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Introduction – From individuals to aggregations: Unifying properties, global framework, and the holy grails of congregation

JULIA K. PARRISH, WILLIAM M. HAMNER,
AND CHARLES T. PREWITT

1.1 Seeing is believing

An aggregation of anything against a background of sameness captures our eye. Congregations of creatures that routinely swarm and cluster or crowd together capture our imagination and generate new descriptive, often florid, collective terms for groups of living things; descriptors that are species-specific and etymologically precise (see Lipton’s “Exaltation of Larks,” 1991). A swarm of bees, a host of sparrows, and a smack of jellyfish generate crisp images in our mind’s eye, while a cloud of goats, a gaggle of flies, and a pod of parrots only generate confusion. There is no collective term in the English language for this wealth of collective adjectives (Lipton 1991), other than terms of “venery” (from the Latin *venari*, to hunt game), words that initially described aggregations of game animals, clustered conveniently for the huntsman.

Some of these terms denote protean behavioral displays that are visually compulsive. However, when our congregations of creatures are behaviorally coordinated in space and time, synchronously moving and wheeling and twisting before us in three-dimensional space, as in a school of smelt or a flock of phalaropes, they subvert our visual ability to focus on an individual animal and, somehow, suddenly the sum of the parts becomes a cohesive whole. Those of us who are terminally entranced with the three-dimensional, hypnotic beauty of synchronized flocks of birds and schools of fish quite simply cannot be cured. We know there is order within these three-dimensional displays, but it is not immediately obvious how to quantify it.

Schools of fish have fascinated evolutionary biologists for many years (Williams 1964) because the individuals in the aggregation do not appear to act selfishly at all; rather they seem to behave and interact as if for the benefit of the school as a whole. Indeed, if the individuals within a school did not look and behave similarly, then one of the primary antipredatory advantages associated with

schooling, anonymity within the aggregation, could not exist. Odd animals are eaten first; however, this does not necessarily mean the dissolution of group structure as all individuals fight to gain access to the best locations (Krause 1994). Natural selection has produced behavioral patterns which emphasize similarity and uniformity within the group, such that coherence and cohesion are hallmarks of many types of animal congregation. It is this tension between survivorship of the individual within the protection of the school and the constraints imposed by living within a group that poses an evolutionary paradox that still has not been resolved. Collective behavior is illustrative of one of the central philosophical issues of biology in particular and science in general, i.e. the issue of individuality, the dichotomy between the sum of the parts and the whole.

1.2 Defining a framework

1.2.1. The phenomena of aggregation

Aggregation is a pervasive phenomenon. At the most basic level, an aggregation is a collection of parts or units which form some coherent, often cohesive, whole. Molecules aggregate to form the basic building blocks of matter and substance as we know them. Inanimate objects of all shapes and sizes aggregate to form the familiar landscape within which we live. Beaches are made of aggregations of sand grains or cobblestones, glaciers are made up of compacted aggregations of snowflakes, planets are aggregated into solar systems, and solar systems are aggregated into galaxies. In many cases, inanimate objects are not only aggregated, but sorted along some set of physical gradients. Adjacent sand grains on a beach are apt to be the same size, having been sorted by the physical force of wave action. But beach material is not all the same size. Thus, a beach contains a gradient of grain sizes instead of a random assemblage of sand, pea gravel, and cobble. Furthermore, the sand on a given beach is likely to be predominantly of a single type. Pink sand beaches in Bermuda are made mostly from coral growing in the adjacent reef, whereas black sand beaches in Hawaii are made from the locally abundant volcanic rock. Both physical sorting and local abundance of source material create nonrandom aggregations which then may be arranged into repetitive patterns. Sand on a dune may be arranged by density and size, but dunes are also repetitively arrayed along a beach. However, aggregation is not only passive sorting. Many objects actively aggregate, such that like materials attract, while foreign materials are repelled. Atoms and molecules are both attracted and repulsed, resulting in cohesion into liquids or solids within which the individual units are held at some minimum distance.

