorable" to be spaced too far apart, so swarms with spacing much larger than $l$ are not expected to occur. At small spacing, i.e. $\delta \ll 1$ in dimensionless units, we use a Taylor expansion of the exponents in equation (16) to obtain the asymptotic expression:

$$\bar{W} = \frac{2}{\delta}(C - l^2) + O(1), \quad \delta \ll 1.$$

From this expression, we note that if $C < l^2$, the net potential diverges to $-\infty$ as $\delta \to 0$. Under this condition, the net potential has no other local minima at finite $\delta$ (see below). Weak repulsion ($R < (a/r)^2 A$) cannot overcome attraction even at short distances. The net potential decreases as the spacing decreases so that **the group collapses whenever**

$$Rr^2 < Aa^2. \tag{17}$$

This condition quantifies explicitly what is meant by the assertion that repulsion has to be *strong enough* to prevent collapse of the group.

A necessary condition for existence of a local minimum of the net potential $\bar{W}$ is $d\bar{W}/d\delta = 0$:

$$\frac{d\bar{W}}{d\delta} = 2\left[\frac{e^{\delta/l}}{(e^{\delta/l} - 1)^2} - \frac{Ce^{\delta}}{(e^{\delta} - 1)^2}\right] = 0. \tag{18}$$

In general, equation (18) is transcendental, but for certain special values of $l$, e.g., $l = 2$ and $l = 3$, it is polynominal in $\exp(\delta/l)$, and can be solved analytically. Details in the appendix then lead to the solutions:

$$\begin{aligned}
\delta &= 2\ln\left(\frac{1}{2}[C - 2 + \sqrt{(C-2)^2 - 4}\,]\right), \quad l = 2, \\
\delta &= 3\ln\left(\frac{1}{2}[\sqrt{C} - 1 + \sqrt{(\sqrt{C} - 1)^2 - 4}\,]\right), \quad l = 3.
\end{aligned} \tag{19}$$

These expressions confirm that the equilibrium spacing exists only for $C > l^2$, and that this spacing is an increasing function of the repulsion strength and a decreasing function of the range of attraction. Expressions (19) also demonstrate that for large $C$ (equivalently, for $l \simeq 1$), the spacing is roughly similar to the comfortable

distance, $\delta \simeq s$. (This can also be verified by approximating (18) with $e^{\delta}$, $e^{\delta/l} \gg 1$, obtaining $\delta \simeq l \ \ln(C)/(l-1) \simeq s$.)

At other values of $l$, equation (18) cannot be solved in closed form. We solved this equation numerically using the bisection method with accuracy 0.05 for various values of $l$ and $C$. In Figure 3, we show the corresponding equilibrium spacing $\delta_l(C)$ (solid line) as a function of $C$, at two values of $l$ (obtained analytically for $l = 2$ and numerically for $l = 1.2$). The spacing increases with the repulsion strength and decreases with the range of attraction. Finite spacing did not exist when $C < l^2$. The dependence of the comfortable distance, $s$ (dashed line), on $C$, given by equation (14) is shown on the same figure. The figure also reveals that $\delta < s$: **The individual distance in a large group is always smaller than the comfortable distance of two organisms on their own**.

In the Appendix, we prove analytically that for repulsion sufficiently strong $(C > l^2)$, a unique minimum of $\bar{W}$ exists at finite $\delta$ (see also Figure 2), while there is no local minimum at $C < l^2$. Thus, the equilibrium spacing in an equidistant group is unique at $C > l^2$. At $C < l^2$, the group collapses. A limiting case of very small spacing occurs close to the onset of collapse of the swarm to a tight cluster, when $(C - l^2) \ll l^2$. The following asymptotic expression for the distance (in terms of dimension-carrying variable, $\delta_{dim}$) is obtained using Taylor expansions of
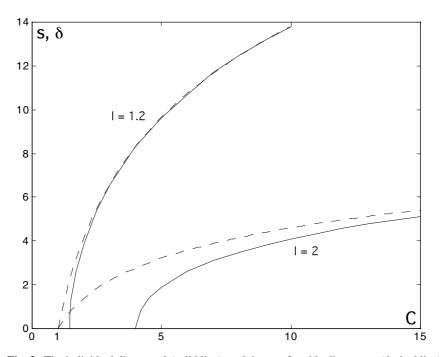


**Fig. 3.** The individual distance, $\delta$ (solid line), and the comfortable distance, $s$ (dashed line) (both scaled in units of $r$), are plotted as functions of the parameter $C$ at two different values of parameter $l$. The function $\delta_l(C)$ is obtained from numerical solution of equation (18), while the form of $s_l(C)$ is given by equation (14).

the exponential functions:

$$\delta_{dim} \simeq \sqrt{12\frac{Rr^2 - Aa^2}{R - A}} \ll s. \tag{20}$$

### 3.2. Inverse power forces

This case was studied by Breder (1951) and Niwa (1994) and further interpreted in terms of resources and predation risk by Beecham and Farnsworth (1999). Effective interaction forces of attraction and repulsion are considered to have the forms:

$$F^a(x) = \frac{A}{x^m}, \quad F^r(x) = \frac{R}{x^n}, \tag{21}$$

where $A$, $R$ are the magnitudes of attraction and repulsion, and the powers, $m, n$, are related to decay over distance.

The treatment of the case of such inverse power forces is similar to that of exponential forces, and is presented in the Appendix. Analysis reveals that the Parr-Breder interaction force $F = A - (R/x^2)$ would lead to a collapsed group at all values of the parameters.

## 4. General results

In this section we discuss gradient forces and obtain some results in the case when the spacing of the individuals is not necessarily equidistant. Generic results for 1D can be obtained by considering changes (positive or negative) in the Lyapunov function that occur when a given configuration is altered. Details are given in the Appendix.

Let $\mathbf{z} \equiv \{z_i\}_{i=1}^{N-1}$ (where $z_i = x_{i+1} - x_i$) denote the $N - 1$ spacing distances between successive neighbors. For $V(x) = F^r(x) - F^a(x)$ the velocities, and $P(x) = P^r(x) - P^a(x)$ the potentials induced by one neighbor on an individual at a distance $x$ away, we assume that $F^r(x), F^a(x) > 0$ and $P^r(x), P^a(x) > 0$ at $x > 0$, and that $P(x)$ is monotonically decreasing to a single minimum at $x = s$ (the comfortable distance) and thereafter monotonically increasing.

- **Result 1: Cohesiveness and individual distance**
  - **(a) At the stable equilibrium, the distance $\delta$ between any two neighboring individuals in the group is not greater than the comfortable distance $s$.**
    We prove this result in the Appendix using an argument by contradiction: we consider a group with large inter-individual distances, allow those distances to shrink, and prove that the value of the Lyapunov function of the "contracted swarm" is lower. This contradicts the possibility that the original configuration was globally stable. The corollary of this result is:
  - **(b) If attraction is long-range, the group is cohesive.**
    More specifically, if $V(x) < 0$ at $x > s$, then the size of the globally stable group cannot exceed $(N - 1)s$.

