



## Review

# Collective motion: Influence of local behavioural interactions among individuals

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Fascinating patterns are displayed in nature due to the collective coherent motion of many living organisms. The origin of collective behaviours is diverse as the group members benefit in various ways: large resources of food, mating choices, nesting, and protection from predators, to name a few. It is still not well understood how complex behaviours emerge from a collective group that are otherwise not displayed at the level of solitary individuals. In recent years, along with field studies, numerous theoretical approaches have been developed to obtain insights into the mechanisms of aggregations and the collective decision-making processes. This brief review focuses on the self-propelled particle models, which have played a significant role in deciphering the underlying dynamics of collective motion in various organisms. Here, we discuss how local behavioural interactions and coordinations among the individual members give rise to complex collective behaviours. We consider the examples of collective motion in the schooling of fishes, flocking of birds, and swarming of prey, and address the emergence of a variety of patterns, a transition from disorder to ordered motion, and survival chances of prey group when under predator attacks.

**Keywords.** Behavioural interactions; collective motion; flocking; prey–predator dynamics; schooling; swarming

## 1. Introduction

Collective motion has been observed in diverse living organisms, such as flocking of birds (Heppner 1990; Ballerini *et al.* 2008; Cavagna *et al.* 2018), swarming of insects (Buhl *et al.* 2006), schooling of fishes (Parrish and Edelman-Keshet 1999; Parrish *et al.* 2002; Hemelrijk and Kunz 2005), organized lane formation by ants (Couzin and Franks 2003), and in human crowds (Moussaïd *et al.* 2011). In all these examples, the interactions among the individual members in the group help them stay close to each other and move together in a coherent manner. Such instances of cohesive motion have also been found on a microscopic length scale, such as the aggregation of cells

during tissue development (Mukhopadhyay and De 2019, 2022), collective cell migration (Friedl and Gilmour 2009; Arboleda-Estudillo *et al.* 2010; De and De 2019, 2022), and bacterial colony formation (Czirók *et al.* 1996; Sokolov *et al.* 2007; Zhang *et al.* 2010), to name a few. Apart from living systems, non-living systems such as artificial microswimmers (Elgeti *et al.* 2015), multi-agent robots (Vásárhelyi *et al.* 2018), vibrated disks (Deseigne *et al.* 2010), and stick-slip systems (Ananthakrishna and De 2006) also demonstrate collective behaviours. In many of the cases, this collective ordered motion emerges through a phase transition from a disordered motion. In nature, collective movements happen for various reasons, such as searching for food, finding a nest, or relocating to a new place. Another important reason for cohesive group formation is to avoid and survive predator attacks. In a large prey group, it becomes more difficult for the predator to focus on an individual prey. On the

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other hand, staying within a group could also become unfavourable as the predator can easily track and attack a group. Therefore, the prey group often tries to find an efficient way to escape a predator attack and optimize its chances of survival. Generally, in a large group, each individual or agent interacts with its neighbours through some local rules. These behavioural interactions often help the system to move in a coordinated way. The interactions could be of the attractive–repulsive type or alignment of velocities in response to the neighbours, in order to maintain collective motion. Moreover, the nature of local interactions may vary from species to species depending on their sensory capabilities such as visual sensing, athleticism, age, physical structures, etc. Due to these limitations, instead of interacting with all members, individuals may interact with a few surrounding neighbours in the group. Moreover, how individuals make their neighbour choices may also widely vary. A review of the existing literature shows that neighbouring interactions can be dependent on metric distances between the neighbours, or they can be topological interactions within a number of close neighbours (Ballerini *et al.* 2008; Camperi *et al.* 2012; Kumar and De 2021).

The general mechanisms of these interactions could be independent of the detailed nature of the specific organisms. For example, bird flocks or fish schools have many common behavioural interactions such as parallel alignment following the heading direction of the neighbours, collision avoidance, or attractive responses. Therefore, studying such universal behaviours of the many interacting units, their characteristic statistical features, and the phase transition from disordered to ordered states provides deeper understandings of large-scale collective motion. In this respect, theoretical investigations could bring many insights into the complex dynamics of large moving groups. Hence, along with experiments, several theoretical studies have been carried out to understand the underlying principle of local interactions in large moving groups.

In this brief review, we discuss some theoretical studies, including our works that have been developed using the self-propelled particle models to understand the collective behaviours of fish schools, bird flocks, and prey swarms under predator attack. In these simple particle-based model frameworks, each individual or agent has been considered an active interacting particle to study collective motion. It is worth noting that particle-based models remain one of the significant theoretical frameworks to study collective dynamics since these models not only provide many insights but also

the model predictions could easily be tested against observations in field studies. In this review, we mainly focus on the influence of the local behavioural interactions among individuals in a group that help to achieve large-scale collective cohesive motion. First, we briefly discuss some theoretical models involving various local interactions that lead to collective coherent motion in the schooling of fishes and flocking of birds. Next, we address the influence of interaction range among the individuals in a group and the emergence of ordered motion in flocks, and various escape patterns and survival of prey swarms.

