Self-organization and collective behavior in vertebrates

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1. Introduction

1.1 <u>Overview</u>

As a ripple of light the fish turn. Like some animate fluid, the school glides and turns again. The synchrony of motion is captivating. A similar integration of behavior can be seen in a bird flock, where the volume and shape of the group changes as it turns and arcs overhead, and yet the aggregate remains cohesive. Many group-living vertebrates exhibit complex, and coordinated, spatio-temporal patterns, from the motion of fish and birds, to migrating herds of social ungulates and patterns of traffic flow in human crowds.

The common property of these apparently unrelated biological phenomena, is that of inter-individual interaction, by which individuals can influence the behavior of other group members. It is on how these interactions result in the collective behaviors of vertebrate animal groups that we focus on here. Specifically, we consider systems in which insights from self-organization theory have been useful in improving our understanding of the underlying mechanics. Self-organization theory suggests that much of complex group behavior may be coordinated by relatively simple interactions among the members of the group. Following this theory, the form, and therefore often the function, of the collective structure is encoded in generative behavioral rules. Self-organization has recently been defined as "a process in which pattern at the global level of a system emerges solely from numerous interactions among the lower-level components of a system. Moreover, the rules specifying interactions among the system's components are executed using only local information, without reference to the global pattern" (Camazine *et al.*, 2001). It should be noted that often in nature, pattern-forming processes may not strictly conform to this classification: in some instances, such as animal migration, individuals may modify their local (self-organizing) interactions with others with reference to global information, such as a general desire to move in a certain direction. This type of system therefore self-organizes within the context of global cues.

In recent years there has been an expanding interest in pattern formation in biological systems (Gerhard and Kirshner, 1997; Maini and Othmer, 2000; Camazine *et al.*, 2001). The field of pattern formation covers a wide range of areas, including attempting to explain fetal development (Keynes and Stern, 1998), patterns on the coats of mammals (Murray, 1981), the structure of social insect nests (Theraulaz and Bonabeau, 1995), and the collective swarms of bacteria (Ben-Jacob *et al*., 1994), army ants (Deneubourg *et al.*, 1989) and locusts (Collett *et al.*, 1998). In particular there is a growing interest in the relationship between individual and population-level properties. A fundamental question is how large-scale patterns are generated by the actions and interactions of the individual components. Many pattern-forming processes in biological systems, such as cellular sorting or the collective organization of group-living (particularly eusocial) insects, are dynamical mechanisms whereby the large-scale patterns (e.g. clustering of cell types, Glazier and Graner, 1993; or periodic activity cycles in ant colonies, Boi *et al*., 1999) can be accounted for by the interactions among the individual components of the system (e.g. differential adhesion among cells; ants responding locally to the activity of others).

Applying such a self-organization viewpoint to vertebrate groupings is a more recent development, and despite the importance of understanding group dynamics for ecological processes (Levin, 1999), many collective behaviors are still only qualitatively understood. Vertebrates often have superior cognitive abilities and more complex behavior patterns than organisms such as social insects. Consequently it may appear that this approach may be less able to account for the collective behaviors of these organisms. However, the self-organization approach is applicable to even the most complex of organisms, such as humans, but is restricted to certain aspects of their behavior, such as the motion of pedestrians within crowds (see sections 2.2a and 2.3) where interactions may be (mechanistically) relatively simple. A further reason that vertebrate groups have been less well studied in this context is that for many vertebrate groups, such as ungulate herds, pelagic fish schools, or human crowds, the interactions among the individuals are much harder to study than in group-living insects, or bacterial swarms, where the manipulative experiments required to understand the underlying mechanisms better are easier to perform (and replicate).

Here we will review progress in this newly emerging field, that of applying self-organization theory to mobile vertebrate groups composed of many interacting individuals (such as bird flocks, ungulate herds, fish schools, and human crowds) in an attempt to improve our understanding of underlying organizational principles.

1.2 Understanding the dynamics of collective behavior

Mathematical modeling is becoming increasingly recognized as an important research tool when studying collective behavior. This is because it is usually not possible to predict how the interactions among a large number of components within a system result in population-level properties. Such systems often exhibit a recursive, non-linear relationship between the individual behavior and collective ('higher-order') properties generated by these interactions; the individual interactions create a larger-scale structure, which influences the behavior of individuals, which changes the higher-order structure, and so on. Consider the movement of ungulates across grassland, or over snow-covered terrain. The motion of an individual is likely to change the environment through which it moves (by compression of the grass or snow). This local change influences the motion of other individuals passing near that point: they exhibit a tendency to maximize their comfort of travel (and hence minimize energy expenditure) and thus have a greater propensity to move over the ground previously walked on. This results in further changes to the environment at that point (further compression of the substratum), which in turn increases the probability of others to choose to move over that point if close to it. Taken over a larger area, this feedback results in the generation, and use of, trail structures. Thus individuals change the local properties of their environment, which influences the motion of others, which further alters the environment, and so on. The generation of animal (including human) trails will be discussed in more detail below, and the results of computer models will be used to reveal the dynamics of this system.

When modeling population-level processes, continuum approaches ('Eulerian' models) have typically been used. These abstract the movement of very large populations to population densities, and movement is usually represented using diffusion and advection

processes. Such approximation procedures are very useful, since there are well-developed mathematical tools for their analysis. Although well suited to the movement of very large populations (e.g. bacterial, planktonic and certain insect aggregations), they are less suitable for most vertebrate animal groups where the number of individuals within an aggregate is relatively small. Furthermore, the analysis of such models is typically greatly complicated when social interactions, or interactions between individuals and their environment, are an important organizing mechanism. Consequently, here we will largely consider the motion of groups as resulting from interactions among the individual group members, and use, where appropriate, individual-based (or 'Lagrangian') models of animal motion to elucidate certain (often generic) principles. This approach to modeling shares certain properties with techniques developed in non-linear statistical physics to simulate the motion of particles, as for example in gases, fluids or magnets. While particles may be subject to physical forces, animal behavior can conceptually be considered to result from individuals responding to "social forces": for example, the positions and orientations of neighbors, internal motivations (e.g. degree of hunger), and external stimuli (such as the positions of obstacles). In understanding the movement decisions of animals we must better understand how and why motivations exist, and how these translate to collective patterns.

The global-level ('emergent') dynamics of the group are usually not explicitly encoded: there is often no global blueprint or template for the pattern (although the formation of trails, as described above, may to some degree be considered as the generation of an interactive, labile template). The form of the collective structure, and hence often the function, is usually encoded in generative behavioral rules. Such rules, being subject to natural selection, allow the generation of self-organized adaptive patterns at the group-level. Since the costs and benefits to individuals when grouping may change dynamically, even as a function of the position of an individual relative to other group members, changes in individual rules are likely to occur as group members attempt to maximize their individual fitness. This can result in groups adopting different shapes, or motions, as well as being a potential driving force for internal structuring within vertebrate groups. Such properties will also be discussed here.

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Environmental factors, such as physical habitat structure or temperature may influence the behavior of individuals within groups, and consequently their motion and structure. These factors may affect the cohesion of groups, or act as 'seeds' for self-organized aggregation processes. Individuals may balance global goal-oriented behavior (such as a desire to move up a temperature gradient) with local conditions, such as avoidance of isolation from a group, or alignment with group members. Such a balance of external and internal social forces may underlie the motion of certain vertebrate groups, such as migrating fish schools. The structure of the environment through which individuals move is also important. In some cases, the spatial heterogeneity in the environment may be temporally stable (relative to the timescale over which grouping mechanisms function), such as the positions of trees, rocks, and other landmarks. Such heterogeneity may influence both the suitability of the environment for locomotion, and the effective range of interaction among individuals. This variability is likely to have a strong influence on both individual movement patterns and interaction range. In other cases spatial variation in habitat is dynamic, such as the flows and turbulent eddies within certain aquatic environments.

A further important factor to consider when understanding the collective behaviors of animal groups (and self-organized pattern-forming processes in general) is the influence of stochastic (random) events. Animal behavior is inherently probabilistic, and stochastic properties of animal movement are likely to strongly influence the structure of many vertebrate groups. It is becoming increasingly evident that self-organized patterns often arise because of the amplification of random fluctuation (Nicolis and Prigogene, 1977; Seeley, 1995), as shall be discussed here when we consider the shape of migrating wildebeest herds. By developing stochastic computer models of animal groups one can aim to capture the essential statistical mechanics of the system. The aim of modeling is often not to attempt to include all the known properties of a system, but rather to capture the essence of the biological organizing principles. One of the principal aims of self-organization theory is to find the simplest explanation for complex collective phenomena. A commonly perceived problem when modeling animal behavior, especially that of humans, is that of the representation of complex organisms through simple behavioral

rules. The apparent complexity of the entities to be represented in a computer model may be misleading, however. In order to gain insight into the dynamics of a collective phenomenon, all of the complex details may not be necessary or even relevant. For example, much of human behavior within crowds is carried out almost automatically with little conscious decision-making, and although the organism is complex, the interactions need not necessarily be so.

Furthermore, when exploring potential grouping mechanisms one often deliberately explores a simplified representation of the system that characterizes a broader range of general mechanisms. That a biological population is described as being self-organized does not suggest that all individuals within the population are simple, identical, or have the same influence on one another. Of course this is not to say that more specific representations of certain systems are not important. To the contrary, developing models of specific cases of a broader mechanism is extremely valuable. However there are currently often limitations in the quality of empirical information available, and thus creating a generalized model can often be more appropriate. Also, without an understanding of the behavior of the simplest system we cannot possibly know how changes made to the model affect its behavior. Even with relatively few parameters, the exploration of parameter space can be time-consuming and complex. A further point to bear in mind is that with collective systems, understanding the behavior of an individual in isolation does not necessarily provide information about the properties of that individual within a collective situation, where non-linear interactions may determine much of the group dynamics.

2. Group shape and motion

2.1 The wave-like front of migrating wildebeest herds

Many collective behaviors result in complex, and coordinated, spatio-temporal patterns, from an undulating flock of birds, to mobile herds of social ungulates and lanes of traffic flow in human crowds. One of the most dramatic examples of collective motion in

vertebrates is that of migrating wildebeest (*Connochaetes taurinus*) that form huge herds that cross the Serengeti grasslands, moving to the north in May-June, and returning south in November. A single herd may include in excess of 100 000 individuals which viewed from above exhibit a common direction of motion, and a broad front that exhibits a characteristic wave-like form (Fig. 1). Interestingly, the wavelength of this front pattern is much larger that the possible interaction range of an individual. To gain a better understanding of how this group shape may be generated, Gueron and Levin (1993) developed a mathematical model of the herd front. They made the simplifying assumptions that individuals have a common directional preference, and that it is likely to be the motion of individuals at the front of the group (leaders) that primarily explains this pattern. How certain individuals within a group may become leaders, and the influence of leadership within vertebrate groups, is discussed more fully in sections 3.2 and 3.4 below.

Since these migrating wildebeest herds are so large, Gueron and Levin abstracted the herd front to a curve evolving in time and space, making the system tractable to mathematical analysis. Given that the phenomenon of interest, the wavy front, has a periodicity much greater than that of the supposed interaction range, individuals within the model were restricted to modify their motion in their desired direction only as a function of that of neighbors within a specified range (the average location of individuals in a local neighborhood). Thus it was possible, using the model, to investigate the potential influence of the range of interaction. Using the following simple rule set, the model was found to generate a wave-like front:

1) Individuals have an intrinsic speed and accelerate or decelerate in response to the positions of neighbors within a local neighborhood.
2) Those lagging behind others in their local neighborhood can fall further behind, until the gap reaches a specified maximum distance. When this distance is reached individuals speed up to reduce the gap.
3) Those ahead of neighbors can speed up until the gap reaches a specified maximum distance, where the behavior is reversed, and they slow down.

Following these rules, an initial uniform herd front (straight line) is unstable. Small perturbations (stochastic irregularities) in the curve representing the herd front appear and tend to grow (amplify), yielding the irregular "wavy" fronts (Fig. 2), similar in appearance to those seen in nature (Fig. 1). Thus a simple and local set of behavioral rules can explain the long-range pattern. Importantly, the solutions to the model were "semi-stable", meaning that although they did change over time, the characteristic feature of the system (the presence of the irregular wavy front) was persistent. The exact shape of the front was found to be largely dependent on the range of interaction, and the model was better able to represent the waveform seen in reality with relatively local interactions (the front becoming flatter as the range of interaction increases). Consequently the model makes broad-level predictions about the type of behavioral interactions herding wildebeest may exhibit, and about how interaction range affects group shape in this system. Furthermore, the model makes it clear that long-range patterns need not be explained by long-range interactions. However, it is unclear how such predictions may be tested in practical terms given the huge spatial scale of the system in question, and therefore, whether alternative local rules may also explain this phenomena. In this case it may be very difficult to test the predictions of computer models. Ideally one would like to be able to manipulate the system such that it would be possible to investigate the consequences of changing the parameters of the model (e.g. manipulate the interaction range of real organisms), or more realistically perhaps, to track the motion of individuals within a subset of the herd to see if they conform to the type of local interactions assumed by the model. This may be achieved by recording how the velocity of individuals depends on the velocities of neighbors (bearing in mind that velocity incorporates the position of an individual, its direction of motion and speed). We discuss the analysis of such groups in more detail below (3.1).

Gueron and Levin also point out that their type of approach may be relevant to understanding the motion of narrow bands of animals only one or a few individuals in width, such as thin streams of ungulates, birds, or bats. One would then consider the direction of travel to be perpendicular to that in their wildebeest model, and that individuals tend to adjust their position to either side, relative to individuals ahead of, and

behind them, for example to avoid collisions or perhaps to improve visual range. Given this formulation, individuals would tend to move to one side (e.g. to avoid collisions) until they reach a maximum distance, at which time they would tend to move back towards the group (representing a tendency to avoid being isolated). In this context, as suggested by Gueron and Levin, it may be beneficial to modify the rules of interaction such that individuals tend to predominantly respond to those ahead (as opposed to equally to those ahead and behind, if one were to abstract the original model exactly). However, similar predictions are likely to result: that perturbations tend to grow, resulting in winding, as opposed to straight, lines and that the exact form of the wave will similarly depend on the interaction range.

2.2 The generation and use of collective trail systems by animals, including humans

A further property that influences the motion of organisms such as herding ungulates is their ability to change the environment through which they move, and to respond to such changes. This recursive feedback loop may also be an important determinant of the types of patterns that form at the population-level. Consider the type of situation outlined previously in section 1.2, where individuals change local properties of their environment as they move through it, such as by trampling of grass or snow. As well as responding to the positions of other group members, individuals respond to their environment. We are not aware of any mathematical approach that has been applied to this problem for organisms that actively aggregate, and thus the theoretical consequence of the balance of these forces has not yet been investigated. However, progress has been made in the case where the effects of direct interactions between individuals can be ignored, such as when they are very rare. Initially this may seem irrelevant in a chapter on animal groups where interactions are known to be very important. However, since the only work on this topic has made this assumption it is still beneficial to understand what pattern forming processes occur when direct interactions are a trivial influence. Furthermore, even when individuals themselves do not interact directly, the pattern-forming mechanism is still collective through indirect interactions by environmental modification. We will then

make suggestions about suitable modifications of this approach to include direct interactions, and the potential outcome of such modifications, to this type of model.

a) Human trails

Helbing *et al*. (1997a, b) developed a model of trail formation by mobile individuals (or "active walkers"). These walkers were considered to have the potential to modify the environment through which they move. In their model these changes represent the trampling of substratum as described previously. Using such a model one can investigate the influence of the degree to which individuals change their environment (and consequently the effect this change has on others) and the lifetime of the environmental changes (simulating the local durability of a change; for example the re-growth of vegetation or further falls of snow will act to return the environment to its former state). Although Helbing *et al.* (1997a, b) restrict their discussion of vertebrate trails to those generated by humans, the type of model is applicable to any system where individuals can modify their environment, and respond to such modifications.

For humans one can consider the situation where people move between certain points in space, each for example representing doors to buildings. Within the model of Helbing *et al*. (1997a) it is assumed that people will tend to take the shortest route to their destination, but tend to reconcile this global goal-oriented behavior with a relatively local preference to walk on previously used (less bumpy) ground. They considered the movement of simulated pedestrians over initially homogenous ground from, and to, specific points in space. Figure 3A shows a trail system forming near the beginning of a simulated run in the case where there are four entrance/destination points, one in each corner of the simulated domain. As can be seen, pedestrians initially tend to take the direct route to their destinations. Over time, however (Fig. 3B), frequently used trails become more comfortable (and hence attractive) and this influences the characteristics of the trail system: sections of trails become shared by walkers with different desired routes, creating a trail system in which the overall length is reduced. Increasing comfort means that a given section of trail is more likely to be used in future, which further increases its

comfort, and so on (autocatalysis). Trails that are not sufficiently reinforced will decay through processes such as the regeneration of vegetation and weathering effects, thus providing a negative feedback within the system. The exact type of collective trail system that forms will depend on the properties of the system that affect these feedbacks. For example, increasing the number of pedestrians within the environment, or the degree to which pedestrians influence the comfort of the ground over which they walk, will increase the positive feedback. Increasing the rate of recovery of the environment, by contrast, will amplify negative feedback. This will influence how individuals reconcile their global and local behavioral tendencies. If pedestrians' desire to use existing trails is very large, the final trail system will be a minimal way system (the shortest system that connects all the points). Conversely if there is no advantage to using trails (as in most urban environments) individuals will use a direct route system (similar to that seen in Fig. 3A). In between these extremes, the simulation suggests that pedestrians collectively will find a compromise between short and comfortable ways.

b) Extending trail-laying/response concepts to other animals

This type of modeling approach is similar to earlier studies investigating the generation of trails by ants (Deneubourg *et al*., 1989; Franks *et al*., 1991). In the latter case positive feedback (amplification) can occur when the orientation of a trail-laying ant depositing chemical pheromone at a certain location influences the direction taken by a further ant passing that point. The latter ant may reinforce the pheromone trail, which can further influence the direction taken by subsequent ants, and so on. This can lead to a selection of trail orientation at that location. Pheromones decay, causing negative feedback. A decaying trail is less likely to be followed, and will therefore be subject to further decay. As in the case of human trails, trail persistence depends on the balance between reinforcement (positive feedback) and decay (negative feedback).