- **Result 2: Condition for a well-spaced group**
  - **If repulsion is strong enough, then there is a well-spaced group configuration that is globally stable.**
    The quantifier "strong enough" means that for some distance $\hat{z} < s$ repulsion dominates attraction according to

    $$P^r(\hat{z}) > P^a(\hat{z}) + 4 \sum_{n=0}^{\infty} P^a(n\hat{z}), \tag{22}$$

    In this case, the Lyapunov function assumes a global minimum at one or more points $\mathbf{x}' \in \mathcal{R}_+^N$, such that each bin of size $z_{min}$ in 1D space contains at most one individual (See Appendix). Here $z_{min}$ is the largest value of $\hat{z}$ that satisfies condition (22). This indicates that in the stable configuration, individuals are distributed into spatial "bins" of some minimal width, $z_{min}$. (See Appendix.) Furthermore, if the repulsion potential increases as $\hat{z} \to 0$ faster than $1/\hat{z}$, while the attraction potential decreases to zero as $\hat{z} \to \infty$ rapidly enough, then the condition (22) is always satisfied at sufficiently small $\hat{z}$. (See Appendix.)
- **Result 3: Group collapse**
  - **Repulsion must be sufficiently strong, i.e. $\int_0^{\infty} P^r(x)dx > \int_0^{\infty} P^a(x)dx$ to prevent the collapse of the group into a tight cluster.**
    This condition is necessary for the stable group to have diameter of order $O(N)$ or greater. The opposite inequality is a sufficient (but not necessary) condition for the collapse of the group. That condition cannot be improved qualitatively (See Appendix).
    In the Appendix, we show that for biologically reasonable, smooth, non-oscillating potential functions, this integral inequality corresponds closely to a related inequality $Rr^2 > cAa^2$, $c \sim 1$ where the parameters $R, A, a, r$ are defined in terms of the (now arbitrary) shapes of the potentials. This is consistent with the related result (17) obtained for exponential forces.

### 4.1. Implications

Results 1 and 2, above, imply that as the number $N$ of individuals in the swarm increases, the average density of the group does not change, but that its physical size is proportional to $N$. Formally, these results assert global stability of a well-spaced group, where the average distances between neighbors are neither too large nor too small, i.e. are bounded from above and below uniformly with respect to $N$.

The condition for result 2 implies that the repulsive force blows up when distance between individuals shrinks to zero. For example, the potentials used by Beecham and Farnsworth (1999) corresponding to effective interaction forces, i.e.,

$$P(x) = \begin{cases} A/x^2 - R/x^3 & \text{if } x \geq r_{safe} \\ -R/x^3 & \text{if } x < r_{safe} \end{cases}$$

satisfy the condition for result 2 for any values of the parameters. Our results therefore predict that the "Cost Potential" of Beecham and Farnsworth (1999) guarantees

existence and stability of a well-spaced group. Furthermore, individual distances in the group are bounded from below uniformly with respect to $N$.

The inequality in result 3 can be interpreted with $Rr$ as an approximate "energetic cost" of repulsion, and $Aa$ an approximate "energetic payoff" of attraction. The range of attraction is $a/r$ times greater than that of repulsion. This means that when the group is enlarged, the relative "energetic changes" per organism, due to repulsion and attraction are $Rr^2$ and $Aa^2$, respectively. For a well-spaced group, the "cost" of the repulsion has to be sufficiently greater than the "payoff" of attraction.

Results 1 and 2 could theoretically be strengthened by showing that when a group contains very many individuals ($N \to \infty$), it stabilizes into a uniform distribution of equidistant individuals regardless of the initial configuration; but this goal, analogous to a longstanding problem in classical physics, is difficult to achieve analytically. With some generalizations, we instead demonstrate numerically that **locally stable near-uniform configurations exist**. Furthermore, **such states are unique and were found to result from a large set of realistic initial conditions**.

## 5. Generalization to higher dimensions

Explicit calculations in the previous sections have been formulated for linear aggregations in 1D. These results can be generalized to higher dimensions (2D and 3D). The positions of $N$ individuals in the group become a set of $N$-vectors. The Lyapunov function is $W(\mathbf{x}) = \frac{1}{2} \sum_{i,j=1,i\neq j}^{N} (P^r(\mathbf{x}_i - \mathbf{x}_j) - P^a(\mathbf{x}_i - \mathbf{x}_j))$, where $P^a$ and $P^r$ are non-negative attraction and repulsion potential functions. Interactions that depend strictly on distance $x_{ij}$ between individuals $i$ and $j$, as $P^{a,r}(\mathbf{x}_i - \mathbf{x}_j) = P^{a,r}(|\mathbf{x}_i - \mathbf{x}_j|) = P^{a,r}(x_{ij})$, $x_{ij} \equiv |\mathbf{x}_i - \mathbf{x}_j|$ are considered here, neglecting angle-dependence: see (Gueron et al., 1996). Both $P^a(x)$, and $P^r(x)$ are monotonically decreasing functions. As in 1-D, short-range repulsion and long-range attraction lead to a potential function having a single minimum at $x = s$: i.e., there exists a distance $s$ such that $P'(x) < 0$ at $x < s$, and $P'(x) > 0$ at $x > s$. We introduce the square (cubic) grid $\mathbb{Z}_{\hat{z}}^d$ with grid spacing $\hat{z}$. We term the smallest square (cube) in such a grid the cell of size $\hat{z}$.

The three results of Section 4 have analogues in higher dimensions. (See the Appendix.)

- **Result 1': The group is cohesive if attraction dominates repulsion at long distances.** If the Lyapunov function has a global minimum at one or more configurations $\mathbf{x}$, then each such configuration is contained in a disc (sphere) of diameter $(N-1)s$ where $s$ is the "comfortable distance".
- **Result 2': For repulsion sufficiently strong relative to attraction, the density of a stable group is bounded from above uniformly with respect to $N$.** If the inequality

$$P^r(\sqrt{d}\hat{z}) > 2C(d)P^a(0) + 2 \sum_{\mathbf{x} \in \mathbb{Z}_{\hat{z}}^d} P^a(\mathbf{x}), \qquad (23)$$

holds for $\hat{z} < s$, then the Lyapunov function has a global minimum at a configuration where at most one organism is found per cell of size $z_{min} \equiv \max\{\hat{z} :$

(23) is satisfied}. The parameter $d$ is the space dimension and $C(2) = 5$, $C(3) = 13$ for 2D and 3D aggregates, respectively.

- **Result 3': A necessary condition to avoid collapse of a group to a tight cluster is**

$$\int_{\mathcal{R}^d} (P^r(\mathbf{x}) - P^a(\mathbf{x})) \, d\mathbf{x} > 0. \tag{24}$$

This condition is necessary for the average spacing in a group of $N$ organisms in a stable state to be bounded from below uniformly with respect to $N$. If this condition fails, the average spacing decreases as a function of the number of individuals, $N$.

In higher dimensions, if short-range repulsion is strong enough, i.e..

$$\int_{\mathcal{R}^d} P^r(\mathbf{x}) \, d\mathbf{x} > c \int_{\mathcal{R}^d} P^a(\mathbf{x}) \, d\mathbf{x}, \quad c \sim 1,$$

then the group is well-spaced: (its average density is bounded from below and above uniformly and independently of $N$). For $R$, $A$ and $r$, $a$ the magnitudes and ranges of repulsion and attraction, respectively, the above criterion can be rewritten as:

$$Rr^{d+1} > cAa^{d+1}.$$

The condition on the repulsion, $R > cA(a/r)^{d+1}$ is more restrictive for the dimension $d > 1$ (since $a/r > 1$ by assumption).

In higher dimension, we can explain analytically features of the cohesiveness of the group, but not its *shape*. However, numerical experiments in 2-D, discussed below, demonstrate that the group is contained in a disc whose diameter is of order $O(N^{1/2})$. Corresponding rigorous analytical results in 2D were proved in theoretical physics (Radin, 1981) for artificial potential functions, using techniques of functional analysis beyond the scope of this paper.

## 6. Non-pairwise interactions

Alternate hypotheses that could account for well-spaced groups include interactions of greater numerosity (i.e., superposition of interactions of triplets, quadruples, etc., within the group). An example of this type is discussed in the Appendix, but simple, realistic, gradient-force examples are more difficult to devise than those for pairwise interactions. Higher numerosity interactions lead to a feature analogous to "density dependence" that is absent in the pairwise interactions case.

