

Review

A review of attraction and repulsion models of aggregation: Methods, findings and a discussion of model validation

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ABSTRACT

Animal aggregates (sparrow flocks, anchovy schools, caribou herds) are complex systems made up of potentially thousands of individuals moving in a coordinated mass. While such aggregates are difficult to study in the field, models of aggregation offer researchers a way to investigate how the interplay of individual behaviour makes aggregation possible and leads to different aggregate-level behaviour. This paper reviews the findings of models of aggregation, both mathematical and computer-based, with a focus on the means used to validate these models. In the context of this review it is argued that the existing *de facto* modelling framework, the Attraction Repulsion (AR) framework, does not allow for an adequate representation of the properties of individuals required to create validatable models of natural aggregation. However, it is further argued that the increasing use of information or perceptual fields in AR models provides a promising direction for future research.

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1. Introduction

Animal aggregation is a pervasive phenomenon in the natural world. European starlings (*Sturnus vulgaris*) move through the air in a tightly packed, fast moving group (Heppner, 1997). Some types of slime mould (*Mycetozoa*) live as a group of unconnected single-celled organisms until these organisms begin to starve, at which point they gather together to form a single slug that moves as a cohesive whole (Camazine et al., 2001; Bonner, 2009). Dolphins move in pods that perform elaborate manoeuvres in order to herd fish (Bel'kovich, 1991), which themselves move in large, coordinated schools (Parrish et al., 2002).

Despite its prevalence, aggregation is not a trivial bi-product of organism interaction, but a behaviour that must be initiated and maintained through the action of specific biological mechanisms. Some aggregating animals, like dolphins, are highly complicated and intelligent organisms, while others, like slime mould cells, could barely be said to have cognitive abilities. Nonetheless, every one of these organisms has the ability to move together with other organisms of the same type in complicated ways to form cohesive, organised groups that often display elaborate spatial and temporal group patterns. This suggests that aggregation is both an evolutionarily important and multiply realisable natural behaviour.

Animal aggregate researchers, an interdisciplinary group comprised of biologists, cognitive scientists, psychologists, sociologists, computer scientists and physicists, attempt to describe, explain and predict the behaviour of animal aggregates. Areas of research include the movement patterns generated by animal aggregates (for example, the swirling cylindrical patterns (mills) seen in fish schools (Parr, 1927)) and the patterns of communication that are generated by these aggregates over time (for example, the synchronised flashing of fireflies (Moiseff and Copeland, 2000)). Within this context, researchers may be interested in describing the nature of the aggregate behaviours seen in a particular species (for example, the people streams observed in human crowd situations (Helbing et al., 2002)) or they may be interested in doing more abstract, theoretical work (for example, studying the effect that access to varying levels of environmental information has on general aggregate behaviour (Couzin et al., 2005)).

Due to difficulties associated with studying aggregate behaviours experimentally and in the wild, this behaviour is an ideal candidate for mathematical and computer modelling. The goal of these models is to increase an understanding of the behaviour of interest, both with respect to its reasons for existing and also with respect to the mechanisms required for its existence. Although in some cases the goal of the models is merely to demonstrate or investigate theoretically the ways in which such behaviour is possible, many models wish to model specific aggregate behaviours occurring in the natural world, whether this is with respect to animal families for which gregarious behaviour is common (e.g., fish species in general) or with respect to the behaviours of specific species (e.g., sticklebacks (*Gasterosteus aculeatus*)). When this is the case, to be considered valid models of the specific phenomenon of interest, the models must be clearly based on observed behaviours and experimentally derived data and validated through reference to observed and derived data as well.

The goal of this paper is to understand the ways in which the origins of aggregate modelling have influenced current modelling practices in this area and, further, to consider how future models

may be better validated by explicitly introducing perceptual factors into the modelling process. The paper begins, in Section 2, with a brief introduction to modelling the act of aggregation and a discussion of the current *de facto* framework used to model this act—the Attraction Repulsion (AR) framework. Then, in Section 3, available techniques for data gathering and some results obtained by each approach are reviewed, demonstrating the ways in which current technology allows for the gathering of data that could be used to calibrate and validate models. Techniques used for studying individual mechanisms of aggregation, and the results of this research are also briefly discussed. Section 4 considers research investigating the perceptual underpinnings of aggregate behaviour.

2. Modelling aggregation

2.1. Breder's model: drawing an analogy with physical forces

One of the challenges of modelling aggregates is the development of modelling techniques that are both computationally tractable and that can take into account the many interactions among individuals in an aggregate. Breder (1951, 1954, 1976) was one of the first researchers to generate mathematically tractable models of the behaviour of schooling fish by drawing an analogy between fish in an aggregate and atoms held in a crystal lattice, and by comparing the responses to social stimuli of fish in an aggregate with the attractive and repulsive forces that exist between atoms. In Breder's 1954 model, aggregation depended simply on a , the attractive force between two individuals, r , the repelling force and d , the distance between the individuals, along with two constants, m and n (see Eq. (1)). These combine to provide c , a measure of the cohesiveness of the school as a whole. Breder then used Coulomb's law of magnetism and electrostatics, in conjunction with some simplifying assumptions, to derive Eq. (2), where r_1 and r_2 are the repulsion of fish 1 (or school 1) and fish 2 (or school 2).

$$c = \frac{a}{d^m} - \frac{r}{d^n} \quad (1)$$

$$c = 1 - \frac{r_1 r_2}{d^2} \quad (2)$$

Breder's models began the practice of simplifying the stimulus and response component of aggregation by making use of a physical forces analogy. While acknowledging the importance of perception in actual aggregate behaviour, by positing the existence of social forces, analogous to physical forces, Breder and later modellers (e.g., Okubo, 1986; Edelstein-Keshet, 2001) were able to avoid modelling the stimulus response aspect of aggregation explicitly. This made models mathematically tractable and allowed modellers to focus instead on the more general question of how attraction and repulsion in individuals could lead to aggregation. This, in turn, led to the widespread incorporation of the concepts of attractive and repulsive social forces as a basic component of aggregation models, which in turn resulted in the adoption of the AR framework as the *de facto* framework for modelling aggregation.

Breder's model also demonstrates the way in which aggregation models generally begin by considering individual properties but then switch to a focus on group properties. The variables a and r reflect individual properties, but it is assumed that all individuals within the group share the same value for these properties. This allows a single value to be used for these properties, which, again, makes the model mathematically tractable and in turn allows con-

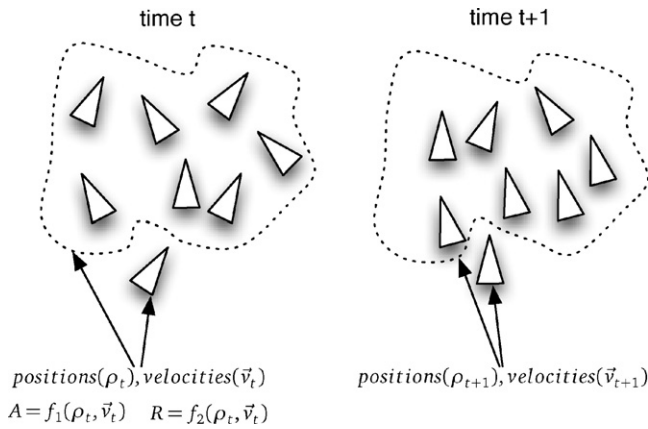


Fig. 1. Calculating the behaviour of individuals within the aggregate over time. Each agent changes its position, ρ_t and velocity, \vec{v}_t based on the position and velocity of nearby agents, and the attraction (A) and repulsion (R) equations assigned to it.

clusions to be drawn about the group property, c . Effectively, a more detailed representation of the heterogeneity and behavioural complexity of actual animals is avoided in order to obtain analytical power. Later models have also followed this pattern. [Adiou et al. \(2003\)](#), for example, have developed a model that considers, as one of its main variables, a state variable that reflects the proportion of individuals in a particular unit of volume that have a certain orientation angle. The modellers then create a system of equations that relate to this state variable and explore the resulting properties of the mathematical model as they relate to group aggregate properties.

2.2. A typical aggregate model

Breder's model is only one example of how the AR framework can be used to model aggregation. More generally, in modelling terms, the AR framework posits that each animal within an aggregate maintains the cohesion of the aggregate by following particular attraction and repulsion rules. Movement through space by an individual at a particular time, t , is determined by:

1. the attraction and repulsion equations (along with equation parameters) associated with individuals in the aggregate.
2. the inputs to the attraction and repulsion equations at that time, t , which themselves depend on the state of the environment at that time—in particular the position and velocity of other individuals in the environment.
3. the outputs of the attraction and repulsion equations, possibly combined with additional reaction equations, which determine how the position and velocity of the individual will change from time t to time $t+1$ (see Fig. 1).