Thus at a certain level of description, vertebrate and insect trail-laying may share some fundamental properties of organization. Consequently, the results of research on ant trail systems may also shed light on fundamental properties of trail formation by vertebrates.

For example, it has been found that ants can find the shorter of two routes between the colony and a food source. Ungulates may create and use trails as they move between feeding areas, or watering holes, and as described above, humans may move between buildings. Fig. 4A shows trails forming in the model of Helbing *et al*. (1997a) where individuals have a desire to move from the top to the bottom of the domain, and vice-versa. Fig. 4B shows similar natural trail systems used by ungulates in the Australia. The potential consequences of such dynamics can be considered in a hypothetical, and deliberately simple, situation shown in Fig. 5A where individuals are considered to desire to move between just two points labeled 1 and 2, and vice versa, but in doing so must move around an impassable landmark in the center. Individuals create and follow trails as described above. Initially, in the absence of any trails, individuals first reaching the landmark, having limited and local visual information, will randomly select a route around it (Fig. 5B). However those individuals that take the shorter route will reach their destination more quickly. This causes that route to be more rapidly reinforced. This means further individuals reaching the point at which trails bifurcate to the right and left around the landmark will tend to be more "attracted" to the shorter route, which will become even more attractive, and so on. Thus the counterbalance of positive and negative feedback could be expected to facilitate the collective selection of the shortest trail to a specific point, without individual decision-making being invoked (Fig. 5C).

A further property highlighted by research on ant recruitment mechanisms that may also relate to vertebrate trails is that of a trade-off between accurate and rapid decision-making. Consider our earlier simplistic scenario, involving the navigation of organisms between two points in space around an asymmetric obstacle. If positive feedback is very high (trails are very attractive, as would be the case, for example, if the ground is very difficult to move over unless you follow a path made previously) then the trail-forming system is very susceptible to initial conditions. For example, if the first individual to pass the obstacle were, by chance, to go the long way around, then it would be very likely that the next individual would also take that route. This would cause rapid fixation of the longer route. Thus the system will be very dependent on the initial (random) choices of individuals. If each individual were to have a weak effect on the ground, or be only

weakly attracted to the trails of others, then it will take a much longer time for one particular route around the obstacle to be dominant, but it is very likely that it will be the shorter route that is "chosen". A further point to be made is that even given a symmetrical obstacle, if positive feedback is relatively strong, then the organisms are still likely to select a (randomly determined) single route around the obstacle.

We are not suggesting here that vertebrates behave just like ants, and the predictions we make above are deliberately speculative. Caution should be used when extrapolating the results between different systems. However, the presence of similar fundamental feedback mechanisms may mean that, as demonstrated by human trail formation, some collective processes exhibited by vertebrate populations may be explained without invoking complex decision-making abilities at the level of the individual.

A further potential property of vertebrate trail systems that has yet to be investigated is the influence of direct interactions among the components of the system. Intuitively one may expect that herding behavior would tend to increase the amplification processes involved in trail formation, since individuals would tend to remain in the proximity of others, and would tend to follow one another. However, in the case of bi-directional traffic on a trail, congestion may cause trails to bifurcate more readily, creating a system with a series of anastomosing trails, as opposed to a single trail. However, it would be important to further develop models of these processes, and to find systems where it would be possible to test the predictions of computer models. For example, it may be possible to compare trails made by organisms moving over vegetation that offers different resistance to locomotion (and consequently the ease of creation and relative comfort of trails). It may also be possible to set up experiments similar to that shown in Fig 5, and investigate the collective solutions 'found' by the organisms in question.

In some cases vertebrates may deposit chemicals that can facilitate trail formation (or complement the mechanisms discussed previously). For example, Norway rats *Rattus norvegicus* (Galef and Buckley, 1996) and naked mole rats *Heterocephalus glaber* (Judd and Sherman, 1996), having found a food source, can deposit odor that can bias the

direction taken by other individuals, somewhat analogous to trail deposition and following by ants and termites. Being central-place foragers, such trails can facilitate information transfer to other (naïve) individuals about the location of resources. It is known in rats that deposition of scent in urine is used as a trail-marker (Wallace *et al.*, 2002), whereas in naked mole rats it is unclear how the scent is deposited by the individual (Judd and Sherman, 1996). For rats it has also been shown that the attractiveness of a trail increases as a function of how many times a trail section has been traversed, and that rats deposit trail only when moving away from the food source (Galef and Buckley, 1996). Furthermore, it has been shown that the odor discriminatory ability of rats allows them to distinguish between self-generated trails, and those of conspecifics (Wallace *et al.*, 2002). Such an ability is also known to occur in certain ant species (Hölldobler and Wilson, 1990), and could be useful for rats when searching within very dark environments in allowing them to retrace their trajectory. Further studies of Norway rats and naked mole-rats are likely to provide an excellent basis for future research efforts since they can be more readily kept in captivity, and their experimental conditions more easily manipulated than for larger organisms such as ungulates

It is possible that trail deposition and following may be widespread in rodents, and may be combined with environmental modification such as trampling or removal of obstacles from the environment. Scent deposition and detection may also be important in other vertebrate trail systems, such as those discussed for ungulates above.

A further extension of the trail formation concepts discussed here can be made to include collective burrow systems, such as those made by naked mole rats. Here, individuals modify their environment by digging, and unmodified environment would need to be considered as resistant to motion. A further modification of the previous concepts would be that the environment would not return to its former state once modified (or would do so only extremely slowly).

c) Collective generation of home ranges through deposition of, and response to, scent

Another collective biological phenomenon that relies on the modification of, and response to modifications of, the environment is the generation of home ranges by vertebrates such as carnivores (Gosling and Roberts, 2001; Macdonald, 2001) and rodents (Brown and Macdonald, 1985; Viitala *et al*., 1995; Gray and Hurst, 1997). In this case individuals, or groups of individuals in the case of pack-living canids (such as coyote or wolf) mark their territory with scent, which diffuses over time. The motion of individuals is dependent on the scent they detect as they move: they will tend to turn around (and hence not occupy space) in which they detect the scent of another individual (or group of individuals in the case of pack animals). Long-range patterns of space use result from these local interactions. Moorcroft *et al*. (1999) developed a mechanistic model based on these basic principles. Individuals were assumed to increase the degree to which they scent-marked after interaction with the scent of another individual/group. Encounters with such foreign scent-marks would also bias the trajectory of individuals towards the center of their own home range. Using a Eulerian approach (using partial differential equations, PDEs) they showed that these rules were sufficient to explain the general properties of territory generation, and were better suited than models in which individuals did not bias their movement after discovering foreign marks, for their experimental system (the coyote, *Canis latrans*, in the Hanford Arid Lands Reserve, Washington, USA).

2.3 The collective behavior of humans within crowds

In our earlier discussion of humans we considered the case where people interact through environmental modification (trail formation), and largely ignored the influence of direct interactions among pedestrians. However, within an urban setting individuals can seldom influence their surroundings in this way. Furthermore, when walking down a busy street, or corridor, one balances global goal-oriented behavior (desire to reach a certain point) with local conditions created by the motion and positions of other nearby pedestrians. Each member in such a crowd is likely to have a limited perceptive radius in which information to determine future movement must be gathered. Consequently, larger scale

patterns in crowds are seldom evident from an individual pedestrian's viewpoint. However, if viewed from above crowds often do display obvious and consistent patterns. One of the most common of these can be seen when there is bi-directional traffic, as for example when people are trying to move both ways along a walkway, or crossing the road at a crosswalk. Under such circumstances 'bands' of pedestrians form: each band composed of a number of pedestrians with a common directional preference (Milgram and Toch, 1969). See Fig. 6A.

The flow of pedestrians under conditions of crowding was likened by Henderson (1971) to the motion of fluids or gases. He used a well-known technique for the mathematical analysis of such materials, the Navier-Stokes equation for fluid dynamics, to simulate a crowd. Although providing an insight into how individual-level (microscopic) properties lead to large-scale (macroscopic) properties, such an approach is difficult to implement since the conservation of energy and momentum assumptions for a physical system do not apply to a biological system in which the individual components are 'self-driven'. Despite this, Helbing (1992) was able to modify such equations with respect to some of these properties, but analytic solutions proved hard to find. The most promising approach to studying crowd behaviors comes from individual-based modeling.

a) Influence of repulsion (collision avoidance)

Helbing and Molnár (1995) developed a simple individual-based model of pedestrian motion in which they consider people moving in opposite directions along a corridor. This simple geometric representation of space allows the assumption that all individuals have a desire to move only in one direction or another along the walkway. However, pedestrians will also tend to avoid collisions by decelerating and turning away if they come into close contact with one another. When no other individuals are within a specified local range, individuals will tend to accelerate to a desired speed, and orient towards their destination. This simple behavioral response alone can account for the formation of bands when there is bi-directional traffic. Individuals meeting others head on will have 'strong' interactions in which they are likely to slow down and move aside

to avoid collisions. Initially this occurs frequently. However, individuals that find themselves behind others moving in the same direction are less likely to have to perform such extreme avoidance maneuver, and in turn they 'protect' others behind them, from head on avoidance moves. Given a sufficiently long corridor (and a sufficiently high traffic flow for interactions among pedestrians to be an important factor) the system will self-organize into lanes. Individuals entering the corridor (at random positions) move around in the direction perpendicular to their desired direction of travel when they interact with oncoming pedestrians. However, if by chance they fall in behind another individual moving in the same direction this is a more 'stable' state. Thus the system naturally self-organizes into a situation where pedestrians are in the 'slipstream' of others moving in the same direction as themselves, thus creating bands, and reducing movement in the direction perpendicular to desired motion (Fig. 6B). Helbing and Molnár (1995) also demonstrated in their model that the number of bands that tend to form scales linearly with the width of the walkway. This demonstrates that there is a characteristic length-scale to the pattern-forming process: that is, from any point in the system statistically similar motions occur one wavelength away.

b) Influence of attraction to other pedestrians

Clearly one does not need to invoke complex individual behavior to explain the banding patterns found in human crowds. The above model shows how individuals would 'naturally' occupy space (in the dimension perpendicular to desired direction of travel) in which others ahead and behind them tend to have a similar direction of motion. It is possible in real crowds, however, that individuals actively (as well as passively) seek such positions. That is, instead of finding such positions by chance, as in the previous model, they will tend to deliberately walk behind individuals moving in the same direction as themselves. For example, Couzin (1999) simulated the motion of pedestrians crossing a road at a crosswalk. Given the type of rules described in 2.3a the system requires some time to 'find' the collision-minimization state. Consequently, in the crosswalk situation, although some banding does occur, congestion is still relatively high (Fig. 7A). However, if one adds a supplementary rule such that an individual will exhibit

a propensity to follow other individuals moving in their desired direction, then bands tend to form much more readily, thus reducing head-on collisions and increasing the rate of flow (Fig. 7B). On a crosswalk, such bands begin to form even before the pedestrians moving in different directions meet. Thus the groups act as 'wedges' when they come into contact with one another allowing the bands to interlace more readily when they reach the central area of the walkway. Thus, although attraction is not a necessary condition for bands to form in crowds, it decreases the time taken for bands to develop, and increases the flow rate more rapidly than does avoidance alone.

c) The influence of the geometry of the environment

In these pedestrian models, the geometry of the environment is very simple. However, what happens when one introduces an obstacle within the environment? Helbing and Molnár (1995) investigated how their model behaved when they placed a doorway in the corridor. What they found was that, given a sufficient density of pedestrians, oscillations in alternating flows of passing direction at the doorway occur. This occurs because the "pressure" of pedestrians at one side of the door eventually results in an individual being able to make it through the door. This makes it easier for individuals with the same desired direction to follow, resulting in a unidirectional flow of individuals through the doorway, as shown in Fig. 8. This reduces the "pressure" of pushing pedestrians at that side of the door, which will then result in a situation where the flow is stopped, and then individuals moving in the other direction are able to pass through (since the "pressure" on their side is now greater), and so on. If the doorway is widened, changes in direction of flow become more rapid.

It was also found that, given the same total width of doorway, two half-sized doors near the walls of the corridor increase the rate of flow of pedestrians relative to a single door. This is because, due to the mechanism of band-formation described above, each door becomes used by pedestrians flowing in a common direction for relatively long periods of time. Individuals leaving their respective doorway in one direction 'clear' the space ahead of the door for their successors.

d) Crowd behavior and emergency situations

Under certain extreme conditions, such as when people are evacuating from a crowded building, panic can result in pedestrians being injured or killed through crushing or trampling. In some cases crushing can occur in the absence of any external factor (e.g. fire) resulting instead from the impatience of queuing individuals, who having predominantly only local information, push forward. The physical interactions among members of a crowd can add up to cause dangerous pressures up to approximately 4,450 Nm^{-1}, which can cause brick walls to collapse, bend steel barriers, and result in a large number of fatalities (Elliott and Smith, 1993). In an attempt to understand better such collective situations, Helbing *et al.* (2000a, b) extended their models of pedestrian behavior to include a 'body force', which counteracts the compression of bodies, and a 'sliding friction force' which impedes relative tangential motion within crowds. Furthermore, they assume that, within such crowd situations, people exhibit a greater degree of stochasticity (fluctuations) in their movement, and a higher desired velocity, due to the psychological effects of panic (Kelly *et al.*, 1965). The model showed that increasing the value of either, or both, of these parameters caused an increase in evacuation time from a building by increasing the degree of interpersonal friction. This resulted in blockages which occurred especially in the vicinity of bottlenecks. Thus, people fleeing from a building can decrease their chances of survival by attempting to move as fast as possible, or by performing uncoordinated movement through nervousness or panic.

Within conditions where individuals have very restricted information about their local surroundings, such as in a smoke-filled room, Helbing *et al*. (2000a) investigated the possibility that people may respond not only individualistically, but also in response to the motion of individuals near them, which they term a 'herding effect'. Under such conditions neither pure individualism nor herding behavior performs well. Following just the individualistic rule, the discovery of an exit becomes a largely random process for each individual. Although herding can result in groups of individuals escaping if an exit

is found, it is more likely that the crowd will move in the same, blocked, direction. However, if people are assumed to use an intermediate strategy combining both individualism and herding, then the rate of escape is maximized, given the assumptions of the model.

These models of human crowds are based on a simplified set of plausible interactions, and as such provide useful insights into the general behavior of such groups under a variety of conditions. There is, however, a need for further empirical studies, which are lacking despite the economic and/or social benefits of such research (e.g. in designing facilities so to reduce risk during evacuation). We encourage initial studies to be made of crowds within relatively simple environments, such as on walkways, where an individual's desired direction of travel can be better judged than for example in a crowded street, where motivations may change dynamically and be influenced by many more factors. Gathering data during genuine evacuation procedures will always be problematic (practically, and in some cases ethically), but data gathered from practice evacuations may be very useful in testing, and further improving, current models. The importance of such safety issues has been further emphasized by the events of September 11th 2001 where large, highly populated buildings ('The World Trade Center' in New York and 'The Pentagon' in Washington D.C.), and the streets around these buildings, had to be evacuated.

2.4 Fish schools and bird flocks

In other animal aggregates, such as fish schools and bird flocks, group shape is often less constrained by environmental structure than in the human crowd examples discussed in section 2.3. In open space these groups can display clear cohesion and structural order, with the behavior of the individuals resulting in such ordered patterns of motion that they appear to move as a single coherent entity. When perturbed, as for example when a predator is detected, rapid waves of turning can propagate across the group (Radakov, 1973; Davis, 1980; Partridge, 1982; Potts, 1984). Many of these kinds of collective

behaviors can only be understood by considering the very large number of interactions among individual group members.

Early work on such collective phenomena hypothesized that birds can transmit information about turning almost instantaneously to other group members by "thought transference" (Selous, 1931), or by the generation by muscles or the brain of an electromagnetic field that could be detected by other group members (Presman, 1970). Heppner and Haffner (1974) argued that that a 'leader' must coordinate the motion of such groups whereas Radakov (1973) concentrated on the possibility that fish schools may interact through the propagation of relatively local information among group members. Radakov made important steps in moving towards quantifying certain aspects of collective motion in these groups, including the propagation of "waves of excitation" which spread across his experimental schools when disturbed. Such waves of turning were shown to share certain properties with physical waves in that they attenuated, potentiated, reflected off the tank walls and even seemed to cancel out if they met mid-school. The essential advance here is that Radakov realized that collective behavior need not be explained as a phenomenon coordinated by a leader, or by global information, but by the rapid propagation of local information about the motion of near-neighbors.

a) Models

Some of the most conceptually simple models of the coordination of such animal groups have focused on explaining how a propensity to align with near-neighbors can result in a longer-range alignment within a population of mobile individuals (Vicsek *et al.*, 1995; Czirók *et al.*, 1997; Czirók *et al.*, 1999). In these models it is assumed that individuals move at a constant speed and assume the average direction of motion (this direction being subject to error) of those within a local neighborhood. Such models are useful because their minimalism allows them to be analyzed using techniques developed for non-equilibrium statistical physics (for a review see Czirók and Vicsek, 2001). This comes at the cost of biological realism, however. For example, the mobile particles in these simulations neither avoid collisions nor exhibit attraction towards others. Consequently

they cannot form a self-bounded group (such as the bird flocks and fish schools described above) when individuals exhibit any error in decision-making, and thus cannot fully explain the clearly defined animal groups seen in many species.

Here we will focus on more biologically realistic (yet still much simplified) models of animal motion, based upon generic abstractions of the aggregation tendencies evident in fish schools and bird flocks (Partridge, 1980; Partridge and Pitcher, 1980; Partridge, 1982; Heppner, 1997). Several authors have developed models in which grouping results from individuals exhibiting local repulsion, alignment and attraction tendencies based upon the positions and orientations of individuals relative to one another (Aoki, 1982; Reynolds, 1987; Huth and Wissel, 1992; Couzin *et al.*, 2002). Repulsion simulates individuals avoiding collisions if they come very close to one another. Alignment reduces collisions among mobile individuals within a group and facilitates collective directional motion of large groups. Attraction allows groups to retain cohesion, and simulates an individual tendency to join groups and to avoid becoming isolated (Hamilton, 1971). In these models the individual behavioral rules result in group formation and cohesion, rather than fixing individual density within a periodic domain[1] (as in the simplest models described above).