In an Eulerian framework, we formerly demonstrated that when the density-dependence of the repulsion is greater than that of the attraction, the density in the interior of the group is constant and independent of $N$ (Mogilner and Edelstein-Keshet, 1999). Interactions based on triplets, quadruples, etc., share some of these features in the Lagrangian context: short-ranged repulsion, and long-ranged attraction, leads to a cohesive group. For large groups, the average 'energy' per individual grows with $N$ for arbitrarily weak repulsion, indicating that a well-spaced group with uniform average spacing is more stable.

Numerical experiments generally support the conclusion that weak, short range, triplet repulsion could maintain a realistic group in the presence of a strong, pairwise, long range attraction. Such triplet repulsion could also cause higher density at the group edges, as observed in some biological cases. Indeed, an organism at the edge interacts with roughly half the number of neighbors as does an organism at the center of the group. This means weaker attraction at the edge, but also *much* weaker repulsion, because the number of *pairs* of individuals repelling the given organism at the edge would decrease roughly *four* times. This relatively weaker repulsion would lead to a decrease of spacing at the edge in such cases.

## 7. Simulations and numerical results

### 7.1. Numerical experiments in 1D

To illustrate and test the analytical predictions, we numerically simulated the full equations of motion with exponential forces and rescaled variables:

$$\frac{dx_i}{dt} = \sum_{j=1}^{N} V(x_i - x_j), \quad V(x) = Ce^{-x} - e^{-x/l}, \quad i = 1 \ldots N, \qquad (25)$$

where the unit of length is the range of repulsion, $r$, and the time unit is the ratio of the spatial scale and velocity scale, $r/A$. The model parameters are thus the number of organisms, $N$, the ratio of repulsion to attraction strength, $C > 1$ and the ratio of attraction to repulsion ranges $l > 1$.

Figure 4 (a,b) illustrates aggregation of two groups from initially uniform distributions over one unit distance, for parameters $C = 1.1$ and $l = 2$. (The condition $C > l^2$ is not fulfilled here.) Equations (25) were integrated using a forward Euler method with an appropriate time step. Within a few tenths of a time unit, the organisms aggregate into a tighter group. Comparing the cases of $N = 20$ and $N = 40$ individuals in Figure (4a) and Figure (4b), we find that the group maintains a roughly constant diameter as $N$ increases. (Found to be satisfied for large $N$ and a variety of initial conditions.) This implies that the spacing in the group decreases as $1/N$ (or the density of the group increases as $N$). Note also that the group diameter is approximately 0.4 distance units, which is on the order of magnitude of the comfortable distance, $s = (l/l - 1)ln(C) \simeq 0.19$, but much smaller than the range of attraction, $a = 2$. Thus, every individual in the group is effectively interacting with all the others. This is the case of group collapse discussed above.

Next, we investigated aggregation under parameter values $C = 10^3, l = 10$. (This is the case of very strong short-range repulsion, $C \gg l^2$, where the analysis predicts the existence of a well-spaced group.) The initially uniformly and widely spaced individuals aggregated into a stationary group within a few hundred time units (Figure 5). Analysis of the spacing within groups of size $N = 20$ and $N = 30$ reveals that, away from the edges, neighbors are roughly equidistant (true at other group sizes and initial conditions.) The spacing in the group is independent of $N$, and the diameter of the group is roughly proportional to the number of individuals, as in biologically realistic 1D groups. Moreover, the simulations confirm the
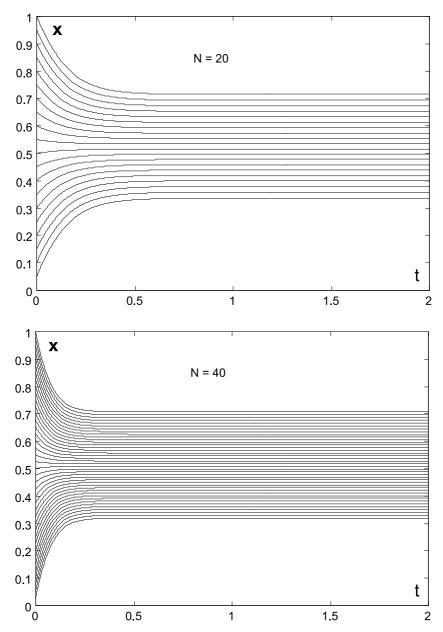
**Fig. 4.** Trajectories of individuals as they aggregate over time are shown here for groups of sizes $N = 20$ and $N = 40$. This is the case of weak short ranged repulsion ($C = 1.1, l = 2$) obtained by numerically solving equations (25). The positions of $N$ individuals (scaled in units of $r$) are initially equidistant and far apart. These converge with time into a tight stationary group, whose size does not depend on $N$.
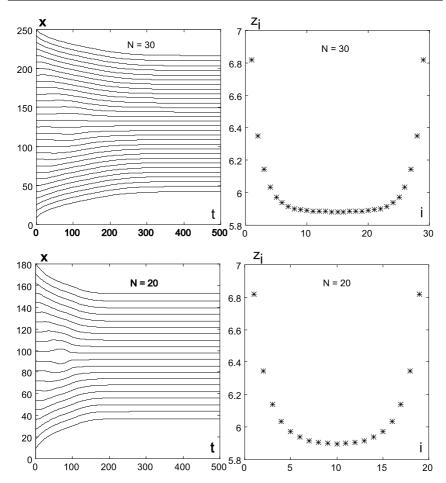
**Fig. 5.** Left column: As in Figure 4, but in the case when the short-range repulsion is strong ($C = 10^3 \gg l = 10$). The individuals converge over time to a well-spaced stationary group, whose diameter is proportional to $N$. Right column: The equilibrium distances between the $i^{th}$ and $(i + 1)^{th}$ organisms, $z_i$ are shown (as a function of $i$) for $i$, $i = 1..(N − 1)$. Note that, aside from edge effects, the spacing tends to a constant, $\delta \approx 5.9$, independent of the size of the group.

conjecture that in the limit $N \gg 1$ the spacing within the group is uniform. Note, also, that the distance between neighbors ($\delta \approx 5.9$) is smaller than the comfortable distance $s$ (which, in this case, is $s \simeq 7.7$).

Finally, at the edges of the group, the spacing of neighbors is larger than at the center (up to $\simeq 6.8$). This results from edge effects not considered in our analytical treatment. Briefly, an individual near the center of the group cannot repel its neighbors effectively, as they all attract one another, leading to tighter packing inside the aggregate than at the edges. Figure 5 can be compared to observations by Parr (1927) who noted that peripheral individuals tend to move towards the center of

the school as they felt a one-sided attraction. When a school of fish was perturbed, the central part of the dispersed school was last to gain normal density. Similarly, Krause and Tegeder (1994) observed that, when frightened by an aerial predator, fish at the periphery of a group start to pack closer together earlier than do fish near the group center. Thus, our simple model misses some features of biological interactions (but see the discussion of non-pairwise interactions).

### 7.2. Numerical experiments in 2D

We simulated a group in 2D, with periodic boundary conditions, using both exponential and inverse-power forces. The results were similar in these cases, so here we report on the numerical experiments with exponential forces. Initially, the positions of individuals are chosen at random. The attractive and repulsive potentials (for each member of the group) are superimposed to form a potential for each individual, $\bar{P}_i(\mathbf{x}_1, ..., \mathbf{x}_N, \mathbf{x}) = \sum_{j \neq i} P(\mathbf{x}_j - \mathbf{x})$, where $P(\mathbf{x}) = C \exp(-|\mathbf{x}|) - l \exp(-|\mathbf{x}|/l)$, $C = R/A, l = a/r$. The deterministic motion of each individual following the gradient of the corresponding potential is computed, and the new positions (and new potentials) are calculated at each time step. The velocity of the $i^{th}$ individual is

$$\mathbf{V}(\mathbf{x}_i) = -\nabla_\mathbf{x} \bar{P}_i(\mathbf{x}_1, ..., \mathbf{x}_N, \mathbf{x})|_{\mathbf{x}=\mathbf{x}_i}.$$

At each step, each individual is moved by $\mathbf{V}_i dt$, $i = 1, ..., N$, where $dt$ is the time step.