Attraction and repulsion equations may vary in form, as long as they produce both attraction and repulsion. [Cousin et al. \(2002\)](#) define the attraction and repulsion behaviour of individuals as follows: If the distance, d , between an individual, i , and other individuals, j , is less than a certain distance, r , then adjust the agent's direction of travel, \vec{d}_i , as follows:

$$\vec{d}_i(t + \Delta t) = - \sum_{j \neq i}^{n_r} \frac{\vec{c}_j(t) - \vec{c}_i(t)}{|\vec{c}_j(t) - \vec{c}_i(t)|} \quad (3)$$

where \vec{c}_j is the position vector of the neighbour at time t , and n_r is the number of neighbours within the specified distance, r at time t . This points the agent away from its neighbours, resulting in it

moving away from them in the next time step. If this is not the case, then:

$$\vec{d}_i(t + \Delta t) = \sum_{j \neq i}^{n_a} \frac{\vec{c}_j(t) - \vec{c}_i(t)}{|\vec{c}_j(t) - \vec{c}_i(t)|} + \sum_{j=1}^{n_o} \frac{\vec{v}_j(t)}{|\vec{v}_j(t)|} \quad (4)$$

where \vec{v}_j is the velocity of the neighbours, n_o are the neighbours within a particular distance o from the individual (but not closer than r) and n_a are the neighbours that are within a particular distance, a from the individual (but not closer than o), at time t . This results in the agent pointing towards its neighbours and matching its velocity with the velocity of the neighbours.

These two equations, when used to calculate the positions of each individual in the aggregate at each moment in time, result in aggregation behaviour by the group of agents over time. They are effectively force equations that describe the influence of the social forces exerted by other agents on a particular agent's position and velocity. As such, they act on agents, and determine the overall behaviour of the model.

This abstraction away from biology towards the adoption of a more simplistic physical forces analogy is a major advantage of the AR framework. Because it does not specify any physical mechanisms of attraction and repulsion, but instead only assigns abstract, descriptive attraction and repulsion rules that act on individuals within the aggregate, models using the AR framework are not tied to any particular aggregating species. Thus, the AR framework functions as a general theory, which can capture the essential aspects of aggregation across species. This, in turn, has allowed animal aggregate researchers to study the general properties of aggregation without the need to refer to the behaviour of particular animal aggregates in the wild.

In addition to this useful generalisability, the AR framework has two other major advantages from a modelling perspective. The first is that generally only a few parameters are required by the framework, so that it is fairly simple to create models. The second is that the modelling concepts of attractive and repulsive forces can be clearly defined with equations, albeit ones that are recognized to serve as abstractions or analogies for the actual mechanisms of aggregate behaviour. This means that there is little doubt as to how abstract models of aggregate behaviour are implemented, and model results can be clearly analysed, explained and compared. Having said this, because of its generalities, the AR framework has difficulties describing animals in specific enough terms to concretely model relevant physical and cognitive differences between animals and, by extension, aggregate heterogeneity. It also has difficulties connecting with particular natural scenarios (for example, transitions in aggregate behaviour when the temperature drops, or when the sun sets). Thus, although the AR framework excels at drawing theoretical conclusions about aggregation, (e.g., [Cousin et al., 2002](#)) it is often difficult to apply or relate these conclusions to aggregates in the natural world. To do this, models must be created that are consistent with, and validated by, data about actual aggregation, a requirement that will be considered further in Section 6.

3. Aggregation research methods used for data collection

To create models that are consistent with, and validated by, aggregate behavioural data, the structures of these models must be compared to what is known about actual aggregates. This, however, raises questions regarding the type of data available for model calibration and validation. Consequently, to understand and evaluate the claims that modellers make for their models, it is important to understand the possibilities that currently exist for gathering data on aggregation and also the qualitative and quantitative findings of this research. In this context, this section of the paper will consider available technologies for gathering data on this behaviour and the

findings arising from the application of these techniques that may be relevant for validating the behaviour of aggregation models.

3.1. Observation and capture

Simple visual observation is sometimes feasible when studying aggregates of smaller aquatic animals, and often entire aggregates can be captured in order to learn about the properties of individuals that make up the group. Using this technique, Spieler (2003) found that tadpoles of the frog *Phrynomantis microps* increased their aggregation size when in ponds with relatively clear water, possibly in response to increased predation risk. Krause et al. (1996) and Krause et al. (2000) observed and collected shoaling banded killifish (*Fundulus diaphanus*), golden shiners (*Netomigonus crysoleucas*) and white suckers (*Catostomus commersoni*). They found that shoals had a mixed composition with respect to species but that composition was still influenced by species and size. When shoals encountered each other there was transfer of individuals between shoals, as well as combination of shoals (fission and fusion phenomena).

3.2. Sonar and echosound

Researchers have obtained a considerable amount of information on the size, shape and aggregate behaviour of fish schools using sonar and echosounder technology. Axelsen et al. (2001) observed herring (*Clupea harengus*) being attacked by Atlantic puffins (*Fratercula arctica*) and recorded a wide variety of shape changes in response to these attacks, (including bend, hourglass, vacuole and split) along with density propagation through the school. Gerlotto et al. (2006) observed anchovies (*Engraulidae*) using multibeam sonar and were able to record the propagation of a flash response (where fish rotate so that their silver side is visible) moving through the aggregate, which they speculate is a means of rapidly communicating predator attack through a large school. Pelagic fish schools (Soria et al., 2003) and clupeid fish schools (Gerlotto and Paramo, 2003) have also been observed using multibeam sonar and echosound, with findings that schools tend to be longer than they are wide, but that there is still considerable variation in school shape and behaviour, even between schools of the same species found in different locations.

3.3. Photography and film

Photography and film have enhanced the ability of aggregate researchers to analyse and quantify their observations, particularly when the individuals in the aggregate can be easily distinguished and identified, either as a result of fortuitous natural circumstances or deliberate laboratory setup. Miller and Stephen (1966) used aerial photography to photograph sandhill crane (*Grus canadensis*) flocks that were feeding in fields and found that the distance between cranes remained consistent, at 5.79 ± 0.16 ft, regardless of group size. Carbone et al. (2003) used a similar method to monitor flock expansion in feeding barnacle geese (*Branta leucopsis*), finding that flocks expanded over feeding time. Caraco and Bayham (1982) used Super-8 film to analyse the effects of temperature and sex of house sparrows (*Passer domesticus*) on flock size and nearest neighbour distance and determined that while sparrow sex did not have a noticeable effect on flock behaviour, lower temperatures led to an increase in flock size, and that nearest neighbour distance decreased as flock size increased.

Moving from naturalistic settings to lab studies, Krause and Tegeder (1994) were able to combine digitised and computer analysed video with a carefully designed experimental setup to determine that sticklebacks (*G. aculeatus*) followed movement rules that minimised their approach time to a single conspecific when aggregating. Miller and Gerlai (2007) used a similar approach

to study zebra danio (*Danio rerio*) shoaling in the laboratory and found that baseline shoaling was altered by both the presence of food (increasing inter-individual distance) and predator presence (an initial increase in inter-individual distance followed by a more cohesive schooling behaviour).

3.4. Stereophotography and videography

Stereophotography and videography, combined with digitisation and computer analysis provide what is potentially the most promising, although technologically most challenging, method for studying aggregate behaviour, particularly in naturalised settings. Aoki et al. (1986) used stereophotography combined with photo digitisation and computer analysis to study the three-dimensional structure of schools of jack mackerel (*Trachurus japonicus*) and mackerel (*Scomber* sp.), determining nearest neighbour distances (1.43 body lengths (BL) and 1.51 BL respectively), individual fish size (20 cm and 14–23 cm respectively) and school density estimates (6.6–19.5/m³ for Jack Mackerel). More recently, Viscido et al. (2004) used two digital video cameras in a laboratory setting, combined with a calibration grid and video analysis software to determine the position and velocity of individual fish within small *Devario aequipinnatus* schools.

The capabilities of stereo techniques for researching aggregates have recently been extended even further by Ballerini et al. (2008) and Ballerini et al. (2008b), who used stereophotography combined with the trifocal technique (Hartley and Zisserman, 2003) and a variety of analysis techniques including statistical physics, image analysis and optimisation theory, to obtain data on the three-dimensional positions of individual European starlings (*S. vulgaris*) moving within flocks over time (for flocks of up to 8000 starlings). Using this technique they were able to obtain quantitative measures for a variety of aggregate properties of starling flocks, as well as properties of individual starlings within these flocks. With respect to aggregate properties, they found that, for the starling flocks they analysed, flocks had a typical shape (thin and long), distinct from size of flock and that flock density was not uniform, but instead was most dense on the periphery of the flock. With respect to individual properties, they found that individuals moved throughout the flock, rather than maintaining a single position within the flock. Using some data extrapolation techniques they have also proposed Ballerini et al. (2008) that individuals within the flock use a number of nearest neighbours to determine their position within the flock, rather than considering all of the starlings within a certain area of three-dimensional space.