Reynolds' model (1987) simulated the motion of computer-animated flocking "boids" within three-dimensional space, and demonstrated how local interactions among individuals can lead to realistic-looking collective behaviors such as polarization within groups, and cohesion of groups, even when moving around environmental obstacles. Incorrectly, this model is sometimes thought to have included global information, perhaps due to Reynolds' use of the term "flock centering". However it is clear from the original model description that information is restricted to local regions around each "boid". Although capable of simulating motion similar to that of real birds, this model is somewhat complicated, including properties such as banking during turns to make it "look better" (this was intended as an animation tool for computer games and films). This

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[1] A periodic domain is one with no boundaries. Individuals leaving the domain at one side reappear at the appropriate position at the opposite side. This is a standard technique in computer modeling to minimize the influence of "edge effects".

makes it difficult to interpret and analyze from a more rigorous scientific perspective. Somewhat simpler models have been developed in 2-dimensional space by Aoki (1982) and Huth and Wissel (1992), and in 3-dimensional space by Couzin *et al.* (2002). Aoki (1982) demonstrated that simple stimulus-response behaviors, similar to those used by Reynolds (1987), could account for the coordinated movement of groups of fish. Extending this model, Huth and Wissel (1992) investigated in more detail the potential interaction processes involved in coordinating such collective motion. They explored the possibility that individuals use a "decision-making process" from which they determine a single near neighbor with which they then interact, or an alternative "averaging process" whereby individuals average the influence of a different number of neighbors. Averaging models in which individuals combined the influence of several nearest neighbors were found to better account for the behavior of real fish, since they produced groups which were better aligned and less likely to fragment. Decision models, by contrast, could not account for the type of highly coordinated motion seen in real groups.

b) Individual behavior and group shape

Couzin *et al.* (2002) developed a model of animal aggregations in 3-dimensional space (e.g. flocking and schooling) similar to those described above. They demonstrated how relatively minor changes in individual behavior can result in dramatic changes in group shape. They also investigated some properties of the transitions between group-shapes that may highlight some fundamental properties of animal groups. Following the approach of Aoki (1982) and Huth and Wissell (1992) they assumed, for tractability, that individuals respond to each other within specified behavioral "zones" (see Fig. 9). The highest priority for individuals was assumed to be maintenance of a minimum distance between themselves at all times to avoid collisions (Krause and Ruxton, 2002). They achieved this by moving away from other individuals within a close-range spherical "zone of repulsion", with radius r_d. If not performing an avoidance maneuver, individuals were assumed to align with others within a "zone of orientation", r_o, and to be attracted to other individuals within a "zone of attraction", r_a. These latter two zones were spherical, except for a volume behind the individual in which neighbors were undetectable. All

behavioral zones in this model were non-overlapping. An individual would perform a correlated random walk if it did not detect any neighbors. Following these rules, individual trajectories were integrated over time at discrete intervals (timesteps), set as 0.1s apart, representing the response latency of fish (Partridge and Pitcher, 1980).

Couzin *et al*. (2002) investigated the consequences to group shape of changing the size of the zone of orientation (its width defined as $\Delta r_o = r_o - r_d$), and the zone of attraction (width defined as $\Delta r_a = r_a - r_o$), given random starting conditions. They calculated two properties from the simulation (after it had reached a dynamic equilibrium) that could allow group shape to be quantified:

1) Group polarization (p_{group}), ranging from $0 - 1$. This increases as the degree of alignment of group members increases,

2) Group angular momentum (m_{group}), ranging from $0 - 1$. This measures the degree of rotation of a group about the group center, increasing as degree of rotation increases.

It was found that, if individuals exhibited attraction to others but little, or no, orientation tendency, they formed a "swarm" group-type (Fig. 10A), characterized as having low p_{group} and low m_{group} (even though individuals do rotate around the group center they do so in different orientations, thus resulting in low group angular momentum). As the size of the zone of orientation increased, however, the group was found not to adopt the swarm formation, but instead would form a "torus" with low p_{group} and high m_{group} in which the individuals perpetually rotated around an empty core (even though individuals are locally polarized, overall group polarization is low) (Fig. 10B). The direction of rotation was random. If the zone of orientation was increased further, however, the group initially adopted a "dynamic parallel" conformation (higher p_{group}, low m_{group}) (Fig. 10C), and then a "highly parallel" arrangement (highest p_{group}, low m_{group}) (Fig. 10D).

This model predicts that these are the four fundamental types of collective state that individuals within such groups can adopt, and between these states the collective behavioral transitions are very sharp (Fig. 10E, F). It also demonstrates that large changes in group properties and organization can result from relatively minor changes in local

individual response, and that animal groups are likely to change rapidly between these states since intermediate group types are unstable. Biologically the ability of groups to change between structural types could be very important in allowing individuals to maximize fitness as conditions change. This may occur, for example, as a response to hunger, or to external stimuli such as the presence of predators. It is known that fish and birds tend to become more polarized within groups (individuals become better aligned) when predators are detected (Wilson, 1975; Partridge, 1982). This is important since it not only allows the individuals within the group to avoid colliding with one another, but also facilitates the transfer of indirect information about the presence of a predator. For example, if only one, or a subset of, individuals turns in response to such a stimulus, the alignment tendency allows this change in direction to be transmitted over a range much larger than the individual interaction radius. This property of groups is discussed in more detail in section 2.4*d* below.

If alignment range in the model is reduced the individuals adopt a torus conformation. This group shape may initially appear uncharacteristic of real animal groups, but is in fact adopted by many species of fish including barracuda, jack and tuna (see Parrish and Edelstein-Keshet, 1999, for a photograph of jack performing this behavior). This behavior results in a quasi-stationary group, yet allows the continual motion of individuals that is required by certain fish species for respiration, while permitting individuals to benefit from local polarization. Furthermore it may allow individuals to save energy since each is in the slipstream of another. If individuals exhibit attraction, but little or no alignment, they form a swarm. This behavior is often seen in aggregates of insects, such as midges (Okubo and Chiang, 1974) and mosquitoes (Ikawa and Okabe, 1997), but can also be exhibited by fish schools (Pitcher and Parrish, 1993). Although cohesive, this group type does not benefit from the advantages of polarization discussed above.

c) Behavioral transitions, collective memory and hysteresis

After initially exploring the types of group shape that form from random starting conditions, as described above, Couzin *et al.* (2002) investigated the consequences of different starting conditions to the collective behavior within their model. In nature, groups are likely to move between collective states as conditions change, and as a consequence of this the previous history of individual orientations and positions may have an influence on the collective behavior as behavioral parameters change. To investigate this possibility, the same simulation was used but the starting conditions were non-random. Keeping the size of the zone of attraction constant, the influence of individuals modifying the size of their zone of orientation was investigated. Starting with no alignment tendency ($\Delta r_o = 0$) the model was run to dynamic equilibrium (resulting in a swarm). Then, without resetting the model to the random starting conditions, the size of the zone of orientation (r_o) was increased slightly, and the model allowed to run to dynamic equilibrium again, and the process repeated until the group entered the dynamic polarized state. Then, the size of the zone of orientation was decreased sequentially in the same way, until eventually the model was returned to the original parameter settings ($\Delta r_o = 0$). Intuitively one would assume that this would simply mean the collective state moves from being a swarm, to a torus, to a parallel group type (as r_o is incrementally increased) and then back to a torus and finally a swarm (as r_o is decreased). As shown in Fig. 11, when the zone of orientation was increased the model behaved as assumed, but if moving through the same parameter space in the opposite direction (as r_o is decreased) the collective behavior was different. The group did not adopt the torus conformation, and instead eventually only returned to the swarm configuration. This demonstrates an important principle: that two completely different collective behavioral states can exist for identical individual behavioral rules, and that the transition between behavioral states depends on the previous history (structure) of the group, even though the individuals have no explicit knowledge of what that history is. Thus the system exhibits a form of "collective memory".

Intuitively one might assume that group-living animals only need evolve a direct interaction between individual internal state (resulting from internal and external stimuli)

and behavior (here the rules of interaction employed). Our results suggest, however, that the situation is not so simple, and that the evolution of collective (extended) phenotypes may be more complex. Importantly, this kind of behavior is likely not to be specific to this model, or even this class of model, but rather may be a generic property of transitions between collective behaviors.

d) Group shape and motion in the presence of external stimuli

Although the fundamental organizing principles defining the shape of aggregates such as fish schools and bird flocks do not rely on external stimuli, such stimuli may also be important in explaining shape under certain circumstances. For example, as suggested in section 2.4b, local interactions allow information (here encoded as the positions and orientations of neighbors) to be propagated across the group. Thus individuals within such groups can perform avoidance maneuvers without direct detection of an incoming signal. Simulating predator attack allows the response of groups to transient disturbance to be investigated. For example, Fig. 12 shows a time-series from an animation of a simulation of grouping developed by Couzin *et al.*, (2002) in which a predator is included (shown in red). Here the predator follows a simple rule; it moves towards the highest perceived density of individuals (Milinski, 1977). A supplementary rule is included to the behavior of prey individuals in the model described in section 2.4b above, which allows them to detect and move away from a predator. The model exhibits the characteristic collective patterns that have been described in natural groups under attack (Partridge, 1982), including "flash expansion" where individuals rapidly move away from the predator as it strikes (Fig.12a); "vacuolation", where the expansion results in a cavity forming around the attacker (Fig. 12c, d); and the "split effect", where a group may be fragmented (Fig. 12h).

The size of the volume in which individuals respond to others is also important in coordinating collective avoidance behaviors (Fig. 13). If this volume is small an individual will behave more or less independently of those around it. This increases the tendency of individuals to become non-aligned, and for groups to become fragmented

(Fig. 13a). As the size of this zone increases, an individual will respond to a greater number of neighbors. This increases the quality of information an individual has access to, and decreases the variance (through averaging over a greater number of influences). The group becomes capable of transferring information (Fig. 13b). The response of individuals not only to nearest neighbors, but also to neighbors further away (but still in a relatively local volume) also increases the speed of information transfer. This can explain the high speed of maneuver waves in birds (Potts, 1984) and fish (Radakov, 1973). If this zone continues to grow, however, the quality of information an individual acquires from the movement of others may decrease. The orientation and position of individuals further away is less likely to encode relevant information (Fig 13c). Large behavioral zones increase the homogeneity of response within the group. If all individuals respond equally to all others within a group, for example, they can collectively select a direction that may be detrimental to all, or almost all, of them. Group members would therefore be expected to respond only to those individuals that are most likely to have information that would benefit them. Proponents of self-organization theory often stress that animals do not *need* long-range information to coordinate group behavior (Bonabeau *et al*., 1997). However, localizing information input may provide significant adaptive benefits to an individual within a group, allowing sensitive response not only to predators but also to environmental obstacles.

Similarly, Inada and Kawachi (2002) investigated how directly changing the number of neighbors that an individual responds to affects the information transfer within such groups. Their model was also able to emulate the escape responses of fish within real schools, and showed that in groups of 50 individuals, responding to a relatively small number of neighbors ($\approx$ 3) was the best strategy for escape. However, their model requires individuals to be able to count the number of neighbors. Currently it is unclear whether fish perform such counts, or whether they perform behaviors such as changing the range over which they respond to others (which would indirectly change the number of neighbors with which they interact).

In addition to allowing collective avoidance behaviors, the rapid changes in turning and group shape in such animal groups may also act to confuse the sensory system of

predators, thus making it difficult to isolate and catch any given individual (Landeau and Terborgh, 1986).

Information transfer among individuals is also likely to influence their response to other stimuli, such as the positions of resources, or favorable regions within a heterogeneous environment. In aquatic habitats, for example, resources such as phytoplankton, the temperature or salinity of the water, and concentrations of dissolved gases are all known to vary in a non-uniform way, and over both small and large length scales. Individuals are therefore expected to modify their positions with respect to these properties so as to maximize resource intake and minimize physiological stress. However, this is a non-trivial task: unpredictability and local fluctuations make finding and moving up or down such environmental gradients (taxis) difficult where an individual has only local knowledge on which to base its motion. In many cases, such as phytoplankton or gaseous concentration, the gradients occur over such large spatial scales (in the order of kilometers) that local detectable gradients are inherently extremely shallow. In the case of thermal gradients, for example, even the steepest horizontal gradients in the open sea are $0.01 - 0.1°C/100m$ (Dizon *et al.*, 1974).

Grünbaum (1998) used computer simulation to investigate the theoretical consequences of grouping to such taxis behavior. He assumed individuals use a simple form of taxis, known as klinotaxis, whereby a moving individual modifies its probability of making a turn as a function of whether conditions are perceived to improve or deteriorate over a given time interval. Such behavior is known to facilitate taxis in even very simple organisms, such as bacteria (Keller and Segel, 1971; Alt, 1980; Tranquillo, 1990). Although they are not directly detecting the gradient, individuals performing such taxes will, on average, spend more time moving in favorable directions than in unfavorable ones. By simulating groups of individuals performing this behavior under conditions where they do not interact with one another (asocial taxis) and do interact by balancing the tendency for taxis with a simple schooling behavior (social taxis), Grünbaum (1998) demonstrated that such social interactions improve the motion of individuals up a gradient. The alignment of individuals, and thus transfer of information, when schooling,

allows averaging of individual errors in gradient detection, and therefore results in reduced deviations in motion from the desired direction of travel. This information-sharing within schools of fish has been likened to a "sensory array" (Kils, 1986) which allows information to be gathered over a wider spatial range than would be possible for a solitary or non-interacting individual, and dampens the influence of small-scale fluctuations in the environment. The model also predicts that the benefits of such information-sharing are dependent on group size. As group size is increased the efficiency of taxis shows an asymptotic increase: initially it increases steeply, but then the rate of increase reduces over time leading to a plateau where further increases in group size have very little effect on taxis accuracy. Owing to the deliberately abstract nature of the model (to characterize a generic property), the absolute group sizes are less important than the general prediction of the type of relationship that should be expected in natural groups.

A further property of individual behavior that Grünbaum (1998) explored was the balance of the taxis and interaction 'social forces' within his simulation, which demonstrated a trade-off between these two tendencies. Individuals that only interacted weakly with others (the taxis response is weighted strongly) would benefit little from averaging of information. At the opposite extreme, where the interactions of individuals with one another are strong relative to taxis, the group will take a long time to adjust to changes in gradients. Thus, in reality, individuals may be expected to evolve an intermediate strategy.

Niwa (1998a) developed a conceptually similar model to investigate how very large fish schools could use klinotaxis to move up heterogeneous temperature gradients when migrating. Migrating pelagic fish such as sardines, anchovies and mackerel form cohesive groups that can extend over kilometers, and contain in excess of 10^6 fish (Pitcher and Parrish, 1993). The memory necessary for thermal klinotaxis (comparing previous and current temperature) may be obtained from internal core temperature providing fish with information about previous thermal history (from internal sensors), and their current temperature detected by sensors in the skin (Neill *et al*., 1974). In

Niwa's model individuals were considered to have a desired internal temperature, and to behave in a similar way as individuals in Grünbaum's (1998) model described above. Even for such large groups, simple and local response behaviors are able to account for the collective migration behavior.

Group shape has also been found to be influenced by parasites. In wild schools of banded killifish (*Fundulus diaphanus*), for example, group geometry is dependent on the overall prevalence of a trematode parasite (*Crassiphiala bulboglossa*) among group members: groups with high parasite prevalence tended to exhibit a broad phalanx-like shape, whereas those with low parasite prevalence tended to be elliptical, with the major axis aligned with the direction of travel (Ward *et al*., 2002). Interestingly, a similar change in group shape has been exhibited in a general model of grouping behavior (of zebra herds, *Equus burchellii*, but also applicable to other group-types) by Gueron *et al*. (1996). The difference in this model resulted not from changes in the interactions among individuals, but simply from a difference in individual speed. Groups in which individuals moved more slowly tended to proceed as a phalanx, whereas groups in which individuals tended to move more rapidly formed a more columnar structure, elongated in the direction of travel (see section 3.2 below for further discussion of this model). If parasite load affects swimming speed, such a difference may be able to account for the difference in group shape in killifish. Ward *et al*., (2002) suggest that the trematode cyst may reduce swimming performance by affecting the dorsal musculature of infected individuals, and/or by reducing the hydrodynamic streamlining of individuals. It should be noted, however, that other changes to behavior in schooling models can also change group shape. For example, decreasing the angle of perception (increasing the frontal bias) will also result in a group more elongated in the direction of travel (Couzin, unpublished data).

e) Parabolic groups of predatory fish

Group shape may also be important to predatory fish. Partridge *et al.* (1983) analyzed the structure of Atlantic bluefin tuna (*Thynnus thynnus*) schools in the wild, from aerial photographs. Such groups are well suited to this kind of analysis because they swim just under the water surface, so the third spatial dimension is not required for the analysis of their positioning behavior. Schools varied in size from 2 to 79 individuals, and group members tended to occupy very defined positions relative to one another. In small schools (≤ 10 members) nearest neighbors tended to be alongside (90º), and consequently groups tended to be more or less straight lines (perpendicular to the direction of travel). For larger groups, however, nearest neighbors tended to occupy positions of 45º and 135º. Perhaps the most interesting type of group shape was a "parabola" with the deflection point in the center of the group with respect to the direction of travel. Partridge *et al.* (1983) suggest that this group shape allows the school to act like a 'seine' net, funneling or encircling the prey fish. They also hypothesize that individuals at the edge of the parabola would be less likely to catch prey (due to increasing overlap of strike zones from the group center), and thus it is possible that some alternative benefit may be associated with these positions, or that individuals change position within the group between hunting events.

3. Group internal structure

3.1 Analyzing spatial positions in natural groups

Despite the ubiquity of animal aggregations, there is limited quantitative information about the internal structure of most vertebrate groups. Groups moving in three-dimensional space present a particular challenge to study since there are significant technical complications involved in recording accurately the spatial positions and orientations of group members. Consequently, attempts to characterize such structure are often limited to qualitative observations (Radakov, 1973), although through the use of inventive camera-based techniques it has been possible to make accurate recordings of spatial positions in fish schools (Cullen *et al.*, 1965; Partridge, 1980; Partridge and

Pitcher, 1980; Partridge *et al*., 1980) and bird flocks (Major and Dill, 1978; Davis, 1980; Pomeroy and Heppner, 1992; Heppner, 1997).