Human societies have all adopted the phenomenon of arranged, or ordered, aggregation as basic to living. We build a brick wall one ordered row at a time

instead of in haphazard arrangements. Engineers and architects instruct us about the structural and aesthetic properties of ordered arrangements designed to make our surroundings both functional and pleasing to the eye. Many of us sort silverware by type: knives with knives and forks with forks. Commuters in automobiles follow each other in columns determined by the locations of roads and freeways, attracted to their ultimate destinations, but repelled from each other for fear of having an accident (not always successful). In short, ordered arrangements of like objects surround us comfortably, as a consequence of our actions.

1.2.2 Animate aggregations

Most of the aggregation that surrounds us, both inanimate and animate, is arrayed in three dimensions, and some of it contains a fourth dimension, time, as well. Like the physical world, animate aggregations and patterns within them can be the result of sorting by physical forces. Assemblages of plants are often found in discrete locations, not only based on where they can grow, but also on where the seeds were carried (Forcell & Harvey 1988). Wind, water, and animals all distribute seeds nonrandomly (e.g. Becker et al. 1985; Skoglund 1990). Animal aggregations also result from physical sorting. In open water, zooplankton are often found in dense aggregations, associated with localized physical phenomena (e.g. Hamner & Schneider 1986). Animals are not necessarily actively attracted to these aggregations; often they are passively transported there via physical processes. These types of assemblages might be called *passive aggregation*, although this does not preclude the possibility of the aggregation members acting and interacting once within the group.

Within the animate world, aggregations often form around an attractive source, with potential members of the aggregation actively recruited to a specific location. Zooplankton aggregate nightly at the surface of the sea as a result of vertical migration. Clumped patches of any resource, such as food or space, attract animals, especially if the resource is limiting. We refer to these types of aggregations as *active aggregations*. In these situations the aggregation is apt to disperse if the source of attraction wanes. Once seeds have been consumed, birds no longer visit a feeder. Individuals also may continuously join and leave the aggregation, rather than remain continuous members. Thus, turnover may be high even if the aggregation as a whole remains fairly constant in terms of size, density, shape, or location.

Although attraction to a common source may be responsible for the creation of the aggregation, repulsion also plays a crucial role in determining group structure (Okubo 1980). Unmitigated attraction would result in an aggregation so

dense that the costs to individual members would quickly outweigh the benefits. As density increases, basic resources, such as oxygen in the aquatic environment, are depleted faster than they can be replenished (see McFarland & Okubo Ch. 19). At the same time, waste products are likely to build up faster than they can be advected out of the group. Repulsion may occur on a global level; i.e. individuals are repulsed from an external source (e.g. Payne 1980), creating an open space or vacuole around the repulsion source (e.g. a predator in a fish school; Pitcher & Parrish 1993). Repulsion also occurs on a local level; i.e. regulation of interindividual density (see Parrish & Turchin Ch. 9). The combination of attractive and repulsive forces should thus define the physical attributes of the group as the spacing between many interacting individuals and forms the emergent pattern we see as group structure.

In contrast to plants and pebbles, animals have the ability to react rapidly to changes in their environment. While a sand grain or a seed may fall among others of equal size and origin, it does not do so by choice. Many animal aggregations are formed and maintained by the mutual attraction of members. When the source of attraction is the group itself, we define this behavior as *congregation* (sensu Turchin 1997). Examples of animal congregations abound: flocks of birds, swarms of insects, schools of fish. Congregations can be shaped by internal, i.e. member-derived, forces, by external forces, and by frictional forces (see Warburton Ch. 20; Okubo 1986). The foraging trails of ant colonies may have structure, determined in part by the surfaces they crawl over. However, given a smooth, featureless environment, the ants would still congregate (Edelstein-Keshet Ch. 18, 1994; Gordon et al. 1993). Thus the phenomenon of congregation may be structured by the larger environment within which the group resides as well (Gordon 1994).

Although a large variety of animals congregate, interactions within the group differ markedly across species (Bertram 1978). Spatially well-defined congregations, such as fish schools, may be composed of individuals with little to no genetic relation to each other (Hilborn 1991), low fidelity to the group (Helfman 1984), and thus no reason for displaying reciprocal altruism. Schooling fish are generally considered “selfish herds” (Hamilton 1971), in that each individual attempts to take the maximum advantage from group living, independent of the fates of neighbors (Pitcher & Parrish 1993). The fact that three-dimensional structure is apparent does not necessarily lead to the conclusion that the individuals within the group interact socially. Rather than active information transfer (i.e. social interaction), information may be transferred passively (sensu Magurran & Higham 1988). For this reason, we refer to these asocial types of congregations as passive. In a *passive congregation* (the FSH of Romey Ch. 12), in-

dividual members are attracted to the group per se, but do not display social behaviors.