We also compute and plot the net potential function $\bar{P}_{\mathbf{x}_1,...,\mathbf{x}_N}(\mathbf{x}) = \sum_{i=1}^{N} P(\mathbf{x} - \mathbf{x}_i)$, which shows the "potential landscape" created by the configuration of the swarm. The surface plots of this net potential function provide a visualization of the direction of movement of an individual at any point in 2D space and the "potential energy" of each individual in the swarm. The model allows experimentation with the numerical size of the group, with magnitudes and ranges of attraction and repulsion, as well as stochasticity, which we do not consider in detail here. The interactive program is available online for further exploration by the reader at: (www.math.ubc.ca/~ais/chemosim/).

Figures 6 and 7 illustrate the outcome of five numerical experiments after 200 time steps. In the first case (Figure 6a,b), we tested a strong short range repulsion and moderate long range attraction, $C = 2, l \approx 1.43, l^3 \approx 2.9$. In this case, $C > 1.5l^3$, corresponding to analytical predictions of a well-spaced group. Indeed, numerics confirm that when the number of organisms increases from $N = 20$ to $N = 45$, the diameter of the group increases, preserving the spacing between neighbors. (The average spacing decreases only from 50.52 to 42.01 units as the group increases by a factor of more than two.) Figure 7a,b shows the corresponding potential landscapes. The potential flattens out to zero away from the group. Inside the group, the potential fluctuates significantly but has a constant average level, indicating that individuals all share a similar environment in the interior. The potential increases to sharp narrow peaks at points where individuals are located due to the strong short range repulsion.

In the second case (Figure 6c,d), we increased the range of attraction (with other parameters as before), so that: $C = 2, l = 2, l^3 = 8$. In this case, $C \ll l^3$, so
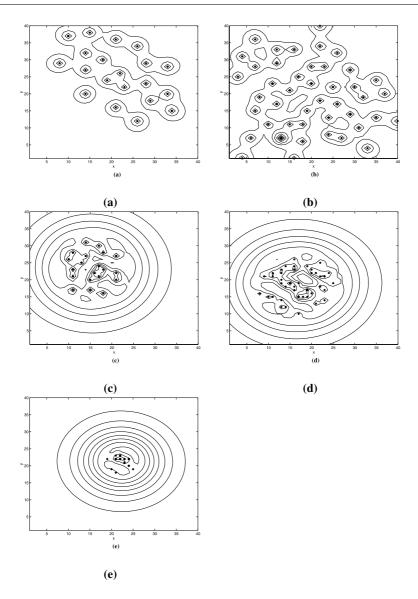
**(a)**

**(b)**

**(c)**

**(d)**

**(e)**

**Fig. 6.** Two dimensional group formation showing positions of individuals and the equipotential contours for the exponential interaction forces. The simulations were started with a random initial distribution on individuals and integrated for 200 time steps in each case.
Part 1: $A = 20, R = 40, a = 2.85, r = 2.0$ was tested with two group sizes (a) $N = 20$ individuals, and (b) $N = 45$ individuals; we find that well-spaced groups form, i.e., when the number of members increases, the diameter of the group increases. Part 2: $A = 20, R = 40, a = 4, r = 2.0$, also tested with two group sizes: (c) $N = 20$ individuals, and (d) $N = 45$ individuals; the swarm diameter is the roughly the same for both sizes, i.e. individuals crowd closer together. Part 3: $A = 20, R = 22, a = 4, r = 2, N = 20$; there is collapse and some individuals are on top of each other. The average spacing distance between individuals in each case was: (a) 50.52, (b) 42.01, (c) 22.90, (d) 11.84, and (e) 3.62.
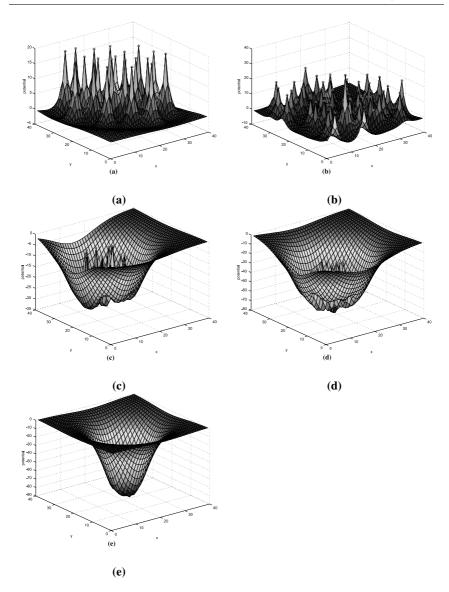
**(a)**

**(b)**

**(c)**

**(d)**

**(e)**

**Fig. 7.**  As in Figure 6 but with a surface plot of the net potential function.

there should not be a well-spaced group. Indeed, increasing group size resulted in closer packing density. (The average individual distance decreased by a factor of two, from 22.90 to 11.84 units, as the number of individuals increased from 20 to 45.) The potential surface (Figure 7c,d) resembles a "potential well": the potential at the center of the swarm is lower than it is at the edges because of a significant energy of attraction at the center. Repulsion is not strong enough to balance attraction here. There are still local maxima, indicating local repulsion, at the positions of the

individuals, but globally, each individual attracts quite a few others. Conditions at the center and the margins of the swarm are different. A new individual introduced to the group would not stay at the margin of the swarm, but would rather "roll down" to the bottom of the potential well at the center of the group without affecting the diameter of the group.

In the last case, we decreased the repulsion amplitude dramatically: $C = 1.1, l = 2, l^3 = 8$. Figure 7e shows that the potential well becomes narrower and deeper. Weak repulsion then completely fails to overcome attraction. Figure 6e shows that clusters of individuals form, some "on top" of each other, as the group collapses. Our results indicate that when the repulsion is significant, but not strong enough relative to attraction, there may be configurations of isolated individuals that are not internally well-spaced. When the repulsion is very weak, locally stable configurations consist of clusters of individuals that have collapsed to a point, and further equilibrium exists among the clusters of various sizes.

In several cases above, we find that the shape of the swarm is nearly round. (This is clear in the last three cases discussed.) For a well-spaced group, this means that the diameter of the swarm increases as the square root of the number of individuals. There is an analogy with minimization of the "surface energy" in physical systems: each individual at the edge of the swarm has a higher average 'energy' than a counterpart at the center. This implies that the perimeter will be minimized. Together with restrictions on the total area (in 2D), or volume (in 3D) per individual, this leads to the round shape of the group as a whole. The simulations shown here do not indicate any regular arrangement of individuals inside the swarm. However, at larger amplitudes of interaction, hexagonal spacing of the individuals starts to emerge.

## 8. Discussion

Many of the original works on fish schools assumed attraction-repulsion forces that are of gradient type (Parr, 1927; Breder, 1951; Sakai, 1973; Niwa, 1994). In some cases, this feature was not recognized, and in others, its consequences were only partly explored. The potential function of Beecham and Farnsworth (1999), for example, is similar to our Lyapunov function, and the derivatives of these potentials correspond to our interaction forces of gradient type. Beecham and Farnsworth (1999) defined a **Cost Potential**, i.e. a superposition of the potential that results from the cost of predation and the cost of interference between group members. They explored consequences numerically. Our paper exploit the mathematical structure of this type of system to reach general conclusions analytically, admittedly in a simplified setting.

