

1 **Upwash exploitation and downwash avoidance by flap phasing in** 2 **ibis formation flight**

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11 **Many species travel in highly organised groups¹⁻³. The most quoted function of these**
12 **configurations is to reduce energy expenditure and enhance locomotor performance of**
13 **individuals within the assemblage⁴⁻¹¹. The distinctive V formation of bird flocks has long**
14 **intrigued researchers and continues to attract both scientific and popular attention^{4,7,9-14}.**
15 **The well held belief is that such aggregations give an energetic benefit for those birds**
16 **which are flying behind and to one side of another bird through using the regions of**
17 **upwash generated by the wings of the preceding bird^{4,7,9-11}, though a definitive account of**
18 **the aerodynamic implications of these formations has remained elusive. Here we show**
19 **that individuals flying within a V flock position themselves in aerodynamically optimum**
20 **positions, in so far as they agree with aerodynamic theoretical predictions. Furthermore,**
21 **we demonstrate that birds exhibit wingtip-path coherence when flying in V positions,**
22 **flapping spatially in phase enabling upwash capture to be maximised throughout the**
23 **entire flap cycle. In contrast, when birds fly immediately behind another bird – in a**
24 **streamwise position – there is no wingtip path coherence; the wing-beats are in spatial**
25 **anti-phase. This could potentially reduce the adverse effects of downwash for the**
26 **following bird. These aerodynamic accomplishments were previously not thought**
27 **possible for birds because of the complex flight dynamics and sensory feedback that**

28 **would be required to perform such a feat^{12,14}. We conclude that the intricate mechanisms**
29 **involved in V formation flight indicate remarkable awareness of, and ability to either**
30 **sense or predict, the spatial wake structures of nearby flock-mates; and suggest that birds**
31 **in V formation have phasing strategies to cope with the dynamic wakes produced by**
32 **flapping wings.**

33 Fixed-wing aerodynamic theories have predicted the exact spanwise positioning that birds
34 should adopt within a V formation flock to maximise upwash capture^{4,9-14}. The primary
35 empirical evidence to confirm that this mechanism is used is a reduction in heart rate and wing-
36 beat frequency in pelicans flying in a V formation⁷. There is a general lack of experimental
37 data from free-flying birds, mainly due to the complications of measuring the intricate and
38 three-dimensional complexity of formation flight, and the lack of appropriate devices to
39 monitor and record such information. Therefore, the precise aerodynamic interactions which
40 birds employ to exploit upwash capture have not been identified. To investigate the purported
41 aerodynamic interactions of V formation flight, we studied a free-flying flock of critically
42 endangered Northern bald ibises (*Geronticus eremita*) (Fig. 1a). We used novel technology^{15,16}
43 to measure the position, speed and heading of all birds within a V formation. We recorded
44 position and every wing flap of 14 birds during 43 minutes of migratory flight using back-
45 mounted integrated Global Positioning System (5 Hz) (GPS) and inertial measurement units
46 (300 Hz) (IMUs) (see Full Online Methods)^{15,16}. The precision of these measurements allows
47 the relative positioning of individuals within a V to be tracked, and the potential aerodynamic
48 interactions to be investigated at a level and complexity not previously feasible.

49 During a 7 minute section of the flight, where the majority of the flock flew in approximate V
50 formation in steady, level and planar direct flight, (see Full Online Methods), we found wing
51 flaps occurred at an angle of, on average, 45 degrees to the bird ahead (or behind), and
52 approximately 1.2 m behind (Fig. 1b, c, d). The most populated 1 m by 1 m region was 0.49 m
53 to 1.49 m behind (“streamwise”) and to the side of the bird ahead. The centre of the most

54 populated (0.25 m) spanwise region was at 0.904 m, resulting in a wingtip overlap⁹⁻¹³ of 0.115
55 m (Fig. 1c, d, wingspan $b = 1.2$ m). This falls within the bounds of fixed-wing theory
56 predictions⁹⁻¹³ for maximising the benefits from upwash, which range from zero wingtip
57 overlap (assuming no wake contraction⁴) to, maximally, 0.13 m (assuming elliptical loading
58 over the pair of wings, and full wake contraction from wingspan b to $\pi b / 4$)⁹.

