



It pays to follow the leader: Metabolic cost of flight is lower for trailing birds in small groups

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Many bird species commonly aggregate in flocks for reasons ranging from predator defense to navigation. Available evidence suggests that certain types of flocks—the V and echelon formations of large birds—may provide a benefit that reduces the aerodynamic cost of flight, whereas cluster flocks typical of smaller birds may increase flight costs. However, metabolic flight costs have not been directly measured in any of these group flight contexts [Zhang and Lauder, *J. Exp. Biol.* 226, jeb245617 (2023)]. Here, we measured the energetic benefits of flight in small groups of two or three birds and the requirements for realizing those benefits, using metabolic energy expenditure and flight position measurements from European Starlings flying in a wind tunnel. The starlings continuously varied their relative position during flights but adopted a V formation motif on average, with a modal spanwise and streamwise spacing of [0.81, 0.91] wingspans. As measured via CO₂ production, flight costs for follower birds were significantly reduced compared to their individual solo flight benchmarks. However, followers with more positional variability with respect to leaders did less well, even increasing their costs above solo flight. Thus, we directly demonstrate energetic costs and benefits for group flight followers in an experimental context amenable to further investigation of the underlying aerodynamics, wake interactions, and bird characteristics that produce these metabolic effects.

locomotion | collective behavior | energy | biomechanics | formation

The coordinated group movement of animals has long engaged popular attention and elicited scientific investigation along many paths of inquiry (1–4). In birds, the possibility of energy savings in group flight has often been raised (5–8), especially in the context of the V, echelon, or line formations where the wingtip vortices shed by the upstream bird are hypothesized to reduce the cost of producing lift for downstream birds. Studies using on-animal loggers measuring biomechanical (9) and physiological (10) correlates of energy expenditure in large birds flying in V formation support such savings but none have directly measured metabolic energy use. Furthermore, studies of biomechanical correlates to energy use by smaller birds in less organized flocks suggest group flight comes with an added energetic cost (11, 12). Thus, the scope of costs or benefits of group flight, or even collective locomotion in general (13), and the requirements for realizing them remain uncertain and the subject of continued research.

Investigations into the possible energy savings achieved in group flight have proceeded along a variety of different fronts. Many studies in this domain begin and end with mathematical or computational models (5, 6, 14, 15), while others combine models with observational data (7, 16–18), or data from sensors placed on freely behaving birds (9–12). Strikingly, despite the long history of using animal flight wind tunnels to investigate bird flight physiology and aerodynamics (19–22), few studies have used such apparatus to study group flight (23). A wind-tunnel-based experimental context offers clear advantages in quantifying many aspects of group flight behavior, from positioning to energy expenditure and aerodynamics. However, the paucity of prior results leaves uncertain what flight modes birds might adopt during group wind tunnel flights. Thus, we first sought to determine whether groups of birds flying in a wind tunnel adopt preferred formations or follow any structuring rules analogous to those seen in nature. Additionally, we used metabolic measurements to quantify the costs of flight, to examine whether flying in a small group of two or three birds affects flight cost and if so, whether it does so in a beneficial or detrimental manner. Specifically, we hypothesized that if birds adopted a follower position consistent with V formation flight, they would save energy relative to their solo

Significance

Our work addresses long-standing questions in bird flight and collective movement through measurements of starlings flying in groups of two or three birds in the controlled environment of an animal flight wind tunnel. During their dynamic group flight behavior, follower birds tended to fly on average with a characteristic offset behind the leader bird, consistent with the V-shaped formation alignment observed in migratory bird flight. Significant energetic cost savings were realized when the follower maintained this characteristic offset. Furthermore, leaders typically had lower solo flight costs than their companions and lower flapping frequencies, while birds with higher flapping frequencies stayed in better alignment as followers.

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flight costs. Finally, we examined whether solo flight costs relate to how individual birds fly when in these small groups.

To address these questions, we repeatedly flew 14 European Starlings (*Sturnus vulgaris*) in a closed-circuit animal flight wind tunnel (Fig. 1A). Birds flew solo, in pairs, and in groups of three. The wind tunnel working section measured 1.2 m wide $\times$ 1.2 m high $\times$ 2.8 m long, compared to the approximately 34 cm tip-to-tip wingspan of the starlings, affording the birds sufficient room to position themselves in a variety of possible configurations while still avoiding direct physical interactions. The birds' flight position in the wind tunnel was continuously recorded by four machine vision cameras operating at 25 Hz. The birds were also equipped with inertial measurement unit (IMU) backpacks that recorded three-axis accelerations at 200 Hz and uniquely identified the birds in the camera recordings via a colored LED attached to the backpacks. We quantified the metabolic energy expenditure of the birds during flight by measuring the washout rate of isotopically labeled $^{13}\text{CO}_2$ delivered as an injection of ^{13}C -labeled sodium bicarbonate just prior to flight (Fig. 2A and [SI Appendix, Fig. S1](#)). In total, we recorded 121 individual flights and 80 metabolic

measurements across the different birds and conditions. Only one metabolic measurement could be taken at a time, and so when two or more birds flew as a group, metabolic expenditure was only measured for one bird, while flight positioning data were collected for all.

Results

Positioning with Respect to Neighbors. We found that starlings' position in the wind tunnel was dynamic during both solo and group flights, with their position in the wind tunnel reference frame and position relative to other birds changing over time (Fig. 1B). For each video frame in the group flight recordings, we categorized the birds as either a "Leader" (the single most upstream bird), or as a "Follower" if they were 1) downstream of another bird, 2) within 1/2 wingspan of that bird in vertical position, and 3) within five wingspans of that bird in total distance. If the bird did not meet either the Leader or Follower criteria it was classified as "Other" (6% of the total group flight time). In some cases, Leader and Follower designations were conserved