3.5. Limitations: technological and theoretical

Some of the research projects discussed here—in particular those by Ballerini et al. (2008b)—have only recently become technologically feasible. Technological limitations, however, are only one of the barriers that stand in the way of creating validatable aggregation models, and cannot fully explain the relative lack of models of naturally occurring aggregate behaviours. It is argued in this paper that another barrier is the use of the AR framework, as used to describe and explain aggregate behaviour. One of the strengths of the AR framework from a theoretical perspective is its abstraction of the perceptual underpinnings of aggregate behaviour. However, this same abstraction means that the AR framework does not easily lend itself to the creation of verifiable models of aggregation. This is because its physics-centred characterisation of attractive and repulsive forces and its relatively simplistic representation of animal properties make it difficult to connect it to species-specific behaviour. It is further argued that in order for the AR framework to take advantage of technological advancements, it needs to return to a consideration of the percep-

tual and other biological underpinnings of aggregate behaviour as investigated by Parr (1927), Partridge and Pitcher (1980), and other researchers discussed in the following section.

4. Perceptual underpinnings of aggregate behaviour

4.1. The role of sensory abilities

Parr (1927) showed, in a very general way, that animals rely on particular sensory abilities to receive and process attractive and repulsive stimuli and thereby maintain their positions within aggregates. He demonstrated this aspect of aggregation by temporarily blinding a number of chub mackerel (*Scombrus colias*) using lampblack, and then returning these fish to the aquarium containing their original school. He observed that, while blinded, these fish remained isolated in the aquarium. Upon regaining their vision, however, they returned to their school and exhibited typical schooling behaviour once again. Parr concluded from this experiment that animals process information from particular senses when forming aggregates. He further noted that different species may rely on different sensory abilities to achieve aggregation.

The importance of specific types of sensation to aggregation has been further supported by more recent experiments that show that fish and other marine animals rely most specifically on visual perception and lateral lines for schooling. Partridge and Pitcher (1980), for example, showed that saithe (*Pollachius virens*) with intact lateral lines but without vision could maintain their position in a school, as long as the school did not suddenly dissolve and reform as the result of a startle reaction. Fish with intact vision and no lateral lines could also school, but their position in relation to other fish in the school was affected by the loss of their lateral line perceptions.

The possible role of other perceptions in fish schooling has also been investigated. Hemmings (1966), for example, investigated the attraction of the roach fish (*Rutilus rutilus*) to visual cues vs. odour cues. He found that, while roach were attracted both to the odour of other healthy roach in the water and to the physical (visual only) presence of other roach, they were more strongly attracted to the visual cues. Hemmings also showed that roaches were repelled by the odour of injured roaches.

Perceptual requirements for the reception of species-specific appropriate attraction and repulsion stimuli have also been investigated. Buskey (2000), for example, investigated the visual acuity of the mysid (*Mysidium columbiae*), a small aggregating crustacean, by having the mysids follow line patterns on a rotating drum, which they did without training. Buskey found that the majority of the mysids swam in the direction of the drum when stripes were 4 mm or larger in width, but that this number dropped as the width dropped until, at under 1 mm the percentage following the drum dropped to less than 60% of the school, suggesting that at this point the visual acuity or resolution of the mysids was insufficient to allow for aggregating behaviour. Buskey concluded that this level of visual acuity was consistent with the survival requirements of the mysids, who had to follow other members of their aggregate at distances within the range of their visual acuity (as measured by the experiment) and also use their vision to locate tree roots of a certain minimum size for concealment from predators.

In some respects it seems almost trivial to acknowledge that animals use their sensory and perceptual abilities to aggregate since, aside from scientifically unsupported theories involving mental telepathy (Selous, 1931, as cited in Heppner, 1997) there are no other apparent aggregation mechanisms available to animals. This may explain the relative dearth of research into the precise role of sensation and perception mechanisms in aggregation. Researchers simply assume that aggregating animals are using one or more of their senses to aggregate and are able to attend to and integrate various sensory inputs in an appropriate manner.

However, what is remarkable, in this context, is the fact that such a wide variety of animals, with a correspondingly wide variety of sensory and perceptual mechanisms, successfully aggregate. For example, although the sensory and perceptual mechanisms of Natterer's bats (*Myotis nattereri*) and guppies (*Poecilia reticulata*) differ quite widely, both of these animals form aggregates (Rivers et al., 2006; Godin et al., 2003). One of the challenges that remain for animal aggregate researchers is to determine how each of these diverse species use their particular perceptual abilities to form and maintain their aggregations, and then to produce models that reflect this diversity and enable an exploration of its evolutionary underpinnings.

5. A review of aggregation models and their findings

There are two main types of models that consider questions relating to aggregate behaviour: models that are mathematical in nature, and individually based spatially explicit models (IBSEMs). IBSEMs are written as computer programs and have individual agents applying particular rules to determine how the aggregate as a whole will behave. Mathematical models of aggregation frequently consider more fundamental aggregate questions (e.g., what are the minimum requirements for the existence of coordinated movement) while IBSEMs frequently consider how varying the values of a particular parameter of interest (e.g., the values of attraction and repulsion) can influence the behaviour of an aggregate. IBSEMs are also frequently interested in the contribution the behaviours of individuals make to aggregate behaviour and are more likely to make claims about the behaviours of particular animals and how they aggregate. Both types of models will be discussed in this section.

5.1. A renewed interest in animal aggregation models

Starting in the early 1990s, particle physicists looking for a new area in which to apply some of their modelling knowledge began to create models of animal aggregates by extending their existing particle physics models (see Section 5.2 for a detailed discussion of these models). At approximately the same time, computer scientists working in the field of distributed artificial intelligence began to develop modelling techniques, now referred to as multi-agent simulations (MAS), that would allow them to understand how individuals work together to produce group behaviours (Bond and Gasser, 1988) (see Section 5.3 for a detailed discussion of these models). MAS modelling techniques were quickly adopted by biological researchers (in particular, ecologists and biologists studying population dynamics), who refer to these types of models as individually based, spatially explicit models (IBSEMs) or sometimes simply as individually based models (IBMs) (see Wiegand et al. (2004) for a discussion of the role of IBSEMs in biology).

The IBSEM modelling methodology is particularly promising for animal aggregate researchers because it allows researchers to methodically change the behaviours of individuals within an aggregate model and observe how these changes affect the movement patterns of the aggregate as a whole. This, in turn, affords aggregate researchers greater insight into the ways in which the behaviours of individuals within an aggregate generate particular aggregate behaviours. It is also much easier in IBSEMs to introduce heterogeneous agents into an aggregate model and investigate the effects of this heterogeneity on aggregate behaviour.

In these respects, IBSEMs differ from traditional mathematical models of aggregation, which frequently avoid individual-level description and focus instead on describing aggregate behaviour using global variables like aggregate density or average aggregate velocity. These models then analyse the change in these variables

over time using differential equations (see, for example, Flierl et al., 1999; Lutscher, 2003). Mathematical models take this approach because their focus is on finding general solutions to aggregate equations for all values of variables. Consequently, most of these mathematical models of aggregates, whether developed by biologists or physicists, are not intended to reflect the behaviour of a particular aggregating species. Instead, their goal is to explore aggregation behaviour more generally.

Researchers using IBSEMs, however, often do wish to claim that their models are predictive or explanatory of either the behaviour of a specific species (e.g., locusts (*Schistocerca gregaria*), (Buhl et al., 2006)) or, more often, a group of species (e.g., schooling fish (Parrish et al., 2002) or ungulates (Turner et al., 1993)). Thus it is important to consider the means by which these IBSEM modellers validate these claims—an issue which will be taken up in detail in Section 6.

5.2. Findings of mathematical models

Vicsek, Czirók and others (Vicsek et al., 1995; Czirók et al., 1997; Czirók and Vicsek, 2000) motivated a renewed interest in aggregate modelling by mathematically describing and exploring the behaviour of what they called interacting self-propelled particles. These were zero mass particles that moved with a constant velocity and set their own alignment based on the alignment of local neighbours (where what constitutes a local neighbour is determined by some chosen function, S). Czirók and Vicsek (2000) give two examples of S , one a circle with radius r , and another a number of nearest neighbours on a lattice. A noise function was also introduced in the model, so that particles could not align perfectly, and equations were developed that connected alignment to particle density. Czirók and Vicsek found that, even in this simple model, aligned moving clumps of self propelled particles formed for some values of particle density and noise.

