

Attraction Based Models of Collective Motion

Daniel Strömbom

Department of Mathematics
Uppsala University
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Abstract

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Animal groups often exhibit highly coordinated collective motion in a variety of situations. For example, bird flocks, schools of fish, a flock of sheep being herded by a dog and highly efficient traffic on an ant trail. Although these phenomena can be observed every day all over the world our knowledge of what rules the individual's in such groups use is very limited. Questions of this type has been studied using so called self-propelled particle (SPP) models, most of which assume that collective motion arises from individuals aligning with their neighbors. Here we introduce and analyze a SPP-model based on attraction alone. We find that it produces all the typical groups seen in alignment-based models and some novel ones. In particular, a group that exhibits collective motion coupled with non-trivial internal dynamics. Groups that have this property are rarely seen in SPP-models and we show that even when a repulsion term is added to the attraction only model such groups are still present. These findings suggest that an interplay between attraction and repulsion may be the main driving force in real flocks and that the alignment rule may be superfluous.

We then proceed to model two different experiments using the SPP-model approach. The first is a shepherding algorithm constructed primarily to model experiments where a sheepdog is herding a flock of sheep. We find that in addition to modeling the specific experimental situation well the algorithm has some properties which may make it useful in more general shepherding situations. The second is a traffic model for leaf-cutting ants bridges. Based on earlier experiments a set of traffic rules for ants on a very narrow bridge had been suggested. We show that these are sufficient to produce the observed traffic dynamics on the narrow bridge. And that when extended to a wider bridge by replacing 'Stop' with 'Turn' the new rules are sufficient to produce several key characteristics of the dynamics on the wide bridge, in particular three-lane formation.

Keywords: flocking, swarming, self-propelled particles, alignment-free models, agent-based modelling, leaf-cutting ant traffic, sheep-sheepdog system, the Shepherding problem

Daniel Strömbom, Uppsala University, Department of Mathematics, Box 480, SE-751 06 Uppsala, Sweden.

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Dedicated to Y and Z

List of papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I **Daniel Strömbom**. (2011) Collective motion from local attraction. *Journal of Theoretical Biology* 283(1) 145-151.
- II **Daniel Strömbom**, Mattias Siljestam, Jinha Park & David JT Sumpter. The shape and dynamics of local attraction. Submitted.
- III **Daniel Strömbom**. On the stability and mobility of shapes in the local attraction model. Manuscript.
- IV **Daniel Strömbom**, Richard P Mann, Alan M Wilson, Stephen Hailes, A Jennifer Morton, David JT Sumpter & Andrew J King. Solving the shepherding problem: Heuristics for herding autonomous, locally interacting agents. Submitted.
- V **Daniel Strömbom** & Audrey Dussutour. Self-organized traffic via priority rules in leaf-cutting ants *Atta colombica*. Manuscript.

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Additional papers not included in the thesis

1. Richard P Mann, Andrea Perna, **Daniel Strömbom**, Roman Garnett, James E Herbert-Read, David JT Sumpter & Ashley JW Ward. (2013) Multi-Scale Inference of Interaction Rules in Animal Groups Using Bayesian Model Selection. *PLoS Comput Biol.* 9(3).
2. Anna Sircova, Fariba Karimi, Petter Holme, Sungmin Lee, Evgeny N Osin, **Daniel Strömbom** & Philip G Zimbardo. Approaching social dilemmas through simulation: The mediating role of personal time perspective in tragedy of the commons. Manuscript.

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1. Introduction

1.1 Moving animal groups

Schools of fish, flocks of birds and other animal groups, can move in a highly coordinated fashion despite the fact that each member only experiences its immediate surroundings and there exists no obvious leader. These groups come in a variety of shapes and their global as well as their internal motion of the group varies widely. The most common discernible shapes include mills, tori, balls, sheets, strings and various combinations of these [1–3]. The shape of the flock as a whole may change spontaneously or in response to environmental changes, such as predator attacks [4]. The internal dynamics in a flock can range from essentially none, where each individual maintains a fixed distance to its neighbours, to extensive, where internal rearrangement of individuals occur constantly [1, 5–7]. The preferred separation between flock members vary significantly between species. From being kept apart by physical size alone [8, 9] to being more sparsely distributed, often with a preferred inter-individual distance [10–14].

Up until recently it has been challenging to study collective motion quantitatively. This is in part because detailed motion data from moving animals was hard/impossible to obtain. However, with the recent technological developments, in for example computing, photography, positioning and tracking systems, there is now a wealth of data for collectively moving organisms across taxa in two dimensions and even three dimensions. Data has been collected in systems ranging from bacteria and cells [8, 9, 15–21] via insects [22–25], fish [26–31], birds [13, 32–37], mammals [38–42] up to humans [43–46].

The advances in 3D are particularly impressive. Research has come a long way from the projected trajectories of a small midge swarm in [47] to today where the individual 3D trajectories of each midge in a larger swarm can be recorded [48], as is currently being done in the COBBS Non-Biting Midge Experiment [49]. Similarly, from being impossible a decade ago, today the trajectory of each bird in a flock of thousands of starlings roosting over a city can be taken [13]. Even when the flock is under attack the group dynamics have been recorded [4]. This new data complements the older qualitative information on the general structure and dynamics of moving animal groups by providing high resolution data of several specific instances of collective motion. Hence we may now theoretically approach the subject sensibly from both

the general question of what types of properties flocks have and the specific details of particular biological systems.

