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Review

# The Aerodynamic Mechanisms of the Formation Flight of Migratory Birds: A Narrative Review

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**Abstract:** Recently, significant advances have marked the scientific knowledge of the formation flight of migratory birds. Both experimental and theoretical research have played a central role in understanding the aerodynamic mechanisms associated with this behavior, laying the groundwork for future investigations into the benefits of group formation. These studies have specifically demonstrated the energy savings achieved by birds adopting this practice. Technological evolution, in turn, has opened new perspectives, allowing an in-depth experimental understanding of the flight behaviors of birds in formation, ranging from their energy saving to sophisticated aerodynamic strategies. Studies converge towards an increasing recognition of the complexity and variability of the mechanisms governing formation flight in different avian species. Recent progress in computer modeling has generated impressive visual representations of V-formation flight, prompting several hypotheses about its functions and mechanisms. However, the challenge persists in the ability to test these hypotheses. In conclusion, a multidisciplinary approach involving biologists, engineers, mathematicians, computer scientists, and physicists is essential to unravel the mysteries of the aerodynamics of V-formation flight in migratory birds. This literature review aims to compile studies addressing aerodynamic questions related to the formation flight of migratory birds, exploring various aspects from aerodynamic modeling to energy saving and formation optimization.

**Keywords:** migratory birds; V-formation; aerodynamics; flight strategies; energy savings



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## 1. Introduction

The synchronized aerial acrobatics of migratory birds have captivated observers since the early days of natural history, spanning over 2000 years. Some of these migratory birds achieve remarkable feats, covering distances of up to 96,000 km per year [1]. This accomplishment holds particular significance for lightweight birds, facing headwinds and challenging weather conditions [2–5]. To achieve this, they have developed exceptional physiological abilities and collaborative strategies, with V-formation flight (Figure 1) becoming emblematic of migratory bird flights [6,7]. The question of formation flight was approached from various perspectives [8–10]. Nowadays, the aerodynamic aspect continues to spark debates, despite undeniable evidence from several scientific studies conclusively demonstrating the energy-saving benefits of well-organized group formation flight [11–13].

One of the proposed hypotheses regarding the reasons for flocking is that group flying provides birds with a better opportunity to communicate with each other, constituting a major advantage in avoiding predators [14–18]. While this dimension is relevant, it alone cannot explain the profound interest in well-organized formation flight [6,19]. Other factors and mechanisms must be considered for a holistic understanding of this complex avian behavior [20]. The study of organized bird flight, which began in the 20th century, highlights Kuhn's concept [21] that scientific progress occurs through the development of new techniques. This paradigm shift reflects a transition from purely biological observations to an

interdisciplinary approach, where aerodynamic modeling plays an increasingly significant role in explaining why birds adopt specific formations in flight [22–24]. Aerodynamics, introduced with modern science, has unveiled some secrets related to the organization of formations of migratory birds in organized flight. By observing how birds exploit the aerodynamic and energy benefits of formation flight, engineers can design similar strategies for aircraft, improving their fuel efficiency and autonomy. This biomimetic approach opens up prospects for optimizing flight operations by drawing inspiration from nature. This is precisely what inspired Airbus' fello'fly project [25], aimed at demonstrating the technical, operational and commercial viability of two aircraft flying close together on a long-haul flight. This collaborative project has the potential to significantly reduce fuel consumption and, consequently, the environmental impact of commercial aircraft thanks to collaborative flight.



**Figure 1.** The V-shaped formation, which is characteristic of the flight of migratory birds (copyright-free image).

The primary objective of this literature review is to scrutinize and dissect studies delving into the aerodynamics associated with the formation flight of migratory birds, particularly concentrating on aerodynamic modeling, energy conservation, and the spatial arrangement of formations. In this comprehensive synthesis, we aim to emphasize that, despite the emergence of novel theoretical, experimental, and numerical approaches, the pivotal role of field observation remains unchanged. However, the progress in this domain, be it recent or anticipated, hinges predominantly on the collaborative efforts of physicists, mathematicians, computer scientists, and, notably, field biologists.

## 2. Materials and Methods

In December 2023, an automated literature search was conducted, employing a search strategy that incorporated electronic bibliographic databases including ScienceDirect, PubMed, Web of Science, and Google Scholar. The goal was to encompass as many relevant studies as possible. Only articles composed entirely in English were considered, with no restrictions imposed regarding scientific domains, publication years, and specific journals. Regarding publication types, only peer-reviewed journal articles were considered, thereby excluding book chapters, theses, and editorials from the search process. The search terms "Formation", "Migratory birds", and "Aerodynamics" were included to refine the search. Two independent authors evaluated each study for eligibility and extracted relevant data. Disagreements between evaluators were resolved through discussion or intervention by a

third reviewer. Citations were initially screened based on their titles and abstracts, and any duplicates or those not meeting eligibility criteria were excluded at this stage.

Subsequently, full texts of relevant studies were scrutinized to compile a final list of studies for inclusion. The processes of inclusion and exclusion were meticulously documented and reported using a methodology aligned with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines [26]. In Figure 2, the PRISMA flow diagram visually represents the systematic identification and selection of documents for an extensive review. The initial search yielded 6 results on PubMed, 6 results on Web of Science, 63 results on ScienceDirect, 154 results on Google Scholar and 13 records identified through other sources.