## 2. Local interactions in the schooling of fishes

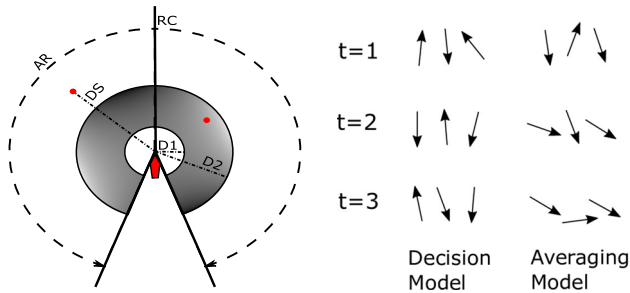
The schooling of fishes is one of the spectacular displays of social interactions observed in the animal kingdom. Fish schools are formed for various reasons, such as efficient foraging, space management, reproduction, and avoiding predator attacks. Many studies show that different patterns arise due to species variation or schooling behaviours (Breder 1959; Shaw 1970; Nursall 1973; Pitcher and Wyche 1983). For example, in a feeding school or resting school, the direction of movements of the fishes are somewhat random. However, fishes become highly polarized while on the move. Velocity alignment, or parallel orientation, changes upon predator attack, and the group forms many exciting patterns such as the formation of a ring around the predator, the fountain effect, where the fishes split into two groups in front of the chasing predator and rejoin behind its tail, or the splitting up into subgroups, etc.

Many theoretical studies have been carried out to understand the coordinated group formations in fish schools. One of the first theoretical models was proposed by Aoki (1982) to investigate the origin of schooling mechanisms. In this work, mutual attraction among the organisms and parallel orientation have been included as significant factors of schooling behaviour, as shown by Shaw (1970) in earlier behavioural studies. A numerical stochastic simulation was performed considering three behavioural interactions between the individuals: collision avoidance interactions, approach motion towards neighbour, and parallel orientation movements. Initially, each individual was positioned randomly in a square box, and their direction of orientation was chosen from a uniform distribution from 0 to  $2\pi$ . Speeds and directions of each member were assumed to be stochastic variables characterized by probability distributions. Velocities

were taken from a gamma distribution, and a normal distribution was chosen to determine the direction of movement of each member:  $P_i(\theta)$ , the probability density for the direction of movement of the  $i$ th individual, is

$$P_i(\theta) = \sum_j W_j \frac{1}{\sqrt{2\pi}S_j} \exp^{-\frac{(\theta-M_j)^2}{2S_j^2}} \quad (1)$$

The mean,  $M_j$ , and variance,  $S_j$ , of the direction of heading are dependent on the positions and directions of neighbours in the sector area as illustrated in figure 1a.  $W_j$  is the weight factor that scales the influence of the neighbour  $j$  ( $\leq 4$ ).  $W_j$  is taken as inversely proportional to the angle between the heading of the  $i$ th individual and the location of its  $j$ th neighbours. The neighbours at the front are given preference if the number of neighbours is higher than 4. If the distance between the  $i$ th particle and its  $j$ th neighbour ( $DS_j$ ) is less than the avoidance distance  $D_1$ , then  $M_j$  deviates  $90^\circ$  from the direction of the  $j$ th neighbour to avoid a collision. On the other hand, parallel orientation is implemented when  $DS_j$  lies between  $D_1$  and  $D_2$  (shaded region shown in figure 1a), i.e.,  $M_j$  is chosen as the



**Figure 1.** (a) The red arrow depicts one representative fish, and the small red dots are its neighbours. The grey shaded region shows the parallel orientation region. The region within the distance  $D_1$  is the collision avoidance region. If a neighbour resides outside a distance  $D_2$  but within the near-field interaction radius  $RC$ , the fish will approach its neighbour.  $AR$  represents the angular range of interaction (redrawn following Aoki 1982). (b) As illustrated, in the ‘Decision’ model, at the starting time step,  $t = 1$ , the two outer fish are directed upwards, and the middle fish is oriented downward. In the next time step,  $t = 2$ , the fish in the middle changes its direction upward since it interacts with the outer fish. However, the outer fish turn downward as they interact with the fish in the middle. This pattern repeats as long as no perturbation destroys this balance. On the contrary, in the ‘Average’ model, the fish group turns into a polarized group as each individual tries to move in the average direction of all the particles (redrawn following Huth and Wissel 1992).

same direction of heading as the  $j$ th neighbour. This model was simulated in standard parameter space, and it successfully generated the schooling patterns. Further, the motion was also studied without considering the parallel orientation and approach interaction, respectively. It has been found that without parallel orientation, particles only aggregate. However, if the approach movement is omitted, then the individuals disperse with parallel orientation. Thus, it shows that both mutual attraction and parallel orientation are necessary to exhibit schooling behaviours.

Based on this model, Huth and Wissel (1992) proposed the ‘Decision’ model and ‘Average’ model as shown in figure 1b. The Decision model is similar to Aoki’s model. In the Decision model, the fish group does not move much, and the direction of movement of the fish group is also not the same for all individuals. This could be called a resting school or feeding school. In this model, individual fish turn their heading direction influenced by the nearest neighbour. This mechanism confuses the fish group more as the maximum turning takes place. However, in the Average model, fish mix up the effects of all the neighbours and use the arithmetic average of the heading angles. Thus, it results in more polarized and cohesive schooling behaviour than the Decision model, as can be seen from figure 1b. Kunz and Hemelrijk have further modified these models and demonstrated how body size and form affect the formation of fish schools (Hemelrijk and Kunz 2005). They proposed three different strategies: (1) active sorting, where each individual agent actively chooses to be close to the related agent; (2) size difference model, in which individuals merely differ in size but behave according to usual schooling rules; and (3) risk avoidance, where small agents avoid the larger ones and each agent tries to stay with the agents of familiar individuals (Hemelrijk and Kunz 2005). In the active sorting, familiar individuals make subgroups that can occur anywhere in the group; however, in the size difference model, agents of different size group concentrically, i.e., small agents are gathered at the centre, and the larger ones stay at the periphery. In contrast, in the risk avoidance model, small agents group together at the periphery, whereas the larger ones occupy the centre of the group. A more modified model with large schools in three dimensions has also been depicted in another work by Hemelrijk and Hildenbrandt (2008). There are also other theoretical approaches in the literature to model fish schooling that can be found in several review articles (Pavlov and Kasumyan 2000; Sumpter 2010; Vicsek and Zafeiris 2012).

