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Energy savings and wake dynamics are conducive to position and flapping phase adaptation in bird formation flight

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Abstract

Formation flight can reduce the energetic cost of bird migration through interactions with the wakes of neighboring individuals. Yet how wake dynamics, flight stabilization and wingbeat synchronization jointly determine these benefits remains poorly understood. Here, through high-fidelity simulations of autonomous flapping flyers within a complex vortical flow, we unveil the links between flight dynamics and wake evolution in formation flight and quantify how relative position and wingbeat phase affect aerodynamic power. We find that followers achieve savings of up to 13.7% when flying approximately one wingspan downstream and laterally from the leader, with their wingbeat synchronized to the advected wake phase. Benefits arise primarily during the downstroke, when high lift production coincides with strong upwash induced by the leader’s downstroke vortices. Wake deformation progressively disrupts this alignment, reducing savings downstream for larger separation distances. Simulations of larger formations show that benefits are governed predominantly by pairwise leader-follower interactions, with additional neighbors contributing marginally. By linking wake evolution, flight control and power consumption, these results provide a physical basis for observed formation geometry and synchronization, bridge aerodynamic predictions and animal flight behavior, and establish a quantitative framework for studying collective locomotion in unsteady flows.

1 Introduction

Efficient locomotion is a fundamental challenge in both biological and engineered systems. Migratory birds, in particular, must minimize the energetic cost of transport during long-distance travel. Many species meet this challenge by flying in organized formations, enabling migratory flights over thousands of kilometers [1]. Formation flight has long been hypothesized to provide energetic advantages [2], and a growing body of experimental evidence supports a measurable reduction in metabolic rate for birds flying in formation [3, 4, 5, 6]. These aerodynamic benefits arise from interactions with the wakes generated by neighboring birds. Formation flight thus creates a highly structured flow environment, varying through time and space, and exposes followers to unsteady aerodynamic conditions. Despite a qualitative understanding and experimental confirmations, the mechanisms that link unsteady wake dynamics to actual reductions in flight power remain insufficiently understood, especially when considering the combined effects of positioning, wingbeat phasing and stabilizing efforts of followers.

The beneficial effect of formation flight can be understood from basic aerodynamic considerations. Aerodynamic forces are typically decomposed into lift and drag, respectively defined as the components normal and parallel to the relative air velocity. In steady, level flight, lift balances the flyer weight and thrust compensates the drag to maintain a constant velocity. An upward velocity component tilts the lift vector forward, effectively contributing to thrust. As a result, net drag is reduced, which lowers the required propulsive effort. The regions of upwash resulting from the lift force of a leader, and present on the sides of their wake, constitute an aerodynamic resource available to following birds flying in formation.

Previous work has contributed significantly to our understanding of formation flight, yet from perspectives that remain only partially connected. Early aerodynamical models based on fixed wing aerodynamics predicted substantial energy savings [2] and described their distribution within the formation [7]. Observations of natural formations have revealed consistent geometrical arrangements [8, 9] and wingbeat phasing [10], suggesting fine-tuned

aerodynamic interactions between individuals. At the same times, experimental studies have demonstrated reduced energetic cost in birds flying in formation using indirect proxies, such as heart rate [3, 5], flapping frequency [4, 5] or CO_2 production [6]. While those approaches demonstrate a reduction in flight power, their nature does not enable a proper quantification of the energy savings or a description of the flow mechanisms leading to them. Furthermore, the interactions between the three-dimensional position and phase of the follower and their impact on the power are difficult to capture, and the altitude readings of GPS trackers are not sufficiently resolved to observe the impact of small relative altitude shifts between individuals on their energy benefits [5].

Advances in computational fluid dynamics have enabled increasingly detailed simulations of formation aerodynamics. The possibilities offered by numerical investigations overcome the reliance on proxies that is inherent to experimental works. They also enable the quantification of aerodynamic forces, resolving the interactions between positioning and phase of the follower with the vortical wake of the leader, even for configurations that would not be naturally adopted by birds. Among the numerical contributions, Maeng *et al.* [11] used Reynolds-Averaged Navier–Stokes (RANS) simulations to examine the effect of phase and wing-tip spacing on energy gains. Tay *et al.* [12] resolved wakes at high fidelity and reported lift and thrust increases, Ghommem and Calo [13] simulated multi-bird formations using an Unsteady Vortex Lattice Method (UVLM) to model the wake, and Beaumont *et al.* [14] employed finite-volume CFD to estimate improvements in aerodynamic efficiency. However, these studies do not consider free flight for birds in formation, but maintain identical flight kinematics and fixed positions. Consequently, the lift and thrust of the follower are affected by the wake and no longer lead to a force equilibrium, while the aerodynamic adaptations required to stabilize the flight within a fluctuating wake are not captured. As a result, no existing framework simultaneously captures unsteady wake evolution, free-flight dynamics control, and aerodynamic power computation, leaving the mechanistic link between these elements unresolved.

Here, we address this gap through a holistic and high-fidelity numerical reproduction of the free-flight dynamics of flapping birds, their flight control through gait modifications, and the long spatio-temporal development of their unsteady wakes. This approach enables direct quantification of aerodynamic power while allowing followers to dynamically stabilize at prescribed positions relative to their leader. By systematically varying streamwise, lateral, and vertical offsets, as well as wingbeat phase, we explore the combined influence of spatial and temporal alignments with the wake on energy savings. This framework allows us to track the evolution of the wake over large distances, tackling the largely unexplored question of possible persistence of energy savings over large separation distances. Indeed, while birds are not observed flying in extended formations, aircraft can exploit wakes over large distances [15]. Understanding this difference between flapping birds and fixed-wing aircraft requires capturing the wake and its deformations over large distances. Finally, we extend our scope to larger flocks of birds, providing an unified framework for investigating formation aerodynamics in flapping flight.

Our results show that optimal energy savings arise from a precise alignment of the follower with the leader’s tip-vortex system, occurring approximately one wingspan downstream, at a lateral offset close to one span, and an altitude difference corresponding to the downward displacement of the wake. These gains are maximized when the follower synchronizes its wingbeat with the advected phase of the wake, such that its downstroke coincides with regions of strongest upwash. The benefits are inherently unsteady, being concentrated during the downstroke, and diminish with downstream distance as wake deformation reduces the overlap between the vortex structures and the follower’s wing motion. Extending the analysis to larger formations, we find that energy savings are primarily governed by pairwise vortex interactions, and interior birds benefit from having both multiple leaders ahead of them and followers behind.

Taken together, these results provide a mechanistic framework linking unsteady aerodynamics, flight control, and energetic performance in formation flight. Beyond explaining observed positioning and synchronization strategies in birds, and contributing to our understanding of the energetics behind long distance migrations [16], this work offers insights for the design of energy-efficient aerial systems and coordinated swarms operating in unsteady flow environments.

2 Results

2.1 Unsteady wake topology and induced upwash of a single flapping bird

We first characterize the unsteady wake generated by a single freely flying bird, as this structure defines the unsteady aerodynamic environment experienced by any follower.

Our numerical framework reproduces flapping flight by coupling a biomechanical model of the bird skeleton, an aerodynamic representation of the wings, a high-fidelity solver for the unsteady wake, and a closed-loop controller stabilizing flight through biologically relevant adaptations of the wing kinematics. This simulates stabilized flight of birds and track the evolution of their wakes over long distances. The bird model replicates a Northern Bald Ibis (*Geronticus eremita*), with span $b = 1.35$ m in steady, level flight at a speed $U_\infty = 15 \text{ ms}^{-1}$. The bird flaps its wings with a constant frequency $f = 4 \text{ Hz}$ (thus the wingbeat period $T = 1/f = 0.25 \text{ s}$). Figure 1 introduces the coordinate system and complementary flow visualizations: instantaneous vorticity fields reveal the evolving wake topology (panel (A)), while period-averaged vertical velocity fields isolate the regions of upwash that could benefit a follower (panel (B)). The video "single_bird_wake.gif" in Supplementary Materials shows the evolution of the wake of a single bird.