How does collective motion work? More precisely, what behavioral rule does each individual use that allows the observed group level shape and dynamics to emerge? As indicated earlier one response to this question is that it depends on the particular species forming the group, the particular environment the group is embedded in and that each individual is different. These statements are certainly true, but it is also true that similarly shaped and behaved groups are seen across taxa, forming in different environments by different aggregations of animals. This suggests that there might be a general and robust local mechanism at work in the groups that is responsible for the overall group level shape and dynamics.

1.2 Models of collective motion

Mathematical models are a central part of understanding collective motion. The models used are often, so called, self-propelled particle (SPP) models. The particles represent the modeled animals. For the most part, these models are Lagrangian, which means the position and velocities of each particle are evolved through time as the particles' interact with their neighbors and the environment. There are two main ways think of and represent such SPP models, either as computer programs where the interaction rules and technical details can be implemented freely, or as a system of coupled difference- (discrete time) or differential equations (continuous time) that can readily be approached mathematically. Going from coupled equations to a computer program is easy but the other way can be impossible even in simple cases, due to for example, the combinatorial nature of the local interactions, positional update scheme, asymmetric interaction zones etc. However, even if a proper system of equations representation exists for a problem, with the Lagrangian approach the number of coupled difference/differential equations increases with the number of particles. Thus even for systems with relatively few particles we are often forced to use simulations for the analysis.

The main complement to Lagrangian models for collective motion are so called Eulerian (or continuum) models, where the density of particles is evolved rather than each particles' position and velocity [50–58]. Eulerian models are often partitioned into kinematic or dynamic depending on whether the flock velocity is calculated directly from the density or if it obey its own evolution equation. The underlying equations are partial differential equations of advection-diffusion type and using established theory for these analytical information can on occasion be obtained. Eulerian models do not have the problem that they increase in complexity with the number of particles, in contrast

to the Lagrangian, but rather fail when a continuum description of the flock is inappropriate.

Thus a rough heuristic for choice of type could be: Lagrangian if the number of particles is small and/or the interaction rules are technically complicated and/or detailed individual information is needed. Eulerian if the number of particles is large and detailed individual information is not required. Although numerical methods are often required to solve the advection-diffusion equations Eulerian methods are preferable if the objective is to obtain analytical information. Motivated, in part, by this schemes for translating Lagrangian to Eulerian models has been investigated and shown to be useful in some cases [59–63] especially in noisy systems and when physics, e.g. hydrodynamics, is to be incorporated into flocking models [53]. In addition, if inherent stochasticity is decided to be crucial using so called self-propelled active Brownian particles might be preferable [64–72]. Active Brownian particles absorb energy from their surroundings and use it to accelerate their motion and the self-propulsion is incorporated via negative friction. The underlying equations are stochastic differential equations of Langevin type, but they can be related to a Eulerian approach.

1.2.1 The boids model

In this thesis the main focus is on flocks with relatively few particles and we will exclusively focus on discrete Lagrangian models. A large number of such models have been proposed in recent years [70, 73–87]. Models are used both for general and specific questions about biology. The general question is on identifying similar mechanisms that underly several different forms of collective motion. More specific questions about the collective motion of a specific species or in a specific environment are also addressed. Models of this type are generally more elaborate as they are often based on a minimal model that is augmented with species or environment specific components.

The main difference between different models lies in the components included in, and the form of, the local interaction rule and how a particle determines who its neighbors are. For example, two main schemes are used for determining the neighborhood of a particle, the metric one in which every particle within a certain distance R is a neighbor, and the topological one where the neighbors are the n nearest particles. One particularly influential metric model, which we now describe, is the classical boid model [73, 78, 88]. In it a number of particles move around in two or three dimensions with constant speed and interact with their neighbors in the following manner. If any neighbor is too close the particle will move away from it (repulsion) and if no particle is too close the particle will be attracted to its neighbors (attraction) while at the

same time trying to take their average heading (orientation). This is illustrated in figure 1.