### 3. Flocking behaviours

Birds often fly collectively with coordinated movements, and this is known as flocking. Sometimes, the group contains thousands of birds and can undertake a long-distance flights, as do migratory birds. The emergence of such flocking behaviours is quite complex, and several studies have been carried out to understand this kind of collective motion. One of the earliest investigations on sandpiper flocks was by Potts (1984), in which a frame-by-frame image analysis showed that any individual could initiate a flock movement which propagates through the whole flock like a wave from the initiation point. Other experiments have also been performed on flocks of birds to study the effect of position on vigilance, flock size, positional effects, and intra-specific aggression in European starlings, etc. (Elgar 1989; Keys and Dugatkin 1990; Beauchamp 2003). Spatio-temporal analysis of the famous V-shaped flock formation in wild geese was done by Hayakawa (2010). Many theoretical models and simulations have also been developed to understand the origin of highly synchronized coherent patterns in flocks. One of the early models was proposed by Reynolds (1987), which successfully generated the dynamics of flocking. His work is based on the three behavioural assumptions similar to the modelling of a school of fish, as discussed in the previous section: (1) collision avoidance, i.e., each bird maintains a minimum specific distance from the other birds in the group, (2) velocity matching, i.e., each bird always tries to match its velocity with those of the neighbouring birds, and (3) attraction among the birds up to a certain distance. Applying these basic rules to interactions could predict natural flocking behaviours.

Another pioneering model on flocking was proposed by Vicsek *et al.* (1995). Vicsek's model was developed to study the emergence of ordered motion in self-driven biological systems. In this model, individuals in a group are considered self-propelled particles. Initially,  $N$  particles are placed in a two-dimensional square box of size  $L^2$  and their positions are updated at each time step,  $\Delta t$ , following the equation

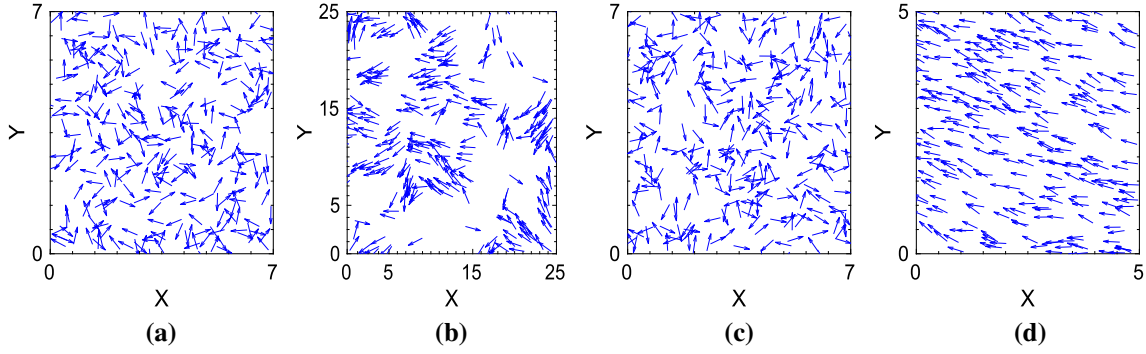
$$x_i(t + \Delta t) = x_i(t) + v_i(t)\Delta t \quad (2)$$

where  $x_i(t)$  is the position and  $v_i(t) = v_0 \cos \theta_i \hat{x} + v_0 \sin \theta_i \hat{y}$  is the velocity of the  $i$ th particle. The magnitude,  $v_0$ , of the velocity of all particles is taken to be constant and the direction is given by the angle  $\theta_i(t)$ . The initial velocity direction of the particles,  $\theta_i(t)$ , are chosen randomly between 0 to  $2\pi$ . Then, the

angles are updated with time as  $\theta_i(t + \Delta t) = \langle \theta(t) \rangle_R + \Delta\theta$ . Here,  $\langle \theta(t) \rangle_R$  is calculated by averaging over the velocity direction of the neighbouring particles within a circle of radius  $R$ , and  $\Delta\theta$  represents a random perturbation which is chosen from a uniform distribution  $(-\eta/2, \eta/2)$ . Simulations have been carried out following the Vicsek model using periodic boundary conditions. Figure 2 shows different flocking patterns observed at various noise strengths ( $\eta$ ) and particle densities ( $\rho$ ). Initially, the particles move in random directions, as shown in figure 2a. However, the particles tend to form small clusters at smaller density and low noise strength, as seen in figure 2b, whereas particles move randomly with small correlation at higher density and higher noise (figure 2c); and at large density and small noise, all the particles propel in an ordered fashion in a specific direction, as shown in figure 2d, mimicking the motion of a flock of birds. Moreover, a phase transition from disorder to order has been observed with decreasing noise strength and increasing particle density of the system (Vicsek *et al.* 1995). Here, the order parameter is defined as the absolute value of the normalized velocity averaged over all particles. These authors have studied the detailed nature of this phase transition and shown that the behaviour of the order parameter is similar to the equilibrium systems close to the critical point (details in Vicsek *et al.* 1995).