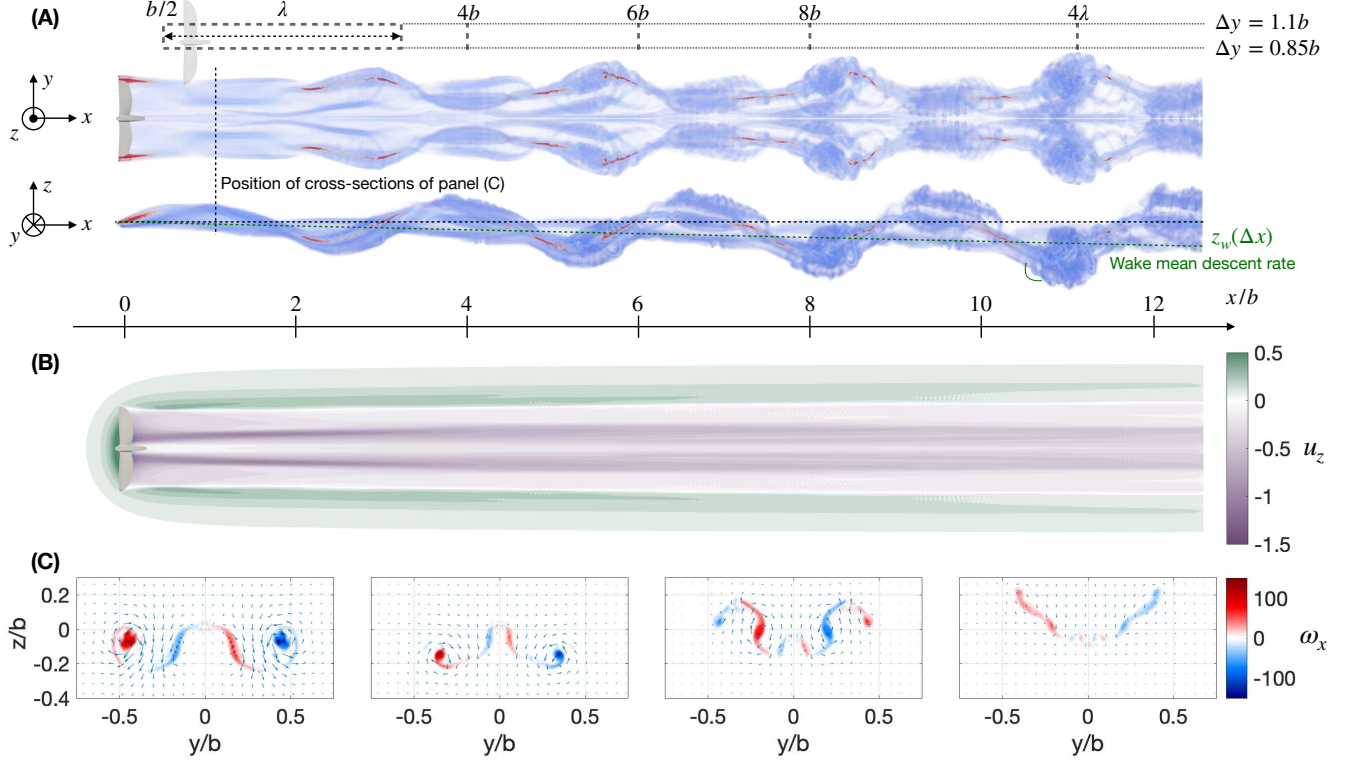


Figure 1: Wake of a freely flying bird. (A) Instantaneous vorticity magnitude (top and side views) highlighting the wake topology, with blue to red indicating increasing vorticity magnitude; candidate follower positions are marked in the top view. With a first volume of one wavelength of the wake (λ) and four subsequent positions at various number of wingspans (b). (B) Contours of period-averaged vertical velocity u_z in a plane tilted by the wake-descent angle, showing regions of upwash (green) and downwash (purple). (C) Streamwise vorticity ω_x and in-plane velocity vectors one wingspan downstream at four wingbeat phases (0%, 25%, 50%, 75% – 0% being mid-downstroke), illustrating the temporal and spatial modulation of the tip-vortex system.

Over each wingbeat, the wings shed a continuous vortex sheet whose strength reflects spanwise and temporal variations of the wing-bound circulation. The largest gradients occur near the wingtips during the downstroke, leading to the formation of strong tip-vortex structures one wake wavelength ($\lambda = U_\infty/f = U_\infty T$) downstream. The instantaneous streamwise vorticity fields of Fig. 1(C) show coherent vortices in both the tip and mid-wing regions. During the upstroke, root, mid-wing, and tip vortices of opposite sign are generated as the outboard wing produces negative lift while the inboard section maintains positive lift. Because circulation varies smoothly over the wingbeat, these structures remain connected in time, often linking upstroke and downstroke vortices across successive phases.

The wake is also advected downward under the influence of its self-induced velocity. We characterize this effect with a linearized mean descent slope of the vortices a_w , such that $z_w(\Delta x) = z_{leader} + a_w \Delta x$ is the vertical position of the wake at a distance Δx from the leader, as represented in green in Fig. 1(A). To estimate a_w , we fit a plane

to the vertical loci of the maximum upwash measured in each x-y position in the mean wake. The value obtained through this process is $a_w = -0.02137$.

The time-averaged vorticity field resembles a horseshoe-like configuration, combining the wing-bound vorticity and the trailing vortex system. This structure induces updraft in a limited region upstream of the bound vortex and in an extended area on the sides of the wake downstream of the bird (Fig. 1(B)). Though the positive velocities upstream of the bird indicate that a bird flying in front would get some benefit, and thus that the leader can save some energy in a formation, we will focus our analysis on the point of view of a follower and on positions downstream in the wake. In the lateral regions, the upwash reaches a local maximum, then decays as one moves downstream. Two mechanisms shape this pattern. First, idealized vortices of constant core size would produce a monotonic asymptotic growth of the upwash with downstream distance, as predicted by the Biot–Savart law. Second, actual viscous diffusion, roll-up, and interactions with spanwise structures increase the effective vortex-core radius, reducing the upwash farther aft. The interplay of these effects creates a local maximum in average upwash approximately one span downstream and half a span laterally from the bird’s center—a location suggestive of optimal exploitation by a follower.

Because lift is generated by flapping wings and both vortices and kinematics are unsteady, a purely time-averaged perspective is insufficient to capture the rich dynamical structure of the wake. Strong upwash gradients near the tip-vortex position mean that local, time-dependent interactions dominate the aerodynamic benefit experienced by a follower. Figure 1(C) therefore presents instantaneous wake cross-sections one wingspan downstream at four phases of the wingbeat (0%, 25%, 50%, and 75%), highlighting the oscillatory nature of the tip vortices and the dynamic environment encountered by a trailing bird.

Together, these wake characteristics define a spatially and temporally structured upwash field whose local maxima and strong gradients suggest that optimal exploitation depends sensitively on the follower’s lateral placement, vertical alignment (relative altitude), and relative phasing with respect to the advected wake—motivating the systematic exploration presented next.

2.2 Follower positioning and phase alignment for optimal wake exploitation

We next quantify how a follower’s relative position and wingbeat phase determine the reduction in aerodynamic power it experiences within the leader’s wake.

Two freely flying birds are simulated, each stabilized by a closed-loop controller displaying biologically relevant dynamics. The video "two_birds_wake.gif" in Supplementary Materials shows the near wake of a pair of birds in free flight. The follower’s configuration is parameterized by its relative position with respect to the leader and its phase. We define the streamwise (Δx) and lateral (Δy) offsets relative to the leader’s position. To account for the leader’s intrinsic wake descent, the vertical position of the follower z_{follower} is compared to the local position of the vortices $z_w(\Delta x)$. The vertical offset Δz is thus corrected with

$$\Delta z_w = z_{\text{follower}} - z_w(\Delta x) = z_{\text{follower}} - (z_{\text{leader}} + a_w \Delta x) = \Delta z - a_w \Delta x ,$$

where Δz is the uncorrected vertical offset between leader and follower. The relative displacements coordinates are illustrated in Fig. 2.

In a similar fashion, the phase offset of the follower $\Delta \phi_w$ is considered relatively to the advected leader phase $\phi_w(\Delta x)$. It corresponds to the phase of the leader’s gait right at the instant it flew through the current follower location, now at a distance Δx . It is thus computed as

$$\phi_w(\Delta x) = \phi_{\text{leader}} - \frac{2\pi \Delta x}{\lambda} .$$

Following Portugal’s hypothesis [10] that birds synchronize with the *advected leader phase* ϕ_w . We consider a follower–wake phase difference, defined as

$$\Delta \phi_w = \phi_{\text{follower}} - \phi_w = \phi_{\text{follower}} - \phi_{\text{leader}} + \frac{2\pi \Delta x}{\lambda} = \Delta \phi + \frac{2\pi \Delta x}{\lambda} .$$

After stabilization, the follower’s aerodynamic power is averaged over one wingbeat