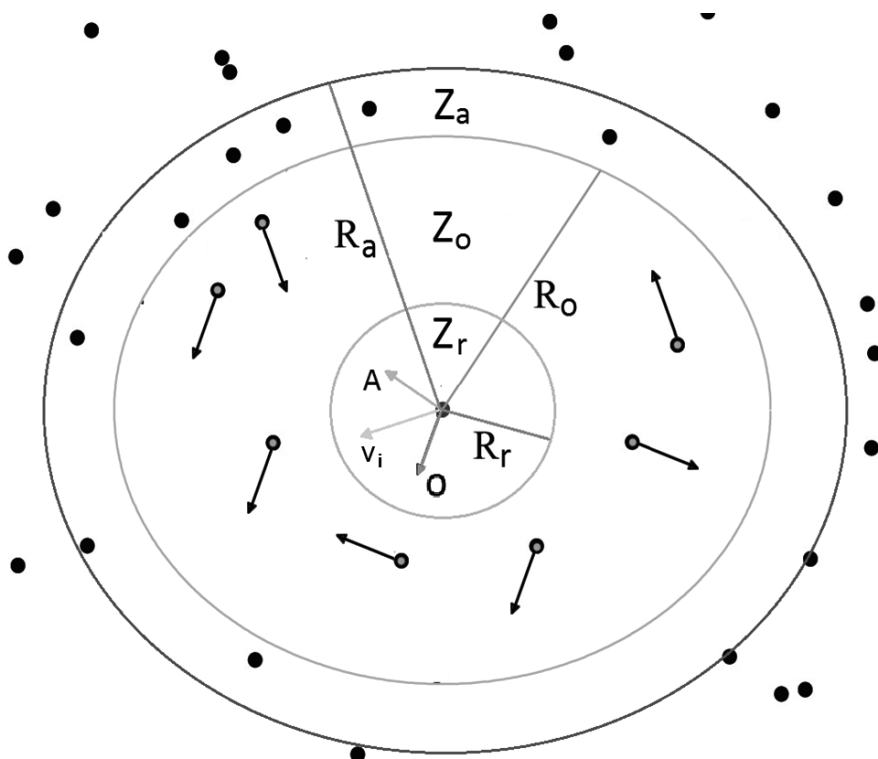


Figure 1.1. How a particle calculates its new heading $v(t+1)$ in the boids model.

More precisely, N individuals with position vectors P_i ($i = 1..N$), and unit direction vectors v_i move with constant speed δ in two or three dimensional space. Each neighbor j of particle i is classified to belong to one of three 'zones' depending its distance to particle i $d_{ji} = |P_j - P_i|$. If $d_{ij} \leq R_r$ then particle j is in the repulsion zone (Z_r) of particle i , if $R_r < d_{ij} \leq R_o$ particle j is in the orientation zone (Z_o) of particle i and finally if $R_o < d_{ij} \leq R_a$ particle j is in the attraction zone (Z_a) of particle i . Discrete time is used and in each time step each particle will calculate which zone each of them is in and based on this decide in which direction $v_i(t+1)$ to move in this time step. Let the number of neighbors in particle i 's repulsion zone be n_r , in its orientation zone n_o and in its attraction zone be n_a . The exact rule for calculating D is the following. If $n_r > 0$ particle i 's new heading is given by

$$v_i(t+1) = - \sum_{i \neq j}^{n_r} \frac{P_j - P_i}{|P_j - P_i|}$$

If $n_r = 0$ the new heading $v_i(t+1)$ will depend on an orientation term O and an attraction term A calculated as

$$A = \sum_{i \neq j}^{n_a} \frac{P_j - P_i}{|P_j - P_i|},$$

and

$$O = \sum_{j=1}^{n_o} \frac{v_j}{|v_j|},$$

respectively. If $n_a, n_o > 0$ then

$$v_i(t+1) = \frac{1}{2}(A + O).$$

Of course one of these zones may be empty and in this case we have that if $n_a = 0, n_o > 0$ then $v_i(t+1) = O$ and if $n_a > 0, n_o = 0$ then $v_i(t+1) = A$. Finally both zones may be empty or $A + O = 0$ and in this case $v_i(t+1) = v_i$. In order to model sensory and movement error the new heading vector $v_i(t+1)$ is rotated by an angle taken from a circular or spherical normal distribution with standard deviation σ . This is the new heading particle i will take, unless the angle between the old $v_i(t)$ and new heading $v_i(t+1)$ is larger than a maximum turning angle θ_m , in which case it will turn this maximum amount toward its intended new heading. The position of particle i is then updated according to

$$P_i(t+1) = P_i(t) + \delta \hat{v}_i(t+1).$$

This process is repeated over a number of time steps in order to simulate group movements.

For this model, it can be shown that in three dimensions four different groups are produced [78]. These range from a swarm (figure 2a), torus (figure 2b), dynamic parallel group (figure 2c) and highly parallel group (figure 2d). The swarm is a cohesive aggregate that is fairly stationary and parallel alignment between particles is very low. The torus (or mill) consists of particles that rotate around an empty core producing a dough-nut shape and this shape is also stationary. The dynamic and highly parallel groups are not stationary and move in space with the particles more or less parallel aligned with each other.

There are lots of questions one can ask about SPP-models. For example, some recent applications attempt model evolution in SPP-models by incorporating birth-death and natural selection [83, 89–92].