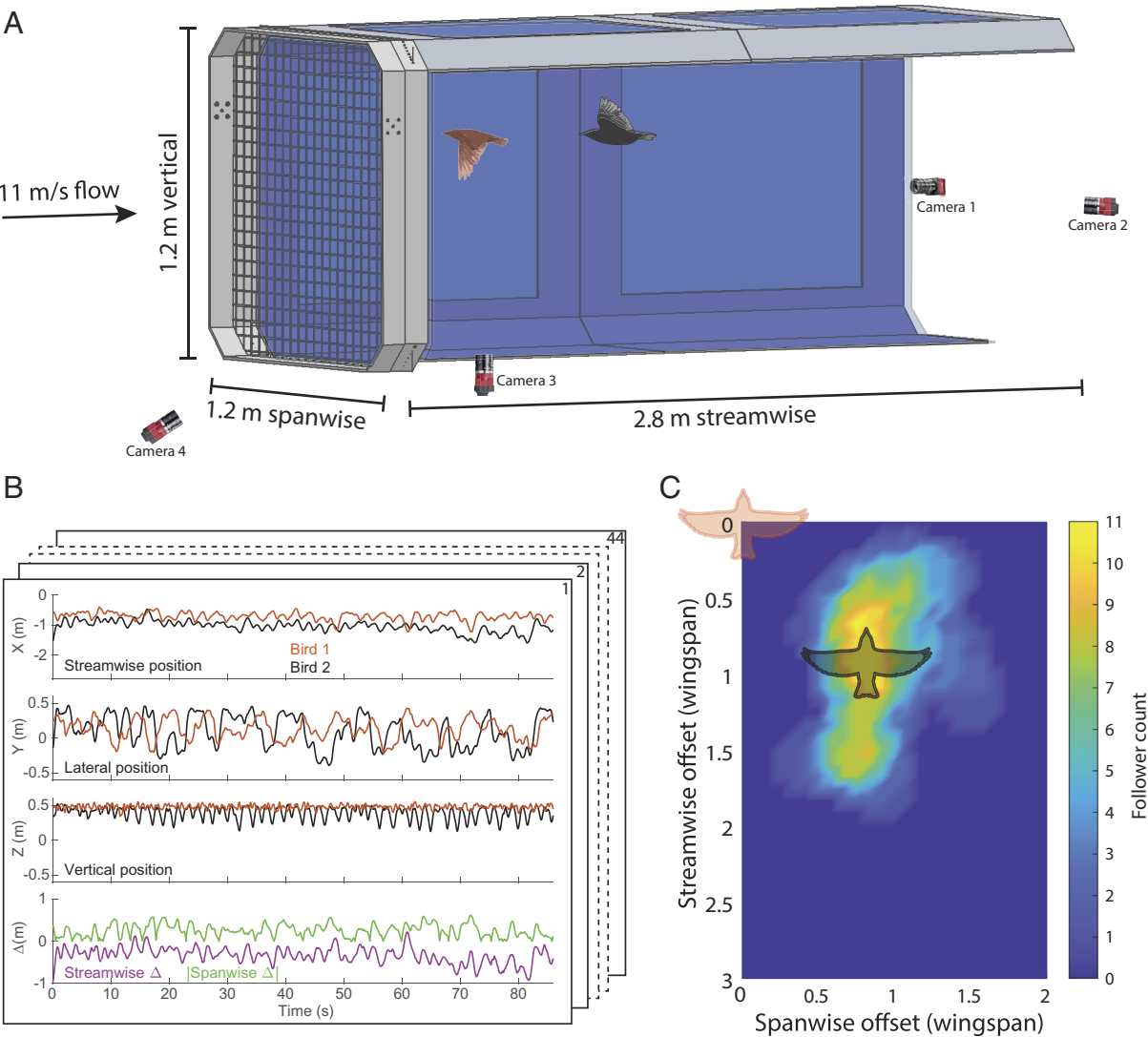


Fig. 1. Overview of bird flight recording and position measurements. (A) shows an illustration of the wind tunnel working section with dimensions, camera placement, and typical bird positioning. The near side and the floor are not depicted to allow illustration of the interior. (B) Position time-series from a single two-bird recording. We collected 44 group flight video recordings. Bird 1 is the leader for the majority of this flight. (C) A spatial histogram of the median spanwise and streamwise offset for birds that were a Follower for more than 40% of a recording. The modal value in this histogram is at an offset of 0.81 tip-to-tip wingspans lateral (i.e., spanwise) and 0.91 wingspans downstream (i.e., streamwise).

