Self-organized collective escape in bird flocks

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Chapter 7.

Synthesis and future perspectives

This PhD thesis aimed to deepen our understanding of collective escape in bird flocks in the context of self-organization with the aid of computational models. Starting with the bird species for which the most empirical data of collective behavior are available [140, 16, 15, 139, 137, 50, 156, 155], in Chapter 2 and 3 we studied the properties of self-organized collective escape in homing pigeons. In Chapter 2, we showed how a distance-dependent pattern of predator avoidance (individual pigeons turn away from the predator more often the closer they are to the predator) may emerge from a rule of escape at the individual level that is independent of an individual's distance to the predator. In Chapter 3, we found that a single turning maneuver by one individual (the initiator) can lead to both patterns of collective escape that we observed in pigeon flocks: the collective turn and the split. Apart from the initiator's angular velocity and centrality, whether a collective turn or a split emerges depended on whether other group members follow the initiator's turn or not.

In Chapter 4, we focused on the most common pattern of collective escape, the collective turn, and its relation to the confusion-effect. We used neighbor instability as a proxy of predator confusion and studied its relation to turns with equal-radii and parallel-paths through a new metric of deviation from the two turning types. We investigated how coordination specifics (that may differ across species [114, 45, 156, 9]) affect the instability of neighbors and the deviation from equal-radii and parallel-paths, during turns towards a roost or away from a predator. We identified that high instability of neighbors may arise when individuals interact with many close-by neighbors (high topological range), very frequently (high reaction frequency) and as part of a large flock. Our model can be adjusted to empirical data to study the complexity of collective turns in detail across species.

In Chapter 5, we studied the species with some of the most complex patterns of collective escape: the European starling [166]. In video observations of flocks under attack by the RobotFalcon, we observed that more than one pattern of collective escape (e.g., the collective turn, the split, the cordon) often co-occur in a single flock. Some of these patterns emerged in our 3-dimensional model, when large flocks are under attack by a predator, from the propagation of a level turn or a diving maneuver executed by a flock member. The patterns of dilution and compacting emerged in our model from mere changes in the frequency with which individuals react to each other and the predator.

In Chapter 6, we have provided technical details of our models, *HoPE* (Chapter 2 and 3), *Colt* (Chapter 4), and *StarEscape* (Chapter 5). Our framework supports the efficient development of new models of collective behavior and facilitates their adjustment to empirical data. In our models, agents move and interact with each other according to an individual-based state machine that makes them perform the discrete escape reactions mentioned above (level turns and dives) and makes their flocks switch between different states (for instance increase the reaction frequency of group members when close to the predator). Given the stand-alone structure of elements in our new framework (e.g., an interaction rule, an escape maneuver, or a state), models can easily be extended or simplified to examine in detail the self-organization of the collective patterns they reproduce: for instance by varying state-specific parameters or removing rules to test their contribution.

7.1 Self-organized collective escape

Self-organized processes are hard to disentangle. One can quickly jump to conclusions about the presence of specific rules at the individual level when a certain individual behavior in a group is observed in empirical data. Whether, however, the observed behavior of an individual when moving as part of a group is caused by a specific rule cannot be inferred by the empirical observations alone. Through computational models, we can search for the simplest rules at the individual level that can lead to a specific collective pattern. Based on the self-organized processes that are identified in a model, we can uncover advantages of being in a group, such as route robustness and efficiency [49, 158] and reduced cognitive costs of minding the position of an attacking predator (Chapter 2), and avoid making assumptions when interpreting empirical findings.

7.1.1 Hysteresis

Hysteresis, when the state of a system depends on its history, is an important aspect of complex systems that has not been well studied in the collective behavior of animals. An example of hysteresis has been identified in previous models of collective motion of fish schools. Simulated schools form mills when individuals increase their alignment tendency while the prior state of the group is swarm-like (low polarization) [33]. When the prior state of the group is a highly polarized group, the same alignment tendency leads the group to transition to a swarm-like state and doesn't form a mill [33]. Another example of hysteresis in animal groups has recently been found in army ants, in the composition of their self-assembled bridges [122].

In our Chapters 2 and 5, we identified hysteresis in the collective escape patterns of pigeons and starlings. To our knowledge, hysteresis has not been studied in bird flocks, and in general in the context of collective escape before. In pigeon flocks, we identified that the increasing predator avoidance closer to the predator (Figure 2.4) would not arise if the predator was not gradually approaching the flock from a distance (for instance if a surprise attack starting from a small predator-prey distance was taking place [35]). In our model of starlings, we found that dilution arises when flock members decrease their reaction frequency after a period of high alertness. Our findings highlight that studying sequences of collective escape (instead of snapshots) is necessary to understand how patterns of collective escape arise.