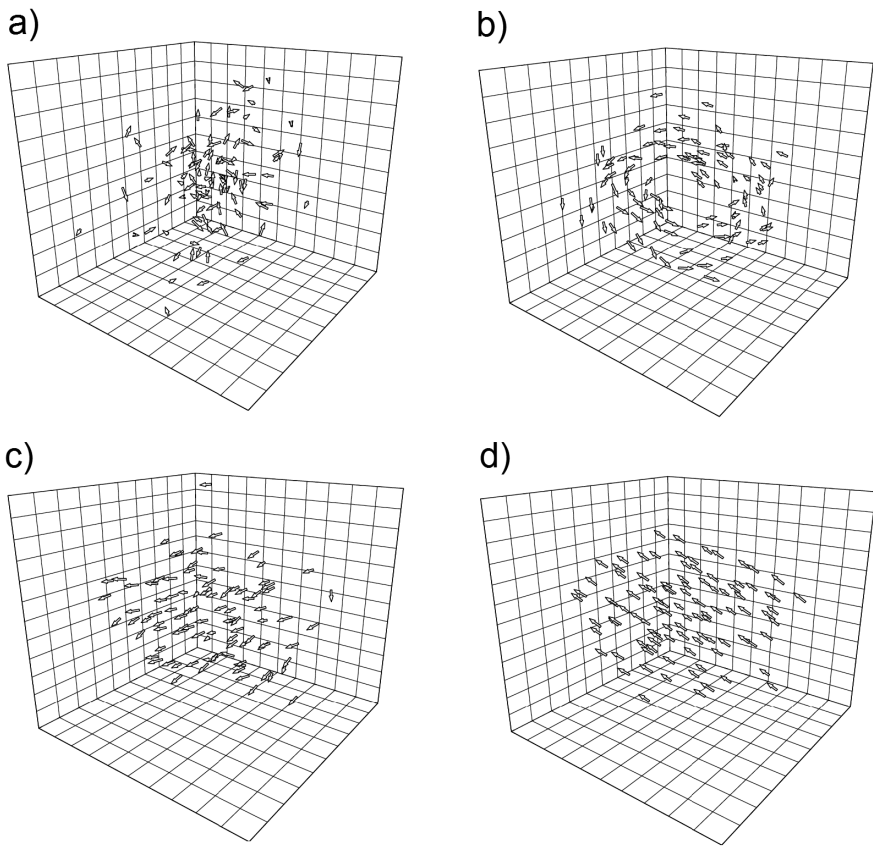


Figure 1.2. The shapes seen in the three dimensional boids model. a) swarm, b) torus (mill), c) dynamic parallel group and b) highly parallel group. Adapted with permission from [78].

1.2.2 Minimal models

One of the goals of work on collective motion is to isolate a minimal set of biologically plausible rules sufficient to produce the general shape and dynamics exhibited by real moving animal groups. In this respect, the boids model, with different zones, is not entirely minimal. The classical example of a truly minimal self-propelled particle model is the Vicsek model [75]. In this, the particles move at constant speed and take the average direction of their current neighbors (orientation), in other words, it is the boid model without attraction and repulsion terms. Vicsek and co-workers studied the competing effects of orientation and noise and showed that a novel type of phase transition occurred between disordered and ordered (polarized) states in the model. Similar pure orientation models have been proposed by and in analytical information regarding convergence have been obtained using methods from control theory [82, 93].

Despite analytical tractability there are, at least, two issues with using these pure orientation models as models of flocking. Firstly, they produce few flock types, typically random, polarized and hybrids in between these. Secondly, local orientation is put in and the main observation is that when it is sufficiently strong in comparison to noise, global orientation (polarized flock) emerges. It would be desirable to have an equally simple one-rule model where polarized flocks emerge without the polarization force being explicitly put in and that this model should be able to produce more shapes and a variety of dynamics. In particular, a minimal model should be able to produce swarms, mills and cohesively moving polarized groups with and without internal dynamics. As described previously it has been known for a long time that the boids model which includes repulsion, orientation and attraction can produce swarms, mills (tori) and cohesively moving (parallel) groups [78]. Can these be found in very minimal models?

In Paper I and the first part of paper II we show that the attraction rule coupled with a blind angle is capable of producing swarms, mills, cohesively moving polarized groups and in addition some novel rotating chain groups in two and three dimensions. These results suggest that attraction, being both biologically plausible and strong enough to produce the three typical shapes, might be the main driving force at work in real flocks. However, a fundamental property of real animals is that they have size and cannot move through each other, so some kind of repulsion should be included in a minimal model. Several attraction-repulsion models exist in the literature [70, 94, 95] but in general the variety of groups produced is small and lack nontrivial internal dynamics. In the second part of Paper II we add to the attraction model a repulsion term that has been designed to be soft enough to allow for internal dynamics but still strong enough to maintain inter-individual distance. The resulting

attraction-repulsion model produce mills, swarms and a whole range of cohesively moving groups some of which exhibit nontrivial internal dynamics in both two and three dimensions. These theoretical findings together with recent studies of individual interactions of mosquito fish [30] and golden shiners [31] indicate that many real flocks and schools may well be formed and driven by attraction and repulsion only, without any orientation rule.

1.2.3 Applications of models

Just like we can establish that a certain minimal model is sufficient to produce swarms, mills and polarized groups with or without internal dynamics we can address the sufficiency issue of interaction rules in real world systems. That is, if the interaction rules at the individual level is thought to be known from a biological point of view, a self-propelled particle model can be used to investigate the sufficiency of these rules to produce some feature at the group level. This is done by implementing the proposed rules in a SPP model mimicking the experimental/observational setting and comparing the outcome of the model with the real system. This approach has been used to model collective motion in a wide variety of different systems, for example fish [27, 96–98], birds [37, 86, 99, 100], insects [22, 23, 48, 70, 101], bacteria [15, 80] and pedestrians [43, 44, 102–104]. In paper II we use this same approach to show, by visual comparison, that attraction and repulsion alone is sufficient to produce the overall shape and orientation of several animal groups previously thought to require additional ingredients for their formation and persistence.