Later, several mathematical models were developed following the Vicsek model to describe different aspects of flocking dynamics. For example, Couzin *et al.* (2005) have investigated how efficient information transfer and decision making can take place in a collectively moving group. Synchronization of the landing of a flock of birds has also been studied using a self-propelled particle model by Bhattacharya and Vicsek (2010). Cavagna *et al.* (2010) have experimentally studied the origin of the collective response by estimating the correlation in velocity fluctuations of birds in a flock. The correlations decay as a scale-free power law, signifying that each individual with an effective perception range greater than the inter-individual interaction range gives rise to the unifying response of the group. Further, another recent experimental study by Ballerini *et al.* (2008) on starling flocks has shown that simple local rules of interaction can give rise to collective behaviour. They have found that each bird interacts with a fixed number of neighbouring birds (on an average, six to seven) irrespective of their metric distance, by analysing the trajectories of





**Figure 2.** Flocking patterns at different noise strength ( $\eta$ ) and particle densities ( $\rho$ ). The snapshot shows the velocities of the particles **(a)** at  $t = 0$  for  $L = 7$ ,  $\eta = 2.0$ ; **(b)** at smaller density and small noise ( $L = 25$ ,  $\eta = 0.1$ ), particles tend to form smaller coherent groups; **(c)** at higher density and large noise ( $L = 7$ ,  $\eta = 2.0$ ), after a certain time, the particles move somewhat randomly with little correlation; and **(d)** particles show ordered motion at higher density and small noise ( $L = 5$ ,  $\eta = 0.1$ ). Keeping the number of particles at  $N = 300$ , simulations have been performed following the Vicsek model (Vicsek *et al.* 1995).

flocks of a few thousand starlings. This kind of neighbour interaction where the metric distance between the birds is not important has been termed topological interaction.

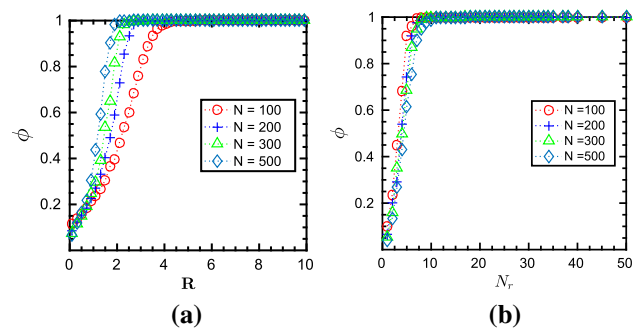
#### 4. Flocking: Metric and topological interactions

Recently our group explored the dynamics of flocking using metric-based and topological interactions (Kumar and De 2021), which we briefly describe here. In this work, initially,  $N$  active particles were placed in two-dimensional space, where  $r_i$  and  $v_i$  denote the position and the velocity of the  $i$ th particle. The particles move in an open space to mimic real-life scenarios. Moreover, the velocity of each particle is influenced by the velocities of its neighbouring particles. The local velocity alignment interaction is confined to an interaction radius,  $R$ , in the case of metric interaction, and for topological interactions, it is limited to a fixed number of neighbours,  $N_r$ . The equation of motion is given as

$$\frac{dv_i}{dt} = \frac{\alpha}{N_{\text{in}}} \sum_{j=1}^{N_{\text{in}}} (v_j - v_i) - \gamma v_i + \eta \quad (3)$$

The first term on the RHS represents the interaction due to the velocity alignment of the  $i$ th particle with its surrounding neighbours,  $\alpha$  defines the strength of interaction,  $\gamma$  is the coefficient of viscous drag,  $N_{\text{in}}$  is the number of interacting neighbours with the  $i$ th particle following the metric or the topological rule of interactions, and  $\eta$  represents the noise in the environment (Kumar and De 2021).

The flocking dynamics have been studied by varying the interaction range,  $R$ , for metric ruling and the number of interacting neighbours,  $N_r$ , in the case of topological ruling. To characterize the ordered state of the system, the absolute value of the average normalized velocity,  $\phi = \frac{1}{N} |\sum_{i=1}^N (v_i/|v_i|)|$ , has been considered as the order parameter of the system. Figure 3a shows that in the case of metric-based local interaction, a certain threshold interaction radius is needed for the group to reach an ordered state. As the flock size increases, the threshold value of the interaction range decreases simply because each individual would get surrounded by more interacting neighbours. Also, the lower speed of the flock turns out to be beneficial to reach the order state as the individuals moving with lower speed would spend substantial time with the same neighbours to align their velocities. On the other hand, in the case of topological interactions, a threshold



**Figure 3.** The order parameter,  $\phi$ , has been plotted for different flock sizes,  $N$ , in the case of **(a)** metric interaction by varying the interaction radius  $R$  and **(b)** topological interaction by varying the number of interacting neighbours,  $N_r$  (keeping a lower flock speed) (as in Kumar and De 2021).

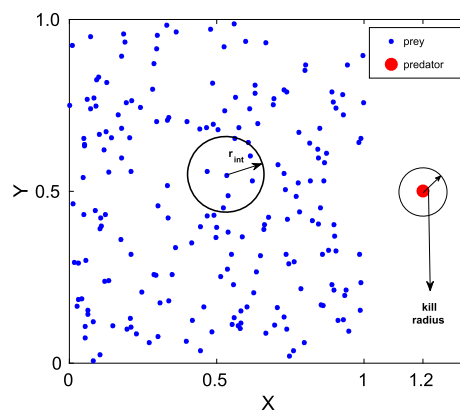
value of the number of interacting neighbours is required to achieve the ordered state as shown in figure 3b. It is found that the variation in flock size does not change the threshold number with lower flock speed; however, a higher flock speed increases the threshold number of interacting neighbours with increasing flock size. Moreover, our study shows that the topological rulings become more efficient than the metric one in attaining the ordered state and the difference in these two ruling gets prominent as the flock size is decreased; a detailed study can be found in the study by Kumar and De (2021). Moreover, Camperi *et al.* (2012) have shown that the condition of maximal stability is achieved when topological neighbours are distributed evenly around each individual. Shang and Bouffanais (2014) have investigated the consensus reaching process using topologically interacting self-propelled particles. They have shown that the rate of convergence to consensus can speed up to an optimal level where the number of neighbours is close to ten. Several other studies have also investigated collective motion using metric and topological rules of local interactions (Hemelrijk and Kunz 2005; Couzin *et al.* 2005; Ballerini *et al.* 2008; Bhattacharya and Vicsek 2010).

