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ORGANIZED FLIGHT IN BIRDS

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ABSTRACT

The organized flight of birds is one of the most easily observed, yet challenging to study, phenomena in biology. Birds that fly in organized groups generally do so in one of two fashions: Line formations and Cluster formations. The former groups are typically demonstrated by large birds like waterfowl, where birds fly arranged in single lines, often joined together. The scientific questions about these groups usually involve potential adaptive functions, such as why do geese fly in a V? The latter, Cluster formations, are typically made up of large numbers of smaller birds like pigeons or blackbirds flying in more irregular arrangements that have a strong three dimensional character. The groups are defined by synchronized and apparently simultaneous rapid changes in direction. Scientific questions about these groups are usually concerned with mechanism; how is synchrony achieved? Although field observations about the phenomenon date to the origins of natural history, experimental studies did not begin until the 1970s. Early experimenters and theoreticians were primarily biologists, but more recently aeronautical engineers, mathematicians, computer scientists, and currently, physicists have been attracted to the study of organized flight. Computer modelling of organized flight has recently generated striking visual representations of organized flight and a number of hypotheses about the functions and mechanisms of organized flight, but the ability to test these hypotheses lags behind the capacity to generate them. It is suggested that a multiple-disciplinary approach to the phenomenon will be necessary to resolve apparently conflicting current hypotheses.

Keywords

animat; bird aerodynamics; bird flight; bird flocking; boid; cluster formations; Canada Goose; *Branta Canadensis*; European Starling; *Sternus vulgaris*; flight formations; flock simulations; flocking simulations; line formations; V formation

The orderly aerial manoeuvres of birds have fascinated and mystified observers since the beginnings of written natural history 2,000 years ago, when Pliny suggested that geese '...travel in a pointed formation like fast galleys, so cleaving the air more easily than if they drove at it with a straight front' (Rackham 1933). Why do geese fly in a V, and how do pigeons all seem to be able to take off and turn at once? The study of these phenomena offers an encapsulated model of the development of knowledge of other behaviours, starting with anecdotal descriptions and speculation, measured observations of increasing precision, formation of testable hypotheses, and then tests of these hypotheses. In the case of the study of organized flight in birds, the first phase began at about the beginning of the twentieth century, the second and third in the 1970s and the fourth in the mid 1980s. The study of bird organized flight also offers a good demonstration of Kuhn's (1962) suggestion that science advances in saltatory fashion, each 'revolution' being prompted by a new technique or apparatus that allows old data to be looked at in a new way.

The early investigators of organized flight were, with a few notable exceptions, biologists. In the 1970s, aeronautical engineers started to be attracted to the phenomenon, followed by computer scientists in the 1980s, and physicists and mathematicians in the 1990s. These later investigators have been primarily interested in modelling the behaviour. The fraction of active investigators with a biological background has steadily decreased over the years. We will try to demonstrate that as the elegance of models has increased, so has their distance from behaviour in the field, and that future progress in the area will depend on collaborations between physicists, mathematicians, computer scientists and biologists rather than specialists working alone.

THE ERA OF ANECDOTE AND SPECULATION

Several ornithologists of the 1930s made visual field observations that would later be very provocative to experimentalists and theoreticians. Nichols (1931) noted that in turning and wheeling pigeon, *Columba livia*, flocks, the position of the birds at the head of a turning flock would be exchanged with birds at the side after the completion of a turn; there did not appear to be consistent ‘leadership’ in such flocks. He speculated that this behaviour might be the result of faster birds in the front of the formation moving ahead of the flock, then turning back to rejoin. The visual stimulus provided by the turnaround might provide a signal for the rest of the birds to turn, apparently simultaneously. He suggested that a change in direction was related to a change of positional leadership.

Selous (1931) made a 30-year series of meticulous visual observations on various species of birds flying in organized flocks, and was convinced that within the limits of unassisted human vision, there were occasions when birds rose from the ground, or made turns simultaneously. He concluded that there could be only two possible explanations for such a phenomenon; disturbance from outside the flock, say the sight of a predator, which would be instantaneously received by all birds in the flock, and would be reacted to in identical manner, or an undefined quality he called ‘thought transference’, or what we might call today ‘telepathy’.

Selous appeared convinced that there were at least some occasions when groups of birds would rise from the ground, apparently spontaneously, with no discernible source of outside disturbance. He also noted in contrast that there were times when a flock on the ground would be indifferent to the rapid approach of an aerial predator, as when members of a flotilla of Eurasian Coots, *Fulica atra*, leisurely swam away as a Great Black-backed Gull, *Larus marinus*, made a low pass over their group. Penrose (1949) made a similar observation when he dove from above toward a large European Starling, *Sternus vulgaris*, flock in a sailplane.

Selous also noted that flocks on the ground would sometimes take to the air in a stepwise fashion. Individuals or small groups of Black-headed Gulls, *Larus ridibundus*, would take flight without any discernible effect on neighbours, and then with no obvious temporal relationship to previous small group departures, the entire remainder of the flock, hundreds of birds, would take flight simultaneously.

‘Thought transference’ had a different standing in the scientific community in Selous’ time than it does today, and it is not surprising that, for want of a better explanation, a careful observer like Selous might be led to something as heterodox as telepathy to explain an otherwise inexplicable phenomenon. Rhine (1983) had started reporting the results of parapsychology experiments using conventional experimental design in 1927, and England, where Selous made his observations was a centre of interest in ‘paranormal’ phenomena. Selous never explored what the nature of thought transference might be.

Gerard (1943) was one of the first individuals to try to quantify turning behaviour in a flock. Whilst pacing a group of approximately 100 unidentified birds in a car being driven at 35 mph (60 km/h), he observed that the entire flock turned left in a flanking movement, rather than a column movement, in military parlance. In a flanking movement all individuals turn at once upon the signal to do so, rather than advancing to a defined point and then turning. He speculated that no bird advanced more than a body’s length beyond any other bird before turning, by his calculation within 5 ms of any other bird. Assuming a minimum reaction time of 100 ms, he proposed that any coordinating signal must have been acted on with great constancy by receiving individuals. Gerard’s own vision must have been remarkable to be able to make this observation while driving a car, but his estimate of probable reaction time was very close to Pomeroy & Heppner’s (1977) laboratory study results of startle reaction times in the European Starling of 70 ms.

Much of the early work on flight flocking was devoted to considerations of the biological utility of flocking, from an ecological or behavioural standpoint, rather than the perspective of organizing principles or mechanisms. Beer (1958) questioned whether large groupings of birds had ‘any’ distinctive utility, and were merely ‘haphazard organizations’. Vine (1971), on the other hand, suggested that a circular grouping provided the best predator avoidance strategy against visual predators. Emlen (1952) looked at flocks from the ethological perspective of the times, and suggested that both flocking itself, and the structure of the flock resulted from the interplay of attractive and repulsive behavioural forces.

One of the annoyances that has persisted over the years for those studying flocks is an etymological one; there has been no consistency in the literature in terms of the definition of ‘flock’ and categories of same. The difficulty is not a trivial one. One author might be describing the properties of a class of behaviours that is quite different than those studied by a different investigator, but both will use the same term.

For example, Emlen (1952, p. 160) described a flock as ‘any aggregation of homogeneous individuals, regardless of size or density’. This definition immediately presents difficulties, because there are very common aerial groupings, such as mixed blackbird groups, composed of different species. Beer’s (1958, p. 78) definition of a flock was ‘...two or more birds which associate with each other due to innate gregarious tendencies’. This definition breaks down in the face of more recent flocking studies, like Reynolds’ (1987), which suggest that coordinated flocking may be the product not simply of ‘gregariousness’, but extremely simple behavioural rules followed by each bird in the group.

Heppner (1974) developed a taxonomy of airborne bird flocks. The primary dichotomy in this scheme was between ‘Flight Aggregations’, which are unorganized groups of flying birds gathered in an area for a common purpose, such as gulls circling about a fishing trawler, and ‘Flight Flocks’, which were organized groups of flying birds coordinated in one or more aspects of flight, such as taking off, turning, landing, etc. However, these distinctions seem not to have been universally adopted in the literature; one regularly sees the term ‘aggregation’ used to describe what Heppner would have called a ‘flight flock’.

Heppner’s second order division of ‘Flight Flocks’ has demonstrated some persistence and consistency in the literature. He differentiated flight flocks into ‘Line Formations’ and ‘Cluster Formations’ (Fig. 1). Line formations are demonstrated by relatively large birds that fly in regular lines or queues, such as geese, cormorants, or ducks. Cluster formations have a three dimensional structure like a sphere, and are typically seen in smaller birds like pigeons, starlings, and smaller shorebirds. Interestingly, line flying birds like geese may sometimes be seen in a cluster, but cluster flying birds like starlings are rarely, if ever, seen flying in single lines.

The categories of biological questions that are raised by each of these formations are quite different. Typically, ‘how’ questions are raised about cluster flocks. Do the birds really turn all at once? How can they achieve synchrony in taking off and landing? How do they decide when to turn, and in what direction? ‘Why’ questions are more characteristic of line flying birds. What might be the biological advantage of flying in this configuration? Are there energy savings to be had? Does the formation shape facilitate communication? A broad question that might apply to both groups is whether there is a general advantage to flying in groups, as opposed to solitary flight?

A literature search suggests that investigators recognize that the two formation categories may represent quite different biological issues. Early key papers on line formations tend to be cited through generations of papers on line formations, but not cluster formation studies, and vice versa. For this review, we recognize the difference between these lines of investigation, and will treat them separately.

LINE FORMATIONS

Line flying birds typically fly in staggered, or ‘echelon’, formations rather than in straight lines nose-to-tail. If two such formations are joined at an apex at the front of the formation, we have a V or a J, its asymmetric variant. Franzisket (1951), von Holst (1952) and Hochbaum (1955) suggested that close formation flight might provide the advantage of a turbulence free zone behind a bird ahead, but that would seem to apply only if the birds flew immediately behind the bird in front, like race cars, which they rarely do.

Two competing, but not necessarily mutually exclusive, hypotheses have been advanced to explain the functionality of staggered line formations (most of the papers to be subsequently cited here refer to V formations and their properties, but Gould & Heppner [1974] found in a study of 104 Canada Goose, *Branta canadensis*, formations that Vs and Js together were less common than single staggered lines, or echelons. Additionally, O’Malley & Evans [1982a, b] found that White Pelicans, *Pelecanus erythrorhynchos*, flying in line formations only flew in Vs

10% of the time). Wieselsberger (1914), an aerodynamacist, was the first to suggest an aerodynamic advantage for line formation flight. He proposed that a V partitioned drag equally between the two legs of the flight, and that birds flying to the left or right of a bird in front could recapture energy lost to an 'upwash' generated off the wingtips of the preceding bird. The alternate, behavioural view suggests that social and perceptual factors have guided adoption of staggered formations. Hamilton (1967) suggested that flying in staggered lines permitted the optimum combination of visibility of neighbours, and a clear visual field to the front. Heppner (1974) suggested that the fixed position of the eyes in the heads of line-flying birds might make a staggered formation advantageous for keeping the image of an adjacent bird on the visual axis of a given bird's eyes. However, Heppner et al. (1985) found that the angle between the legs of a V formation of Canada Geese that would place the image of a leading bird on the visual axis of the eyes of a following bird (128°) was considerably more obtuse than the measured V-angles of V-formation flying birds in previous studies (Gould & Heppner 1974; Williams et al. 1976; O'Malley & Evans 1982a). They also noted that although Canada Geese have a limited amount of binocular vision to the front, despite having eyes located on the sides of their heads, they also have a 'blind cone' in back of them of 29° on either side of the midline. Thus, a V angle of 58° or greater would enable every bird in the formation to see every other bird, even those following behind.

Warnke (1984) offered a third hypothesis that, judging by the number of subsequent citations, seems not to have generated much enthusiasm in the V formation community. He suggested that the V formation could be explained by the interaction of electrostatic fields generated by flapping flight. He did not discuss how birds would be able to detect such fields, nor did he explore the advantage that might accrue to a bird by basing its proximity to a neighbour on the basis of these fields. There was much interest in the biological effects of electromagnetic fields in the 1970s and 1980s; Heppner & Haffner (1974) suggested that coordinated cluster flocks might be explained by signals sent by a leader to all birds in a flock by means of a hypothetical radiated electromagnetic field. Interestingly, Hill (1972) described a device he patented that was a wing-levelling autopilot for model aircraft that operated by the differential in electrostatic fields between wingtips of a moving model airplane, so Warnke's idea was not totally implausible.