Considering aggregate movement, Toner and Tu (1998), motivated by Vicsek et al. (1995), used a mathematical model to investigate how aggregates that begin without cohesive movement in a particular direction are able to break this symmetry and begin moving in a particular direction. They found that over time high and low density fluctuations build up within the aggregate, which in turn lead to a spontaneous breaking of symmetry and group movement in a particular direction. Aldana and Huepe (2003) also considered an extension of Vicsek's simple particle model, where particles could interact via direct random connections instead of only local connections. They referred to this variant as a vectorial network model. They found that even when interactions were determined randomly (analogous to moving at infinite velocity), there were still transitions between ordered and disordered states simply as a result of there being long-range interactions of some kind.

Building on these more general findings, a variety of mathematical models explored the implications of varying attraction and repulsion equations and coefficients for aggregate behaviour. Grégoire et al. (2003) developed a model that was an extension of Vicsek et al.'s (1995) simple particle model by adding attraction and repulsion forces (described as body forces) in addition to the original alignment force. They added weights to the alignment, attraction and repulsion parts of their equations and found that, depending on the strength of the alignment force as compared to the attraction and repulsion force, the aggregate moved through phases which they compared to the gas, liquid and solid phases of a physical material. For weak body forces, the aggregate did not remain cohesive and was in a gas-like state. For stronger body forces, the aggregate behaved in a manner analogous to a liquid or solid. Strength of the alignment forces then determined whether or not this liquid/solid was stationary or moved through space.

Also investigating the formation of aggregates, Lutscher (2003) used a mathematical, one-dimensional AR model to analyse how attraction and repulsion could lead to grouping of individuals over time when the model began in a homogeneous state. Agent influence was local and a variable was included in the model equations to represent a 'radius of perception', which served to limit the influence of group density on the individual. Lutscher found that this AR model could produce both stable and unstable states, depending on how individuals reacted to a departure from their preferred density in the surrounding area, and that areas of high and low density could emerge from homogeneous states.

Modelling attraction and repulsion forces explicitly, and also using a one-dimensional model (but mathematically extending their findings into higher dimensions) Mogilner et al. (2003) explored how changing values of A and R (the strength of attraction and repulsion force in these areas) along with values of a and r (the radius of attraction and repulsion) affected the structure and cohesion of an aggregate. In this model, agents could be influenced by all individuals in the group, but the farther an individual was from an agent, the less their influence on the agent was. Mogilner et al. found that in order for well spaced, globally stable aggregation to occur, it was necessary that the force of attraction be weaker than the force of repulsion, and the range of attraction had to be greater than the range of repulsion, although this was not also sufficient for aggregation in all circumstances. They also found that the distance between individuals within a stable group was smaller than that of the preferred distance of an individual with respect to other individuals.

Addressing factors influencing aggregate level alignment, in an extension of an earlier model by Grünbaum (1999), Adiou et al. (2003) and Adiou et al. (2003) considered the effect of individual alignment and diffusion with respect to aggregate behaviour, with the alignment of an individual defined as the angle between a head-to-tail vector representing individual orientation and a pre-defined reference vector, and alignment of the group measured with reference to the portion of individuals within a chosen unit volume that had a particular orientation. Their models incorporated an approximation of attraction and repulsion (what they refer to as an orientation analogue of attraction and repulsion) by assuming that fish would turn left or right depending on where the majority of other individuals already in the group were pointing, but that this would be offset by a Fickian dispersion mechanism. They found that the extent to which the aggregate as a whole aligned depended on the ratio between the diffusion force and individual alignment tendencies, in that the ability of the aggregate to align depended on a certain minimum ratio of alignment and diffusion and that as the ratio increased aggregate alignment also increased, and time required to align decreased.

Yates et al. (2009) investigated the role of noise in the creation of coherent collective swarm motion. A self-propelled particle model adapted from Czirók et al. (1999) was used to model the collective motion of a swarm of aggregating animals focusing specifically on the directional switching property of the swarm. The study concluded that loss of coherence results in an individual increasing randomness of its motion until alignment is once again achieved. While closed form solutions for average velocity were not derived, the authors hypothesized their existence and use computer-based approximations and modelling to justify this. Model behaviour was supported and informed by experimental locust (*S. gregaria*) nymph behaviour data, with very good agreement between mean switching time and number of locusts in the swarm.

Thus the general finding of these mathematical models was that the behaviour of an aggregate—in particular its level of alignment and cohesion—can be significantly altered by altering the weights and equations associated with individual attraction, repulsion and alignment behaviours. Specifically, by altering attraction

and repulsion equations, the behaviour of the group may range from disordered and stationary, to aligned and moving through space, to remaining in an ordered but stationary state. This suggests that, within a particular aggregating group of animals, members of the group may control behaviour at the aggregate level by varying their individual attraction and repulsion behaviours in a coordinated manner.

However, as can be seen from the research presented here, the representations of animals in these models are highly abstract (often represented in one-dimensional models as zero dimension points moving along a line), and the findings of these models are also abstract. Thus, although findings of these models are relevant with respect to what is possible in aggregates at a theoretical level, it is not clear how these findings relate to, or can be directly validated by, actual aggregate behaviour because representations of aggregating animals in these models are so simplified that it is very difficult to relate them clearly and directly to actual animals. Part of the reason for this simplification is that mathematical equations quickly become intractable when significant abstractions are not made. Computer-based models that represent individuals directly, avoid this problem to some extent by simplifying and increasing the number of equations involved and then transferring the increased computational load to the computer. These types of models will be discussed in the next section.

5.3. Findings of individually based, spatial explicit computer models (IBSEMs)

To some extent, IBSEMs are automatically less abstract than mathematical models because they are composed of multiple discrete agent objects that each follow assigned rules based on their internal states and the state of the simulated environment. As a result of this representation of individuals, there is a subtle shift away from viewing agents merely as objects upon which social forces act, towards viewing them as actors that react to their environment (although the term *social forces* is still generally used to describe attraction and repulsion). As a result, there is a more tangible connection between the agent and the animal and the agent rules and the behaviour of the animal. As well, because IBSEMs represent individual animals explicitly, IBSEMs can more clearly examine how measurable individual properties, behaviours and interactions with the environment contribute to group properties, with a focus on exploring the parameter space of the model to establish cause-and-effect relationships between individual and group properties.

Generally speaking, in aggregate IBSEMs, all agents follow the same assigned rules, but the specific instantiation of these general rules depends on the situation of the agent at time t . As well, for each agent, different rules often operate on different areas or volumes of space, relative to the position of the agent, with modellers referring to these areas or volumes of space as zones, ranges or areas (see, for example, Couzin et al., 2002; Huth and Wissel, 1992, see also Fig. 2). Within this general format, IBSEMs may be two or three-dimensional. They may also be entirely abstract models, like the mathematical models discussed above, or models that incorporate experimental data and model specific aggregating species. All of these model types will be discussed below.

5.3.1. Abstract computer models, two-dimensional

Two-dimensional models assume that some aspects of aggregate behaviour can be accurately modelled on a two-dimensional plane. This seems particularly plausible for aggregates like ungulate herds, fish swimming in shallow water and insects moving on the surface of land or water. However, like the mathematical models discussed in Section 5.2, many two-dimensional models are not created in order to derive particular conclusions about spe-

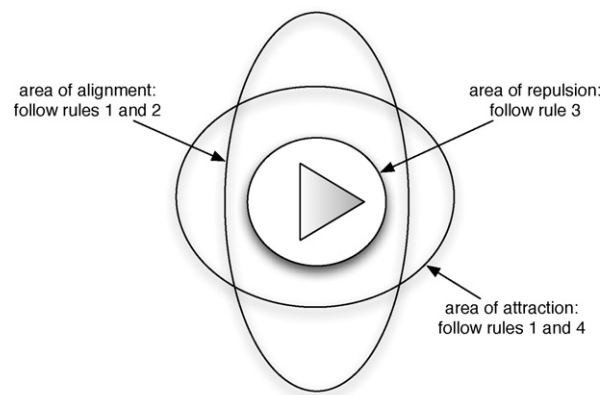


Fig. 2. Individual rules, operating with particular zones of behaviour.

cific aggregates but instead are created to derive more general conclusions about aggregate mechanics. An early two-dimensional simulation model created by Aoki (1982), for example, explores in a very general manner how unified group movements can occur even in the absence of a specific leader or global knowledge of the group by individuals within the group. Multiple combinations of model parameter values were run for the model in order to explore the parameter space of the model, with the finding that model results were consistent across changes in group size but that changing behavioural rules (e.g., removing agents' alignment rule) resulted in changed movement patterns for the aggregate as a whole.