Many animal congregations, however, are socially developed. Often the individual members are related, sometimes highly so, as in the social insects (see Edelman-Keshet Ch. 18; Wilson 1975). Unrelated congregation members will often engage in social interactions if group fidelity is high, such that the chance of each individual meeting any of the others is high (Alexander 1974). *Social congregations* display a variety of interindividual behaviors, necessitating active information transfer. Antennal contact in ants may be used to transfer a variety of information about individual identity or location of resources (Gordon et al. 1993). The rate of contact may also, to some extent, define the structure of the group (see Edelman-Keshet Ch. 18). Social congregations frequently display a division of labor, such that large tasks unassailable by an individual are accomplished by the group (e.g. hunting in social carnivores – Kruuk 1972, 1975; Packer & Ruttan 1988). The way in which both passive and social congregations transfer information between members about the larger environment which is unsensible by any single individual is the subject of Chapter 15 by Schilt and Norris. Highly social congregations, such as felid or canid packs, or any number of primate groups, may actually display a lack of regularly defined spatial pattern within the group (e.g. Janson 1990), perhaps because of the level of social development. In these cases, constant proximity of neighbors is no longer a requirement for information transfer and the “structure” of the groups is by relatedness and social hierarchy rather than interindividual distance.

1.3 Properties of animal congregations

Regardless of species or circumstance, many animal congregations share one or more of the following features.

1. Congregations have *edges* which are usually very distinct; the change in density from inside to outside is abrupt. This is one operational way to define a group. When a congregation moves or changes shape, the edges remain intact. Thus, individuals are either members or isolates, depending on their location.
2. Many types of animal congregations have fairly *uniform densities*, particularly when on the move (e.g. herds, flocks, schools). Other types of animal congregations may have a broader distribution of densities most of the time (e.g. midge swarms), yet retain the ability to assemble almost instantaneously into a more uniform mass. Feeding birds often display non-uniform distribu-

tions around food sources, but if a predator comes into view the flock will take wing as a cohesive, structured unit.

3. Congregations which exist largely as groups of uniform density are often also *polarized*, with all members facing in the same direction. When a flock of birds is in flight, for instance, it is obvious why this should be so. A bird in the interior of the flock, flying at right angles to the rest, would quite possibly create a significant hazard. However, some animal congregations, notably schooling fish, remain in polarized configurations even at rest. Why this occurs is not known.
4. Within the volume of the group, polarized or not, individuals have the *freedom to move* with respect to their neighbors. In a resting group this may mean that individuals are constantly shifting positions, even if the position or shape of the congregation as a whole remains static. In moving groups individuals can also re-sort without disturbing the integrity of the group. The ability to shift positions means that individuals can take selfish advantage of moment-to-moment circumstances as well as accrue the more general benefit of group membership.
5. Many congregations display *coordinated movement patterns* of an almost balletic nature. Flocks on the wing appear to turn simultaneously. Fish in schools arc in a fountain-like pattern in response to attack by a predator, completing the move by reaggregating behind the predator. Ant trails branch out in dendritic structures which coalesce back into main paths.

1.4 On adopting new perspectives

We live in a three-dimensional medium and we constantly, albeit unconsciously, make thousands of three-dimensional calculations each second. A disproportionately large portion of the human brain is committed to these very functions, yet tiny creatures, like hover flies, make lightning judgments in space and time with hardly any neurological equipment. Even with our stereoscopic, full color, visual abilities we cannot track an individual sardine within a rapidly wheeling school. Perhaps, if we could slow everything down, we would be more effective. So, as scientists, we record the behavior with film or video, and replay the images at slower speed. Again, we are lost. Our films are in two dimensions, and we begin our analysis of three-dimensional behavior at the 0.66% level of confidence. If we film with two or more cameras to capture the third spatial dimension, we then must analytically treat the resulting data set using classical three-dimensional photogrammetric calculations (see Osborn Ch. 3). And then we learn the bad news. Automatic three-dimensional data collection and analysis, for any length of time over several seconds, requires the dedicated attention

of the biggest computers currently on the market. A cloud of gnats obviously does not engage in such time-intensive calculation. There must be simple traffic rules for species' engaging in collective movement.