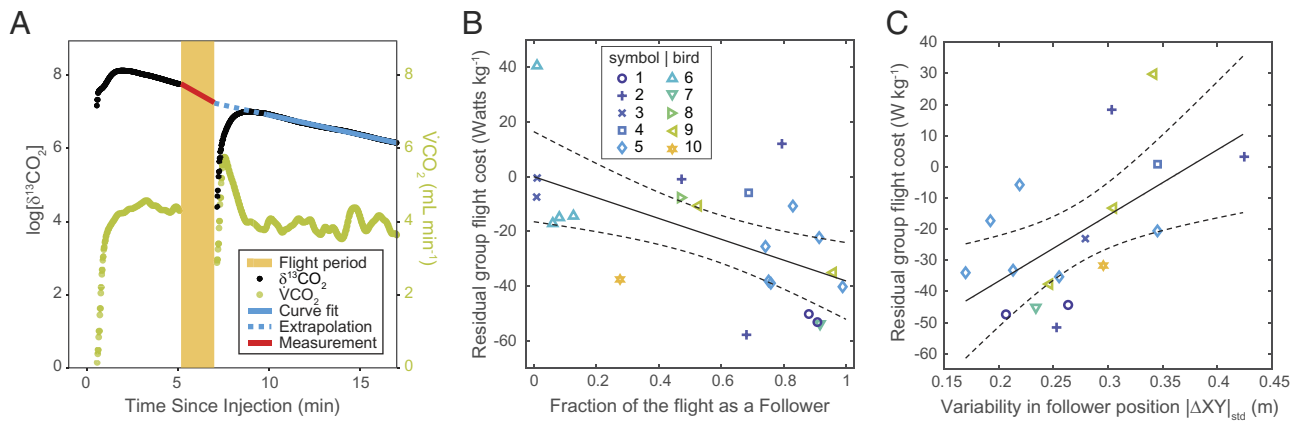


Fig. 2. Following behavior relates to cost of flight in pairs and trios. Panel (A) shows a typical ^{13}C NaBi trace. The bird is given an injection of ^{13}C labeled NaBi, which equilibrates and then begins washing out during the preflight period. The bird then flies in the wind tunnel and is returned to the respiratory chamber where the washout rate is again measured during the postflight period. The increase in washout rate during the flight is directly proportional to increased CO_2 production during that time. (B) Time spent as a Follower in pair and trio flight correlated with lower costs ($P = 0.013$; Table 1—b). Data points are individual recordings, with the vertical axis providing flight cost after accounting for the per-bird average solo flight costs and individual random effects specified in the Table 1—b statistical model. The solid line shows the trend, and the dashed lines show its 95% CI. Panel (C) shows that for birds that were a follower for more than half the time, flight costs were also correlated with the variability in the horizontal plane distance from the follower to the leader. Followers that maintained a more consistent position had lower costs ($P = 0.009$, see Table 1—g). The residual flight cost here accounts for the other fixed and random effects in the Table 1—g statistical model.

throughout the flight while in other cases they were occupied in nearly equal proportions by all birds. Despite continual variation in instantaneous position (Fig. 1B and Movie S1), the average relative position of the followers revealed a V formation-like structure (Fig. 1C and SI Appendix, Fig. S2). Specifically, birds that spent at least 40% of the flight as a Follower in either two or three bird groups had median relative flight positions 0.75 to 1.25 wingspans lateral to and 0.5 to 1.75 wingspans downstream of their leader; the most common following location (the “surfing spot”) was 0.81 wingspans lateral and 0.91 downstream (Fig. 1C).

As a comparison to the observed positioning of birds flying in pairs and trios, we computed a similar relative location map by combining the solo flight recordings from the birds used in the actual small group flights and processing them as if the birds had flown together. This revealed an expected follower offset of 0.59 wingspans lateral and 1.61 wingspans downstream (SI Appendix, Fig. S3). Thus, the birds flying in pairs and trios were approximately 40% closer together than expected based on their solo flight positions, but with greater spanwise spacing.

Metabolic Cost of Solo and Small Group Flight. Solo flight metabolic measurements were collected from 10 birds, with an average of 4.7 samples per individual (range of 2 to 7 for a total

of 47 flights). For comparison with the pair and trio flight results, we computed the average solo flight metabolic power for each bird ($\bar{P}_{\text{solo}}$), which had an among-individual mean and SD of 6.00 ± 0.85 W. The mass-specific equivalent, $\bar{P}_{\text{solo}}^*$, was 85.3 ± 12.6 W kg^{-1} (mean $\pm$ std) among individuals. These measurements are the entire metabolic expenditure during flight, including expenditures for biological functions other than locomotion.

Metabolic measurements were conducted during the flights of 25 pairs and 8 trios. Having observed V formation positioning as described above, we evaluated our hypothesis that Follower birds would save energy relative to their solo flight cost by using a statistical model for group flight costs that related the mass-specific cost of group flight, P_{group}^* , to the average solo flight cost for that bird, $\bar{P}_{\text{solo}}^*$, and the fraction of the flight spent as a Follower. Both the solo flight cost and fraction of flight spent as a Follower were significant (Table 1—a and b). Furthermore, birds spending more time following had lower costs (Fig. 2B). Despite this general result, not all consistent followers (i.e., birds that had a Follower fraction > 0.5) had lower flight costs than their solo benchmark, and so, we examined this set of birds for other factors related to success in saving energy when following another bird. Within this subset, variation in the relative position between Leader and

Table 1. Results from mixed-effects statistical models related to flight cost

Dataset	Formula	Fixed-effect P values	R^2	AICc
All pair and trio flight recordings with known positions ($n = 24$)				
a	$P^* \sim 1 + \bar{P}_{\text{solo}}^* + (1 * \text{pipe} * \text{BirdID})$	$P = 0.004$	0.33	253.5
b	$P^* \sim 1 + \bar{P}_{\text{solo}}^* + F + (1 * \text{pipe} * \text{BirdID})$	$P < 0.001, P = 0.013$	0.47	257.2
c	$P^* \sim 1 + \bar{P}_{\text{solo}}^* + F + \Delta XY _{\text{std}} + (1 * \text{pipe} * \text{BirdID})$	$P < 0.001, P = 0.012, P = 0.05$	0.55	265.4
d	$P^* \sim 1 + \bar{P}_{\text{solo}}^* + \text{PoT} + (1 * \text{pipe} * \text{BirdID})$	$P = 0.007, P = 0.923$	0.33	263.5
Pair and trio flight recordings with known positions and $> 50\%$ Follower ($n = 18$)				
e	$P^* \sim 1 + \bar{P}_{\text{solo}}^* + (1 * \text{pipe} * \text{BirdID})$	$P = 0.009$	0.33	201.7
f	$P^* \sim 1 + \bar{P}_{\text{solo}}^* + F + (1 * \text{pipe} * \text{BirdID})$	$P = 0.002, P = 0.098$	0.43	213.4
g	$P^* \sim 1 + \bar{P}_{\text{solo}}^* + \Delta XY _{\text{std}} + (1 * \text{pipe} * \text{BirdID})$	$P = 0.001, P = 0.009$	0.55	209.0

Symbols: P^* : mass-specific metabolic during pair or trio flight (W kg^{-1}); BirdID : unique bird identifier; $\bar{P}_{\text{solo}}^*$: average P^* during solo flight; F : proportion of the flight spent as a Follower; $|\Delta XY|_{\text{std}}$ the SD of the horizontal plane distance from Leader to Follower; PoT pair or trio categorical designation. AICc is only comparable within a dataset. Entries a–d use only recordings with the highest possible flight quality score, entries f–h use recordings with the highest and second-highest possible flight quality to ensure sufficient sample size.

Follower, computed as the norm of the SD of the offset positions $|\Delta XY|_{std}$ was highly significant, and birds with more variation in their relative position had higher flight costs (Table 1—e to g and Fig. 2C). Incorporating all these factors into a statistical model for all group flight recordings produced the most explanatory model tested here (Table 1—c). We found no statistically significant difference between results for Followers from two or three bird recordings (Table 1—d).