There have been more papers addressing the aerodynamic hypothesis of staggered flight than other hypotheses, and a bit of aerodynamic theory here will make the subsequent references more intelligible. For a bird to fly by use of a wing requires a 'relative wind'; a passage of air over the wing. If the front of the wing is tilted up slightly relative to the wind, the relative wind is deflected downward. The result is a positive force on the underside of the wing, 'Newtonian lift' (Fig. 2). Additionally, airplane wings are typically constructed so that the top of the wing is curved and air moves faster over the top of the wing, creating a negative pressure on the top of the wing; 'Bernoulli lift'. In still air, we must generate the relative wind by moving the aircraft forward. To do so, we must have a force called 'thrust', generated, for example, by a propellor. In general, the faster the aircraft goes, the more lift is generated by the wing. Unfortunately, as the aircraft accelerates, 'drag' is produced, at least in part by friction between the air and the surface. One type of drag, 'induced drag', is especially germane to bird flight. Lift is, partly, created by the angle with which the wing meets the air (referred to also as the angle of attack). Up to a limit, the steeper the angle, the greater the lift—but also, the greater is the induced drag, which is produced as a by-product of lift. Compared to airplanes, birds are typically low-speed aircraft whose wings produce a lot of induced drag.

The inner part of a bird's wing provides most of the lift, the outer part, by a kind of rowing action, provides the thrust. As air streams over a wing generating lift, it tends to form vortices, which typically stream off the wing as 'tip vortices', essentially horizontal tornadoes. These tip vortices have a rising and falling component, and in an airplane, may carry sufficient energy to upset a smaller aircraft following a larger one in for a landing. It is this energy, which essentially represents a cost of flight using wings, that the aerodynamic hypothesis of V formation suggests might be partially recaptured by a following bird whose own wingtip was located in the upward rising part of the tip vortex, or upwash, streaming off the wing of the preceding bird (Fig. 3). The diameter of the vortex increases with distance from the producing bird's wingtip, and tends to dissipate with increasing distance. The placement of a following bird's wingtip in relationship to the vortex from a preceding bird's wingtip should, in theory, affect how much energy is recaptured by the following bird. To recapture tip vortex energy from a preceding bird, a following bird would have to be positioned to the left or right of a preceding bird, suggesting that a V (or at least a staggered, or echelon) formation would be advantageous for birds flying in a group.

Lissaman & Schollenberger (1970) produced the first quantitative suggestion, based on aerodynamic theory, of exactly how much energy might be saved by a group of birds flying in a V formation. They proposed that a group of 25 (unspecified species) birds flying in a V would have 71 percent more range than a single bird. Their optimum V angle appeared to be about 120° between the legs of the V. For later investigators, this paper was both stimulating and frustrating because they did not present the calculations and formulae used to arrive at their conclusions, ignored the quantitative effects of flapping rather than fixed wing flight, and did not apparently consider the difference between air flowing over a smooth metal surface and a feathered wing nor the aerodynamic scaling effects of small birds flying at low speeds compared to aircraft. Nonetheless, this paper provided a 'target' for experimental and quantitative observational work.

Haffner (1977) flew Budgerigars, *Melopsittacus undulatus*, in a wind tunnel and used a smoke stream to visualize the airflow over the bird's wing. He concluded that flapping wing flight is aerodynamically complex, and that calculations of energy saving for the V formation using fixed wing models were oversimplified, and probably overgenerous. Using Cone's (1968) theoretical studies on flapping wing flight and his own experimental work, he concluded that potential energy saving of V formation flight compared to solitary flight was a much smaller maximum of 22%.

Willis et al. (2007) examined the theoretical energy savings in formation flight with respect to basic positioning and wing beat phase relationships between a preceding bird and a following bird. Nachtigall (1970) found a phase synchrony in a field study of wing beats in Canada Goose formations, but Gould (1972), in a similar study, failed to do so. Willis et al.'s (2007) study is preliminary as they do not consider the optimal formation shape or detailed flapping kinematics or wing shapes. Nonetheless, their results suggest that optimal flapping phase synchrony accounts for up to 20% of induced flight power savings, but that precision phase locking is not required for energy savings to occur. They also observed that ideally, the following bird would not be vertically elevated above or below the lead bird's wake if flapping started in phase. If flapping is not in phase, however, it may be advantageous to take on a vertical displacement relative to the preceding bird to most effectively capture its strongest upwash regions. They suggest that vertical displacements in nature probably do not happen for aerodynamic benefit, as for that to occur precision flight dynamics and sensing would be required.

Determination of the distance between birds, and the angle of the legs of the V would be necessary to test V formation hypotheses. Gould & Heppner (1974) performed the first field measurement of both parameters in Canada Geese using projective geometry and still photography. They reported a mean angle between the legs of the V ±SD of 34±6°, N=5, with a mean distance between bird bodies ±SD of 4.1±0.8 m, N=3 and a mean flock size ±SD of 18±12 birds, N=5. Two years later, Williams et al. (1976) examined V angles in Canada Goose formations using a radar technique. They found a range of 38−124° in the feeding flights they recorded. Further, they noted that the angle in a single formation varied from 5−40° between successive sweeps of the radar beam (duration of sweep not reported). Both groups of authors used their respective photographic and radar techniques on the same flocks of birds in 1975, and found no significant difference between the two.

Higdon & Corrsin (1978) refined Lissaman & Schollenberger's (1970) hypothesis by considering the effects of flying in three-dimensional fashion, i.e. in a cluster, like starlings. As one might suspect, the physics is considerably more complex, but they suggested that it was aerodynamically disadvantageous to fly directly behind another bird, and that a tall, narrow cluster flock (such as is often seen in mixed blackbird flocks) is aerodynamically disadvantageous compared to solitary flight. May (1979) also re-examined Lissaman & Schollenberger's (1970) suggestions, and concluded that the aerodynamic advantage of line flight in large birds was 'slight', perhaps as little as 10% compared to solitary flight.

Badgerow & Hainsworth (1981) re-examined Gould & Heppner's (1974) data on distances between Canada Geese to obtain 'wingtip spacing', a variable they felt was more appropriate than 'distance between body centres' in testing the aerodynamic hypothesis of V formation flight. When they did this, they found a number of birds had wingtips that overlapped the position of the wingtips of a bird ahead, a problematic situation for producing an energy advantage in Lissaman & Schollenberger's (1970) hypothesis. In contrast to Lissaman & Schollenberger's (1970) predicted maximum range increase of 71% for V formation flight, Badgerow & Hainsworth's (1981) revision predicted a maximum increase of 51%, with a range increase of 2−23% for the birds in a selected Gould & Heppner (1974) flock. Hainsworth (1987) later provided an excellent description of the modified projective geometry technique he and Badgerow used in the study above for examination of goose flocks, and applied it to his own photographs of Canada Goose flocks. He noted that birds frequently shifted positions laterally relative to the bird ahead, although the basic energy saving model of Lissaman & Schollenberger (1970) predicted that there was an optimum position for energy saving. Using their model, he concluded that the goose flocks he filmed were only enjoying a 36% energy advantage over solitary flight, about half of the Lissaman & Schollenberger (1970) model. He cautioned against a simplistic engineering model for explaining in toto a behaviour that might be highly variable, depending on circumstance.

O'Malley & Evans (1982a, b) broadened the examination of line formation flight by studying line flight in White Pelicans, *Pelecanus erythrorhynchos*. They used a variant of Gould & Heppner's (1974) projective geometry technique to measure angles of Vs and Js, and distance between birds, with much larger sample sizes (45 flocks) than in the Gould & Heppner (1974) study. The angles ranged from 24−122°, with a mean ±SD of 67±8°, *N*=12, for V formations, and 70±5°, *N*=33, for J formations. As in the earlier goose formation measurements, there was wide variation in the measured angles, and the means were well below Lissaman & Schollenberger's (1970) predicted optimum angle of 120° for maximum aerodynamic advantage. Again, as in the goose studies, V formations were less common than single line formations.

Hummel (1983), an aerodynamacist, further refined the theoretical aspects of formation flight by considering wing shape, homogeneous vs. non-homogeneous spacing, size of bird, flight speed, and straight vs. curved lines. He concluded that, under optimum conditions of the above, energy savings for formation flight were possible due to aerodynamic considerations, but the wide variance seen in the arrangements of flocks in the field suggested that aerodynamics might not be the only factor in formation flight.

Badgerow (1988) took a fresh look at the aerodynamic and visual hypotheses, and tried to organize the scant real field data in such a way that they could be subject to test. He suggested that if aerodynamic advantage was the primary driver of line flight, there should be a certain geometric relationship between birds in a formation, but if visual considerations were paramount, there should be a different configuration. Unfortunately, the variation in data between flocks was sufficiently large to prohibit a clear distinction between the hypotheses, although Badgerow felt that there was a non-trivial (about 10%) energetic advantage of formation flight over solo flight.

Cutts & Speakman (1994) also found wide variation in placement of individuals in their study of formation flight of Pink-footed Geese, *Anser brachyrhynchus*. They photographed 54 skeins from directly beneath, simplifying the extraction of distances and angles. They found that large numbers of birds flew outboard of the position predicted by theory to maximize aerodynamic savings, resulting in a postulated mean energy saving of 14%. Further, after a discussion of optimum flight speed for optimum range, they suggested that if the birds in their sample flew at a speed that would maximize their range, the savings would drop to 2% of that predicted by Lissaman & Schollenberger (1970). Speakman & Banks (1998) later used the same technique to photograph 25 formations of Greylag Geese, *Anser anser*. They found a great deal of variation in positioning and that only 17% of birds flew in the predicted optimum position for aerodynamic savings. They suggested, using the same assumptions as the Cutts & Speakman (1994) paper, that the mean saving in induced power was 27%, and the reduction in total flight costs was 5–9% of the whole. Hainsworth (1988) also found in film studies of Brown Pelicans, *Pelicanus occidentális*, that there was wide variation in wingtip spacing, and that there was no evidence that the birds spaced to optimize possible aerodynamic effects.

Shortly after the turn of the new century, several papers appeared with a decidedly more mathematical bent than had been seen previously, from investigators with backgrounds in the control of multiple autonomous unmanned aerial vehicles, like the Predator, and Global Hawk. Seiler et al. (2002) noted the wide variation in distances and angles reported in bird formations in previous field studies, and in a rather puzzling table suggested that the average number of birds in a V formation appeared to be small, typically under 10 birds. Other studies (Gould & Heppner 1974; Hainsworth 1987) had reported mean V formation sizes closer to 20 birds. Seiler et al. (2002, p. 122) noted that, on theoretical grounds, maintenance of a specific spacing and angular relationship between a 'leader', and following autonomous robotic vehicles is a daunting task, and that errors in spacing rapidly multiply with each subsequent vehicle, so much so that '—flying in close formation is *not possible* (italics added) with information only about the predecessors'. In other words, if a vehicle attempts to maintain position in the formation only by maintaining position with its immediate predecessor in line, the formation itself will quickly break down. However, they proposed two potential resolutions:

1. the formations should be very small, and/or
2. leader positional information should be simultaneously communicated to all members of the formation; in other words, a trailing bird should maintain its position with respect to the leader, rather than its immediate predecessors.

The same team expanded this idea, and explored the concept of 'string instability', the phenomenon where the trailing vehicle in a line has such difficulty tracking predecessors that it oscillates in position to such a degree that it eventually cannot stay with the formation (Seiler et al. 2003). In particular, they explored the difficulties of maintaining lateral positioning in a line formation. They proposed that the difficulty in maintenance of position increases markedly with position back from the leader; the 'positional error' (assuming the birds were 'trying' to maintain an optimum position for either aerodynamic or visual reasons) of the number four bird in relation to the lead bird would be twice as much as that of the number two bird. Seiler et al. (2003, p. 279) concluded by suggesting '—that (avian) formation flight is *inherently* (italics added) difficult'. A glance overhead at a winter waterfowl assembly area displaying a panorama of dozens of birds flying in each of hundreds of separate line flocks suggests a variant of the catch phrase of the late Spanish ventriloquist, Señor Wences, 'Difficult for me; easy for you'. Seiler et al. (2003) suggested that their hypothesis could be tested by examining whether birds further back in the formation have a greater variation in wingtip spacing than those closer to the leader. This hypothesis, of course, rests on the prior hypothesis that there is an optimum spacing that the birds are attempting to maintain.