Warburton and Lazarus (1991) used a two-dimensional model of between 2 and 9 agents to consider how attractive and repulsive forces of individuals in the model lead to common inter-individual distance in the group and group stability. By varying parameters associated with attraction and repulsion equations they were able to determine that the shape of these equations (i.e., linear, inverse sigmoid, convex, concave) influenced the average inter-individual distance in the group and that for 4 of the 8 functions considered, similar to findings by Mogilner et al. (2003), actual inter-individual distance was smaller than the preferred distance used by individuals. They also considered how the number of nearest neighbours influenced by an individual might interact with the social force equations. In this model, group size was small and all agents could be influenced by all other agents but did not necessarily use information about all agents when determining movement. They found that only a single influential neighbour was required for aggregate cohesion under some circumstances—specifically when there was no random vector (referred to as a 'searching vector') included in the movement rules—but that when the searching vector was included a minimum number of neighbours that was close to half the group size was required for group cohesion.

Huth and Wissel (1992) also considered how aggregation is influenced by the decision rules that individual agents use to react to the location of other local agents. In particular, they considered how different turning angle algorithms influence aggregation by analysing the effects when a fish agent either determined its turning angle by considering a particular number of its neighbours but then responding only to the 'best' one, as defined by its angle from the front of the agent (the D-model) or took all neighbours into account in determining its response (the A-model). They found that averaging across all neighbours (the A-model) led to a faster moving, more aligned group (although both groups remained cohesive) as measured by the expanse of the aggregate. Reducing the maximum turning angle improved the behaviour of the D-models. Huth and Wissel also varied the radius of the areas of attraction, repulsion and orientation in order to evaluate their effects on model behaviour and found that the larger the orientation range, the more

aligned but less cohesive the aggregate. It is interesting to note that in the process they state that these areas represent “sense capabilities” and suggest that they vary for different species.

Considering aggregation in a larger environmental context, Zheng et al. (2005) investigated how the presence of predators might affect the behaviour of individual fish in schools, and how this, in turn might affect the behaviour of the entire aggregate. They modelled this by varying the behaviour rules fish agents chose to follow when they received information about a predator. In some cases the fish agent responded only to the predator, while in other cases the fish agent also took into consideration the presence of the other fish in the aggregate when deciding how to move. They found that optimum predator evasion occurred when fish divided their behaviour between schooling and evasion, and when they had some tolerance for the presence of the predator, rather than immediately switching to an evasion behaviour.

Romanczuk et al. (2009) proposed a simple model of Brownian particles with interactions moderated by pursuit and escape motivations in order to explore the effect of these motivations on group movement patterns. The model was characterized by physical and social forces and could be described as being of the attractive-repulsive class. The authors derived results for stationary velocity for particle pairs for their abstract self-propelled particle model and reported excellent agreement with numerical simulation results across a wide range of parameter values. They noted that their model and results were consistent with recent results from Bazazi et al. (2008) concerning marching insects and their flight from predators, although they further noted this to be an open question. The model proposed predicts phase transition behaviour that is consistent with the results of Buhl et al. (2006). This model represents a starting point for more realistic theoretical models with the kind of zonal considerations found (for example) in Edelstein-Keshet et al. (2000)

5.3.2. Abstract computer models, three-dimensional

Three-dimensional models offer researchers the chance to incorporate more realistic physical interactions and movement rules into models, particularly for animals like birds, fish and flying insects, which can move in three-dimensions. Parrish et al. (2002) used a three-dimensional model to consider how varying attraction and repulsion rules, as well as movement algorithms, influenced fish aggregate behaviour. They based several of their modelling parameters (e.g., fish speed and acceleration, fish visual blind spots) on qualitative fish movement and physiology data—in particular from giant danio (*Danio aequipinatus*) behaviour—making the model more explicitly grounded from an empirical perspective. Similarly to Warburton and Lazarus (1991), they found that varying attraction and repulsion equations caused corresponding variability across most aggregate measures, with the exception of aggregate alignment. They also found that the number of neighbours, and scaling functions applied to neighbour influence, affected size and cohesion of the aggregate, as well as polarity and speed of the group.

Viscido et al. (2005, 2007) used a similar three-dimensional model to consider how population size and number of nearest neighbours used by individuals to determine movement could influence aggregate properties Viscido et al. (2005) and how the functional form of a variety of forces applied to the individual (social forces including alignment, attraction, repulsion and neighbour influence, as well as random forces and frictional forces) affected aggregate behaviour Viscido et al. (2007). They found that group properties are influenced by overall size of population and number of neighbours considered by individuals, and that, in general, all forces, with the exception of the random force, significantly influence aggregate behaviour. They also found specific patterns of influence for specific force forms. For example, they determined

(similar to the results of Mogilner et al. (2003)) that a strong repulsion force was required for aggregation to occur and also that speed of motion, weighting of neighbours considered, and alignment impulses influenced both aggregate structure and the ability of the aggregate to maintain structure over time.

Eriksson et al. (2010), in their three-dimensional particle model, proposed a method for determining local interaction rules in swarms, their hypothesis being that individual behaviour can be treated as a set of rules. The methodology used to induce rule descriptions was to vary model parameters and minimize deviations between the observed swarm (in this case also simulated, due to a lack of available field data) and modelled movements. Their agent-based framework used a force matching model adapted from the domain of complex molecular simulations (Noid et al., 2008) to generate agent trajectory data. Two hypotheses for interaction rules were investigated: geometric and topological. In the geometric hypothesis, agents within the swarm based their movement decisions on relative positions and velocities. In the topological hypothesis, agents used a fixed number of nearest neighbours to support coherent swarm movement. Their results indicated that only by simultaneously fitting all forces can these competing hypotheses be separated. However, the authors acknowledged the difficulties associated with making high fidelity observational measurements and concluded that it is unclear how well the method “handles the natural variability found in biological systems” (p. 1110). This behavioural variability may also be related to environment factors; however, the authors do not comment on this issue.

In general, abstract IBSEM models of aggregates have been able to explicitly explore the behaviour of the aggregate with respect to how individual behaviours lead to group behaviours, with an emphasis on how particular attraction and repulsion rules of individuals determine model behaviour across parameter sets. Abstract IBSEM models have also been able to draw more detailed conclusions about the effects of different movement rules on aggregation—rules which are relatively straightforward to define and change in IBSEM models. However, with some exceptions they are generally unconcerned with relating their findings directly or concretely to actual animal aggregates, and their representations of the sensory and perceptive aspects of aggregation (e.g., integration of information from multiple sources, shifting attention) are restricted to representing either the presence or absence of information.

5.3.3. Models incorporating more concretely observable properties of individuals

All of the models discussed to this point consider how either unobservable abstractions of individual properties (attraction and repulsion forces) or difficult to observe individual properties (behavioural or cognitive reaction algorithms for responding to observed individuals) might influence aggregate behaviour. Many fewer models discuss results that relate more directly to observable animal properties (e.g., body size, movement capabilities or perceptual abilities). However, as computer simulations have become more sophisticated, a number of IBSEMs have been produced that attempt to determine how some of these observable properties influence aggregation. These models, in order to answer questions relating to physical properties of animals, have started to include more physically realistic perception and movement rules, as well as more realistic, fully embodied agents.

With respect to agent embodiment, Reynolds (1987) was arguably the first to create fully embodied aggregating agents, with multi-component, articulated three-dimensional bodies. However, his simulation was intended for animation rather than research. With respect to research on the behaviour of embodied agents in an aggregate, Brogan and Hodgins (1997) created an aggregate

model consisting of two groups of dynamically simulated, physically realised agents. They replicated one legged robots and bicycle riders, along with a control group consisting of point mass agents, in order to study agents with different dynamic movement properties (physically simulating both the bicycle and the rider). They used this model to explore how movement dynamics influence aggregate behaviour. Agents considered their n nearest neighbours when calculating movement (with n varying between 1/3 and all of the group) and attempted to move to a position based on the weighted location of these neighbours (with movement being influenced by body dynamics). Brogan and Hodgins found that the point mass version of the model was most successful at moving tightly together while avoiding obstacles, the one-legged robot group required more spacing between individuals to avoid collision and the bicycles had a difficult time avoiding collisions when turning.

In terms of being embodied in the sense of responding to environmental conditions in a physically realistic manner, Flierl et al. (1999) used a combined mathematical and individual-based approach to examine how social aggregate forces interact with environmental factors to influence aggregate behaviour of aquatic organisms. They began by considering what aggregate effects can arise simply as a result of environmental conditions and then added social forces to the model to consider how these would interact with the environmental conditions being modelled (e.g. turbulence). With respect to these later models they found that although high amounts of turbulence can impede aggregation, low amounts of turbulence can enhance aggregation by providing more opportunities for agents to encounter each other, at which point social forces lead to the formation of aggregates.

Couzin et al. (2002) considered, in a three-dimensional point-agent model, how two observable properties of individuals—turning rate and speed—influence aggregate behaviour, along with the influence of the spatial range over which agents receive information and population size. Their model included heterogeneity across these variables to reflect heterogeneity in actual populations. They found that aggregate properties were influenced by attraction and repulsion values, neighbour selection and movement algorithms. With respect to movement algorithms they varied speed and turning rate among individuals within the aggregate and determined that faster individuals remained within the aggregate but moved to the front of the aggregate. Individuals with a higher turning rate, however, tended to be positioned nearer to the centre of the group.

