

# Complexity, Pattern, and Evolutionary Trade-Offs in Animal Aggregation

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One of the most striking patterns in biology is the formation of animal aggregations. Classically, aggregation has been viewed as an evolutionarily advantageous state, in which members derive the benefits of protection, mate choice, and centralized information, balanced by the costs of limiting resources. Consisting of individual members, aggregations nevertheless function as an integrated whole, displaying a complex set of behaviors not possible at the level of the individual organism. Complexity theory indicates that large populations of units can self-organize into aggregations that generate pattern, store information, and engage in collective decision-making. This begs the question, are all emergent properties of animal aggregations functional or are some simply pattern? Solutions to this dilemma will necessitate a closer marriage of theoretical and modeling studies linked to empirical work addressing the choices, and trajectories, of individuals constrained by membership in the group.

Aggregation occurs at all sizes from bacteria to whales, from groups of 10 to 10 million, and across a range of temporal stability from the ephemeral assemblages of midges to the obligatory schools of herring (1). What the eye sees is the collective—the flock, the school, the swarm—regardless of whether its members work in synchrony (fish, birds) or not (insects). Aggregations often behave as a unit with properties that are not merely a sum of the individual behaviors. In some cases, this results in new functions: the ability to build a nest or thermoregulate the hive (bees, termites), form a spore-bearing structure (slime mold), or mob predators (birds) (2, 3). In other cases, the properties are meaningful only in the context of a group, for example, a well-defined edge (hopper bands of locusts), a well-regulated density profile (schooling fish), polarity without a leader, or a distinct shape whose topology varies to suit the tasks (branched army ant raiding column) (4). Some aggregations also display fluidity and uniformity of response, such as mills, vacuoles, fountains, and flash expansion of fish schools (Fig. 1) (5). Emergent properties of groups are not surprising in view of recent research on complexity demonstrating the ability of large populations of simple, identical units (for example, spin magnets) to self-organize, form patterns, store information, and reach “collective decisions” (6). Even with rather simple individual rules, nonlinear

interactions can lead to complex and non-intuitive behavior in large groups (7).

Operationally, animal aggregations fit into two classes: those that “self organize” and those that form in response to external cues such as light or food. The former, for example bird flocks, fish schools, and ungulate herds, are of primary interest in complexity theory. In some congregations, an external attractant nucleates the group: schools of tuna initially form beneath floating objects but quickly grow in size, dwarfing the original stimulus (8). Once formed, many aggregations persist even though membership turns over. Relatedness to, or knowledge of, neighbors may be minimal, and the group is maintained through collective individual responses. Simple mechanisms, such as allelomimesis—or doing

what your neighbors do (7)—can prevent structural breakdown provided individuals are physically close enough to interact.

## Evolutionary Functions

Why do animals aggregate? Responses to this question are based on the evolutionary assumption that joining a group must increase the survivorship or reproductive success of the new member. Juvenile survival increases in protective, physically structured herds, with the strongest adults at the periphery (9). Classically, protection from predators has been viewed as an important selective advantage to group membership, with benefits including dilution of predation, group vigilance, and the confusion effect (an inability of predators to visually lock onto one target among many) (10). However, persistent aggregations also attract predators (11). Marine mammals use the tendency of their prey to be concentrated to facilitate successful attack (12). The consummate concentration predator—humans—can net up to 40 million metric tons of schooling marine finfish and invertebrates annually (half of the world catch of marine biomass) because these species aggregate so densely (13).

Other selection factors also favor aggregation. Mating and mate choice lead to small, ephemeral assemblages (swarms of mosquitoes, leks of sage grouse) as well as large, predictable aggregations (herds, pods, and schools migrating to and from spawning



Fig. 1. Fish schools provide an example of emergent pattern such as milling in which individual members circle about an unoccupied core. [Photo: ©1999 Norbert Wu]

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grounds). Energetic benefits for flying or swimming may derive from specific relative positions of individuals (14). Survival strategies in adverse conditions may require cooperation, as in the slime mold amoebae that aggregate, form a multicellular spore-bearing structure, and disperse a fraction of their members to other sites (3). Food finding is enhanced in aggregations that act as an interacting array of sensors and effectors, gathering and analyzing more information about the world than could a lone individual. These sensory integration systems transduce physical signals into social cues, which amplify or attenuate group responses (15–17).