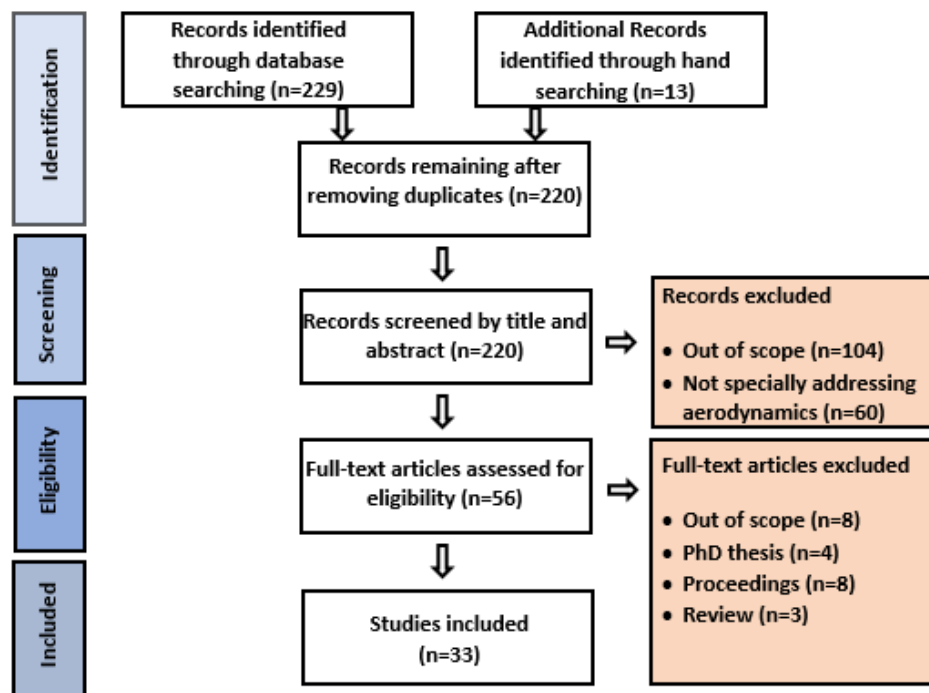


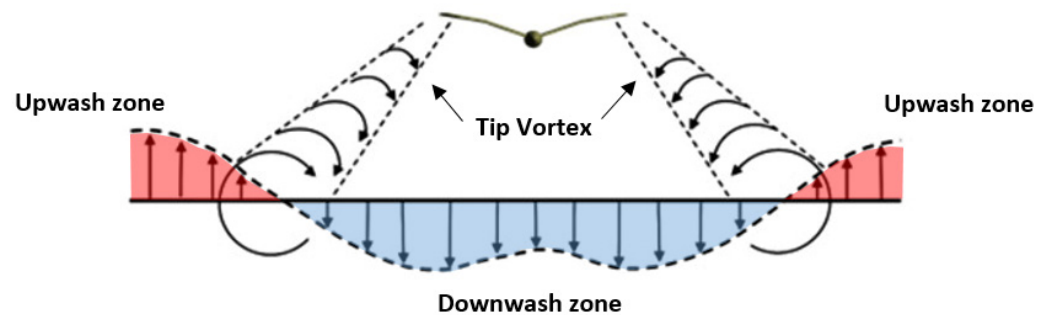
Figure 2. PRISMA flow diagram.

### 3. Results

#### 3.1. Theoretical and Experimental Studies

In 1969, Pennycuick [27] presented a study on the mechanics of flight in migratory birds, covering topics such as the power required to fly and the effects of altitude, which he expressed algebraically. His study, rooted in the classical aeronautical theory, was considered fundamentally reliable, despite some simplifications. The text also provided mathematical models for calculating the performance estimates of different bird species. However, Pennycuick pointed out that the accuracy of these estimates depended both on the theory and on the accuracy of the experimental data, which were scarce at the time of the study's publication. The text emphasized the imperative of accumulating experimental measurements for different types of flying animals in order to improve the accuracy of performance estimates. The study that has truly been considered a pioneer in the study of the aerodynamics of migratory birds flying in formation is that of Lissaman and Shollenberger [28]. Their study was the first to theorize the aerodynamic advantages of formation flying, particularly those of V-formation (see Figure 1). Their theoretical model provided an estimate of the aerodynamic drag induced by birds flying in formation, concluding that V-formation was aerodynamically advantageous and generated substantial energy saving for birds following the leader. The authors developed a theoretical aerodynamic model that considered the optimal positioning of birds side by side in a V formation. This model described how optimal positioning could reduce induced power, i.e., the power required

to maintain sufficient lift and overcome gravity for each bird in the group. Their study was based on the idea that as wingtip spacing decreases, the induced power required also decreases, as the next bird now flies into an increasingly strong upward vortex from the vortices generated by its neighbor (Figure 3). Similarly, beyond a critical wingtip spacing, as the V-formation becomes tighter, the following bird begins to fly in the wake generated by the preceding bird, resulting in increased energy costs rather than energy saving (Figure 3). Thus, optimal wingtip spacing should exist that maximizes the benefits of formation flight while minimizing the potential costs resulting from the wake. Lissaman and Shollenberger expressed their analysis by comparing formation flight with solo flight. Specifically, the induced power of a single bird in formation was expressed as the ratio of the induced drag of a bird flying in formation to that of a bird flying alone.



**Figure 3.** Diagram of the vortex flow developing in the wake of a large bird gliding at high speeds.

At the time of its publication, Lissaman and Shollenberger's 1970 paper was essentially theoretical, mainly due to the lack of appropriate technology to experimentally study the dynamic flight of birds within a V-formation. This article has been a source of inspiration for many researchers, who have continued the work based on their preliminary results and theories. Although the authors omitted to present the calculations and formulas leading to their conclusions, this study remains a pioneer in the field.

Based on the hypothesis of Lissaman and Schollenberger [28], Higdon and Corrsin [29] used the simplest stationary aerodynamic theory to model the induced drag of birds flying alone or in formation. The results of their study suggested that flying directly behind another bird would be detrimental in terms of aerodynamics. One of Higdon and Corrsin's mathematical models was based on the horseshoe vortex model, a major drawback being the assumption that wake vortices extend to infinity, whereas in reality vortex trails dissipate gradually. The authors raised the question of whether a "drafting" effect, now well known in the field of sport [30–32], could offset the adverse wake effect induced when one bird flies directly behind another. In line with theoretical studies by Lissaman and Shollenberger [28], they pointed out that migratory birds such as geese, flying within a V-shaped formation, could save a significant amount of energy through mutual aerodynamic interaction. They also suggested that a tall, narrow flock would actually experience an increase in drag. They also tentatively concluded that improved flight efficiency was not a sufficient reason for migration in large, three-dimensional flocks. Their theoretical study did, however, make a significant contribution to the scientific literature of the time.

A few years later, Gould and Heppner [6] questioned the theory of formation flight and focused on the V-formation observed in Canadian geese. Gould and Heppner's measurements on Canadian geese initially cast doubt on the aerodynamic advantage of V-formation. This theory, originally proposed by Lissaman and Shollenberger [28], suggested that birds could save energy by flying in a specific formation. However, an in-depth analysis, taking into account the spacing between the wingtips of birds in formation, confirmed that the theory was valid. The methodology employed in their study involved making videos of groups of Canadian geese, then measuring the V-angle and distance between birds flying in formation. The study highlighted the importance of considering non-aerodynamic factors

such as group cohesion and navigation parameters. The results showed variations in the apparent angle of V formations as birds moved along their flight path. Measurements taken from images of migratory bird groups determined that the average angle between the arms of the V-formation was  $34^\circ$ , while Lissaman and Schollenberger [28] estimated this angle at  $120^\circ$ . Table 1 summarizes the range of apparent V-formation angles reported by various authors. The article by Gould and Heppner [6] underlined the need for further studies with other species and taking into account various factors such as weather, wind, altitude, group size, season, etc... Thus, Gould and Heppner's study played a crucial role in empirically examining the validity of formation flight theory in migratory birds, contributing to a better understanding of bird flight behavior. A few years later, May [33] continued the work of his predecessors, addressing various aspects of the dynamics and aerodynamics of migratory birds and the V-formation of Canadian geese (*Branta canadensis*). May [33] takes up the theories of Lissaman and Schollenberger [28] and determines that the aerodynamic advantage for large birds of flying in formation is "minimal". He estimates the gain at around 10% compared with solitary flight, which nevertheless confirms the aerodynamic advantage of flying in a group. May also suggests using depth to quantify the distance between birds measured along the flight path.