Weimerskirch et al. (2001) have provided the best (and to date) most realistic attempt to resolve in the field whether there is an energy advantage to line formation flight. They trained a flock of eight Great White Pelicans, *Pelecanus onocrotalus*, to fly in formation behind a motorboat. Energy consumption during flight was not recorded directly, but inferred from heart rate data. They measured heart rate from selected individuals in the flock, and from a solitary bird flying under the same conditions. Heart rates of the birds in formation were 11–15% lower than that of the solitary bird. From this, they concluded that they had provided empirical evidence of an aerodynamic advantage to formation flight, in about the same fractional proportion as the heart rate difference.

An alternate interpretation of the data is possible, especially given the relatively scant proposed saving compared to most aerodynamic theory-based predictions. Pelicans are highly social animals and the experience of flying solo might have been stressful compared to normal social flight. Späni et al. (2003) found that laboratory mice housed individually had a heart rate 4% higher than that of mice housed in pairs. So the effect seen may have been due, at least in part, to social stress rather than aerodynamic advantage.

Modelling, Simulations and Application

The development of very powerful, relatively inexpensive computers in the late 1990s permitted a more sophisticated mathematical analysis of V formations. The first to report a model producing V formations was Flake (2000, pp. 270–275), who extended Reynolds' (1987) model (to be discussed later) with an additional rule; each artificial bird, or 'animat' (Wilson 1985; Watts 1998), 'attempted' to move laterally away from any animat that blocked its view to the front, and with that achieved V-formation flocks.

Assuming that there is, in fact, a reduction in collective aerodynamic drag experienced by members of a flock in a V, Dimock & Selig (2003) went a step further and developed a computer simulation that actually modelled the induced drag. They extended Reynolds' (1987) model to 'detect' potential drag reductions by adding a rule by which each animat acted to reduce the drag, and observed how the animats self-organized themselves. There was an evolutionary component to this study—they used genetic algorithms to evolve the model's parameters and as each animat acted so as to reduce its own drag, the collective result was that the drag reduction of the flock as a whole was maximized. Limiting the utility of the model, their induced drag calculations were based on a rigid wing just as Lissaman & Schollenberger's (1970). In relatively short simulations, their model correctly penalized collisions, and ultimately produced rigid/stable flocks of perfect Vs. Using the same evolutionary theme, Andersson & Wallander (2004) suggested that kin selection might explain why there appeared to be so much variation in V formation structure. Most aerodynamic advantage studies propose that the lead position is to some degree less advantageous than following positions, but Andersson & Wallander (2004) suggested that if the flock is composed of kin, the leader might enjoy a gain in inclusive fitness, even if at a personal energetic disadvantage. A casual glance at feeding or migrating flocks suggests considerable shifting of position, and 'leadership' changes within the flock, but it would be useful if there were a quantitative study indicating whether all or most birds assume the 'leader' position during a flight.

Nathan & Barbosa (2008) developed a comprehensive computer model that produced V formations. Their model evolved from a series of simulations that yielded cluster flocks (discussed below). The animats in their model followed simple rules; each bird attempted to seek the proximity of the nearest bird (while avoiding collision), each bird attempted to find a position that offered an unobstructed longitudinal view (if the first rule was not applicable), and each bird attempted to position itself in the upwash of a leading bird. Using these rules, they were able to produce Vs, Js and echelons; as well as inverted Vs which are rarely seen in nature. The model was limited in its ability to handle flock turning movements as it assumed a constant heading and the rules produced only lateral displacements. An attractive feature of the model was, nonetheless, that it offered the opportunity to test the relative importance of aerodynamic, or communication hypotheses, by changing the values of parameters.

So, Why do Birds Fly in a V Formation?

After over 30 years of active interest in the field, we may be reasonably certain of the following things;

1. Many large birds (but not all) fly in line formations; small birds almost never.
2. The V and J formations are the most striking and eye catching line formations for humans to observe, but they are not the most common for birds to fly in; the echelon has that distinction.
3. There is wide variation, from flock to flock and species to species, in positioning and distances of individual birds in a line. Aerodynamic theory predicts, however, that there is an optimum position and distance between birds if aerodynamic advantage is to be maximized, both for individuals and flocks.
4. The lines are wavy as often as they are straight.

One of us (FH) once asked a WWII B-17 pilot why bombers flew in a V. His reply was, ‘To keep a clear field of fire for the guns to the front, and to keep an eye on the leader, who does the navigation.’ Birds clearly need not worry about the former, but if in fact the ‘leader’ is determining the direction the flock is to take, it would be an advantage to keep it in sight, an advantage in a large flock accruing to a curved or irregular line.

Why not fly directly to the side of the leader, or directly in back? If a bird flew to the immediate left or right of another bird, a gust of wind or a startled response from the neighbour might precipitate a collision. Similarly, if the bird ahead were to suddenly slow down for any reason, a rear-end collision might be possible. On an uncrowded motorway, drivers rarely prefer to drive for long distances alongside a car in an adjacent lane, or tuck in close behind a leading car if there is an opportunity to pass, possibly for similar anti-collision reasons. If the object of the staggered line formation is primarily to avoid collision while keeping a leader in sight, one would expect to see wide variation in spacing and alignment, simply because there is no particular advantage to one spatial relationship rather than another. Similarly, one would expect to see undulations in the line. As the body of a neighbour momentarily blocked the view of the leader, perhaps due to a wind gust, an individual bird could simply speed up a bit or drop back to regain sight of the leader, thus precipitating a wave.

But what of the potential aerodynamic advantage of V flight? Aerodynamic theory suggests that one exists, under certain conditions. One must ask about its relative importance and need, however, as it is noted that most of the field studies of line formations have not been made on migration flights, where energy savings, even small ones, might well be of importance, but on short feeding flights of 10–20 km, where the energy expended in flight represents a small fraction of the birds' daily energy budget, and that whereas staggered lines are common, Vs and Js are much less so. We simply do not know what kinds of formations large birds use on their long migratory flights, which are often over water. Additionally, there may be an energetic cost to flying in close formation. The stress level in flying in very close proximity to other birds, with consequent collision risk, might (on migration flights) raise metabolic levels enough to partially negate any aerodynamic energy advantage of close formation flight.

The 'crucial' experiment, to determine if, in formation flight, there is a worthwhile energy advantage to be gained for aerodynamic reasons, might be to train a group of imprinted line-formation birds like geese to fly in a wind tunnel, and then use modern airflow visualization techniques to empirically determine what the upwash properties of birds flying in formation really are (Pennycuick et al. 1997; Rayner 1995).

CLUSTER FLOCKS

There is an extensive literature discussing the biological value of flocking in general (Krebs & Barnard 1980), but very few papers have appeared with specific reference to the highly organized turning and wheeling ('cluster') flocks of some small birds. The most commonly offered hypothesis is that the closely spaced cluster flocks offer protection against aerial predators like hawks, presumably by increasing the risk of collision to the predator (Tinbergen 1953). Examples have been reported where flocks of starlings and shorebirds bunch up tightly when attacked by a hawk (Major & Dill 1978). This hypothesis appears reasonable, but leaves a commonly seen behaviour in some cluster flying species to be explained. At sunset, or just before, large flocks of European Starlings will form over a roost from smaller foraging flocks that have dispersed during the day from that roost. These flocks will engage in some of the most spectacular group movements seen in flocking birds for periods of 30–45 min before settling into the roost for the night. Two questions immediately present themselves: 1) Do not these movements 'waste' energy in species for which energy is important (Hamilton et al. 1967)? and 2) by occurring every night in the same location, and being highly visible from up to a km away, do they not almost invite predator attack? A loitering predator would have an excellent opportunity to pick off a straggler (we have seen many pre-roosting turning and wheeling flocks that generate stragglers as the flock splits and rejoins). Why do these flocks not land immediately in the roost after returning from foraging, and why are there often 10–15 min of coordinated turning and wheeling before a flock descends to a feeding area, both expending energy, and facilitating predation?

Wynne-Edwards (1962) proposed instead that these movements represented 'epideictic' displays that might enable individual flock members to assess the population numbers and density of the flock as a whole; information that might be used in regulating breeding behaviour. This suggestion was part of a larger concept that is called today 'naïve group selection'. This hypothesis received little support at the time (Crook 1965), but has enjoyed a recent re-examination (Wilson & Wilson 2007) that may be useful in considering how organized flight evolved. Another hypothesis was provided by Major & Dill (1978) who suggested that these turning and wheeling movements were 'protean' (Driver & Humphries 1970); irregular movements designed to confuse potential predators. A number of recent studies (Biro et al. 2006; Codling et al. 2007; Dell'Ariccia et al. 2008) have suggested that flying in a group improves homing performance in pigeons, but it is not clear that the structure of the flock has anything to do with this improvement.

There are several questions that are usually asked when considering the mechanism, rather than the function of cluster flocks:

1. Do the flock members truly turn simultaneously during a turning movement, or is there a wave of movement starting at a centre somewhere and passing through the flock?
2. Is there a leader in the flock who communicates an action intention in some fashion to other members of the flock, or is there some emergent property of flocking itself that produces coordinated movement?
3. What mechanism governs the departure of flocks from the roost, ground, or perch, in which sometimes the whole flock departs, and at other times, subgroups will depart before the main group?

Simultaneity (or not) of individuals making a turn has relevance to the related question of leadership. A wave of turning in the flock would suggest (but does not necessarily provide evidence for) a relatively simple model where a leader turns, followed by a turn by neighbours after a suitable reaction time (which was established by Pomeroy & Heppner [1977] to be under 100 ms in laboratory studies of starlings), then a wave passing through the flock as birds respond to a turn by birds distant from the leader, but who ultimately have responded to a turn initiated by the leader. Vision would be the most parsimonious medium for information transmittal in such a model. If birds turn simultaneously instead (within the limits of the recording instrumentation), the question becomes more interesting; either a putative leader has to communicate a message instantaneously to all members of the flock, seemingly ruling out sound and vision in large flocks (because the bodies of nearby neighbours would block the view of more distant birds), or it would be necessary to propose an organizing principle that could produce synchronized turns without leadership. Such a model only became available in the 1980s.

Davis (1980) filmed turning flocks of Dunlin, *Calidris alpine*, with a slow-motion cine camera (72 frames/s). Dunlin are differentially coloured on their dorsal and ventral surfaces, and Davis observed that some individuals in flocks of approximately 40 birds all appeared to turn within 120 ms, giving the appearance of a 'flash'. Potts (1984) using a similar technique with Dunlin, noted some examples of waves of turning that propagated from neighbour to neighbour within 14 ms, considerably faster than the measured reaction times in birds. He proposed a 'chorus-line' hypothesis to account for rapid turns, in which one bird or a small group could initiate the movement, which would then be followed by neighbours who responded to their immediate neighbours and whose speed of response would depend on their own reaction times, but more distant birds would be able to estimate and anticipate the passage of the wave, as in the 'Mexican wave' in stadiums (Farkas et al. 2002). However, Heppner (1997) suggested the possibility that a perceived wave of turning in differentially turning birds might be an artefact of observer position relative to the near and far borders of the flock, and that individuals in a flock apparently turning in wave fashion might in fact be turning nearly simultaneously.

Early on it was realized that to approach these questions, some idea of the geometric relationship between birds in a cluster flock would be needed, and that meant the development of three-dimensional (3D) analysis techniques. These techniques are well developed for laboratory studies of fish schools (Partridge et al. 1980), but are much more challenging for birds in the field.