In view of the prediction of complexity theory that patterns emerge as epiphenomena in the inanimate world, it is hard to argue the case that all animal aggregations have a functional purpose. Numerous examples of strikingly beautiful aggregations form spontaneously through combined physical forces and individual properties, with no clear evolutionary benefit or drive. Currents, eddies, convergent zones, and other fluid dynamic phenomena can result in patchy and highly clumped distributions of organisms (18). Other examples such as branching morphology in bacteria colonies (19) occur under specific, possibly contrived, laboratory settings. Pattern and structure can arise as epiphenomena through nonlinear interactions, whether or not the units are alive, and whether a purpose exists or not (20). Aggregation can also be the result of individuals assorting uniformly relative to resource availability and quality, with the result that high-quality patches have the densest groups (21). Once convened, biological factors such as predation can operate

as selective agents for the maintenance of emergent properties of the aggregation—including group size, shape, and architecture—and the constraint of membership (as the cost of straggling is often death).

### The Paradox of Individuality

An aggregation may form initially by random encounter and grow by density-dependent interactions. Group size is then determined by the balance of payoffs to individual members, where size of the group affects its performance. At very small sizes, mistakes by individuals are magnified in group response, social transmission is compromised such that reproduction may be jeopardized, and predation is not well mitigated (22). At very large sizes, individuals compete for resources, succumb to concentration predators and disease, and even to the self-pollution of the group (23). Within the midrange are the theoretically optimum group size ( $n^*$ ), the point at which benefits to the average member are maximal relative to a loner, and the equilibrium or critical group size ( $\bar{n}$ ), at which the benefits equal those of a loner. For the foraging case,  $n^* < \bar{n}$  and group size tends to be larger than optimal. For the predation case,  $\bar{n}$  may be less than, greater than, or essentially equal to  $n^*$ , depending on predator abundance and type. In reality,  $n^*$  and  $\bar{n}$  are dynamic variables, responding to external forcing factors (for example, predatory pressure, flow, time of day), group factors (for example, density, shape), and individual internal state (for example, hunger, breeding state). In human societies optimal group size is often exceeded (24), with the consequent societal result that in the largest, densest human aggregations (cities) the costs of

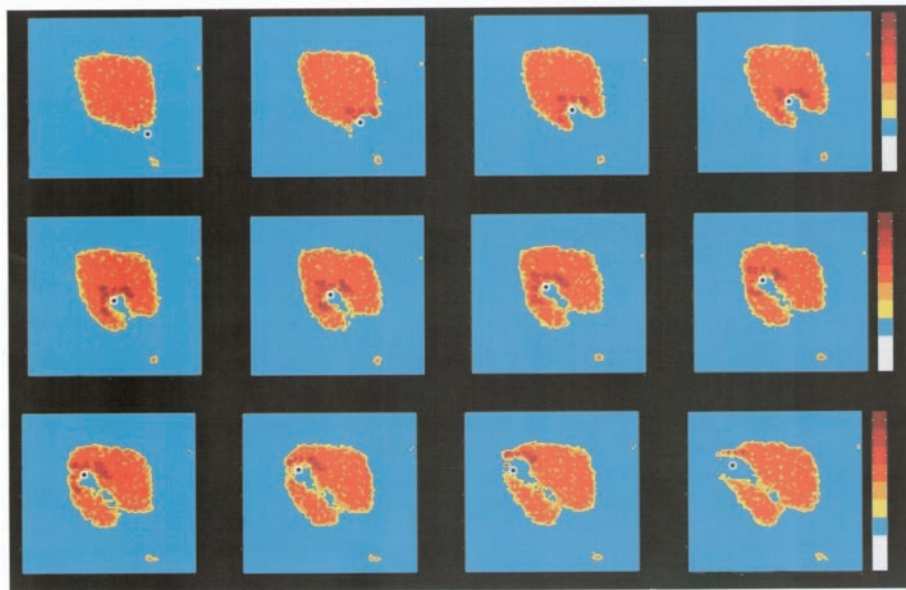
pollution, epidemics, and aggression overwhelm the benefits of gregariousness and lead to environmental degradation (25).

