Effect of Stochasticity and Variable Speed on Collective Dynamics of Finite Fish Schools

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of BS-MS dual degree in Science

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Certificate of Examination

This is to certify that the dissertation titled **"Effect of Stochasticity and Variable Speed on Collective Dynamics of Finite Fish Schools"** submitted by **Vivek Jadhav** (MS15080) for the partial fulfillment of BS-MS dual degree programme of the Institute, has been examined by the thesis committee duly appointed by the Institute. The committee finds the work done by the candidate satisfactory and recommends that the report be accepted.

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Dated: June 15, 2020

Declaration

The work presented in this dissertation has been carried out by me under the guidance of Dr. Vishwesha Guttal at the Indian Institute of Science, Bengaluru and Dr.N.G. Prasad at the Indian Institute of Science Education and Research Mohali.

This work has not been submitted in part or in full for a degree, a diploma, or a fellowship to any other university or institute. Whenever contributions of others are involved, every effort is made to indicate this clearly, with due acknowledgment of collaborative research and discussions. This thesis is a bonafide record of original work done by me and all sources listed within have been detailed in the bibliography.

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In my capacity as the supervisor of the candidate's project work, I certify that the above statements by the candidate are true to the best of my knowledge.

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Abstract

Various mathematical models have been developed to understand schooling in fish. Most of these models are built on three main rules - alignment, attraction and repulsion. They differ from each other in terms of defining social interactions and individual properties. However, the criticism of these models is that the model assumptions are unrealistic. In the majority of these models, individuals move at a constant speed, or their speed is independent of neighbours. Also, in most models, the position and orientation of all individuals are updated at the same time. Therefore neglecting the inherent stochasticity observed in a school of fish that results in ansynchronous changes in the direction of movement and neighborhood-dependent dynamic variation in the speed.

In this thesis, we develop a more realistic model to understand schooling in fish. In our model, we incorporate both stochasticity and the ability of individuals to adjust their speed as a response to neighbours' behaviour. School size range from 10 to 60 and the model is two-dimensional. We find that cohesive groups and high polarisation is achieved through pairwise alignment and attraction. This is in contrast to direction averaging in Vicsek like models. We show that schools of all size are oblong and the density is equally distributed about the centre of the group.

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Chapter 1

Introduction

We notice similar patterns in seemingly different set-ups. We form a queue whether to buy coffee after a class or to buy tickets for a cricket match. We make an unspoken decision to move to an empty table, spread ourselves symmetrically before we begin our discussion. Similar behaviour can be observed when we enter the cricket stadium, this time maybe with a preference for a seat where the batsman is clearly visible. Individuals' behaviour starting from how they form a queue to occupy a seat is perfectly predictable across all cafes and stadiums. These are a few examples of free individuals behaving collectively in our daily routine ([Sumpter 05]).

These behaviours, which are common to all of us, are examples of collective behaviour in humans or animals, in general. Collective behaviour refers to the emergence of coordinated group-level behaviour by repeated interactions among neighbouring individuals. Essentially, collective behaviour is the tendency to form group-level patterns. Conspecifics aggregate due to external physical forces, such as clustered resources or due to mutual attraction among themselves.

Irrespective of the forces that cause collective behaviour, group living offers various benefits to individuals. Studies have shown that group-living provides better access to mates and better reproductive success ([Robinson 88], [Cameron 09]). Other benefits include cooperative breeding, parental care ([Balshine 01], [Clutton-Brock 02]) and an increase in foraging efficiency ([Rypstra 89]). Members of the group are protected from aggression or predation through communal territory defence ([Krebs 08], [Port 11]), mobbing behaviour ([Krams 02]), confusion effect, risk dilution and enhanced predator detection ([Turner 86]). Another manifestation of group-living is animals moving

in groups—for example, fish schools or bird flocks. Studies have shown that coordination among individuals moving together reduces the chances of predator attacks ([Ioannou 12]) possibly due to confusion effect ([Landeau 86]). And, it is also shown to reduce the energetic costs of locomotion ([Bill 76], [Herskin 98a], [Filella 18]). Even though group-living offers various benefits, they come at a cost. It can increase the rate of infection or disease ([Tella 02], [Godfrey 09]), increase in competition for limited resources ([Skogland 85]), such as food and mates ([Schradin 10]).

To continue living as a group and reap the benefits of group-living, animals need to move as a group. Through repeated local interactions, animals tend to travel collectively. This behaviour often results in the emergence of fascinating group-level patterns across biological systems. The spectacular swirling of starlings as a collective; V-formation of migrating geese; ants marching in the bidirectional lane of infinite length; gliding and turning fish schools; migrating herds of social ungulates; swarms of marching locusts; or even human crowds in busy streets ([Sumpter 05]).

Researchers have tried to characterise the underlying local interactions that result in a wide range coordinated motion in animals. Different methods were employed by biologists and physicists (and mathematicians) to understand the emergent properties. Biologists mainly focused on studying how animals process the information from their neighbours, which is generally noisy and inaccurate. On the other hand, physicists and mathematicians have tried to develop theories and models assuming simple behavioural rules - which describes the interactions between individuals. This aids in identifying the behavioural rules that might result in patterns resembling natural systems ([Jhawar 19b]). However, to better understand the collective motion and predict natural systems, we need to develop models where the behavioural rules are guided by empirical observations. Recent advancement in tracking technologies has helped us obtain high-resolution spatiotemporal data. Hence we can now better infer underlying local interactions ([Jhawar 19a]).

Most of the mathematical models are developed on the principle of self-organisation theory. Self-organisation theory suggests that most of the complex coordinated behaviour can emerge through relatively simple repeated interactions among the group members. This theory suggests that behavioural rules dictate the form and consequently, the function of the collective structure ([Couzin 03]). Self-organisation is

defined as "a process in which pattern at the global level of a system emerges solely from numerous interactions among the lower-level components of a system. Moreover, the rules specifying interactions among the system's components are executed using only local information, without reference to the global pattern" ([Camazine 03]). However, it should be noted that in certain systems like migrating animals; animals may modify their local interactions with neighbours based on global information, such as a common consensus to move along a specific direction ([Couzin 03]). Various studies have tried to understand group-level patterns in biological systems on the foundation of self-organisation. Few of them are fetal development ([Kenynes 88]), coats of mammals ([Murray 81]), nests of social insects ([Theraulaz 95]), swarms of bacteria ([Ben-Jacob 94]), marching army ants ([Deneubourg 89]), locusts ([Collett 98]), bird flocks ([Hemelrijk 12]), fish schools ([Radakov 73a]), and human crowds ([Couzin 03]).

Mathematical modelling is widely used to study collective behaviour. It is difficult to deduce how the interactions among large number of group members result in complex population-level structure. In these systems, there is a non-linear relation between interactions among neighbours and the emergent structure - a result of local interactions. Interactions between individuals create larger patterns, which in turn influence the behaviour of group members, and this further alters the higher-order structure. This feedback loop continues ([Couzin 03]).

For example, ants deposit pheromone to mark their way to a food source ([Wilson 71]). Other ants, which encounter the pheromone trail, follow the trail which leads them the food source. As ants use the trail, which leads them to the food source, they reinforce the trail by secreting more pheromone to the initial trial. Ants which carry food from the source also leave pheromone on their way back to the nest. Through the positive reinforcement, the pheromone trail builds-up, and a larger number of ants can be seen marching between food source and nest. This steady-state of the ant trail formed is "more than sum of its parts" ([Sumpter 05]).

One of the influential models in the field of collective behaviour is the *Vicsek model* ([Vicsek 95]). In the standard *Vicsek model*, N self-propelled particles move at a constant speed s in a finite volume, V with periodic boundary conditions. All the particles move in the average direction of their neighbours. Particles are assumed to make an error while copying the average direction. Mathematically, at time t each

individual i {i ϵ 1, 2, 3, ..., N} updates its direction θ_i synchronously as

$$\theta_i(t + \delta t) = \bar{\theta}_i + \Delta\theta(t) \tag{1.1}$$

where the overbar represents an average over all the neighbours within a fixed radius *r* from the *focal* individual, *i*. The second term on the right-hand side represents an error focal individual makes while copying the average direction. The error is typically chosen from a uniform distribution over the range $[-\frac{\eta}{2}, \frac{\eta}{2}]$, where $\eta \leq 2\pi$. The particle now moves in the calculated direction at speed *s* for time δt. After time δt the angles are re-calculated.
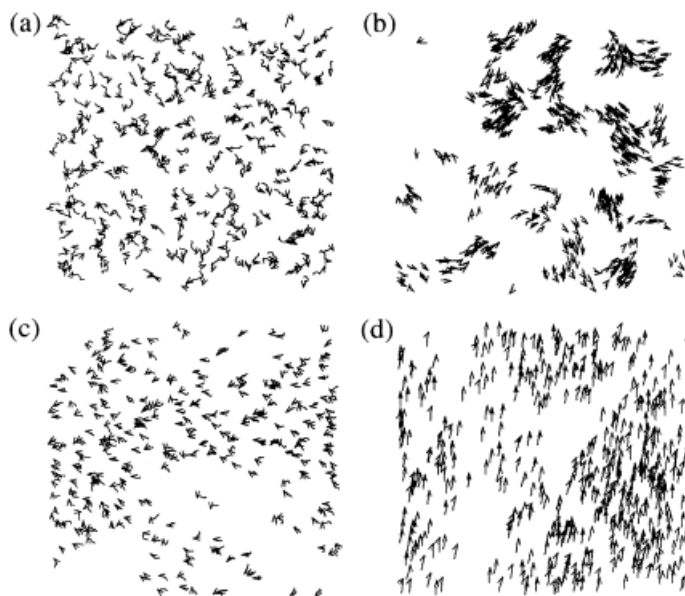
FIG. 1. In this figure the velocities of the particles are displayed for varying values of the density and the noise. The actual velocity of a particle is indicated by a small arrow, while their trajectory for the last 20 time steps is shown by a short continuous curve. The number of particles is $N = 300$ in each case. (a) $t = 0$, $L = 7$, $\eta = 2.0$. (b) For small densities and noise the particles tend to form groups moving coherently in random directions, here $L = 25$, $\eta = 0.1$. (c) After some time at higher densities and noise ($L = 7$, $\eta = 2.0$) the particles move randomly with some correlation. (d) For higher density and *small noise* ($L = 5$, $\eta = 0.1$) the motion becomes ordered. All of our results shown in Figs. 1–3 were obtained from simulations in which v was set to be equal to 0.03.