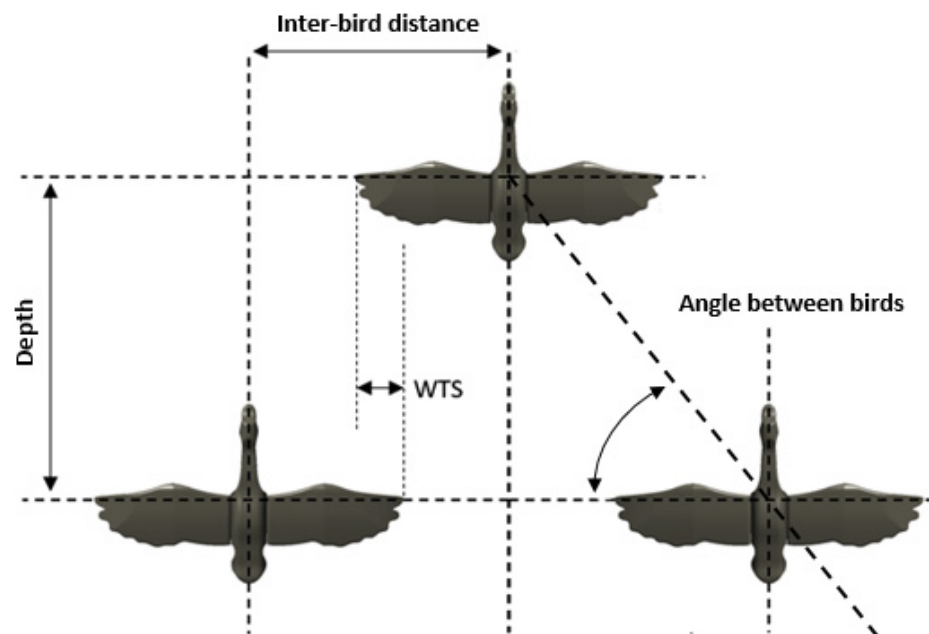
**Table 1.** Formation angle range of V-formation from various authors.

Lissaman and Schollenberger [28]	$120^\circ$
Gould and Heppner [6]	$27.5^\circ$ – $44^\circ$
Williams et al. [34]	$38^\circ$ – $124^\circ$
Heppner et al. [16]	$24^\circ$ – $124^\circ$
O'Malley and Evans [35]	$24^\circ$ – $122^\circ$

A few years later, Badgerow and Hainsworth [11] continued their research into V-flight in Canadian geese. In their study, they re-evaluated the data of Gould and Heppner [6] using wingtip spacing instead of the distance between body centers to test the aerodynamic hypothesis of V-flight. They observed that several birds had wingtips that overlapped with the wingtips of the preceding bird, thus contradicting the hypothesis of Lissaman and Schollenberger [28]. Completing the aerodynamic theory of V-flight, Badgerow and Hainsworth [11] estimated that V-flying birds could save 51% energy compared with flying alone, whereas Lissaman and Schollenberger [28] estimated an energy saving of 71%. Using the description of the velocity field induced by a finite wingspan in the case of formation flight, Hummel [36] demonstrated that each wing in formation flies within an upwash field generated by all the other wings in the formation, leading to a significant reduction in flight power demand. Aerodynamic theory methods have been used to calculate the reduction in flight power for formations of arbitrary shapes with any number of birds. The total power reduction is strongly dependent on the lateral distance between the wings. In addition, he showed that a longitudinal displacement of the wings in the direction of flight has no influence on the total reduction in flight power, but only on its distribution among the individuals involved. He also addressed the communication aspects of formation flying. Still based on Lissaman and Schollenberger's initial theory [28], Hainsworth [37] also looked at the aerodynamics of formation flight in migratory birds. In this study, Hainsworth meticulously described the projective geometry technique used in his collaboration with Badgerow. He applied this technique to his own photographs of Canadian goose formations and observed that the birds frequently changed lateral positions relative to the preceding bird. This observation contradicted the basic energy conservation model proposed by Lissaman and Schollenberger [28], which predicted an optimal position for energy conservation. Using their model, Hainsworth concluded that photographed goose formations demonstrated only a 36% energy advantage over solitary flight, about half that predicted by Lissaman and Schollenberger's model [28]. He warned

against adopting a simplistic engineering model to fully explain behavior that could be highly variable depending on environmental parameters.

Badgerow [38] also focused on the formation flight of Canadian geese and evaluated energetic advantages by testing various hypotheses on the geometric characteristics of the formation. Badgerow examined the positioning of birds within different diagonal line formations (V, J, echelon, etc.) and proposed hypotheses on how geese maximize benefits. Positioning was defined in relation to the leader bird and could vary in three ways: along the flight path (depth), perpendicular to the flight path (wingtip spacing), or both (see Figure 4). Each hypothesis predicted a characteristic pattern of flight behavior in the form of a relationship between depth and wingtip spacing. He postulated that if the aerodynamic advantage was the main driver of line flight, there should be a specific geometric relationship between birds in a formation. Badgerow proposed an energy advantage of around 10% for formation flight over solitary flight, a value significantly lower than the estimates of Hummel (who proposed saving of 30% saved energy for follower birds) or Gould and Heppner [6] who estimated energy saving of 51%.



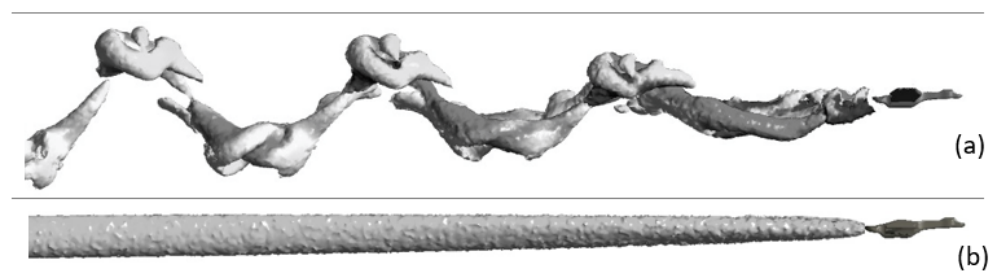
**Figure 4.** Geometric positioning of birds relative to each other within an organized formation flight.

Along with his predecessors, Hainsworth [39] investigated the energetic benefits of formation flight in Canadian geese (*Branta canadensis*). His study analyzed the variation in vortex position induced by wing movements in V-shaped formations. The researchers measured various parameters, such as wingtip spacing, formation depth, wingbeat frequency, and relative extreme wing positions, to assess the use of these variations in vortex positioning. The results showed that only 48% among 73 birds from eight different formations had wing-beat frequencies similar to those of the bird in front of them (difference  $\leq 0.1$  beats per second). The study suggests that birds at the rear of a formation adjust wingtip spacing (WTS) in response to changes in the horizontal position of the bird in front of them. Some birds, around 20%, maintain positions leading to relatively low economies, highlighting individual variability in the use of aerodynamic strategies. Table 2 shows some of the WTS values estimated by various authors, together with an estimate of the associated energy savings.

**Table 2.** Wing-tip spacing (WTS) of the follower bird compared to the leader bird (Canadian geese). In brackets, energy savings expressed as a percentage.

	WTS	Energy Savings
Badgerow and Hainsworth [11]	−16 cm	51%
Hainsworth [37]	−19.8 cm	36%
Hainsworth [39]	−33.7 cm	30–40%

Many years after the pioneering study by Lissaman and Schollenberger [28], theoretical methods aimed at deciphering the mechanisms contributing to energy savings during formation flight have evolved considerably. Kshatriya and Blake [40] developed an optimal formation pattern aimed at reducing the power required during formation flight in birds by approximating the wing with a horseshoe vortex. The analysis was based on a rigid, rectangular wing without flapping, which the authors believed would be suitable for large birds flying in formation over long distances and flapping their wings slowly. Assuming strict uniformity between all birds, encompassing factors such as wingspan, weight, and aspect ratio, the authors used a method in which the vortex system is simplified. The aerodynamic profile is replaced by a bound vortex, while the trailing wake is represented by two tip vortices. As Figure 5 suggests, the wake of a flapping bird is different from that of a gliding bird. Various models of leader position change were also investigated, comparing the rates of power reduction required.