In addition to group-size benefits, individuals gain selfishly because payoffs are not evenly distributed but a function of position (26). In “selfish herds” the interior is safest, whereas in fish schools the opposite may be true; the vanguard is most advantageous for exploiting resources, whereas individuals on the trailing edge may fall behind and get lost or eaten (27). Selfish individuals should constantly vie for optimal positions as the moment-by-moment conditions change. However, individual movement patterns that contrast too sharply with the group may create behavioral stragglers more easily targeted by predators (28). Furthermore, in large aggregations most individuals are located in interior positions, unaware of the distance to an edge. The cost of suboptimal location and incomplete information must be balanced against the (usually greater) cost of noncooperation. Here is one of the conundrums of animal aggregation—if all individuals act with maximal short-term selfishness, the average benefits are lost to everyone and the group dissolves in the scuffle. If all individuals act for maximum group benefit, then the principles of evolution, as we understand them, are violated.

Positional benefits are also a function of group shape (29, 30). The food-finding advantage to the vanguard individual is diluted as the group switches from an oblate ellipsoid to a sphere to a flat forward surface. Shape is a function of summed individual response to the environment, constrained by the responses of neighbors. Thus, a shape may be adaptive, as in the paraboloid formations of hunting bluefin tuna (31); maladaptive, as in balls of herring under attack by marine mammals (12); or a simple epiphenomenon, as in trunk trails or ramified, fan-shaped structures of army ants under different life-cycle stages (32, 33).

### Modeling Aggregation

Theoretical work on aggregation has complemented biological observation and focused on conditions leading to aggregation—how individual decisions influence the overall shape, size, function, and dynamics of the collective, and the interplay between deterministic and stochastic effects. Three theoretical approaches to the study of aggregation are prevalent. The first describes the mean-field density of a swarm using “Eulerian” continuum equations (partial differential equations), based on a diffusion approximation of random motion. Other terms for attraction and repulsion to conspecifics or external sources are superimposed (34). Because the theory of partial differential equations is rich, analytical progress is possible, although the realism of these models is re-



**Fig. 2.** Output from a cellular automata model demonstrating the emergent property of uniformity and fluidity of group-level response to a predator (large black dot) producing a vacuole which tracks the predator movement through the school. Darker red indicates higher density; yellow is low density. [Photo: Figure 9 in (38), reprinted with permission]



stricted to large, dense aggregates with no sharp discontinuities. Some models allow for nonlocal interactions, such as visual or auditory sensing (35). From recent models of this type, certain important properties of self-organized swarms can be deduced. First, at low densities, attraction should dominate over repulsion to keep the aggregation from disintegrating, but the opposite should hold at high densities to prevent unrealistic compaction. Restated, repulsion should have a more nonlinear density dependence than attraction. Second, nonlocal interactions are essential for long-lasting mobile groups, but even these cannot prevent loss of members at the trailing edge on some slow time scale.

A second theoretical approach is based on individual trajectories, with "Lagrangian" equations of motion and detailed forces and velocities attributed to individuals (18, 34). Stochastic effects are often included to incorporate noise or imperfect responses of individuals. Such models can be more accurate descriptions of what the members of a group are actually doing, although their analysis is difficult. Numerical simulations or approximate solutions are then investigated.

A third approach dispenses with equations of motion and relies directly on discrete (for example, cellular automata or lattice gas) simulations of individual behavioral rules and motion (36–38) (Fig. 2). For instance, the "multi-agent" simulation system "Swarm" (39) has been applied to bees, fish, and other collectives. It is argued that the discrete approach gives vivid visual predictions of how individuals contribute to collective behavior. However, many sets of rules can lead to lifelike group behavior, so that the results, though visually appealing, may be uninformative—it is not always possible to deduce individual behavior from emergent properties. Furthermore, detailed behavior of real organisms may be very complex and hard to reproduce in a simulation. The fact that simple rules generate a lifelike behavior is no guarantee that living systems actually follow simple rules.

**Pattern Versus Function**

Emergent properties are a hallmark of animal aggregation but are not necessarily evolutionarily advantageous. Which ones convey fitness benefits and which are simply epiphenomena is a fundamental question. Put another way, what is the scale of selection (40)? With the wide variety of living aggregates, it is hard to make sweeping generalizations; however, there are a few commonalities. (i) Group size and shape fluctuate as a function of resources, physiology, predominant activity, and limitations on the sensing abilities of the members. Extremes of size are disadvantageous. (ii) As a unit, aggregations remain stable even though membership is in constant flux. New members can transfer experience; however, rapid replacement of the majority can compromise this social storage function. (iii) Shape,

internal structure, and motion of the group are emergent properties dictated by constrained collective decision-making. What appears as cooperation resulting in cohesion may in fact be conflict veiled by the necessity to minimize the cost of disintegration.