Figure 1.1: Patterns formed in Vicsek model
Image Take From: [Vicsek 95]

The Vicsek model is a simple model in continuous space where the position and

direction of particles are updated synchronously based only on the local information (directions of the neighbouring particles). Yet, the model could demonstrate a wide range of patterns of collective motion (Figure 1.1). Through numerical simulation, they showed that group polarisation exhibits a phase transition in two dimensions as the group density is increased, and noise is decreased ([Vicsek 95]). The Viscek model inspired various similar SPP models of collective motion ([Czirók 99], [Couzin 02], [Mishra 12], [Hemelrijk 08]).

Vicsek model and similar SPP models were successful in providing novel insights on the collective patterns observed in natural systems. However, most of these studies try to understand collective behaviour in the macroscopic scale, i.e. in the limit of infinite group size ([Jhawar 19b]). But, group size is finite in many biological systems, especially vertebrates. Therefore, they tend to ignore the role of stochastic due to finite group size. Also, *Vicsek* like models, where all the group members behave alike at every time step, fail to account for the stochasticity that arises due to differences in interactions among group members ([Couzin 03], [Jhawar 19a]).

As mentioned above, stochasticity can arise from multiple factors. The behaviour of animals in the group are inherently probabilistic, either when they act on their own or when they interact with their neighbours. Such stochastic behaviour of animal movement can determine the group structure in many taxa. Groups are usually finite in size, often relatively small. Finite group size can give rise to group-level stochasticity, also known as *intrinsic noise* ([Jhawar 19a]). Even though stochasticity is an integral part of animal decision making and group dynamics, it is usually regarded as a nuisance which destroys order or obscures patterns in most of the earlier works. Hence, various statistical tools were developed to get rid of randomness in-order to study the underlying patterns ([Boettiger 18]).

In most of the *Vicsek like* models, individuals are considered to move at the same constant speed. However, in biological systems, the speed of an individual can vary in response to its neighbours' dynamics ([Mishra 12]). Members of the group adjust their speed by either slowing down to avoid collisions or increase their speed to prevent being isolated ([Hemelrijk 08]). They also change their speed stochastically ([Huth 92a], [Jhawar 20]). Put simply, individuals adjust distance and alignment with neighbours primarily through manipulating their speed. Studies have shown that the speed of an individual determines its spatial position in the group. Faster moving

individuals usually occupy positions at the front of the group, and slower ones flow them ([Couzin 02], [Gueron 96]). Recent experiments on fish schools have shown that faster moving schools are highly aligned compared to that travelling at slower speeds ([Mishra 12], [Hemelrijk 12]). Consequently, variations in the speed of individuals' can strongly influence the collective behaviour—primarily collective states such as polarisation, inter-individual distances and group density.

However, in the past few decades, the notion that stochasticity is a nuisance and obscures patterns has been challenged. Studies have recognised noise as a force driving novel phenomena that could not have been understood from the underlying deterministic skeleton alone ([Boettiger 18]). Many biological systems such as schooling fish or flocking birds show different types of collective motion at different times. The transition between different types of collective motion can be caused by environmental factors or change in behavioural rules. Additionally, they can happen entirely due to stochastic effects as shown in some studies ([Kolpas 07], [Yates 09], [Dyson 15]). In fact, it is shown that stochasticity itself creates order. When a colony of ants is presented with two identical sources of food, we may expect them to divide equally between two choices. Therefore, not reaching a consensus. But, this is true only when the colony size is infinitely large, i.e. under the deterministic limit. If we consider the intrinsic noise due to the finite colony size, ants do arrive at a consensus. But, this is true only when the colony size is less than the certain critical value ([Biancalani 14]).

In another study on fish groups of *Etroplus suratensis*, it is shown that schooling is noise-induced. Noise emerged from the intrinsic stochasticity due to finite group size. One important finding is that fish aligns with only one neighbour at a given time, unlike standard *Vicsek* like models where the heading is calculated by local direction-averaging ([Jhawar 20]). They also derive a mesoscopic model for the group order-parameter (polarisation) by considering noise as a function of both - inherently probabilistic nature of interactions and finite group size ([Jhawar 19b]). The model could describe empirically observed group polarisation. However, as the model assumed constant speed, various questions such as the relation between group-polarisation and speed, inter-individual distances, group density remain unaddressed.

In this thesis, we incorporate both stochasticity and the ability of individuals to adjust their speed in response to neighbours' state, into a numerical model to simulate

and understand schooling in fish. There are models in which events or interactions such as alignment and attraction are formulated to be stochastic, but, all the particles move at a constant speed, or their speed is assumed to be independent of other particles ([Calovi 18], [Bode 10], [Strömbom 19], [Jhawar 20]). Similarly, there are models where all the interactions are assumed to occur synchronously, but the speed is a function of local neighbourhood ([Mishra 12], [Filella 18], [Hemelrijk 08]). However, we know that the behaviour of animals in the group is inherently probabilistic and their speed depends on the neighbours' dynamics. To our knowledge, models do not incorporate both - probabilistic nature of animal behaviour and speed as a function of neighbours position and orientation.

Also, the way attraction and repulsion are modelled is distinct from previous models. In most of the earlier models ([Huth 92b], [Huth 94], [Couzin 02], [Bode 10]), attraction and repulsion interactions depended just on the angle between the focal individual's orientation and the line joining the focal individual and the neighbour ($\measuredangle(\mathbf{v}_i^0, \mathbf{x}_j - \mathbf{x}_i)$, where $\mathbf{v}_i$ and $\mathbf{x}_i$ are velocity and position vectors of *ith* particle). In other words, the interactions were independent of the relative distance between neighbours ($\mathbf{x}_j - \mathbf{x}_i$). In the metric formulation (which is assumed in most of these models), the interactions are confined to respective zones. This, in turn, accounts for relative distances, but studies show that interactions are governed by topological distances rather than metric ([Ballerini 08]). However, in some studies ([Hemelrijk 05], [Hemelrijk 08], [Calovi 18]), attraction and repulsion interactions are functions of both relative angle and distance ($\measuredangle(\mathbf{v}_i^0, \mathbf{x}_j - \mathbf{x}_i)$ and $\mathbf{x}_j - \mathbf{x}_i$) but, they are different from our formulation.

Stochasticity is modelled through continuous-time Gillespie simulations (details in the next section). This work is an extension of the previously studied spatial model with stochasticity and constant speed ([Jhawar 20]). Such a model ([Jhawar 20]) will help us study the shape and internal structure of travelling groups of fish. We can further comment on the differences in shape and internal structure between fish schools travelling at different group speeds. We finally discuss the importance of stochasticity and variable speed in understanding collective motion in biological systems.

Chapter 2

Model and Specifics of Interactions

As mentioned in the introduction, the model we build is an extension of the spatial model developed by [Jhawar 20]. Particles in the model are characterised by position and direction of motion—the direction of particles change due to spontaneous turning and pair-wise alignment interaction. For the group to be cohesive, they include medium-range attraction and avoid collisions through short-range repulsion. As the interactions (spontaneous turning, attraction and pair-wise alignment) are modelled to be stochastic, they occur at a fixed rate. They employ continuous-time Gillespie ([Gillespie 76], [Gillespie 77]) simulations for interactions with position updated synchronously at discrete-timestep.

We incorporate stochasticity in our model similarly as done by [Jhawar 20]. However, we model alignment, attraction and repulsion more realistically ([Parrish 05], [Hemelrijk 08]) as elaborated in the next section.

2.1   Model

We consider N particles ($i = 1, 2,..., N$) in 2-D continuous space. Each particle is characterised by its position $\mathbf{r}_i$, speed v_i and orientation $\mathbf{e}_i$. Individuals move along their orientation (Figure 2.1). As is usual in similar agent-based models, particles align with their neighbours and attract to them. Individuals maintain minimum distance with their neighbours to avoid collision and also turn spontaneously ([Huth 92b], [Huth 94], [Couzin 02], [Hemelrijk 05], [Hemelrijk 08], [Jhawar 20]). Unlike earlier models, where speed is an independent parameter, particles adjust their speed in response to neighbours' dynamics. Also, as mentioned earlier, interactions are stochastic owing to

inherent probabilistic nature of animal interactions. Hence the speed and orientation of individuals change stochastically - due to spontaneous rotation, alignment and attraction, and deterministically due to short-range repulsion. We use continuous-time Gillespie simulation ([Gillespie 76], [Gillespie 77]) for attraction, spontaneous turning and alignment events with position updated synchronously at discrete time-steps. We emphasise the readers to notice that the state of an individual change stochastically. Put simply, the events (alignment, attraction and spontaneous rotation) occur at different times for different individuals.

