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Self-organized collective escape in bird flocks

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Chapter *1.*

Introduction

From the beginning of the 20^{th} century, scientists across disciplines have been intrigued by large collective events that spontaneously emerge in human societies [128]. Interactions among individuals (often without established behavioral rules or instructions) trigger complex collective phenomena, such as traffic congestion [96], crowd surges at music festivals [103] and financial crises [119]. Apart from in human societies, collective behavior is widely seen in nature, forming an extremely interdisciplinary field of research.

Collective behavior appears in a large spectrum of biological systems, at different scales and levels of complexity. Collective movement of cells appears in a number of tumor types of cancer during cell invasion [51] and leads to intriguing growth patterns in bacterial colonies [14]. In invertebrates, social insects demonstrate some captivating collective activities: ant colonies create trail networks during foraging, termites work together to construct pillars of complex architecture [19] and desert locusts (*Schistocerca gregaria*) form huge swarms during migration, with clear phase transitions between an individual and a collective state [176].

In vertebrates, striking motifs are formed at the front of migrating wildebeest herds [60]. Schooling behavior appears in at least one life stage of around 50% of all fish species [160], with thousands of individuals grouping together and displaying a big variety of dynamically changing shapes [133]. The murmurations of European starlings (*Sturnus vulgaris*) above their sleeping sites are a great example of the mesmerizing patterns that birds demonstrate when flying in flocks.

A main selective driver of grouping across species is the protection it offers against predators [133]. Three aspects of grouping are proposed to underlie this anti-predatory function: the selfish-herd hypothesis [61], the many-eyes hypothesis [102], and the confusion effect [102, 83]. The selfish-herd hypothesis predicts that individuals will have a tendency to aggregate and move towards the center of their group in order to not be the one caught (increasing the number of group mates between themselves and the predator). According to the many-eyes hypothesis, individuals can detect predators sooner when they are aggregated and thus the whole group will have a higher chance of escaping. The confusion effect implies that the predator may struggle to single out a group member and catch it while many individuals are rapidly passing through its field of view.

When groups are threatened by a predator, a great variety of collective patterns (referred to as patterns of collective escape) arises while members are interacting with each other and reacting to the threat [143, 166, 141] (Figure 1.1). Even though these patterns are hard to miss, the mechanisms behind them are far from clear. Their high complexity has been a barrier in identifying the underlying mechanisms of such patterns: how do individuals move and coordinate to produce them?

