Self-organized collective escape in bird flocks

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Thesis Summary

Bird flocks show fascinating patterns of collective motion, particularly when escaping a predator. Little is known, however, about how these patterns come to be. This thesis aimed to fill this gap by analyzing empirical data of bird flocks under attack by a robotic-predator and studying birds' collective escape in computer simulations. This approach was based on self-organization: the process with which patterns at the level of a group emerge from local interactions among individuals [24].

In Chapter 2 and 3, we took advantage of GPS data of pigeons flocks under attack by an artificial predator (a RobotFalcon [164]) to study in detail the way that pigeons collectively escape. We developed an agent-based model and adjusted it to characteristics of motion and coordination among individuals that are specific to pigeons. A previous study on pigeons has revealed that flock members turn away from the predator more the closer they are to the predator, leading the authors to conclude that pigeons prioritize predator avoidance over group coordination under increased threat [156]. Using computer simulations, in Chapter 2, we studied what rules of predator avoidance at the individual level may underlie this distance-dependent pattern. We showed that, even if individuals do not intend to escape more when closer to the predator, their escape frequency still increases when the predator gets closer. This happens by self-organization from the coordination among individuals. A key aspect of this process is the increasing consensus among flock members over the escape direction when the predator gets closer.

In Chapter 3, we investigated what patterns of collective escape arise in pigeons and studied how these pattern emerge by self-organization. We observed that pigeon flocks are collectively turning or splitting into two sub-flocks. In our computational model, both collective patterns emerged from a single escape maneuver (a turn away from the predator). When a flock member maneuvered sharply and was positioned further away from the center of the flock, there was a higher probability that the flock would split rather than turn collectively. By measuring individual turns in the empirical data of pigeons attacked by the RobotFalcon, we validated the prediction of our model that high angular velocity and low centrality are linked to more splits and fewer collective turns.

The collective turn is probably the most common pattern of collective escape in bird flocks [165]. To deepen our understanding of this pattern, in Chapter 4 we built an agent-based model in which flocks turn to escape a predator, either by directly evading it by turning away from its heading (like pigeons [156]) or by turning towards a point in space (for instance their roost, like starlings [25, 81], or cover, like corvids [165]). We also developed a measurement for the resemblance of a collective turn to two previously identified types: the equal-radii and the parallel-paths turn. Collective escape of prey is expected to confuse the predator and decrease its hunting success. We thus used our model to investigate how these turning types and the specifics of coordination among individuals (that differ across species [9, 114, 113, 45]) relate to the predator's confusion. We observed that when individuals interact with more neighbors and more often (properties previously related to the presence of a predator [79]), their relative position to each other changes faster. This may make it harder for the predator to single out and catch a prey [83]. We also identified non linear relationships between this reshuffling of individuals and the two turning types, that varied depending on the parameters we varied in our simulation. Our findings emphasize on the complexity of collective turning and the need to be further studied in the future.

In Chapter 5 we focused on the species demonstrating the most complex patterns of collective escape, the European starlings [166]. Even though their murmurations are well known [98] and their collective motion well studied [26, 10, 81, 25], the emergent mechanism of only one, of many [166], patterns of collective escape has been studied in detail (namely the agitation wave [74, 143]). We filled this gap by developing a 3-dimensional agent-based model and adjusting it to the specifics of starlings. By analyzing videos of starling flocks pursued by the RobotFalcon, we identified that more than one pattern of collective escape may simultaneously co-occur in a single flock. In our model, collective turns and splits emerged from level turns by a few flock members and from their turns being propagated through the group by individuals copying the turn from their close-by neighbors. Cordons and columnar flocking emerged through diving maneuvers of flock members away from the predator. We also showed that dilution emerges from a decrease in the reaction frequency of individuals after the predator retreats. Thus the emergence of this pattern depends also on the previous state of the group, rather than only the parameters that underlie it (a phenomenon called *hysteresis* [33, 122]).

The three models we used in Chapters 2 to 5 are developed in our new framework that uses clusters of interconnected rules of motion at the individual level (state machines) to simulate collective escape in a data-inspired manner. In this framework, the user can build an agent-based model by composing sets of behavioral blocks (e.g., interactions among group members, escape reactions to a predator), adjusting them to a specific species, and simulate complex collective phenomena by chaining these sets together. We presented this framework in Chapter 6 and emphasized its contribution to the modeling of collective behavior in animal groups.

Data of collective motion of animals in nature are increasingly becoming available. With technological advances, more data on collective escape can also be collected in the future [164, 108]. These data can inform computational models and increase our understanding of how the mesmerizing and complex patterns that bird flocks demonstrate emerge. We hope that this Thesis sets the ground for a deeper understanding of collective escape and highlights the importance of computational models in this endeavor.