The equations of motion are

$$\dot{\mathbf{r}}_i = v_i \mathbf{e}_i \tag{2.1}$$

$$\mathbf{e}_i = (\cos \theta_i, \sin \theta_i)^T$$

$$\dot{\theta}_i(t) = \begin{cases} \omega & 0 \leq \theta_{id} - \theta_i(t) < \pi \\ -\omega & \theta_{id} - \theta_i(t) \geq \pi \\ \omega & \theta_i(t) - \theta_{id} > \pi \\ -\omega & 0 \leq \theta_i(t) - \theta_{id} \leq \pi \end{cases} \tag{2.2}$$

$$\tau \frac{dv_i}{dt} = v_0 - v_i + \Delta v_{int} + \Delta v_r \tag{2.3}$$

where v_0 is the speed of an individual in case of no interaction, this is equivalent to the "cruise speed" defined by ([Hemelrijk 08]). For simplicity, we assume v_0 to be same for all individuals (however, in general, v_0 can be different for different individuals depending upon their size, position and environmental factors). τ is constant with dimensions of time. τ is the response time taken by an individual to change from its current speed to desired speed. Say if $\tau << 1 time\ step$ then the fish achieves the desired speed instantaneously. However, if $\tau \approx O(1) of\ time\ step$ then inertia prevents an instantaneous change in speed. Therefore, τ is a function of the mass of the fish, friction and drag due to fluid. Δv_{int} is the desired change in speed due to events.

In case of an event (alignment, attraction, obstacle avoidance or spontaneous rotation) heading of the individuals change. To achieve the desired direction, i.e. the desired orientation of the particle, (θ_{id}), individuals rotate at a constant angular speed, ω. If the desired heading is within $|\omega|dt$ then the individuals rotate and move in the
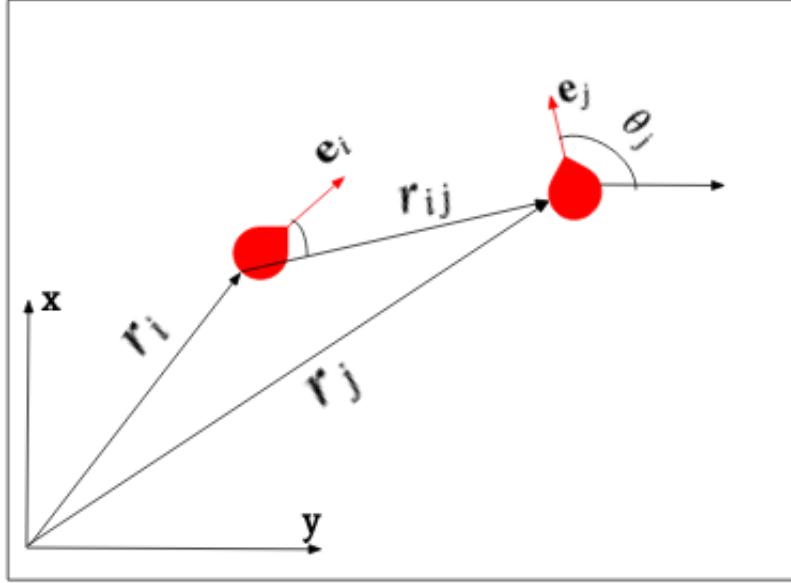
Figure 2.1: Sketch of two interacting fish where $\mathbf{r}_i$ is the position of ith particle with orientation $\mathbf{e}_i$. $\mathbf{r}_{ij}$ is the distance between two fish.

desired direction else, they rotate by $|\omega|$dt towards the desired direction.

Fish have a rare blind angle, i.e. fish cannot see its neighbour if the angle between its orientation and the vector $\mathbf{r}_{ij}$ is greater than θ_m. Therefore fish aligns and attracts only to the neighbours present within its sight. Mathematically, θ_{ij} should be less than θ_m:

$$\theta_{ij} = \cos^{-1}\left(\frac{\dot{\mathbf{r}}_i \cdot \mathbf{r}_{ij}}{|\dot{\mathbf{r}}_i|\,|\mathbf{r}_{ij}|}\right) \tag{2.4}$$

where $\mathbf{r}_{ij} = \mathbf{r}_j - \mathbf{r}_i$. In some studies ([Hemelrijk 05], [Hemelrijk 08]), the blind zone depends upon the type of interaction. However, in our model, similar to [Couzin 02], the blind angle is constant and independent of the type of interaction.

Further, our model follows topological approach, i.e, an individual can sense K nearest neighbours and, align/attract with k ($k \leq K$) individuals randomly chosen from K nearest neighbours ([Couzin 02]).

Why topological interaction and not metric? Experimental results on flocks of starlings by [Ballerini 08], showed that the nature of interaction to be topological, i.e., each individual interact with a fixed number of closest neighbours, independent

of their distances. Topological interaction ensures robust cohesion and hence, higher biological fitness. In the case of metric formulation, whenever the interindividual distances exceed the metric range, there will not be any interaction between the individuals. Therefore, high chance of cohesion to be lost.

Additionally, to build a realistic model, we need to account for the fact that individuals behaviour is influenced only by those they can perceive. Metric formulation neglects the density-dependent perception of group members, i.e., higher group density limits the perception of individuals which are further away. In [Hemelrijk 08] study, they overcome the shortcomings of the metric formulation by modelling the range of perception as inversely proportional to density.

2.1.1 Interactions

In this section, we explain the interaction dynamics in detail.

1. Alignment

At a constant rate per unit time c, individuals try to match their heading and speed with the nearest neighbours. They identify K nearest neighbours and then randomly select k_c individuals from the set. However, when we account for finite vision, fish can only align with neighbours present in its sight. Therefore, if there are not K fish in sight of the focal individual, it identifies all the fish (K') in its sight. If $K' > k_c$ then the focal individual randomly chooses k_c from the set to align. Else, if $K' \leq k_c$ then the focal fish aligns with all the fish in its sight, i.e $k_c = K'$.

The desired heading is,

$$\mathbf{e}_{ic} = \frac{1}{k_c} \sum_{j=1}^{k_c} \mathbf{e}_j \tag{2.5}$$

Individuals adjust their speed to the mean speed of the neighbours. Hence the rate of change of speed due to alignment is:

$$\tau \frac{dv_i}{dt} = v_0 - v_i + \Delta v_c \tag{2.6}$$

$$\Delta v_c = \frac{1}{k_c} \sum_{j=1}^{k_c} (v_j - v_0) \tag{2.7}$$

2. Attraction

If any individual is farther away from its closest neighbour, it increases its speed and moves toward the neighbour to avoid being isolated. Hence in the model, if an individual is at a significant distance from its neighbour, it increases its speed and approaches the neighbour. However, if the group is already cohesive, and the distance between individuals is less than few body sizes of fish, then attraction should not have any qualitative effect on the group dynamics. The desired speed and direction depends upon the magnitude of $\mathbf{r}_{ij}$ ($|\mathbf{r}_{ij}| = r_{ij}$) i.e, desired speed is high if r_{ij} is large and low if r_{ij} is small.

At rate r, every individual identifies K nearest neighbours and randomly chooses k_a neighbours from the set and is attracted to them. Similar to alignment, fish is attracted only to the neighbours in its sight. Hence, if the number of fish in its sight is less than K but greater than k_a, the focal individual identifies all the K' individuals in its sight and randomly selects k_a neighbours from the set to attract. But, if the number of fish in the sight of the focal individual is less than k_a, it gets attracted to all the fish in its sight.

Rate of change of speed due to attraction:

$$\tau \frac{dv_i}{dt} = v_0 - v_i + \Delta v_a \tag{2.8}$$

$$\Delta v_a = \frac{\kappa_a}{k_a} \sum_{j=1}^{k_a} \left(\frac{|\mathbf{r}_{ij}| - 2r_{rp}}{l} \right)^{\gamma} \tag{2.9}$$

where r_{rp} is fish body length.

Nevertheless, individuals cannot move faster beyond a limit. The maximum achievable speed is v_m. Therefore,

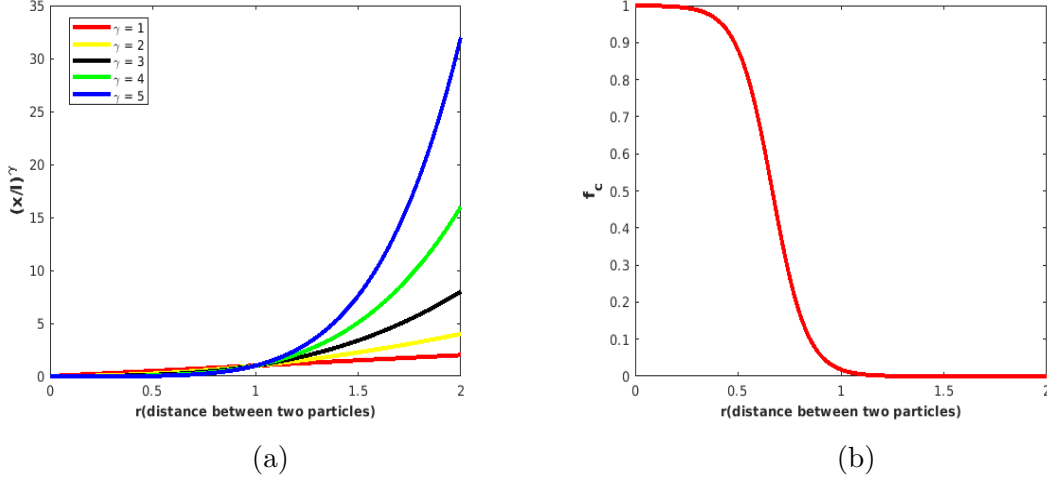$$\Delta v_a = \begin{cases} \Delta v_a & \Delta v_a \leq v_m \\ v_m & \Delta v_a > v_m \end{cases} \tag{2.10}$$

Figure 2.2: (a) $\frac{r}{l}$ vs x for different γ, x is the distance between two particles. (b) f_c as a function of inter-particle distance.

l (0.6 m in this study) is a constant. If the particles are within this distance change in speed and orientation due to attraction will be very small. Hence, if $r_{ij} - 2r_{rp} < l$, attraction will not have any effect on the group dynamics (Figure 2.2). As shown in the Figure 2.2, if γ is large, $(\frac{r_{ij}-2r_{rp}}{l})^\gamma$ will only have an effect when the fish are at a significant distance apart.