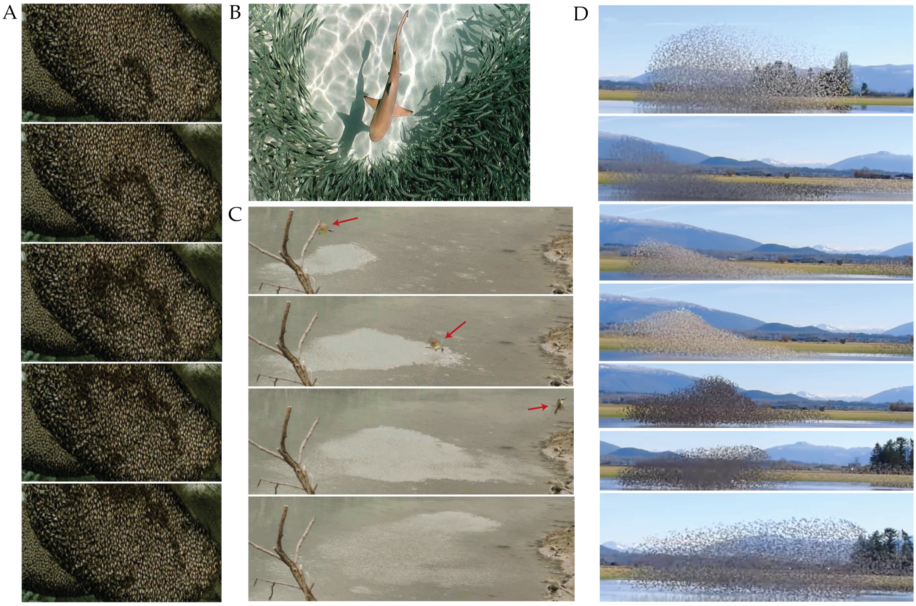

Figure 1.1: Patterns of collective escape. (A) Propagation of a shimmering wave in giant honeybees (*Apis dorsata*) as a reaction to a hornet (*Vespa* sp.) attack [95]. Screenshots taken from Video S1 of Kastberger et al. (2008). (B) A fish school escaping an approaching shark [174]. Photo from Touahmi et al. (2012). (C) Propagation of a 'diving' escape wave in schools of sulphur mollies (*Poecilia sulphuraria*) as a response to the attack of a great kiskadee (*Pitangus sulphuratus*) [43]. Red arrows indicate the predator. Screenshots taken from Video S3 of Doran et al. (2022). (D) Aerial displays of flock of dunlins (*Calidris alpina*) reacting to the attack of a peregrine falcon (Falco peregrinus). Screenshots taken from the video 'Dance of the Dunlins' (2013) by Ray Hamlyn.

1.1 Self-organization

Almost 100 years ago, patterns of collective behavior were thought to be the result of 'thought transfer' between individuals concerning their movement [159].

Later, it was hypothesized that collective behavior may arise from one individual leading the group [22] or from all individuals following a pre-designed plan [24]. However, the scale and spontaneity of some collective phenomena (involving a large number of individuals that instantaneously react to external stimuli) make these hypotheses seem less likely [24]. Using computer simulations, modeling studies on collective behavior have shown that complex patterns can emerge from the local transmission of information between a few neighbors, without the presence of a centralized coordination system, a leader or the need for individual knowledge of the group's global features [4, 150, 85, 33, 68, 81]. Thus, the collective behavior of animals is attributed to self-organization [169].

Self-organization is defined as: 'a process in which a pattern at the global level of a system emerges from numerous interactions among its lower-level components' [24]. These interactions are represented by a set of rules that the components (group members) execute using only local information, without reference to the global pattern [24]. The link between the interactions of the members of a group and the observed collective behavior is not intuitive [133], since the global characteristics of the system (at the level of the group) is more than the sum of each individual's behavior [24]. Individual-based (or agent-based) models based on self-organization are used to link the behavioral rules at the individual level with the emerging collective patterns.

1.2 Computational models of collective motion

In order to disentangle the mechanisms behind collective motion of animal groups, different types of models have been developed based on the organism of interest and the biological question of each study. The aim of these models is not to fully reconstruct the system, but to capture its organizing principles and provide a simple explanation of a complex phenomenon [31]. Spatially-explicit agent-based models, in particular, have uncovered a large spectrum of mechanisms underlying the collective motion of fish schools and bird flocks [69, 73, 72, 33].

Agent-based models (ABM) of collective motion simulate individual agents, acting in space and time based on simple behavioral rules [85, 4, 150]. At each time step, interactions between nearby neighbors affect the motion of each group member, resulting in the change of its position and heading. Specifically, individuals in a group are modeled to coordinate by following three main rules: 1. 'attraction' (reflecting the tendency of individuals to join a group [61]), 2. 'alignment' (making individuals adjust their headings to others within a local neighborhood to move towards the same direction), 3. 'repulsion' (ensuring the avoidance of collisions when two individuals are too close to each other [150, 31]). The specifics of these rules are often modeled differently across studies.

To relate the models' results to reality, several characteristics of a group are measured and compared to empirical data, for instance the shape and density of a group [81]. This comparison provides a test of naturalism of the computational model and supports or rejects the assumptions made for the model's underlying behavioral rules. To unify the modeling of complex biological systems through agent-based models, Grimm et al. (2005) established a 'pattern-oriented' framework. This framework dictates that the highest pay-off of a model is achieved by balancing the complexity of the model between focusing solely on the pattern of interest and resembling all empirical data available (Figure 1.2). In essence, through pattern-oriented modeling one can develop a model that reproduces a few aspects of a collective system and can then be used to investigate the emergence of one particular pattern [59].

Continuous feedback between empirical and computational studies is essential in order to understand the mechanisms behind collective phenomena, define the parameters that influence them and form new predictions that can be empirically validated [55]. Lack of empirical data can thus pose constraints to the development of biologically-relevant computational models.