### 5. Effect of interaction range on survival of a prey swarm

As discussed, one of the main reasons for cohesive group formation in animals is to defend against and survive predator attacks. However, cohesive movements sometimes become disadvantageous when the predator can easily track down the prey. For example, marine predators can easily track and catch fish schools (Parrish and Edelstein-Keshet 1999). Moreover, the prey situated at the periphery of the swarm are more vulnerable to predator attacks, so each prey competes within the group for a safer position. So, usually, there is a trade-off between moving in a group versus individual needs. So, prey groups often attempt effective strategies to survive under predator attacks (Humphries and Driver 1970; Hayward and Kerley 2005; Caro 2005; McKenzie *et al.* 2012). Several escape pathways have been observed in nature. For example, a school of marine fish arranged themselves in a circular ring around the predator, or they would divide into smaller groups and scatter away from the predator, creating visual confusion (Partridge 1982; Pitcher and Wyche 1983). Other kinds of escape trajectories include various kinds of swarming patterns such as circling,

spinning, chasing, etc. (Humphries and Driver 1970; Domenici and Batty 1997; Edut and Eilam 2004; Caro 2005; Domenici *et al.* 2011). A clear understanding of local interactions within the prey group leading to different complex patterns and increasing survival chances of prey swarm is still due because of the challenges in field studies. In such situations, theoretical studies have provided many insights to understand the collective dynamics of prey–predator systems (Oshanin *et al.* 2009; Zhdankin and Sprott 2010; Angelani 2012; Olson *et al.* 2013; Chen and Kolokolnikov 2014). For example, collective predation and escape strategies have been studied using self-propelled particle models to look into the predation rate and total catch time of the group (Angelani 2012). In another model proposed by Chen and Kolokolnikov (2014), it has been shown that the prey swarm could easily escape the attack of a weak predator. However, as the strength of the predator increased, a transition was observed from the confused state of the predator to chasing dynamics. Besides, other theoretical models have also investigated different interaction mechanisms between predators and prey (Zhdankin and Sprott 2010). Recently, we also studied how the range of cooperative interactions within the prey swarm affects its survival under a predator attack (Chakraborty *et al.* 2020), which we will briefly discuss below.

We have considered a particle-based model where a group of  $N$  prey is positioned randomly on a two-dimensional space in an unit square and the predator approaches the prey swarm from a nearby place, as illustrated in figure 4. Each prey is represented by its position,  $\vec{r}_i$ , and velocity,  $\vec{v}_i$ , and they interact through attractive and repulsive interactions with the



**Figure 4.** The blue dots represent prey and the big red dot denotes the predator. Here,  $r_{\text{int}}$  is the interaction radius within which a prey interacts with the other neighbouring prey. The kill radius has been shown for the predator (as in Chakraborty *et al.* 2020).

neighbouring prey in the group. The equations of motion of prey and the predator are given as

$$\mu \frac{d\vec{r}_i}{dt} = \vec{f}_{i,prey-prey} + \vec{f}_{i,prey-predator} \quad (4)$$

$$\mu_p \frac{d\vec{r}_p}{dt} = \vec{f}_{predator-prey} \quad (5)$$

Here, for simplicity, we consider the dynamics in the overdamped limit and  $\vec{f}_{i,prey-prey}$  is the prey-prey interaction force of the  $i$ th prey,

$$\vec{f}_{i,prey-prey} = \frac{1}{N_{in}} \sum_{j=1}^{N_{in}} \left( \beta(\vec{r}_j - \vec{r}_i) - \alpha \frac{\vec{r}_j - \vec{r}_i}{|\vec{r}_j - \vec{r}_i|^2} \right)$$

Each prey interacts with the neighbouring prey residing within a certain interaction radius,  $r_{int}$ , due to its physical and sensory constraints.  $N_{in}$  is the number of prey interacting with the  $i$ th prey situated within the radius  $r_{int}$ .  $\beta$  and  $\alpha$  signify the strength of attractive and repulsive interactions of the prey, respectively. Prey–predator repulsive interaction has been modelled as

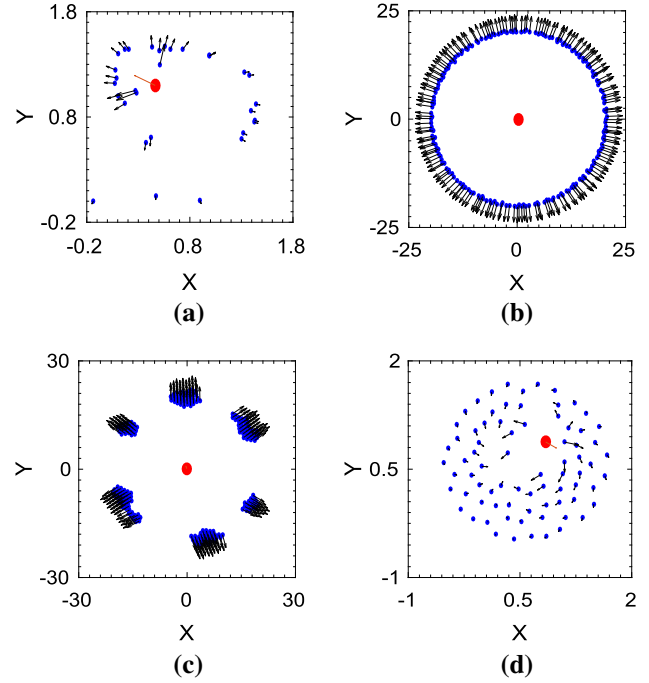
$$\vec{f}_{i,prey-predator} = -\gamma \frac{\vec{r}_p - \vec{r}_i}{|\vec{r}_p - \vec{r}_i|^2}$$

where  $r_p$  is the predator's position and  $\gamma$  signifies the strength of prey–predator interaction. In the predator equation, the predator–prey attractive force is given by averaging over all prey as

$$\vec{f}_{predator-prey} = \frac{\delta}{N} \sum_{i=1}^N \frac{\vec{r}_i - \vec{r}_p}{|\vec{r}_i - \vec{r}_p|^3}$$