$$\bar{P} = \frac{1}{T} \int_{t-T}^t P(t') dt' ,$$

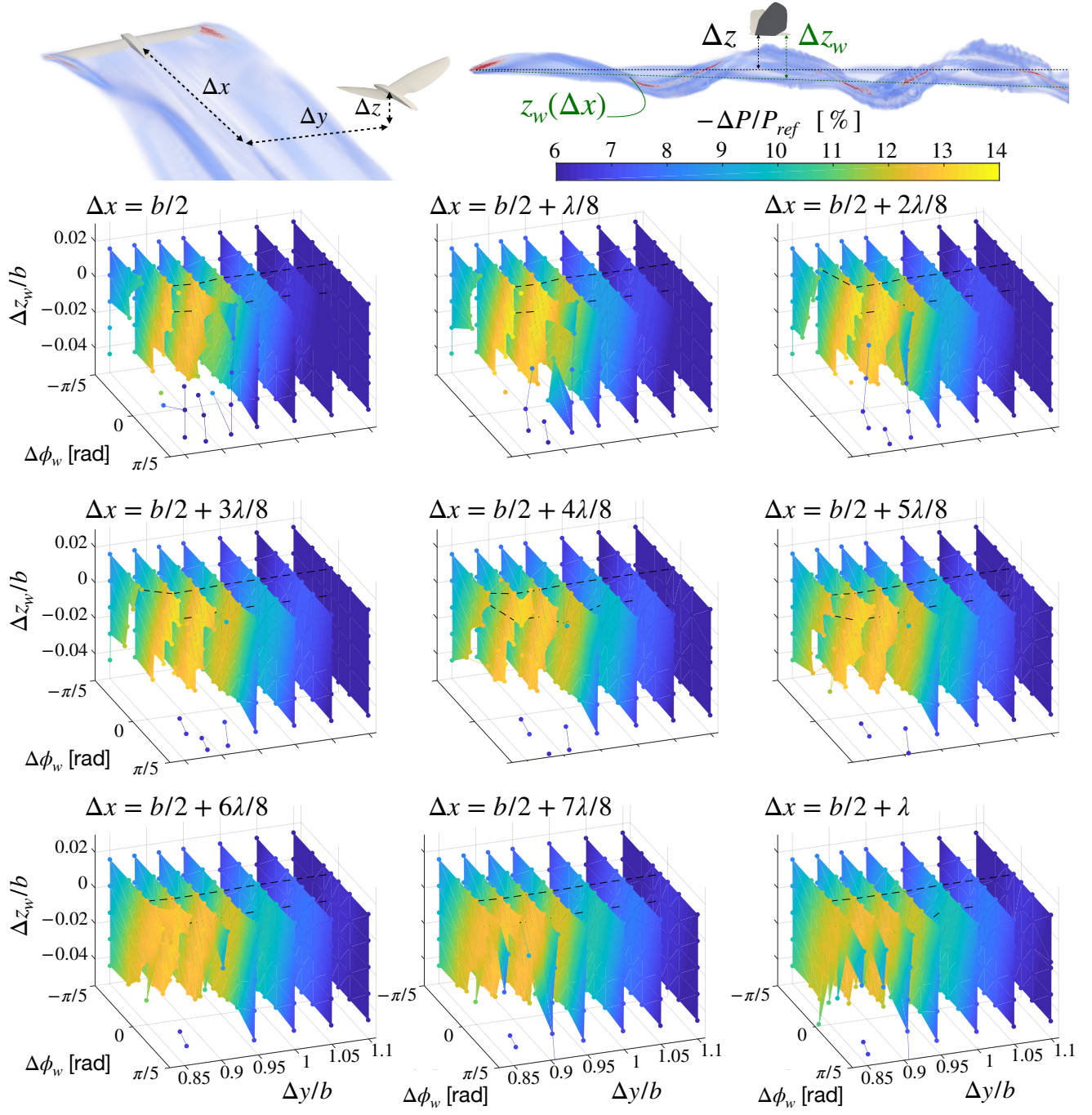


Figure 2: **Reduction of flight power across the 4-D parameter space.** The top panels illustrate the different variables for the positioning of the follower, namely the streamwise separation Δx , the lateral offset Δy and the vertical offset Δz_w . The top right panel shows the difference between the raw vertical offset Δz , and Δz_w , which is corrected for the mean descent rate of the vortices $z_w(\Delta x)$. Each subfigure corresponds to a fixed streamwise separation Δx within the primary sampling volume ($\Delta x \in [b/2, b/2 + \lambda]$). Within a subfigure, each plane corresponds to a lateral offset $\Delta y/b \in \{0.85, 0.883, 0.917, 0.95, 1.00, 1.05, 1.10\}$; axes are vertical offset (Δz_w) versus phase offset ($\Delta \phi_w$) relative to the *advected* wake at that Δx . Missing points indicate configurations that did not stabilize within 40 s. Dashed lines denote loci extracted for the Δx - Δy contour analysis in Fig. 4.

and compared against the reference from a single flyer P_{ref}

$$\Delta P = \bar{P} - P_{\text{ref}} .$$

Configurations that did not stabilize within 40 s of simulation are excluded from the analyses. The parameter space was sampled from $\Delta x = b/2$ to $b/2 + \lambda$ with additional planes at $\Delta x \in \{4b, 6b, 8b, 4\lambda\}$, totaling 2205 configurations in the primary sampling region. The tested positions are marked in Fig. 1 and reported in Table 2.

Stabilization and proximity to tip vortices. Figure 2 shows the power savings across all stabilized configurations in the first sampling volume. Stabilization is highly sensitive to Δy : many configurations near the wake centerline ($\Delta y/b \in [0.85, 0.917]$) fail to stabilize, particularly when the follower’s phase aligns with the local wake ($\Delta\phi_w \approx 0$). In this regime the follower’s wingtip intersects the leader’s tip-vortex cores, where sharp velocity gradients induce strong force fluctuations. As Δx increases, stabilization improves because wake diffusion enlarges the vortex-core radius and reduces these gradients. Although controller performance contributes to the precise stability limits, the underlying mechanism—vorticity-induced force variability—is physically robust.

Power-saving structure across the 4-D space. Savings are largest at moderate lateral offsets and steadily decline beyond $\Delta y \approx 0.92b$. At smaller Δx , a consistent local maximum emerges at $\Delta y/b \approx 0.883$, rather than at the closest available offset, reflecting the geometry of the tip-vortex-induced upwash. As Δx increases, these maxima initially strengthen, then weaken, while gradients in ΔP diminish—indicating greater positional robustness farther downstream. Each Δy -plane contains a region of maximum benefit centered on $\Delta\phi_w \approx 0$ and $\Delta z_w \approx 0$. These regions form tilted ellipses in the $(\Delta z_w, \Delta\phi_w)$ plane, revealing a compensatory mechanism: phase lead or lag partially offsets vertical misalignment. Followers positioned slightly above the mean wake benefit from a small phase advance, while those slightly below benefit from a phase delay. As illustrated in Fig. 3, such combinations allow the follower’s wingtip to track the leader’s downstroke tip vortex—the period of strongest circulation—throughout its own downstroke. This alignment concentrates the aerodynamic benefit during the follower’s downstroke, when its wing produces the most lift and the upwash most effectively tilts the lift vector forward.

Dependence on streamwise and lateral offsets. Contours in Fig. 4 reveal that, when Δz_w and $\Delta\phi_w$ are fixed near their per-plane optima, savings peak at a streamwise separation of roughly one wingspan, with lateral placement exerting a larger influence than streamwise offset. At $\Delta z_w = 0$, small Δy configurations near the centerline often fail to stabilize; at $\Delta z_w = 0.015b$, the maximum savings occur near $\Delta y \approx 0.9b$. Positions too far inboard place a portion of the follower’s wing in downwash, degrading the benefit. As Δx increases, the contours flatten, indicating increased robustness. Additionally, when the follower is positioned further laterally, the optimal streamwise separation shifts downstream; along $\Delta y = b$, savings increase modestly with Δx .

Optimal configurations and decay of benefit. For each streamwise offset Δx , we identified the $(\Delta y, \Delta z_w, \Delta\phi_w)$ configuration yielding the lowest power consumption (Fig. 5). A clear optimum emerges near one span behind the leader, laterally at $\approx 0.88b$, slightly above the advected wake, and in slight phase advance. Beyond this position, optimal savings gradually decline with Δx . The optimal lateral offset increases with distance as the wake widens, the optimal vertical position follows the mean wake descent, and the optimal phase remains close to the advected wake phase. Wake visualizations reveal why the benefit decays: near the leader, tip vortices follow trajectories close to the wingtips, enabling sustained exploitation. Farther downstream, inner vortices roll-up and merge with the tip vortex, along with spanwise vortical structures resulting from time variations of the wing circulation. The resulting deformations of the wake reduce overlap with the follower’s wingtip motion. Time-resolved power traces confirm that while peak downstroke savings remain similar across distances, the shortening of the saving window with Δx reduces the period-averaged benefit.

2.3 Scaling to multi-bird formations: distribution of aerodynamic benefits

We finally examine how wake-exploitation benefits distribute across larger formations.

To isolate group-level effects while avoiding stabilization issues near the strongest tip vortices, all birds are assigned a single, robust configuration relative to their direct predecessor, i.e. $\Delta x = 0.89b$, $\Delta y = 0.95b$, $\Delta z_w = 0$,

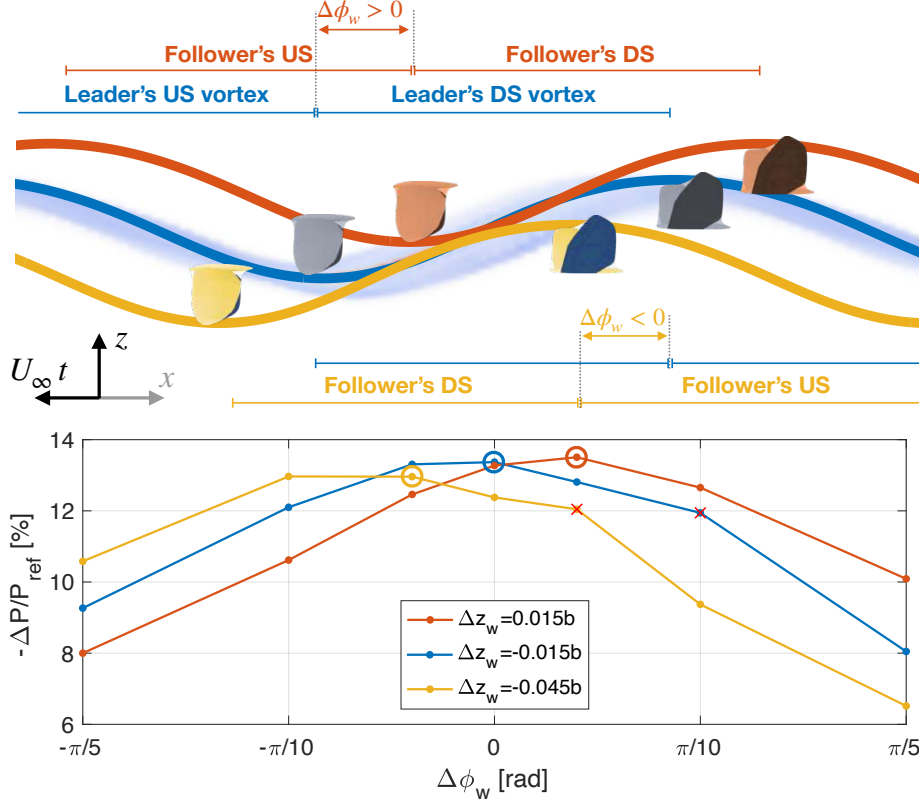


Figure 3: **Phase–height compensation and downstroke-dominated savings.** Top: schematic showing how phase lead/lag can compensate height offsets. A follower above the mean wake ($\Delta z_w > 0$) with positive $\Delta\phi_w$ keeps its wingtip near the leader’s downstroke tip vortex during its own downstroke; conversely for $\Delta z_w < 0$ with negative $\Delta\phi_w$. The axes of the schematic correspond to time (multiplied by flight speed U_∞) and vertical position, as the follower is at a quasi-fixed streamwise position. Time increases from right to left and is aligned with x for visualization. DS/US denote downstroke/upstroke. Bottom: savings versus phase for three heights at $\Delta x = 0.85b$ and $\Delta y = 0.92b$, showing plateau-like benefits when the wingtip tracks the downstroke vortex and confirming that most gains accrue during the follower’s downstroke.