**Figure 5.** Representation of the wake shape behind a migratory bird in flapping flight (a) and gliding flight (b) as determined by numerical simulation. Results obtained by numerical simulations were carried out by the authors of the present study.

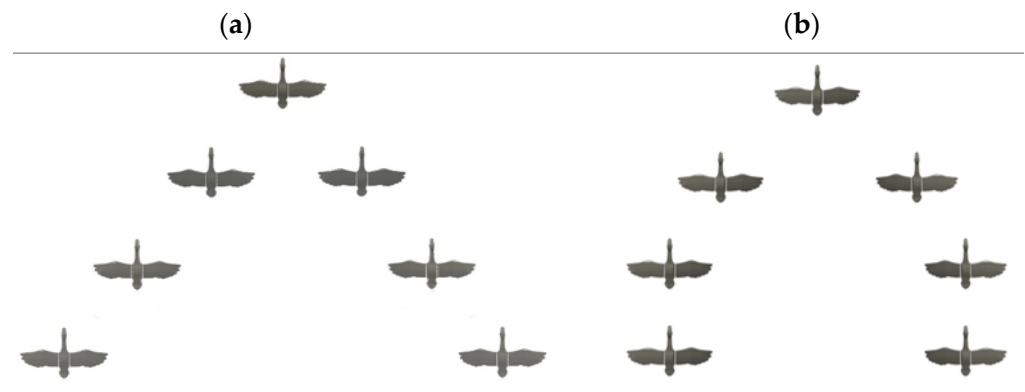
The theoretical study of the aerodynamics of formation flight has revealed that V-formation is optimal for long-distance flights. This configuration offers a significant reduction in power requirements and an even distribution of drag among the birds, resulting in significant energy saving. Cutts and Speakman [41] used an innovative approach, drawing on both observation of formation flight in pink-footed geese (*Anser brachyrhynchus*) and aerodynamic theory. In their study, they photographed 54 birds from the ground to assess distances and angles, revealing that a significant number of birds did not correspond to the position theoretically predicted to maximize aerodynamic economies. They estimated that with an average wingtip spacing, the induced power saving would be 14%. A few years later, Speakman and Banks [42] applied the same technique to photograph 25 formations of greylag geese (*Anser anser*). Their results revealed substantial variation in positioning, with only 17% of birds corresponding to the optimal position expected for aerodynamic saving. Using the assumptions of Cutts and Speakman [41], they proposed an average induced power saving of 26.5%, resulting in a 5–9% reduction in total flight costs. With the leitmotiv of understanding the aerodynamic implications leading to a reduction in the power required for formation flight, Hummel [43] demonstrated that for maximum power reduction, the trailing bird wing should be located as close as possible to the wake of the leading bird wing. He also suggested that the total reduction in flight power for the whole formation depends strongly on the number and lateral distance of the wings.



Observations of migrating cranes from a helicopter have shown that, in formations of this species, the bird at the top flies at the lowest position, and all the other birds are slightly offset in height. This subtle arrangement is necessary to achieve maximum energy saving in the case of a wake vortex. He also noted that in low-level formation flights of geese, the birds are extremely sensitive to disturbances from the ground, making it unlikely to find phase relationships between wingbeats. The first theoretical studies [28] were often carried out with simplifications, as the experimental facilities of the time were unable to quantify the forces exerted on the birds' wings, or to obtain precise information on the relative positions of the birds in relation to each other. It was only with the development of biologgers, capable of measuring energy expenditure, body movements (accelerometers), and individual positioning (GPS), that many of the key ideas could be tested [44–46]. One study, also considered pioneering for its experimental approach conducted with birds in flight, was carried out by Weimerskirch et al. [13]. In this study, the authors used wireless technologies and miniaturized sensors to train eight white pelicans (*Pelecanus onocrotalus*) to fly in a V formation behind a motorboat and an ultralight glider in Djoudj National Park, Senegal. Flight sessions were filmed and sensors were used to measure wingbeat frequency and heart rates and estimate the birds' energy expenditure in flight. Pelicans flying in V formation showed a significant reduction in heart rate compared to birds flying solo. The observed reduction in heart rate suggests that flying in formation enables the birds to increase their flight endurance. Although some pelicans had difficulty maintaining their position in formation, the energy savings were nevertheless significant. The study concludes that the main advantage of V-formation flight may lie in the pelicans' ability to glide for longer periods by flying in the vortex wake, thus achieving substantial energy savings. This strategy translates into energy saving of between 11.4% and 14.0%. These energy saving values, although lower than those estimated in the theoretical studies of geese [11,28], should be considered significant because pelicans flap their wings more slowly and glide for longer periods. Formation flying offers birds the opportunity to extend their range on migratory flights or foraging expeditions. The difficulty of studying living birds has prompted most researchers to adopt a purely theoretical approach. This is the case of Seiler et al. [47], who theoretically analyzed the V-formation of migratory birds, testing the two main hypotheses: aerodynamic advantage and enhanced visual communication. In this study, each bird is assumed to fly at a constant speed, and each segment of the linear formation is modeled as a chain of  $(N + 1)$  birds. The authors drew on the work of Pennycuik [48] to estimate the forces acting on the birds. The motion of each bird was modeled using Newton's equations, and force generation was analyzed using a linear model. The results suggested that spacing control is difficult when a predecessor-following strategy is implemented. The dynamics of the linearized system showed that tracking errors are amplified, requiring higher accelerations for birds far from the leader. The study by Seiler et al. provides a better understanding of bird organization strategies within a V formation, and these results can also be applied to Unmanned Aerial Vehicle (UAV) control devices.

Sugimoto [49] also adopted a mathematical approach to better understand how birds manage to maintain an aerodynamically efficient formation. In his study, he sought to understand the mechanisms behind energy conservation by examining the existence, stability and self-organization of the formation flight used by migratory birds. The author argues that, due to the low flight speed and high Reynolds number, it is appropriate to treat air as an inviscid, incompressible fluid. While modeling air with this approach may offer simplifications, it inherently carries risks of underestimating or overestimating actual aerodynamic forces and overlooking significant phenomena. To mitigate these potential problems, the authors have incorporated the fundamental effects of viscosity using the concept of zero drag. Formation flight was defined as the steady-state solution to the basic equations, particularly the solution in which all birds fly at the same speed. Still on a purely theoretical approach, Kawabe [50] analyzed the potential reduction in power when flying in formation by considering the wing as a horseshoe vortex. Various patterns of leader

change were investigated, comparing the rates of power reduction required, including V-formations. Using an approach similar to that of Kshatriya and Blake [40], a rigid, rectangular, non-flapping wing was considered. Kawabe's theoretical study revealed that the U-formation (see Figure 6) would be optimal for long-distance flying. The U-formation would provide a significant reduction in power requirements compared to solo flight, and significant energy savings on extended flights. To our knowledge, Kawabe's study [50] is the only one that argues in favor of U-shaped formation. The theoretical results of this study need to be compared with experimental data to evaluate the potential energy savings of U-shaped formation compared to other types of formations.