This book is all about animal aggregations in four dimensions, three in space and one in time. It is not confined to just an experimental treatment of the subject. We believe that it will require much more than biology to understand how and why animals do (or do not) congregate in more or less ordered arrangements. Two of us (Parrish and Hamner) experienced the limitations of a purely biological approach, first independently and then together, when we tried to answer questions about how individuals move within groups and how those movements are patterned in space and time. As biologists we found ourselves immersed in a rich literature on why animals aggregate. Hypotheses describing where animals should be in a group, and why they should be there, abound (Alexander 1974; Hamilton 1971; Lazarus 1979; Pitcher et al. 1982b), but the literature on how animals aggregate is much sparser. While we found information on how individuals might match retinal images (Parr 1927), how they might match their speeds (Shaw & Tucker 1965), or how quickly individuals might detect and respond to a stimulus, these papers did not point the way to answering our questions about how these individuals organize themselves in space and time within aggregations. When we pressed these issues, we quickly found ourselves in a technological morass.

Following individual animals (or units of anything within a moving aggregation) in space and time turns out to be very difficult. Tracking requires a known frame of reference within which the object moves. If an object moves very fast, the rate at which its position is sampled must also be fast to accurately record changes in speed and direction. For confined objects, such as a fish in a tank, this is relatively easy. However, tracking a fish in the ocean is more difficult, as it is likely to swim away. If a tracking device such as a transponder is attached to a fish, then the receiving array must also move with the fish, and it in turn must be accurately tracked. Quite quickly the limits of technology are reached. Following individual units moving in space and time within a group which also moves is nearly impossible. Even if we did manage to collect the requisite four-dimensional data, analytical tools were not readily available. Distilling four-dimensional data on identified individuals into a form where interesting biological questions can be addressed is a daunting task.

We were faced with interesting questions and no way to answer them. So, we did what most of us do when confounded, we found someone with complementary skills to help us solve our problems. Prewitt is a crystallographer, used to thinking about the structure of three-dimensional aggregations and trained in how to detect three-dimensional patterns. In the course of our collaboration we

subsequently discovered other people working in the general field of three-dimensional aggregation, many from perspectives that we had not initially considered. Eventually, we came to the conclusion that examining four-dimensional animal aggregations was a multidisciplinary “field” of its own. Like most individuals within any group, researchers interested in four-dimensional problems generally only have a sense of their own work, and little appreciation of that of their “nearest neighbors.”

Because intellectual disciplines move forward as new ideas are injected into an existing framework, we decided that it was time to reevaluate the framework for the study of animal aggregations. We convened a group of scientists who work on many different aspects of aggregation, both animate and inanimate. This book is the product of our interactions. Because each of us soon saw our studies in a new perspective (new ways to collect data, new methods of analysis, new phenomena to model, new systems for comparison, new questions to ask), we decided to begin at the beginning and review all aspects of the multidisciplinary study of animal aggregation in space-time. This new field encompasses aspects of animal behavior, ecology, and evolution as well as crystallography, geology, photogrammetry, and mathematics. The thread that ties us together is the how and why of aggregation. Sand grains on a beach and fish in a school share some similar properties. Might models of the former elucidate the latter?

1.5 Central themes and “big picture” questions

A defining aspect of any field is the set of questions it attempts to answer. As a multidisciplinary group, we have come up with what we refer to as Big Picture Questions (BPQs) — issues central to the study of animal aggregation (a non-inclusive list of which follows). One of the central themes connecting all of these questions deals with the basic conundrum of how a set of selfish individuals can apparently act as a cohesive, coherent whole.

What are the costs and benefits of group membership?

Are they positionally dependent?

What information can, and do, individuals use?

Do individuals have a sense of the whole?

Is there an optimal group size?