7.2 Patterns of collective escape across bird species

Empirical studies of collective escape have so far been focusing on a single species per study. To our knowledge, no patterns of collective escape have been compared across species. Such comparisons can be highly beneficial to our understanding of how patterns of collective escape emerge. For instance, how do species with different traits (aerodynamics properties and flock size) differ in their patterns of collective escape? Dunlin flocks are known to quickly alternate their color between dark and bright (a pattern called 'flashing flight') when attacked by a predator ([21], see also Figure 1.1D). These flashes are caused by changes in the exposure of the back (black) and the belly (white) of group members during an escape maneuver [37]. A similar orientation maneuver has been proposed to underlie agitation waves in starlings [74]. When individuals maneuver after their neighbors have maneuvered, dark bands seem to move through the group since starlings have a homogeneously dark body and the observer instantaneously sees a larger area of the birds' wings while they are banking to maneuver [143, 74]. It is thus possible, that collective patterns that have been labeled differently across species (e.g., the flashing flight in dunlins and the agitation wave in starlings) emerge from the same individual behavior.

The influence of the body color (or other species-specific traits) should be considered when studying patterns of collective escape. In computational models, by including a visualization of agents that resembles the study species (Chapter 5, [74, 67]), visual comparisons of patterns between simulations and empirical data are possible. This visual component can also help study a pattern in detail;

for instance, in the computational model StarDisplay, the blackening of starling flocks has been studied by measuring the luminance of non-background pixels in pictures of flocks in the model [30]. Such quantitative approach (see also measurements of milling in fish schools [23, 29] and Chapter 4) can be used to study more complex patterns of collective escape (e.g., the cordon, the vacuole) in the future.

7.2.1 Computational models of bird flocks

For a simulated flock to resemble a real flock during collective escape, the collective motion in a model should first be adjusted to the species of interest. Apart from the species we studied in this thesis (pigeons and starlings), available data of collective motion of others, such as gulls [184] and jackdaws [113], can be used to create new species-specific models in our framework (Chapter 6), given large differences in flock characteristics across species (Figure 7.1). Based on such species-specific models, we can make predictions about the expected patterns of collective escape in those species by incorporating known escape reactions, and guide the future collection of empirical data during collective escape. Studies on individual maneuvers across bird species [144] can thus highly benefit research on collective escape.

The effect of aerodynamics of flying, and especially maneuvering, on collective behavior is not well known; most studies have been focused on the energetic costs of flocking [171]. The collective patterns of airborne flocks may be influenced by the different types of flight performed by the group members, for instances the alteration between continuous flapping, gliding, and bouncing flight [127]. In collective escape, the specifics of some patterns (e.g., vertical agitation waves) may be caused by flight aerodynamics rather than the mere interactions among individuals. For instance, if an individual is losing altitude while performing a maneuver, the shape and diffusion of the flock will be affected. Another specific aspect of flying, head stabilization [139], may also influence the emerging patterns, given that individuals in a flock sense their closest neighbors through their field of view (head frame) which while maneuvering (e.g., during banking) is not aligned to their body frame. This head stabilization is the main specific of flight (along with banking) that has been incorporated in models of starlings (StarDisplay [81] and StarEscape, Chapter 5). Given advances in our understanding of flight aerodynamics and aerial maneuvering [108], more details can be added in future models of collective motion by birds to test whether they play a role in the emergence of the complex collective patterns we observe.

Another aspect of collective behavior not well studied in computational models is individual heterogeneity [89]. In a bird flock, individuals differ in certain traits. First, in physical characteristics, such as weight or age; they may influ-

Figure 7.1: Flocks of: (A) starlings (Chapter 5), (B) pigeons [156], (C) jackdaws [112], and (D) gulls [184].

ence the speed and position of a bird in the flock [155]. Secondly, in experience: less experienced individuals may be more susceptible to imitate their neighbors while flying in the flock [138]. Thirdly in social relationships: the flock's spatial structure may be influenced by biased interactions between individuals (e.g., flock members may stay closer to their mating pair than the rest of their surrounding neighbors, [90, 113], but see also [26]). These differences may have an influence on collective escape. Our pigeon model (Chapter 2 and 3) is the first, to our knowledge, model of bird flocks that includes individual variation as identified in the empirical data: agents differ in their preferred speed and deviate from it to stay in the flock [155]). With our new framework (Chapter 6) more models of collective behavior that include individual heterogeneity can be developed in the future, providing the missing theoretical link between research on differences among individuals in animals [90, 88, 89] and self-organization.

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7.3 Outlook

Insight in the ways that bird flocks react to their predators can be valuable for other fields of research. First, our models can inform practices for bio-herding [97], and especially bird deterrence using robotic predators by proposing species-specific strategies for the artificial predator to approach the flocks [164], while also providing a simulation environment in which pilots of remote-controlled artificial predators can be trained [83]. Secondly, our models can be adjusted to the specifics of motion and the coordination among drones, which along with the insight into the self-organized processes we investigated in this thesis, may aid the development of better systems of autonomous swarms of drones [108].

Overall, our modeling framework can help towards unifying the modeling of collective escape across species and taxa. Using our framework, detailed model documentation [58] and, thus, reproducibility that is currently lacking in the field of collective behavior can be assured, while offering efficiency for the development of new models. To conclude, we hope that this thesis sets the grounds for the systematic study of collective escape across species.