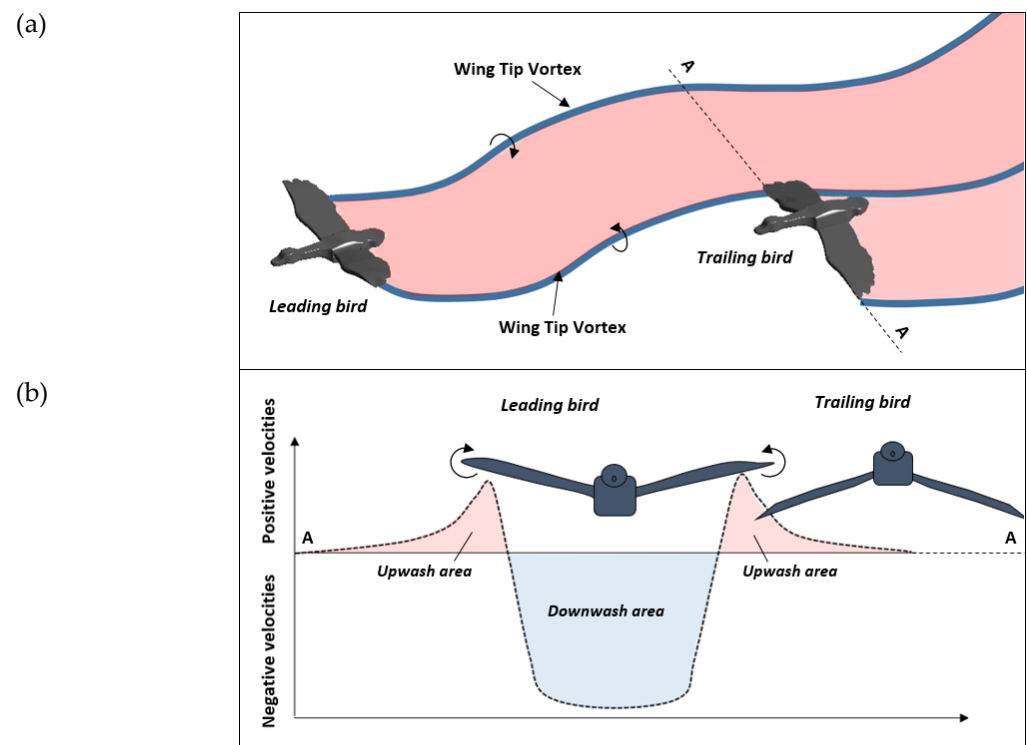
**Figure 6.** Example of an inverted V-formation (a) and an inverted U-formation (b).

The constant development of algorithms has led Duman et al. [51] to use a new approach called metaheuristics, which mimics the behavior of migratory birds. This so-called “Migratory Bird Optimization” (MBO) algorithm is inspired by the V-shaped formation of migratory birds. Parameters such as bird number, speed, wingtip spacing (WTS), and wing flapping were incorporated into the optimization model. Nevertheless, crucial details on bird species or size, which play a fundamental role in energy savings, are not disclosed.

One of the studies that can be considered a major contribution to the scientific literature in the field of migratory bird aerodynamics was published in 2014. In this study, Portugal et al. [52] investigated the V-formation flight of bald ibises (*Geronticus eremita*). The findings of their study indicate that, in V-formation flight, ibises occupy positions mathematically predicted by fixed-wing aerodynamics, as described notably by Lissaman and Shollenberger [28]. In-flight measurements showed that the birds flew precisely as predicted by theoretical simulations, about one meter behind the lead bird and another meter to the side. Some ibises showed a preference for flying on the right or left side of the V, while others favored the center or edges. However, the overall pattern indicated frequent exchanges of positions, and the group lacked a consistent leader. They also suggested that the wake of flapping birds (in their study, ibises spent 97% of their time flapping) is likely to be much more complex than predicted by theoretical studies.

In addition, they showed that the birds exhibited coherence in wingtip trajectories when flying in V formation, beating their wings spatially in phase to maximize upwash capture throughout the wingbeat cycle (Figure 7). In contrast, when flying directly behind another bird, they adopted a spatially antiphase wingbeat, potentially to mitigate the detrimental effects of the downwash. Portugal et al. also suggested that energy saving could be increased by 20% when wing flapping is performed optimally in a spatial phase compared to out-of-phase wing flapping. These aerodynamic achievements, which might be considered impossible for birds due to the complexity of their flight dynamics, suggest an awareness of the spatial structures generated by the wakes of neighboring birds. These results provide an in-depth understanding of the complex aerodynamic interactions in birds' V-formation flight, demonstrating their remarkable ability to anticipate or detect these dynamic wakes. The investigation carried out by Portugal and colleagues, incorpo-

rating experimental data collected from birds in flight, is undoubtedly among the major contributions of the last decade.



**Figure 7.** The flapping of the wings creates a vortex that starts at the bird’s wingtips. A-A represents a virtual line that extends through the wingtips of the trailing bird (a). Vertical velocity can be plotted along this line A-A (b). From (b), we can see that the airflow at the center of this wake is directed downwards (downwash; in blue); in this area, the velocity is negative, while the area outside each wing represents an upwash region (in red), where the velocity is positive. A bird flying in the wake of the one preceding it can reduce its energy expenditure by taking advantage of the upwash in the wake of the leading bird (a, side view; b, front view).

In 2015, Voelkl et al. [53] used a similar research methodology to Portugal et al. [52] and Weimerskirch et al. [13], training 14 young northern bald ibises (*Geronticus eremita*) to follow an ultralight paraglider in flight. The authors demonstrated a strong correlation between the duration during which a bird was leader of a formation and the time during which it had previously benefited from the wake of another bird. This temporal correlation suggests cooperation between birds directly taking turns to lead the formation. Interestingly, analyses revealed that these changes in pairs had a significant impact on the overall cohesion of the V-formation. With the aim of better understanding the organization of birds within the group, Li et al. [54] used a mathematical method to investigate the intrinsic mechanism of V-formation. Using control-engineering principles, the authors incorporated visual communication constraints into a standard gradient-based control algorithm. Their simulation results show that the group of birds gradually converges towards a stable V-formation, which is consistent with flight phenomena observed in biology. This paper presents the development of a cost function aimed at achieving V-shape formation in bird groups, using control-engineering principles. This cost function incorporates visual communication constraints to ensure that each bird maintains a correct collision-free formation. In summary, the paper proposes a mathematical and control framework for achieving stable V-formation in bird flocks, balancing visual communication and collision avoidance through a carefully designed cost function and control algorithm.