The study of animal aggregation can be attempted at several levels. The former questions acknowledge the central importance of the individual member and they attempt to examine the group through the combined action of its members. However, one can also look at the entire group as a unit possessing certain prop-

erties. The second core theme embedded in our BPQs addresses the group as a whole.

Why are there discrete boundaries?

What is the appropriate scale for assessing pattern?

Why should pattern exist in three-dimensional aggregations?

Is observed three-dimensional structure no more than would result from optimal packing?

The third theme attempts to integrate elements of the individual with those of the group – Essentially, trying to define the whole as some function of the parts.

What are the assembly rules?

Which properties of the group are epiphenomena and which are functional properties that have been selected for?

Can models which predict epiphenomena be used to make predictions about individual behavior?

None of the BPQs are easy to answer, and several of them are outside the framework of the scientific method, that is, they do not lend themselves to testable predictions. However, we believe these questions are a starting point from which we will launch our studies. In this book, we attempt to address some of these questions, as well as others which are logical extensions of the few presented here.

1.6 Organization – from measurement to models

We have organized this book around four central issues: collecting data, analyzing data, the functional biology of aggregation, and modeling aggregation. Within each section the reader will find several chapters devoted to examples of how to address the issue or define the approach. However, each chapter addresses other issues as well. It is impossible to analyze data without first collecting it. It is useful to have model predictions when examining the functional role of individual position within the group. Rather than read cover-to-cover, we encourage readers to follow their own path through the book as each chapter leads to others within and across sections.

Neither group structure, nor individual movement within that structure, can be described, analyzed, or modeled without the ability to collect data in X , Y , Z over time. In this respect, many of us have been limited by technology. It is only recently that off-the-shelf systems with the ability to collect four-dimensional information have become available. Prior to the advent of automated data collection, researchers interested in collecting four-dimensional data sets had to repeatedly digitize hundreds, if not thousands, of points. Methods sections in

several fish schooling papers from the 1960s and 1970s are full of agonizing descriptions of the number of frames analyzed (e.g. Partridge et al. 1980 hand digitized over 1.2 million points). The endless hours of data collection were enough to turn anyone away. Today technology offers us not only visual options for data collection but also acoustic methods. In concert, these sensory modalities will eventually allow us to examine animal aggregations at the level of the individual, the group, and the habitat.

The first section of the book – Imaging and Measurement – reviews the technology and specific methods available to resolve three-dimensional images and track moving points through space-time. Jaffe (Ch. 2) gives a broad overview of three-dimensional technology before focusing in on acoustic techniques. Greene and Wiebe (Ch. 4) give a specific example of data collected via three-dimensional acoustic technology. While Jaffe uses sound to attempt to follow individual plankters (his FTV system), Greene and Wiebe use sound to map plankton aggregation over several kilometer volumes of open ocean. Thus, acoustic technology lends itself to a tremendously broad range of spatial scales. Osborn (Ch. 3) reviews three-dimensional optical methods which rely on the principles of photogrammetry and gives four short examples of photogrammetric analyses in aquatic systems. The final two chapters provide examples of optical collection of three-dimensional data in aerial systems. Heppner (Ch. 5) discusses the development of devices to follow birds in flocks, along with the underlying reasons for flocking. Ikawa and Okabe (Ch. 6) discuss a system for following the movements of swarming mosquitoes.

The search for three-dimensional structure or animal architecture has been one of the holy grails of animal aggregation research. Early attempts to detect structure used physical world examples, such as crystals, as a model (Breder 1976). These attempts were largely unsuccessful because the spacings of animals in a school or flock are not as regular as are atoms or molecules in a crystal and perhaps because these investigators did not employ the full range of possibilities for description that exist in the crystallographic literature. We believe that research on animal aggregations should embrace physical models, especially those created from the study of inanimate aggregation. Several authors in this volume, notably in the sections on Analysis and Models, adapt concepts from the physical sciences that can be useful in a more biological context. For example, the concept of diffusion is used by several authors to describe relative movement of aggregations and/or the movement of individuals within those aggregations. Most people think of diffusion as something that occurs when there is a physical or chemical gradient present in a system. McFarland and Okubo (Ch. 19) use advection and diffusion equations to model oxygen depletion as a function of school size. In contrast to much of the existing literature on