κ (3×10^{-2} in this study) and γ (3 in this study) are constants which determine the intensity of attraction interaction.

Desired heading is towards the individual farther away from the focal individual. However, if the group is cohesive to begin with, the desired direction will be the focal individuals current heading. Mathematically, the desired heading is given as:

$$\mathbf{e}_{ia} = \frac{1}{2} \left(\mathbf{e}_i + \frac{1}{k_a} \sum_{j=1}^{k_a} \left(\frac{|\mathbf{r}_{ij}| - 2r_{rp}}{l} \right)^\gamma \frac{\mathbf{r}_j}{r_j} \right) \tag{2.11}$$

NOTE: In the above description of alignment and attraction, we considered a general case of selecting k individuals randomly from K ($K > k$) closest neighbours to align and attract. A special case when $k = 1$ is called pair-wise alignment ([Jhawar 20]) and pair-wise attraction. So in pair-wise interaction, a focal individual identifies K closest neighbours (if K individuals are not in sight, it follows the same method described above) and randomly selects one neighbour ($k = 1$) from the set to align and attract.

Hence eq 5 and 11 can be written as:

$$\mathbf{e}_{ic} = \mathbf{e}_{j\epsilon\mathcal{L}} \tag{2.12}$$

and

$$\mathbf{e}_{ia} = \frac{1}{2}\left(\mathbf{e}_i + \left(\frac{|\mathbf{r}_{ij}| - 2r_{rp}}{l}\right)^{\gamma} \frac{\mathbf{r}_{j\epsilon\mathcal{L}}}{r_{j\epsilon\mathcal{L}}}\right) \tag{2.13}$$

respectively. Where $\mathcal{L}$ is set of K nearest neighbours. Similarly, eq 7 and 9 are

$$\Delta v_c = v_{j\epsilon\mathcal{L}} - v_0 \tag{2.14}$$

and

$$\Delta v_a = \kappa_a \left(\frac{|\mathbf{r}_{ij,j\epsilon\mathcal{L}}| - 2r_{rp}}{l}\right)^{\gamma} \tag{2.15}$$

respectively.

3. Spontaneous Rotation

Individuals spontaneously change their heading and speed at a rate of s.

The desired heading of the ith particle is

$$\theta_s = \theta_i + \mathcal{N}_{\mathsf{trunc}}(0, \varepsilon_\theta, -\pi, \pi)$$

$$\mathbf{e}_{is} = (\cos\theta_s, \sin\theta_s)^T \tag{2.16}$$

$\mathcal{N}_{\mathsf{trunc}}(0, \sigma^2, a, b)$ is a truncated normal distribution with mean μ, variance σ^2 with interval (a,b). Rate of change of speed due to spontaneous rotation:

$$\tau\frac{dv_i}{dt} = v_0 - v_i + \Delta v_s \tag{2.17}$$

and

$$\Delta v_s = \mathcal{N}_{\mathsf{trunc}}(0, \varepsilon_v, -v_m, v_m)$$

15

4. Short-range repulsion

Fish occupy a finite volume. Individuals maintain minimum distance among themselves to prevent collisions. Therefore if individuals approach their neighbours, they reduce their speed and change orientation. At every update, we ensure that individuals do not collide.

Unlike [Jhawar 20], other events are not restricted by repulsion interaction. In their model, other events occur only if the focal individual maintains a certain minimum distance with every individual of the school. However, in this model other events can happen at any time-step independent of repulsion interaction but, if individuals are too close to each other, short-range repulsion dictates the desired heading and speed.

The rate of change of speed due to this interaction is

$$\tau \frac{dv_i}{dt} = v_0 - v_i + \Delta v_r \tag{2.18}$$

where Δv_r is the desired change in speed due to repulsion and is given as:

$$\Delta v_r = \frac{1}{\mathcal{N}_r} \sum_{j=1}^{n} f_{app_j} f_{prox_j} f_{c_j} \tag{2.19}$$

$$f_{app_j} = H\left[\mathbf{v}_i \cdot \mathbf{r}_{ij}\right] H\left[\mathbf{v}_i \cdot \mathbf{r}_{ij} + \mathbf{v}_j \cdot \mathbf{r}_{ji}\right] \tag{2.20}$$

$$f_{prox_j} = \left(\mathbf{v}_i \cdot \mathbf{r}_{ij} + \mathbf{v}_j \cdot \mathbf{r}_{ji}\right) \frac{\kappa_r}{\left(|r_{ij}| - 2r_{rp}\right)^\beta} \tag{2.21}$$

$$f_{c_j} = 1 - \frac{1}{e^{-c_1|r_{ij}|+c_2}+1} \tag{2.22}$$

$$f_{c_j} = 1 - \frac{1}{e^{-c_1|r_{ij}|+c_2}+1} \tag{2.23}$$

$H[x]$ is the Heaviside step function.

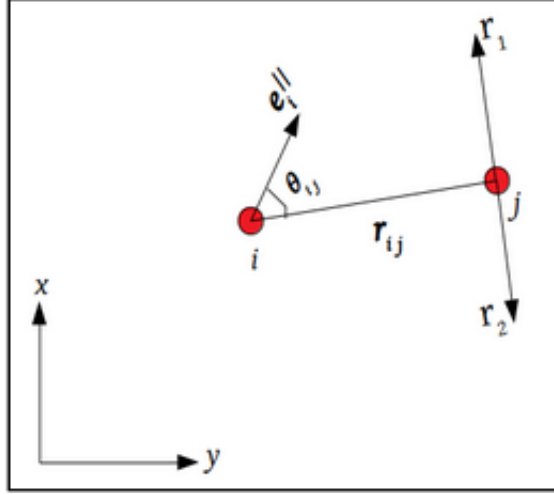$$H[n] = \begin{cases} 0 & n < 0 \\ 1 & n \geq 0 \end{cases}$$

Figure 2.3: Two perpendicular vectors to the line joining two interacting particles ($\mathbf{r}_{ij}$).

$\mathcal{N}_r$ is the number of particles in the repulsion zone

Here, f_{app_j} is non zero (i.e $f_{app_j} = 1$) only if i is approaching j and the rate of change of $\mathbf{r}_{ij}$ is negative. Put simply, only when the focal individual is moving towards its neighbour and, the distance between focal individual and its neighbour is decreasing with time $f_{app_j} = 1$ else it is zero. Magnitude of f_{prox_j} increases as the distance between to individuals decrease and f_{c_j} indicates whether the repulsion term is significant or not. As shown in Figure 2.2, f_c decreases as the distance between two fish increases and is zero beyond a point ($r = 1$ in Figure 2.2). κ_r (fixed to be -10^{-3}), c1 and c2 are constants ().

The desired heading of focal individual (i) is perpendicular to $\mathbf{r}_{ij}$ weighted with f_{app_j}, f_{prox_j} and f_{c_j} ([Calovi 18]). Let us denote the unit perpendicular vector as $\mathbf{r}_\perp$. Now, for a given vector $\mathbf{r}_{ij}$ there are two perpendiculars in 2-D space. Individual chooses a perpendicular vector which is at shorter angular distance from its current orientation (Figure 2.3). That is, if $\mathbf{r}_{\perp 1}$ and $\mathbf{r}_{\perp 2}$ are two perpendicular vectors to $\mathbf{r}_{ij}$ the desired heading $\mathbf{r}_{ij\perp}$ is along:

$$\mathbf{r}_{ij\perp} = \begin{cases} \mathbf{r}_{\perp 1} & \cos^{-1}\frac{\mathbf{e}_i \cdot \mathbf{r}_{\perp 1}}{|\mathbf{e}_i||\mathbf{r}_{\perp 1}|} \leq \frac{\pi}{2} \\ \mathbf{r}_{\perp 2} & \cos^{-1}\frac{\mathbf{e}_i \cdot \mathbf{r}_{\perp 1}}{|\mathbf{e}_i||\mathbf{r}_{\perp 1}|} > \frac{\pi}{2} \end{cases} \tag{2.24}$$

Therefore the desired heading $\mathbf{e}_{ir}$ is given by,

$$\mathbf{e}_{ir} = \frac{1}{\mathcal{N}_r} \sum_{j=1}^{n} f_{app_j} f_{prox_j} f_{c_j} \mathbf{r}_{ij\perp} \tag{2.25}$$

In [Couzin 02] like models, the desired direction of the focal individual is independent of its distance from neighbours. However, the strength of neighbours' influence depends upon how far they are from the focal individual ([Reuter 94], [Hemelrijk 05], [Hemelrijk 08]). Most of these models assume the speed of particles to be independent of other agents and is considered to be a stochastic variable. But, the speed of fish can vary as a response to neighbours' dynamics ([Mishra 12], [Filella 18]). Therefore, we incorporate both speed and direction of particles as a function of their distance and orientation with neighbours.