$\Delta\phi_w = 0$. While this position is not the optimum for energy savings of a single follower, it induces a more robust stabilization, pending only slightly lower power benefits. The video "five_birds_wake.gif", in Supplementary Materials, shows the wake of a formation of five free-flying birds after stabilization in this configuration. For any pair of birds, we use *inboard* for the direction toward the center of the pair and *outboard* for the direction facing outward. We simulate echelon formations ranging from 2 to 6 birds and compute period-averaged power relative to solo flight; we then extend to an 11-bird echelon and a 21-bird V-formation to examine the influence of a second branch, as represented in Fig. 6.

Echelon formations (results and mechanism). Across 2–6 birds in echelon, savings increase systematically with position along the line, except for the last bird, which gains less because it lacks a follower which would induce vertical velocities in front of it (Fig. 6(A)). The underlying mechanism is a *cancellation-dominated superposition*. For two successive birds in the formation, the inboard vortices of the pair induce velocities that partially cancel each other. Their contribution to the vertical velocity induced at the location of another follower in the formation is thus negligible. What remains is a *two-term balance*: (i) an upwash from the outboard tip vortex of the direct predecessor (closest and dominant) and (ii) a weak downwash from the formation leader’s opposite-side outboard tip vortex acting at large lateral/streamwise separation. Because this residual downwash decays with lateral distance, its influence weakens with rank. The net savings thus increase asymptotically for further followers, competing with the absence of followers for the last birds of the formation. A small benefit is also observed for the leader, consistent with upwash induced immediately ahead of the followers.

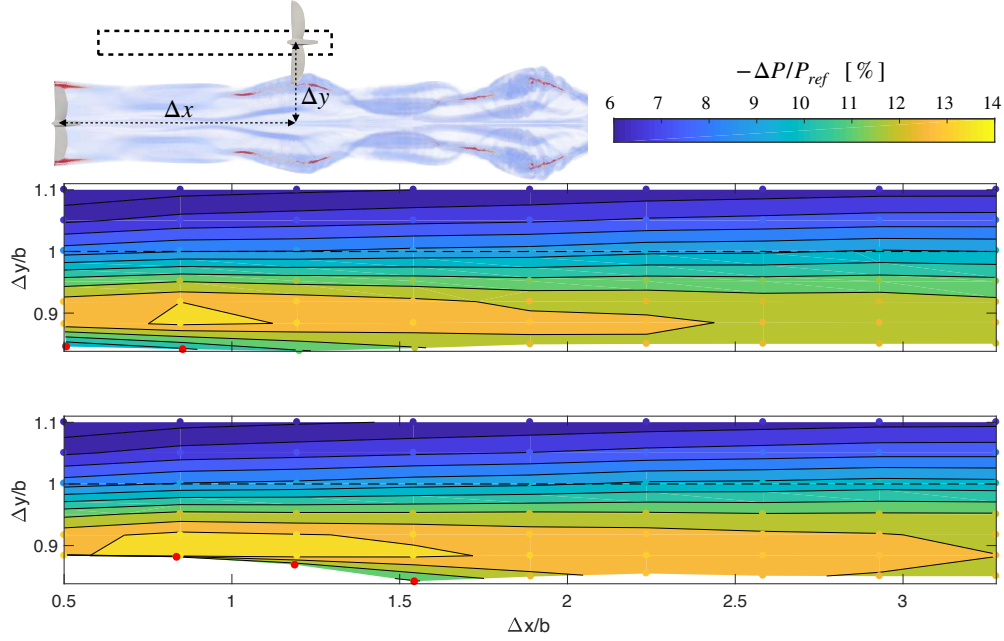


Figure 4: **Savings versus streamwise and lateral separation at fixed height and phase.** Contours of power reduction as functions of Δx and Δy for two settings near the per-plane optimum: (top) $\Delta z_w = 0.015b$ with $\Delta\phi_w = 0$; (bottom) $\Delta z_w = 0$ with $\Delta\phi_w = 0$. Red markers denote points not fully stabilized (values shown with caution). The dashed line on the contours highlights the tip-to-tip configuration ($\Delta y = b$). The dashed box in the illustration above situates the x-y range of the measurements to scale with the leader’s wake. Savings peak near one span downstream and are more sensitive to lateral than streamwise placement; gradients are steeper at smaller Δx , indicating greater robustness downstream.

V-formation versus single-branch echelon. The same cancellation logic applies when a second branch is introduced. For a given rank, the residual downwash term at a follower’s position now comes from the outboard-most tip vortex on the opposite branch, compared to the outboard vortex of the formation leader in the echelon formation. For birds in the front of the V formation, the outboard vortex is situated at a large lateral distance and induces a weaker downwash as a result. Consequently, early ranks in the V-formation exhibit modestly higher savings than their single-branch echelon counterparts (Fig. 6(B)). As rank increases, the branches diverge laterally and the opposite-branch contribution becomes negligible relative to the direct predecessor–follower interaction within the same branch.

Synthesis. Benefits in multi-bird formations are therefore governed by a pairwise-cancellation mechanism with a simple residual structure: followers exploit the direct predecessor’s outboard tip vortex, while the only meaningful opposing contribution, a far-field downwash from the formation leader (or opposite branch), weakens with distance and geometry. This clarifies why echelon and V geometries concentrate energy savings toward interior ranks and why V-formations offer slightly larger gains in the first rows.

3 Discussion

Wake structure and deformations

The wake structure obtained in our simulations is comparable to experimental observations of bird wakes in laboratory environments. Such a comparison was previously performed in [17]. Tip vortices as a main feature correspond to most observations [18, 19, 20], and previous works have also identified root [19, 20, 21] and spanwise vortices [22, 23].