Major & Dill (1978) obtained the first 3D measurements of distances between birds in free-flying flocks of Dunlin, *Caladris alpina*, and European Starlings by using a stereoscopic photographic technique that utilized two 35 mm film cameras whose optic axes were parallel, and which were firmly fixed on an aluminium bar 5.5 m long. They were particularly interested in nearest-neighbour distances, and the angles between neighbours, as these would provide an index of condensation of the flocks. They reported that the nearest neighbour to a reference bird was typically behind and below a reference bird, a pattern often seen in fish shoals.

Pomeroy (1983) and Pomeroy & Heppner (1992) used an orthogonal 3D photographic technique to obtain sequence pictures of semi-domestic Rock Pigeons, *Columba livia*, turning in flocks of 8–11 birds. Using this technique, they were able to plot the flight paths of individual birds, as well as nearest neighbour distances. They reported that the flight paths of individual birds crossed over each other, such that in a 90° turn, a bird that had been in the lead would be to the right or left of the flock, and after a 180° turn, would be in the rear of the flock. They suggested that an individual bird would find it difficult to 'lead' a flock by positioning itself at the head of the flock.

Ballerini et al. (2008a, b) and Cavagna et al. (2008a, b) have developed a powerful tool for the analysis of cluster flocks by essentially solving the 'correspondence problem' that has bedevilled photographic 3D analysis techniques. Most such methods involve taking a pair of pictures from slightly different viewpoints, and noting the displacement of the image of a single bird in one view from the other member of the pair. With large numbers of birds of identical appearance, how do you match the image of the same bird in the two views? By using a novel statistical method, they were able to determine the positional relationships of over 1,000 birds in a European Starling flock flying over Rome. Using data obtained by this technique, Ballerini et al. (2008a) suggest that the significant factor in determining interaction between birds in cluster flocks is not the distance between birds ('metric' distance), but the number of birds between any two birds ('topological' distance, in their terminology).

Modelling, Simulations and Application

Davis (1980), after reviewing the deficiencies of a leadership model for cluster flock turning and wheeling movements, suggested the possibility that a 'self-generated synchronous activity' might provide a model for coordinated movements. Within a decade, the development of accessible and powerful computers and programming languages produced such models. Working independently, Okubo (1986), Reynolds (1987) and Heppner & Grenander (1990) each developed flock flight models based on the concept that each bird in a flock followed simple behavioural rules in relation to its neighbours, and that the interaction of these rules produced the emergent property of a coordinated flock. Moreover, Okubo (1986) and Reynolds (1987) suggested that the same concept could be employed to model schools and herds, which lead to numerous studies in all three fields based on similar models, as if to find a universal theory. To some extent the conceptual ancestor of all models was John Conway's 'Game of Life', (Gardner 1970), one of the first cellular automata that demonstrated how complex global behaviours can arise as a product of self-organization by simple components following simple local rules.

To be specific, Reynolds (1987) proposed that for the purpose of computer animation a flock could be modelled as a group of animats (or 'boids', using his terminology) that followed three simple rules, which might behaviourally be rephrased as 'drives'. These drives caused the animats to attempt to avoid collisions with nearby neighbours ('separation' or 'repulsion'), match velocity with nearby neighbours ('velocity matching'), and stay close to nearby neighbours ('cohesion' or 'attraction'). The term 'nearby' was used to describe the animat's localized perception of the universe. In all incarnations of the model, Reynolds (1987, 1999, 2004) used drive dependent perception volumes (nearby neighbours were all animats within a sphere of a predefined diameter centred at the currently observed animat's origin) with a biologically realistic perception model (limitations of visual perception were accounted for; a 'blind cone' [the three-dimensional equivalent of a 'blind spot'] was subtracted from the perceptual sphere at the back of the observed animat). At the time of proposal the approach represented a giant step forward compared to the traditional techniques used in computer animation for motion pictures. The first animation created with the model was 1987's '(Stanley and Stella in) Breaking the Ice', followed by a feature film debut in Tim Burton's 1992 film 'Batman Returns' with computer generated bat swarms and 'armies' of penguins marching through the streets of Gotham City. The current state of the art in computer animation for motion pictures has evolved even further (Massive 2008); these advanced models, however, due to the obvious financial consequences, remain proprietary.

Heppner & Grenander's (1990) distinguishing features were the approach used to model perception and the animats' drives. In their case the same perception volume (a sphere of a predefined diameter centred at the currently observed animat's origin) was used for all drives and limitations of visual perception were not accounted for. The animats attempted to stay in the roosting area ('homing'), attempted to fly with a predefined flight speed ('velocity regulation'), and attempted to move apart if too close, or closer if not too distant ('interaction'). An additional feature was 'random impact', which was intended to simulate the random distractions that are present in a natural environment (wind gusts, distractions from moving objects on the ground, etc.). Heppner & Grenander (1990) implemented the latter by using a Poisson stochastic process and admitted that without its inclusion they were unable to produce a flock-like behaviour.

In the mid 1980s and early 1990s, computer processing power was limited and real time simulations of large flocks consisting of more than a few dozen birds were infeasible. The first step to simulations that would allow observing an animated output while running the simulation and interactively changing the model's parameters was performed by Lorek & White (1993), who, just a few years after Reynolds' (1987) paper was published, used a Meiko Transputer System with up to 50 processors to run flight flock simulations, consisting of merely 100 birds at slow, but interactive rates (6 frames/s). The recent advances in multicore technology (Gschwind et al. 2006) and computer graphics dedicated hardware (NVIDIA 2007), and their use for scientific research (Khanna 2007; Sijbers & Batenburg 2008) give the impression that barriers to real time simulations and interactivity will soon be breached.

Reynolds (2006), for example, reported a multicore solution, which takes advantage of the Sony PlayStation 3 Cell processor for running simulations of 10,000 fish with animated output of cinematic quality at 60 frames/s. More recently, at the SIGGRAPH 2008 conference, the Game Computing Applications Group of AMD, Inc. was showing a cinematic quality technology demo titled 'March of the Froblins' (AMD 2008; Shopf et al. 2008), a graphics processing unit (GPU) based crowd simulation of 65,000 agents at 30 frames/s.

The techniques used for achieving high frame rates might at times be at the expense of biological realism. It is also true that for a scientific study centred on behaviour, the ability to interactively change the model's parameters and observing the effects in real time is a welcome plus. In computer animation for games and virtual reality (Brogan et al. 1998) high frame rates are important and the modelling of flocking behaviour has a niche of its own—it falls under the subject of 'controlling groups of objects'. Disregarding the cost of achieving the desired degree of visual realism, the simplicity of achieving high frame rates depends on the class of the controlled group of objects. Using Parent's (2002) terminology, there are three principal classes of controlled groups: 1) 'particles', characterized as large collections of individual objects, each of which obeys simple physical laws, such as momentum and conservation of energy, but has no 'intelligence', or decision making capacity; usually, such particles interact mostly with their environment, and there is little, if any, inter-individual exchange (typical examples are models of fluids, gaseous phenomena, hair, fur, etc.); 2) 'flocks', characterized as medium (fewer in number than particles) size collections of individual objects, with some incorporated physics and intelligence—interaction with the environment and inter-individual exchange (typical examples are models of schools, swarms, herds, crowds, traffic, etc.); 3) 'autonomous agents', characterized as small collections, with little, if any, incorporated physics and much intelligence (typical examples are intelligent agents, autonomous robots, software agents, computer viruses, etc.). All three classes are examples of independently behaving members of groups with varying levels of autonomy, physical characteristics and simulated motions.

Kennedy & Eberhart (1995) were the first to incorporate elements from artificial life and artificial intelligence (AI) studies to allow bird flocking behaviour models to serve as exemplars for more general kinds of behaviour, including human social behaviour (Helbing & Molnár 1995). A group of interacting animats is a ‘swarm’ in AI terms, and Kennedy & Eberhart (1995) presented algorithms by which a swarm might optimize its behaviour, or adapt to serve some end, such as increasing energy input. The animats in a swarm make decisions about their own behaviour based on the behaviour and knowledge gained from their neighbours, as well as the perceived elements of their surroundings, such as locations of ‘feeding areas’. From the swarm's collective behaviour emerges the animats' indirect approach to relatively-good solutions. These algorithms are also known as ‘particle swarm optimization’, or PSO for short (Kennedy et al. 2001; Engelbrecht 2006). Macgill & Openshaw (1998) and Macgill (2000), for example, later on used flocking behaviour to assist the analysis of geographical data. Subsequent AI studies started introducing more and more intelligence in individual animats while reducing their number; Odell (1998) provided a summary of the terminology and properties attributed to ‘agents’ in computer studies.

In the mid-1990s, physicists began to show interest in the mathematics and physics of organized flocks, using a perspective very different from those found in earlier biological and aerodynamic studies. Vicsek et al. (1995) and Toner & Tu (1995, 1998) viewed the birds in a flock as particles, behaving much as molecules in a fluid or atoms in a crystal might, and that they were responsive to the same mathematical rules. The models were all based around the same perception model as in Heppner & Grenander (1990); inter-individual influences occurred between animats that were not further apart than a predefined distance. Additionally, an overall constant flight speed was assumed and the number of drives was reduced to merely one, attempting to match flight direction with nearby neighbours. A stochastic component had been added in these models, perhaps on similar presumptions as the random impact used by Heppner & Grenander (1990). As theoretical physicists, Toner & Tu (1998, p. 4830) may have been somewhat removed from realities in the field when they suggested, ‘This correlation function should be *extremely easy* (italics added) to measure in simulations, and in experiments on real herds or flocks, in which, say, video tape allows one to measure the positions ... of all the birds ... in the flock at a variety of times *t*'. Vicsek et al. (1995) suggested that the physics concepts associated with phase transitions, as in the transition from solid to liquid forms of materials, might serve to explain the puzzling shifts between orderly and disorderly flock formations often seen in birds like European Starlings. All in all, their models represent a substantial simplification in biological assumptions over the initial ones proposed by Okubo (1986), Reynolds (1987) and Heppner & Grenander (1990). Using Parent's (2002) terminology, these models fall perfectly under the particles category. The model devised by Vicsek et al. (1995) is also known as the 'self-propelled particles' model, or SPP. Physicists embraced these minimalist models and a number of subsequent studies have been published (see Czirók et al. 1997; Czirók & Vicsek 1999, 2000; Tu 2000; Li et al. 2007; Li & Xi 2008; Chaté et al. 2008; Gönci et al. 2008; Huepe & Aldan 2008, for example). Recent field observations by Ballerini et al. (2008a, b) and Cavagna et al. (2008a, b) seem to be making an impact in the physics community and even physicists are starting to acknowledge the importance of inclusion of attractive-repulsive drives (Grégoire et al. 2003; Grégoire & Chaté 2004; Feder 2007). An additional result of these field observations, is one that somewhat contradicts the approach commonly assumed by flock flight models. These typically assume a fixed radius of interaction. Data obtained by Ballerini et al. (2008a, b) and Cavagna et al. (2008a, b) seems, on the other hand, to suggest that it is not the radius, but the number of influencing individuals, which remains constant.

Just as Kennedy & Eberhart (1995) incorporated AI elements into flight flock models to devise PSO, other computer science studies applied AI algorithms to evolve the models themselves. Reynolds (1993a, b), Zaera et al. (1996), and Spector et al. (2005), used genetic programming, a technique for automatically creating computer programs that satisfy a specified fitness criterion, to evolve the individual animat's rules, or in this case 'programs', which, when the animats interacted, produced flocking behaviour. All previous models employed constants like 'perception radius' (diameter of the sphere centred at the currently observed animat's origin, by the use of which nearby neighbours are selected), 'weights' (typically the direction of flight [and flight speed] of the currently observed animat is computed as a weighted sum of the individual 'desired' flight directions that would meet the individual drives, respectively), etc. Heppner & Grenander's (1990) approach was to modify these by hand and analyse the results. The AI approach was to use evolutionary computing. Genetic algorithms were used to vary the parameters to optimize the behaviour to a specified fitness criterion. Dimock & Selig (2003), for example, used genetic algorithms on a modified Reynolds (1987) model to find parameters for minimum power consumption in a flock of simulated birds. Wood & Ackland (2007), on the other hand, using a Couzin et al. (2002) model, studied the evolution of group formation when subjected to simulated predation and foraging. Their results replicate conventional evolutionary behaviour—foraging animats prefer a narrower perception volume, while the hunted prefer a wider one.