At every time-step, we check if the agent undergoes any of the interactions (alignment, attraction or spontaneous rotation). If more than one type of interaction occurs at a given time-step, then the desired direction is given as:

$$\mathbf{e}_{id} = \mathbf{e}_{ic} + \mathbf{e}_{ia} + \mathbf{e}_{ir} + \mathbf{e}_{is}$$

and

$$\mathbf{e}_{id} = (e_{idx}, e_{idy})$$

hence

$$\theta_{id} = \tan^{-1} \frac{e_{idy}}{e_{idx}} \tag{2.26}$$

Similarly, $\Delta\mathbf{v}_{int}$ is the average of all the interactions at that time-step. For example if alignment and attraction events occur at a given time-step then,

$$v_{int} = \frac{\Delta v_c + \Delta v_a}{2} \tag{2.27}$$

Chapter 3

Analysis and Results

3.1 Analysis of the model

The model described in the previous chapter was implemented on the commercial software Matlab. We studied the model for different numbers of agents ($N = 10$, 15, 30, 60). Simulations were run for 4×10^5 time-steps and 8 replicas. Parameter values explored are given in Table 3.1. This set of parameters ensure cohesive and polarised schools. At each time-step, the following statistics were calculated. To confirm if the model resulted in cohesive schools, we calculated 'expanse' (a) as defined by [Huth 92a]. If the schools are cohesive and do not break apart, the expanse value lies between fixed values dependent on school size. And, if schools are not cohesive the expanse value diverges (see Figure 3.5)

$$a(t) = \sqrt{[\mathbf{x}_i(t) - \mathbf{X}_{(t)}]^2} \tag{3.1}$$

$$\mathbf{X}_t = \frac{1}{N} \sum_i \mathbf{x}_i(t) \tag{3.2}$$

Where $\mathbf{X}_t$ is the position of the centre of the school. This variable quantifies the spatial size of the school. We calculate group polarisation (m) ([Jhawar 20]) to quantify the orientation of the agents.

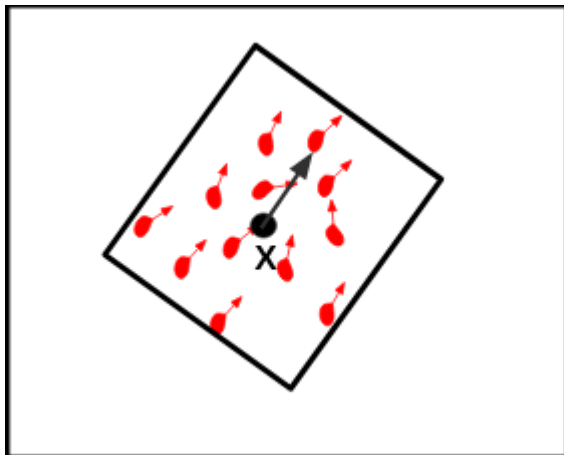$$m(t) = \left| \frac{1}{N} \sum_{i=1}^{N} \mathbf{e}_i(t) \right| \tag{3.3}$$

Figure 3.1: Method of measuring group width (w), group length (l) and distance to front (f). Snapshot of positions (red circles), velocities (red arrows), centre of mass (black circle) and group velocity (black arrow).

Parameter	Unit	Symbol	Value(s) explored
Number of individuals	1	N	$10 - 60$
Time step	2	Δt	0.02
Zone of repulsion	m	r_{rp}	0.2
Sight	Degrees	–	210
Rate of spontaneous rotation	s^{-1}	s	1.5
Rate of alignment	s^{-1}	c	3.5
Rate of attraction	s^{-1}	r	2
Rate of rotation	Degrees s^{-1}	ω	60
Cruise Speed	ms^{-1}	v_0	0.2 and 0.4
Max speed	ms^{-1}	v_m	1
Variance in angle	Degree	ϵ_θ	45
Variance in angle	ms^{-1}	ϵ_v	0.06
Response time	seconds	τ	0.2

Table 3.1: Summary of model parameters.

where $\mathbf{e}_i$ is the orientation of the *ith* agent. m = 1 implies all the agents are pointing in the same direction (order) and, m = 0 indicates that agents are pointing at random direction (disorder).

To study the form of the school, the school was enclosed within the smallest rectangle, whose length was parallel to the group direction (Figure 3.1). To calculate the elongation of the school, we divide the group length (length of the rectangle parallel to the group direction) by the group width (width of the rectangle orthogonal to group direction). Further, to calculate the degree of centrality of the position of the group centre, we divide the distance of the group centre to the front by group length. We used the 'boundary' function available on Matlab to enclose the school within the smallest boundary and area of the same was calculated. The school size was then divided by the area to calculate the group density. All the calculations are done for two cruise speeds (v_0) - 0.2 m/s (slow) and 0.4 m/s (fast).

3.2   Results

We found that schooling was achieved for various sets of interaction rates (alignment, attraction and repulsion). However, for this study we stick to one set of interaction rates given in Table 3.1.

Groups were cohesive when only attraction interaction or both alignment and attraction interactions were considered along with spontaneous rotation (Figure 3.3). However, when only attraction interaction along with spontaneous rotation and no alignment is modelled, groups behave like swarms, i.e. low group polarisation (disorder). But when both alignment and attraction interaction rates are non-zero, groups are highly polarised (order). Further, the polarisation decreases with an increase in school size (Figure 3.4). When only attraction interactions are considered, the spread in polarisation decreases with an increase in group size. But, a reverse trend is observed when both alignment and attraction interactions are considered (Figure 3.4). High polarisation and group cohesion were achieved only through pair-wise attraction and pair-wise alignment.
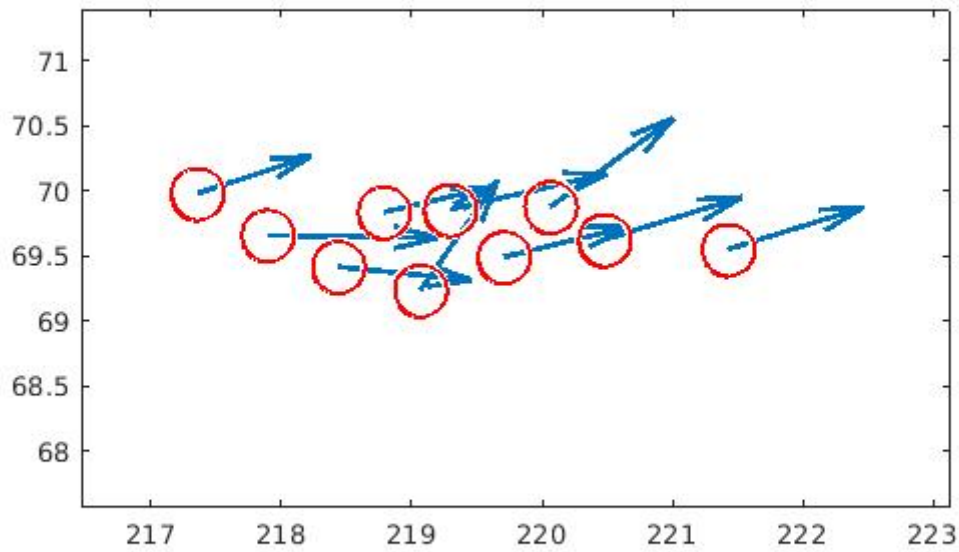
Figure 3.2: Snap shot of typical simulation run. Centre of the circle denote the position of agents. Blue arrows indicate the direction of motion of particles and their length is proportional to the magnitude of particles' speed. Red circles denote the average area occupied by fish. No two circles can intersect.
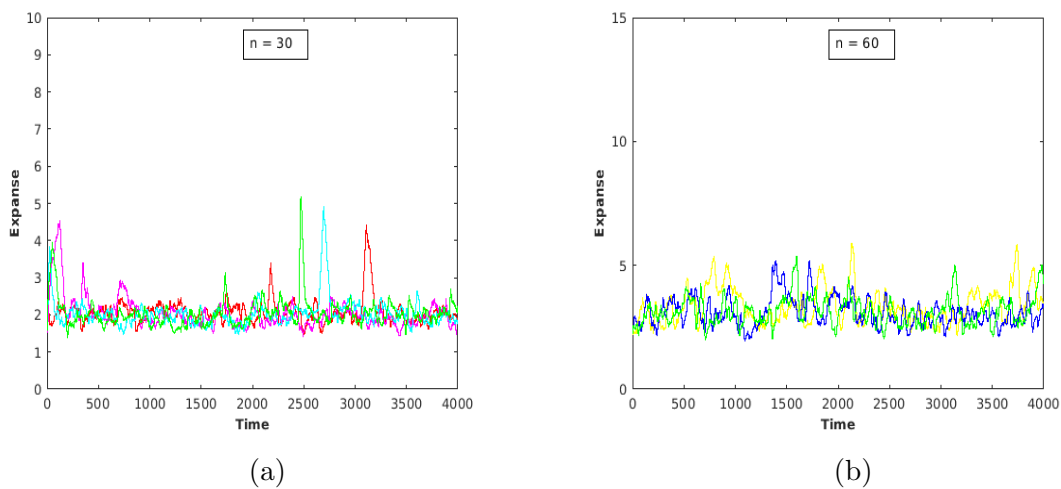
Figure 3.3: (a) Time series of expanse with both alignment and attraction interactions included for group size 30. (b) Time series of expanse with only attraction interaction for group size 60. Different line colours denote different trials.
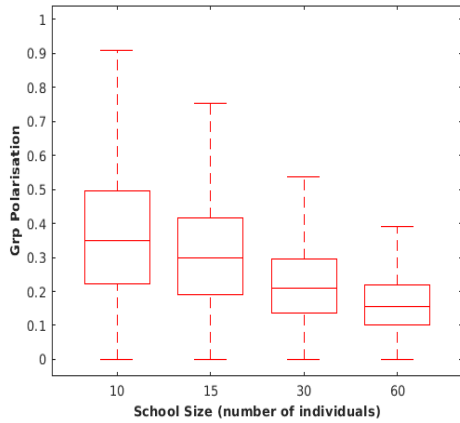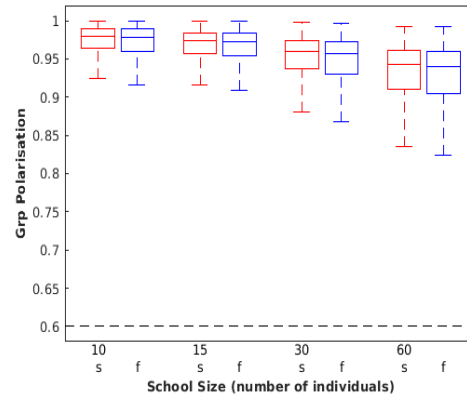
$$(a) \qquad (b)$$