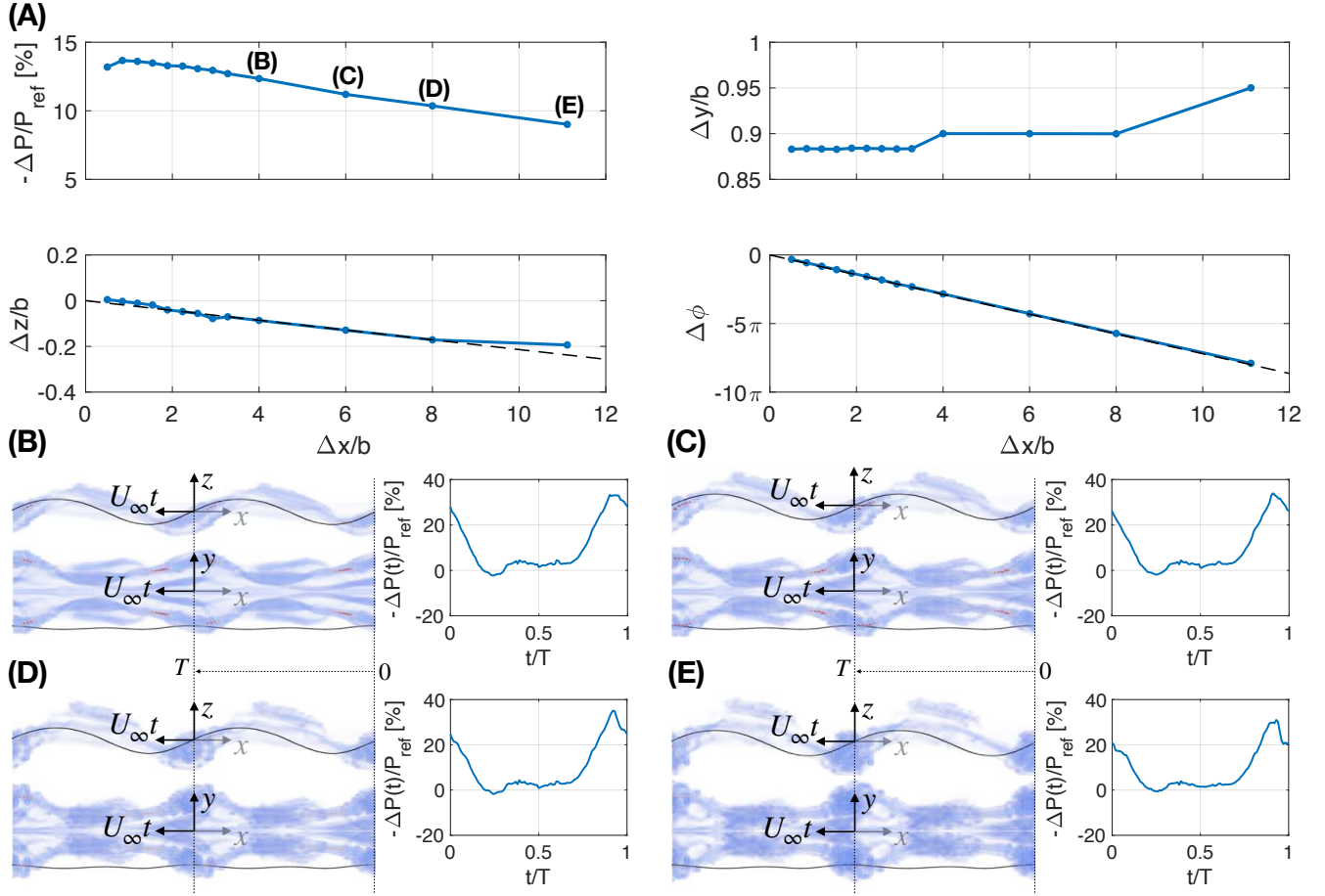


Figure 5: Best attainable savings versus distance and wake-evolution effects. Minimum period-averaged power (relative to solo flight) and corresponding optimal configurations as functions of Δx . The optimal lateral offset Δy increases with distance (widening wake), optimal height Δz follows the mean wake descent $z_w(\Delta x)$ (dashed), and optimal phase $\Delta \phi$ remains close to the advected phase $-2\pi\Delta x/\lambda$ (dashed). Volume renderings (panels B–E) at $\Delta x = 4b, 6b, 8b, 4\lambda$ show the follower’s wingtip trajectory superimposed on the wake. As in Fig. 3, the horizontal axis corresponds to time multiplied by the flight speed U_∞ and is aligned with $-x$. Adjacent traces of $\Delta P(t)$ demonstrate that peak downstroke reductions remain similar, but the duration of the saving window shrinks with Δx , reducing the period average.

Averaging the wake upwash over a flapping period (Fig. 1(B)) delivers valuable predictions. When simulating the flight of a follower and integrating its instantaneous power savings, a maximum benefit is achieved at a streamwise separation distance corresponding to the local maximum of the average upwash (Fig. 5(A)). Laterally, the follower positions itself in such a way that its wing tip does not enter the regions of downwash in the leader’s wake. This indicates that maximizing upwash leads to a minimization of flight power for the follower.

Wake deformations are linked to decays in energy savings for larger streamwise separation distances. The tip vortices change shape following their self-induction and the absorption of spanwise vorticity present in the wake (Fig. 1(A)). As a result, the spatio-temporal window during which the wingtip of a follower remains close to the region of maximal upwash becomes narrower at further positions, and the average reduction in power is reduced (Fig. 5). This phenomenon is characteristic of flapping wing wakes, and is not observed for fixed wings, which enables extended formation flight with large separation distances [15]. It is worth noting that our framework uses a laminar inflow without turbulence. While atmospheric perturbations will have a relatively low impact on the vortical structure of the near wake, they will exacerbate the wake deformations and further reduce the potential savings at large separation distances. Our simulations thus provide a *best-case* scenario for wake exploitation at large distances, yet still demonstrate a clear decay of savings.

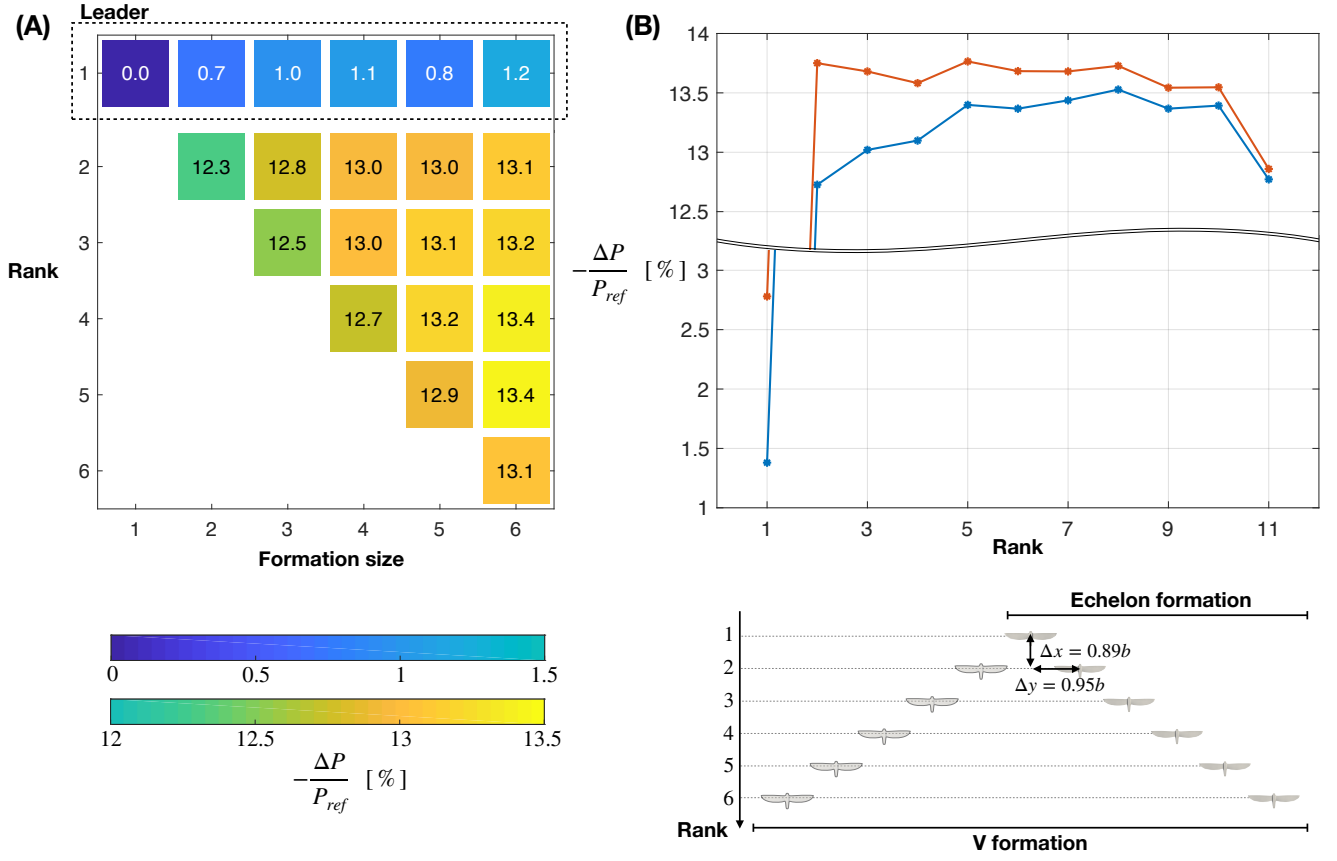


Figure 6: **Distribution of power savings in larger formations.** (A) Echelon formations with 2–6 birds: period-averaged power reduction (relative to solo flight) as a function of position in the line. Savings generally increase with rank (except for the last bird, which gains less because it lacks a follower) and formation size for a given rank. Even the leader displays a small benefit that grows with formation size due to induced upwash ahead of followers. (B) Comparison between a 21-bird V-formation (red) and an 11-bird echelon (blue): the upwash induced by the other branch in the V yields additional savings in the first few rows, diminishing with rank as the branch spacing increases. V- and echelon formations are defined, (the echelon being a single branch of the V), as well as relative spacing between successive birds.

Follower position and configuration

By simulating the flight of two free-flying birds in formation, we analyze the configuration of the follower and the impact of position and phase on the energy savings. The maximum amount of power that can be saved by the follower is found to be 13.7%. This value is comparable with previous findings in flapping flight, whether experimental (11.4–14% observed in Pelicans [3]) or numerical (14–19% in [11]). It is also of the same order as energy savings for fixed-wing formation flight [24, 25], which is remarkable given the unsteady nature of the flow induced by flapping wings as compared to fixed ones.

Regarding the variations of energy savings with the follower’s position, we find that the position maximizing the gains is at a spanwise position of about 0.9 spans, which corresponds to predictions based on simplified models [2] and real-life observations [10]. We also confirm the observation of [10], where followers synchronize their wingbeat to the *advected* phase of the leader. In our results, such a phase shift maximizes the power that can be saved from the wake exploitation. We further notice that most of the savings are obtained during the downstroke of the follower. This is demonstrated by the interactions between the phase and the vertical offset to maintain high levels of energy extraction (Fig. 3) and the traces of instantaneous savings (Fig. 5(B-E)). Our results indicate that the physical reasoning for the phase adaptation goes further than path coherence. The vortices corresponding to the downstroke of the leader have a higher circulation and induce more upwash on the follower. Given that the drag reduction comes from a forward-tilt of the lift vector proportional to the upwash, combining moments of high lift

in regions of high upwash leads to maximal savings, and this is what we observe in our results.

The maximum savings being observed in the close vicinity of the tip vortices, the follower finds itself close to regions where stabilization is challenging. While the observed stabilization issues may come from our controller implementation, the strong gradients of velocity near the tip vortices are faithful to bird wakes and are expected to create instabilities regardless of the controller. Furthermore, the power savings vary more steeply in the vicinity of the global maximum than further in the downstream or spanwise direction (Fig. 4). These observations indicate that there should be a trade-off between seeking maximum wake exploitation or obtaining a smaller but more robust benefit.