In Paper IV we apply this method to evaluate a proposed shepherding algorithm against experiments where a flock of sheep was herded by a sheepdog. The underlying model was an attraction-repulsion model similar to that in paper II. The main difference in this case is the presence of one special agent, the shepherd, which follow its own rules. Models with two types of agents are frequently used to model leader-follower systems [105, 106] and shepherding systems similar to ours [107–111]. In paper V we investigate the sufficiency of a set of empirically determined traffic rules proposed in [25] to govern the traffic on leaf-cutting ant trails. In this case we have four different types of ants moving in the same environment and ant's behavior in each encounter depends on its own type, the type of the ant it encounters and to some degree its history of previous encounters.

1.3 Analyzing self-propelled particle models

When attempting to construct a biologically realistic model of flocking the problem of complexity arises. Often the known biology of the phenomenon we want to model indicate that several potentially spatio-temporal dependent

factors are crucial, e.g. distribution of neighbors, current speed, noise, type of flocking agent, memory etc. Naturally these factors may also depend on each other in a nontrivial way. On top of this, the local interactions between particles may be complicated (e.g. non-physical) so our choice of model type is often very limited. Given the correct set of rules, SPPs are flexible enough to accurately model any given phenomenon, but the price we pay for this flexibility is loss of analysis tools. Even in the simplest cases frequently the only way to analyze an SPP is by computer simulations. In addition, even if we are willing to make simplifications so that the SPP can be represented as a system of difference- or differential equations, that may be approached by conventional mathematical methods, success is not guaranteed. This lack of analytical tractability is because the size of the system grows with number of individuals, since both position and velocity of each particle is evolved through time. The latter problem can be circumvented in some cases if only the behavior at the macro level is of interest and the flock (density) can be approximated well by a continuum. However, then information at the micro level is lost. The resulting PDEs themselves are frequently hard to analyze and in many relevant biological systems the number/density of individuals is too low for a continuum approximation to be appropriate. In a few simple cases model specific rigorous analysis of certain aspects, e.g. existence, stability, convergence and phase transitions, has been carried out but it is unclear if and to what extent these approaches can be generalized and used to analyze other or more realistic models. Therefore, novel and generalizable methods for analyzing SPPs are needed.

In Paper III we outline a particular approach to the analysis of SPP within the framework of the local attraction model introduced in Paper I. This approach does not increase in complexity with number of particles or even require that an approachable system of equations for individual motions can be written down, but still provides some information about the individual behavior as well as the collective. The key idea is to focus on particle interaction and dynamics with respect to an interaction mediating object rather than explicit interactions with the collective of neighbors. Then we specify the dynamics of this mediating object in order to address questions regarding formation, persistence, stability, mobility and ultimately classification of shapes, each being a key issue in the analysis of any model.

1.4 Issues: past, present and the future

As with most fields of research there are several problematic issues concerning self-propelled particle models of collective motion. These range from philosophical and conceptual via technical to practical. Some are well known and considered, some are well known and less considered and some cannot really

be addressed nor resolved at present. In a review from 2005 [81], Parrish et al. sum up several issues relating to the realism of individual based models proposed up until that time. In particular they mention technical issues such as the simulations typically consist of few particles (up to 128), ignorance of density dependence on individual perception and not properly local interactions. They also highlight the key practical problem which was the non-existence of trajectory data from real animals over long enough periods. The technical issues are now generally considered and some have even devoted entire papers to explicitly implement models where they, by construction, are avoided, e.g. [96], and the data issue is currently being overcome. Moreover, several important general insights have been gained since 2005. In particular, they stated that only models including an explicit alignment term, or an implicit alignment term via leaders, exhibit polarized groups and that "rule sets need to be explored that allow individuals to shift location within the school, rather than simply aggregate and remain in a static configuration." Since 2006 we have been aware, via [70, 94, 95], that attraction and repulsion alone can produce polarization but non-trivial internal shifts remained a problem. In papers I and II we show that attraction alone can produce polarization and in addition produce non-trivial internal dynamics via the 'figure of eight'. Furthermore, as established in Paper II, adding a tailored repulsion term to the attraction only model allow groups to exhibit non-trivial internal dynamics which appear more realistic than the 'figure of eight'.

Parrish et al. [81] then question the relevance of concepts such as stability and convergence to models of, in particular, fish since it is an observable fact that schooling fish typically rearrange within the group, leave the group only to re-join it immediately and even leave the group in search for a new group to join. In particular, they state that "In the next generation of agent-based schooling simulations, rule sets must allow a simultaneous exploration of individual movements provoking group-level pattern and fission-fusion of groups." This point of view appear not to have been taken by many researchers since even today models are frequently being simplified/modified in order to allow stability and convergence results to be established, and although this might be the correct approach in engineering applications reconsidering it for biological applications seems unavoidable.