Figure 3.4: (a) Box plot of group polarisation vs school size when only attraction interaction was included. (b) Box plot of group polarisation vs school size when both alignment and attraction interactions were modelled. Red and blue box denote slower (0.2m/s) and faster (0.4 m/s) cruise speeds

When only alignment interaction with no attraction was modelled, the groups were not cohesive, and agents travelled in random directions (Figure 3.5). Expanse is observed to remain constant for a certain amount of time further followed by a sudden increase and remain constant till the next abrupt increase.
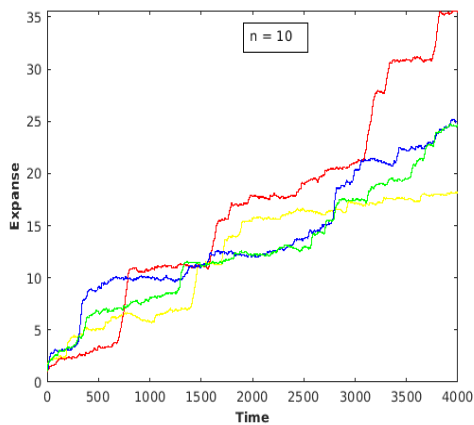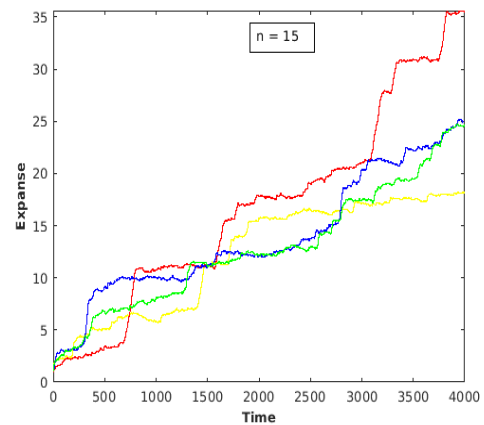
$$(a) \qquad (b)$$

Figure 3.5: Time series of expanse with only alignment interaction for group sizes 10 and 15. Different line colours denote different trials.

We also found that schools are oblong for all group sizes. At larger group sizes schools become more oblong (Figure 3.6). Also, faster schools were more oblong. A reverse trend was observed in group density. Group density decreased with an increase in group size. Schools with lower cruise speed were denser compared to faster schools (Figure 3.6).
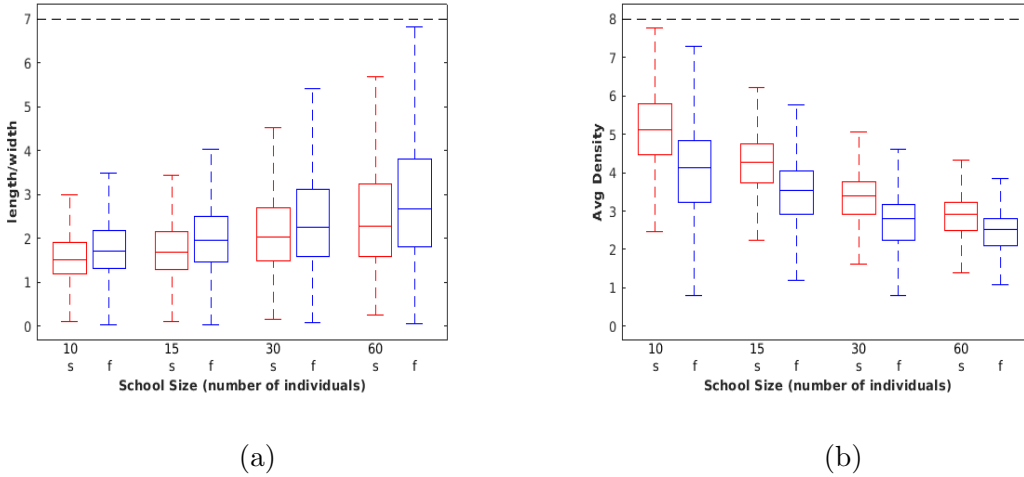
Figure 3.6: (a) box plot of length/width ration vs school size. (b) box plot of density vs school size. Red and blue box denote slower (0.2m/s) and faster (0.4 m/s) cruise speeds

To understand the distribution of density, we calculated the degree of centrality of the position of the group centre. Values significantly less than 0.5 would suggest that a larger number of agents are located in front of the group centre and higher frontal density. Furthermore, if the values were significantly greater than 0.5 would mean higher density in the tail. However, we found the value very close to 0.5, indicating that agents were equally distributed over the school. Further, we also found that at almost all times, the equal number of agents were in-front and back of the group centre (Figure 3.7). The results were the same for both schools moving at slower cruise speed and faster cruise speed.

Speed distribution as expected was centred around 0.2 ms^{-1} and 0.4 ms^{-1} for slower and faster schools respectively (Figure 3.8). When an agent undergoes spontaneous rotation interaction, a random speed from a normal distribution is chosen as the desired change in speed. If the computed resultant speed is less than zero, we set the speed of the agent to zero as speed cannot be negative. Also, when agents are

(a)

(b)
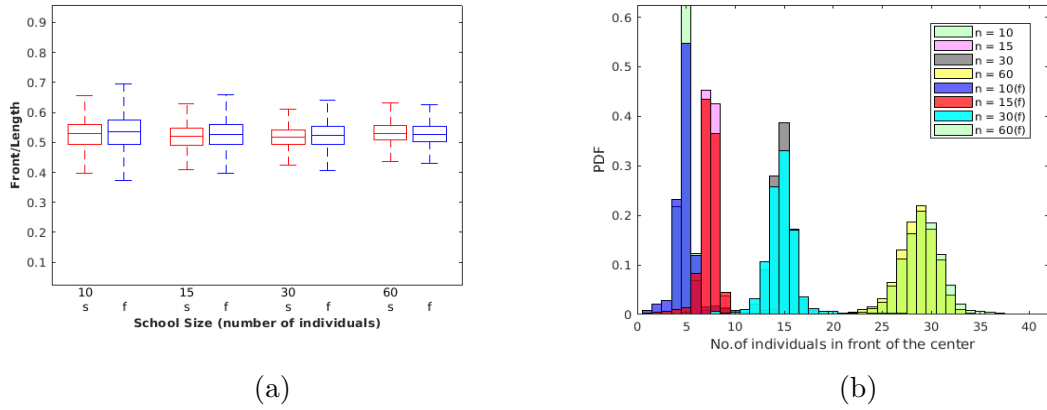
Figure 3.7: (a) Box plot of location of the group centre. (b) Distribution of the number of agents in front of the group centre. Red and blue box denote slower (0.2m/s) and faster (0.4 m/s) cruise speeds

too close to each other, the one approaching its neighbour comes to rest to avoid the collision. This is manifested as a peak around $v = 0$.

(a)

(b)
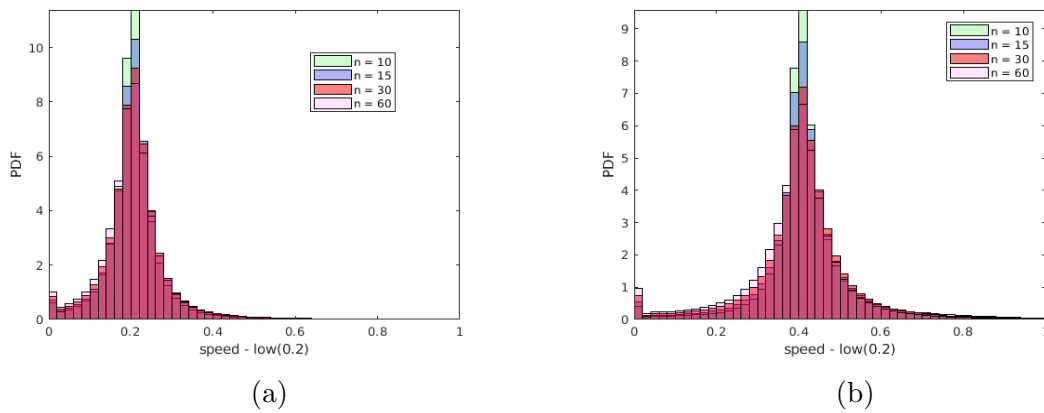
Figure 3.8: (a) Speed distribution of agents with slower cruise speed (0.2 m/s). (b) Speed distribution of agents with faster cruise speed (0.2 m/s).

Chapter 4

Discussion

In this study, we show that patterns of spatial organizations - oblong schools and uniform group density, emerge as a consequence of modelled behavioural rules of coordination in fish. The behavioural rules governing the fish motion - speed control, perception of neighbours and interactions are modelled more realistically ([Hemelrijk 08]).

We find that group cohesion and high group polarisation are achieved in all groups sizes only through pairwise alignment and pairwise attraction. [Jhawar 20] show that schooling in *Etroplus suratensis* to be noise-induced. The noise is arising from the intrinsic stochasticity due to the finite group size and inherent probabilistic nature of interactions. The mathematical model built to simulate the fish motion shows that fish align with one neighbour at a time. This is different from the local direction averaging in *Vicsek* like models. However, due to the constant speed of agents and the way interactions were defined, to achieve cohesive groups, the focal individual had to move towards the centroid of neighbouring $N/4$ agents. Where N is the total number of agents in the group.