Couzin et al. (2002) and Couzin & Krause (2003) added the next level of sophistication in flocking models. The substantial difference was not in the animats' drives, but in the perception model, or when these drives were actually in effect. Whereas Heppner & Grenander (1990) used one perception volume for all three drives, Reynolds (1987, 1999, 2004) three non-exclusive perception volumes with biologically inspired limitations, Couzin et al. (2002) and Couzin & Krause (2003) introduced a different approach; in their model there were three exclusive perception volumes, or 'zones', using their terminology: 1) 'zone of repulsion', 2) 'zone of orientation' and 3) 'zone of attraction'. If there were neighbours in the zone of repulsion, then only the separation drive was active and the other two ignored. If, however, there were no neighbours in it, the other two drives were averaged, but the animat attempted to match velocity only with the neighbours in the zone of orientation and attempted to stay close only to the neighbours in the zone of attraction. Additionally, the zone of repulsion was modelled as a sphere, whereas the other two were modelled as a sphere with a blind cone subtracted at the animats' back. Couzin et al. (2002) considered what would happen to group movements if individuals in the group modified their behavioural rules in response to experience with the flock as a whole. More specifically, what would happen if the diameter of the zone of orientation was variable, while keeping the zones of repulsion and attraction constant. They found that, as the diameter of the zone of orientation increased, the group went from a loosely packed stationary swarm, to a torus where individuals circle round their centre of mass and, finally, to a parallel group moving in a common direction (see also Sumpter 2006). Further on they discovered that the transitions were rapid, and as the diameter decreased, the collective behaviour was different. They established that two completely different behavioural states can exist for identical parameters, and that transition between behavioural states depends on the previous history (structure) of the group, even though the individuals have no explicit knowledge of what that history is. Consequently, they suggested that the system exhibits a form of 'collective memory'. In a later study, Couzin et al. (2005) examined leadership and decision making in animal groups on the move by giving knowledge of a preferred flight direction only to a proportion of the simulated animals. The study revealed that the larger the group, the smaller the proportion of informed individuals needed to guide the group, and that only a small proportion is required to achieve great accuracy. Several recent experimental studies (Biro et al. 2006; Codling et al. 2007; Dell'Ariccia et al. 2008) investigated the 'many-wrongs principle' in pigeon homing and suggest that pigeons flying in a group have better navigational performance than birds flying alone, but it is not clear whether the spatial organization of the flock is significant in this observation.

Lebar Bajec et al. (2003a, b, 2005) and Lebar Bajec (2005) introduced the concept of fuzzy logic to flocking models. The basic concept of the model remained the same; three drives and perception modelled as a sphere with a blind cone removed from the back. But in previous models, the animats would react to their surroundings in a 'crisp' way. For example, if we are interested in two moving animats that are on a closing course with one another, there might be some specific threshold distance at which they would deviate to avoid collision (e.g. when they enter each other's zone of repulsion [Couzin et al. 2002]). Or, in a slightly more complex example, there might be a gradient for different closing angles such that the animats would deviate proportionately, but still in deterministic fashion depending on the closing angle. However, with fuzzy logic, vague qualities like ‘close’ or ‘far’ rather than a specific distance or angle can be used to describe the behavioural repertoire of the animat. In this fashion, a more naturalistic type of behaviour can be produced. Indeed, Heppner & Grenander (1990) used a single perception volume, Reynolds (1987, 1999, 2004) three overlapping perception volumes, and Couzin et al. (2002) and Couzin & Krause (2003) advanced the model by introducing three non-overlapping perception zones, the use of vague qualities enabled Lebar Bajec et al. (2005) to produce a mixture of these approaches with partially overlapping perception zones. The issue this model has, with respect to the others, is that it is two dimensional; animats can move left or right, but not up or down. As real birds exist in three dimensions, a genuinely realistic simulation needs to feature the third dimension. Moškon et al. (2007) expanded the fuzzy model to account for foraging behaviour by including hunger as a drive. While doing so, they also modelled foraging fields and landing and taking off from them; while this has not been achieved by promoting the drives to work in three dimensions, they upgraded the model to pseudo 3D nonetheless.

So, How do Birds Seem to Turn and Wheel Together?

In the 1970s, there was no conceptual alternative to a leadership model for producing simultaneous or near-simultaneous turning movements in cluster flocks. With the advent of the many models that treat flocks as collections of independently acting agents that produce turning movements as the product of individual movement decisions, a viable alternative to leadership models now exists, but such models 1) do not rule out the possibility that under certain circumstances, particularly with small, or family flocks, leadership might still play a role in cluster flock movements, and 2) do not provide evidence that birds use the same algorithms as the models. Just as there may be several biological functions for line formations, it may be that there are multiple mechanisms for producing cluster flock movements.

CONCLUSION

Advances in the understanding of the function and mechanisms of organized flight have been strongly linked to the introduction of new techniques or technologies. Heppner (1997) identified several areas that might be expected to produce such advances, but a decade later, although it has been possible to refine and more closely define these needs, much still needs to be done.

1. Three dimensional simulations. Some of the existing simulations (Vicsek et al. 1995; Lebar Bajec et al. 2005; Moškon et al. 2007; Nathan & Barbosa 2008), although capable of producing realistic-appearing flocks on a computer screen, feature animats that travel in a two dimensional universe. They may travel left or right, but not up or down. As real birds exist in a 3D world, a genuinely realistic simulation would have to feature the third dimension. Adding the additional dimension is not a trivial programming task, but its accomplishment could be expected to pay large dividends.
2. Non-homogeneous models. To date, flight flock models have assumed that flocks are composed of identical subjects. In reality, there will be individual differences in age, gender, sensitivity to hunger, health, and other factors that may well influence the collective behaviour of the flock.
3. Fast, cheap, field data acquisition. Cavagna et al.'s (2008a) technique for obtaining the 3D positions of thousands of birds in a flock has yielded remarkable results, but the method requires custom-made synchronizing equipment for the cameras, skilled operators, lengthy processing, and a fixed location. As a result, it is difficult to compare species, conditions, or fine structure over time. The current generation of digital still and video cameras offers the potential for both high resolution and a high frame rate at a reasonable cost. Commercial wireless technology, such as that used to simultaneously fire multiple remote flash units, offers the potential of synchronizing

two (or more) cameras in the field without the necessity for custom made synchronizing devices.

4. User-friendly simulations. The current generation of flocking simulations is primarily designed to be used and manipulated by their designers, who may or may not be familiar with the behaviour of animals in the field. The programs are not easily used or modified by other users unfamiliar with programming. It would be very helpful if future simulations came with a 'console', or control panel that would allow non-programmers to change the parameters or their values in the simulation, such as preferred velocity, or attractiveness of feeding site, thus allowing field biologists to examine the results of changing inputs to the program based on their field experience. It might also be possible to set up 'detectors' in the program, as is done in experimental particle physics, to allow many different combinations of parameters and values to be run in sequence, and the program would flag interesting behaviours, such as the appearance of a V, when they appear. For example, the Boston Museum of Science in Massachusetts has a large public display called the 'Virtual Fishtank' (Nearlife, Inc. 2001) that enables visitors to interactively change the behaviour of individual fish in a 'school', and immediately see the change in the behaviour of the school.
5. Metrics for 'truth testing'. Current simulations offer naturalistic appearing virtual flocks, but it cannot be certain that real birds use the same algorithms employed in the simulation. Ideally, one would produce a simulation of a particular species' flocking behaviour, and use it to make predictions about the behaviour of the real flock, and then test those predictions in the field. To do this, one would have to have a metric that could be derived from the simulation, and then measured in the field. For example, some simulations produce flocks that apparently turn and wheel much like real flocks. Perhaps 'turning and wheeling' could be quantified, such that one could say that, for example, a flock of X number of birds of species Y will make a turn,

defined as a departure of more than 20° from the mean direction exhibited in the previous 5 s, every 8.2 s. If this variable were measurable in the field, it could then be possible to refine the model to produce more accurate predictions. Successful prediction would, of course, not be prima facie evidence that the algorithms in the real and virtual worlds were the same, but would certainly provide stronger evidence than a superficial, qualitative similarity. Dill et al. (1997) discussed this issue more extensively.

The last 40 years have seen remarkable progress in the understanding of this intriguing and aesthetically spectacular phenomenon. In addition to being a phenomenon worthy of examination in its own right, the study of organized flight in birds has provided a model system that has demonstrated utility in the study of crowd behaviour, bird strikes on aircraft, traffic theory, complex systems, particle swarms, computer animation, and control of (remotely piloted) autonomous aircraft. At this time, it is possible to foresee that with the assistance of biologists, physicists, mathematicians and computer scientists working together, we will, before long, truly be able to say how and why birds fly in organized groups.

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REFERENCES

AMD 2008. *ATI Radeon HD 4800 series real-time demos*. (accessed February 2009) http://developer.amd.com/documentation/videos/pages/froblins.aspx

Andersson, M. & Wallander, J. 2004. Kin selection and reciprocity in flight formation? *Behavioral Ecology*, **15**(1), 158–162. doi: 10.1093/bheco/arg109.

Badgerow, J. P. 1988. An analysis of function in the formation flight of Canada Geese. *The Auk*, **105**(4), 749–755.

Badgerow, J. P. & Hainsworth, F. R. 1981. Energy savings through formation flight? A reexamination of the Vee formation. *Journal of Theoretical Biology*, **93**(1), 41–52. doi: 10.1016/0022-5193(81)90055-2.

Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., Lecomte, V., Orlandi, A., Parisi, G., Procaccini, A., Viale, M. & Zdravkovic, V. 2008a. Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study. *Proceedings of the National Academy of Science*, **105**(4), 1232–1237. doi: 10.1073/pnas.0711437105.

Ballerini, M., Cabibbo, N., Candelier, R., Cavagna, A., Cisbani, E., Giardina, I., Orlandi, A., Parisi, G., Procaccini, A., Viale, M. & Zdravkovic, V. 2008b. Empirical investigation of starling flocks: A benchmark study in collective animal behaviour. *Animal Behaviour*, **76**(1), 201–215. doi: 10.1016/j.anbehav.2008.02.004.

Beer, J. R. 1958. The composition of bird flocks. *The Flicker*, **30**, 78–83.

Biro, D., Sumpter, D. J. T., Meade, J. & Guilford, T. 2006. From compromise to leadership in pigeon homing. *Current Biology*, **16**(21), 2123–2128. doi: 10.1016/j.cub.2006.08.087.

Brogan, D. C., Metoyer, R. A. & Hodgins, J. K. 1998. Dynamically simulated characters in virtual environments. *Computer Graphics and Applications*, **18**(5), 58–69. doi: 10.1109/38.708561.

Cavagna, A., Giardina, I., Orlandi, A., Parisi, G. & Procaccini, A. 2008a. The STARFLAG handbook on collective animal behaviour: 2. Three-dimensional analysis. *Animal Behaviour*, **76**(1), 237–248. doi: 10.1016/j.anbehav.2008.02.003.

Cavagna, A., Giardina, I., Orlandi, A., Parisi, G., Procaccini, A., Viale, M. & Zdravkovic, V. 2008b. The STARFLAG handbook on collective animal behaviour: 1. Empirical methods. *Animal Behaviour*, **76**(1), 217–236. doi: 10.1016/j.anbehav.2008.02.002.

Chaté, H., Ginelli, F., Grégoire, G. & Raynaud, F. 2008. Collective motion of self-propelled particles interacting without cohesion. *Physical Review E*, **77**(4), 046113. doi: 10.1103/PhysRevE.77.046113.

Codling, E. A., Pitchford, J. W. & Simpson, S. D. 2007. Group navigation and the 'many-wrongs principle' in models of animal movement. *Ecology*, **88**(7), 1864–1870. doi: 10.1890/06-0854.1.

Cone, Jr, C. R. 1968. *The aerodynamics of flapping birdflight*. Special Scientific Report 52, Gloucester Point, VA: Virginia Institute of Marine Science. 133 p.

Couzin, I. D. & Krause, J. 2003. Self-organization and collective behavior in vertebrates. *Advances in the Study of Behavior*, **32**, 1–75. doi: 10.1016/S0065-3454(03)01001-5.