The importance of interplay between attraction and repulsion in the behavior of a group of organisms has been stressed in the past. For example, Warburton and Lazarus (1991) state that ".. it is useful to compare attraction/repulsion functions in terms of their potential for achieving a high degree of group cohesion". Detailed estimates of relative magnitudes and ranges of these interactions leading to specific group structures were missing in previous studies. Our non-trivial, novel result is that strong short-ranged repulsion, and long range attraction **do not** always

guarantee a well-spaced group. The fact that an isolated pair of individuals tend to preserve an individual distance also does not guarantee that this applies to a large group under identical interaction forces. Our paper quantifies a sufficient condition for existence of a well-spaced large group. That condition, relating magnitudes and ranges of interactions is:

$$Rr^{d+1} > cAa^{d+1}, \ c \sim 1$$

where $c$ is a constant of order 1, $d$ is spatial dimension ($d = 1, 2, 3$), $R$, $A$ are the magnitudes, $r$, $a$ the ranges of exponential repulsive and attractive forces. More generally, for other pair-wise interactions expressed in the integral form, the condition can be stated as follows:

$$\int_{\mathcal{R}^d} (P^r(\mathbf{x}) - cP^a(\mathbf{x})) \, d\mathbf{x} > 0, \ c \sim 1,$$

where $P^{r,a}$ are the repulsion/attraction potential functions.

The above result for a well-spaced group does not guarantee that a uniform distribution of equidistant individuals will always form from an arbitrary initial configuration. This amounts to proving uniqueness of the global minimum of the Lyapunov function and periodicity of the configuration at that minimum in the limit $N \to \infty$. Mathematically, the problem of finding a global minimum of the Lyapunov function corresponding to the sum of short ranged repulsive and long ranged attractive forces is equivalent to a famous long-standing problem of proving the existence of crystals in the limit of absolute zero temperature in classical physics (Radin, 1981). In theoretical physics, this problem has been solved in the case of the well-known Lennard-Jones potential, $P(x) = x^{-12} - x^{-6}$, which is the potential energy of interaction between atoms via Van-der-Waals forces (Gardner and Radin, 1979). Gardner and Radin proved uniqueness of the corresponding globally stable ground state and its periodicity using the detailed expression for the Lennard-Jones potential, matrix theory, and functional analysis. However, they also proved that neither uniqueness nor periodicity are robust: specifically, arbitrarily small perturbations of the potential function can destroy both properties.

Analytical results were given for the case of deterministic groups. Simulation experiments with superimposed random motion (using piece-wise constant and Gaussian interaction forces) led to similar outcomes: Noise was found not to change the group structure qualitatively, but it did introduce a finite probability that neighbors at the edge of a group could exchange places, move away, and/or separate from the group. (Large stochasticity leads to rapid dispersal and breakup of the aggregates.)

Numerical experiments complement the analytical results and confirm that if the short ranged repulsion is sufficiently stronger than the long range attraction, then a "well spaced" group forms, such that the distance between neighbors away from the group edges does not depend on the group size. We derived explicit dependencies of this inter-individual spacing in 1D as function of the strength and ranges of the repulsion and attraction. The formulae can be easily generalized to higher dimensions.

A connection exists between the Lagrangian, individual-based approach, and the continuous Eulerian framework. Some results related to our current findings are discussed in a preceding work in the Eulerian framework (Mogilner and Edelstein-Keshet, 1999). A requirement for the validity of the Eulerian approximation is that many organisms are located on a spatial scale on the order of the range of interactions. Our results demonstrate that this holds only when the repulsion is relatively weak: $0 < (Rr^2/Aa^2) - 1 \ll 1$. This restrictive inequality suggests that a continuous description of group structure is valid only in very special cases.

### 8.1. Connection to biology

The "persistently uniform density" of a school of fish such as herring, mackerel, and sprat was noted by Parr (1927). Similarly, the density of herring is reported to be independent of the size of the shoal (Misund, 1990; Misund, 1993). Many previous models for mutual interactions, however, predict densities that increase as $N$, the size of the group increases, contrary to these observations: see the reviews of such models in (Beecham and Farnsworth, 1999; Warburton and Lazarus, 1991). This trend has been observed in some rare cases, e.g. in sparrow flocks (Caraco and Bayham, 1982). Recent tuna image data, collected and analyzed by Newlands (2002) presents nearest-neighbor distances for a variety of basic formations, and a range of group sizes. The decreasing distance between neighbors is seen in some, but not all formations, as the number of individuals increases. Analysis of the data against predictions of our model will be undertaken in a future follow-up study.

There are several ecological implications of our model. Under threat of predation, for example, individuals tend to cluster or huddle together as a possible defensive strategy. This corresponds to Hamilton's (1971) idea of the Domain of Danger. For a specific example, see the responses of fiddler crabs (Viscido et al., 2001) or sticklebacks (Tegeder and Krause, 1995) to a predator. Schools of anchovies considerably reduce their packing density at night (Graves, 1976). This may be accomplished by changes in any of the parameters associated with effective attraction and repulsion from conspecifics: e.g. increase in magnitude or range of attraction, or decrease in magnitude or range of repulsion. Our results would indicate how changes in such attraction or repulsion might affect the clustering of individuals in groups, and specifically, conditions for tight packing of the group.

The distribution of resources can affect the tendency of individuals to separate. As noted by Beecham and Farnsworth (1999), the distance between animals is correlated to resource abundance and predation threat. Mean spacing would therefore be expected to decrease if foraging constraints decrease relative to predation risk.

Our results suggest the solution to the following problem originally posed by Warburton and Lazarus (1991): "The problem is to..measure equilibrium distance in the group.. where an animal is substantially influenced by many or all others in the group..". Under assumption of the linear superposition of the pairwise gradient interactions in the group, we have shown analytically that the distance between isolated pairs of organisms is greater than the distance between members of a large swarm, as suggested by these authors. We have also demonstrated that the size of a linear (1D) group is proportional to the number $N$, of individuals, and, that as

the size of a finite group increases, the density of the group becomes uniform away from the edges. Similarly, for 2D and 3D groups, the size of the group increases as $N^{1/d}$, where $d$ is the space dimension, and the distance between neighbors away from the group's edges is independent of the group size.

In the case of bacteria, the secretion of chemical signals provides a mechanism for attraction and repulsion. Rates of secretion, types of molecules secreted (e.g. their diffusion and half lives), and sensitivity of the cells to chemical gradients are biological parameters that may vary in response to conditions. These, in turn, affect the attraction/repulsion parameters $(A, a, R, r)$ as shown in a recent model (Lee et al., 2001). The importance of social behavior in microorganisms has been highlighted recently (Crespi, 2001). In some cases (e.g. conditions of starvation), cells must aggregate tightly as a preliminary step in the formation of fruiting bodies (Myxobacteria and Dictyostelium). In other cases, the so-called "quorum sensing" based on chemical signaling serves some other purpose, such as plasmid transfer, or coordination of a massive attack in infection. Techniques here developed can help to understand dispersal and clustering mechanisms at the micro as well as the macro scale.

## 9. Appendix

### 9.1. Analysis of the net potential function

Here we use calculus to analyze the net potential (16) as a function of $\delta$. Critical points of the function $\bar{W}(\delta)$ are given by equation (18). Define the variable $x = e^{\delta/l}$. Note that biologically meaningful solutions require $x \geq 1$, $\delta \geq 0$. Equation (18) can be re-written in terms of $x$ as

$$\frac{x}{(x-1)^2} = C \frac{x^l}{(x^l-1)^2}.$$

For integer values of $l$, the denominator $(x^l - 1)$, has $(x - 1)$ as one of its factors. This greatly simplifies the situation. Cancelling common factors then leads to a polynomial with coefficients that depend on $C$. In the case $l = 2$ and $x > 1$, this results in a quadratic equation $x^2 + (2 - C)x + 1 = 0$ whose solution is given in (19). (The second root of the quadratic equation is not biological, because we require $x \geq 1$.) When $l = 3$, a similar procedure leads to the quadratic equation, $x^2 + (1 - \sqrt{C})x + 1 = 0$, and the second formula in equation (19).