Physiological Correlates to Leadership. In addition to showing that followers in two- and three-bird groups flight expended energy at a reduced rate compared to their solo flight benchmarks, we also found that solo flight metabolic measurements were predictive of the flight roles adopted by different birds. Specifically, birds with lower mass-specific solo flight costs ($\overline{P^*_{solo}}$) had an overall tendency to spend more of the flight as the Leader (Table 2—a). We refined this relationship by computing the difference in $\overline{P^*_{solo}}$ between the birds in each specific group flight, denoted $\Delta \overline{P^*_{solo}}$. Birds with lower costs than others in their specific flight group were significantly more likely to be the Leader (Fig. 3A and Table 2—b). Body mass at the time of flight was also a significant factor such that larger birds were more likely to be a Leader (Table 2—c). This was true even in the presence of the mass-specific term $\Delta \overline{P^*_{solo}}$ (Table 2—d), although the addition of a second term to the model increased AICc (Akaike Information Criterion corrected for small sample sizes) compared to other models.

Flapping Frequency in Group Flight. Flapping frequency during group flight was related in part to both previously described results—the reduction in flight cost experienced by followers and the determination of group flight roles of different birds. Flapping frequency in small group flight was generally similar to frequency in solo flight and was strongly associated with leadership, such that leaders typically had lower flapping frequencies than followers. This effect was significant for frequency data recorded during the two- and three-bird flights (Table 2—e), with a nonsignificant trend but similar direction trend when average solo flapping frequencies were used instead of the pair and trio data ($\overline{f_{solo}}$, Table 2—f). Flapping frequency by followers was also associated with performance such that followers with higher flapping frequencies had less variation in their position with respect to the leader as measured by $|\Delta XY|_{std}$ (Fig. 3B and Table 2—g).

Discussion

Here, we provide substantial information on how bird flight in small groups can affect the metabolic energy expenditure of individuals in the group. In our flight experiments with pairs and trios of European Starlings in an animal flight wind tunnel, the birds exhibited dynamic flight behavior, but on average adopted a characteristic positioning relative to each other. This positioning was similar to that observed by large birds in V and echelon formation flocks (7, 8) and the “compound-V” spacing identified for shorebird cluster flocks (24). The most common follower location was located approximately one wingspan behind the leader, and 0.8 wingspans lateral, providing a slight overlap in wing-tip alignment along a streamwise path. Followers had reduced flight costs, predicated on the degree to which they stayed in consistent alignment with a leader. The estimated savings for a follower that achieved the best-observed alignment consistency for an entire flight was a 25% reduction in flight cost, close to the maximum predicted energy saving based on analytical aerodynamic models (25) and exceeding the savings extrapolated from data based on heart rate monitoring of pelicans in natural V formation flight (10).

Although we present no physical evidence for a reason for the measured cost savings by followers, it seems plausible that it is associated with the tip vortices generated by the leading bird. All flying objects at moderate to high Reynolds numbers—birds, bats, aircraft—generate tip vortices as a consequence of producing lift. Those vortices trail behind the animal and induce a downwash immediately behind the body and an upwash outboard of the wings (26). For fixed-wing aircraft or gliders, a follower positioned in the upwash region behind and outboard of a leader benefits from the upward airflow which reduces the energy requirements to maintain flight. This energy savings of formation flight has been quantified both experimentally and theoretically for fixed-wing aircraft flying in a V- or Diamond pattern (25), but until now has never been measured for a flying animal. The average positioning measured here for follower birds is a close match to the ideal position for energy savings from theoretical models of formation flight (14, 25). Thus, our results are consistent with energy savings for follower birds derived from beneficial aerodynamic interaction with the tip vortices of a lead bird.

If a physical mechanism based on tip vortex interactions is the basis for energy savings by followers, then we would also expect that followers flying out of alignment with the leader would not experience a benefit. However, because most followers examined here flew in locations where energy saving is expected, we do not have a sufficiently large sample of birds flying in other locations

Table 2. Results from mixed-effects statistical models related to leadership and positioning

Dataset	Formula	Fixed-effect P values	R ²	AICc
Group flight recordings with known positions and $\overline{P^*_{solo}}$ for all birds (n = 29)				
a	$L \sim 1 + \overline{P^*_{solo}} + (BirdID)$	$P = 0.088$	0.59	42.8
b	$L \sim 1 + \Delta - \overline{P^*_{solo}} + (1 BirdID)$	$P = 0.018$	0.67	39.9
c	$L \sim 1 + M_b + (1 BirdID)$	$P = 0.018$	0.63	40.0
d	$L \sim 1 + \Delta - \overline{P^*_{solo}} + M_b + (1 BirdID)$	$P = 0.026, P = 0.025$	0.70	41.8
Group flight recordings with known positions along with f and $\overline{f_{solo}}$ for the focal bird (n = 21)				
e	$L \sim 1 + f + (BirdID)$	$P = 0.013$	0.68	35.8
f	$L \sim 1 + \overline{f_{solo}} + (1 * pipe * BirdID)$	$P = 0.19$	0.71	39.0
Group flight recordings > 5% Follower with known f (n = 18)				
g	$ \Delta XY _{std} \sim 1 + f + (1 BirdID)$	$P = 0.001$	0.62	—

Additional symbols: L: proportion of the flight spent as a Leader; $\Delta \overline{P^*_{solo}}$: difference in mass-specific average solo flight metabolic power between the focal bird and the lowest cost other bird in a group flight; M_b : body mass; f: flapping frequency; $\overline{f_{solo}}$: average solo flight flapping frequency.