Viscido et al. (2002) considered how the manner in which agents decide to move, based on the information available to them, influences aggregate behaviour. They consider 4 different movement rules—random movement, simple nearest neighbour (similar to the decision rule considered by Huth and Wissel (1992)) a Hamiltonian rule (which required agents to consider their nearest neighbour and the nearest neighbour of their nearest neighbour) and a collection of rules which they refer to as the Local Crowded Horizon rule. Although most of these rules refer to cognitive variables, this last rule could be considered to be a perceptual rule. For the Local Crowded Horizon movement rule, the influence of other agents was mediated by what they refer to as a ‘perception function’, so that animals farther away have less influence on the behaviour of the animal, because they are smaller and harder to see. They tested 6 different variants of this perception function to see how it influenced aggregate behaviour. In their conclusions they note that changing the perceptual function strongly influenced the behaviour of the aggregate, as did the other movement rules, and that all rules produced results that differed statistically significantly from each other, based on the aggregate measures used.

Also relating to animal perception, Ward et al. (2001) developed a two-dimensional evolving aggregate model using artificial neu-

ral networks. In this model, agents detected other agents in two different regions of space, inspired by a distinction between the lateral line and visual perceptions of fish. Weights associated with each of these fields could change so that agents could choose which agent information to use in their movement rules (where agents included predators and food as well as other aggregating agents). Movement rules were simply ‘turn left’ or ‘turn right’, with constant speed. Predators and food (along with an energy measure) were introduced to the modelling environment to provide selection pressure and model weights evolved over time. Ward et al. found that, although aggregation was not explicitly programmed into agents at the start of the simulation, with each successive generation prey agents moved closer together (with respect to average distance from other prey agents). They also showed, through an analysis of weights in the neural nets of individual agents, that agents valued staying close (schooling) more than eating, and that the field based on vision was used to turn towards food while the field based on the lateral line was used to avoid predators.

Kunz and Hemelrijk (2003) constructed a two-dimensional model that considered the effects of body size on aggregate behaviour. Fish were modelled as lines of two sizes (big and small), in addition to being modelled as points. Both vision and lateral line perceptions were explicitly modelled, and the shape of the area for which the fish received information was influenced by its body shape. The visual field for line agents was spherical, but the lateral line field was elliptical based on the argument that actual lateral line sensors would result in an elliptical information field. As well, attraction and repulsion equations were different for fish of different sizes, since larger fish would be expected to have longer lateral line fields. Kunz and Hemelrijk found that larger agents had larger inter-individual distances, that aggregate homogeneity was reduced when agent bodies were represented by lines rather than points, and that elliptical fields resulted in more frequent turning by agents within the aggregate and smaller aggregates over all.

Hemelrijk and Hildenbrandt (2008) followed this two-dimensional model with a three-dimensional model created specifically in order to take into account criticisms, like those by Parrish and Viscido (2005), that some of the movement and perceptual rules used in the earlier model (Kunz and Hemelrijk, 2003) were unrealistic, in addition to school size being too small. In this model, agents moved through a three-dimensional space at a preferred speed, but could change this speed in response to information about neighbouring fish. Agents had a blind zone that represented the visual blind spot of actual fish. The range of agent detection was decreased as density increased, to take into account the fact that at higher densities some fish are occluded by other fish. Agents followed attraction and repulsion rules, with each rule operating only in a particular volume of space. Hemelrijk and Hildenbrandt found that model aggregates were oblong with a higher density at the front than the back of the school, a group phenomenon that occurred in the model as a result of individual agents avoiding collisions while at the same time trying to maintain desired distances between themselves and neighbouring agent.

5.4. Models of naturally occurring aggregation phenomena

There have been relatively few models of aggregation that have been created in order to investigate the behaviour of specific, naturally occurring aggregate systems, arguably due in part to the limitations of both technology and the AR framework. Nonetheless, some researchers have made considerable efforts to generate phenomenon-specific or species-specific models based at least in part on experimental data about their species of interest. As well, some modellers, although referring to their models in a more generic way (for example, as fish models) have based their model parameters on, or compared the behaviour of their model to, exper-

imental data gathered about the behaviour of specific aggregating species. Lastly, other models, while general enough to be easily applied to a variety of aggregating species, are species-specific in the sense that they have been created in order to provide their creators with insight into species-specific behaviours of interest. All three types of models will be reviewed in this section.

It is not uncommon for model creation to be motivated by observations of species-specific behaviour, but for the model itself to be a more general model of animal aggregation. A good example of this is the model by Hoare et al. (2004), which is motivated by the observed behaviour of banded killifish (*F. diaphanus*). Although the model itself is a generic aggregation model with no species-specific characteristics, Hoare et al. used it to further their understanding of the way in which interaction distance influenced the size of banded killifish aggregates under various circumstances. Similarly, a model (Stöcker, 1999) inspired by tuna behaviour, although not informed by experimental measures of tuna (*sp. Thunnus*) behaviour, allowed the researcher to gain an increased understanding of the way in which the energetics of school formation might influence maximum group size in fish, in order to better estimate tuna fish stocks.

In other cases, researchers wish to model a specific aggregate behaviour of a particular species and base at least one of their model parameters on experimental data gathered about either the individual behaviour or group behaviour of the species in question. Movement rates are relatively easily observed so this experimental data is most frequently incorporated. Dagorn and Freon (1999), for example, were motivated by the tendency of tuna (*sp. Thunnus*) to gather under floating objects (generically referred to as 'logs') to create a two-dimensional model of tuna aggregation in the presence of logs. Swimming speeds of tuna in the model (3.5 km/h) were based on experimental data and size of the model and position and frequency of logs were also based on experimental data. Several recent models of fish aggregation, already discussed in Section 5.3 (Parrish et al., 2002; Viscido et al., 2005, 2007), have also incorporated experimental data on fish movement of particular species in their models. Parrish et al. (2002) and Viscido et al. (2005, 2007) base the movement parameters (agent speed and agent velocity) for their agents on *Danio aequipinatus* movement gathered using Tracker 3D, a two camera tracking system (Grünbaum et al., 2005).

In other cases, the relevant experimental data is behavioural rather than movement based. In their two-dimensional cockroach larvae model, Jeanson et al. (2005) based probabilities of cockroach larvae (*Blatella germanica*) behaviour (stopping, starting moving after a collision, starting moving in the absence of a collision and exiting the aggregate) on detailed laboratory observations of cockroach larvae in a large circular arena. They found that chance encounters arising out of an initial uniform distribution of cockroach larvae led to eventual large scale aggregation as a result of a process of gradual cluster amplification. In other cases the behavioural data is more general. Two models of daphnia (*Daphnia* sp. behaviour (Mach and Schweitzer, 2007; Vollmer et al., 2006) based the behaviour of agents in their models on the known attraction of daphnia to light sources, along with experimental data gathered on movement abilities (self propulsion and movement rate) and possible avoidance behaviours of daphnia.

Investigating the behaviour of an abstract two-dimensional particle model, but then including a comparison of their model with the behaviour of cockroaches (*Blatella germanica*) interacting with robots, You et al. (2009) studied a swarm consisting of particles with two group types using a Langevin equation based attraction-repulsion model. This model demonstrated that spatial separation can occur between groups under certain critical conditions. Specifically, two results were included that showed one group circling outside of another and group separation with one group following another. Furthermore, analytical results were provided for several of the critical values (e.g., the self-propelling strength). The model

environment was then augmented to include different types of shelter objects that particles were attracted to, to varying degrees. The resulting behaviour of the model was compared to the results of an experiment examining the behaviour of cockroaches and robots in an environment with two types of shelters. As in the experiment, analysis of the model behaviour showed that altering the level of shelter attraction for one type of particle could result in a change in the shelter choice of the second type of particle, even when the behavioural parameters of the second particle type were not themselves altered.

Also considering a two-dimensional real-world aggregate system—surf scoter (*Melanitta perspicillata*) flocks sitting on water—Edelstein-Keshet et al. (2000) created an agent based model to investigate surf scoter flock cohesion, structure and synchronized behaviour. They supported the behaviour of this model using data gathered on surf scoter flock positioning, and set some of the model parameter values relating to the behaviour of individual agents using this data. The authors noted that zonal models have provided many insights into collective motion (e.g., dynamic switching between collective patterns and leadership effects on uninformed agents). The paper then used a zonal interaction model to fit the data obtained for the scoter flocks with results indicating that strong short-range repulsion, intermediate-range alignment and longer-range attraction (with circular zones) were associated with a weak, but significant, frontal sector interaction with a single neighbour. While this model was based upon attraction-repulsion principles, the more realistic sensory apparatus associated with the scoter agents generated very good agreement for angular and radial densities.