In the future, evolutionary theory based on individual return will have to be reconciled with the emergent patterns created when individuals assort in stable groups—what is pattern and what has become function? Following groups, tracking individuals, and scaling up from small groups remain the biggest areas where work is needed. Until experimental progress is made, it seems unlikely that we will gain a true understanding of animal aggregation, let alone decipher rules underlying such complex systems. Mathematically, models that include local and long-range effects, as well as deterministic and stochastic components, provide promising directions. Linking this output with real-world aggregation phenomena, however, will still be a challenge. Beyond this integration of approaches and fundamental questions lies the possibility of shaping aggregation phenomena, for example crowd control, by manipulating the socioenvironmental parameters under which aggregation occurs. Will the lessons of complexity contribute to our understanding? The importance of fluctuation for attaining globally optimal states suggests that noise plays an important role in group organization; whether other lessons contribute to biological insight remains to be seen.

**References and Notes**

1. W. C. Allee, *Animal Aggregations* (Univ. of Chicago Press, Chicago, 1931).
2. Nest building: B. Holldobler and E. O. Wilson, *The Ants* (Belknap, Cambridge, MA, 1990). Thermoregulation: B. Heinrich, *Science* **212**, 565 (1981); J. Watmough and S. Camazine, *J. Theor. Biol.* **176**, 391 (1995). Mobbing: B. C. R. Bertram, in *Behavioural Ecology: An Evolutionary Approach*, J. R. Krebs and N. B. Davies, Eds. (Sinauer, Sunderland, MA, 1978), pp. 64–96.
3. J. T. Bonner, *Am. J. Bot.* **31**, 175 (1944).
4. Edges: P. E. Ellis, *J. Exp. Biol.* **30**, 214 (1953). Density: O. A. Misund, *Behaviour of Schools Related to Fish Capture and Acoustic Abundance Estimation* (University of Bergen, Bergen, Norway, 1991). Polarity: W. L. Romey, *Ecol. Model.* **92**, 65 (1996). Shape: (32).
5. T. J. Pitcher and J. K. Parrish, in *Behavior of Teleost Fishes*, T. J. Pitcher, Ed. (Chapman & Hall, New York, ed. 2, 1993), pp. 363–440.
6. H. Haken, *Synergetics, An Introduction: Nonequilibrium Phase Transitions and Self-Organization in Physics, Chemistry, and Biology* (Springer-Verlag, New York, 1983); R. Graham and A. Wunderlin, Eds., *Lasers and Synergetics: A Colloquium on Coherence and Self-Organization in Nature* (Springer-Verlag, New York, 1987).
7. J. L. Deneubourg and S. Goss, *Ethol. Ecol. Evol.* **1**, 295 (1989).
8. J. R. Hunter and C. T. Mitchell, *U.S. Fish Wildl. Serv. Fish. Bull.* **66**, 13 (1966).
9. L. D. Mech, *The Wolf: The Ecology and Behavior of an Endangered Species* (Natural History Press, New York, 1970); M. Edmunds, *Defense in Animals* (Longman, London, 1974).
10. G. C. Williams, *Mich. State Univ. Biol. Ser.* **2**, 349 (1964). Dilution: W. D. Hamilton, *J. Theor. Biol.* **31**, 295 (1971). Vigilance: D. L. Lack, *The Natural Regulation of Animal Numbers* (Clarendon, Oxford, 1954); J. Lazarus, *Anim. Behav.* **27**, 855 (1979); J. L. Hoogland, *ibid.*, p. 394. Confusion: L. Landeau and J. Terborgh, *ibid.* **34**, 1372 (1986).