As stated above, the implementation of the flight controller is one limitation of our framework. It failed to stabilize the follower in some regions of the wake, which prevented us from mapping the energy savings when a significant portion of the wing enters the wake vortices. However, we did capture an increase of flight power at the closest spanwise positions (Fig. 2), and we can assume that the gains decrease further as the follower approaches the wake. While an improved controller could lead to stable flight in these regions, the lack of stabilization is a result in itself. The strong velocity gradients pose an obstacle to maintaining a fixed position for our simulated bird, and we can expect this to be the case for real birds as well. Another limitation linked to the controller is that we used a single strategy to adapt the wingbeats kinematics and compensate for rolling and yawing moments induced by the wake. Other adaptations could lead to changes in our results, for example if the follower adapts the trajectory of its wingtip to follow the tip vortices of the leader, thereby increasing exploitation at further downstream distance. The physical origin of the savings (forward-tilt of the lift vector in upwash) is however independent of the controller and thus remains valid.

Large formations

Our results show the variation in savings between different formation sizes and between individuals within a given formation (Fig. 6). To ensure stability for all birds in the formation, we perform other simulations with a more robust relative positioning, although with lesser wake exploitation. The marginal increase of gains towards the later ranks of the formation corresponds to theoretical predictions made for fixed wings in [7]. They result from the horseshoe structure of the wake vortices, and the oscillatory nature of the wake does not play a combined role with the size of the formation. The reduction of savings at the last ranks of the formation was also predicted in [7]. In our results, we notice that an individual benefits from flying in a larger group, independently of its rank. Though birds participating in formations might also be motivated by social factors or predator evasion, aerodynamics are sufficient to explain the emergence of large V-shaped or echelon formations and the observed relative positions between individuals.

The results of the comparison between echelon and V formations can be explained by the same mechanisms, with equivalent horseshoe vortices that partially cancel each other and the birds at the front of the formation benefiting from the opposite branch. Similar results were predicted in [7]. However, we obtain higher gains for the second rank than later ones within the V formation. This result cannot be interpreted with the same mechanical principle, and its origin is uncertain. Since the difference in power reduction between successive birds is relatively low, it could be linked to positioning errors of the free-flying birds. At the end of the simulation when the power is evaluated, some individual birds are stabilized at a slightly offset vertical and lateral period-averaged position (of $\approx 10^{-3}$ spans), and all birds in the simulation naturally oscillate around their mean position under their unsteady force production (amplitude of the oscillations of $\approx 10^{-2}$ spans). The combination of these displacements could lead to slight variations in power, given the steep gradient of the energy savings in the vicinity of the leader's wake.

Conclusions

Taken together, our results explain how the evolution of the wake and the kinematics of the follower jointly govern the energetic benefits of formation flight in flapping birds. By combining controlled free-flight with a high-fidelity wake model, this study bridges the gap between idealized aerodynamic predictions and observations of real bird formations. The simulations show that the commonly observed lateral spacing and phase synchronization of followers coincide with maximal wake exploitation, which emerge from alignment of the follower's downstroke with the leader's downstroke tip vortices. At the same time, the progressive deformation of flapping-wing wakes imposes a fundamental limitation on extended formation flight, explaining why large separation distances—common in fixed-wing formations—are not exploited by birds. Extending the analysis to larger formations further reveals

how pairwise wake interactions and vortex cancellation shape the distribution of benefits within the flock, favoring interior positions while still providing a small advantage to leaders.

Beyond supporting existing biological hypotheses with quantitative aerodynamic evidence, this paper presents a mechanistic framework for interpreting formation geometry in birds. This establishes a basis for investigating how animals interact with and exploit complex flow environments. Future studies could incorporate environmental turbulence, heterogeneous individuals, sensory feedback, or adaptive control strategies to examine how robust formation flight emerges under natural conditions. The insights gained from these biological systems may also inspire new control strategies for autonomous aerial swarms, in which coordinated vehicles actively exploit unsteady aerodynamic interactions to improve endurance, efficiency, and collective performance.

4 Methods

4.1 Numerical model of a flapping bird

The analysis of formation flight is performed using a numerical model of a flapping bird. The present framework, described extensively in [26], is based on the coupling of a multibody model of a bird with articulated wings with a fluid solver using a vortex particle-mesh method. The first model handles the motion of the bird and its wings and the fluid solver computes the aerodynamic forces produced during flight, and computes the flow in the wake of the birds.

In the present application, the model is used to represent the formation flight of Northern Bald Ibises (*Geronticus Eremita*). The modeled birds are all identical and have mass of 1.2 kg. The formation flies at a velocity $U_\infty = 15 \text{ m s}^{-1}$, and the birds flap their wings at a frequency $f = 4 \text{ s}^{-1}$. The wavelength of the wake is thus $\lambda = U_\infty/f = 3.75 \text{ m}$. The span mid-downstroke is $b = 1.35 \text{ m}$, the mean aerodynamic chord of the birds is $\bar{c} = 0.18 \text{ m}$ and the Reynolds number is thus defined as $Re = U_\infty \bar{c}/\nu = 1.8 \cdot 10^5$ where $\nu = 1.48 \cdot 10^{-5} \text{ m}^2 \text{ s}^{-1}$ is the kinematic viscosity of air. The flapping amplitude of the birds is variable and, as it depends on it, the Strouhal is not constant. For a representative flapping amplitude of 26 degrees about the shoulder joint, the Strouhal number based on the vertical displacement of the wingtip is $St = 0.149$.

Figure 7 pictures the various models used to represent the bird in the simulation, and a photograph of the Ibis to provide a point of comparison. Panels of this figure will be further used to support the description of these models throughout this section.

Multibody model of a bird

Each bird in the simulations is modeled in a multibody framework as a rigid body and two articulated wings, as in [26]. The wing skeleton is composed of three rigid segments corresponding to the main bones of the wing, as represented in panels (A) and (B) in Fig. 7. Representative *control-feathers* are attached to these bones to represent the plumage. Their motion is governed by the aerodynamic forces, elastic joints at their attachment points, and spring-like elements linking each feather with its neighbors.

The dynamics of the skeleton and feathers are handled by the multi-body solver ROBOTRAN [27]. A local frame is defined after each joint rotation, in which the subsequent rotation angle is defined. In our model, the shoulder joint has three rotations, the elbow is rotating about the local z axis only, and the wrist rotates about three successive orthogonal axes.

Bird aerodynamics

The aerodynamic forces acting on the birds are computed using an Immersed Lifting and Dragging Line method (ILDL)[28]. That is, the aerodynamic properties of the wing are gathered on a single line immersed in the fluid, and the forces are computed at multiple points of this line based on the 2D airfoil at the location, and the local flow conditions. The values of lift and drag are obtained through lookup of the coefficients in previously obtained polar data. In this case, the coefficients are those of an AS6092 airfoil [29]. It is a bird-like airfoil, and its polar is available in [29], where it is computed using XFOIL [30].

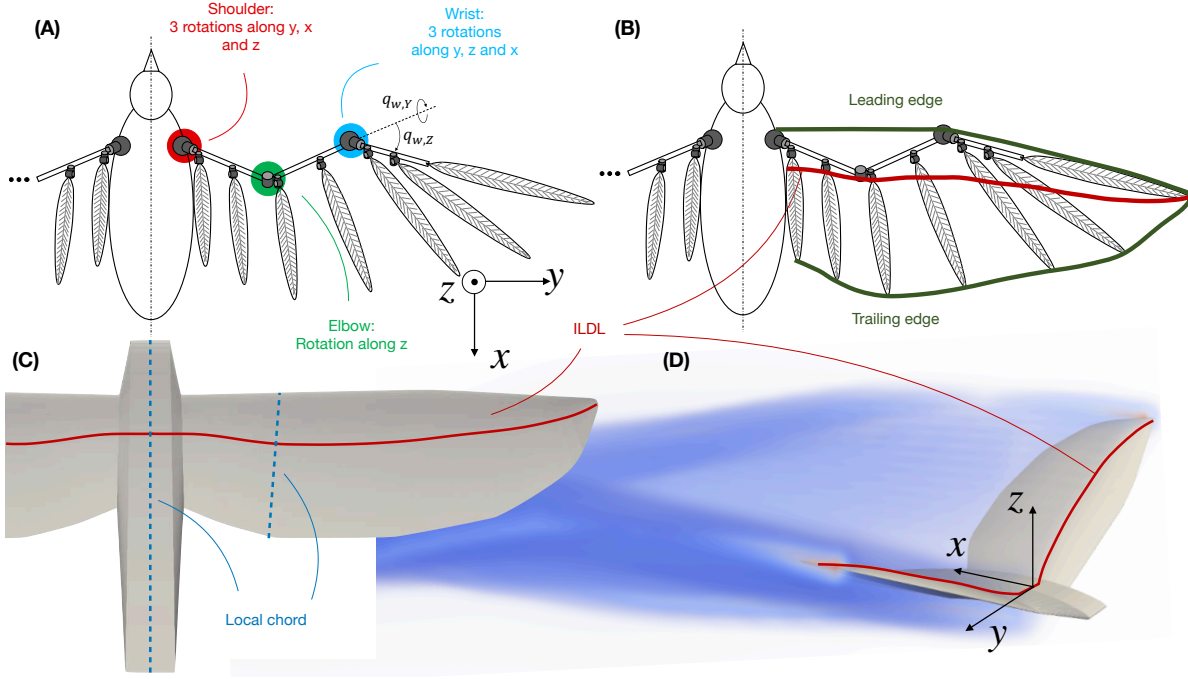


Figure 7: **Various models are used to capture the bird in the simulation framework.** (A) bio-mechanical model of the skeleton and feathers, with the actuated joints being highlighted and two rotations of the wrist being represented as examples. (B) Immersed Lifting and Dragging Line (ILD) obtained in a particular configuration. (C) final planform represented in the fluid solver. (D) Simulated bird and its near wake, where red to blue indicates increasing values of the norm of the vorticity field. This figure is adapted from the methodological framework presented in [17].