Using classical aerodynamic theory, Mirzaiena and Hassalanian [55] theoretically investigated the aerodynamic advantages and energy efficiency of V-flight in Canadian

geese. The results of their study confirmed that the lead bird consumes the most energy, while subsequent birds benefit from reduced drag. They calculated the energy required for migration and the total drag of the flock, demonstrating the benefits of position rotation in increasing flight time and distance. Their study revealed that changing position within the flock can improve flight time and distance travelled by over 44.5%. This research highlights strategic formation and load balancing in migrating Canada geese, optimizing their energy consumption and flight efficiency through collaborative behaviors and aerodynamic advantages. Also theoretically, Mirzaiana et al. [56] investigated the effects of wingtip spacing on total drag in a group of bald ibises. Using existing mathematical models [9,40], the authors carried out an aerodynamic study on bald ibises in flocked flight. They determined the percentage drag reduction of individual ibises and showed that ibises can save energy by flying in formation. The results indicated that as the number of ibises in a group increases, the drag force of each individual ibis decreases. Depending on whether the number of birds is even or odd, there are always one or two ibises in the middle with the lowest drag value. For a group of 15 ibises, it was shown that drag is reduced by 34% for the lead and trailing ibises by changing the wingtip spacing, while the rest of the ibises see a drag reduction of 65 to 73%. Note that this level of drag reduction is close to the estimates of Lissaman and Shollenberger [28] and well above the predictions of other authors (see Table 3). Building on their previous study [56], Mirzaiana et al. [57] again investigated the effects of not only wingtip spacing but also wingspan on the individual drag of each ibis in the flock. An algorithm was applied for the replacement mechanism and load balancing of ibises during flight. In this replacement mechanism, ibises with the highest remaining energy value are iteratively replaced by ibises with the lowest energy. After four replacement stages, ibises with wingspans of 1.39 m and 1.37 m were found to have the lowest remaining energy. In addition, small birds were found to have a chance of taking the lead position during group flight.

**Table 3.** Energy savings for a trailing bird in formation flight. The potential energy savings in formation flight are quantifiable by considering the ratio between the induced drag coefficient for solo flight and the average drag coefficient of a bird within the formation, as proposed by Lissaman and Shollenberger [28].

	Energy Savings	Bird Species
Lissaman and Shollenberger [28]	71%	-
Badgerow and Hainsworth [11]	51%	Canada Geese
Hainsworth [37]	36%	Canada Geese
Cutts and Speakman [41]	14%	Pink Footed Geese
Speakman and Banks [42]	26.5%	Greylag Geese
Weimerskirch et al. [13]	11.4–14%	White pelicans

Still based on aerodynamic theory, the study by Mirzaenia et al. [7] reaffirmed the effectiveness of V-formation in reducing induced drag. The Mirzaenia et al. study [7] examines aerodynamic drag forces for individual Canada geese as well as for the overall group to understand how flock size affects drag and energy conservation. Theoretical modeling demonstrated a significant reduction in drag as group size increased. The study also explored the effects of wingtip spacing on total group drag. The results showed that by reducing wingtip spacing to a certain point, total group drag decreased. Their study provided information on optimizing energy consumption by repositioning leaders and followers, which could improve the range and flight endurance of these migratory birds by over 44.6%. Previous research had already confirmed the principle that birds exhibit cooperative behavior, taking turns at the front of formations to optimize energy use. Table 3 summarizes the theoretically estimated maximum energy savings that following birds

could experience in a formation flight. Remarkably, the theoretically estimated energy savings decrease as predictive models evolve and become more refined over time.

Over time, researchers have compiled information on the structure and spatial organization of migratory birds in formation flight. Based on existing data, Corcoran and Hedrick [58] studied the interaction rules of a limited sample of migratory bird species. Based on available flight data, they postulated that groups composed of larger shore-bird species would show improved organization compared to those composed of smaller species, reflecting the tendency of larger birds to fly in well-structured V-formations. In addition, they anticipated that larger species would more regularly display aerodynamic formations. Contrary to expectations, all the species studied flew in a group structure that the researchers termed a “composite V-formation”. Corcoran and Hedrick’s results are consistent with theoretical and empirical studies supporting the hypothesis that birds flying in simple V formations benefit from aerodynamic and energetic advantages. They proposed that these advantages might also explain why birds adopt the composite V formation.

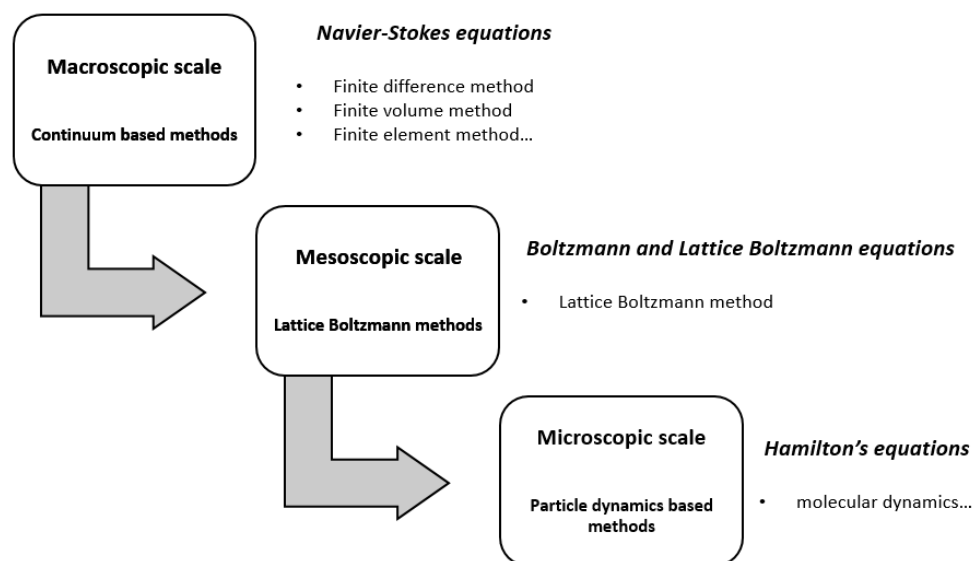
With a different approach but still using classical aerodynamic theory, Shi and Hendrickx [59] focused on the 2D echelon training of multi-agents seeking to maximize benefits according to their relative position in the group. Agents can either maximize their own benefits or optimize the group’s total benefit. As in many theoretical studies, a fixed-wing assumption was used. This method could, according to the authors, explain their failure to numerically reconstruct these migratory formations. By modeling the birds with fixed wings and ignoring the slow wave motion of the wings, the authors assume that wing flapping plays a more important role than expected. They also show that this type of formation may not emerge if bird behavior is guided solely by energy conservation. In addition, non-aerodynamic factors, such as collision avoidance and improved vision, could also contribute to the development of migratory formation.

### 3.2. Numerical Studies

Numerical studies of the aerodynamics and organization of birds in formation use computational models to simulate and comprehend the complex phenomena associated with formation flight. These models help researchers handle a range of variables and conditions to analyze how birds interact aerodynamically and organize their formation. These numerical studies help deepen our understanding of the aerodynamic mechanisms and organization of birds in formation flight, providing valuable information for the biology of flight and the design of nature-inspired drone systems. Among the methods used are the standard two-dimensional lattice Boltzmann method (LBM), computational fluid dynamics (CFD), including the vortex lattice method, and tools such as Matlab and Ptera software. As shown in Figure 8, the system of equations depends on the scale of modeling (microscopic, mesoscopic, or macroscopic).