Samenvatting

Vogelzwermen vertonen fascinerende patronen van gezamenlijke beweging, vooral als ze aan een roofdier ontsnappen. Er is echter weinig bekend over hoe deze patronen tot stand komen. Dit proefschrift wilde dit hiaat vullen door empirische data te analyseren van vogelzwermen die werden aangevallen door een robot-predator en door de collectieve ontsnapping van vogels te bestuderen in computersimulaties. Deze benadering was gebaseerd op zelforganisatie: het proces waarbij patronen op het niveau van een groep ontstaan uit lokale interacties tussen individuen [24].

In hoofdstuk 2 en 3 maakten we gebruik van GPS-gegevens van duivenzwermen die werden aangevallen door een kunstmatige roofvogel (een RobotFalcon [164]) om in detail te bestuderen hoe duiven collectief ontsnappen. We hebben een agent-gebaseerd model ontwikkeld en hebben dit model uitgerust met eigenschappen van beweging en coördinatie tussen individuen die specifiek zijn voor duiven. Uit een eerdere studie over duiven is gebleken dat de leden van de zwerm zich meer van het roofdier afwenden naarmate ze er dichter bij zijn. Hierdoorconcludeerden de auteurs dat duiven het vermijden van roofdieren meer prioriteit geven boven groepscoördinatie naarmate de dreiging groter is [156]. Met behulp van computersimulaties hebben we in hoofdstuk 2 onderzocht welke regels van roofdiervermijding op individueel niveau ten grondslag kunnen liggen aan dit afstandsafhankelijke patroon. We toonden aan dat, zelfs als individuen niet in toenemende mate van plan zijn te ontsnappen als ze dichter bij het roofdier zijn, hun ontsnappingsfrequentie toch toeneemt als het roofdier dichterbij komt. Dit gebeurt door zelforganisatie als gevolg van de coördinatie tussen individuen. Een belangrijk aspect van dit proces is de toenemende overeenkomst in de bewegingsrichting tussen de leden van de zwerm wanneer het roofdier dichterbij komt.

In hoofdstuk 3 onderzochten we welke patronen van gemeenschappelijk vluchtgedrag ontstaan bij duiven en hoe ze ontstaan door zelforganisatie. We zagen dat duivenzwermen collectief omkeren of zich opsplitsen in twee sub-zwemen. In ons computermodel ontstonden beide collectieve patronen als gevolg van een enkele ontsnappingsmanoeuvre (een draaibeweging weg van het roofdier). Als een lid van de zwerm scherp manoeuvreerde en zich verder van het centrum van de zwerm bevond, was de kans groter dat de zwerm zich zou splitsen in plaats van collectief te draaien. Door individuele draaibewegingen te meten in de empirische gegevens van duiven die werden aangevallen door de RobotFalcon, hebben we de voorspelling van ons model gevalideerd dat hoge draaisnelheid en lage centraliteit samenhangen met meer splitsingen en minder collectieve draaiingen.

Het gezamenlijke draaien is waarschijnlijk het meest voorkomende patroon van collectiefvluchtgedrag in vogelzwermen [165]. Om dit patroon beter te begrijpen hebben we in hoofdstuk 4 een agent-gebaseerd model ontwikkeld waarin zwermen draaien om aan een roofdier te ontsnappen, hetzij door het roofdier direct te ontwijken door weg te draaien van zijn koers (zoals bij duiven [156]) hetzij door te draaien naar een punt in de ruimte (bijvoorbeeld naar hun slaapplaats, zoals bij spreeuwen [25, 81], of naar bedekking, zoals bij kraaiachtigen [165]). We hebben ook een maat ontwikkeld voor de overeenkomst van een collectieve draaibeweging met twee eerder geïdentificeerde types: de draaiing met gelijke-radii en die met parallelle-paden. Verwacht wordt dat het collectief ontsnappen van prooien de predator in verwarring brengt en zijn jachtsucces vermindert. Daarom hebben wij ons model gebruikt om te onderzoeken hoe deze draaitypes en de specifieke kenmerken van de coördinatie tussen individuen (die verschillen tussen de soorten [9, 114, 113, 45]) samenhangen met de verwarring van de predator. We stelden vast dat als individuen met meer buren en vaker interacteerden (eigenschappen die eerder in verband gebracht zijn met aan de aanwezigheid van een roofdier [79]), hun relatieve positie ten opzichte van elkaar sneller veranderde. Dit kan het voor het roofdier moeilijker maken om een prooi uit te kiezen en te vangen [83]. Daarnaast hebben we niet-lineaire relaties ontdekt tussen deze herschikking van individuen en de twee draaitypes, die afhankelijk waren van de parameters die we in onze simulatie onderzochten. Onze bevindingen benadrukken de complexiteit van gemeenschappelijk draaien en de noodzaak om dit in de toekomst verder te bestuderen.