As in [26, 17], the position of this line is obtained from the current position of the bones and feathers embodied into the bio-mechanical model. As shown in Fig. 7(B), the leading edge of the wing is defined as the line starting from the shoulder, going straight to the wrist joint (thus following the propatagial tendon), and then following the hand segment and the last primary feather. The trailing edge links the tip of the feathers, from the last secondary (the closest to the body), to the last primary (at the wingtip). The ILDL is then defined as the line passing through the quarter of the local chord, i.e. the line connecting the leading and trailing edges, at each point along the wing, and normal to the chord.

The ILDL includes the body-tail ensemble of the bird, where the chord length is set to the length of the bird body. The aerodynamic performance of the airfoil between the wings degraded in terms of lift-to-drag ratio. The lift coefficient value obtained from the polar is divided by 3 in the simulations, while keeping the same drag coefficient. This value roughly corresponds to the increase of chord length between the wing root and the body, and thus reduces the spanwise variation of the circulation at that location. This value is arbitrary, but avoids the shedding of too strong vortices at the wing root, and has little effect on the aerodynamics of the wings, which contribute the most to the total forces.

Solving the unsteady wake flow

The incompressible Navier-Stokes equations are solved in their vorticity-velocity ($\omega - \mathbf{u}$) formulation in the vicinity and the wake of the birds, using a hybrid vortex particle-mesh method [31, 28, 26]. The vorticity field is represented through discrete particles advected using the velocity field. The differential operations in the vorticity equation, and the Poisson equation used to obtain the velocity field are solved on a Cartesian grid, hence the coupled approach. The information is passed back and forth between the particles and the grid through high order interpolation schemes. This is achieved using the PPM library [32].

The mesh is also used to *reset* the particles on grid points every 5 timesteps to prevent clustering or depletion of particles in some areas. Finally, particle discretization does not ensure that the vorticity field remains divergence-

free. To prevent errors related to this, a reprojection operation is performed on the vorticity field every 20 timesteps. Both of these operations are described in details in [31].

The ILDL representing the bird acts as a source of vorticity in the fluid solver and vortical structures related to the production of lift and drag are shed from it. Vortex particles are emitted to represent the shedding due to both the variations of circulation along the line and through time. In addition, vortex dipoles are shed to represent the signature of drag in the wake. More detail on these methodological aspects can be found in [28]. Panel (D) of Fig. 7 shows the intensity of the vorticity field behind the ILDL of a representative simulation scenario of a single bird.

The momentum in the wake has been confirmed to correspond to the actual aerodynamic forces produced by a simulated bird in [26, 17], and for fixed wings in [28]. The model used to simulate the wing aerodynamics, the shedding of vorticity and the wake evolution has been compared to experimental data in the challenging case of rotorcraft in [33], where the aerodynamic forces and their variations with the control parameters of the rotor were accurately modeled. The coupled bio-mechanical and aerodynamic model used to simulate bird flight have been compared to reference results regarding flight power in [26], and regarding the wake structure of a flapping bird in [17].

Power computations

The simulation framework allows multiple ways to compute the power consumption of the bird. The chosen method in this paper is to compute the aerodynamic power. We obtain it from the ILDL, by multiplying the local force at each point of the line with its velocity in a ground-fixed frame. This corresponds to the energy flux from the wing to the fluid. Since the velocity of the points of the line results from a combination of the flight speed of the bird (almost aligned with the x axis) and smaller velocities due to the flapping motion, the main contribution to the power comes from the multiplication of this velocity and the drag component of the aerodynamic force. The drag being always positive, the power is also always positive at each point of the line. Given that the actuation of the bird model is done with imposed kinematics of the wing skeleton, considering the aerodynamic power does not require us to make assumption about how the joint moments are generated. The aerodynamic power computed here represents the minimum power that has to be produced by the bird, independently on the type of actuation.

When considering power savings, we choose to represent them as $-\Delta P/P_{\text{ref}}$, with P_{ref} being the power of a bird flying alone, and $\Delta P = P - P_{\text{ref}}$. The minus sign ensures that $-\Delta P$ remains positive in case of energy savings.

Flight controller

The multibody model of the birds' wings are actuated by imposing the kinematics of the skeletal model. Each joint angle q_i follows a sinusoidal trajectory with an offset average and with a single constant frequency f equal to the wingbeat frequency. This results in three parameters – the mean angle $q_{0,i}$, the amplitude of oscillations A_i and the initial phase of the sine ϕ_i – and thus $q_i(t) = q_{0,i} + A_i \sin(2\pi ft + \phi_i)$. All parameters were adjusted in order to resemble bird kinematics measured experimentally in [34], then adjusted for the current species [26]. The resulting default values of each parameter are reported in Table 1.

Joint	Shoulder Y	Shoulder X	Shoulder Z	Elbow Z	Wrist Y	Wrist Z	Wrist X
$q_{0,i}$ [deg]	0.63 ⁽¹⁾	0	−9.59 ⁽¹⁾	16.67	0 ⁽²⁾	−16.67	0
A_i [deg]	2.14 ⁽¹⁾	22.22 ⁽¹⁾	11.11	16.67	1.85 ⁽²⁾	16.67	0
$\phi_{0,i}$ [rad]	$-\pi/2$	0	$\pi/2$	$-\pi/2$	$-\pi/2$	$\pi/2$	−

Table 1: Kinematic parameters used in the simulations for the right wing. The left wing is symmetrical. Superscripts (1) indicate parameters that are adjusted for the longitudinal stabilization and superscripts (2) indicate parameters adjusted asymmetrically for the lateral stabilization.

To stabilize the flight, some of these parameters are actually closed-loop controlled. Although many combinations are possible, the chosen parameters governing flight control are the flapping amplitude ($A_{s,X}$, impacting thrust), the wing pitch ($q_{0,s,Y}$, impacting lift), the pitching oscillations of the wing ($A_{s,Y}$, impacting thrust), the sweep

($q_{0,s,Z}$, impacting pitching moment), the distal wing twist ($q_{0,w,Y}$, impacting rolling moment when asymmetrical) and the oscillations of distal wing twist ($A_{w,Y}$, impacting yawing moment when asymmetrical).

The control strategy is summarized as follows. The velocity of the bird is controlled so that it reaches a moving point, and adopts the velocity of its target (known *a priori*). Forces along the x and z axes as well as moments about x (rolling), y (pitching) and z (yawing) are generated by variations in the wing kinematics, and lateral forces (along y) are achieved by flying with a non-zero bank angle (i.e. a rotation along the x axis, which gives a sideways component to the lift force). The values of the kinematic parameters are obtained through a linearization of their effect on the forces. Inverting these linear relationships provides us with combination of kinematics that output a force along a single axis. The reference forces to be produced are obtained as the output of P, PI or PID controllers, depending on the degree of freedom. Detailed explanations of the development of the controllers are provided in a dedicated document provided as Supplementary Material, and a similar controller was used in [26].

4.2 Simulations setup

In the volume, we consider 9 equally spaced streamwise positions, 7 lateral positions ($\Delta y/b = 0.85, 0.883, 0.917, 0.95, 1, 1.05$ and 1.1), 5 relative vertical positions equally spaced between $\Delta z_w = -0.06$ m and 0.02 m, and 7 relative phase differences $\Delta\phi_w = -0.2\pi, -0.1\pi, -0.04\pi, 0, 0.04\pi, 0.1\pi$ and 0.2π . This amounts in total to 2205 tested configurations. In the subsequent streamwise positions, we consider 7 lateral positions ($\Delta y/b = 0.85, 0.875, 0.9, 0.95, 1, 1.05$ and 1.1), 5 vertical positions equally spaced between $\Delta z_w = -0.09$ m and 0.03 m, and 9 relative phases ($\Delta\phi_w = -0.3\pi, -0.2\pi, -0.1\pi, -0.04\pi, 0, 0.04\pi, 0.1\pi, 0.2\pi$ and 0.3π). For the final position at $\Delta x = 4\lambda$, we add two additional vertical positions at $\Delta z_w = 0.06$ m and 0.09 m after finding minimum power at an edge position. Table 2 summarizes the tested configurations.

Variable	Number of tested values	Values
Large volume		
Δx	9	$b/2 + \{0, 0.125, 0.25, 0.375, 0.5, 0.625, 0.75, 0.875, 1\} \lambda$
Δy	7	$\{0.85, 0.883, 0.917, 0.95, 1, 1.05, 1.1\} b$
Δz_w	5	$\{-0.06, -0.04, -0.02, 0, 0.02\}$ [m]
$\Delta\phi_w$	7	$\{-0.2\pi, -0.1\pi, -0.04\pi, 0, 0.04\pi, 0.1\pi, 0.2\pi\}$ [rad]
First three planes		
Δx	3	$\{4, 6, 8\} b$
Δy	7	$\{0.85, 0.875, 0.9, 0.95, 1, 1.05, 1.1\} b$
Δz_w	5	$\{-0.09, -0.06, -0.03, 0, 0.03\}$ [m]
$\Delta\phi_w$	9	$\{-0.3\pi, -0.2\pi, -0.1\pi, -0.04\pi, 0, 0.04\pi, 0.1\pi, 0.2\pi, 0.3\pi\}$ [rad]
Last plane		
Δx	1	4λ
Δy	7	$\{0.85, 0.875, 0.9, 0.95, 1, 1.05, 1.1\} b$
Δz_w	7	$\{-0.09, -0.06, -0.03, 0, 0.03, 0.06, 0.09\}$ [m]
$\Delta\phi_w$	9	$\{-0.2\pi, -0.1\pi, -0.04\pi, 0, 0.04\pi, 0.1\pi, 0.2\pi\}$ [rad]

Table 2: Values considered for the relative position and phase of the following bird relative to the leader.