Sewatkar et al. [60] used the two-dimensional lattice Boltzmann method (LBM) to solve the Navier-Stokes equations. The authors introduced a model for investigating the flow over cylinders placed in a V-formation, and drew a basic comparison with birds in flight. The impact of formation angle, spacing in the flow direction and number of cylinders on parameters such as the drag coefficient, lateral force coefficient and Strouhal number was investigated. The results indicated that reducing the formation angle resulted in lower drag, with the leading cylinder experiencing the lowest drag. This counter-intuitive finding contradicts the observations of other researchers, as the lead bird is generally the one that expends the most effort [7,37,61]. This increase in drag for the leader of a formation is generally accompanied by a decrease for athletes in the leader’s wake. This is what is observed in sports, where the principle of drafting stipulates that an athlete can benefit from the aerodynamic wake created by the athlete in front of him, while protecting himself against air resistance [30,62]. The simplicity of this study provided a basic understanding of some aspects of birds in flight in V-formation, revealing a trade-off between energy conservation and lateral forces. The results were in line with the positioning rules proposed

by previous studies for artificial birds in V-formation. Overall, the study offered insights into the forces exerted on birds in V-formation and their implications in energy conservation.

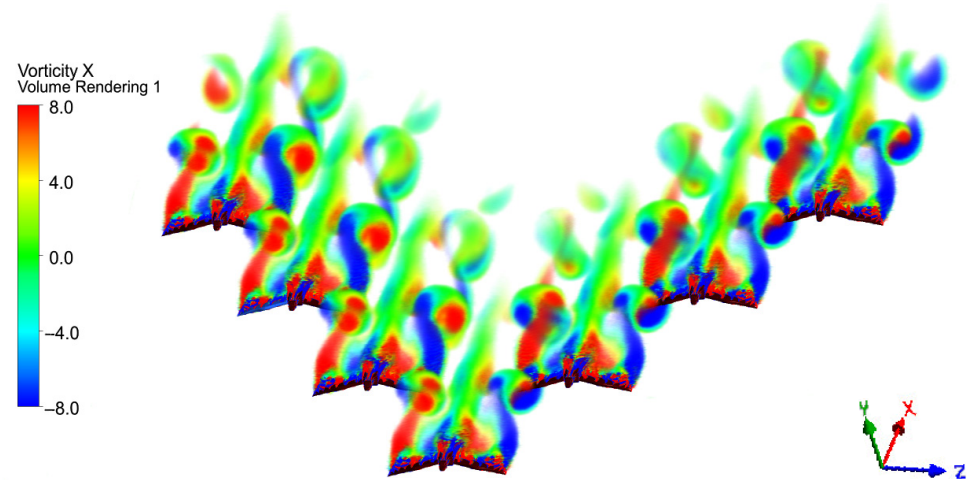


**Figure 8.** Unlike CFD methods that numerically solve the conservation equations for macroscopic properties (i.e., mass, momentum, and energy), LBM models the fluid as fictitious particles, and these particles undergo successive processes of propagation and collision on a discrete lattice.

Some studies are based on mathematical modeling and numerical simulation methods. This is the case of Klotsman and Tal's study [63], which presents an approach to animating flocks of birds flying according to line formation models. The method used distinguishes between the behavior of these flocks during initiation and their behavior during stable flight. A data-driven approach using an energy-saving model was proposed for animating stable flight. The authors showed that this problem could be formulated as a system of nonlinear equations and solved. The authors calculated the power reduction value for each bird in the flock. Using a mathematical model [36] which assumes a two-dimensional flock, with equal speeds and non-flapping wings. Although interesting, the initiation algorithm has several limitations, such as the inability to handle inverted shapes (such as inverted U's or V's) that exist in nature. The method, which is inspired by the actual position of birds within formations, offers interesting prospects, although it cannot, for the moment, model the flapping of bird wings.

Among the numerical approaches used to study the unsteady dynamics of flapping or fixed wings, computational fluid dynamics (CFD) is one of the most widely used. An example of the results obtained with the CFD method is shown in Figure 9. Maeng et al. [64] used this method to study the flight mechanics of the Canadian goose. A two-joint arm model was used to assess unsteady aerodynamic performance and estimate potential energy savings for geese during migration. The flow around a Canadian goose wing geometry was studied using a CFD code that implements the solution of the time-averaged Navier-Stokes equations (RANS). From the velocity and pressure distributions on the wing, the researchers found that modifying the wing morphology reduced the induced drag and saved around 15% energy. Analysis of the flow in the wing wake revealed that a pair of beneficial alternating three-dimensional flapping vortices (FAVs) were generated. A goose positioned behind could save around 19% of its energy during the wing's downward phase and 14% during the upward phase. The researchers deduced an optimum depth of around 4 m from the wingtip and an optimum spacing between wingtips ranging from 0 to −0.40 m. The differences in drag and lift coefficients between the different wing-flapping modes showed that the typical wing-flapping case was the most effective in terms of drag reduction, resulting in energy saving of around 16%, which is consistent with estimates

from the most recent studies [13,41,42] that estimated these energy saving values to range between 11.4 and 26.5%.



**Figure 9.** Example of numerical simulation result obtained using the RANS method. Visualization of the interaction of the vortex wake between birds in a V-formation using the volume rendering method. Results obtained by numerical simulations carried out by the authors of the present study.

Ghommem et al. [65] used the unsteady vortex lattice method (UVLM) to simulate the flight of flapping wings in formation. Their simulation considered the aerodynamic coupling between flapping wings and their interactions with wake vorticity. Motivated by field observations of migratory birds, the numerical analysis revealed that flying in a V-formation with optimal spacing led to a significant increase in lift and thrust, while saving energy costs. This improvement is explained by the inherent interaction between the following birds and the wake vorticity generated by the lead bird. The researchers also examined the effect of wake decay on the aerodynamic performance of flapping wings, reporting a limited influence on the generation of aerodynamic forces and power. It should be noted that the unsteady vortex lattice model (UVLM) does not account for viscous effects, and neglects wing deformability and fluid-structure interactions. This limitation limits its accuracy in modeling scenarios involving flow separation and high levels of interaction with the wing wake, introducing a potential risk of discrepancy between the results of this study and the true physical nature of this complex phenomenon. Vortex lattice methods (VLM) are often used in the early stages of aerodynamic studies because they calculate the flow around a wing with a rudimentary geometric definition. However, several authors have employed this method for advanced aerodynamic analyses. For example, Rubin et al. [66] used Ring and Horseshoe Vortex Lattice Methods to analyze the drag of wings arranged in a V-formation with different wingtip spacings. In addition, the authors 3D printed NACA 2412 airfoils and arranged them in a V-formation in a laminar flow water tunnel. They subsequently carried out Particle Image Velocimetry (PIV) measurements to study downwash and upwash flows. Theoretical investigations into drag reduction during formation flight were reviewed. It should be noted that in this study, analytical fluid dynamics was carried out with certain assumptions to model the aerodynamics of V-formation flight. In modeling the drag, the authors have assumed that the wings fly in a laminar flow regime (low Reynolds number). They also assumed that the flow pattern was incompressible and the air density constant. Furthermore, their study was carried out assuming that the downwash velocity of the wing was constant along the span, and that there was no turbulence in the wake. Despite these simplifying assumptions, the results of the numerical study are consistent with literature data showing that wing tip spacing (WTS) plays an important role in wing-induced drag. Their study shows that by increasing wingtip spacing over a certain distance, there is no change in drag coefficients, and maximum drag

coefficients occur when the trailing wings are positioned in the downwash region of the leading wing.