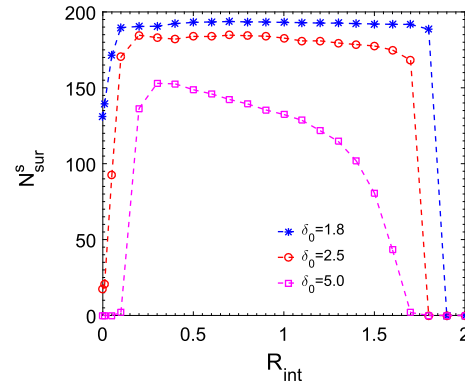
and  $\delta$  denotes the predator's strength. Moreover, kill radius has been introduced to mimic the natural prey capturing process as shown in figure 4.

The coupled equations (equations 4–5) are solved numerically for different parameter values. Simulation results show the emergence of various escape patterns with varying interaction range,  $R_{int}$  (the parameters are presented in dimensionless units) (Chakraborty *et al.* 2020). At  $R_{int} = 0$ , i.e., when there is no interaction within the prey swarm, the predator is able to catch the randomly moving prey over time as the prey move away due to prey–predator repulsive force shown in figure 5a. As we increase the interaction radius to  $R_{int} = 0.5$ , the prey group forms a ring around the predator, which confuses the predator about which direction to attack from, as seen figure 5b. Further increase of the interaction radius to  $R_{int} = 1.2$  would result in prey escaping the predator by dividing into



**Figure 5.** Various escape patterns formed by the prey swarm with different interaction radius: (a)  $R_{int} = 0.0$ , (b)  $R_{int} = 0.5$ , (c)  $R_{int} = 1.2$ , and (d)  $R_{int} = 2.0$ . The blue dots represent prey and the red dot shows the predator (as in Chakraborty *et al.* 2020).

smaller subgroups as in figure 5c. However, at a large interaction radius,  $R_{int} = 2.0$ , chasing dynamics has been observed, i.e., the predator could chase down all the prey as shown in figure 5d; similar dynamics are also observed when each prey interacts with all other prey in the group. Further, the number of surviving prey,  $N_{sur}^s$ , at the steady state has been calculated as a function of interaction radius,  $R_{int}$ , as shown in figure 6. It can be seen that very short-range or long-range



**Figure 6.** The number of surviving prey,  $N_{sur}^s$ , with varying interaction range,  $R_{int}$ , for different predator strengths ( $\delta_0$ ) and initial prey group size,  $N = 200$  (Chakraborty *et al.* 2020).

interactions within the prey swarm are disadvantageous for the survival of the prey swarm. However, in the intermediate range of interaction radius, the survival of the prey swarm is maximum. For a small range of interaction, the prey are not able to establish coordinated motion in the group in order to escape from the predator. On the other hand, in the case of a large interaction radius, each prey interacts with almost all other prey in the group. Thus, the prey group moves together cohesively, which is why the predator can easily track and catch the prey over time. Interestingly, at an intermediate interaction radius, the cooperative interaction within the prey swarm helps the prey group to initiate a coordinated motion in order to confuse the predator by forming a circle or splitting up into subgroups or by other escape routes so as to survive in the long run. Moreover, it is observed that the optimal range of interaction for the survival of the prey swarm depends on the strength of the predator and also on the prey group size. The details of this study can be found in Chakraborty *et al.* (2020).

## 6. Conclusion

In this brief review, we have discussed self-propelled particle-based theoretical models that could shed light on how local interaction rules among individuals could give rise to coherent collective motion in diverse species such as the schooling of fishes, flocking of birds, and swarming of prey while being chased by a predator. Several studies have shown how the varying range of interactions can influence the emerging patterns of various shapes, such as spinning, circling, splitting up into smaller groups, or chasing, as observed in natural scenarios. Moreover, the nature of local interactions in a group could be governed by the metric distance between the individuals or determined by a fixed number of surrounding neighbours, namely, topological interactions, which vary from species to species. Apart from the particle-based model, there are other theoretical approaches; for example, continuum hydrodynamic models have been developed to explain the dynamics of flocking at large scales (Toner *et al.* 2005). There are also lattice models which have investigated the chase and escape strategies of prey–predator systems (Kamimura and Ohira 2010; Bonato 2011; Patwardhan *et al.* 2020). The study of prey–predator dynamics in complex networks has also received much attention in recent times as many real-world systems can be efficiently modelled using complex networks (Albert *et al.* 1999; Strogatz 2001; Benson *et al.* 2016). Theoretical studies,

along with experiments, thus enable us to understand the complex dynamics of collective motion of diverse species at various length and time scales.