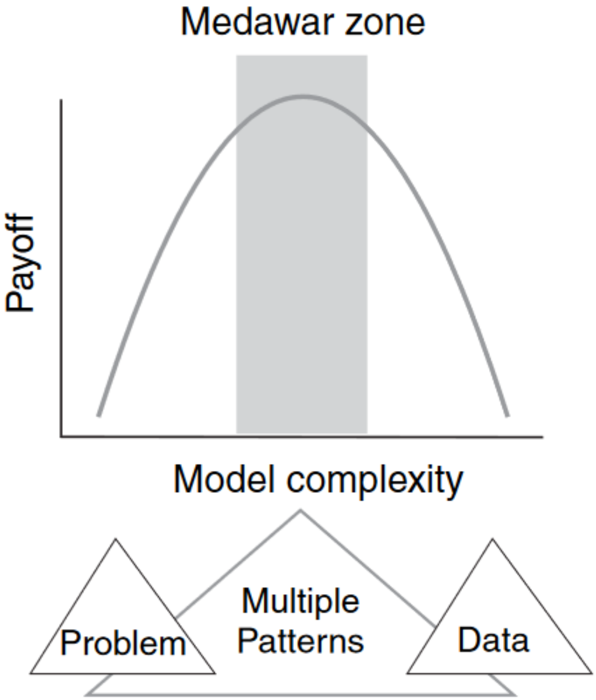

Figure 1.2: Figure from Grimm et al. (2005): pay-off of agent-based models in relation to their complexity based on pattern-oriented modeling [59].

1.3 Computational models of collective escape

In contrast to the large number of models of collective motion, models of collective escape are scarce. As a result, our knowledge about how patterns of collective escape emerge is still limited. The first model of collective escape, developed by Inada and Kawachi (2002), simulated the escape motion of small fish schools under predator attack (in 2D). Seven patterns of collective escape were produced by the model: the herd, the split, the hourglass, the vacuole, the flash expansion, the flash turn and the fountain effect (Figure 1.3)[141, 86]. It is noteworthy that this variety of patterns emerged from only a single escape rule at the individual level: individuals were turning away from the position of the predator while coordinating with each other [86]. Different weighted averages between coordination and predator avoidance led to different frequency of emergence of each pattern.

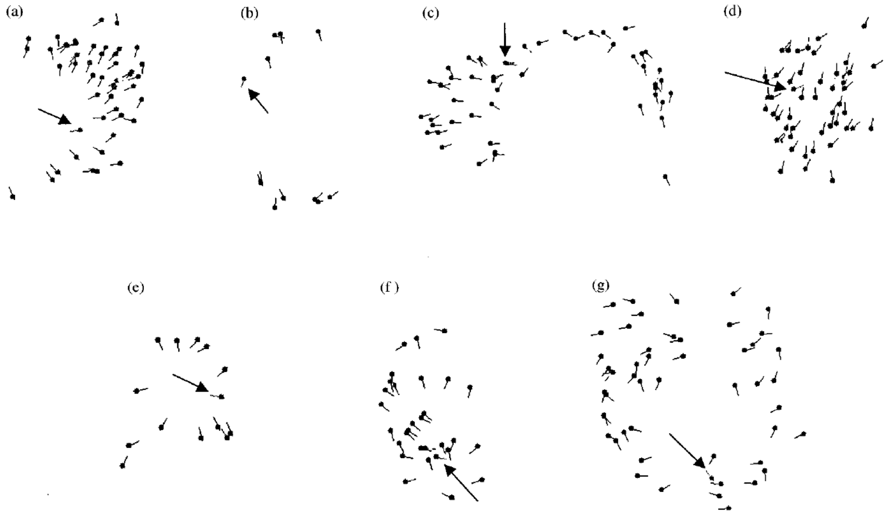

Figure 1.3: Figure from Inada and Kawachi (2002): simulated patterns of collective escape in their agent-based model. Arrows indicate the predator. Every screenshot represents a pattern: (a) Herd, (b) Split, (c) Hourglass, (d) Vacuole, (e) Flash expansion, (f) Flash turn, (g) Fountain effect. The descriptions of each pattern are given in Table 1.1.

Other studies on collective escape in fish have focused on the emergence of a single pattern: the escape wave. Instead of the continuous avoidance of the predator in the model of Inada and Kawach (2002), escape waves emerge in fish schools by individuals turning instantaneously and speeding up away from a threat (a ‘discrete’ reaction, e.g., performing a U-turn). This discrete action performed sequentially by all individuals causes a density wave that propagate through the group [80, 120].