More recently, Billingsley et al. [67] have used the UVLM to investigate the combined effects of active bending, twisting and group organization on the aerodynamic performance of flapping wings. The UVLM model was used to assess the aerodynamic forces generated on flapping wings in V-shaped formations of three to five members. The study explored the effects of morphing on lift, thrust and power coefficients, as well as propulsive efficiency, demonstrating improvements in thrust and power coefficients in solo flight and in V-formation. The model used by Billingsley et al. employs active morphing in the UVLM-based solver. Unlike various numerical studies [61,64,68], the wing is not modeled as a rigid, non-deformable solid. Nevertheless, the study is based on the use of a rectangular-shaped wing, which generates a different wake from a complex-shaped bird's wing.

In a recent paper, Urban [69] used the open-source Ptera software (V2.0.0), which employs the unsteady vortex lattice method (UVLM) to analyze flapping wing V-formations. The author of the study validated the results with experimental data while demonstrating its ability to analyze simple ornithopters. A major limitation of this method is that the fluid is considered to be inviscid. In this scenario, the model does not take into account some aerodynamic phenomena such as flow separation, leading to some inaccuracies in the results. Nevertheless, this method, less commonly used to date, seems promising for simulating, in a simplified way, the organized flight of migratory bird flocks.

Different numerical methods can be used to study the aerodynamics of migratory birds, each having its own advantages and disadvantages. Among the most commonly used methods are the Lattice Boltzmann method and the CFD method. A comparison of these models for aerodynamic purposes was conducted in a recently published study [70].

Among the authors who have used the CFD method, we can mention Beaumont et al. [61]. They used CFD to determine the optimum position of gliding Canada geese within a V-shaped formation, taking into account the influence of wingtip spacing and depth (see Figure 6). A computational code based on the finite volume method was used to analyze the wake and three-dimensional vortex structures developing behind the birds. The results demonstrated that flying in formation could reduce energy expenditure by minimizing aerodynamic drag while improving lift. A significant finding suggested that wingtip spacing should be around  $-26$  cm to optimize aerodynamic efficiency. These results are quite close to previous estimates by Badgerow and Hainsworth [11], who suggested that maximum energy saving was obtained for a wingtip spacing of  $-16$  cm, while another study by Hainsworth [37] experimentally determined a median wingtip spacing of  $-19.8$  cm, and yet another study [38] reported a wingtip spacing of  $-33.7$  cm. It should be noted that this optimal position requires a lateral overlap of the birds' wingtips (see Figure 6) to achieve the best aerodynamic efficiency [11]. Seiler et al. [71] have shown that the spacing between the wingtips of leader and follower birds is highly variable, suggesting that tracking the lateral position of the preceding bird is a difficult task. The study by Beaumont et al. [61] also highlighted an imbalance of forces between the left and right wings of the second bird, which could be attributed to the interplay of wakes. This observation, although logical at first sight, does not seem to have been reported by other studies. Pressure distributions and vortex wake structures were also analyzed to understand aerodynamic dynamics, with the results suggesting that the lateral displacement of the birds in the V-formation influences aerodynamic efficiency and the forces exerted on each wing. As observed in the study by Maeng et al. [64], the numerical model incorporates certain limitations, such as the assumption of a rigid, non-deformable body to simulate the bird's wings. These simplifications can influence the results, underlining the need for meticulous validation of the numerical model.

We have explored various numerical methods, each with its own specific advantages and disadvantages. Let's not forget to mention the Boundary Element Method (BEM), which stands out for its ability to efficiently handle infinite domains. This method is particularly relevant in aerodynamic studies [72,73], where the domain of interest extends far beyond



the immediate vicinity of the wings or bodies under study. BEM reduces the dimensionality of the problem by focusing on the boundaries rather than the whole volume. This can lead to significant reductions in complexity and computation time, making this method a potentially more efficient option for simulating large-scale aerodynamic formations. The boundary element method is often more efficient than other methods, including finite elements, in terms of computational resources for problems characterized by a low surface-to-volume ratio. However, for many other problems, the BEM is significantly less efficient than volume discretization methods such as the finite element method, the finite difference method and the finite volume method.

#### 4. Conclusions

In recent decades, significant progress has been made in the understanding of bird formation flight. Theoretical studies have played a central role in elucidating the aerodynamic mechanisms of formation flight, laying the foundation for considering the benefits of birds migrating in groups. Pioneers such as Lissaman and Shollenberger [28] initiated in-depth discussions on the causes and advantages of formation flight, inspiring other researchers like Gould and Heppner [6] and Badgerow and Hainsworth [11]. Subsequently, the increasing influence of algorithm development and other mathematical modeling added a new dimension to this research, confirming the advantages of V-formation and prompting in-depth investigations into the associated energy savings and social dynamics of this flight behavior.

Technological advancements have opened new perspectives, allowing a thorough understanding of the formation flight behaviors in birds, ranging from their energy savings to sophisticated aerodynamic strategies. Weimerskirch et al. [13] and Portugal et al. [52] demonstrated the potential of wireless instrumentation to obtain real-time quantitative data on the physical and biological parameters of birds in flight. These studies converge towards a growing recognition of the complexity and variability of mechanisms governing formation flight across different avian species. Recently, computer techniques have been used to simulate and enhance the understanding of complex aerodynamic mechanisms associated with the formation flight of birds. Numerical models, aiming to replicate specific formations adopted by migratory birds in flight, integrate aerodynamic factors such as drag, lift, air resistance, and other forces influencing bird movement in flight. Ghomem et al. [65], and more recently, Billingsley et al. [67], used the unsteady vortex lattice method (UVLM) to simulate flapping-wing formation flight. Other authors, such as Maeng et al. [64] and Beaumont et al. [68], used computational fluid dynamics (CFD) to model the aerodynamic behavior of Canadian geese. The numerical modeling of bird flight often involves an interdisciplinary approach, integrating concepts from biology, aerodynamics, mathematics, and computer science. Despite these advancements, numerical modeling remains challenging due to the complexity of individual interactions and environmental factors. Researchers strive to improve model accuracy to best reflect the reality of formation flight. While numerical modeling represents a powerful and reliable tool for deepening the understanding of various issues, it is crucial to remain vigilant regarding the faithful representation of the physics of a phenomenon and the relevance of the obtained results to avoid misinterpretation.

Overall, experimental, theoretical, and numerical approaches complement each other. Experimental studies provide fundamental data, theoretical studies develop conceptual models, and numerical studies allow precise modeling. By combining these approaches, researchers can achieve a more comprehensive understanding of the aerodynamics of migratory birds. However, there are still many phenomena to understand given the complexity of flight physics of flapping birds. This literature review shows that much of the research remains largely theoretical, as experimentation on living animals is still in its infancy. The advent of numerical methods will undoubtedly enable increasingly precise modeling of the complex interactions in the wakes of migratory birds flying in formation. Nature has not yet revealed all its secrets. Currently, it seems feasible that with

collaboration between biologists, physicists, mathematicians, and computer scientists, a profound understanding of why birds fly in organized groups will soon be achieved.

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