Partridge *et al*., (1980) used photographic techniques to record the positioning of individuals within fish schools in three-dimensional space within a large circular channel (1.8m wide and 31m in circumference) in the laboratory. A moving gantry projecting from the center allowed fish schools to be filmed from above. Fish were trained to swim over a "speckled spot of light" projected onto the floor of the tank, and thus by rotating the gantry at a constant speed they could film the school as it swam to keep pace with the spot. To reconstruct the three-dimensional positions and orientations of the fish they used a shadow method (Cullen *et al*., 1965) in which a secondary light shone at a known angle on to the school casts shadows of the fish. The area filmed included that where the shadows were cast, and a calculation involving the known position of the light and the depth of the water allowed the height of the fish in the water column to be estimated, thus providing the third spatial dimension. There are, however, limitations to this method. Firstly, it is very time-consuming, and somewhat subjective, to relate a shadow to an individual fish within the video sequence. Secondly, in situations where fish become closely packed, it is not possible to record the positions of all fish due to individuals occluding one another. A third limitation to this particular study was that an extraneous stimulus controlled the position and speed of the group. Such a stimulus was likely to have an influence on the grouping behavior of fish by constraining their natural movement tendencies, and by forcing fish to balance two social forces: their motion with respect to one another, and their motion with respect to the stimulus.

Nevertheless, this technique is still vastly superior to qualitative observations, and Partridge *et al*. (1980) were able to investigate positioning behavior in groups of up to 30 individuals for three species of fish: cod (*Gadus morhua*), saithe (*Pollachius virens*) and herring (*Clupea harengus*). As well as being commercially important, these fish possess different degrees of schooling tendency. Cod are weakly facultative schoolers, whereas saithe, although facultative schoolers, spend the majority of their time in polarized groups (individuals within the group are aligned). Herring are obligate schoolers, and form

highly polarized groups. In order to examine internal group structure, both nearest neighbor distances, and the elevation and bearing of group-members to their nearest neighbors were recorded. Elevation and bearing correspond to the angle between the current orientation of the reference individual and the position of the nearest neighbor, in the vertical and horizontal plane, respectively. The angles 0º and 180º refer to directly ahead of, and behind, the reference individual, respectively.

Individuals were shown to exhibit a minimum approach distance (analogous to the "zone of repulsion" described in section 2.4b). To ascertain whether positioning was non-random, the elevation and bearing distributions were compared to those generated by a random (null) model in which individuals were assigned positions at random within a volume equal to that of the real school. Fish within the real schools were found to occupy non-random positions in all experiments. In cod and saithe, the distribution of bearings had a peak at 90º, showing that individuals tended to be closest to lateral individuals. The distribution was more peaked for the relatively more polarized saithe groups. In herring schools, however, the distribution of bearings was found to be bimodal with nearest neighbors found most frequently at angles of 45º and 135º, showing that these fish adopt a more lattice-like structure. Dill *et al.*, (1997), however, questioned the use of the null model used in these analyses, arguing that the results may actually be an artifact of using such a simplistic model with which to compare the data. They demonstrate how more complex, and perhaps more biologically meaningful, null models can be constructed.

There are relatively poor data available to quantify the internal structure of bird flocks. Using stereo photography it was possible for Major and Dill (1978) to record the positions of birds within flocks of European starlings, *Sternus vulgaris*, and dunlin, *Calidris alpina*. They concluded that there were "striking similarities" between the internal organization of bird flocks and fish schools, although the large variance in the data from bird flocks, and the limited number of species investigated, makes rigorous comparison difficult. Furthermore, they were unable to record the flight-paths of individual birds over time. Davis (1980) observed the coordinated turns in flocks of dunlin, but had a very small sample size (nine "analyzable incidents"), and just recorded

the number of birds with light plumage visible over very short time-periods (700 milliseconds). The main problem with this type of analysis, as Heppner (1997) points out, is that as a flock moves relative to an observer, a 'wave' of brightness (through revealing light plumage, or the reflection of light from the body) may appear to cross the flock, indicative of a turn. However, such an effect is likely to be an artifact of the change in the position of individuals relative to the stationary observer and the light source.

In both bird flocks and fish schools it appears that the internal structure of groups is usually dynamic, with individuals frequently shifting position. For example, Pomeroy and Heppner (1992) filmed a flock of 11 pigeons in flight, and found that during a turn birds in the front of the flock can readily fall to the back, or those on one side change to the other. This was a consequence of the birds seeming to employ a relatively constant turning rate during a turn, resulting in positions being rotated.

Sinclair (1977) (in conjunction with J. M. Cullen) used aerial photographs to analyze the spatial positions of individuals within grazing African buffalo (*Syncercus caffer*) herds. They used a manually operated plotting machine (in a nuclear physics laboratory, designed to plot the tracks of particles in bubble chambers) to record the positions and orientations of adults and calves. From these data the distances and bearings to nearest neighbors were calculated. To search for non-random patterns they compared the nearest neighbor data with those generated by a model in which individuals were randomly assigned positions within the same area. In all five herds analyzed, the distance of individuals to their nearest neighbor had a significantly higher than expected number high values. This suggests that the animals are over-dispersed when grazing. When the angles to nearest neighbors were analyzed there appeared to be no consistent pattern. However, in sheep it appears that grazing herds display more evident structure, with nearest-neighbors tending to be at a bearing of about 55º ahead (Crofton, 1958). These data suggest that in sheep herds individuals become progressively more crowded towards the front of the group, since, if this were not the case, nearest neighbors should be expected to be as often behind as in front. Until further studies are made, however, it is difficult to interpret what these results mean with regard to the interactions among individuals within

herds. We encourage any researchers who have any relevant data on the distribution and/or orientation of individuals within herds to make this information publicly available so more rigorous analysis of the grouping behavior, and comparisons between species, can be made.

Throughout this paper we have emphasized the need for empirical studies to test existing models, and develop new theoretical approaches. One of the principal limitations to the study of collective behavior is the difficulty in recording and analyzing the movement of many organisms concurrently. However, only by obtaining accurate recordings of the movement of individuals from which behavioral properties such as the interactions among individuals, and between individuals and their environment can be made, can we begin to understand the processes that underlie collective behaviors. As described above, the manual recording of the positions of individuals over time is extremely laborious. Through recent technological advances, however, a new possibility has been introduced: that a computer can be programmed to 'see' and record the movement of animals automatically. In this way it is possible to track a large number (tens or hundreds) of organisms simultaneously in 2-dimensions (e.g. fish within shallow water) by analyzing film made from above (Couzin, 1999; Roditakis *et al*., 2000) or fewer individuals within three-dimensional space (where occlusion of individuals in the center of large groups is inevitable) from film made by two or more cameras (e.g. one camera filming from directly above a group, and another from the side) (see Osborn, 1997; Parrish and Turchin, 1997). Once trajectories have been obtained it is possible to perform time-series analyses of the velocities of each individual with respect to other group-members, investigating cross-correlations between the velocities of individuals, as well as auto-correlation of the focal individual's velocity (see Okubo, 1980; Partridge, 1980; Parrish and Turchin, 1997). Parrish and Turchin (1997), for example, examined a range of potential "foci" that may influence the behavior of individual fish (juvenile blacksmith, *Chromis punctipinnis*). Such foci were assumed to either be attractive, repulsive or neutral depending on the distance separating it from the fish and ranged from the individual's nearest neighbor to the centroid (center) of the entire group. They found that individuals appear to pay most attention to their nearest neighbor and to the school as an

entire unit, although it is currently difficult to determine from these results what behavioral rules are being used by the fish.

It would be interesting to further develop analysis techniques for such groups. One attractive avenue of research may be to use computer models of grouping to make predictions about where one would expect individuals to move to, from one instance (in time) from a video sequence, to a future instance. Thus one could search for theoretical behavioral rules that have the highest predictive power (over a range of time-intervals) when compared to a real data set. It would also be possible, using the type of computer vision systems mentioned above, to recreate the visual information available to each individual at an instance in time. This may provide further insight into the actual information available to individuals within groups (e.g. for fish that predominantly use vision, such as the stickleback, *Gasterosteus aculeatus*; or ungulate herds filmed from above). Since the imaging software can calculate the size, orientations and positions of individuals, it would be possible to program it to calculate where each individual's eyes are, and generate an impression of what visual information is available when making movement decisions. This is important because there may often be limits (which may vary with environmental conditions and the degree of local crowding) to the distances at which individuals are able to detect, and respond to, neighbors. The influence of external stimuli (such as the perception of obstacles) could also be investigated in this way. Thus, we believe further developments of imaging and behavioral analysis systems could provide new, and important, insights into the mechanisms of grouping behavior.

3.2 Differences among group members and the internal structure of groups

Radakov (1973) considered fish within schools as being behaviorally identical and interchangeable with regard to position. In the simulations described above, it is also assumed that individuals are identical. This is necessary to demonstrate how patterns form with the simplest possible assumptions and information input. However, the positions that individuals take within groups, relative to others, have important

evolutionary and ecological consequences (Hamilton, 1971; Okubo, 1980; Krause and Ruxton, 2002); see Krause, 1994, for a review.

In many cases group members are not intrinsically equivalent (Pitcher *et al*., 1985; Parrish, 1989a; DeBlois and Rose, 1996; Krause *et al*., 1996). Differences among individuals, such as age, nutritional status and sex, may all influence the position adopted by an individual within a group. For example, Krause (1993a), in a study of schooling fish (roach *Rutilus rutilus*), showed that starved individuals would tend to occupy positions towards the front of the group. It is likely that this increases food capture rate by these individuals since they are more likely to be able to detect and consume floating food items than are individuals towards the rear of the group. However, being at the front also increases the chance that these individuals will be the first to encounter predators (Bumann *et al*., 1997). Furthermore, there is evidence for certain mobile fish schools that individuals occupying positions whereby they are in the slipstream of others may need less energy for locomotion (Herskin and Steffensen, 1998). Consequently, there may be both benefits and costs to spatial positions. Individuals within groups may therefore be expected to modify their positions relative to neighbors as a function of their internal state; hungry individuals, for example, being more willing to risk dangerous positions if that will benefit their resource intake. When the advantage of being in a frontal position is outweighed by the perceived risk of predation, however, one may expect that individuals will avoid the group front, perhaps occupying positions closer to the group center (Hamilton, 1971). Krause (1993b) found that minnows, *Phoxinus phoxinus*, respond to perceived danger by moving to positions where they tend to be surrounded by near neighbors on all sides. However, the center need not necessarily be the safest position within a group. Individuals in the center may not be able to detect a threat directly and may also be constrained in their escape movement by the proximity of others. Parrish (1989a), for example, found that Atlantic silversides, *Menidia menidia*, suffered higher predation from black sea bass, *Centropristis striata*, if they occupied central positions within the school. McFarland and Okubo (1997) suggested that central positions in fish schools may also be detrimental for another reason. Individual fish consume dissolved oxygen and increase local ammonium concentrations. In the center of large groups the

modification of dissolved gases may be such that respiration is inhibited, which may be a group-structuring factor in large (particularly stationary) groups.

To investigate the influence of individual behavioral heterogeneity on grouping dynamics, Gueron *et al.* (1996) developed a simple model of herding animals. Their model is conceptually similar to those described above to investigate fish schools and bird flocks, in that individuals are assumed to respond to others within local zones. In their model, individuals attempt to maintain a minimum separation distance. This behavior has the highest priority. Outside this zone is a "neutral zone" extending to the sides, and ahead of, the focal individual. In this zone, individuals do not respond to neighbors unless all neighbors are on the same side, in which case the focal individual will move towards neighbors, but not change speed (representing avoidance of isolation). Lower in priority is the "attraction zone", which extends beyond the neutral zone, again to the sides and front. The rule employed if individuals are found within this zone is to bias both direction and speed to maintain proximity to neighbors. If no individuals are detected in any of these zones, then individuals respond to neighbors (if any) that are present to their rear. An individual that only has neighbors to the rear is termed a "leader". Note that this definition emerges from the relative positions of individuals within the group, as opposed to being explicitly specified. A leader is assumed to reduce its speed to remain in proximity of other group members. Individuals that do not detect any neighbors within their behavioral zones are termed "trailers". Such individuals speed up to represent their attempting to maintain contact with the group.

In the case where all individuals are assumed to be identical, it was found that for a wide range of walking speeds, large groups (up to 100 individuals) could maintain cohesion for long time periods. At low walking speeds the group adopted a phalanx-like structure, with individuals forming a flat moving front. As individual speed was increased, however, the group structure became more columnar.

As a next step, groups were considered to be composed of two subpopulations, each with a different speed. Not surprisingly, individuals in the faster subpopulation tended to

occupy positions at the front of the groups, becoming "leaders" irrespective of their positions within the group when the simulation was started. Without individuals responding to others behind them (in the "rear zone") these subpopulations will inevitably separate, given time. If individuals did respond to those behind them, it was possible to retain cohesion, but as the difference in speed between the two subgroups increased this became less likely, and subgroup fission occurred more rapidly. However, given that the rear zone was set as the 'lowest priority' in this model, it is possible that fragmentation of subpopulations would occur even when the difference in speed was relatively low, since it is possible that individuals would not respond to those to the rear for sufficiently long periods of time. Gueron *et al*. (1996) suggest that differences in speed between lactating and non-lactating zebra (lactating individuals moving more slowly) may explain the segregation of these individuals into subpopulations. This segregation occurs particularly in circumstances where individuals tend to move quickly, such as when the perceived threat of predation is high (for example, when moving near waterholes).

Couzin *et al.* (2002) also investigated the consequences of behavioral heterogeneity on the spatial positions individuals occupy within mobile animal groups, by modifying the model of grouping in 3-D space outlined in section 2.4b. Unlike Gueron *et al.* (1996), they assumed a continuous distribution of individual phenotype within the population, as opposed to just two classes of individual. To simulate variation they modified the behavioral parameter under investigation by adding a Gaussian-distributed random deviate centered on 0 (independently drawn for each individual). Therefore the standard deviation of this distribution determined the degree to which individuals within the group differed with respect to that parameter. They investigated the consequence of variation in individual properties, including speed, turning rate, error, and the size of each of the three behavioral zones. In order to quantify the spatial positioning behavior of individuals, the correlation between these parameters and the distance between individuals and the group center, and the distance to the front of the group, were measured (Fig. 14A-D).

Individuals' speed was positively correlated with their being at the front of the group, and slightly further away from (negatively correlated with) the group center (Fig 14A). Those with a higher rate of turning tended to be at the rear, and slightly closer to the center, of the group (Fig. 14B) and individuals with higher degrees of error in movement tended to occupy the rear of groups. The size of the immediate personal space around individuals, represented as the zone of repulsion (r_r), was important in structuring groups: individuals with small values of r_r tended to occupy positions at the center of, and towards the front of the group (Fig. 14C, E). For all parameters investigated the strength of the correlation (degree of sorting) increased as the variation within the population increased.

These results suggest that behavioral and/or motivational differences among individuals may constitute an important organizational principle within animal groups. As explained above, there may be many reasons why individuals within groups may be expected to modify their positions relative to others. This model provides potential self-organizing mechanisms whereby this may occur. Importantly the sorting within the model depends on "local rules of thumb" and not on the absolute parameters, but rather the relative difference between individuals. Thus an individual decreasing its zone of repulsion relative to near neighbors will tend to move towards the center of the group, even if it has no knowledge of where the center actually is. This is important, because in many naturally occurring large collectives of vertebrates it is extremely unlikely that individuals have the cognitive or sensory capabilities to calculate their absolute position within the group (individuals are often closely packed, restricting perception range). For example, pelagic fish schools can extend over kilometers and may consist of hundreds of thousands of individuals (DeBlois and Rose, 1996), so it would be impossible for individuals to measure their distance from the edge. Thus natural selection is likely to favor local self-organized mechanisms that individuals can use to modify their position relative to others, without necessitating a specific destination or knowledge of current location.

Another point to note about this type of sorting mechanism is that, due to the interaction mechanics involved, individuals with similar phenotypes will become more closely

associated within groups. In many fish schools individuals tend to be close to others similar in size (Pitcher *et al*., 1985; Parrish, 1989a; DeBlois and Rose, 1996; Ward *et al*., 2002) or, in multi-species groups, to conspecifics (Parrish, 1989a). Couzin *et al*'s model suggests a mechanism whereby this would occur without invoking complex individual recognition capabilities: if size, or species, is correlated with behavioral response, then this could account for the assortment seen. A further property of this self-organized sorting is that given consistent differences among individuals, the system will re-assemble to form the same configuration (statistically) after it has been perturbed from that state.

Self-organized sorting may also improve our understanding of the spatial positions taken up by parasitized individuals within groups. For example, Krause and Godin (1994) in the laboratory, and Ward *et al*. (2002) in the field, studied the influence of parasitism on the positioning behavior of individuals within natural fish schools (banded killifish). They found that individuals parasitized by the digenean trematode *Crassiphiala bulboglossa* tended to occupy peripheral positions in the group (see also Barber and Huntingford, 1996, for a similar host-parasite system). It has been suggested that the parasite may be manipulating the behavior of the host, resulting in it modifying its position with respect to others within the group, to increase the chances of propagation of the parasite to its definitive host, the belted kingfisher, *Megaceryle alcyon* (Barber *et al*., 2000). Investigating this behavior in the context of the type of sorting mechanisms we have outlined here may improve the understanding of the behavioral modifications that occur in such parasitized individuals.