More generally, we can show that equation (18) has at most one solution. Re-write the problem as:

$$\zeta(x) = \frac{1}{\sqrt{C}}, \quad \zeta(x) = \frac{x^{(l-1)/2}(x-1)}{(x^l-1)}. \tag{26}$$

The first three derivatives of the function $\zeta(x)$ have the form:

$$\zeta'(x) = \zeta_1[(1-l)x^{l+1} + (l+1)x^l - (l+1)x + (l-1)]$$

$$\zeta''(x) = \zeta_2[(1-l)x^l + lx^{l-1} - (l+1)]$$

$$\zeta'''(x) = \zeta_3[l(l-1)x^{l-2}(1-x)]$$

where $\zeta_1, \zeta_2, \zeta_3 > 0$. $\zeta'''(x) \le 0$ because $x \ge 1, l > 1$. Integration of the third derivative and the fact that $\zeta''(1) = -l < 0$ proves that the second derivative is negative. Integration of the second derivative and the fact that $\zeta'(1) = 0$ proves that the first derivative is negative at $x > 1$. Thus, $\zeta(x)$ is a decreasing function at $x > 1$. Therefore, equation (26) has a unique solution if $\zeta(0) > 1/\sqrt{C}$, and no solutions if $\zeta(0) < 1/\sqrt{C}$. Simple application of calculus demonstrates that the former case corresponds to the inequality $C > l^2$, while in the latter case, $C < l^2$. Further simple analysis reveals that if $C > l^2$, the net potential (16) decreases as a function of $\delta$ from 0 to a unique finite value of the equilibrium spacing and increases at greater values of $\delta$. On the other hand, if $C < l^2$, the net potential (16) is an increasing function at all values of $\delta$. Then there is no finite equilibrium spacing, and the global minimum corresponds to $\delta \to 0$.

### 9.2. Inverse power forces

Consider the case of the inverse power attraction and repulsion forces given by equation (21). The parameters can be related to the (spatial) ranges of attraction and repulsion with the identification $m = 1/a$ and $n = 1/r$. The net force due to mutual interactions, restated in terms of $a, r$ is

$$F(x) = \frac{R}{x^n} - \frac{A}{x^m} = \frac{R}{x^{(1/r)}} - \frac{A}{x^{(1/a)}}, \tag{27}$$

The outcome of interactions between two individuals depends on which function, the attraction or the repulsion dominates at small and/or large distances. We distinguish four cases as before:

*Cases 1, 2, 3.* Identical qualitatively to case 1 of the exponential forces.

*Case 4.* $R > A$ and $a > r$. This is the case of short-ranged repulsion and long-ranged attraction: A comfortable distance, $s$ exists at which $F(x) > 0$ at $0 < x < s$, and $F(x) < 0$ at $x > s$, and, at $s$, attraction and repulsion between a pair of neighbors exactly balance, $F(s) = 0$. The comfortable distance between two individuals would satisfy:

$$s = \left(\frac{R}{A}\right)^{1/(n-m)} = \left(\frac{R}{A}\right)^{ra/(a-r)}. \tag{28}$$

The potential function is:

$$P(x) = -\frac{R}{1-n}x^{1-n} + \frac{A}{1-m}x^{1-m}.$$

The net potential for a very large group ($N \to \infty$) arranged with equidistant spacing $\delta$ along a straight line (1D), is:

$$\bar{W} = 2 \sum_{j=1}^{\infty} W_j = 2 \sum_{j=1}^{\infty} P(j\delta) = -\frac{2R}{1-n} \sum_{j=1}^{\infty} (j\delta)^{1-n} + \frac{2A}{1-m} \sum_{j=1}^{\infty} (j\delta)^{1-m}$$

$$= (-\frac{2R\delta^{1-n}}{1-n} S_n + \frac{2A\delta^{1-m}}{1-m} S_m), \quad S_k = \sum_{j=1}^{\infty} \left(\frac{1}{j}\right)^{k-1}.$$

The system will evolve to minimize the above Lyapunov function. We assume $n > 2, m > 2$ (i.e. $a < 1/2, r < 1/2$) so that the series converges. (In particular for the Parr-Breder forces where $m = 0$ and $n = 2$ the infinite series would diverge and for $m = n = 2$, the series is the well-known divergent harmonic series.) Using the integral approximation (for $p > 1$),

$$\sum_{j=1}^{\infty} \left(\frac{1}{j}\right)^p \approx \int_{x=1}^{\infty} \left(\frac{1}{x}\right)^p dx = \frac{1}{p-1},$$

we obtain,

$$S_k \approx \frac{1}{k-2}.$$

To determine the uniform spacing $\delta$ that minimizes the functional $\bar{W}$, we set $d\bar{W}/d\delta = 0$ yielding:

$$\delta \approx \left[\frac{(m-2)}{(n-2)} \frac{R}{A}\right]^{1/(n-m)},$$

or, in terms of the parameters $a, r$,

$$\delta = s \left[\frac{a\,(1-2r)}{r\,(1-2a)}\right]^{ar/(r-a)}.$$

where $s$ is the comfortable distance defined by equation (28). Note, that in the biologically realistic case, $n > 2, m > 2, n > m$. If either $n$, or $m < 2$, there is no equilibrium finite spacing in the group.

### 9.3. Result 1: Cohesiveness of the group in 1D

We can verify Result 1 of Section 4 in the following way: Suppose the group configuration is given by the vector $\mathbf{z} = \{z_i\} \in \mathcal{R}_+^{N-1}$). We will show that the net potential decreases in a contracted swarm, and thus contradict the assumption that the original configuration was globally stable. The contraction is achieved by defining new coordinates $\mathbf{z}' \in \mathcal{R}_+^{N-1}$ as follows:

$$\mathbf{z}' = \begin{cases} z_i & \text{if } z_i \leq s, \\ s & \text{otherwise.} \end{cases}$$

The new vector of distances, $\mathbf{z}'$, has no components larger than $s$, and, thus, represents a configuration in which individuals are, on average, closer together, so the

swarm is more compact. Some terms in the new expansion (11) of the potential $W(\mathbf{z}')$, will be preserved (for cases in which the given pair of organisms are no closer than before), while other terms will have *decreased* (i.e if the pair of organisms are now closer to each other.) This follows from the fact that the potential function is an increasing function of $x$ at $x > s$. Thus, $W(\mathbf{z}') < W(\mathbf{z})$, i.e. the potential of the contracted swarm is lower than that of the original swarm. *Q.E.D.*

### 9.4. Result 1': Generalization to 2D or 3D

Choose the two most widely separated individuals in the group, and project the 2-D (respectively 3-D) coordinates of all other organisms on the straight line joining these two. Next, tighten the group so that none of the projected distances are greater than $s$. By this procedure, individuals have moved closer wherever they were "too far" apart. Terms in the expansion for the Lyapunov function are either unchanged, or strictly smaller than before, since the potential is an increasing function of $x$ at $x > s$ and distances have contracted to at most $s$. This verifies that the potential of the contracted swarm is lower than that of the original group. Repeat the process: Choose the next two most widely spaced individuals and contract along new direction. With this process, we can prove that in a group with the lowest potential, the distances between individuals cannot exceed $(N - 1)s$.

### 9.5. Result 2: Sufficient condition for a well-spaced group

Suppose that the swarm configuration vector, $\mathbf{x} \in \mathcal{R}_+^N$, is given. Choose a bin size $z_{min} \le s$ small enough such that inside each bin repulsion would dominate. Subdivide the swarm into bins of size $z_{min}$, and consider the number of individuals in each of these intervals. For definiteness, an individual at the edge of an interval will be assigned to the interval on its left.