In addition to problems with the biological realism of the rules themselves and the results they produce, there appears to be a generic problem with model selection from data. It is well known that the same rule can produce different shapes depending on initial conditions [78, 85, 112]. It is also known that different rules can produce the same shapes and dynamics [101, 113–115]. Both these issues naturally reduce the explanation and predictive power of these models. The resolution to this problem, or even establishing whether the degeneracy is a problem [116], remains unclear. However, the research

community seems to have adopted a number of sensible strategies. In addition to requiring biologically plausible rules, the aim is to seek minimality in the general setting (minimal models), in part because of an Occam's razor type argument. In particular cases where data exists the use of statistical model selection methods is used to try as far as possible to distinguish between competing models (or infer the rules) [30, 31, 98, 115, 117–120]. However, it is always important to think about if the models are indeed competing/mutually exclusive with respect to their underlying assumptions and the question(s) being addressed in the first place [116].

Just as important as the establishment of interaction rules from biological observations is the question of how they are implemented. When implementing a SPP model as a computer program many decisions have to be made not directly involving the interaction rules we wish to investigate. It could be everything from large decisions such as choosing between lattice or continuous environment, constant or variable speed, continuous or discrete time, interaction update scheme (simultaneous, sequential or Gillespie), open space or special topologies, restrictions on neighbor detection or possible movement, type of noise, to apparently smaller decisions such as if a particle is considered its own neighbor. Logically each such choice results in a different model and generally it is not clear a priori how different the models are going to be. As has been pointed out several times in mathematical biology, each assumption, or line of code, may be important and failure to consider this properly may have undesirable consequences [121, 122].

It is often not feasible to try every possible choice of model so again heuristics are needed and it is clear that the choice depends heavily on the purpose of the model. Two common heuristics seem to be 1. Make decisions that preserve the analytical tractability of the model and 2. Make each decision as biologically realistic as possible. The first one is frequently adopted by engineers, physicists and mathematicians and the latter frequently by biologists. However, both of these are problematic. The first because analytical tractability typically comes at the expense of realism and the second because in striving for the ideal of realism on the micro scale an understanding of the connection between the micro and the macro scales can be lost. In the worst case a complicated model cannot even be analyzed sensibly via simulations. Therefore, it is crucial to strike a proper balance between these extremes, biological realism and simplifying assumptions, where a limited set of key components and decisions are included/made. The most natural choices are those thought to crucially influence the phenomenon the model is intended to shed light. However, one may consciously or unconsciously be drawn toward one of these extremes by a-priori assumptions on how big this set of key assumptions should be. This can happen, for example, because of the norms in ones original field of study and/or publication opportunities. In order to avoid this personally,

coming from mathematics and physics, I constantly remind myself of what I have heard Prof. Mats Gyllenberg say once in a lecture at the Royal Academy of Sciences, namely that (in mathematical biology) "we must stop adapting the problems to the methods and start adapting the methods to the problems". This is in conjunction with 'specific question'-oriented modeling, be it data driven or purely theoretical, seems like a sensible way forward.

2. Paper Summary

2.1 Paper I

Collective motion from local attraction

Daniel Strömbom. (2011) Collective motion from local attraction. *Journal of Theoretical Biology* 283(1) 145-151.

Many animal groups, for example schools of fish or flocks of birds, exhibit complex dynamic patterns while moving cohesively in the same direction. These flocking patterns have been studied using self-propelled particle models, most of which assume that collective motion arises from individuals aligning with their neighbours. Here, we propose a self-propelled particle model in which the only social force between individuals is attraction. We show that this model generates three different phases: swarms, undirected mills and moving aligned groups. By studying our model in the zero noise limit, we show how these phases depend on the relative strength of attraction and individual inertia. Moreover, by restricting the field of vision of the individuals and increasing the degree of noise in the system, we find that the groups generate both directed mills and three dynamically moving, rotating chain structures. A rich diversity of patterns is generated by social attraction alone, which may provide insight into the dynamics of natural flocks.

2.2 Paper II

The shape and dynamics of local attraction

Daniel Strömbom, Mattias Siljestam, Jinha Park & David JT Sumpter. Submitted.

Moving animal groups, such as flocks of birds or schools of fish, exhibit complex internal dynamics while moving cohesively in the same direction. This kind of flocking behavior has been studied using self-propelled particle models, in which the ‘particles’ interact with their nearest neighbors through repulsion, attraction and alignment responses. Recently, it has been shown that models based on attraction alone can generate a range of dynamic patterns. Here we investigate the conditions under which attraction-based models are

able to reproduce the three dimensional, complex, dynamical patterns seen in natural animal groups. We provide a phase diagram of how attraction strength and blind angle determine the pattern generated in this model. We show that adding repulsion to the model changes the shapes produced, making them look more like natural flocking patterns. We compare our simulations to observations of surf scoters, starlings, moving and rotating fish schools and other flocks. Our results suggest that many biological instances of collective motion might be explained without animals explicitly responding to each others direction. Instead, complex collective motion is explained by the interplay of attraction and repulsion forces.

2.3 Paper III

On the stability and mobility of shapes in the local attraction model

Daniel Strömbom. Manuscript.