[Huth 92b] studied two kinds of models: 'Average model' and 'Decision Model'. In the average model, the individuals moved in the average direction of their neighbours. This is similar to *Vicsek* like models. In the decision model, fish randomly selects a neighbour to adjust its position and orientation (pairwise interaction). Both models result in cohesive groups. However, only the schools formed by the averaging model were polarised. The groups formed from decision model were always "confused", i.e. the group polarisation was low. In contrast, we found groups to be cohesive and highly polar when individuals attract and align with only one neighbour at a time.

[Strömbom 19], in their study, demonstrate that asynchronous updating of orientation and attraction (alignment free) can result in polarised schools. Similarly swarming in locusts was shown to achieve only through selective attraction and repulsion ([Romanczuk 12]). In our study, even though only attraction interaction can result in cohesive groups, they are not highly polarised.

[Jhawar 19a] discuss in detail the importance of stochasticity while modelling biological systems. However, they do not compare the different ways asynchrony are modelled. There are different ways to model asynchrony ([Strömbom 19], [Bode 10]). In [Bode 10], asynchrony is built through stochastic neighbour selection. In other words, the focal individual randomly chooses a neighbour from the group to interact irrespective of its position in the group. Further, the interaction with the selected neighbour is probabilistic (50% chance of alignment interaction and 50% chance of attraction interaction). But, the studies have shown that neighbours tend to remain the same while fish move collectively ([Gerlotto 10], [Magurran 94]). Hence in such systems, it might be an unrealistic way of modelling interactions.

In [Strömbom 19], asynchrony is modelled by randomizing the orders of individuals. But, in their model, all the interaction occur at all times. We employ asynchrony by accounting for the probabilistic nature of interactions. Such modelling of asynchrony can best describe schools in which neighbours tend to be same for longer periods.

Schools are usually oblong ([Partridge 80], [Hemelrijk 08], [Hemelrijk 05]). [Hemelrijk 08] develop a realistic model with variable speed to explain the emergence of oblong schools. In their model, oblong schools emerged because individuals try to avoid collisions. When fish avoid collisions, they tend to fall back. Now those who were on the sides move together to fill the gap. This results in longer schools. In their model, slower schools were more oblong. However, we observe that faster schools to be more oblong similar to various empirical studies ([Radakov 73b], [Breder 59], [Kent 19]). According to Breder's hypothesis, this is because swimming movement occurs along the horizontal plane, and this demands greater distance among individuals along the axis of motion. As a result, schools with faster speeds are more oblong as fish require greater reaction distances ([Breder 59]). Recent empirical work by [Kent 19]

has shown faster groups to be more oblong in contrast to [Hemelrijk 08]. Nevertheless, there might be other mechanisms which might result in oblong schools. As shown in multiple studies swimming at the back might cost less due to hydrodynamic advantages. Hence oblong schools might be a side effect of fish trying to reduce their energetic costs of locomotion ([Herskin 98b], [Svendsen 03], [Filella 18]).

[Hemelrijk 08] found larger schools to be denser—also, high frontal density in schools of all sizes. However, we do not find similar results. We observe density to decrease with an increase in school size. In schools of all sizes, the group centre was located midway of the school length (Figure 3.7). We also found that at most times, an equal number of agents were in front and behind of the group centre. Therefore in schools of all sizes, the density was equally distributed about the centre of the group.

4.1   Future Perspective

In our model, we assume all the agents to be identical. However, in real biological systems, individuals are of different size and age. Motivational differences between group members are shown to influence group structures ([Couzin 02]). Hence it is essential to build models in which agents tend to interact often with neighbours of their own kind. In most of the mathematical model, vision is assumed to be symmetric around the axis of motion, but this not always true in real systems ([Krause 02]). We also do not study the effect of hydrodynamics on schooling. Similar ways of incorporating variable speed along with hydrodynamics can be of focused in future studies.

Bibliography

[Ballerini 08] Michele Ballerini, Nicola Cabibbo, Raphael Candelier, Andrea Cavagna, Evaristo Cisbani, Irene Giardina, Vivien Lecomte, Alberto Orlandi, Giorgio Parisi, Andrea Procaccini *et al.* *Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study.* Proceedings of the national academy of sciences, vol. 105, no. 4, pages 1232–1237, 2008.

[Balshine 01] Sigal Balshine, Brenda Leach, Francis Neat, Hannah Reid, Michael Taborsky & Noam Werner. *Correlates of group size in cooperatively breeding cichlid fish (Neolamprologus pulcher).* Behavioral Ecology and Sociobiology, vol. 50, pages 134–140, 01 2001.

[Ben-Jacob 94] Eshel Ben-Jacob, Ofer Schochet, Adam Tenenbaum, Inon Cohen, Andras Czirok & Tamas Vicsek. *Generic modelling of cooperative growth patterns in bacterial colonies.* Nature, vol. 368, no. 6466, pages 46–49, 1994.

[Biancalani 14] Tommaso Biancalani, Louise Dyson & Alan J. McKane. *Noise-Induced Bistable States and Their Mean Switching Time in Foraging Colonies.* Phys. Rev. Lett., vol. 112, page 038101, Jan 2014.

[Bill 76] Robert Bill & WILLIAM Herrnkind. *Drag Reduction by Formation Movement in Spiny Lobsters.* Science (New York, N.Y.), vol. 193, pages 1146–8, 10 1976.

[Bode 10] Nikolai WF Bode, Jolyon J Faria, Daniel W Franks, Jens Krause & A Jamie Wood. *How perceived threat increases synchronization in collectively moving animal groups.* Proceedings of the Royal Society B: Biological Sciences, vol. 277, no. 1697, pages 3065–3070, 2010.

[Boettiger 18]   Carl Boettiger. *From noise to knowledge: how randomness generates novel phenomena and reveals information*. Ecology letters, vol. 21, no. 8, pages 1255–1267, 2018.

[Breder 59]   Charles Marcus Breder. *Studies on social groupings in fishes. Bulletin of the AMNH; v. 117, article 6*. 1959.

[Calovi 18]   Daniel S Calovi, Alexandra Litchinko, Valentin Lecheval, Ugo Lopez, Alfonso Pérez Escudero, Hugues Chaté, Clément Sire & Guy Theraulaz. *Disentangling and modeling interactions in fish with burst-and-coast swimming reveal distinct alignment and attraction behaviors*. PLoS computational biology, vol. 14, no. 1, page e1005933, 2018.

[Camazine 03]   Scott Camazine, Jean-Louis Deneubourg, Nigel R Franks, James Sneyd, Eric Bonabeau & Guy Theraula. Self-organization in biological systems, volume 7. Princeton university press, 2003.

[Cameron 09]   Elissa Z. Cameron, Trine H. Setsaas & Wayne L. Linklater. *Social bonds between unrelated females increase reproductive success in feral horses*. Proceedings of the National Academy of Sciences, vol. 106, no. 33, pages 13850–13853, 2009.

[Clutton-Brock 02]   Tim Clutton-Brock. *Breeding Together: Kin Selection and Mutualism in Cooperative Vertebrates*. Science (New York, N.Y.), vol. 296, pages 69–72, 05 2002.

[Collett 98]   Matthew Collett, Emma Despland, Stephen J Simpson & David C Krakauer. *Spatial scales of desert locust gregarization*. Proceedings of the National Academy of Sciences, vol. 95, no. 22, pages 13052–13055, 1998.

[Couzin 02]   Iain D Couzin, Jens Krause, Richard James, Graeme D Ruxton & Nigel R Franks. *Collective memory and spatial sorting in animal groups*. Journal of theoretical biology, vol. 218, no. 1, pages 1–12, 2002.

[Couzin 03]   Iain Couzin & Jens Krause. *Self-Organization and Collective Behavior in Vertebrates*. Advances in The Study of Behavior - ADVAN STUDY BEHAV, vol. 32, pages 1–75, 12 2003.

[Czirók 99]   András Czirók, Mária Vicsek & Tamás Vicsek. *Collective motion of organisms in three dimensions*. Physica A: Statistical Mechanics and its Applications, vol. 264, no. 1-2, pages 299–304, 1999.

[Deneubourg 89]   Jean-Louis Deneubourg, Simon Goss, Nigel Franks & JM Pasteels. *The blind leading the blind: modeling chemically mediated army ant raid patterns*. Journal of insect behavior, vol. 2, no. 5, pages 719–725, 1989.

[Dyson 15]   Louise Dyson, Christian A Yates, Jerome Buhl & Alan J McKane. *Onset of collective motion in locusts is captured by a minimal model*. Physical Review E, vol. 92, no. 5, page 052708, 2015.

[Filella 18]   Audrey Filella, Fran çois Nadal, Clément Sire, Eva Kanso & Christophe Eloy. *Model of Collective Fish Behavior with Hydrodynamic Interactions*. Phys. Rev. Lett., vol. 120, page 198101, May 2018.

[Gerlotto 10]   Francois Gerlotto, Emma Jones, Nicolas Bez & David G Reid. *When good neighbours become good friends: observing small scale structures in fish aggregations using multibeam sonar*. Aquatic Living Resources, vol. 23, no. 2, pages 143–151, 2010.

[Gillespie 76]   Daniel T Gillespie. *A general method for numerically simulating the stochastic time evolution of coupled chemical reactions*. Journal of computational physics, vol. 22, no. 4, pages 403–434, 1976.

[Gillespie 77]   Daniel T Gillespie. *Exact stochastic simulation of coupled chemical reactions*. The journal of physical chemistry, vol. 81, no. 25, pages 2340–2361, 1977.