3.3 Social dominance relationships and structuring within groups

Several authors have suggested that self-organized structuring may also occur within animal groups as a result of dominance interactions among individuals (Hogeweg and Hesper, 1983; Hogeweg and Hesper, 1985; Theraulaz *et al*., 1995; Bonabeau *et al*., 1996; Hemelrijk, 1998; Bonabeau *et al*., 1999a; Hemelrijk, 1999). Dominance relationships among individuals within a group have been recorded for many animals, such as birds

(Schjelderup-Ebbe, 1913, 1922), primates (Kummer, 1968; Mendoza and Barchas, 1983; Barchaz and Mendoza, 1984; Thierry, 1985), ungulates (Tyler, 1972; Barton *et al*., 1974), fish (Francis, 1983; Beugrand and Zayan, 1984; Hsu and Wolf, 1999) and insects (Franks and Scovell, 1983; Heinze, 1990; Bourke, 1988; Oliveira and Hölldobler, 1990). Dominance interactions are typically considered to be "pairwise": that is, most contests involve just two individuals at a time. Individuals that tend to "win" such interactions (termed high rank individuals) are often thought to increase their access to resources (such as mates or food) so individuals should be expected to strive to increase their rank within the group (Datta and Beauchamp, 1991). However, dominance interactions with others are often aggressive, and thus may be energetically costly and time-consuming. Individuals may therefore also be expected generally to avoid conflict, instead relying on passive recognition mechanisms once the hierarchy has been established (Karavanich and Atema, 1998). When such a hierarchy (network of dominance-submission relationships) persists, it should therefore be expected to organize the group in such a way that the costs of the dominance interactions do not offset the benefits of group membership.

Within the context of self-organization theory, it has been proposed that a double reinforcement mechanism may explain certain properties of the dominance hierarchies seen in natural groups. Simplistically, such a mechanism assumes that winners of interactions increase their probability of winning future interactions, whereas losers increase their future probability of losing (Chase, 1982a, b). If it is assumed that all individuals are initially similar with regard to their probability of winning interactions, then the outcome of early contests will be relatively unpredictable. However, if by chance an individual wins, this increases its chance of winning a future contest. Similarly, a losing individual is more likely (probabilistically) to lose in future. Thus, this process of feedback and amplification of initial stochastic events can result in progressive differentiation of the group. Such effects have been reported in real animal groups (Ginsburg and Allee, 1975; Chase, 1980, 1982a, b, 1985; Francis, 1983; Beugrand and Zayan, 1984). However, in reality it is likely that differences among individuals affect their real propensity to be successful in such contests (Slater, 1986), and the initial assumption that all individuals are similar in this respect merely acts to show that

inherent differences are not *essential* to explain the generation of a hierarchy. Of course, a model could be constructed in which individuals have different intrinsic rates of feedback: that is, for some individuals positive and/or negative reinforcement may be stronger than in others. It should be noted, however, that experimentally it may be difficult to differentiate from a model based on pre-existing differences, a so-called "correlational model" (Chase, 1980) from self-organized alternatives that either do, or do not, incorporate inherent heterogeneity in response to interactions. Even in cases where the data are relatively detailed, such as for some social insects such as *Polistes* wasps (Theraulaz *et al*., 1989; Theraulaz *et al*., 1992; Theraulaz *et al.*, 1995), it is currently not possible to determine to what degree self-organized reinforcement structures dominance hierarchies since the empirical data can be explained by both correlational and self-organized approaches (Bonabeau *et al.*, 1999a). Interestingly, recent evidence suggests that even simple organisms such as *Polistes* may be able to recognize nest-mates, and that this ability influences the intensity of dominance interactions (Tibbetts, 2002).

Hogeweg (1988) and Hemelrijk (1998, 1999) extended the self-organized models of hierarchy formation to investigate potential spatial effects that may emerge in populations of individuals that exhibit the type of feedback mechanism described above. Individuals exhibit a simple grouping tendency and can perform double reinforcement dominance interactions. It should be noted that although a centripetal force (tendency to move towards the group center) has not been explicitly encoded in these models, the propensity of individuals to approach others if they become isolated would result in a mean acceleration of individuals towards the group center (see Okubo, 1980, 1986). Without such an inward-oriented force (relative to the current group center) the group would tend to dissipate by randomness of motion. After a dominance interaction, both the winner and loser of such interactions turn a randomly determined angle of 45º either clockwise, or anticlockwise, and move forward. The loser is assumed to move further in a given time-interval, simulating it being "chased" away (thus it moves more rapidly). The model therefore assumes that the dominance rank of an individual influences the mobility of individuals; more submissive individuals being more mobile. In these models this rule-set results in subordinate occupying peripheral positions, and dominant individuals the group

center. Given a physical system in which particles move at different rates, similar spatial structuring often results. A commonly known example of this is that more active particles within a liquid or gas often rise (e.g. hot air rising). In this case gravity can be considered analogous to the net centripetal force.

The degree to which groups are structured in this manner is related to the difference in motion among individuals, and hence the "steepness" of the hierarchy, with the distance from the group center and dominance level being increasingly negatively correlated as the steepness increases. Thus Hemelrijk's model suggests that this spatial structure will be more defined for despotic societies (where the hierarchy gradient is steep) than for egalitarian societies (where the gradient is relatively shallow). Further extensions of this model allow investigations of other properties, including the importance of memory of previous interactions, and different strategies with regard to the perceived risk of encounters, and thus provides a useful tool with which to make predictions about dominance relationships in real animal groups (Hemelrijk, 2000). However, it may still be difficult to differentiate between different explanations for the same phenomena, as discussed by Bonabeau *et al.* (1999a).

3.4 Leadership

The models we have introduced above demonstrate that leadership is not a necessary requirement for collective organization of groups. We have also described how leadership may 'emerge' within mobile groups, as a result of the interactions among individuals. In some cases the behavioral properties of an individual may bias its probability of being a leader (Gueron *et al.*, 1996; Couzin *et al.*, 2002; see Krause *et al.*, 2000a for a review of leadership in fish), whereas in the case of essentially identical individuals the probability of being a leader of a group may be largely random, or be dependent on the initial starting conditions. This concept of leadership is quite different from that used by early researchers such as Selous (1931) and Pressman (1970), who assumed a leader has control of all other group members. This is clearly not the case. However, individuals that happen to be at the front of a group, or whose behavior increases their probability of

occupying frontal positions, are likely to have a stronger influence on the motion of the group than are individuals further back, even if all individuals are identical and follow exactly the same rules.

Consider a simplistic situation. Assume you are walking at the front of a group which is moving forward in a straight line. If you were to suddenly stop, this would be likely to impact on the motion of other group members, who must now avoid you to continue their journey. If a group is sufficiently fast moving and tightly packed, this can cause great disturbance. However, consider that you perform the same stop behavior, but instead of starting at the front of the group, you were to start at the back. Your behavior would have little, or no, effect on other group members who are not impeded by you. Similarly, within a herd, school, or flock an individual changing speed at the front of a group will have a larger influence on other group members than if it were at the rear. If an individual at the front performs a turn, for example, this also reduces its speed relative to the direction of group motion. Thus it is likely to interact with a large number of other group members, and its orientation is much more likely to be propagated to other group members than if it were in the rear of the group.

Such leadership effects may be further enhanced if individuals have a tendency to interact more strongly with those ahead, so called "frontal bias" (Huth and Wissel, 1992), which has found support from empirical work on fish shoals (Bumann and Krause, 1993). This may be a result of having a blind area to the rear in which they cannot detect others, or individuals having evolved to bias their movement decisions more heavily to those ahead of themselves in moving groups. This makes sense since the individuals at the front of a group are more likely to encounter stimuli, such as environmental obstacles, sit-and-wait predators or resources.

4. Group size and composition

In the previous sections of this chapter we have considered how the interaction dynamics among individuals result in the formation, internal structuring and collective behaviors of

vertebrate groups. In this section we consider the distribution of grouping individuals over larger spatial and temporal scales, and discuss how individual behaviors lead to population-level dynamics. At an ecological scale, the distribution of social organisms (such as schooling fish and herding ungulates) results from the processes of amalgamation (fusion) and splitting (fission) of groups (here we consider isolated individuals as being in a group of size 1) within the context of their environment. Understanding these properties is essential if we are to understand better disease transmission and the transfer of information among individuals (e.g. social learning). In section 4.1 we discuss how the timescale over which fission and fusion occurs can result in stationary frequency distributions of group size within a population, and how modeling may help determine the underlying mechanisms of such processes when only group-size distributions are available (as in many natural systems where the distribution of group sizes is easier to record than the underlying interactions among groups). In section 4.2 we will explore how the spatial dimension through which individuals move, and habitat properties such as fragmentation may affect the distribution of grouping organisms. We then consider how phenotypic differences among individuals may influence fission-fusion systems in 4.3. We conclude the section by considering how the theory of optimal group size can be considered from a self-organization perspective, in 4.4.

4.1 Fission, fusion and group size distributions

The fission-fusion processes described above may often occur sufficiently rapidly (relative to the temporal and spatial scale over which ecological properties may change) that the group-size distribution is stable (stationary) (Okubo, 1986; Gueron and Levin, 1995; Bonabeau and Dagorn, 1995; Niwa, 1998b; Bonabeau *et al*. 1999b; Sjöberg *et al*., 2000). The type of shape of group sizes found within a population is shown in Fig. 15 for African buffalo. Okubo (1986) discusses some of the behavioral and ecological constraints which may result in the equilibrium distribution of group size being unstable within given intervals of time, including sudden changes in the behavior of grouping individuals, or of the environment (e.g. availability of resources, or visibility). We will

return to the influence of these variables later. However, for simplicity it is reasonable at the offset to assume stability in these properties.

In cases where fusion is high relative to fission, then the number of groups with few individuals should tend to decrease (larger groups will be more likely to persist) and the group-size distribution would be expected to have a relatively long tail. If fusion is low relative to fission, however, groups tend to be unstable, and large groups are less likely to form. Consequently group-size distributions would be more rapidly decreasing. Several studies have recorded exchange rates between groups of fish. Hilborn (1991), for example, studied skipjack tuna, *Katsuwonus pelamis*, and found that 16-63% of individuals changed shoals within a day, although Bayliff (1988) found much more stable groupings in the same species. Klimley and Holloway (1999) for yellowfin tuna, *Thunnus albacares*, and Bayliff (1988) for skipjack tuna, found that cohesion of schools was high, and the half-life of schools was likely to be in the order of weeks. Krause (1993a) found in roach shoals (*Rutilus rutilus*) that a turn-over of more than 50% of the individuals occurred within 2 days. In killifish (*Fundulus diaphanus*) shoal encounters were observed very frequently (on average every 1.1 min for a given shoal) resulting in high rates of exchange of individuals between shoals and a complete mixing of fish in the population within 24 hrs (Krause *et al*., 2000c). A similar result was found by Seghers (1981) in spottail shiners (*Notropis hudsonius*) and Helfman (1983) reported an absence of shoal fidelity in the yellow perch (*Perca flavescens*). In summary, these data indicate that fission-fusion processes occur more frequently in freshwater where density of individuals is high and thus encounters more common than for pelagic marine species. Thus we would expect that the group size distributions would reflect the different fission-fusion dynamics of these groups.

It is important to note when looking at group-size distribution data, that the pattern seen results from a dynamic process. Even though such a distribution can often be relatively stationary, it is the continuous splitting and fusion of groups that makes it so. Consequently it represents the probability distribution of a given individual being in a group of a certain size at any given moment of time. Considering the large scale over

which fission-fusion dynamics takes place, some modelers (Okubo, 1986; Gueron and Levin, 1995) have made the assumption that the population properties can be described by a non-spatial approach, where one may attempt to define the average rate of fusion or fission of groups. However, if we consider the mechanisms at the level of the individual it will become clear that both the probability of a group encountering another (and fusing) and the probability of a group spontaneously fragmenting (fission) will be dependent on the size of the group in question. For example, the range over which individuals can interact (and/or the strength of interaction) is likely to influence group cohesion. As described above (section 2.4), groups much larger than the range of individual interactions can form. However, as group size increases, it will be increasingly likely that a group will fragment (due to the inherent stochastic nature of interactions and motion). Such fragmentation may be exacerbated by interactions with other groups and/or the environment (see section 4.2 below). As group size increases other properties may also change, such as the velocity of the group, and the probability of a group encountering other groups (Flierl *et al.*, 1999). Thus, although one can relatively easily describe a system in terms of a time-dependent dynamical function of the number of groups of a given size incorporating size-dependent fission and fusion rates (see Okubo, 1986; Flierl *et al.*, 1999), defining (and verifying) realistic fission-fusion functions used can be a complex task. Flierl *et al.*, (1999) use individual-based models of fish schooling to estimate some of these functions (e.g. fission-rates as a function of school size), and group-size distributions in their model tend to be very nearly exponentially distributed.

Using an alternative technique involving a "maximum entropy" principle, Okubo (1986) also predicted that all group-size distributions should be exponentially decreasing (see Okubo, 1986, for a detailed mathematical description of the model), and fitted this model to a range of experimental data from fish species, including the spottail shiner, *Notropis hudsonius,* and ungulates including American bison, *Bison bison*, and Desert bighorn, *Ovis canadensis*. However Bonabeau *et al.* (1998, 1999b) argue that Okubo's (1986) model assumes that there is a fixed average size to animal groups (and thus that there is a well-defined mean to such distributions), and that in reality when maximum group size is large, group size distributions may exhibit longer tails than predicted by a decreasing

exponential function. Furthermore they argue that such long-tailed distributions are likely to be truncated since populations are ultimately finite, and are rapidly decreasing at large sizes. Consequently they propose that animal group-size distributions may conform to a 'truncated power law', where the number $N(s)$ of groups of size s is proportional to s^{-b} where b is the scaling exponent, up to a cut-off group size C. If group-size distributions do follow a power law, then Bonabeau *et al*. (1998, 1999b) suggest that biotic factors that may influence the stability of groups, such as resource availability, should be expected to affect the cut-off size, but not the power index, b (which corresponds to the slope of the function when plotted on a log-log scale) which is scale-invariant. They were able to show that experimental data on group-size distributions from fish schools (tuna and sardinella) and ungulate herds (African buffalo) exhibit long-tailed distributions characteristic of the truncated power law (indicating that such species form relatively cohesive, stable groups). Where data were available, for tuna fish, they also demonstrated that cut-off size does vary between years, but b appears relatively constant.

If this model does indeed fit the observed data, they also suggest that this may indicate that the underlying aggregation mechanism may be relatively simple (at least in terms of the join-leave probabilities), whereas the cut-off size could be used to reflect biologically important properties, such as changes in individual behavior, individual density or the environment. The ability to determine the cut-off point, which may represent a critical, and biologically meaningful, aggregate size, is one of the potential strengths of applying the truncated power law model, as opposed to the other methods described above, to group-size distributions. However, the prediction that cut-off size would vary with density-dependent properties was not explicitly tested by Bonabeau *et al*. (1998, 1999b), presumably due to insufficient data. Sjöberg *et al*. (2000) demonstrated that they could fit truncated power laws to data from gray seals (*Halichoerus grypus*) aggregating on haul-out sites (see Fig. 16), larvae of tephritid flies (*Paroxyna plantaginis*) clumping in flower heads and aphids (*Aphidiodea* spp.) aggregating on stems. However, they also provide some evidence that cut-off size does vary as a function of density-dependent effects (resource density and individual density) for some insects (aphids), although in their system the resource distribution is also likely to influence the group-size distribution.

They also provide evidence that for aphids and tephritid fly larvae, that the exponent of the power law (the slope *b*) may be influenced by biotic factors. Thus they conclude that the simple mechanistic approach to understanding aggregation phenomena proposed by Bonabeau *et al.* (1998, 1999b) may not necessarily be suitable for other biological systems.

Niwa (1998b) modified a balance-equation model by Gueron and Levin (1995) in which the fission-fusion processes were shown to result in a stationary solution. Like Bonabeau *et al.* (1998, 1999b) he applied this modeling approach to understanding the group-size distributions, inferring (as did Flierl *et al.* 1999) the fission-fusion rates from models of schooling dynamics (see Niwa, 1994, 1996). This model was fitted to data from free-swimming tuna (as used by Bonabeau *et al.*, 1998, 1999b), Japanese sardine (*Sardinops melanosticta*), northern anchovy (*Engraulis mordax*) and flying fish (*Cypselurus opisthopus hiraii* and *Cypselurus heteruu döderleini*). Niwa argued that the school size distributions fit a truncated power law with a crossover to an exponential decay around a certain cut-off size. This cut-off was dependent on the total population size, and is a result of fission-fusion within a finite population. Thus when the cut-off size is small (when populations are relatively small compared to these pelagic marine examples, as may be the case for some freshwater species: see Seghers, 1981 and Okubo, 1986), the exponential decay may be the only part of the function evident. As the population size increases one may therefore predict that the group-size distribution would better fit a power law. The model of Niwa (1998b) also predicts that the exponent of the power law does depend on population size, and that as population size increases the exponent should approach 1 over a wider range of group sizes (the population exhibiting a longer tail in the group-size distribution).

4.2 The influence of habitat structure

Continuing the discussion of the truncated power law description of animal group-size distributions proposed by Bonabeau *et al.* (1998, 1999b), a further prediction was made that the power index, *b*, should vary predictably as a function of the spatial dimension of

the system in question (also see Takayasu, 1989). The reason b increases is because at a low spatial dimension the spatial constraints mean that groups have a higher probability of meeting and fusing, relative to that at a higher dimension (given all other properties of the system are constant). Thus the truncated power law model predicts that b increases with effective dimension, but that where the effective spatial dimension is less than 3 (as in all biologically reasonable cases) then $b < 3/2$. Specifically $b = 4/3$ (1.33…) for $d = 1$, $b = 1.465 \pm 0.003$ for $d = 2$, $b = 1.491 \pm 0.007$ for $d = 3$ (although it should be noted that Niwa, 1998b and Sjöberg *et al*. 2000 question whether b must be less than 3/2).