These models reveal that it is possible to base model parameters and agent behaviours on experimental data—an important step in the creation of models that can be connected to specific species, and a generally desirable feature of scientific models. At the same time, it is important to note that, although these models are at least to some extent created based on experimental data, models are much less frequently validated by experimental data—in particular, by comparing aggregate-level behaviour in the model with new experimental data. As well, models are rarely used to make predictions of novel behaviour within actual aggregates but instead tend to be used to explain existing behaviour. It is also worth noting that although movement and behaviour data are incorporated into these models, perceptual data is much less frequently incorporated into species-specific models. In those cases where it is considered at all, as in Parrish et al. (2002), perceptual data frequently relates to more general cross-species findings, and effects of perceptual factors specific to the particular species of interest are not explored.

Thus, although the models discussed in this section have increased researchers' awareness of what is possible with respect to aggregation, they have been less successful at answering questions about what is actually occurring in real world aggregates. In the next section methodological concerns regarding the AR framework will be discussed.

6. Methodological issues with the AR framework

6.1. Challenges validating AR models

Particularly with the introduction of IBSEMs, modellers more and more frequently wish to move away from making very general claims about the theoretical underpinnings of aggregate behaviour towards making more specific claims about how aggregation actual works in the context of specific biological systems (e.g., Viscido et al., 2005; Hemelrijk and Hildenbrandt, 2008; Gueron and Levin, 1993). However, some animal aggregate researchers (e.g., Parrish and Edelstein-Keshet, 1999; Rohani et al., 1997) have been criti-

cal of the idea that IBSEM aggregation models can be informative with respect to the behaviour of particular aggregating species or groups of species. Their scepticism is largely derived from the fact that a wide variety of behavioural rules can produce IBSEM models that exhibit aggregate behaviour. Putting this concern succinctly, (Parrish and Edelstein-Keshet, 1999, p. 101), state “[M]any sets of rules can lead to lifelike group behaviour, so that the results, though visually appealing, may be uninformative”. In other words, aggregation is a multiply realisable phenomenon. As a result, it is difficult to determine when an aggregate model truly reflects the behaviour of an aggregating species or when it does not but simply looks like it does. In order to successfully defend themselves against these criticisms, researchers must demonstrate that the models they produce are sufficiently constrained such that they are a match to the aggregate or aggregates of interest rather than to animal aggregation in a more general sense.

To address this criticism, researchers need to produce data-driven and experimentally verifiable models of animal aggregates. Generally speaking, in order for a model, IBSEM or otherwise, to be validated through experimental evidence, the component parts of the model must first be clearly and explicitly connected to the phenomenon of interest by gathering data relevant to the components of the model and creating these components according to this data, a posteriori, rather than constructing them prior to data collection. This connection between components and phenomenon constrains the design of the model so that the behaviour of the model cannot simply be adjusted in an *ad hoc* manner until it matches the behaviour of the phenomenon. As a result, the behaviour of the model can then also be compared with experimental evidence in order to validate the model. In the case of IBSEMs, which are focused on and driven by individual behaviour, this means that the model must be connected in some way to the phenomenon of interest at the level of the individual. If relevant properties of individuals in the model are clearly matched with relevant properties unique to the animal of interest, then the model will be constrained in such a way that it is provably a model of the specific phenomenon of interest, with emergent group level behaviour that is a legitimate reflection of the actual behaviour of the aggregate in question.

Connecting measurable individual properties to concepts in the AR framework is difficult, however. As discussed previously, the AR framework describes individuals in an aggregate as being acted on by social forces that cause them to be attracted to and repulsed by the individuals around them. Each individual's particular combination of reactions to these forces leads to the behaviour of the aggregate as a whole. Supplying the model with different attraction and repulsion rules—for example, changing the distances at which individuals begin and cease to be attracted or repulsed, or the number of agents it uses to calculate attraction and repulsion—can cause the aggregate as a whole to behave differently. As can be seen from this description, although the AR framework allows for the creation of individuals with detailed and specific attraction and repulsion rules, models created in the AR framework are not required to, and frequently do not, directly attribute to individuals in the model properties that are typically used when describing actual organisms: size, shape, colour, physical abilities, perceptual abilities, cognitive abilities, movement abilities. Instead, these properties are either ignored, incorporated abstractly into the attraction and repulsion equations or, in some of the more recent models mentioned in Section 3.3, incorporated into the model on top of the AR framework in some *ad hoc* manner. As a result, individuals in the AR framework are largely, if not entirely, defined by their position, their velocity and their attraction and repulsion equations. This minimal quality of the AR framework has its advantages when it comes to understanding the underpinnings of aggregation. However, it can cause problems when the framework must be applied to specific aggregating species. In particular, as has

already been stated, this lack of familiar, observable properties makes it difficult to successfully match, even in the presence of experimentally-derived data on individual properties, a particular theoretical model of aggregation with a particular aggregation in the wild.

To more clearly appreciate the problems, consider using a model constructed in the manner described above to predict the behaviour of a particular aggregate under changing environmental circumstances. For instance, suppose that the level of light in the environment of the aggregate were to change over time. In this case, how should the attraction and repulsion equations be changed? Should individuals react by becoming more attracted to individuals, or less attracted to them? Or should, instead, both attraction to and repulsion from other animals become a weaker influence on the behaviour of the individual? In general, it is unclear how the AR equations should be altered as the environment is changed. As a result, it is hard to use these models to make predictions about aggregate behaviour under changing environmental circumstances.

The lack of connection between the AR framework and known animal properties also becomes a problem when trying to use this methodology to model a heterogeneous aggregation of animals. It seems likely that in the case of a heterogeneous aggregation, different animals in the aggregation might have different attraction and repulsion behaviours, as a result of variability in the underlying mechanisms being used to carry out these behaviours (due, for example, to age, size, social position, health, energy level). One way to capture this heterogeneity using the described methodology might be to first derive average attraction and repulsion equations for individuals within the model and then to vary these attraction and repulsion equations for different individuals within the aggregate model. Unfortunately, it is not clear how the aggregation equations should be varied with respect to individual differences between actual animals within the aggregate. For example, should larger animals be more strongly attracted to other animals, or less? How should the attraction and repulsion equations reflect this? And what experimental evidence should the modeller use when making these decisions? Again, these issues are not as much of a concern when investigating aggregate behaviour in a very abstract sense. They become a problem, however, when trying to understand the behaviour of actual aggregates (e.g., the behaviour of herds of female caribou (*Rangifer tarandus*) with their calves (see Miller et al., 1972; Fancy, 1983; Harrington and Veitch, 1991)).

These problems may be overcome by incorporating into the model at least some properties of individual behaviour that are derived from observations of individuals, and which are clearly tied to properties and behaviours of the species of interest. Aggregate behaviours that result from these individual behaviours will then also be connected to the species of interest. However, this again raises the question of which aspects of the AR framework are directly observable. The main features of the AR framework—attractive and repulsive social forces—are not directly observable, because animals do not literally exert attractive and repulsive forces on each other. Other model elements (e.g., agent body shape, agent perception, agent movement) are also generally abstracted in order to increase the generalisability of the model. Consequently, tying AR models to specific natural aggregates is difficult at best.

Some researchers have already recognised that a more concrete and behaviourally detailed animal aggregate IBSEM modelling framework is required to improve the current modelling situation. Parrish et al. (2002) note, in the context of models of fish schooling, that the current inability of modellers to directly compare models and resolve conflicting model results might be remedied by the presence of a common fish school modelling framework. This point made by Parrish et al. in the context of fish schooling—that