In hoofdstuk 5 concentreerden we ons op de soort die de meest complexe patronen van collectieve ontsnappingsvlucht vertoont, de Europese spreeuw [166]. Hoewel hun murmuraties goed bekend zijn [26, 10, 81, 25], is het ontstaansmechanisme van slechts één van de vele [166] patronen van collectieve ontsnapping in detail bestudeerd (namelijk de agitatiegolf [74, 143]). Wij hebben dit hiaat gevuld. Hiervoor ontwikkelden we een 3-dimensionaal agent-gebaseerd model en pasten het aan aan de specifieke eigenschappen van spreeuwen. In onze analyse van video's van spreeuwen die door de RobotFalcon werden achtervolgd, stelden we vast dat meer dan één patroon van collectief vluchtgedrag tegelijkertijd kan voorkomen in één zwerm. In ons model kwamen het draaien en splitsen van een zwerm voort uit draaibewegingen van een paar leden van de zwerm die op een en dezelfde hoogte vlogen en doordat de draaibewegingen door de groep werden verspreid via het kopieren van de draai van hun naaste buren. Cordons en zuilvormige zwermen ontstonden door duikmanoeuvres van individuen, weg van het roofdier. We hebben aangetoond dat verdunning ontstaat door een afname van de reactiefrequentie van individuen nadat de predator zich terugtrekt. Het ontstaan van dit patroon hangt dus ook af van de eerdere toestand van de groep, en niet alleen van de parameters die eraan ten grondslag liggen (een fenomeen dat *hysteresis* heet) [33, 122]).

De drie modellen die wij in de hoofdstukken 2 tot en met 5 hebben gebruikt, zijn ontwikkeld in ons nieuwe theoretische kader waarin we clusters van onderling verbonden bewegingsregels op individueel niveau (toestandsmachines) gebruiken om collectieve ontsnappingen te simuleren op een door data geïnspireerde manier. Dit kader stelt de gebruiker in staat om een agent-gebaseerd model te ontwikkelen door sets van gedragsblokken samen te stellen (bv. interacties tussen groepsleden, ontsnappingsreacties op een roofdier), deze aan te passen aan een specifieke soort, en complexe collectieve fenomenen te simuleren door deze sets aan elkaar te koppelen. Dit theoretische kader stellen we in hoofdstuk 6 voor en we benadrukken hoe dit kader bijdraagt aan het modelleren van collectief gedrag in diergroepen.

Data over collectieve bewegingen van dieren in de natuur komen steeds meer beschikbaar. Met de technologische vooruitgang kunnen ook in de toekomst meer gegevens over gemeenschappelijk vluchtgedrag worden verzameld [164, 108]. Deze gegevens kunnen de basis van computationele modellen vormen en ons begrip vergroten over hoe de betoverende en complexe patronen van vogelzwermen ontstaan. Wij hopen dat dit proefschrift de basis legt voor een beter begrip voor het collectieve vermijdingsgedrag van dieren in een zwerm en het belang van computermodellen in dit streven benadrukt.

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My friends are the words we don't speak,
the hugs we don't share, the kisses we don't give.
My friends are the phone calls we forget to make. [...]
With such friends you have no need to go on vacation, to rest, you always remain ready for war, for the heaviest winter, for the toughest pandemic, the most unbearable solitude.

- Tellos Filis, 2021

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About the author

Marina Papadopoulou

Marina was born in Thessaloniki, Greece in 1994. She is a computational biologist with an interest in self-organization, collective behavior and complex systems. She completed her BSc degree in *Biology* at Aristotle University of Thessaloniki in 2016. During her graduate studies she conducted a thesis on species-distribution modeling of sea turtles in the group of Dr. Antonis Mazaris, conducting field work in the National Marine Park of Zakynthos, and a research internship at Glasgow University under the supervision of Dr. Sophie Spatharis and Prof. Dr. Jason Matthiopoulos. She continued her education in Imperial College London, getting a MSc degree on *Computational Methods in Ecology and Evolution* in 2017, with a thesis on 'The Cultural Evolution of Evolution', under the supervision of Dr. James Rosindell, Prof. Dr. Armand Marie Leroi and Prof. Dr. Timothy Barraclough. In autumn 2017, she started her PhD at the University of Groningen in the group of Prof. Dr. Charlotte Hemelrijk on self-organization of social systems, under the day to day supervision of Dr. Hanno Hildenbrandt, working on computational models of bird flocks. At the time of publication of this Thesis, Marina is a post-doctoral researcher at the group of Dr. Andrew King at Swansea University, studying collective motion across species with applications to swarm robotics.

"It turns out life isn't a puzzle that can be solved one time and it's done. You wake up every day, and you solve it again."

– Chidi Anagonye, The Good Place