Despite the fact that some animals, such as fish, move in three-dimensional space, the individuals may not actually use the space available, as in the case of the schools of Atlantic bluefin tuna (*Thynnus thynnus*) discussed above (section 2.4e) which may predominantly occupy two-dimensional space, cruising just below the water surface (Partridge *et al.*, 1983). Bonabeau *et al.* (1998, 1999b) tested this prediction using data from fish species that differ in their space use. Free swimming tuna (a mixed population of yellowfin tuna *Thunnus albacares*, skipjack tuna *Katsuwonus pelamis* and bigeye tuna *T. obesus*) often move in open ocean, but are still likely not to use the space available to them fully. For example they are more likely to be parallel to, rather than perpendicular to, the surface (due to the influence of gravity). Bonabeau *et al* (1998, 1999b) term the dimensionality of space actually used by the organisms as the "effective dimensionality" of the system. In the case of the free-swimming tuna their effective space use will be somewhere between 2 and 3 dimensions. Environmental structure is likely to influence this space use. Sardinellas (*Sardinella maderensis* and *S. aurita*), for example, tend to follow the coastline of West Africa, above the continental shelf (which limits water depth from 1 to 200m (Bonabeau *et al.*, 1998, 1999b). Therefore the effective spatial dimension would be somewhere between 1 and 2. Space use may be reduced even further in some instances, such as when pelagic fish gather under artificial buoyant objects, known as 'fish aggregating devices' (FAD). Bonabeau *et al.* (1998, 1999b) argue that the effective dimension of tuna fish schools caught in the vicinity of an FAD is less than 1 because the FAD is a point (relative to the large-scale spatial movements of tuna fish). It should also

be noted that such a device also affects the aggregation dynamics by introducing an attractive focus to individuals.

Comparing the predictions of their model to the data from sardinella and tuna, described above, Bonabeau *et al* (1998, 1999b) demonstrated a qualitative, but not a quantitative fit ($b = 1.49$ for freely swimming tuna fish, $b = 0.95$ for free swimming sardinellas, and $b = 0.698$ for tuna fish caught in the vicinity of an FAD). This shows that, as expected, the exponent b of the power law is inversely related to the spatial dimension used by the animal. Since these animals (as described above) use an unknown dimensionality of space it is perhaps not surprising that the fit to 3, 2 and 1 dimensions for the free-swimming tuna, sardinellas and aggregated tuna is only qualitative, although Bonabeau *et al.* (1988, 1999b) argue that the lack of perfect agreement with the empirical data with which they tested their model may result from biases in available data. Firstly, their data came from schools caught by purse seine nets, and consequently a catch made may include only a subsection of a school (and this would be more likely as school size increased). Furthermore, because fishermen are not necessarily interested in small schools (and may use technology such as acoustic imaging to focus on larger groups) these are likely to be under-represented in these data. Another limitation to these data is that school size is based not on an actual count of the number of individuals, but an estimate made from the weight of each haul. As discussed above in section 3.2 phenotypically similar individuals become associated within such groups, and this can result in groups, when they fragment, becoming phenotypically assorted (see section 4.3 below). This means that in a fisheries sample (which is assessed by weight) a small group of large individuals would be indistinguishable from a larger group of smaller individuals, given that the two are of similar weight.

In all grouping animals the effective space is likely to be an important consideration when attempting to understand their distribution in space and time. Animals are likely to live in heterogeneous habitats, and their behavior may often be influenced by habitat type. To some degree the effective dimensionality of the environment may be characterized as the fractal dimension of the spatial distribution of patches suitable for

movement. However, the situation becomes complicated in cases where there is more complex variation in habitat type (rather than a binary classification of merely suitable and unsuitable habitat). Some habitat may act to attract individuals (e.g. areas with high food abundance) whereas others may restrict motion (e.g. where there is structural complexity, as in forest).

Habitat structure is also likely to affect other properties important in determining the fission-fusion dynamics. For example, some habitat (e.g. forest) may restrict the range over which individuals can respond to one another, and hence limit the interaction range. This is likely to have the effect of increasing the fragmentation of groups. In the case of animal groups that are mobile, motion around obstacles in the environment is also likely to increase the probability of splitting, and so one may expect the detailed nature of the habitat structure (such as the size and distribution of obstacles) to be an important influence on group size distribution.

In some cases habitat structure may change very rapidly. Flierl *et al.* (1999), for example, used computer modeling to investigate the consequences of turbulent flow in aquatic environments on the grouping dynamics of fish. In many fluid environments changes in flow regime may be rapid (for example the volume of water on a given stretch of a freshwater waterway may change very rapidly as a result of flooding). Furthermore where conditions are turbulent there are likely to be rapidly changing shear and strain fields that will exert physical forces on animals. Under turbulent conditions one may expect that groups will be more likely to fragment since individuals may be expected to have insufficient control over their locomotion (relative to the strong physical forces exerted on them by the flow conditions) to maintain cohesion. At the very least it may be expected that even weak turbulence will act to impose largely stochastic physical forces which would decrease cohesion. In the model of Flierl *et al.* (1999), which incorporated a simple schooling tendency similar to that used by Grünbaum (1997, 1998), strong turbulence was shown to fragment groups, but where turbulence is weaker groups can form in temporary "refuges". Once formed turbulence actually acts to increase the size of groups that form because the flow acts to increase the encounter rates between groups

since individuals tend to occupy the spaces in-between high turbulence areas. This suggests that the turbulent regime of aquatic environments is likely to have a strong influence on fission-fusion processes of grouping and consequently will affect the resulting group sizes in the population. This model also highlights the importance of considering physical properties of the environment that are potential pattern-forming processes.

It is clear that there is still much debate about the processes involved in fission-fusion systems, yet the diverse range of mathematical techniques used has provided constructive and thought provoking discussion of a topic that is relevant not only to our understanding of collective behaviors and ecological questions, but also conservation issues where the models may allow a better understanding of how changes to the environment, or to the density of organisms, may affect group- and population-level processes.

4.3 Phenotypic assortment: active or passive?

There is considerable empirical evidence that animals (most of the data come from fish shoals) tend to be assorted by phenotype between groups (Krause *et al*. 2000b). This includes sorting by body length, species, parasite load and body color. In section 3.2 above, we discussed how differences among individuals within a group can lead to 'natural' sorting: individuals with similar behaviors tend to become more closely associated as a result of the interaction mechanics. We hypothesized that, if properties such as body size, or species, are correlated with behavioral response, that this could explain the fact that fish within schools tend to be close to others of similar size (Pitcher *et al*., 1986; Parrish, 1989a; DeBlois and Rose, 1996, Ward *et al*., 2002) or, in multi-species groups, to conspecifics (Parrish, 1989a). However, we did not consider the consequences of such self-sorting processes to population-level properties. Here we consider such sorting processes within the context of a fission-fusion system, and show how we can make some predictions about how these mechanisms are likely to influence group-level properties.

The close association of individuals with similar phenotypes within a group means that, when groups fragment, individuals will tend to remain with others that are more similar to themselves (Croft *et al*., in press). Thus phenotypically heterogeneous groups, when they fragment, will tend to do so into more homogenous groups. This phenotypic assortment is counteracted to some degree by the merging of groups of different phenotypes. To better understand how this process works at a population-level we construct a deliberately simplistic model of grouping. This model is similar to that outlined in section 2.4b (see Couzin *et al*., 2002, for further details), except here we simplify the model further: individuals have a close-range zone of repulsion that simulated their tendency to maintain a minimum distance between themselves, and a single 360º zone of perception that extends beyond this in which they can detect others. As before, the zone of repulsion has highest priority, but if there are no individuals within this zone, individuals will align with, and be attracted to neighbors within the zone of perception (for simplicity these forces are assumed to have equal weighting). This grouping behavior is subject to slight error (stochastic effects). If no others are detected, individuals perform a correlated random walk. Further details of the formulation of this model can be found in Hoare *et al.*, (submitted).

In our model, individuals are 4cm long, move at 5cms^{-1}, and have a maximum turning rate of 100º/sec, corresponding to the killifish *Fundulus diaphanus*. However, this model is generic, and the processes we describe are not dependent on the exact parameters used. We assume individuals have localized perception, and respond to others within two body-lengths. Again, changing this parameter changes the results quantitatively but not qualitatively. Our simulated organisms move in continuous space on a two-dimensional plane with periodic boundary conditions. Within this model individuals form mobile groups that exhibit fission and fusion. To investigate how differences among individuals can change group composition, we assume that there are two subpopulations that may, or may not, differ with respect to their behavior. This may correspond, for example, to two species, or to two classes of individuals (such as hungry vs. satiated individuals). Clearly further modifications, such as simulating continuous variation in behavior, would be

interesting, but for simplicity here we assume just two 'types' of individual within the population.

Within this model, even slight behavioral differences between the two sub-groups results in groups becoming phenotypically assorted (see Fig. 17). One of the strongest sorting influences is a difference in speed between the two groups (Fig. 17A, B). Fig 17C shows how individuals assort when there is a difference in the size of the zone of repulsion between the two sub-populations (in section 3.2 above we discussed how this property affects the positioning of individuals within groups).

Thus if different species, or 'types' of conspecific, differ with respect to their behaviors (for example tend to move at different speeds, or tend to respond to others over different ranges), this may result in them becoming 'naturally' self-sorted within a population. One need not necessarily invoke complex recognition and decision-making capabilities on behalf of the organism, although to the human observer it may appear that individuals are behaving in a more complex way. For example, within our computer model a naïve observer watching the individuals move around on the computer screen is likely to assume that they have been programmed to make complex decisions about whether to associate with others. This misconception results from biases in our perception since we often tend to consider behavior from too anthropocentric a point of view. We suggest that natural selection may act on such local 'rules of thumb' to facilitate phenotypic assortment within groups if that confers a benefit to individuals.

Our model suggests that heterogeneity within animal groups may make them more susceptible to fragmentation: groups of individuals that differ with respect to certain behaviors (e.g. speed, or desired personal space) will tend to be less 'stable' (and therefore more likely to fragment) than those in which individuals are phenotypically similar. Our results also suggest that the population will become more phenotypically assorted as the difference between the two sub-populations (behavior types) increases (Fig. 17B, C).

Typically when researchers have observed phenotypic assortment within populations they have assumed that individuals are making active choices with whom they group. A preference for conspecifics over heterospecifics is assumed to have functional significance. Firstly conspecifics may be more likely to be in spatial proximity after hatching, and thus may be expected to develop anti-predator maneuvers with conspecifics as opposed to with heterospecifics (Krause *et al.*, 2000b). Furthermore, individuals are thought to avoid being phenotypically 'odd' individuals within a group since this may enhance their risk of predation (through the predator being more likely to 'lock' its attention on the odd individual; Landeau and Terborgh, 1986; Theodorakis, 1989). There is some evidence that in mixed-species shoals the less common species may leave when the perceived threat of predation is high (Wolf, 1985). Furthermore, Allen and Pitcher (1986) reported that multi-species shoals separated into their component species when under predation threat. A similar explanation (avoidance of oddity) has been put forward to explain body-length sorting in single-species groups (reviewed in Ranta *et al.*, 1994 and Krause *et al.*, 2000b). It may seem from our explanation of self-sorting that we contradict this view by suggesting a passive sorting strategy and not an active decision-making process. However, this is not the case. We do, however, point out that in some instances it may be difficult to determine whether individuals are actively sorting (i.e. making an active decision to leave a group), or whether this is an inevitable consequence of different behavior types that have evolved for another reason. However, we must stress that the type of self-sorting processes we describe above may result from selection to allow assortment of individuals for the functional benefits we describe here. Thus, just as we argue that this type of self-organizing mechanism may be selected to allow individuals to modify their position within a group without necessitating complex cognitive abilities (or knowledge that would be difficult or impossible to obtain), natural selection may also select "rules of thumb" that individuals could use to become assorted by phenotype.

The case, described by Wolf (1985), where less-common species in mixed species groups leave under threat of predation is consistent with a self-sorting type of mechanism. The perturbed group is likely to fragment, with odd individuals being 'shed' as the group

performs avoidance maneuvers. Another interesting point is that the empirical literature so far appears to be contradicting itself. Landeau and Terborgh's (1986) study clearly showed that individuals are at a higher risk in a group where they are phenotypically odd compared to one comprising phenotypically similar group members (provided both groups are of the same size). The higher predation risk explains why an individual should switch from a group where it is odd to one where it 'fits in' and do so particularly under predation threat. However, Landeau and Terborgh (1986) also convincingly demonstrated that, if there is no such alternative, then an odd individual does much better by staying in a group where it is odd then being on its own because when alone the predation is even higher. Furthermore, they reported that no cost due to oddity occurred, provided shoals were larger than about 15 fish, because the antipredator effects of grouping became so efficient at this group size that the predator could not make any captures regardless of whether the group did or did not contain an odd fish. In this context it seems very surprising that Allan and Pitcher (1986) and Wolf (1985) found that different species separated under predation threat. We should expect to see the opposite, namely different species merging into shoals so that all individuals benefit from a large shoal size that renders oddity irrelevant. We suggest that multi-species groups split into single-species ones in such situations because of constraints imposed by species-specific behaviors (including potential differences in response latency, speed of locomotion and interaction rules). Thus the split into single-species groups is not an adaptive behavior that lowers predation risk when under attack but a result of a constraint that is likely to increase risk but which fish cannot overcome in this situation. Interestingly, another benefit of phenotypic assortment may be that information transfer (in terms of changes in individual velocity being propagated across the group) may be more efficient in homogenous than in heterogeneous groups (see section 2.4d) and we encourage further research in this area.

In the case of individuals within groups being assorted by size, it would be interesting to determine whether this is a consequence of individuals somehow assessing the size of others relative to themselves (which introduces the problem of how individuals know their own size, and assess the size of others in the absence of stereo vision, as is the case over much of the field of view of most grouping animals) and choosing to associate with

similar individuals. An alternative possibility is that size is correlated with a behavior that results in groups becoming assorted by the type of mechanism we propose here. Similarly, groups within populations in which there are parasitized and non-parasitized individuals may be expected to become assorted by parasite prevalence, and/or load (Ward *et al.*, 2002). However, in some instances body-length and parasite load may be correlated (Hoare *et al.*, 2000) so it may be difficult to determine what causes the sorting.

In reality it may also be difficult to determine whether the behavioral difference that results in a population being self-sorted has evolved for that purpose, or whether sorting is an epiphenomenon that merely does not incur a cost. Researchers should perhaps bear in mind that assortment may result from self-sorting processes. It should be noted that we are not saying that grouping individuals cannot, or do not, use more complex recognition and response behaviors. Rather we just aim here to introduce the possibility that complex phenomena at the level of the population may also be explained by alternative (and sometimes simpler) mechanisms.

4.4 Optimal group size

There are costs and benefits to individuals of being in groups (Ritz, 1997; Krause and Ruxton, 2002). Grouping individuals may, for example, decrease their chances of being consumed by a predator by positioning themselves near others (Hamilton, 1971). This is sometimes known as the 'dilution effect' because, if a predator randomly selects prey, then an individual having near neighbors may 'dilute' its chances of being consumed. As discussed in section 2.4d, individuals within a group may benefit from information exchange about the positions of predators, and perhaps the 'confusion effect' if individuals perform synchronized escape maneuvers (Partridge, 1982). A potential disadvantage of aggregation is that a group of individuals is more likely to be conspicuous to predators than a single individual. With regard to foraging behavior, grouping may benefit individuals by allowing transfer of information about resources (see section 2.4d), but costs may also result from individuals within groups competing for resources once they are found (Krause and Ruxton, 2002).

Since the costs and benefits of grouping vary as a function of group size, we may expect that individuals will modify their choice of group size (by joining or leaving groups) as ecological conditions change to maximize their fitness (Pulliam and Caraco, 1984). One problem with this possibility is that individuals within a group may not be able to exclude solitary individuals, and consequently individuals will continue to join a group exceeding the "optimal group size" (Sibly, 1983). Thus solitary individuals, by joining a group, may increase their own fitness, but decrease that of all other group members. When the costs of grouping become greater than the benefits individuals should be expected to leave (see Krause and Ruxton, 2002 for further discussion of the costs and benefits of group size).

Laboratory studies involving fish have shown that individuals, when presented with a simple binary choice of associating with one of two stimulus shoals (within containers so the perceived group size can be modified experimentally) that individuals usually 'select' the larger group (Krause and Ruxton 2002). However, see van Havre and FitzGerald (1988) for an exception. There are several potential problems with such studies. First, test fish may be stressed when alone in the test compartment and second, the range of shoal sizes that can be presented is limited due to the confined space in the laboratory, and rarely comprises more than 20 individuals. In nature, however, fish can often be found in shoals of hundreds or thousands of individuals. Thus there is a real need for more fieldwork to be carried out in this area (see Hensor *et al.*, in press).

In a laboratory study where individuals could freely associate with others, Hoare *et al.* (submitted) investigated the influence of ecological factors (perceived food availability and predation risk) on the schooling behavior of banded killifish. Since natural group sizes will result from the interactions among all individuals it is important, as they point out, to consider what group sizes result when all individuals can make membership decisions. They subjected groups of 10 size-matched fish to four treatments: (i) food, (ii) control, (iii) food and alarm, and (iv) alarm. The food treatment involved adding food odor to the water (but to prevent competition for food items themselves no food particles were introduced), and predation risk was simulated through the use of killifish skin

extract (which contains chemicals that cause alarm in fish, and are naturally released when fish are injured or captured by predators). In the control treatment no odor was added, and in treatment (iii) both food and alarm odor were added to the water.

Group sizes were shown to be context dependent, with individuals tending to be in the smallest group sizes in the presence of food odor (Fig. 18a, (i)), and the probability of individuals being found within larger groups increasing under control conditions (yet groups of five or more individuals are still very rare, Fig. 18a, (ii)). In the presence of alarm substance, however, the fish tended to form large groups, with individuals spending the majority of time in the maximum group size of 10 (Fig. 18a (iv)). When alarm substance and food odor were present, fish exhibited a response intermediate to that in the presence of food odor or alarm odor alone (Fig. 18a (iii)).

This demonstrates that group size in this organism is context-dependent. Individuals increase their probability of being within small groups when food odor is detected since this may reduce intra-group competition for resources when found. When alarm odor is detected, however, individuals would be expected to form large groups, since by doing so fish may reduce per capita predation risk. In the case of both food odor and alarm odor, the fish seemed to have conflicting tendencies resulting in them performing an intermediate behavior. This is interesting, as the fish seem to be trading off foraging benefits and safety from predators in their movement decisions.