Many animal groups, for example schools of fish or flocks of birds, exhibit complex dynamic shapes while moving cohesively in the same direction. The main theoretical tools used to study the formation and dynamics of these shapes are so called self-propelled particle models. However, even the simplest models typically require computer simulations for their analysis, especially when the number of particles is small. For example, this is the case for the local attraction model with a blind angle. Here we explore three geometrical ideas based on transferring the attention from the particles themselves to the local center of mass they detect and the shapes they constitute. We use these methods to investigate the persistence and mobility of shapes in a local attraction model with a blind zone. More specifically, we address the persistence/stability of the mill shape. Then we investigate how the dynamics of the detected local center of mass relate to the shapes we observe, including a moving figure of eight shape generated by the model. Finally, we provide some insight into why some rotating chains exhibit translational motion and some do not. Although this work is in its infancy we believe that these ideas have potential and may facilitate analysis of similarly complex models.

2.4 Paper IV

Solving the shepherding problem: Heuristics for herding autonomous, locally interacting agents

Daniel Strömbom, Richard P Mann, Alan M Wilson, Stephen Hailes, A Jennifer Morton, David JT Sumpter & Andrew J King. Submitted.

The herding of sheep by dogs is a powerful example of how one individual can cause many unwilling individuals to move in the same direction. Similar phenomena are seen in systems as diverse as crowd control, cleaning the environment, and collecting other animals or robot drones. Although single dogs are seen to solve this "shepherding problem" every day around the world, it remains unknown which algorithm they employ or whether a general algorithm exists for shepherding. Here we describe such an algorithm, based on adaptive switching between collecting the sheep when they are too dispersed and driving them once they are aggregated. We show, in a self-propelled particle model, that our shepherding algorithm can effectively herd large numbers of autonomous, locally interacting agents. A side-to-side motion of the shepherd behind the group emerges from interactions between the dog and the sheep. We show that this and other aspects of the herding interactions in our model are consistent with empirical data of real sheep herds. It appears that the shepherding algorithm applied by dogs is simpler and more effective than those previously proposed by engineers, suggesting new methods for the development of mobile robots designed to influence movements of living and artificial agents.

2.5 Paper V

*Self-organized traffic via priority rules in leaf-cutting ants *Atta colombica**

Daniel Strömbom & Audrey Dussutour. Manuscript.

Ants, termites and humans often form well-organized and highly efficient trails between different locations. Yet the microscopic traffic rules responsible for this organization and efficiency are not fully understood. Recent experimental work with leaf-cutting ants (*Atta colombica*) on a very narrow trail has suggested a set of priority rules thought to govern the traffic dynamics. Here we implement an agent-based model to investigate the sufficiency of these rules with respect to producing the observed spatio-temporal properties of the traffic. We compare the model results to four statistics of the real ant flow and find that they share several key characteristics. Then we extend the model to a wider trail and compare the simulation results with new experimental data from this setting. We find that the extended model is able to reproduce the general features of the flow seen in the experiments, including the formation of three-lane traffic. The experimental finding that *Atta colombica* indeed organize the flow into three-lane traffic is important in its own right and contradicts the previously held belief that *Atta* in general do not. Due to the simplicity of the proposed rules we believe that they may be responsible for organizing the

traffic flow on trails in other species of ant, and perhaps even other trail forming animals such as termites and humans.

3. Summary in Swedish

Djurgrupper i rörelse, exempelvis fiskstim och fågelflockar, rör sig ofta på ett mycket koordinerat sätt trots att varje medlem endast kan uppleva och interagera med sin närmaste omgivning, och utan att någon självklar ledare för gruppen finns. Välkända exempel är ankor som går på rad, ringformade fiskstim, bisvärmar och gigantiska tubformade starflockar. Hur fungerar detta? Mer specifikt, vilka lokala regler använder individerna i en grupp som möjliggör att gruppens övergripande form och dynamik kan uppstå? Ett svar på denna fråga är att det beror på vilken art som utgör gruppen, miljön som gruppen rör sig i och att varje individ är unik. Dessa påståenden är sanna, men det är också sant att grupper av djur från vitt skilda arter uppvisar samma form och rörelsemönster, uppstår i olika miljöer med olika individer. Detta tyder på att det kan finnas en allmän och robust lokal mekanism som verkar i grupperna och ger upphov till den övergripande gruppstrukturen och dess dynamik. Sökandet efter, och analysen av, en sådan generell mekanism (minimal modell) är en av huvudinriktningarna inom forskningsområdet kollektiv rörelse. En annan är modellering av kollektiv rörelse hos djur av en viss art och/eller i en specifik miljö. Modeller av denna senare tillämpade typ är allmänt mer komplicerade då de ofta bygger på en minimal modell som är utökad med art- eller miljöspecifika komponenter. I båda fallen används ofta partikel-modeller (SPP-modeller) där en samling självframdrivna partiklar följer ett antal inprogrammerade/definierade interaktionsregler medan de rör sig runt i rummet.