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## References

- Albert R, Jeong H and Barabási A-L 1999 Diameter of the world-wide web. *Nature* **401** 130–131
- Ananthakrishna G and De R 2006 Dynamics of stick-slip: Some universal and not so universal features. *Lect. Notes Phys.* **705** 423–457
- Angelani L 2012 Collective predation and escape strategies. *Phys. Rev. Lett.* **109** 118104
- Aoki I 1982 A simulation study on the schooling mechanism in fish. *Bull. Japan. Soc. Sci. Fish* **48** 1081–1088
- Arboleda-Estudillo Y, Krieg M, Stühmer J, *et al.* 2010 Movement directionality in collective migration of germ layer progenitors. *Curr. Biol.* **20** 161–169
- Baggio JA, Salau K, Janssen MA, Schoon ML and Bodin O 2011 Landscape connectivity and predator–prey population dynamics. *Landscape Ecol.* **26** 33–45
- Ballerini M, Cabibbo N, Candelier R, *et al.* 2008 Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study. *Proc. Natl. Acad. Sci. USA* **105** 1232–1237
- Beauchamp G 2003 Group-size effects on vigilance: a search for mechanisms. *Behav. Processes* **63** 111–121
- Benson AR, Gleich DF and Leskovec J 2016 Higher-order organization of complex networks. *Science* **353** 163–166
- Bhattacharya K and Vicsek T 2010 Collective decision making in cohesive flocks. *New J. Phys.* **12** 093019
- Bonato A and Nowakowski RJ 2011 *The game of cops and robbers on graphs* (American Mathematical Society)
- Breder Jr C 1959 Studies on social grouping in fishes. *Bull. Am. Mus. Nat. Hist.* **117** 393–482
- Buhl J, Sumpter DJ, Couzin ID, *et al.* 2006 From disorder to order in marching locusts. *Science* **312** 1402–1406
- Camperi M, Cavagna A, Giardina I, Parisi G and Silvestri E 2012 Spatially balanced topological interaction grants optimal cohesion in flocking models. *Interface Focus* **2** 715–725
- Caro T 2005 *Antipredator defenses in birds and mammals* (University of Chicago Press)
- Cavagna A, Cimarelli A, Giardina I, *et al.* 2010 Scale-free correlations in starling flocks. *Proc. Natl. Acad. Sci. USA* **107** 11865–11870



- Cavagna A, Giardina I and Grigera TS 2018 The physics of flocking: Correlation as a compass from experiments to theory. *Phys. Rep.* **728** 1–62
- Chakraborty D, Bhunia S and De R 2020 Survival chances of a prey swarm: how the cooperative interaction range affects the outcome. *Sci. Rep.* **10** 8362
- Chen Y and Kolokolnikov T 2014 A minimal model of predator–swarm interactions. *J. R. Soc. Interface* **11** 20131208
- Couzin ID and Franks NR 2003 Self-organized lane formation and optimized traffic flow in army ants. *Proc. R. Soc. B Biol. Sci.* **270** 139–146
- Couzin ID, Krause J, James R, Ruxton GD and Franks NR 2002 Collective memory and spatial sorting in animal groups. *J. Theor. Biol.* **218** 1–11
- Couzin ID, Krause J, Franks NR and Levin SA 2005 Effective leadership and decision-making in animal groups on the move. *Nature* **433** 513–516
- Czirók A, Ben-Jacob E, Cohen I and Vicsek T 1996 Formation of complex bacterial colonies via self-generated vortices. *Phys. Rev. E* **54** 1791
- De PS and De R 2019 Stick-slip dynamics of migrating cells on viscoelastic substrates. *Phys. Rev. E* **100** 012409
- De PS and De R 2021 Does cellular adaptation to force loading rate determine the biphasic vs monotonic response of actin retrograde flow with substrate rigidity? *bioRxiv* <https://doi.org/10.1101/2021.04.23.441062>
- De R and De PS 2022 A brief overview on mechanosensing and stick-slip motion at the leading edge of migrating cells. *Indian J. Phys.* <https://doi.org/10.1007/s12648-022-02297-0>
- Deseigne J, Dauchot O and Chaté H 2010 Collective motion of vibrated polar disks. *Phys. Rev. Lett.* **105** 098001
- Domenici P and Batty RS 1997 Escape behaviour of solitary herring (*Clupea harengus*) and comparisons with schooling individuals. *Mar. Biol.* **128** 29–38
- Domenici P, Blagburn JM and Bacon J. P 2011 Animal escapology i: theoretical issues and emerging trends in escape trajectories. *J. Exp. Biol.* **214** 2463–2473
- Edut S and Eilam D 2004 Protean behavior under barn-owl attack: voles alternate between freezing and fleeing and spiny mice flee in alternating patterns. *Behav. Brain Res.* **155** 207–216
- Elgar MA 1989 Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev. Camb. Philos. Soc.* **64** 13–33
- Elgeti J, Winkler RG and Gompper G 2015 Physics of microswimmers-single particle motion and collective behavior: a review. *Rep. Prog. Phys.* **78** 056601
- Friedl P and Gilmour D 2009 Collective cell migration in morphogenesis, regeneration and cancer. *Nat. Rev. Mol. Cell Biol.* **10** 445–457
- Gao J, Havlin S, Xu X and Stanley HE 2011 Angle restriction enhances synchronization of self-propelled objects. *Phys. Rev. E* **84** 046115
- Hamilton WD 1971 Geometry for the selfish herd. *J. Theor. Biol.* **31** 295–311
- Hayakawa Y 2010 Spatiotemporal dynamics of skeins of wild geese. *Europhys. Lett.* **89** 48004
- Hayward MW and Kerley GI 2005 Prey preferences of the lion (*Panthera leo*). *J. Zool.* **267** 309–322
- Hemelrijk CK and Hildenbrandt H 2008 Self-organized shape and frontal density of fish schools. *Ethology* **114** 245–254
- Hemelrijk CK and Kunz H 2005 Density distribution and size sorting in fish schools: an individual-based model. *Behav. Ecol.* **16** 178–187
- Heppner F 1990 A stochastic nonlinear model for coordinated bird flocks; in *The ubiquity of chaos* (American Association for the Advancement of Science)
- Humphries D and Driver P 1970 Protean defence by prey animals. *Oecologia* **5** 285–302
- Huth A and Wissel C 1992 The simulation of the movement of fish schools. *J. Theor. Biol.* **156** 365–385
- Kamimura A and Ohira T 2010 Group chase and escape. *New J. Phys.* **12** 053013
- Keys GC and Dugatkin LA 1990 Flock size and position effects on vigilance, aggression, and prey capture in the european starling. *Condor* **92** 151–159
- Kumar V and De R 2021 Efficient flocking: metric versus topological interactions. *R. Soc. Open Sci.* **8** 58
- McKenzie HW, Merrill EH, Spiteri RJ and Lewis MA 2012 How linear features alter predator movement and the functional response. *Interface Focus* **2** 205–216
- Moussaïd M, Helbing D and Theraulaz G 2011 How simple rules determine pedestrian behavior and crowd disasters. *Proc. Natl. Acad. Sci. USA* **108** 6884–6888
- Mukhopadhyay D and De R 2019 Aggregation dynamics of active cells on non-adhesive substrate. *Phys. Biol.* **16** 046006
- Mukhopadhyay D and De R 2022 Growth kinetics and power laws indicate distinct mechanisms of cell-cell interactions in the aggregation process. *Biophys. J.* **121** 481–490
- Nursall J 1973 Some behavioral interactions of spottail shiners (*Notropis hudsonius*), yellow perch (*Perca flavescens*), and northern pike (*Esox lucius*). *J. Fish. Res. Board Can.* **30** 1161–1178
- Olson RS, Hintze A, Dyer FC, Knoester DB and Adami C 2013 Predator confusion is sufficient to evolve swarming behaviour. *J. R. Soc. Interface* **10** 20130305
- Oshanin G, Vasilyev O, Krapivsky P and Klafter J 2009 Survival of an evasive prey. *Proc. Natl. Acad. Sci. USA* **106** 13696–13701
- Parrish JK and Edelstein-Keshet L 1999 Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science* **284** 99–101
- Parrish JK, Viscido SV and Grunbaum D 2002 Self-organized fish schools: an examination of emergent properties. *Biol. Bull.* **202** 296–305