A similar pattern, the agitation wave (a dark band moving through the group), is thus far the only pattern of collective escape of whose emergence has been studied in bird flocks. In a computational model of starlings (named StarDisplay [81]), these waves, surprisingly, arise not by individuals temporarily decreasing the distances among them, but from the sequential changes in individuals' orientations while they are executing a 'zig-zag' maneuver to escape [74]. This orientation change creates the optical effect of blackening due to a larger surface of the starlings' bodies being exposed to the observer while each individual is banking to maneuver. The emergence of other collective patterns in bird flocks is not well understood, not only because of their high complexity, but also from the lack of empirical data of collective escape in nature.

1.4 Collective escape in bird flocks

Aerial displays of collective escape have been studied in few bird species, given the practical and technological constrains in collecting data of birds under attack in the wild. Dunlins (*Calidris alpina*) and starlings (*Sturnus vulgaris*), in the presence of a predator, create large and dense spherical flocks, increase their speed and demonstrate a variety of collective pattern with their flocks turning, expanding, compressing, ascending and descending, splitting in subflocks and merging [118, 25, 166]. An extensive list of patterns along with their descriptions is given in Table 1.1 (and see Figure 1.4 for patterns of collective escape in starlings). The flock's reaction seems to be influenced by various factors such as the predator's attack strategy [188] and the intensity of the attack [166].

From an evolutionary perspective on defensive mechanisms, individual birds should develop an aerial escape strategy which will give them an advantage over their predator, depending on their aerodynamics of flight and biological characteristic ('escape specialism') [65]. Different factors at the individual level can influence the escape tactic, such as the predator's characteristics (e.g., species, size), the relative distance between the predator and the prey, the relative velocities of prey and predator at the beginning of the attack (e.g., speed and direction of attack), and the state of the prey under attack (e.g., alarmed) [65, 41]. When an individual is part of a flock, its reactions may further vary [186]. It remains unknown whether different bird species or individuals in a group react in the same way to the attack of a predator and whether they use a continuous tendency to turn away from the predator [86, 186] or a discrete escape maneuver [80].

1.5 This Thesis

The main aim of this thesis is to push towards a better understanding of collective escape in bird flocks through the interaction between empirical data and

Table 1.1: Patterns of collective escape across studies on bird species: starlings (*Sturnus vulgaris*), dunlins (*Calidris alpina*), and pigeons (*Columba livia*), insects -giant honeybees (*Apis dorsata*) and whirligig beetles (*Dineutes discolor*)-, and several fish species such as sand-eel (*Ammodytes sp.*), rummy-nose tetra (*Hemigrammus rhodostomus*), and Pacific blue-eyes (*Pseudomugil signifer*).

Pattern	Description	Bird species	Other taxa	
Collective turn	The group changes its moving direction.	starling, dunlin, pigeon	fish	[156, 115, 8, 107, 141, 21]
Split	A group separates into two or multiple smaller subgroups	starling	fish	[166, 141]
Herd	The group takes a quarter-moon shape with group members being polarized.	starling	fish	[141, 166]
Hourglass	When the two sides of a herd formation are turning to the same direction and a small bridge of individuals is connecting the two main clusters of the group.	-	fish	[141]
Cordon	A thin line of few individuals interconnects two relatively large parts of the group.	starling	-	[166]
Flash expansion	Individuals suddenly move radially outward from the group and away from the predator.	starling	fish, beetles	[141, 166, 153]
Flash turn	Some individuals move radially away from the predator while the rest of the group moves forward.	-	fish	[86]
Vacuole	The group has a hole-like opening and the individuals around it are polarized.	starling	fish	[141, 166]
Fountain effect	The group splits in front of the approaching predator and rejoins behind it.	-	fish	[141]
Compacting	The group reduces its area.	starling	-	[166]
Blackening	The group darkens, as a whole or a part of it.	starling	-	[166]
Dilution	The group increases its area, lightens in color and decreases in density.	starling	-	[166]
Columnar flight	The group takes a vertical shape, elongated in the direction of altitude.	dunlin	-	[21]
Escape wave	An escape reaction of turning and accelerating that propagates through a group.	-	fish	[80, 107]
Agitation wave	One or multiple optically darkened bands propagate through a group.	starling	-	[143]
Flashing flight	The flock's color rapidly alternates between light and dark while the group is turning.	dunlin	-	[21]
Rippling flight	Light colored bands pass through the flock without the group changing its flight directions, resembling a wave.	dunlin	-	[21]
Shimmering wave	A dark band moves through the group by individuals sequentially flipping their abdomen upwards resembling a Mexican wave.	-	honeybees	[94]