Choose the interval that contains the most individuals, say $m$. (If there is more than one such interval, choose one of these intervals arbitrarily.) Then these $m$ organisms all repel one another (provided $m > 2$). Further, for $z_{min} < s$, the potential function $P(\hat{z})$ decreases with distance, so that the minimal 'energy' of interaction between a pair of organisms within the chosen interval would be $P^r(z_{min}) - P^a(z_{min})$.

Move one of the $m$ organisms to infinity. In so doing, we lower the contribution of the repulsion energy in the interval by at least $(m-1)(P^r(z_{min}) - P^a(z_{min}))$. The energy due to attraction to *all* neighbors is also affected. The immediately adjacent right and left neighboring bins contain at most $m + m$ members, resulting in attraction energy at most $2m P^a(0)$. The next two bins contribute at most $2m P^a(z_{min})$ to the attraction energy. Similar terms corresponding to further bins contribute $2m P^a(2z_{min})$, etc. The total contribution that accrues is $2m \Sigma_{n=0}^{\infty} P^a(nz_{min})$. Putting these together verifies that removal of one individual lowers the total energy by more than $(m - 1)(P^r(z_{min}) - P^a(z_{min})) - 2m \sum_{n=0}^{\infty} P^a(nz_{min})$. Because $\max\{m/(m-1)\} = 2$, the latter will be positive if the inequality (22) holds. *Q.E.D.*

If the repulsion potential increases as $\hat{z} \to 0$ faster than $1/\hat{z}$, while the attraction potential decreases to zero as $\hat{z} \to \infty$ rapidly enough, then the condition of Result

2 is always satisfied at sufficiently small $\hat{z}$. Indeed, let $P^r(\hat{z}) \geq \hat{z}^{-1-\epsilon}$, for some $\epsilon > 0$, and choose $\hat{z}$ small enough so that the Riemann sum on the r.h.s. of (22) can be approximated by the integral:

$$\Sigma_{n=0}^{\infty} P^a(n\hat{z}) \simeq \hat{z}^{-1} \int_0^{\infty} P^a(x)dx.$$

Then, inequality (22) assumes the form:

$$\hat{z}^{-\epsilon} > \hat{z}P^a(\hat{z}) + 4 \int_0^{\infty} P^a(x)dx,$$

which holds at sufficiently small $\hat{z}$ for finite values of $P^a(0)$ and $\int_0^{\infty} P^a(x)dx$.

### 9.6. Result 2': Generalization to 2D or 3D

Choose a grid with spacing $z_{min}$, and select a cell containing the largest number of individuals, say $m$. Remove any one of these $m$ organisms to infinity. The minimal 'energy' of repulsion between a pair of organisms within the given cell is $P^r(\sqrt{d}\hat{z}) - P^a(\sqrt{d}\hat{z})$. By removing one of the organisms, we have lowered the energy of interaction within the cell by at least $(m-1)(P^r(\sqrt{d}\hat{z}) - P^a(\sqrt{d}\hat{z}))$. Simultaneously, the energy of attraction to *all* neighbors is increased by at most $m((C(d)-1)P^a(0) + \sum_{\mathbf{x} \in \mathcal{Z}_{\hat{z}}^d} P^a(\mathbf{x}))$. The process of removal lowers the total energy if $m > 1$ and (23) holds. Iterating this process of removal, we end up with a configuration with no more than one organism per cell. Because the energy is lowered at each step of the process, the energy of this final configuration is smaller than that of the initial configuration, completing the proof.

### 9.7. Result 3: Insufficient repulsion may lead to collapse

For smooth, non-oscillating potential functions (e.g. similar to those in Section 3) we expect that the maximum of the expression $\hat{z}P^r(\hat{z})$ would occur approximately at a distance on the order of the range of repulsion ($\hat{z} \sim r$). Multiplying (22) by $\hat{z}$ and approximating the Riemann sum on the r.h.s. by an integral of the form $\int_0^{\infty} P^a(x)dx$, we have:

$$rP^r(r) > c \int_0^{\infty} P^a(x)dx,$$

where the constant $c \sim 1$. We now use the fact that the order of magnitude of the potential function is a product of the velocity and the range of interaction, while the integral of the potential has a magnitude related to the product of the scale of the potential and range of interaction. This leads to the rough approximations:

$$P^r(r) \sim Rr, \quad \int_0^{\infty} P^a(x)dx \sim Aa^2.$$

Using these approximations, an order of magnitude estimate for a sufficient condition guaranteeing existence of a well-spaced group is:

$$Rr^2 > cAa^2, \quad c \sim 1. \tag{29}$$

The inequality in Result 3 provides a sufficient but not a necessary condition for group collapse. This condition cannot be improved qualitatively. Indeed, suppose this condition is not met, and that

$$\int_0^\infty P^r(x)dx < \int_0^\infty P^a(x)dx, \quad \text{or} \quad Rr^2 < cAa^2, \ c \sim 1.$$

Then the "net cost" of placing a large number, $N$ of individuals in an equidistant formation with small spacing $\delta$ (with $\delta \ll r, a, \ \delta N \gg r, a$) can be estimated, neglecting edge effects, as

$$(N/\delta) \left[ \int_0^\infty (P^r(x) - P^a(x))dx \right] < 0.$$

Now chose $\delta \sim N^{-1/2}$, and note that $\delta$ approaches zero as $N$ increases, implying collapse of the swarm to tighter grouping as the number of individuals increases. The negative cost of this collapsed group is proportional to $-N^{3/2}$, much lower than that of any well-spaced group, proportional to $-N$. This makes the collapsed group more "energetically favorable", i.e more optimal biologically, which is ordinarily not the case in social aggregations.

## 9.8. Result 3': Generalization to 2D or 3D

For $N \gg 1$, choose the spacing $\delta(N) \sim N^{-1/(d+1)}$ in the group and place an organism at each grid point of $\mathcal{Z}_{\delta(N)}^d$ within a square (cube) of size $\delta(N)N^{1/d}$. Then the total energy of such group is a Riemann sum which can be approximated by the integral:

$$N\delta(N)^{-1} \int_{\mathcal{R}^d} (P^r(\mathbf{x}) - P^a(\mathbf{x})) \, d\mathbf{x} \sim N^{(d+2)/(d+1)} \int_{\mathcal{R}^d} (P^r(\mathbf{x}) - P^a(\mathbf{x})) \, d\mathbf{x}.$$

If the integral is negative, the corresponding energy, $\sim -N^{(d+2)/(d+1)}$, is lower than that of a well-spaced group, $\sim -N$, and the group has collapsed.

## 9.9. Non-pairwise interactions

In our Lagrangian, individual based model, higher density dependence of the repulsion corresponds to a velocity of the $i^{th}$ individual as:

$$V_i(x_i) = -\sum_{j \neq i} F^{(2)}(x_i - x_j) + \sum_{k \neq j \neq i} F^{(3)}(x_i - x_j, x_i - x_k).$$

where $F^{(2)}(x_i - x_j)$ is the attraction force (velocity) of the $i^{th}$ to the $j^{th}$ organism, while $F^{(3)}(x_i - x_j, x_i - x_k)$ is the repulsion force (velocity) for the $i^{th}$ organism moving away from the pair $j, k$ (e.g. from the center of mass of these individuals). The Lyapunov function of such a system has the form:

$$W(x_1, ..., x_N) = -\sum_{i,j} P^{(2)}(x_i - x_j) + \sum_{i,j,k} P^{(3)}(x_i - x_j, x_i - x_k),$$

provided a potential function $P^{(3)}$ describing a *triplet repulsion* exists.