11. J. F. Wittenburger and G. L. Hunt, *Avian Biol.* **8**, 1 (1985).
12. B. Würsig and M. Würsig, *U.S. Fish Wildl. Serv. Fish. Bull.* **77**, 871 (1980); V. M. Bel'kovich et al., in *Dolphin Societies: Discoveries and Puzzles*, K. Pryor and K. S. Norris, Eds. (Univ. of California Press, Los Angeles, 1991).
13. J. K. Parrish, *Environ. Biol. Fishes*, in press.
14. Birds: P. B. S. Lissaman and C. A. Shollenberger, *Science* **168**, 1003 (1970). Fish: D. Weihs, *Nature* **241**, 290 (1973).
15. D. Grunbaum, in *Animal Groups in Three Dimensions*, J. K. Parrish and W. M. Hamner, Eds. (Cambridge Univ. Press, London, 1997), pp. 257–300.
16. C. R. Schilt and K. S. Norris, in *ibid.*, pp. 225–244.
17. K. S. Norris and C. R. Schilt, *Ethol. Sociobiol.* **9**, 149 (1988).
18. T. J. Pedley and J. O. Kessler, *Annu. Rev. Fluid Mech.* **24**, 313 (1992); G. Flierl et al., *J. Theor. Biol.* **196**, 397 (1999).
19. J. Wakita et al., *J. Phys. Soc. Japan* **67**, 3630 (1998); E. Ben-Jacobs and H. Levine, *Sci. Am.* **279**, 56 (1998).
20. A. M. Turing, *Philos. Trans. R. Soc. London Ser. B* **237**, 37 (1952).
21. Ideal free distribution: S. D. Fretwell and H. J. Lucas, *Acta Biotheor.* **19**, 16 (1970).
22. Individual mistakes: (15). Loss of social function: W. C. Allee et al., *Principles of Animal Ecology* (Saunders, Philadelphia, 1949); (16). Loss of reproduction: J. Forcada et al., *Mar. Mamm. Sci.* **10**, 137 (1994).
23. Resource competition: C. W. Clark and M. Mangel, *Theor. Popul. Biol.* **30**, 45 (1986); L.-A. Giraldeau, in *The Ecology of Social Behavior*, C. N. Slobodkinoff, Ed. (Academic Press, San Diego, CA, 1988), pp. 33–53. Concentration predators: (30). Disease: W. O. Kermack and A. G. McKendrick, *R. Stat. Soc. J.* **115**, 700 (1922). Self pollution: W. N. McFarland and S. A. Moss, *Science* **156**, 260 (1967).
24. E. A. Smith, in *Hunter-Gather Foraging Strategies*, B. Winterhalder and E. A. Smith, Eds. (Univ. of Chicago Press, Chicago, 1981), pp. 36–65.
25. J. M. Diamond, *Guns, Germs, and Steel: The Fates of Human Societies* (Norton, New York, 1997).
26. J. Krause, *Biol. Rev.* **69**, 187 (1994).
27. Interior safety: J. C. Coulson, *Nature* **217**, 478 (1968). Interior risk: J. K. Parrish, *Anim. Behav.* **38**, 1048 (1989). Trailing edge risk: L. Edelman-Keshet et al., *J. Math. Biol.* **36**, 515 (1998).
28. T. J. Pitcher and C. J. Wyche, in *Predators and Prey in Fishes*, D. L. G. Noakes et al., Eds. (Dr. W. Junk, The Hague, 1983), pp. 193–204.
29. M. V. Abrahams and P. W. Colgan, *Environ. Biol. Fish.* **13**, 195 (1985).
30. J. K. Parrish, *Netherlands J. Zool.* **42**, 358 (1992).
31. B. L. Partridge et al., *Environ. Biol. Fishes* **9**, 253 (1983).
32. T. C. Schneirla, in *A Study in Social Organization*, H. R. Topoff, Ed. (Freeman, San Francisco, 1971).
33. C. W. Rettenmeyer, *Univ. Kansas Sci. Bull.* **44**, 281 (1963).
34. A. Okubo, *Diffusion and Ecological Problems: Mathematical Models* (Springer-Verlag, New York, 1980); *Adv. Biophys.* **22**, 1 (1986); L. Edelman-Keshet et al., *J. Math. Biol.* **36**, 515 (1998).
35. M. Mimura and M. Yamaguti, *Adv. Biophys.* **15**, 19 (1982); A. Mogilner and L. Edelman-Keshet, *J. Math. Biol.*, in press.
36. C. W. Reynolds, *Comput. Graphics New York* **21**, 25 (1975).
37. G. B. Ermentrout and L. Edelman-Keshet, *J. Theor. Biol.* **160**, 97 (1993).
38. R. Vabø and L. Nøttestad, *Fish. Oceanogr.* **6**, 155 (1997).
39. C. G. Langton, *Artificial Life: An Overview* (MIT Press, Cambridge, MA, 1995).
40. S. A. Levin, in (15), pp. 245–256.
41. We acknowledge helpful comments on earlier drafts of the manuscript by R. T. Paine and P. D. Boersma. K. Jensen provided invaluable help. Figure 1 was taken by N. Wu, www.norbertwu.com, ©1999, and appears with permission. Figure 2 was originally published as figure 9 in (38) and appears by permission of the publisher Blackwell Scientific.