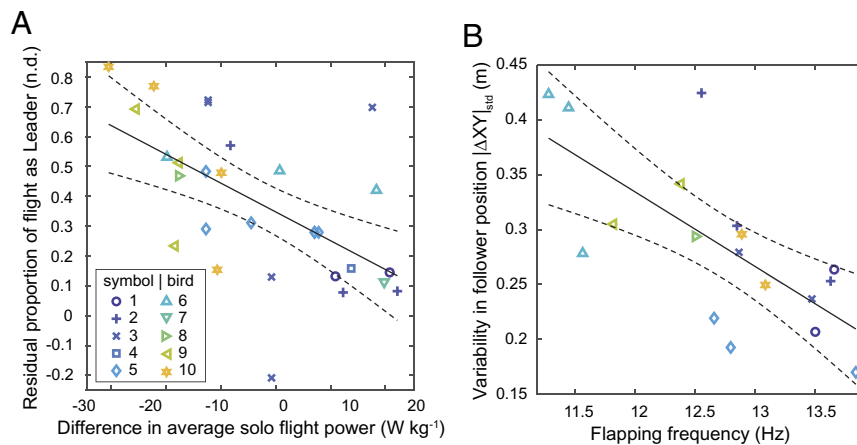


Fig. 3. Determinants of group flight role and follower effectiveness. (A) Solo flight costs predict role in pair and trio flights. In a pair or trio flight, the Leader is the single most upstream bird, and each bird in the group spends some proportion of the flight, ranging from 0 to 1, as the Leader. The difference in average solo flight costs between birds in a pair or trio, calculated as the difference between a focal bird and the lowest-cost other bird in the group, relates to the proportion of the flight the focal bird spent as a Leader. Lower solo flight costs were significantly associated with leadership ($P = 0.018$, Table 2—b). Data points represent flights, the vertical axis shows the proportion of the flight spent as a Leader after including the per-bird random effects estimated in the statistical model. The solid line shows the statistical trend, and the dashed lines show its 95% CI. (B) Follower birds with higher flapping frequencies had significantly less variability in their flight position with respect to the leader ($P = 0.001$, Table 2—g). Only recordings with at least 5% of flight time as a follower are shown.

to statistically identify costs associated with follower mispositioning. We note that flying directly behind the leader, in the downwash, incurs the highest energetic penalty, and we almost never see the follower in this position (Fig. 1 C). Streamwise positioning has less effect on the predicted energetic benefit for followers, and in our results, birds used a variety of streamwise offsets from their leader. This variation in streamwise position was not significantly associated with follower flight costs. Finally, the trailing vortex wake behind flapping animals has a characteristic streamwise structure associated with the upstroke and downstroke (21) and European Ibis in free flight were observed to fly in a V formation with a flapping phase-to-spacing relationship (9), with the trailing bird synchronizing its wingstroke, presumably to take optimal advantage of the leading bird's vortex wake. We were unable to make this measurement in the current study, but it could be addressed in future studies by using synchronized high-speed videography and accelerometry and by quantifying the vortex wake structure using particle image velocimetry.

In the lab frame of reference, the wind tunnel flight recordings give the visual impression of rapidly changing bird–bird positioning, contrary to the impression given by casual observation of starlings in free flight. However, the wind tunnel view is misleading. The average variation in the birds' airspeed during group flights was only 0.71 m s^{-1} , or $\pm 3.2\%$ of their 11 m s^{-1} flight sustained flight speed and they remained highly directional during the flight (reorientation of trajectory less than $3.7 \text{ degrees s}^{-1}$). Consequently, the birds' flight was more stable than casual observation might suggest.

The observed Leader–Follower positioning in these wind tunnel flights is distinct from those measured in free flight from starling murmuration flocks (27). In those recordings, starlings flew with their nearest neighbor in a directly lateral position, but with a minimum mean spacing similar to the modal leader–follower distance reported here. The lateral positioning observed in the murmurations would minimize aerodynamic interactions (beneficial or detrimental), and analysis of flocks from a closely related species (*Corvus momedula*) suggested that such lateral neighbor positioning would also reduce maneuvering costs associated with staying in formation (18). The size of our wind tunnel test section does allow sufficient lateral space for side-by-side flight, and this arrangement was observed in three of our two-bird flights, with the follower bird

slightly downstream the leader but more than 1.5 wingspans lateral. The measured energy savings in those three cases was less than those for other followers, but not statistically significant, possibly owing to the small sample size. Given these observations, it is possible that Starlings in murmuration flocks of hundreds to tens of thousands of birds adopt energetically suboptimal positioning to maintain group spacing during the highly dynamic large-group maneuvers. In contrast, a starling-size shorebird species (dunlin; *Calidris alpina*, 56 g, 0.34 m wingspan) was found to adopt V-formation-like substructures in a cluster flock (24), so it may also be the case that starlings in free flight would adopt the average V formation positioning seen in our wind tunnel recordings if minimizing the cost of transport was a dominant consideration.

Finally, our results also support recent findings on the relationship between group leadership and flight ability in bird flocks. Pettit et al. show that in homing pigeon flocks, solo flight speed determines flock leadership (28). Here, flight speed was constrained to 11 m s^{-1} by the wind tunnel, but we found that the birds with the most economical solo flights in terms of W kg^{-1} and the lowest solo flight flapping frequency were most likely to be leaders, and the strength of the effect related most directly to the difference in flight economy or flapping frequency between the birds in the group. Birds that fly most economically at the fixed speed used here, determined during training to be near the minimum power speed for the starlings, may also be able to sustain a greater maximum speed in unconstrained flight, making our results fully consistent with Pettit et al. (28).

Materials and Methods

Birds and Bird Training. We captured 34 European Starlings from local populations near Amherst, MA, in Spring 2022 using box traps. The birds were then transferred to an indoor aviary in the Brown University animal care facility where they were habituated to captivity for 68 d before wind tunnel training began. Throughout the experiment, birds were maintained on 12 h light:12 h dark photoperiod and fed an ad libitum diet of turkey starter and *Tenebrio* mealworms. The birds were flown daily and encouraged to maintain steady flight via food reward. At the end of the initial training period, 18 birds were selected as good candidates for flight recordings and the others released. Following completion of all measurements, the 18 recording birds were also released. These and subsequently described animal procedures were authorized as Brown University IACUC protocol

2022-03-0006 and University of Massachusetts IACUC protocol 2022-2825. The Starlings used in this study had an average mass of 70.8 g (*SI Appendix, Table S1*), measured via electronic balance before each metabolic measurement flight, and an average wingspan of 33.5 cm, measured as the wingtip-to-wingtip distance at mid-downstroke using the calibrated video recordings.