Couzin, I. D., Krause, J., Franks, N. R. & Levin, S. A. 2005. Effective leadership and decision-making in animal groups on the move. *Nature*, **433**(7025), 513–516. doi: 10.1038/nature03236.

Couzin, I. D., Krause, J., James, R., Ruxton, G. D. & Franks, N. R. 2002. Collective memory and spatial sorting in animal groups. *Journal of Theoretical Biology*, **218**(1), 1–11. doi: 10.1006/jtbi.2002.3065.

Crook, J. H. 1965. Adaptive significance of avian social organization. *Symposia of the Zoological Society of London*, **14**, 181–218.

Cutts, C. J. & Speakman, J. R. 1994. Energy savings in formation flight of Pink-footed Geese. *Journal of Experimental Biology*, **189**(1), 251–261.

Czirók, A., Stanley, H. E. & Vicsek, T. 1997. Spontaneously ordered motion of self-propelled particles. *Journal of Physics A: Mathematical and General*, **30**(5), 1375–1385. doi: 10.1088/0305-4470/30/5/009.

Czirók, A. & Vicsek, T. 1999. Collective motion. In: *Statistical Mechanics of Biocomplexity*, Vol. 527/1999 of Lecture Notes in Physics (Ed. by D. Reguera, J. M. G. Vilar & J. M. Rubí), pp. 152–164. Berlin: Springer. doi: 10.1007/BFb0105002.

Czirók, A. & Vicsek, T. 2000. Collective behavior of interacting self-propelled particles. *Physica A*, **281**(1), 17–29. doi: 10.1016/S0378-4371(00)00013-3.

Davis, J. M. 1980. The coordinated aerobatics of Dunlin flocks. *Animal Behaviour*, **28**(3), 668–673. doi: 10.1016/S0003-3472(80)80127-8.

Dell'Ariccia, G., Dell'Omo, G., Wolfer, D. P. & Lipp, H.-P. 2008. Flock flying improves pigeons' homing: GPS track analysis of individual flyers versus small groups. *Animal Behaviour*, **76**(4), 1165–1172. doi: 10.1016/j.anbehav.2008.05.022.

Dill, L. M., Holling, C. S. & Palmer, L. H. 1997. Predicting the three-dimensional structure of animal aggregations from functional considerations: The role of information. In: *Animal Groups in Three Dimensions* (Ed. by J. K. Parrish & W. M. Hamner), pp. 207–224. New York: Cambridge University Press.

Dimock, G. A. & Selig, M. S. 2003. The aerodynamic benefits of self-organization in bird flocks. In: *Proceedings of the 41st AIAA Aerospace Sciences Meeting and Exhibit, Reno, NV*. AIAA 2003-0608. Reston, VA: AIAA.

Driver, P. M. & Humphries, D. A. 1970. Protean displays as inducers of conflict. *Nature*, **226**(5249), 968–969. doi: 10.1038/226968a0.

Emlen, J. T. 1952. Flocking behavior in birds. *The Auk*, **69**(2), 160–170.

Engelbrecht, A. P. 2006. *Fundamentals of Computational Swarm Intelligence*. Chichester, UK: John Wiley & Sons Ltd.

Farkas, I., Helbing, D. & Vicsek, T. 2002. Social behaviour: Mexican waves in an excitable medium. *Nature*, **419**(6903), 131–132. doi: 10.1038/419131a.

Feder, T. 2007. Statistical physics is for the birds. *Physics Today*, **60**(10), 28–30. doi: 10.1063/1.2800090.

Flake, G. W. 2000. *The Computational Beauty of Nature: Computer Explorations of Fractals, Chaos, Complex Systems, and Adaptation*. Cambridge, MA: MIT Press.

Franzisket, L. 1951. Über die ursachen des formationsfluges. *Vogelwarte*, **16**, 48–55.

Gardner, M. 1970. Mathematical games: The fantastic combinations of John Conway's new solitaire game 'life'. *Scientific American*, **223**(4), 120–123.

Gerard, R. W. 1943. Synchrony in flock wheeling. *Science*, **97**(2511), 160–161. doi: 10.1126/science.97.2511.160.

Gönci, B., Nagy, M. & Vicsek, T. 2008. Phase transition in the scalar noise model of collective motion in three dimensions. *The European Physical Journal Special Topics*, **157**(5), 53–59. doi: 10.1140/epjst/e2008-00630-2.

Gould, L. L. 1972. Formation flight in the Canada Goose (*Branta c. canadensis*). MSc thesis, University of Rhode Island, Kingston, RI.

Gould, L. L. & Heppner, F. H. 1974. The Vee formation of Canada Geese. *The Auk*, **91**(3), 494–506.

Grégoire, G. & Chaté, H. 2004. Onset of collective and cohesive motion. *Physical Review Letters*, **92**(2), 025702. doi: 10.1103/PhysRevLett.92.025702.

Grégoire, G., Chaté, H. & Tu, Y. 2003. Moving and staying together without a leader. *Physica D*, **181**(3–4), 157–170. doi: 10.1016/S0167-2789(03)00102-7.

Gschwind, M., Hofstee, H. P., Flachs, B., Hopkins, M., Watanabe, Y. & Yamazaki, T. 2006. Synergistic processing in Cell's multicore architecture. *IEEE Micro*, **26**(2), 10–24. doi: 10.1109/MM.2006.41.

Haffner, J. 1977. A flapping wing model for avian formation flight. MSc thesis, University of Rhode Island, Kingston, RI.

Hainsworth, F. R. 1987. Precision and dynamics of positioning by Canada Geese flying in formation. *Journal of Experimental Biology*, **128**(1), 445–462.

Hainsworth, F. R. 1988. Induced drag savings from ground effect and formation flight in brown pelicans. *Journal of Experimental Biology*, **135**(1), 431–444.

Hamilton, III, W. J. 1967. Social aspects of bird orientation mechanisms. In: *Animal Orientation and Migration* (Ed. by R. M. Storm), pp. 57–71. Corvallis, OR: Oregon State University Press.

Hamilton, III, W. J., Gilbert, W. M., Heppner, F. H. & Planck, R. J. 1967. Starling roost dispersal and a hypothetical mechanism regulating rhythmical animal movement to and from dispersal centers. *Ecology*, **48**(5), 825–833.

Helbing, D. & Molnár, P. 1995. Social force model for pedestrian dynamics. *Physical Review E*, **51**(5), 4282–4286. doi: 10.1103/PhysRevE.51.4282.

Heppner, F. H. 1974. Avian flight formations. *Bird-Banding*, **45**(2), 160–169.

Heppner, F. H. 1997. Three-dimensional structure and dynamics of bird flocks. In: *Animal Groups in Three Dimensions* (Ed. by J. K. Parrish & W. M. Hamner), pp. 68–89. New York: Cambridge University Press.

Heppner, F. H., Convissar, J. L., Moonan, D. E. & Anderson, J. G. T. 1985. Visual angle and formation flight in Canada Geese (*Branta canadensis*). *The Auk*, **102**(1), 195–198.

Heppner, F. H. & Grenander, U. 1990. A stochastic nonlinear model for coordinated bird flocks. In: *The Ubiquity of Chaos* (Ed. by S. Krasner), pp. 233–238. Washington DC: American Association for the Advancement of Science.

Heppner, F. H. & Haffner, J. D. 1974. Communication in bird flocks: An electro-magnetic model. In: *Biological and Clinical Effects of Low-Frequency Magnetic and Electric Fields* (Ed. by J. G. Llaurado, A. Sances & J. H. Battocletti), pp. 147–162. Springfield, IL: Charles C. Thomas.

Higdon, J. J. L. & Corrsin, S. 1978. Induced drag of a bird flock. *The American Naturalist*, **112**(986), 727–744. doi: 10.1086/283314.

Hill, M. L. 1972. Introducing electrostatic auto pilots. *AIAA Astronautic Journal of Aeronautics*, **10**(11), 22.

Hochbaum, H. A. 1955. *Travels and traditions of waterfowl*. Minneapolis, MN: University of Minnesota Press.

Huepe, C. & Aldan, M. 2008. New tools for characterizing swarming systems: A comparison of minimal models. *Physica A*, **387**(12), 2809–2822. doi: 10.1016/j.physa.2008.01.081.

Hummel, D. 1983. Aerodynamic aspects of formation flight in birds. *Journal of Theoretical Biology*, **104**(3), 321–347. doi: 10.1016/0022-5193(83)90110-8.

Kennedy, J. & Eberhart, R. C. 1995. Particle swarm optimization. In: *Proceedings of the IEEE International Conference on Neural Networks, Perth, WA*, Vol. 4, pp. 1942–1948. New York: IEEE. doi: 10.1109/ICNN.1995.488968.

Kennedy, J., Eberhart, R. C. & Shi, Y. 2001. *Swarm Intelligence*. San Francisco, CA: Morgan Kaufmann Publishers.

Khanna, G. 2007. *PlayStation3 gravity grid*. (accessed February 2009) http://gravity.phy.umassd.edu/ps3.html

Krebs, J. R. & Barnard, C. J. 1980. Comments on the function of flocking in birds. In: *Proceedings of the XVII International Ornithological Congress (Symposium on Flocking Behavior), Berlin, Germany*, Vol. 2, pp. 795–799. Berlin, Germany: International Ornithological Congress.

Kuhn, T. 1962. *The Structure of Scientific Revolutions*. Chicago, IL: University of Chicago Press.

Lebar Bajec, I. 2005. Fuzzy model for a computer simulation of bird flocking. PhD thesis, Faculty of Computer and Information Science, University of Ljubljana, Slovenia.

Lebar Bajec, I., Zimic, N. & Mraz, M. 2003a. Boids with a fuzzy way of thinking. In: *Proceedings of Artificial Intelligence and Soft Computing (ASC 2003)*, Banff, Canada (Ed. by H. Leung), pp. 58–62. Anaheim: ACTA Press.

Lebar Bajec, I., Zimic, N. & Mraz, M. 2003b. Fuzzifying the thoughts of animats. In: *Fuzzy Sets and Systems: Proceedings of the 10th International Fuzzy Systems Association World Congress (IFSA 2003)*, Istanbul, Turkey, Vol. 2715 of Lecture Notes in Artificial Intelligence (Ed. by T. Bilgiç, B. De Baets & O. Kaynak), pp. 195–202. Berlin: Springer-Verlag. doi: 10.1007/3-540-44967-1_23.

Lebar Bajec, I., Zimic, N. & Mraz, M. 2005. Simulating flocks on the wing: The fuzzy approach. *Journal of Theoretical Biology*, **233**(2), 199–220. doi: 10.1016/j.jtbi.2004.10.003.

Li, X., Cai, Z. & Xiao, J. 2007. Biologically inspired flocking of swarms with dynamic topology in uniform environments. In: *Proceedings of the 46th IEEE Conference on Decision and Control*, New Orleans, LA, pp. 2522–2527. Piscataway, NJ: IEEE. doi: 10.1109/CDC.2007.4434572.

Li, X. & Xi, Y. 2008. Flocking of multi-agent dynamic systems with guaranteed group connectivity. *Journal of Systems Science and Complexity*, **21**(3), 337–346. doi: 10.1007/s11424-008-9117-7.

Lissaman, P. B. S. & Schollenberger, C. A. 1970. Formation flight of birds. *Science*, **168**(3934), 1003–1005. doi: 10.1126/science.168.3934.1003.

Lorek, H. & White, M. 1993. Parallel bird flocking simulation. In: *Proceedings of BCS International Conference on Parallel Processing for Graphics and Scientific Visualization*, Edinbourgh, Scotland, pp. 1-13. London, UK: British Computer Society. (accessed February 2009) http://citeseer.ist.psu.edu/53206.html

Macgill, J. 2000. Using flocks to drive a geographical analysis engine. In: *Artificial Life VII* (Ed. by M. A. Bedau, J. S. McCaskill, N. H. Packard & S. Rasmussen), pp. 446–453. Cambridge, MA: MIT Press.