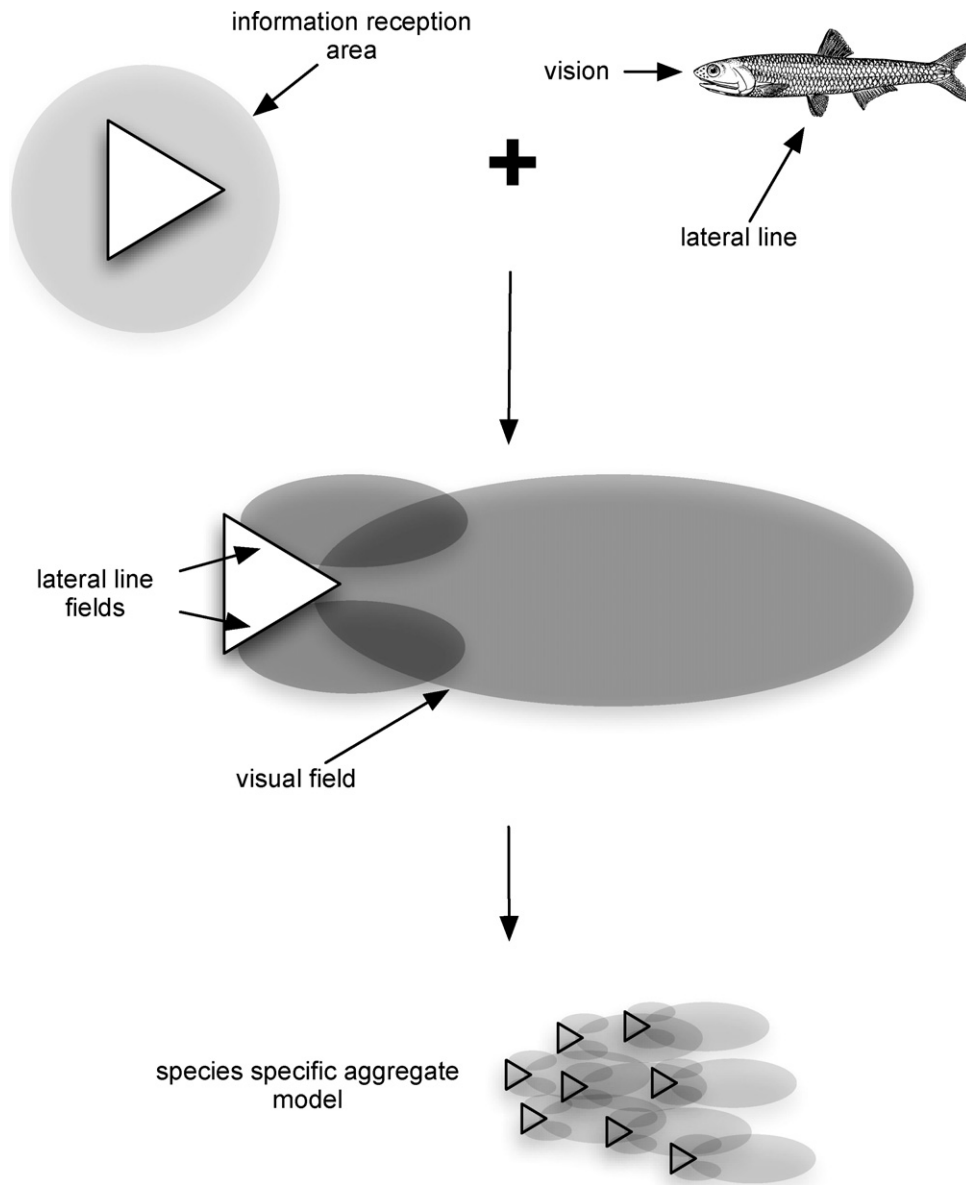


Fig. 3. Combining the concept of the information area with what is known about animal perception results in an experimentally validatable model of individual agents. This in turn allows modellers to create species-specific aggregation models. (Anchovy drawing in figure from (Pearson Scott Foresman, n.d.))

a common modelling framework is required to move research forward—is also applicable to animal aggregate modelling more generally. Ideally, this common framework would find ways to overcome the current difficulties that modellers in this area face when trying to connect their models to the behaviour of a particular aggregating species, in addition to allowing them to compare their resulting models with other aggregation models.

6.2. Updating the AR framework using the information processing paradigm

By acknowledging that agents do not have perfect knowledge of their surroundings, and restricting access to environmental information using an area or volume in which agents can receive information, aggregate modellers are implicitly recognising the key role of perception mediated information processing in aggregation.

Grünbaum and Okubo (1994), for example, describe Lagrangian models (i.e., individual based mathematical models) as typically incorporating what they refer to as a 'sensing range', which limits

the interactions between individuals (see, for example, Mogilner et al., 2003; Tu, 2000). Similarly, as discussed, Zheng et al. (2005), in their IBSEM model of the reaction of fish schools to attack by a predator, provide agents with what they term a 'visible area', outside of which the agent does not receive information about the environment. This is in keeping with the idea that actual senses and perceptual abilities are limited and imperfect (for further examples of this, see Aoki, 1982; Couzin et al., 2002).

Other researchers have made more explicit efforts to include sensation and perception in their models, in some cases modelling perception in a general sense (as in Viscido et al., 2002) while in other cases specifically referring to the sensory and perceptual abilities of a particular species (as in Ward et al., 2001). Most explicitly, (Hemelrijk, 2003; Hemelrijk and Hildenbrandt, 2008), in their models of fish schooling, refer to their agents as having a *range of perception*, and adjust the shape of what they refer to as the agents *behavioural zones* based on data about lateral line ranges of fish species. Viscido et al. (2005) also restrict the angle of the volume in which agents react to other agents to ± 150 degrees,

based on the fact that most fish have a rear blind spot. Thus, while in some models the role of perceptions and the types of information received by these perceptions are mentioned only in passing or are left unacknowledged altogether (e.g., [Adiou et al., 2003](#); [Toner and Tu, 1998](#)), in other models perception is clearly alluded to as being relevant.

There are a number of theoretical and experimental advantages to be had in making the implicit role of sensation and perception explicit, and clearly connecting the physical space in which model agents are able to receive information to the perceptual abilities and aggregating behaviours of the animal being modelled (see Fig. 3). First, and most importantly, perceptual, cognitive and movement abilities can be determined through the experimental study of the individual properties of animals (e.g. the average speed or turning radius of the individual, either in the context of its aggregate or in an isolated context), rather than properties of groups of animals (e.g. the density of the aggregate or the average space between members of the aggregate). This, in turn, allows for emergent group properties, rather than assumed group properties, and overcomes some of the difficulties discussed associated with model validation ([Schellinck, 2008](#)).

Secondly, animal behaviourists already have some understanding of how perceptions, cognition and movement are affected by the state of the environment and other properties of the individual (for example, how vision is affected by light levels ([Levenson and Schusterman, 1999](#)) or how visual acuity changes as an organism ages ([Schneck et al., 2004](#)). These effects may then be incorporated into models of aggregation and used to make predictions about the behaviour of actual animal aggregates in particular environmental conditions. The concept of perceptual fields also allows for a more concrete consideration of sensory information integration and the role of attention in aggregation.

Finally, since a perception-focused information processing framework is consistent with the AR framework, theoretical work may still be carried out using the AR framework. However, in instances where specific animals are involved, an information processing framework that takes into account the perceptual, cognitive and movement abilities of the animal being modelled can be used and data from animal behaviour research more directly incorporated into aggregation models. The connection between aggregate behaviour and observable animal properties will also serve to connect animal aggregation models more directly to experimental research on animal aggregation, as well as to the larger field of animal behaviour.

7. Conclusion

A wide variety of research is relevant to animal aggregation, due to its complex and difficult-to-observe nature. This paper has reviewed both the findings of aggregation models as well as key findings in aggregate research areas particularly relevant to the creation of validatable models of aggregation. The paper began with a discussion of experimental findings on aggregate properties, with an emphasis on the research methods that enabled these findings and continued its experimental review by considering experimental findings relevant to the role of perceptual abilities in aggregation. Mathematical and computer-based (simulation) models of aggregation were then considered, with attention focused on findings related to unobservable individual properties like attraction and repulsion, as well as more observable properties, like animal shape and speed. Lastly, aggregation models of specific species were reviewed, with attention to how these models were supported or verified using experimental results.

Although these models have increased researchers' awareness of what is possible with respect to aggregation, they have been less

successful at answering questions about what is occurring in natural aggregates. In particular, they do not answer questions about the mechanisms that specific species are using to aggregate, or why some aggregate-level phenomena are similar in widely differing species, while other aggregate-level phenomena can vary widely, even within the same species, from moment to moment. When considering this issue it must be recognized that aggregation is not an automatic phenomenon, nor one that is uniform across species. Species aggregate in species-specific ways, driven by species-specific mechanisms. To capture this diversity of behaviour and begin to move away from simply understanding the basis of aggregation, aggregates need to be modelled in ways that pay attention to the unique characteristics and aggregating mechanisms of the individuals within the aggregate.

At the core of many aggregation models are the concepts of attractive and repulsive forces, which are analogies for physical processes taking place inside aggregating animals. This presents problems for aggregate researchers who are trying to make validatable models, because the concepts of simple attractive and repulsive forces cannot easily be matched with the biological properties of individual animals. This, in turn, does not allow for verification of models using experimental data, particularly with respect to predictions concerning novel environmental circumstances. Thus, although theoretical aggregation models created with the AR framework may increase the level of understanding of basic aggregation concepts and requirements for aggregation, these models will have difficulty explaining how individuals from particular species interact to form aggregates, or why these aggregates have group-level properties that differ from the aggregates of other species. In order to create validatable aggregation models, researchers need to incorporate properties that clearly differentiate animals with respect to how they are aggregating.

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