[Godfrey 09]   Stephanie S. Godfrey, C. Michael Bull, Richard James & Kris A. Murray. *Network structure and parasite transmission in a group living lizard, the gidgee skink, Egernia stokesii*. Behavioral Ecology and Sociobiology, vol. 63, pages 1045–1056, 2009.

[Gueron 96]   Shay Gueron, Simon A Levin & Daniel I Rubenstein. *The dynamics of herds: from individuals to aggregations*. Journal of Theoretical Biology, vol. 182, no. 1, pages 85–98, 1996.

[Hemelrijk 05] Charlotte K Hemelrijk & Hanspeter Kunz. *Density distribution and size sorting in fish schools: an individual-based model*. Behavioral Ecology, vol. 16, no. 1, pages 178–187, 2005.

[Hemelrijk 08] Charlotte K Hemelrijk & Hanno Hildenbrandt. *Self-organized shape and frontal density of fish schools*. Ethology, vol. 114, no. 3, pages 245–254, 2008.

[Hemelrijk 12] Charlotte K Hemelrijk & Hanno Hildenbrandt. *Schools of fish and flocks of birds: their shape and internal structure by self-organization*. Interface focus, vol. 2, no. 6, pages 726–737, 2012.

[Herskin 98a] J. Herskin & J. F. Steffensen. *Energy savings in sea bass swimming in a school: measurements of tail beat frequency and oxygen consumption at different swimming speeds*. Journal of Fish Biology, vol. 53, no. 2, pages 366–376, 1998.

[Herskin 98b] J Herskin & JF Steffensen. *Energy savings in sea bass swimming in a school: measurements of tail beat frequency and oxygen consumption at different swimming speeds*. Journal of Fish Biology, vol. 53, no. 2, pages 366–376, 1998.

[Huth 92a] Andreas Huth & Christian Wissel. *The simulation of the movement of fish schools*. Journal of theoretical biology, vol. 156, no. 3, pages 365–385, 1992.

[Huth 92b] Andreas Huth & Christian Wissel. *The simulation of the movement of fish schools*. Journal of theoretical biology, vol. 156, no. 3, pages 365–385, 1992.

[Huth 94] Andreas Huth & Christian Wissel. *The simulation of fish schools in comparison with experimental data*. Ecological modelling, vol. 75, pages 135–146, 1994.

[Ioannou 12] C. C. Ioannou, V. Guttal & I. D. Couzin. *Predatory Fish Select for Coordinated Collective Motion in Virtual Prey*. Science, vol. 337, no. 6099, pages 1212–1215, 2012.

[Jhawar 19a] Jitesh Jhawar & Vishwesha Guttal. *Noise-induced Effects in Collective Dynamics and Inferring Local Interactions from Data*, 2019.

[Jhawar 19b] Jitesh Jhawar, Richard G. Morris & Vishwesha Guttal. *Chapter 13 - Deriving Mesoscopic Models of Collective Behavior for Finite Populations*. In Arni S.R. [Srinivasa Rao] & C.R. Rao, editeurs, Integrated Population Biology and Modeling, Part B, volume 40 of *Handbook of Statistics*, pages 551 – 594. Elsevier, 2019.

[Jhawar 20] Jitesh Jhawar, Richard G Morris, UR Amith-Kumar, M Danny Raj, Tim Rogers, Harikrishnan Rajendran & Vishwesha Guttal. *Noise-induced schooling of fish*. Nature Physics, vol. 16, no. 4, pages 488–493, 2020.

[Kent 19] Maud IA Kent, Ryan Lukeman, Joseph T Lizier & Ashley JW Ward. *Speed-mediated properties of schooling*. Royal Society open science, vol. 6, no. 2, page 181482, 2019.

[Kenynes 88] ROGER J Kenynes & CLAUDIO D Stern. *Mechanisms of vertebrate segmentation*. Development, vol. 103, no. 3, pages 413–429, 1988.

[Kolpas 07] Allison Kolpas, Jeff Moehlis & Ioannis G. Kevrekidis. *Coarse-grained analysis of stochasticity-induced switching between collective motion states*. Proceedings of the National Academy of Sciences, vol. 104, no. 14, pages 5931–5935, 2007.

[Krams 02] Indrikis Krams & Tatjana Krama. *Interspecific reciprocity explains mobbing behaviour of the breeding chaffinches, Fringilla coelebs*. Proceedings. Biological sciences / The Royal Society, vol. 269, pages 2345–50, 12 2002.

[Krause 02] Jens Krause, Graeme D Ruxton, Graeme D Ruxton, Ibls Graeme Ruxton*et al.* Living in groups. Oxford University Press, 2002.

[Krebs 08] John Krebs, Michael MacRoberts & J. Cullen. *Flocking and feeding in the Great Tit Parus major– An experimental study*. Ibis, vol. 114, pages 507 – 530, 04 2008.

[Landeau 86] Laurie Landeau & John Terborgh. *Oddity and the 'confusion effect' in predation*. Animal Behaviour, vol. 34, no. 5, pages 1372 – 1380, 1986.

[Magurran 94] AE Magurran, BH Seghers, PW Shaw & GR Carvalho. *Schooling preferences for familiar fish in the guppy, Poecilia reticulata*. Journal of Fish Biology, vol. 45, no. 3, pages 401–406, 1994.

[Mishra 12] Shradha Mishra, Kolbjørn Tunstrøm, Iain D Couzin & Cristián Huepe. *Collective dynamics of self-propelled particles with variable speed*. Physical Review E, vol. 86, no. 1, page 011901, 2012.

[Murray 81] J. D Murray. *A pre-pattern formation mechanism for animal coat markings*. Journal of Theoretical Biology, vol. 88, no. 1, pages 161–199, 1981.

[Parrish 05] Julia K Parrish. *Traffic rules of fish schools: a review of agent-based approaches*. Self-organization and evolution of social systems, 2005.

[Partridge 80] Brian L Partridge & Tony J Pitcher. *The sensory basis of fish schools: relative roles of lateral line and vision*. Journal of comparative physiology, vol. 135, no. 4, pages 315–325, 1980.

[Port 11] Markus Port, Peter Kappeler & Rufus Johnstone. *Communal Defense of Territories and the Evolution of Sociality*. The American naturalist, vol. 178, pages 787–800, 12 2011.

[Radakov 73a] Dmitrii Viktorovich Radakov. *Schooling in the ecology of fish*. 1973.

[Radakov 73b] Dmitrii Viktorovich Radakov. *Schooling in the ecology of fish*. 1973.

[Reuter 94] Hauke Reuter & Broder Breckling. *Selforganization of fish schools: an object-oriented model*. Ecological Modelling, vol. 75, pages 147–159, 1994.

[Robinson 88] John Robinson. *Group size in wedge-capped capuchin monkeys Cebus olivaceus and the reproductive success of males and females*. Behavioral Ecology and Sociobiology, vol. 23, pages 187–197, 09 1988.

[Romanczuk 12] Pawel Romanczuk & Lutz Schimansky-Geier. *Swarming and pattern formation due to selective attraction and repulsion*. Interface focus, vol. 2, no. 6, pages 746–756, 2012.

[Rypstra 89] Ann Lundie Rypstra. *Foraging success of solitary and aggregated spiders: insights into flock formation*. Animal Behaviour, vol. 37, pages 274 – 281, 1989.

[Schradin 10] Carsten Schradin, Barbara König & Neville Pillay. *Reproductive competition favours solitary living while ecological constraints impose group-living in African striped mice*. The Journal of animal ecology, vol. 79, pages 515–21, 05 2010.

[Skogland 85] Terje Skogland. *The effects of density-dependent resource limitations on the demography of wild reindeer*. 1985.

[Strömbom 19] Daniel Strömbom, Tasnia Hassan, W Hunter Greis & Alice Antia. *Asynchrony induces polarization in attraction-based models of collective motion*. Royal Society open science, vol. 6, no. 4, page 190381, 2019.

[Sumpter 05] David J. T. Sumpter. *The principles of collective animal behaviour*. Philosophical Transactions of the Royal Society B: Biological Sciences, vol. 361, pages 22 – 5, 2005.

[Svendsen 03] Jon C Svendsen, Jakob Skov, Mogens Bildsoe & John Fleng Steffensen. *Intra-school positional preference and reduced tail beat frequency in trailing positions in schooling roach under experimental conditions*. Journal of fish biology, vol. 62, no. 4, pages 834–846, 2003.

[Tella 02] J. L. Tella. *The evolutionary transition to coloniality promotes higher blood parasitism in birds*. Journal of Evolutionary Biology, vol. 15, no. 1, pages 32–41, 2002.

[Theraulaz 95] Guy Theraulaz & Eric Bonabeau. *Coordination in distributed building*. Science, vol. 269, no. 5224, pages 686–688, 1995.

[Turner 86] George F. Turner & Tony J. Pitcher. *Attack Abatement: A Model for Group Protection by Combined Avoidance and Dilution*. The American Naturalist, vol. 128, no. 2, pages 228–240, 1986.

[Vicsek 95] Tamás Vicsek, András Czirók, Eshel Ben-Jacob, Inon Cohen & Ofer Shochet. *Novel Type of Phase Transition in a System of Self-Driven Particles*. Phys. Rev. Lett., vol. 75, pages 1226–1229, Aug 1995.

[Wilson 71] Edward O Wilson *et al. The insect societies.* The insect societies., 1971.

[Yates 09] Christian A. Yates, Radek Erban, Carlos Escudero, Iain D. Couzin, Jerome Buhl, Ioannis G. Kevrekidis, Philip K. Maini & David J. T. Sumpter. *Inherent noise can facilitate coherence in collective swarm motion*. Proceedings of the National Academy of Sciences, vol. 106, no. 14, pages 5464–5469, 2009.