- Partridge BL 1982 The structure and function of fish schools. *Sci. Am.* **246** 114–123
- Patwardhan S, De R and Panigrahi PK 2020 Survival probability of a lazy prey on lattices and complex networks. *Eur. Phys. J. E* **43** 1–9
- Pavlov D and Kasumyan A 2000 Patterns and mechanisms of schooling behavior in fish: a review. *J. Ichthyol.* **40** S163
- Peruani F, Schimansky-Geier L and Baer M 2010 Cluster dynamics and cluster size distributions in systems of self-propelled particles. *Eur. Phys. J. Spec. Top.* **191** 173–185
- Pitcher TJ and Wyche CJ 1983 Predator-avoidance behaviours of sand-eel schools: why schools seldom split; in *Predators and prey in fishes* (Springer) pp. 193–204
- Potts WK 1984 The chorus-line hypothesis of manoeuvre coordination in avian flocks. *Nature* **309** 344–345
- Rainolds CW 1987 Flocks, herds and schools: A distributed behaviour model. *Comp. Graphics* **21**. <https://doi.org/10.1145/37402.37406>
- Reynolds CW 1987 Flocks, herds and schools: A distributed behavioral model. *Proceedings of the 14th Annual Conference on Computer Graphics and Interactive Techniques* pp. 25–34
- Salau K, Schoon ML, Baggio JA and Janssen MA 2012 Varying effects of connectivity and dispersal on interacting species dynamics. *Ecol. Model.* **242** 81–91
- Shang Y and Bouffanais R 2014 Influence of the number of topologically interacting neighbors on swarm dynamics. *Sci. Rep.* **4** 1–7
- Shaw E 1970 Schooling in fishes: Critique and review; in *Development and evolution of behavior* (eds) (Aronson LR, Tobach E, Lehrman DS and Rosenblatt JS) (Freeman) 452–480
- Sokolov A, Aranson IS, Kessler JO and Goldstein RE 2007 Concentration dependence of the collective dynamics of swimming bacteria. *Phys. Rev. Lett.* **98** 158102
- Strogatz SH 2001 Exploring complex networks. *Nature* **410** 268–276
- Sumpter DJ 2010 *Collective animal behavior* (Princeton University Press)
- Toner J, Tu Y and Ramaswamy S 2005 Hydrodynamics and phases of flocks. *Ann. Phys.* **318** 170–244
- Vásárhelyi G, Virágh C, Somorjai G, *et al.* 2018 Optimized flocking of autonomous drones in confined environments. *Sci. Robot.* **3** <https://doi.org/10.1126/scirobotics.aat3536>
- Vicsek T and Zafeiris A 2012 Collective motion. *Phys. Rep.* **517** 71–140
- Vicsek T, Czirók A, Ben-Jacob E, Cohen I and Shochet O 1995 Novel type of phase transition in a system of self-driven particles. *Phys. Rev. Lett.* **75** 1226
- Weng T, Yang H, Gu C, *et al.* 2019 Predator-prey games on complex networks. *Commun. Nonlinear Sci. Numer. Simul.* **79** 104911
- Zhang H-P, Be'er A, Florin E-L and Swinney HL 2010 Collective motion and density fluctuations in bacterial colonies. *Proc. Natl. Acad. Sci. USA* **107** 13626–13630
- Zhdankin V and Sprott J 2010 Simple predator-prey swarming model. *Phys. Rev. E* **82** 056209

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