One may initially think that these killifish regulate group size by assessing how many individuals they are currently schooling with, and making a decision to stay or leave (or approach others) based on that. However, this is a rather anthropocentric view of the behavior of these animals that assumes they can count the number of individuals within their group. Hoare *et al*. (submitted) suggest that we need not invoke such complexity in the individual decision-making process, and that group-size may be an emergent property resulting from fish following relatively simple "rules of thumb". To support this conjecture, they develop an individual-based model of their experiment, similar to that we used above to examine self-sorting within animal populations (see section 3.2). In

their model they assumed that fish change the range over which they interact with others as environmental conditions change: individuals that detect food tend to respond only to very near neighbors, whereas those that experience alarm odor will increase the range over which they interact with others, so that they aggregate, thus avoiding isolation. By modifying this range of interaction within their model they could investigate its consequence on the group-size distribution at the level of the population (Fig 18b). This change in local response was shown to be able to account well for the shift in group-size distributions from small to large groups recorded experimentally (see Fig. 18a, where the model data are compared to experimental data).

This type of simple model demonstrates how individuals can modify their probability of being within a group of a certain size by changing a local behavior and, as Hoare *et al.* (submitted) point out, their aim was not to determine the exact rules used by their fish, but rather to show that individuals can modify their probability of being in a group of a certain size *without* making explicit decisions about membership of particular groups. Thus their model demonstrates the logical consistency of their argument. An individual fish need not know the range of possible group sizes available to it: rather the group size distribution can be an emergent property of local interactions. This approach is appealing (and plausible) for other systems where it is unlikely that individuals can assess the size of the group they join, such as in pelagic fish populations where group sizes may frequently be in the order of thousands or even hundreds of thousands, or where interactions must be local, as in turbid water. As this model demonstrates, the 'decisions' made by individuals may be much simpler than they may initially appear.

Interestingly, in a study of African buffalo, *Syncercus caffer*, Sinclair (1977) found that the size of herds changes throughout the year. During the wet season herd sizes tend to be large, but in the dry season groups tend to be much smaller. Sinclair (1977) suggests that the groups may get larger during the rut, which begins at the start of the wet season. Furthermore, aggregation may act to protect the young produced in the wet season. However most conceptions occur at the end of the wet season in this species, so Sinclair also argues that changes in resource availability (productivity is greater in the wet season)

may also be important. Thus, the buffalo may be responding to resource availability for similar reasons as do the fish described above, reducing competition for resources when food is limited, and increasing group size when the productivity of their environment increases.

In the study by Hoare *et al.* (submitted) described above, all individuals should be expected to have the same motivations (all individuals had the same pre-experiment feeding regime, and all had the same stimulus and stimulus intensity). In reality, however, the situation is likely to be more complex than this. Satiated individuals, for example, would be expected to respond less strongly (if at all) to food odor, when compared with hungry fish. In addition to variation in individual state, there is also likely to be variation in the perceived stimuli, and also in the inherent propensity of individuals to respond (for example, variation in general schooling tendency is known to occur within populations; Magurran *et al.*, 1995). Individuals within the types of fission-fusion systems we have considered here would be expected, therefore, to change their behavioral response to others dynamically in order to increase their probability of being in groups of a size that approximate their current 'optimal' group-size. We therefore encourage further research into understanding whether, and how, potential self-organizing mechanisms can result in individuals maximizing their fitness by changing their probability of being in groups of a certain size. Such an approach should consider both current experimental evidence that shows how grouping individuals can regulate group sizes with the properties we have discussed previously in this chapter, such as intra-group self-sorting processes, and the resulting group-size distributions seen at the level of the population.

5. Summary

We have looked at different taxonomic groups to reveal where self-organization theory can make an important contribution to explaining collective behavioral patterns. Since this a recently emerging field of research, and because vertebrate groups may be difficult to study, developing theories of self-organization for these groups (which can then be

tested empirically) is particularly important. Consequently we focused on how modeling approaches (particularly those that are individual-based) have been, and are being, used to help reveal the organizational principles in human crowds (2.2a and 2.3), ungulate herds (2.1), fish schools and bird flocks (2.4) and primate groups (3.3). The collective behavior of such systems is largely characterized by the interactions among individual components, and thus are well suited to an approach that seeks to elucidate generative behavioral rules. We also discussed the evolution of collective behaviors (2.4c). Here, theory has been important in demonstrating that different collective behaviors can exist for identical individual behaviors, suggesting that the evolution of collective (extended) phenotypes may be more complex than it may, at first, appear.

Behavioral differences among individuals within a group may have an important internal structuring influence, and using simulation models we showed how individuals can modify their positions relative to other group-members (e.g. to move relative to the front or center of a group) without necessitating information about their current position within the group (3.2). This is important because it is unlikely that individuals within large groups (e.g. pelagic fish schools) can calculate their absolute position relative to all other group members; thus we argue that natural selection is likely to act on the kind of local rules we discussed.

In section 4 we discussed how local self-organized interactions result in the distribution of animals at a larger spatial and temporal scale, showing how mathematical studies of group-size distributions are being used to make testable predictions about how individual behavior translates to that at the level of a population (4.1, 4.2) and how differences among individuals within a population may lead to phenotypically assorted groups within a population (4.3). We also addressed "optimal group size" concept (4.4). As an alternative to the view in which individuals explicitly assess the size of groups and then make a decision to leave or join, we showed how local 'rules of thumb' could be used by individuals to modify their probability of being within a group of a given size. We demonstrated that in real organisms (schooling fish) group-size distributions (and hence the probability of an individual being within a group of certain size) is context dependent,

and that this behavior is entirely consistent with a self-organized mechanism whereby individuals change local interactions as conditions change.

In considering self-organization within vertebrate groups it is evident that the organization at one level (e.g. that of the group) relates to that at higher levels (e.g. that of the population). For example, self-sorting processes that lead to internal structuring within groups also result in population-level patterns when such groups fragment (e.g. phenotypic assortment), thus affecting the probability that an individual will be in a group of a given size and composition at any moment in time. These population properties then feed back to the individual interactions by changing the probability of encounters among different members of a population. Thus to fully understand collective behaviors one cannot necessarily consider these properties in isolation.

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Fig. 1. Herd of wildebeest showing a wave-like herd front. (From Sinclair, 1977; used with permission)

Fig. 2. Model of a wildebeest herd front that produces wave-like herd fronts from initially aligned individuals (along the x-axis). (Modified from Gueron and Levin, 1993)

Fig. 3. Computer simulation of human trail systems. (A) Initially walkers will take more-or-less direct routes between the four entry/exit points in the corners. The instantaneous velocities of walkers are shown as arrows. (B) After a period of time a shared trail system forms. (From Helbing *et al.*, 1997b; used with permission)

Fig. 4. (A) A model of trail formation from Helbing et al. 1997b (used with permission), and (B) natural trails made by ungulates (© 2002 Iain Couzin).

Fig. 5. (A) Hypothetical scenario in which individuals move between points 1 and 2, around an obstacle in-between. (B) Initially individuals will randomly select a direction around the obstacle. However the shorter route is reinforced more quickly. (C) The feedback in the trail formation-following system means that the shortest route can be selected collectively.

Fig. 6. Simulation of pedestrian dynamics showing lane formation (from Couzin, 1999). The successive positions (trajectories) of individuals with a desire to move to the left are shown in gray. The positions of those individuals intending to move to the right are shown in black.

Fig. 7. Simulation of pedestrians attempting to move across a crosswalk. Gray = individuals intending to move left. Black = individuals attempting to move right. (A) Where individuals just exhibit repulsion from others flow is less smooth than when, (B) they exhibit repulsion but also attraction towards others that have a similar desired direction.

Fig. 8. Simulation of pedestrians at a doorway exhibiting oscillations of flow. Here individuals moving to the left have temporarily monopolized the doorway. The decrease in "pressure" to the right of the door, caused by this exodus, will shortly allow those standing to the left of the doorway to block, and then to temporarily monopolize the doorway, and so on. Image modified from that available from the simulation at http://www.helbing.org/Pedestrians/Door.html

Fig. 9. Representation of an individual in the model of grouping in three-dimensional space, centered at the origin and pointing in the direction of travel. zor = zone of repulsion, zoo = zone of orientation, zoa = zone of attraction. The possible 'blind volume' behind an individual is also shown. α = the field of perception. (From Couzin *et al.*, 2002)

Fig. 10. The collective behaviors exhibited by the model: (A) swarm, (B) torus, (C) dynamic parallel group, (D) highly parallel group. Also shown are the group polarization p_{group} (E) and angular momentum m_{group} (F) as a function of changes in the size of the zone of orientation Δr_o and zone of attraction Δr_a. The areas denoted as (a-d), correspond to the area of parameter space in which the collective behaviors (A-D), respectively, are found. Area (e) corresponds to the region in parameter space where groups have a greater than 50% chance of fragmenting. (From Couzin *et al.*, 2002)

Fig. 11. The change in group polarization p_{group} (A) and angular momentum m_{group} (B) as individuals within a group increase (bold line) or decrease (dotted line) the size of the zone of orientation r_o. The group patterns that form depend on the previous history of the group (hysteresis). (From Couzin *et al.*, 2002)

Fig. 12. Computer simulation of 1000 grouping individuals (white) responding to attack by a predator (red). (a-h) show a successive snapshots of the simulation as the predator attacks.

Fig. 13. Theoretical influence of the size of the zone in which individuals respond to others. The predator is shown in red, individuals that directly perceive the predator in blue, and all others in black. (a) one individual detects the predator, but the small size of the behavioral zones does not allow other individuals to respond to its change in orientation. (b) only two individuals detect the predator directly, but the behavioral zones are sufficiently large to allow group cohesion and the spread of relevant information about the location of the predator (the change in direction of blue individuals) to other individuals nearby. (c) if behavioral zones are too large, individuals are swamped with information from both near and distant sources. This reduces the ability of individuals to respond to local perturbation.

Fig. 14. Sorting as a function of variation in (A) speed s, (B) turning rate θ, (C) zone of repulsion r_r, and (D) zone of orientation r_o. A typical group sorted by r_r is shown in (E). Sorting is measured as the Spearman rank correlation coefficient (rho) of individuals calculated from the front (solid line) or center (dotted line) of the group. (From Couzin *et al.*, 2002)

Fig. 15. Frequency distribution of group sizes of African buffalo, *Syncercus caffer* (From Sinclair, 1977 used with permission).

Fig. 16. Frequency distribution of group sizes of gray seals, *Halichoerus grypus*, resting on an island. The fit shows a truncated power law with a cut-off at group size 21 (whole model: b_1 (slope of line from group size 1 – 21) = -0.35, b_2 (group size > 21) = -0.93, R^2 = 0.91, $P < 0.001$). (From Sjöberg *et al.*, 2000; used with permission).

Fig. 17. Simulation model demonstrating how self-organized sorting can result in phenotypic assortment within groups in a population. (A) Typical snapshot of the simulation at dynamic equilibrium: Total number of individuals = 300, with the two 'types' of individual (150 of each) shown in black (moving at 5cms^{-1}) and gray (moving at 7cms^{-1}); the domain size is 5m x 5m with completely periodic boundaries. The mean degree of assortment (where 1 = all individuals identical) within groups consisting of 3 or

more individuals as a function of (B) the difference in speed between the two 'types' (kept constant at 5cms^{-1} in one 'type' and increased in the other), and (C) the difference in the size of the zone of repulsion (kept constant at 4cm, 1BL, in one group and decreased in the other).

Fig. 18. Percent frequency distribution of median group sizes. (a) Model results demonstrating that increasing the range of interaction produces changes in group size distribution. These are similar to those obtained experimentally (b). (b) Experimental data compared with the results of the model

(i) Interaction radius = 1.2 BL; Food treatment

(ii) Interaction radius = 1.5 BL; Control treatment

(iii) Interaction radius = 1.6 BL; Food + alarm treatment

(iv) Interaction radius = 2.9 BL; Alarm treatment

Fig. 1
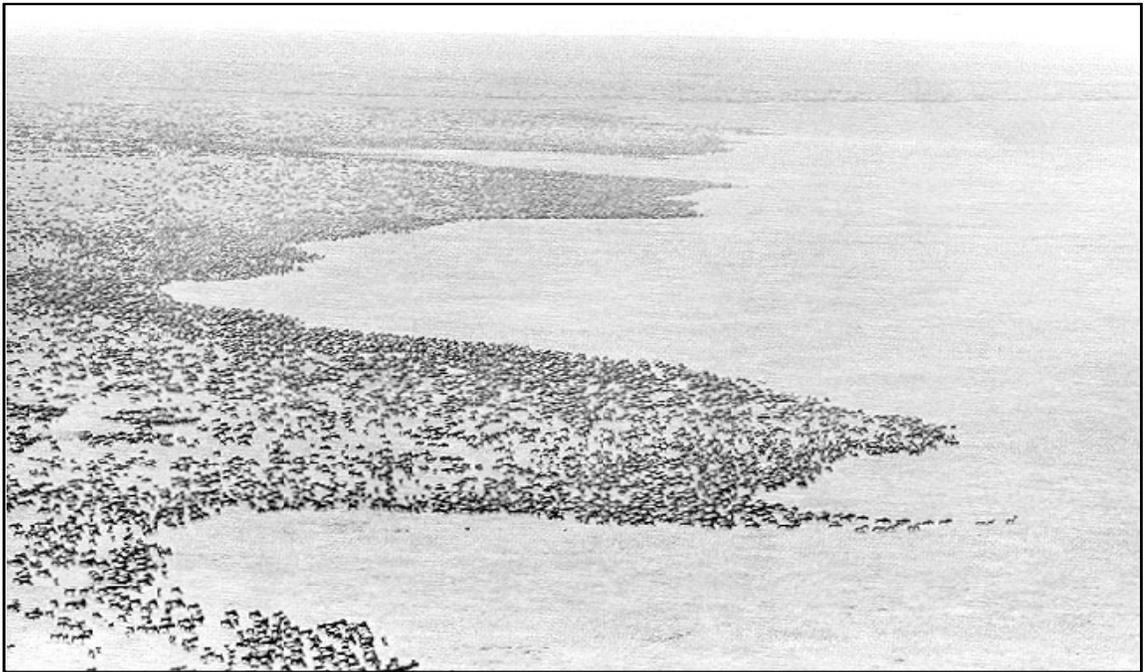
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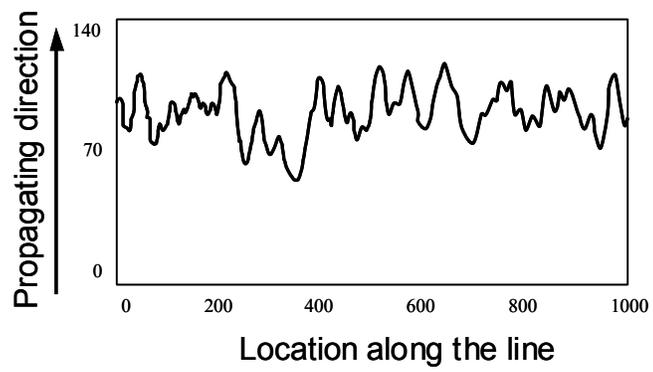
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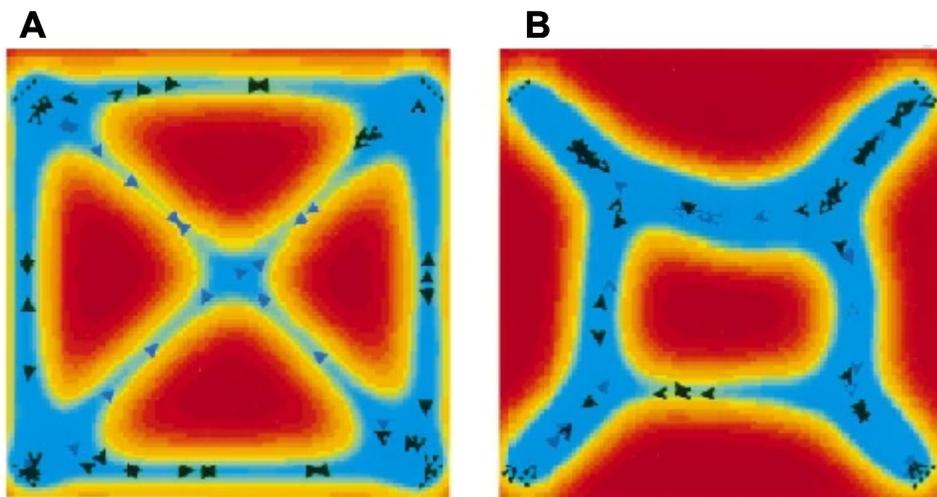
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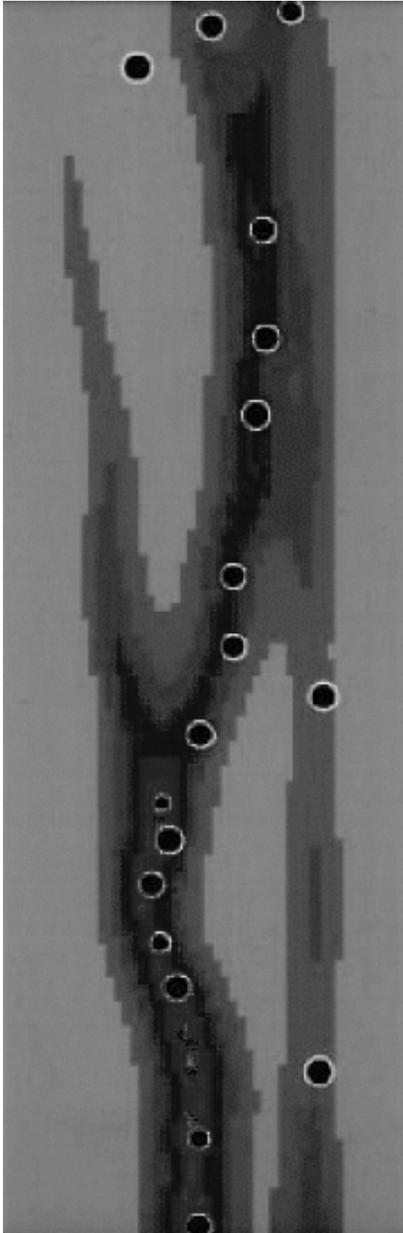
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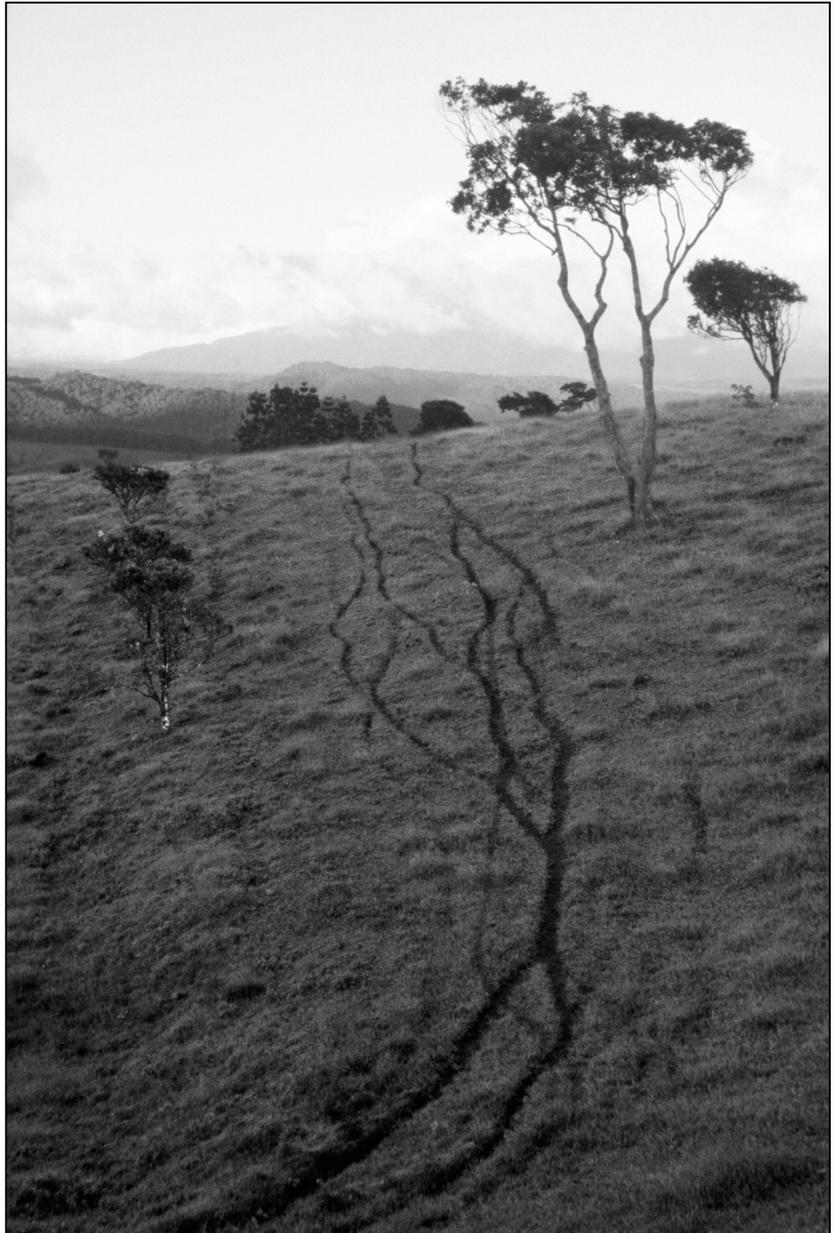
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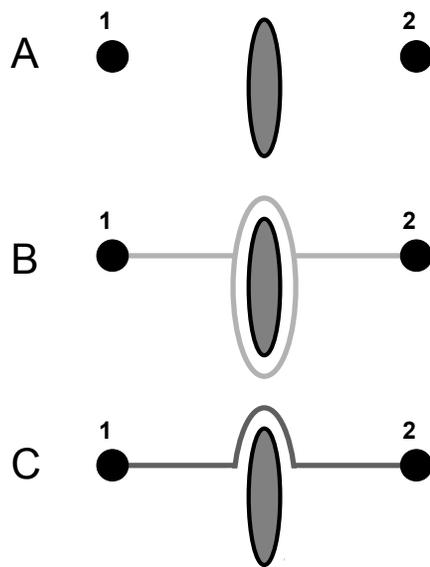
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A