3.1 Minimala modeller

Ett av målen när det gäller minimala modeller är att isolera en minimal uppsättning biologiskt rimliga regler tillräckliga för att producera verkliga djurgrupperns allmänna form och rörelsemönster. I nuläget bör en minimal modell åtminstone kunna producera svärmar, cirklar och grupper som förflyttar sig linjärt med och utan inre dynamik. Det har länge varit känt att en speciell minimal modell bestående av tre regler är tillräcklig för att kunna producera dessa tre former. Dessa tre regler är: varje individ rör sig från grannar som är alltför nära (repulsion), varje individ tar medelriktningen av grannarna som varken är för nära eller för långt bort (orientering) och varje individ rör sig mot grannar som är långt borta (attraktion). Denna modell har varit väldigt inflytelserik och använts för att modellera ett stort antal olika situationer som involverar kollektiv rörelse. I artikel I och första delen av artikel II visar vi att

attraktionsregeln ensam kan generera svärmar, cirklar och grupper som förflyttar sig linjärt med och utan inre dynamik i både två och tre dimensioner. Detta indikerar att lokal attraktion, som både är rimlig från ett biologiskt perspektiv och stark nog för att producera de tre typiska formerna, kanske är huvuddrivkraften i många verkliga flockar och stim. En grundläggande egenskap hos riktiga djur är dock att de har storlek och inte kan röra sig genom varandra, så någon typ av repulsion bör ingå i en minimal modell. Flera modeller av attraktion-repulsion-typ modeller finns i litteraturen, men ofta är antalet olika grupper som kan genereras få och dessa saknar i allmänhet icke-trivial inre dynamik. I den andra delen av artikel II utökar vi vår attraktionsmodell med en speciell repulsions-term. Denna har utformats för att vara mjuk nog för att tillåta inre dynamik, men fortfarande stark nog för att upprätthålla ett visst avstånd mellan individerna. Resultatet är en attraktion-repulsionsmodell som kan generera svärmar, cirklar och en uppsjö grupper som förflyttar sig linjärt och samtidigt uppvisar icke-trivial inre dynamik i både två och tre dimensioner. Dessa teoretiska resultat tillsammans med nya experimentella studier av interaktionsregler hos fiskar [30] [31] indikerar att många verkliga flockar och stim kanske bildas och drivs av endast attraktion och repulsion, utan någon orienteringsregel.

Trots att minimala modeller är relativt enkla måste vi ofta förlita oss på datorsimuleringar för att analysera dem, och inte ens detta är alltid gångbart. Den huvudsakliga orsaken till detta är de lokala interaktionernas kombinatoriska karaktär. Vi kan ofta utan större problem analysera en modell för två partiklar och för oändligt många partiklar. Men i de för tillämpningar viktigaste storlekarna, hundratal eller tusental, kan vi endast i bästa fall analysera dem via datorsimuleringar. I artikel III presenterar vi tre relaterade idéer som kan ge oss helt nya möjligheter att analysera modeller av denna typ. Huvudidén är att flytta fokus från de lokala interaktionerna i sig till dynamiken hos det interaktionsmedierande objektet och dess påverkan på en eller flera testpartiklar. Vi illustrerar idéerna med hjälp av den lokala attraktionsmodellen i enkla typfall och beskriver hur de kan användas för att i förlängningen förhoppningsvis besvara frågor rörande stabilitet, mobilitet, klassificering etc. av denna modell och andra modeller av samma komplexitet. Det bör dock understrykas att detta arbete är i sin linda, men att det finns anledning att vara optimistisk.

3.2 Tillämpningar

Precis som vi kan fastställa att en viss minimal modell är tillräcklig för att producera vissa gruppstrukturer kan vi undersöka om en mängd föreslagna interaktionsregler är tillräckliga för att producera gruppstrukturen och dynamiken i verkliga system. Det vill säga om interaktionsreglerna på individnivå tros vara kända från biologisk synvinkel kan en SPP-modell användas för att un-

dersöka huruvida dessa regler är tillräckliga för att producera vissa egenskaper på gruppnivå. Detta genom att implementera de föreslagna reglerna i en SPP-modell som härmar den experimentella/observationella miljön och jämföra resultatet av modellen med det verkliga systemet. I artikel II använder vi denna metod för att visa att endast lokal attraktion och repulsion är tillräckliga för att generera den övergripande strukturen och rörelsemönstret hos flera djurgrupper som tidigare förmodats kräva ytterligare ingredienser för att bildas och drivas. I artikel IV tillämpar vi denna metod för att utvärdera en föreslagen vallningsalgoritm mot experiment där en flock får blir vallade av en fårhund. Den underliggande modellen är en attraktion-repulsion modell liknande den i artikel II. Den största skillnaden är i detta fall förekomsten av en speciell individ, herden, som följer sina egna regler. Naturligtvis är vi inte begränsade till endast en speciell individ utan kan ha ett valfritt antal olika klasser av individer. I artikel V undersöker vi om en uppsättning empiriskt isolerade trafikregler för lövskärrmyror är tillräckliga för att styra trafiken på en lövskärrmyrstig. I detta fall har vi fyra olika typer av myror som rör sig i samma miljö och en myras beteende i varje möte beror på dess egen typ, typ av myra den möter och till viss del sin historia av tidigare möten.

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