Macgill, J. & Openshaw, S. 1998. The use of flocks to drive a geographic analysis machine. In: *Proceedings of the 3rd International Conference on GeoComputation*, Bristol, United Kingdom. GeoComputation CD-ROM. (accessed December 2008) http://www.geocomputation.org/1998/24/gc24_01.htm

Major, P. F. & Dill, L. M. 1978. The three-dimensional structure of airborne bird flocks. *Behavioral Ecology and Sociobiology*, **4**(2), 111–122. doi: 10.1007/BF00354974.

Massive 2008. *Massive software – artificial life solutions*. (accessed February 2009) http://www.massivesoftware.com

May, R. M. 1979. Flight formations in geese and other birds. *Nature*, **282**(5741), 778–780. doi: 10.1038/282778a0.

Moškon, M., Heppner, F. H., Mraz, M., Zimic, N. & Lebar Bajec, I. 2007. Fuzzy model of bird flock foraging behavior. In: *Proceedings of the 6th EUROSIM Congress on Modelling and Simulation*, Ljubljana, Slovenia, Vol. 2 (Ed. by B. Zupančič, R. Karba & S. Blažič), pp. 1–6. Vienna, Austria: ARGESIM.

Nachtigall, W. 1970. Phasenbeziehungen der flügelschläge von gänsen während des verbandflugs in keilformation. *Journal of Comparative Physiology A*, **67**(4), 414–422. doi: 10.1007/BF00297909.

Nathan, A. & Barbosa, V. C. 2008. V-like formations in flocks of artificial birds. *Artificial Life*, **14**(2), 179–188. doi: 10.1162/artl.2008.14.2.179.

Nearlife, Inc. 2001. *Virtual fishtank*. (accessed February 2009) http://www.virtualfishtank.com

Nichols, J. T. 1931. Notes on the flocking of shore birds. *The Auk*, **48**(2), 181–185.

NVIDIA 2007. *High performance computing (HPC) – NVIDIA Tesla many core parallel supercomputing*. (accessed February 2009) http://www.nvidia.com/object/tesla_computing_solutions.html

Odell, J. April 1998. Agents and beyond: A flock is not a bird. *Distributed Computing*, 52–54.

Okubo, A. 1986. Dynamical aspects of animal grouping: Swarms, schools, flocks, and herds. *Advances in Biophysics*, **22**, 1–94. doi: 10.1016/0065-227X(86)90003-1.

O'Malley, J. B. E. & Evans, R. M. 1982a. Flock formation in white pelicans. *Canadian Journal of Zoology*, **60**(5), 1024–1031. doi: 10.1139/z82-143.

O'Malley, J. B. E. & Evans, R. M. 1982b. Structure and behavior of white pelican formation flocks. *Canadian Journal of Zoology*, **60**(6), 1388–1396. doi: 10.1139/z82-187.

Parent, R. 2002. *Computer Animation: Algorithms and Techniques*. San Francisco, CA: Morgan Kaufmann Publishers.

Partridge, B. L., Pitcher, T., Cullen, J. M. & Wilson, J. 1980. The three-dimensional structure of fish schools. *Behavioral Ecology and Sociobiology*, **6**(4), 277–288. doi: 10.1007/BF00292770.

Pennycuick, C. J., Alerstam, T. & Hedenstrom, A. 1997. A new low-turbulence wind tunnel for bird flight experiments at Lund University, Sweden. *Journal of Experimental Biology*, **200**(10), 1441–1449.

Penrose, H. 1949. *I flew with the birds*. London, UK: Country Life Ltd.

Pomeroy, H. 1983. Three-dimensional analysis of turning within airborne bird flocks. PhD thesis, University of Rhode Island, Kingston, RI.

Pomeroy, H. & Heppner, F. H. 1977. Laboratory determination of startle reaction time in the European Starling (*Sternus vulgaris*). *Animal Behaviour*, **25**(3), 720–725. doi: 10.1016/0003-3472(77)90121-X.

Pomeroy, H. & Heppner, F. H. 1992. Structure of turning in airborne Rock Dove (*Columba livia*) flocks. *The Auk*, **109**(2), 256–267.

Potts, W. K. 1984. The chorus-line hypothesis of manoeuvre coordination in avian flocks. *Nature*, **309**(5966), 344–345. doi: 10.1038/309344a0.

Rackham, H. 1933. *Pliny's Natural History*. Vol. X:XXXII. Cambridge, MA: Harvard University Press.

Rayner, J. M. V. 1995. Dynamics of the vortex wakes of flying and swimming vertebrates. In: *Biological Fluid Dynamics*, Vol. 49 of Symposia of the Society for Experimental Biology (Ed. by C. P. Ellington & T. J. Pedley), pp. 131–155. Cambridge: The Company of Biologists Ltd.

Reynolds, C. W. 1987. Flocks, herds, and schools: A distributed behavioral model. *Computer Graphics*, **21**(4), 25–34. doi: 10.1145/37402.37406.

Reynolds, C. W. 1993a. An evolved, vision-based behavioral model of coordinated group motion. In: *From Animals to Animats 2: Proceedings of the Second International Conference on Simulation of Adaptive Behavior (SAB92)* (Ed. by J.-A. Meyer, H. L. Roitblat & S. W. Wilson), pp. 384–392. Cambridge, MA: MIT Press.

Reynolds, C. W. 1993b. An evolved, vision-based model of obstacle avoidance behavior. In: *Artificial Life III*, Vol. XVI of Santa Fe Institute Studies in the Science of Complexity (Ed. by C. G. Langton), pp. 327–346. Redwood City, CA: Addison-Wesley.

Reynolds, C. W. 1999. Steering behaviors for autonomous characters. In: *Proceedings of GDC 1999*, San Jose, CA, pp. 763–782. San Francisco, CA: Miller Freeman Game Group. (accessed February 2009) http://www.red3d.com/cwr/papers/1999/gdc99steer.html

Reynolds, C. W. 2004. *Opensteer library*. (accessed February 2009) http://opensteer.sourceforge.net

Reynolds, C. W. 2006. Big fast crowds on PS3. In: *Sandbox '06: Proceedings of the 2006 ACM SIGGRAPH Symposium on Videogames*, Boston, MA, pp. 113–121. New York, NY: ACM. doi: 10.1145/1183316.1183333.

Rhine, J. B. 1983. *Extra-sensory Perception*. Boston, MA: Branden Books.

Seiler, P., Pant, A. & Hedrick, J. K. 2002. Analysis of bird formations. In: *Proceedings of 41st IEEE Conference on Decision and Control*, Las Vegas, NV, Vol. 1, pp. 118–123. Piscataway, NJ: IEEE. doi: 10.1109/CDC.2002.1184478.

Seiler, P., Pant, A. & Hedrick, J. K. 2003. A systems interpretation for observations of bird V-formations. *Journal of Theoretical Biology*, **221**(2), 279–287. doi: 10.1006/jtbi.2003.3191.

Selous, E. 1931. *Thought-transference (or what?) in birds*. London, UK: Constable & Co.

Shopf, J., Barczak, J., Oat, C. & Tatarchuk, N. 2008. March of the Froblins: Simulation and rendering massive crowds of intelligent and detailed creatures on GPU. In: *SIGGRAPH '08: ACM SIGGRAPH 2008 classes*, Los Angeles, CA, pp. 52–101. New York, NY, USA: ACM. doi: 10.1145/1404435.1404439.

Sijbers, J. & Batenburg, J. 2008. *FASTRA GPU SuperPC*. (accessed February 2009) http://fastra.ua.ac.be

Speakman, J. R. & Banks, D. 1998. The function of flight formation in Greylag Geese *Anser anser*; energy saving or orientation? *Ibis*, **140**(2), 280–287. doi: 10.1111/j.1474-919X.1998.tb04390.x.

Spector, L., Klein, J., Perry, C. & Feinstein, M. 2005. Emergence of collective behavior in evolving populations of flying agents. *Genetic Programming and Evolvable Machines*, **6**(1), 111–125. doi: 10.1007/s10710-005-7620-3.

Späni, D., Arras, M., König, B. & Rülicke, T. 2003. Higher heart rate of laboratory mice housed individually vs in pairs. *Laboratory Animals*, **37**(1), 54–62. doi: 10.1258/002367703762226692.

Sumpter, D. J. T. 2006. The principles of collective animal behaviour. *Philosophical Transactions of the Royal Society B*, **361**(1465), 5–22. doi: 10.1098/rstb.2005.1733.

Tinbergen, N. 1953. *Social behavior in animals*. London, UK: Methuen.

Toner, J. & Tu, Y. 1995. Long-range order in a two-dimensional dynamical *XY* model: How birds fly together. *Physical Review Letters*, **75**(23), 4326–4329. doi: 10.1103/PhysRevLett.75.4326.

Toner, J. & Tu, Y. 1998. Flocks, herds, and schools: A quantitative theory of flocking. *Physical Review E*, **58**(4), 4828–4858. doi: 10.1103/PhysRevE.58.4828.

Tu, Y. 2000. Phases and phase transitions in flocking systems. *Physica A*, **281**(1–4), 30–40. doi: 10.1016/S0378-4371(00)00017-0.

Vicsek, T., Czirók, A., Ben-Jacob, E., Cohen, I. & Shochet, O. 1995. Novel type of phase transition in a system of self-driven particles. *Physical Review Letters*, **75**(6), 1226–1229. doi: 10.1103/PhysRevLett.75.1226.

Vine, I. 1971. Risk of visual detection and pursuit by a predator and the selective advantage of flocking behaviour. *Journal of Theoretical Biology*, **30**(2), 405–422. doi: 10.1016/0022-5193(71)90061-0.

von Holst, E. 1952. Diskussionsbemerkung. *Journal für Ornithologie*, **93**(2), 191.

Warnke, U. 1984. Avian flight formation with the aid of electromagnetic forces: A new theory for the formation alignment of migrating birds. *Electromagnetic Biology and Medicine*, **3**(3), 493–508. doi: 10.3109/15368378409027710.

Watts, J. M. 1998. Animats: Computer-simulated animals in behavioral research. *Journal of Animal Science*, **76**(10), 2596–2604.

Weimerskirch, H., Martin, J., Clerquin, Y., Alexandre, P. & Jiraskova, S. 2001. Energy saving in flight formation. *Nature*, **413**(6857), 697–698. doi: 10.1038/35099670.

Wieselsberger, C. 1914. Beitrag zur erklärung des winkelfluges einiger zugvögel. *Zeitshrift FlugTechnologie MotorLuft*, **5**, 225–229.

Williams, T. C., Klonowski, T. J. & Berkeley, P. 1976. Angle of Canada Goose V flight formation measured by radar. *The Auk*, **93**(3), 554–559.

Willis, D. J., Peraire, J. & Breuer, K. S. 2007. A computational investigation of bio-inspired formation flight and ground effect. In: *Proceedings of the 25th AIAA Applied Aerodynamics Conference*, Miami, FL, AIAA 2007-4182. Reston, VA: AIAA.

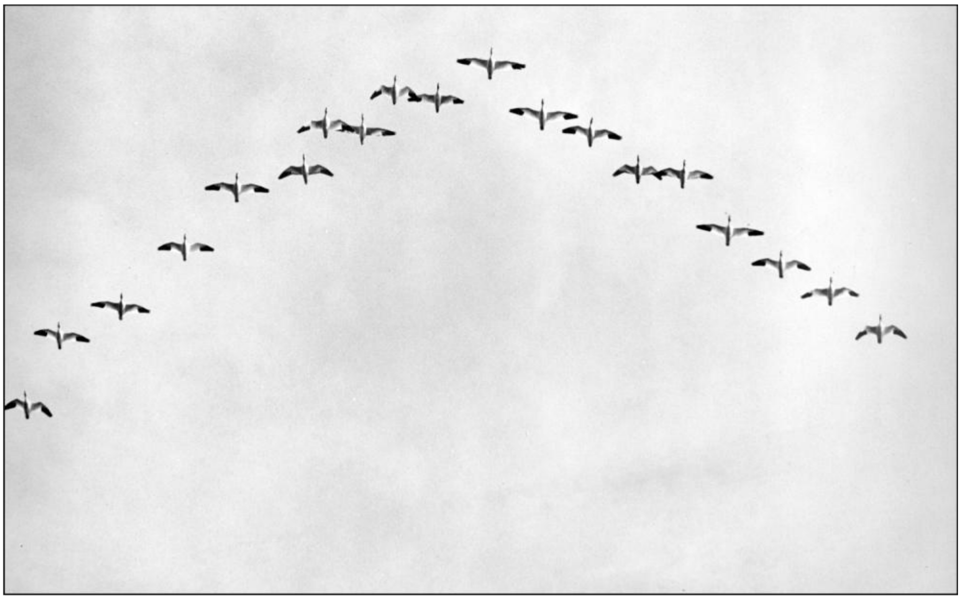
Wilson, D. S. & Wilson, E. O. 2007. Rethinking the theoretical foundation of sociobiology. *The Quarterly Review of Biology*, **82**(4), 327–348. doi: 10.1086/522809.