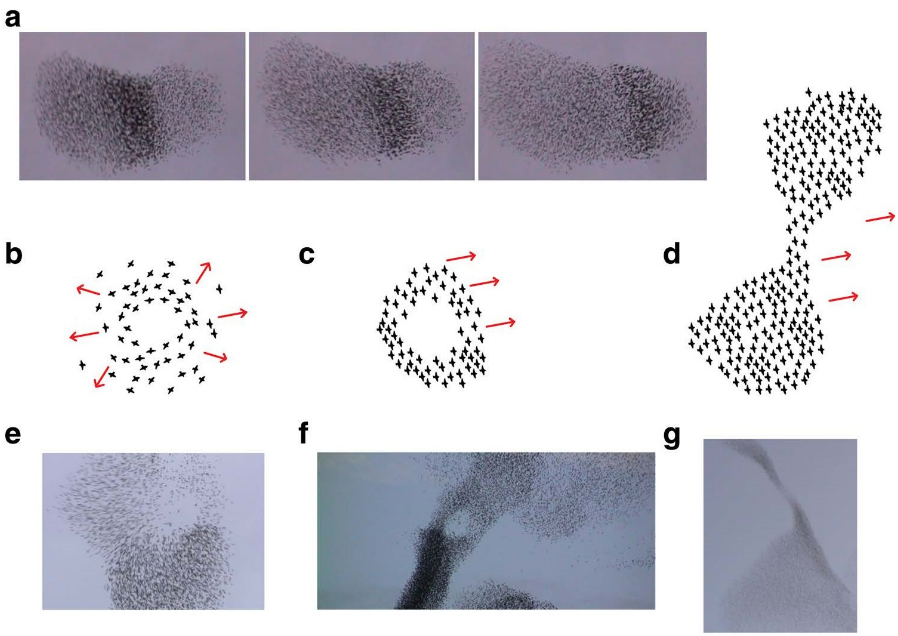

Figure 1.4: Figure from Storms et al. (2019): some complex patterns of collective escape in starling flocks. (a) Video still of the progression of an *Agitation wave*. (b and e) Caricature and video still of a *Flash expansion*. (c and f) Caricature and video still of a *Vacuole*. (d and g) Caricature and video still of a *Cordon*.

computational models of self-organization. Since different bird species may react differently to a predator's attack, here, we develop a framework that enables the construction of species-specific models. We build three such data-inspired agent-based models of collective escape and study how patterns at the group level may emerge through interactions among flocking individuals and between them and a predator. To make our models as biologically relevant as possible, we include some aspects of collective motion that have been disregarded in many previous models, such as individual variation in preferred speed within a group, variable speed that resembles flying motion, and several escape reactions (both continuous and 'discrete' maneuvers).

In Chapters 2 and 3, we study the collective escape of flocks of pigeons, taking advantage of new quantitative data of flocks under attack by a robotic, remotely-control predator, the RobotFalcon [164]. We develop an agent-based model of pigeons and use it to first (Chapter 2) test whether the pattern of increasing predator avoidance over group cohesion, as the RobotFalcon gets closer to the flock, can emerge without individuals minding their distance to the predator. Secondly, we extend our model (in Chapter 3) and study whether the patterns of collective escape of pigeons (splits and collective turns) can emerge from a single escape maneuver.

In Chapter 4, we focus on collective turning, one of the most common patterns of collective escape across species. We develop a model in which flocks turn towards a roost or evade a predator and investigate which specifics of coordination and flocking characteristics may lead to higher predator confusion.

In Chapter 5, we study the species with the most complex patterns of collective escape, the European starling. After analyzing videos of starlings under attack by the RobotFalcon, we develop a 3-dimensional model, adjust it to starlings, and study how patterns of collective escape emerge from simple escape maneuvers at the level of the individual.

Having presented our three models of collective escape, in Chapter 6 we dive into the specifics of our modeling framework that underlie them. We explain how we can approach collective escape through individual-based state-machines and easily build agent-based models that are adjustable to specific species or ecological contexts.

In Chapter 7, we summarize our results, discuss our conclusions and identify research gaps and perspectives for future work.