Wind Tunnel, Cameras, and Lighting. We used the Brown University animal flight wind tunnel (29), a purpose-built, temperature-controlled low-speed wind tunnel with a 1.2 m wide, 1.2 m tall, and 2.8 m long working section with mesh barriers upstream and downstream of the working section. During bird training, we identified 11 m s^{-1} as the most comfortable flight speed for the starlings and all flight recordings were conducted at this flow speed and with temperature fixed at 19°C . The wind tunnel working section sides were covered with opaque blue Lexan sheets and the working section lit from within via six compact LED lights (Litra LitraTorch 2.0, $38 \times 38 \times 48 \text{ mm}$) positioned on the tunnel floor in the middle (four lights) and rear (two lights). Four machine vision cameras (Allied Vision Alvium 1800 U-511c) were positioned around the wind tunnel at the left and right middle-rear, directly underneath the upstream portion of the working section and ahead of the working section looking downstream and upward. These cameras were synchronized via an external programmable function generator (BNC 575, Berkeley Nucleonics) and continuously recorded color video at 25 Hz with 1232×1024 pixel resolution to a host computer during the experiments.

Camera Calibration and Bird Tracking. The four cameras were calibrated for 3D tracking using direct linear transformation (DLT) calculated from a 14-point calibration frame following optical distortion correction using a pinhole camera model with second- and fourth-order radial parameters. The DLT calibration frame was defined by fiducial markers placed on the interior of the working section. These markers were identified automatically in each recording by a custom neural network. Birds were tracked in the videos using another set of neural networks trained on manually digitized data, followed by custom processing in MATLAB to unite 2D detections from several cameras into a 3D track, and to keep the tracks of the multiple birds in the tunnel separate. Tracks were validated by human inspection and corrected as necessary; bird individual identities during tracking were set by the color of the LED on their IMU backpack. The median-of-medians 3D reconstruction error across all group flight data was 0.88 pixels, corresponding to a dimensional uncertainty of approximately 3 mm.

IMU Backpack. Birds wore an IMU recording backpack (Vesper, ASD Technologies, Haifa, Israel) which recorded three degrees of freedom (DoF) in linear acceleration at 200 Hz, three DoF of angular velocity at 200 Hz, and 8-bit audio at 20.8 kHz. The backpacks were attached using custom elastic harnesses (Stretch Magic Elastic Cord, Soft Flex Company, Sonoma, CA). Backpack mass was 4.05 to 4.10 g, about 5.6% of the average mass of the birds in this study and therefore not expected to affect cost of flight (30). IMU and video data were in principle synchronized by an external indicator that simultaneously flashed a light in the camera field of view and sounded a tone in the working section. However, feather noise often masked the indicator tone and combined with internal drift between different backpack CPU clocks; this prevented matching of events among birds or to video records. Finally, in some cases, the accelerometers did not record correctly for a variety of reasons including battery failure, loose wiring, or failure of the magnetometer-based on-off switch, so IMU data are not available for all recordings.

Metabolic Measurements. We measured the metabolic energy expenditure of the starlings in flight using the ^{13}C -labeled Na-bicarbonate method (31–34). First developed more than 20 y ago, this metabolic measurement method saw little use for many years, but the advent of low-cost cavity ring-down spectrophotometers for making the ^{13}C measurements has recently increased its popularity. The method was applied as follows (Fig. 2A and *SI Appendix, Fig. S1*), similar to Hedh et al. (33). Birds were weighed immediately before the start of each flight sequence. Following that measurement, the birds flew for 1 to 2 min alone in the tunnel as a warm-up to establish a baseline activity level. Following the end of the warm-up flight, the birds received a bolus intraperitoneal injection of $0.6 \text{ M } ^{13}\text{C}$ -labeled Na-bicarbonate in solution ($\sim 150 \mu\text{L}$) prior to their measurement flight, and the initial washout of ^{13}C was measured from the bird at rest in a respirometry chamber using a high-resolution cavity ring-down spectrometer (Picarro, Santa Clara, CA). Immediately after injection, the bird was placed in the chamber and the $^{13}\text{C}/^{12}\text{C}$ fraction peaked quickly and a steady rate of decay was recorded for 1 to 5 min. The bird was then quickly transferred

to the wind tunnel to fly for 1 to 2 min. To end the flight, the bird was rapidly caught mid-flight and immediately placed in the metabolic chamber where the postflight $^{13}\text{C}/^{12}\text{C}$ fraction and decay rate were measured for up to 15 min along with the rate of CO_2 production. The postflight CO_2 measurements occasionally began with a peak potentially associated with a short period of postexercise oxygen consumption, so we characterized the postflight ^{13}C decay rate beginning three minutes after the bird was returned to the chamber, then extrapolated backward in time to the actual end of the flight. This procedure effectively includes any postexercise peak in the flight cost estimates. We used the postflight data to determine the relationship between $\dot{V}\text{CO}_2$ and the rate of isotope decay to calibrate the method for each recording, in order to calculate in-flight $\dot{V}\text{CO}_2$ as in ref. 32. Because only one metabolic chamber, CO_2 analyzer and cavity ring-down spectrometer were available for project use, metabolic data were only collected from one bird at a time. Furthermore, because metabolic measurements required an injection, measurements were collected from individual birds no more frequently than every 48 h.

Flights were scored on a 1 (poor) to 5 (excellent) scale by the experimentalists at the time of collection based on observed flight behavior in the tunnel. Lower scores were assigned to birds that repeatedly veered toward the floor, attempted to land on the floor or cameras, or clung to the front or rear mesh. Only flights with a score of 4 or 5 were included in the data presented here. Removal of the bird from the tunnel and transfer to the respirometry measurement chamber was also scored on a 1 to 5 scale, and only transfers with a score of 4 or 5, which indicate a clean catch, mid-flight, and a quick transfer to the metabolic chamber, were included in the analysis.