If repulsion is short ranged, and attraction is long ranged, then the group will be cohesive. In this case, it is possible to prove that in the limit $N \gg 1$ the average spacing in the group is bounded from below uniformly and independently of $N$, and thus **a well-spaced group is globally stable for arbitrarily weak triplet-like repulsion**. Indeed, if we assume the opposite, and the average spacing in the group, $\delta(N)$, is a decreasing function of $N$, then the energy per individual would be $w \sim -\bar{P}^{(2)}(a/\delta(N)) + \bar{P}^{(3)}(r/\delta(N))^2$. Here $\bar{P}^{(2)}$ and $\bar{P}^{(3)}$ are the magnitudes of the attraction and repulsion potentials respectively, and $a$ and $r$ are as before. The ratio $(a/\delta(N))$ is the characteristic number of others attracting the given individual, while $(r/\delta(N))^2$ is the characteristic number of *pairs* repelling the given individual. At large $N$, $(r/\delta(N))^2 \gg (a/\delta(N))$, and the average 'energy' per individual would increase with $N$ at arbitrarily weak repulsion. This indicates that a well-spaced group with uniform average spacing is more stable.

## References

Aoki, I., Inagaki, T.: Photographic observations on the behaviour of Japanese anchovie. *Engraulis japonica* at night in the sea. Mar. Ecol. Prog. Ser. **43**, 213–221 (1988)

Beecham, J.A., Farnsworth, K.D.: Animal group forces resulting from predator avoidance and competition minimization. J. Theor. Biol. **198**, 533–548 (1999)

Breder, C.M.: Structure of a fish school. Bull. Amer. Mus. Nat. Hist. **98**, 1–27 (1951)

Breder, C.M.: Equations descriptive of fish schools and other animal aggregations. Ecology **35**, 361–370 (1954)

Caraco, T., Bayham, M.C.: Some geometric aspects of house sparrow flocks. Animal Behaviour **30**, 990–996 (1982)

Conder, P.J.: Individual distance. Ibis **91**, 649–655 (1949)

Crespi, B.J.: The evolution of social behaviour in micro-organisms. Trends in Ecol. Evol. **16**(4), 178–183 (2001)

Cross, M.C., Hohenberg, P.C.: Pattern formation outside of equilibrium. Rev. Mod. Phys. **65**, 851–1112 (1993)

Emlen, J.T.: Flocking behaviour in birds. Auk **69**, 160–170 (1952)

Flierl, G., Grunbaum, D., Levin, S., Olson, D.: From individual to aggregations: the interplay between behaviour and physics. J. Theor. Biol. **196**, 397–454 (1999)

Gardner, C.S., Radin, C.: The infinite-volume ground state of the Lennard-Jones potential. J. Stat. Phys. **20**, 719–724 (1979)

Graves, J.: Photographic method for measuring spacing and density within pelagic fish schools at sea. Fish. Bull. **75**, 230–234 (1976)

Grunbaum, D., Okubo, A.: Modelling social animal aggregation. In: S. Levin (ed.), Frontiers in Mathematical Biology, Springer N.Y. 1994, pp. 296–325

Gueron, S., Levin, S.A., Rubenstein, D.I.: The dynamics of herds: From individual to aggregations. J. Theor. Biol. **182**, 85–98 (1996)

Haken, H.: Synergetics; An Introduction: Nonequilibrium Phase Transitions and Self-Organization in Physics, Chemistry, and Biology, New York, 3rd edition 1983

Hamilton, W.D.: Geometry for the selfish herd. J. Theor. Biol. **31**, 295–311 (1971)

Holmes, E.E., Lewis, M.A., Banks, J.E., Veit, R.R.: PDE in ecology: spatial interactions and population dynamics. Ecology **75**(1), 17–29 (1994)

Huth, A., Wissel, C.: The simulation of movement of fish schools. J. Theor. biol. **156**, 365–385 (1992)

Keller, E.F., Segel, L.A.: Initiation of slime-mold aggregation viewed as an instability. J. Theor. Biol. **26**, 399–415 (1970)

Krause, J., Tegeder, R.W.: The mechanism of aggregation behaviour in fish shoals: individuals minimize approach time to neighbors. Anim. Behav. **48**, 353–359 (1994)

Lee, C.T., Hoopes, M.F., Diehl, J., Gilliland, W., Huxel, G., Leaverand, E.V., McCann, K., Umbanhowar, J., Mogilner, A.: Non-local concepts and models in biology. J. Theor. Biol. **210**, 201–219 (2001)

Miller, R.S., Stephen, W.J.D.: Spatial relationships in flocks of sandhill cranes. Ecology **47**(2), 323–327 (1966)

Misund, O.A.: Sonar observations of schooling herring: school dimensions swimming behaviour and avoidance of vessel and purse seine Rapp. P.-v. Reun. Cons. int. Explor. Mer **189**, 135–146 (1990)

Misund, O.A.: Dynamics of moving masses: variability in packing density shape and size among herring sprat and saithe schools. ICES. J. mar. Sci. **50**, 145–160 (1993)

Mogilner, A., Edelstein-Keshet, L.: A non-local model for a swarm. J. Math. Biol. **38**, 534–570 (1999)

Newlands, N.: PhD Thesis: Shoaling dynamics and abundance estimation: Atlantic Bluefin Tuna (Thunnus thynnus), Fisheries Center UBC, Vancouver BC Canada, 2002

Niwa, H.-S.: Self-organizing dynamic model of fish schooling. J. Theor. Biol. **171**, 123–136 (1994)

Niwa, H-S.: Newtonian dynamical approach to fish schooling. J. Theor. Biol. **181**, 47–63 (1996)

Okubo, A.: Diffusion and Ecological Problems: Mathematical Models. Springer Verlag, New York, 1980

Okubo, A.: Dynamical aspects of animal grouping:swarms, schools, flocks, and herds. Adv. Biophys. **22**, 1–94 (1986)

Parr, A.E.: A contribution to the theoretical analysis of the schooling behaviour of fishes. Occasional Papers of the Bingham Oceanographic Collection **1**, 1–32 (1927)

Parrish, J., Edelstein-Keshet, L.: Complexity, pattern, and evolutionary trade-offs in animal aggregation. Science **284**, 99–101 (1999)

Parrish, J.K., Hamner, W.M., Prewitt, C.T.: From individuals to aggregations: Unifying properties, global framework, and the holy grails of congregation, In: J.K. Parrish, W.M. Hamner (eds.), Animal Groups in Three Dimensions 1997 Cambridge University Press pp. 1–13 Cambridge U.K.

Radin, C.: The ground state for soft discs. J. Stat. Phys **26**, 365–373 (1981)

Sakai, S.: A model for group structure and its behavior. Biophysics Japan **13**, 82–90 (1973)

Sinclair, A.R.E.: The African buffalo: a study of resource limitation of populations, University of Chicago Press, Chicago 1977

Suzuki, R., Sakai, S.: Movement of a group of animals. Biophysics Japan **13**, 281–282 (1973)

Tegeder, R.W., Krause, J.: Density dependence and numerosity in fright stimulated aggregation behaviour in shoaling fish. Phil. Trans. R. Soc. Lond. B **350**, 381–390 (1995)

Turchin, P.: Beyond simple diffusion: models of not-so-simple movement in animals and cells. Comments on Theor Biol **1**, 65–83 (1989)

Uvarov, B.P.: Locusts and Grasshoppers, Imperial Bureau of Entomology. London, 1928

Vabo, R., Nottestad, L.: An individual based model of fish school reactions: predicting antipredator behaviour as observed in nature. Fisheries Oceanography **6**(3), 155–171 (1997)

Viscido, S.V., Miller, M., Wethey, D.S.: The response of a selfish herd to an attack from outside the group perimeter. J. Theor. Biol. **208**, 315–328 (2001)

Viscido, S.V., Wethey, D.S.: Quantitative analysis of fiddler crab flock movement: evidence for 'selfish herd' behaviour. Animal Behaviour **63**(4), 735–741 (2002)

Warburton, K., Lazarus, J.: Tendency-distance models of social cohesion in animal groups. J. Theor. Biol. **150**, 473–488 (1991)