Wilson, S. W. 1985. Knowledge growth in an artificial animal. In: *Proceedings of the 1st International Conference on Genetic Algorithms* (Ed. by J. J. Grefenstette), pp. 16–23. Hillsdale, NJ: Lawrence Erlbaum Associates.

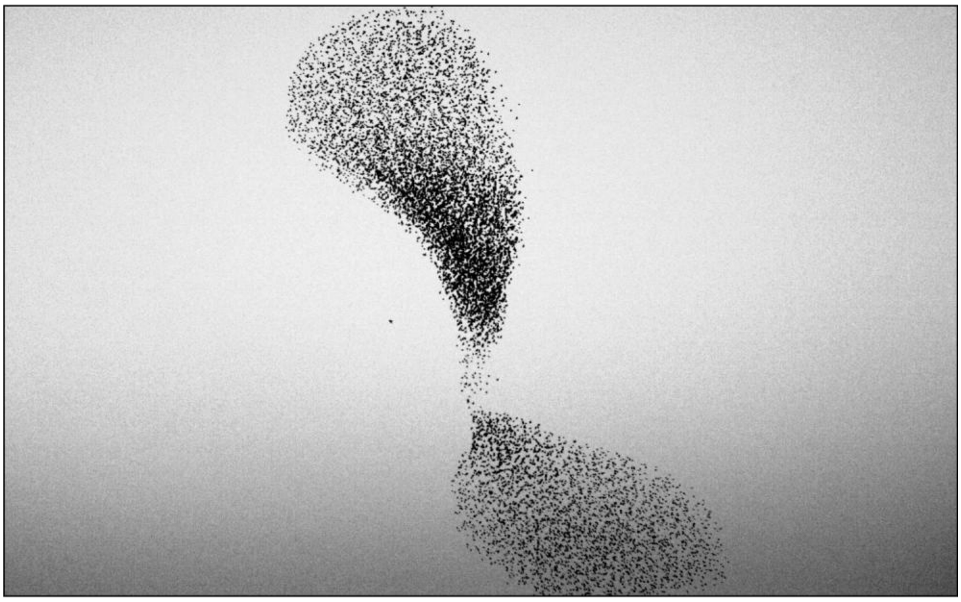
Wood, A. J. & Ackland, G. J. 2007. Evolving the selfish herd: Emergence of distinct aggregating strategies in an individual-based model. *Proceedings of the Royal Society B*, **274**(1618), 1637–1642. doi: 10.1098/rspb.2007.0306.

Wynne-Edwards, V. C. 1962. *Animal dispersion in relation to social behaviour*. Edinburgh, UK: Oliver & Boyd.

Zaera, N., Cliff, D. & Bruten, J. 1996. (Not) evolving collective behaviours in synthetic fish. In: *From Animals to Animats 4: Proceedings of the Fourth International Conference on Simulation of Adaptive Behavior*, Cape Cod, MA (Ed. by P. Maes, M. J. Matarić, J.-A. Meyer, J. Pollack & S. W. Wilson), pp. 635–644. Cambridge, MA: MIT Press.

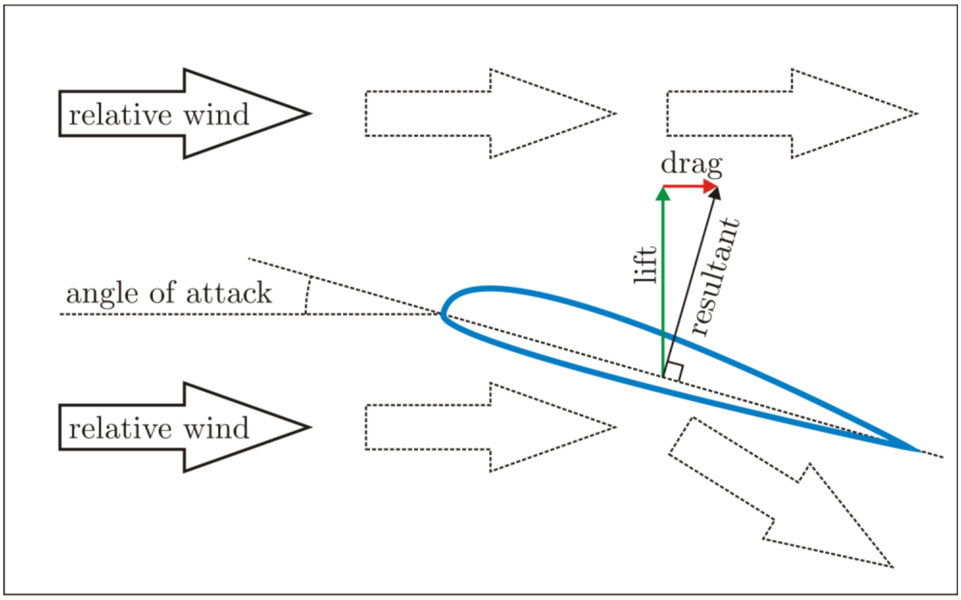


A) Line formation

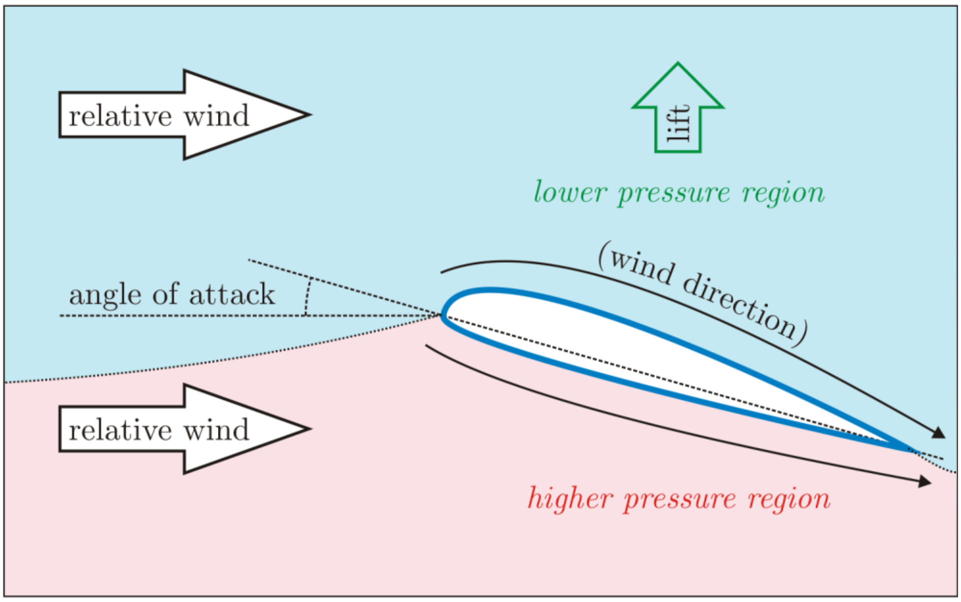


B) Cluster formation

Figure 1. A) Line formation of Snow Geese, *Chen hyperborea*. B) Cluster formation of European Starlings, *Sternus vulgaris*, over Rome (© 2009 STARFLAG project, INFM-CNR).

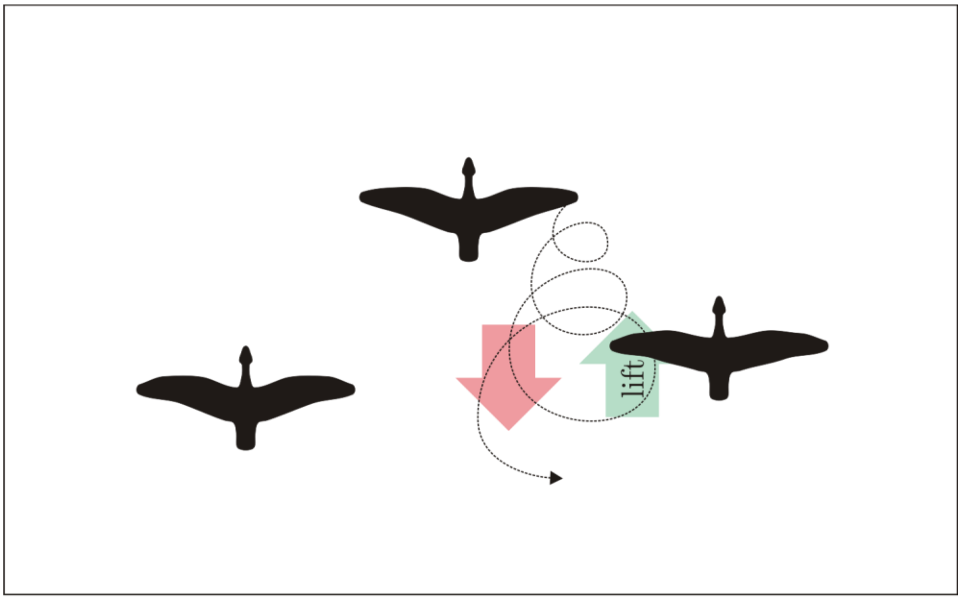


A) Newtonian lift

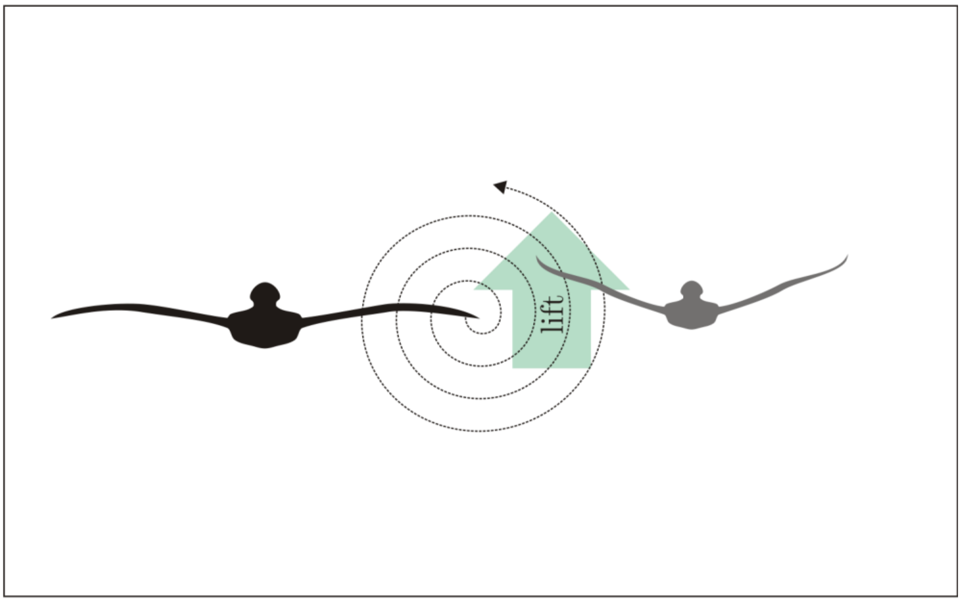


B) Bernoulli lift

Figure 2. Lift is generated in two principal ways. A) Air is deflected downward when there is a positive angle of attack between a wing and the relative wind. This deflection produces a reactive 'Newtonian lift' force. B) When air moves faster over the top of the wing than the bottom, a reduced pressure area is created on the top of the wing, generating 'Bernoulli lift'.



A) Top view



B) Front view

Figure 3. Air streams off of a bird's wingtip as a horizontal vortex that has a rising and falling component. If the wingtip of a following bird were positioned in the rising component of the vortex generated by a preceding bird, some of the energy lost by that bird into the tip vortex, as a product of generating lift, might be recaptured by a following bird.