The ^{13}C NaBi method also produces occasional poor recordings due to bird activity in the respirometry chamber before or after flight, or the injected ^{13}C -labeled Na-bicarbonate becoming unevenly incorporated into the body CO_2 pool. Metabolic data were rejected when the statistical fit of the decay equation to the data yielded an $R^2 < 0.95$ or when the decay rate inferred for flight was less than the decay rate measured postflight. Results with a decay equation fit with an $R^2 < 0.98$ were manually inspected and rejected if the decay curve revealed an atypical shape. Finally, outliers in the metabolic data were identified and removed by iteratively selecting results more than 2.5 SD from the global mean metabolic rate, a process that removed three additional results. The total number of metabolic recordings reported earlier (i.e., 80) is the total after applying these data cleaning procedures.

Datasets for Analysis. Our final dataset of flights for quantifying solo and group flight costs along with group positioning effects included 80 metabolic measurements, of which 47 were solo flights, 25 were with a single companion, and 8 were with two companions. Metabolic measurements were collected from 10 different birds. Because only one metabolic measurement could be collected per flight session, and only one measurement per subject bird per 48 h, these 10 birds commonly flew as companions during group flights where they contributed only overall positioning information (Fig. 1C). An additional four birds flew as group flight companions only and contributed no metabolic measurements. The median number of solo and group metabolic measurement flights per individual was 4.5 and 3.5. In two group flights, the camera system did not function properly, and no position data were collected. IMU data were successfully collected from 55 of the 80 metabolic measurement flights. For analyses to establish bird positioning with respect to neighbors and for determining the average Leader role fraction for each bird, all possible birds were included, regardless of whether or not they were subject to a successful metabolic measurement. This yielded 97 relative bird position measurements from 44 group flight recordings.

Data Reduction. Because the metabolic measurement method used here provides one value for each flight, for analysis purposes, data collected from the other inputs were similarly reduced to single measurements per flight as follows.

Bird positions. In processing the position time series data acquired from the cameras, the data were first low-pass-filtered using a four-pole digital Butterworth filter with a 4 Hz cutoff, removing higher frequency effects due to body oscillations at flapping frequency (approximately 11 Hz) and noise introduced by the automated video data acquisition pipeline. From these smoothed data, a bird was identified as the Leader in a particular video frame if it was the most upstream bird. This value was summarized for a flight as a value from 0 to 1 representing the proportion of the flight time during which the bird was the Leader. Birds were categorized as a Follower if they were downstream of another bird and within 0.5 wingspans vertical distance to that bird and

5 wingspans total 3D distance from it. This value was also summarized for a flight as a value from 0 to 1 representing the proportion of the flight in which the bird was a Follower. Note that by the above criteria, a bird might not be a Leader or Follower in some video frames, e.g., by flying downstream and far from the other birds. Thus, the sum of the leader and follower proportions was less than or equal to 1. Recordings from two-bird and three-bird recordings were analyzed using this same definition for Leader and Follower roles, with the primary difference being that because the Leader is the single most upstream bird, three-bird recordings typically include one Leader and two Followers. In all cases, wingspan used for calculations was 0.335 m, the average value for birds in this study (SI Appendix, Table S1).

For each frame in which a bird was a Follower, its streamwise, lateral, and vertical offsets from the Leader were collected, and these were also summarized by median values for the entire flight. In cases where three birds were flying together, the middle bird by streamwise position could only be a Follower of the most upstream bird, but the last bird by streamwise position might be a Follower of the middle bird or first bird. In this case, the closest neighbor that also met the criteria described above was treated as the Leader for relative positioning calculations for the most downstream bird. See SI Appendix, Fig. S1 for an example recording from a single bird in a single group flight.

For the determination of bird speed in the tunnel reference frame, the position data were first low-pass filtered using a four-pole digital Butterworth filter with an 8 Hz cutoff, preserving more of the original signal than was used for position analysis but still avoiding the 11 Hz flapping frequency. These first derivatives of the 3D position data with respect to time were then measured by fitting a quintic spline polynomial to the smoothed data and differentiating the polynomial. A final speed measure was then computed from the norm of the 3D position derivative.

IMU measurements. Because IMU measurements often could not be precisely synchronized to the camera timebase, values were instead calculated for the entire flight record, trimmed to the period of active flapping, and smoothed using a low-pass filter with a 20 Hz cutoff. This cutoff is above the expected starling flapping frequency, reported elsewhere (34, 35) as approximately 10 Hz. Preliminary analysis of the IMU data did not reveal any relationship between accelerometer signal power and metabolic power, so the IMU analysis was restricted to the characteristic oscillation frequency, which is reflective of the flapping frequency of the bird. This value was calculated from the IMU recordings by computing the

signal power spectrum for the smoothed vertical acceleration, then identifying the frequency at peak signal power.

Solo flight metabolic measurements. For each bird, we calculated the mean solo flight metabolic expenditure for comparison to group flight recordings from that same bird. These solo flight means were calculated after applying the criteria described above for removing outliers from the metabolic measurements.

Statistical analysis. Unless otherwise noted, the statistical analyses presented in this paper are from mixed-effects models, with model quality assessed by Akaike's Information Criterion adjusted for small sample sizes (AICc). Because our dataset includes repeated measurements from the same birds, we included a per-bird random effect in all models, along with fixed effects. These per-bird random effects were left in place even when they worsened AICc or had $P > 0.05$. Because these per-bird random effects are included as degrees of freedom in the AICc calculation, and AICc strongly penalizes the inclusion of additional degrees of freedom in a model, most of our best models include only one fixed effect. In cases where multiple fixed effects were significant at $P < 0.05$ and we believe the results to be informative, we also present the alternative model, noting the AICc of all models presented. Statistical tests were performed in MATLAB r2022a with the Statistics and Machine Learning toolbox.

Data, Materials, and Software Availability. Mixed data types including metabolic measurements, bird flight positions, and inertial measurement outputs along with the scripts and code used to produce the results in the paper have been deposited in Figshare.com (36).