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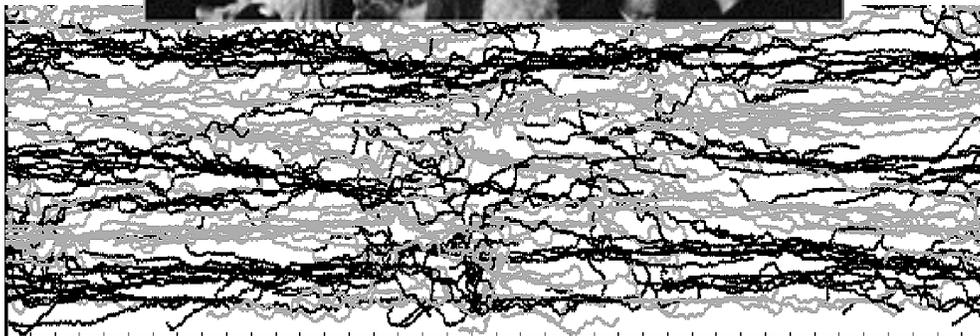
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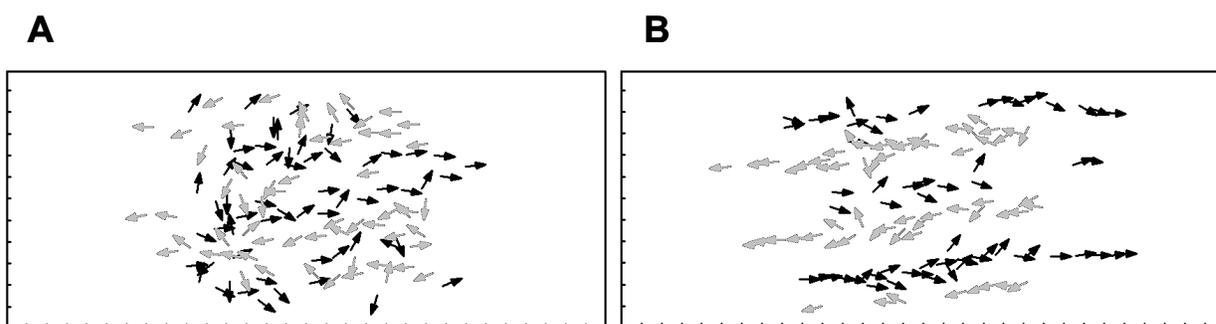
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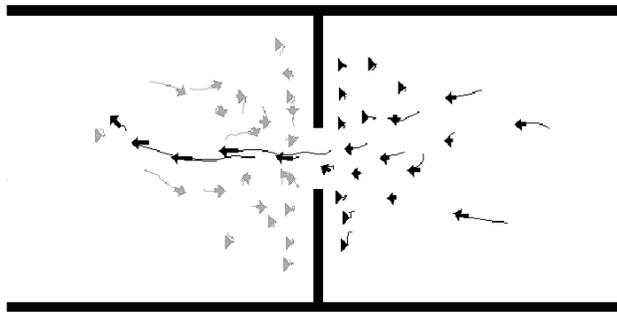
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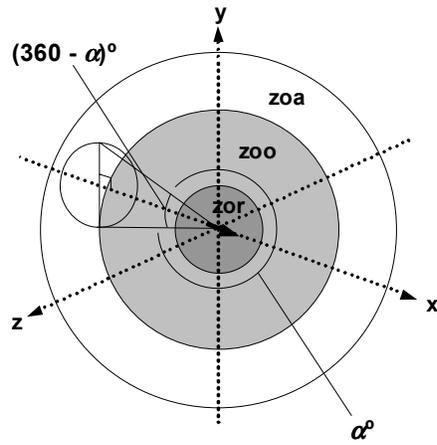
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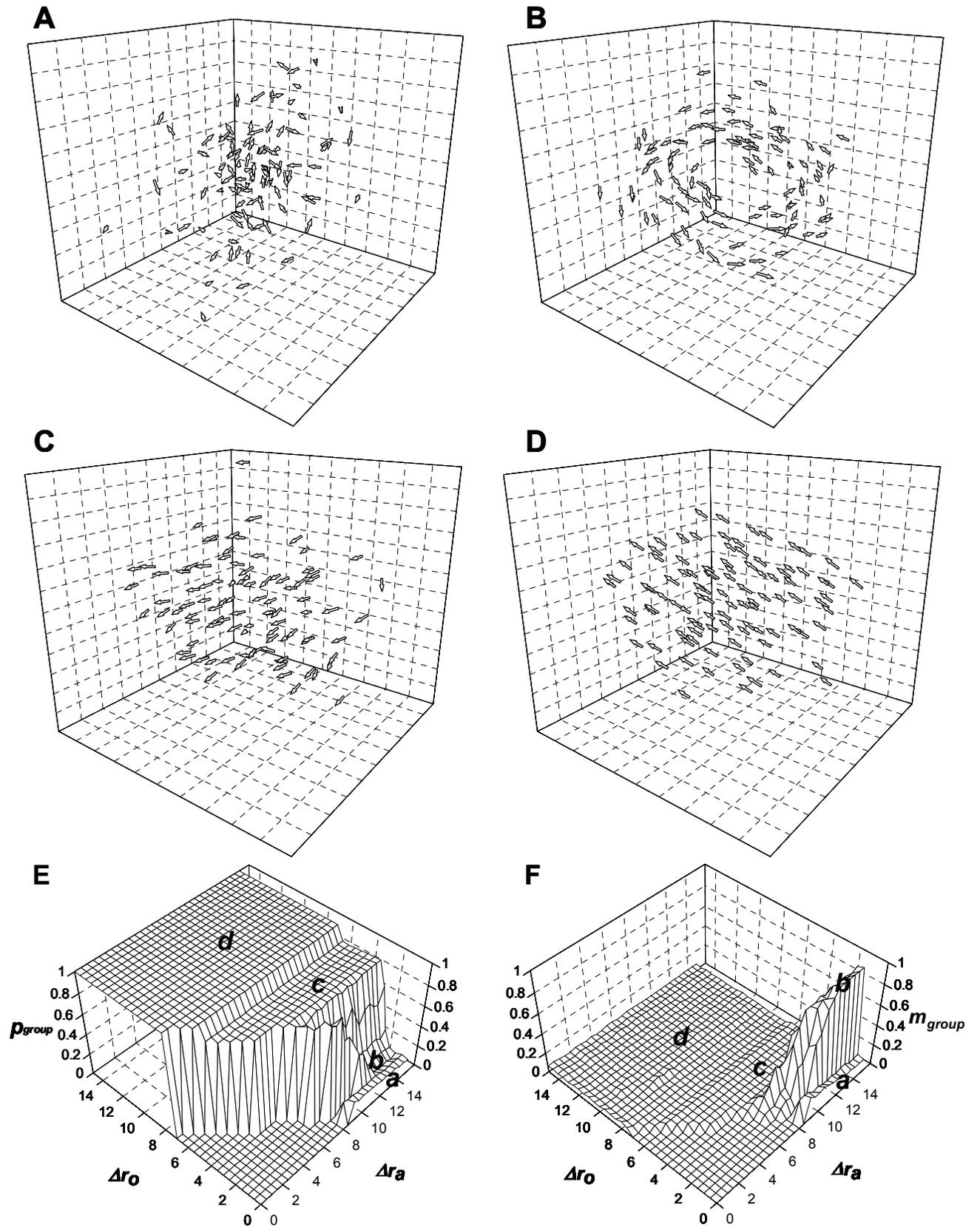
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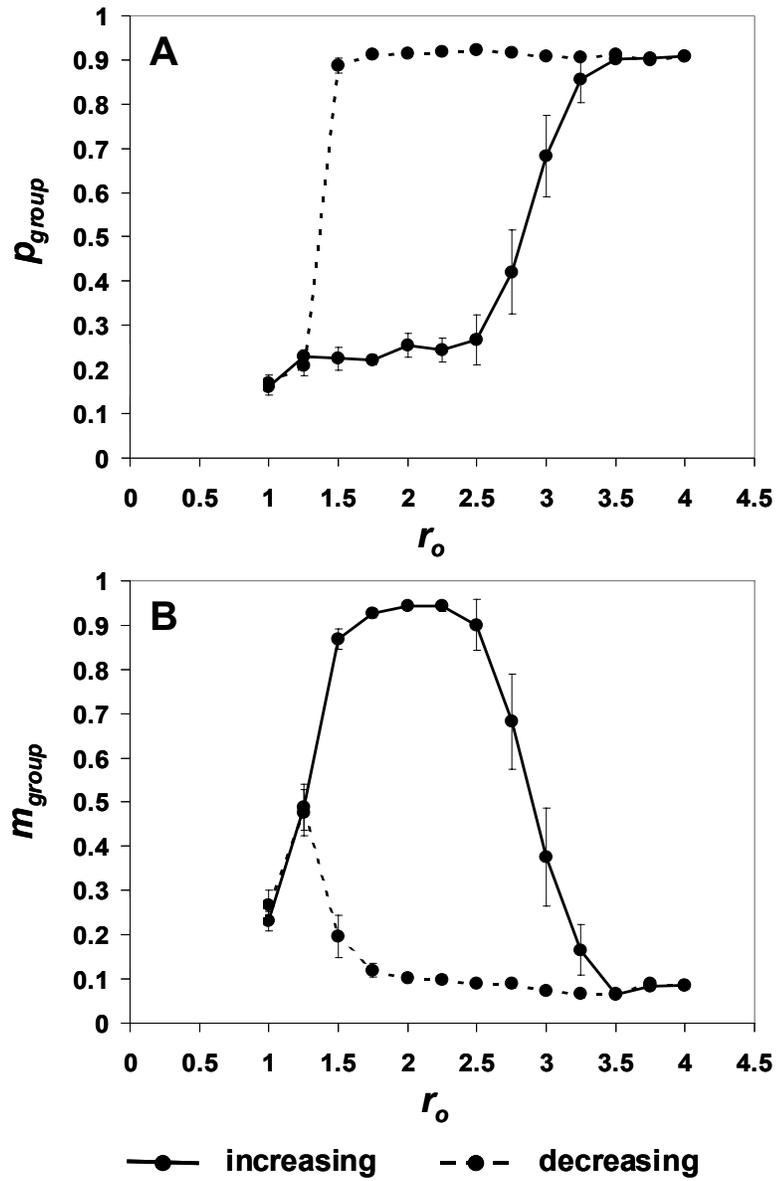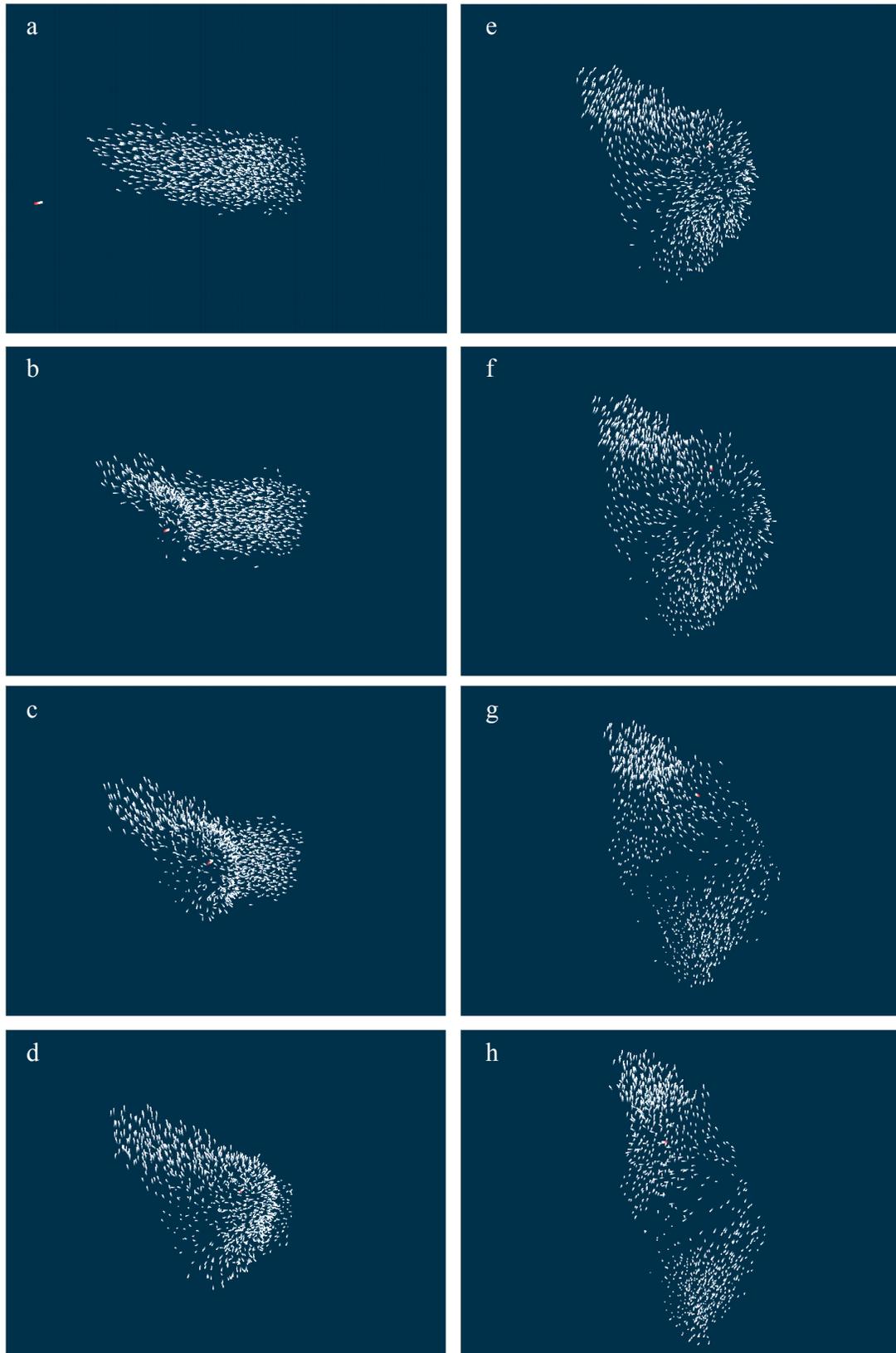
Fig. 12

Fig. 13

Fig. 14

Fig. 15

African buffalo: herds

Fig. 16

Fig. 17

Fig. 18

(a)

(b)