For all simulations, the leader is initially positioned at $(x, y, z) = (0, 0, 0)$, and its controller maintains it on average in that position. The follower is initially positioned at its target location, relatively to the leader, and then controlled to stay there on average over the wingbeat period. In the first second of the simulation, both birds are artificially fixed so that the wakes can develop. They are then freed and the controller stabilizes the birds at their target positions. The power calculations are performed after 40 seconds, if stable flight is achieved.

References

- [1] Robert E Gill Jr, T Lee Tibbitts, David C Douglas, Colleen M Handel, Daniel M Mulcahy, Jon C Gottschalck, Nils Warnock, Brian J McCaffery, Philip F Battley, and Theunis Piersma. Extreme endurance flights by landbirds crossing the pacific ocean: ecological corridor rather than barrier? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 276(1656):447–457, 2008.
- [2] P.B.S. Lissaman and Carl A. Shollenberger. Formation flight of birds. *Science*, 168(3934):1003–1005, 1970.
- [3] Henri Weimerskirch, Julien Martin, Yannick Clerquin, Peggy Alexandre, and Sarka Jiraskova. Energy saving in flight formation. *Nature*, 413(6857):697–698, 2001.
- [4] Helena Wehner, Johannes Fritz, and Bernhard Voelkl. Soaring and intermittent flap-gliding during migratory flights of northern bald ibis. *Journal of Ornithology*, pages 1–11, 2022.
- [5] Elisa Perinot, Ortal Mizrahy Rewald, Johannes Fritz, Marco Salvatore Nobile, Alexei Vyssotski, Thomas Ruf, Leonida Fusani, and Bernhard Voelkl. Small energy benefits of in-wake flying in long-duration migratory flights. *Proceedings of the Royal Society B: Biological Sciences*, 291(2030):20241173, 2024.
- [6] Sonja I. Friman, Cory R. Elowe, Siyang Hao, Laura Mendez, Raul Ayala, Ian Brown, Caylan Hagood, Yseult Hedlund, Dayna Jackson, Justin Killi, Gabriella Orfanides, Evrim Ozcan, Jared Ramirez, Alexander R. Gerson, Kenneth S. Breuer, and Tyson L. Hedrick. It pays to follow the leader: Metabolic cost of flight is lower for trailing birds in small groups. *Proceedings of the National Academy of Sciences*, 121(26):e2319971121, 2024.
- [7] Dietrich Hummel. Aerodynamic aspects of formation flight in birds. *Journal of Theoretical Biology*, 104(3):321–347, 1983.
- [8] C. J. Cutts and J. R. Speakman. Energy savings in formation flight of pink-footed geese. *The Journal of Experimental Biology*, 189(1):251–261, 1994.
- [9] Aaron J Corcoran and Tyson L Hedrick. Compound-v formations in shorebird flocks. *eLife*, 8:e45071, 2019.
- [10] Steven J. Portugal, Tatjana Y. Hubel, Johannes Fritz, Stefanie Heese, Daniela Trobe, Bernhard Voelkl, Stephen Hailes, Alan M. Wilson, and James R. Usherwood. Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature*, 505(7483):399–402, 01 2014.
- [11] Joo-Sung Maeng, Jae-Hyung Park, Seong-Min Jang, and Seog-Young Han. A modeling approach to energy savings of flying canada geese using computational fluid dynamics. *Journal of Theoretical Biology*, 320:76–85, 2013.
- [12] Wee-Beng Tay, Kishen Raj Murugaya, Woei-Leong Chan, and Boo-Cheong Khoo. Numerical simulation of flapping wing mavs in v-formation. *Journal of Bionic Engineering*, 16(2):264–280, 2019.
- [13] M. Ghommem and V.M. Calo. Flapping wings in line formation flight: a computational analysis. *The Aeronautical Journal*, 118(1203):485–501, 2014.
- [14] Fabien Beaumont, Sébastien Murer, Fabien Bogard, and Guillaume Polidori. Aerodynamic mechanisms behind energy efficiency in migratory bird formations. *Physics of Fluids*, 37(2), 2025.
- [15] Andrew Ning, Tristan C Flanzer, and Ilan M Kroo. Aerodynamic performance of extended formation flight. *Journal of Aircraft*, 48(3):855–865, 2011.
- [16] Theunis Piersma, Jr Gill, Robert E, Daniel R Ruthrauff, Christopher G Guglielmo, Jesse R Conklin, and Colleen M Handel. The pacific as the world’s greatest theater of bird migration: Extreme flights spark questions about physiological capabilities, behavior, and the evolution of migratory pathways. *Ornithology*, 139(2):ukab086, 2022.
- [17] Victor Colognesi, Philippe Chatelain, and Renaud Ronsse. Numerical assessment of wake-based estimation of instantaneous lift in flapping flight of large birds. *PLoS One*, 18(5):e0284714, 2023.
- [18] G. R. Spedding. The wake of a kestrel (*falco tinnunculus*) in flapping flight. *Journal of Experimental Biology*, 127(1):59, 01 1987.

- [19] L. C. Johansson and A. Hedenström. The vortex wake of blackcaps (*Sylvia atricapilla* l.) measured using high-speed digital particle image velocimetry (dpiv). *Journal of Experimental Biology*, 212(20):3365–3376, 2009.
- [20] P. Henningsson, F. T. Mujires, and A. Hedenström. Time-resolved vortex wake of a common swift flying over a range of flight speeds. *Journal of The Royal Society Interface*, 8(59):807–816, 2010.
- [21] Florian T. Muijres, L. Christoffer Johansson, Melissa S. Bowlin, York Winter, and Anders Hedenström. Comparing aerodynamic efficiency in birds and bats suggests better flight performance in birds. *PloS one*, 7(5):e37335, 2012.
- [22] GR Spedding, Mikael Rosén, and Anders Hedenström. A family of vortex wakes generated by a thrush nightingale in free flight in a wind tunnel over its entire natural range of flight speeds. *Journal of experimental biology*, 206(14):2313–2344, 2003.
- [23] L Christoffer Johansson, Masateru Maeda, Per Henningsson, and Anders Hedenström. Mechanical power curve measured in the wake of pied flycatchers indicates modulation of parasite power across flight speeds. *Journal of The Royal Society Interface*, 15(138):20170814, 2018.
- [24] Dietrich Hummel. Formation flight as an energy-saving mechanism. *Israel Journal of Zoology*, 41(3):261–278, 1995.
- [25] Curtis E Hanson, Joe Pahle, James R Reynolds, Stephanie Andrade, and Nelson Brown. Experimental measurements of fuel savings during aircraft wake surfing. In *2018 Atmospheric Flight Mechanics Conference*, page 3560, 2018.
- [26] Victor Colognesi, Renaud Ronsse, and Philippe Chatelain. Model coupling biomechanics and fluid dynamics for the simulation of controlled flapping flight. *Bioinspiration & Biomimetics*, 16(2), jan 2021.
- [27] Nicolas Docquier, Antoine Poncelet, and Paul Fiset. Robotran: a powerful symbolic generator of multibody models. *Mechanical Sciences*, 4(1):199–219, 2013.
- [28] Denis-Gabriel Caprace, Grégoire Winckelmans, and Philippe Chatelain. An immersed lifting and dragging line model for the vortex particle-mesh method. *Theoretical and Computational Fluid Dynamics*, 34:21–48, 2020.
- [29] Gavin K. Ananda and Michael S. Selig. Design of bird-like airfoils. In *2018 AIAA Aerospace Sciences Meeting*, page 0310, 2018.
- [30] Mark Drela. Xfoil: An analysis and design system for low reynolds number airfoils. In *Low Reynolds number aerodynamics*, pages 1–12. Springer, 1989.
- [31] Philippe Chatelain, Alessandro Curioni, Michael Bergdorf, Diego Rossinelli, Wanda Andreoni, and Petros Koumoutsakos. Billion vortex particle Direct Numerical Simulations of aircraft wakes. *Computer Methods in Applied Mechanics and Engineering*, 197(13):1296–1304, Feb 2008.
- [32] I. F. Sbalzarini, J. H. Walther, M. Bergdorf, S. E. Hieber, E. M. Kotsalis, and P. Koumoutsakos. PPM A highly efficient parallel particle mesh library for the simulation of continuum systems. *J. Comput. Phys.*, 215:566–588, jul 2006.
- [33] Denis-Gabriel Caprace, Philippe Chatelain, and Grégoire Winckelmans. Wakes of rotorcraft in advancing flight: A large eddy simulation study. *Physics of Fluids*, 32(8):087107, 2020.
- [34] Bret W. Tobalske and Kenneth P. Dial. Flight kinematics of the black-billed magpies and pigeons over a wide range of speeds. *The Journal of Experimental Biology*, 199(2):263–280, 1996.

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