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- I. D. Couzin, J. Krause, N. R. Franks, S. A. Levin, Effective leadership and decision-making in animal groups on the move. *Nature* **433**, 513–516 (2005).
- T. J. Pitcher, "Functions of shoaling behaviour in teleosts" in *The Behaviour of Teleost Fishes* (Springer, 1986), pp. 294–337.
- A. Strandburg-Peshkin *et al.*, Visual sensory networks and effective information transfer in animal groups. *Curr. Biol.* **23**, R709–R711 (2013).
- M. Ballerini *et al.*, Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 1232–1237 (2008).
- D. Hummel, Aerodynamic aspects of formation flight in birds. *J. Theor. Biol.* **104**, 321–347 (1983).
- P. Lissaman, C. A. Shollenberger, Formation flight of birds. *Science* **168**, 1003–1005 (1970).
- C. Cutts, J. Speakman, Energy savings in formation flight of pink-footed geese. *J. Exp. Biol.* **189**, 251–261 (1994).
- F. H. Heppner, Avian flight formations. *Bird-banding* **45**, 160–169 (1974).
- S. J. Portugal *et al.*, Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature* **505**, 399 (2014).
- H. Weimerskirch, J. Martin, Y. Clerquin, P. Alexandre, S. Jiraskova, Energy saving in flight formation. *Nature* **413**, 697 (2001).
- J. R. Usherwood, M. Stavrou, J. C. Lowe, K. Roskilly, A. M. Wilson, Flying in a flock comes at a cost in pigeons. *Nature* **474**, 494 (2011).
- L. A. Taylor *et al.*, Birds invest wingbeats to keep a steady head and reap the ultimate benefits of flying together. *PLoS Biol.* **17**, e3000299 (2019).
- Y. Zhang, G. V. Lauder, Energetics of collective movement in vertebrates. *J. Exp. Biol.* **226**, jeb245617 (2023).
- J.-S. Maeng, J.-H. Park, S.-M. Jang, S.-Y. Han, A modeling approach to energy savings of flying Canada geese using computational fluid dynamics. *J. Theor. Biol.* **320**, 76–85 (2013).
- J. P. Badgerow, F. R. Hainsworth, Energy savings through formation flight? A re-examination of the vee formation. *J. Theor. Biol.* **93**, 41–52 (1981).
- W. Nachtigall, Phasenbeziehungen der Flügelschläge von Gänsen während des Verbandflugs in Keilformation. *Z. Vgl. Physiol.* **67**, 414–422 (1970).
- A. Mirzaeinia, F. Heppner, M. Hassanalian, An analytical study on leader and follower switching in V-shaped Canada Goose flocks for energy management purposes. *Swarm Intell.* **14**, 117–141 (2020).
- H. Ling *et al.*, Collective turns in jackdaw flocks: Kinematics and information transfer. *J. R. Soc. Interface* **16**, 20190450 (2019).
- R. Brown, The flight of birds: II. Wing function in relation to flight speed. *J. Exp. Biol.* **30**, 90–103 (1953).
- C. J. Pennycuik, A wind-tunnel study of gliding flight in the pigeon *Columba livia*. *J. Exp. Biol.* **49**, 509–526 (1968).
- G. Spedding, M. Rosén, A. Hedenstrom, 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. *J. Exp. Biol.* **206**, 2313–2344 (2003).
- B. W. Tobalske, K. P. Dial, Flight kinematics of black-billed magpies and pigeons over a wide range of speeds. *J. Exp. Biol.* **199**, 263–280 (1996).
- F. Arnold *et al.*, Vision and vocal communication guide three-dimensional spatial coordination of zebra finches during wind-tunnel flights. *Nat. Ecol. Evol.* **6**, 1221–1230 (2022).
- A. J. Corcoran, T. L. Hedrick, Compound-V formations in shorebird flocks. *eLife* **8**, e45071 (2019).
- D. Hummel, "The use of aircraft wakes to achieve power reductions in formation flight" in *AGARD FDP Symposium on "The Characterization & Modification of Wakes from Lifting Vehicles in Fluid"* (1996).
- J. Anderson, *Fundamentals of Aerodynamics* (McGraw-Hill, ed. 6, 2017).
- M. Ballerini *et al.*, Empirical investigation of starling flocks: A benchmark study in collective animal behaviour. *Animal Behav.* **76**, 201–215 (2008).
- B. Pettit, Z. Akos, T. Vicsek, D. Biro, Speed determines leadership and leadership determines learning during pigeon flocking. *Curr. Biol.* **25**, 3132–3137 (2015).
- K. Breuer, M. Drela, X. Fan, M. Di Luca, Design and performance of an ultra-compact, low-speed, low turbulence level, wind tunnel for aerodynamic and animal flight experiments. *Exp. Fluids* **63**, 169 (2022).
- J. A. Gessaman, G. W. Workman, M. R. Fuller, Flight performance, energetics and water turnover of tippler pigeons with a harness and dorsal load. *Condor* **93**, 546–554 (1991).
- R. von Busse, S. M. Swartz, C. C. Voigt, Flight metabolism in relation to speed in Chiroptera: Testing the U-shape paradigm in the short-tailed fruit bat *Carollia perspicillata*. *J. Exp. Biol.* **216**, 2073–2080 (2013).
- C. Hambly, E. Harper, J. Speakman, Cost of flight in the zebra finch (*Taenopygia gutata*): A novel approach based on elimination of ¹³C labelled bicarbonate. *J. Comp. Physiol. B* **172**, 529–539 (2002).
- L. Hedh *et al.*, Measuring power input, power output and energy conversion efficiency in un-instrumented flying birds. *J. Exp. Biol.* **223**, jeb223545 (2020).
- T. Urca, E. Levin, G. Ribak, Insect flight metabolic rate revealed by bolus injection of the stable isotope ¹³C. *Proc. R. Soc. B* **288**, 20211082 (2021).
- S. Ward *et al.*, Metabolic power, mechanical power and efficiency during wind tunnel flight by the European starling *Sturnus vulgaris*. *J. Exp. Biol.* **204**, 3311–3322 (2001).
- T. L. Hedrick *et al.*, Data for "It pays to follow the leader: metabolic cost of flight is lower for trailing birds in small groups." Figshare. <https://doi.org/10.6084/m9.figshare.24585780>. Deposited 17 November 2023.