59 During this 7 minute section of V formation flight, individual birds show a certain degree of
60 positional infidelity within the V flock (Fig. 2, see also Supplementary Figure 1 and
61 Supplementary Video 1). While individuals contribute to the statistical V formation, their
62 positioning is inconsistent. Certain individuals showed general preferences for a particular area
63 within the V formation, but the variability in positioning within the flock resulted in no clear
64 leader (see Supplementary Information for further discussion).

65 While we observe that, when flying in a V, ibises position themselves in fixed-wing
66 mathematically predicted positions^{4,9-11}, the wake of flapping birds (in this study, ibises spent
67 97% of their time flapping; Full Online Methods) is likely to be complex⁹⁻¹⁴. Wingtip path
68 coherence, where a flying object flaps its wings in spatial phase with that of the individual it is
69 following, has been proposed as a method that would maximise upwash capture in V formation
70 flight of birds and flying robotic devices¹². Whether birds are able to take advantage of this
71 additional level of complexity present in flapping flight (in comparison to that of fixed-wing
72 flight) had previously remained unanswered.

73 Within the ibis flock, individual flaps for each bird were described from the dorsal acceleration
74 signal from the IMU¹⁵. The temporal phase $\phi_{temporal}$ is defined here as the proportion of a flap
75 cycle of a leading bird at which a following bird initiates a flap. Spatial phase $\phi_{spatial}$ makes use
76 of the temporal phases, and takes account of the number of wavelengths, λ , between the bird
77 ahead and the bird behind:

78 $\phi_{\text{spatial}} = \phi_{\text{temporal}} - 2\pi\lambda$

79 A spatial phase of zero would indicate that, were the birds to be directly following each other,
80 the wingtip paths would match.

81 In the most populated 1 m by 1 m favoured V position (Fig. 1c), Rayleigh's test¹⁷ for circular
82 statistics indicates a significant unimodal bias in both temporal (Rayleigh, $P = 0.018$, mean
83 phase = 0.857; Hodges-Ajne, $P = 0.012$) and, more strongly, spatial (Rayleigh, $P = 0.003$, mean
84 phase = -1.155; Hodges-Ajne, $P = 0.004$) phases (Fig. 3a, b) (see Supplementary Table 1 for
85 further statistics; Supplementary Figure 2a, 3a, 4a). Flapping in spatial phase indicates that the
86 wing of a following bird goes up and down following the path through the air previously
87 described by the bird ahead. The following bird then benefits from consistently flapping into
88 the upwash region from the preceding bird (Fig. 3b, c), presumably reducing the power
89 requirements for weight support^{12,14}

90 In contrast, birds flying directly behind, tracking the bird ahead in a streamwise position
91 (sampled region 0.5 m across, 4 m streamwise, Fig. 1c) flap in close to spatial antiphase
92 (median = 2.897, where precise antiphase would be +/-3.142), significantly ($P < 0.05$) deviating
93 from flapping 'in' spatial phase (see Supplementary Table 1 for further statistics;
94 Supplementary Figure 2b, 3b, 4b). As such, the wingtip paths of the following bird do not
95 match those of the bird they are following, and the wingtip paths are close to maximally
96 separated. Birds flying directly behind another bird in a streamwise location flap in spatial
97 antiphase (Fig. 3d, e, see also Supplementary Figure 2b, 3b), potentially reducing the adverse
98 effects of downwash (Fig. 3f), both in terms of magnitude and direction. If this position was
99 aerodynamically adaptive, it would be predicted to be favoured at higher speeds, where parasite
100 power is relatively high¹⁸, compared with the induced power costs of weight support; forms of
101 slipstreaming can reduce the drag experienced by followers^{5,6,8,19}, even in cases where there is
102 zero net horizontal momentum flux in the wake (i.e. drag=thrust) – as in steady swimming –
103 due to temporal or local spatial^{5,20,21} fluctuations from mean wake conditions. Whether the

104 position immediately behind is accidental or intentional, and whether it offers any aerodynamic
105 advantage or cost, is currently unclear. However, the wing-beat phasing observed when in this
106 position would serve to displace the following bird's wings from regions of greatest downwash
107 (presumably immediately inboard of the trailing wing tip vortices, close to wing tip paths
108 described by the previous bird), through most of the flap cycle.

109 In transects both directly streamwise and in line favoured V position (Fig. 1c), temporal phase
110 increases in proportion with distance behind the focal bird (Fig. 3a, d), with a full 2π cycle
111 change in phase over a complete wavelength; spatial phase is approximately maintained up to
112 4 m behind the leading bird. Previously, there was much uncertainty about spatial wing-beat
113 phasing and wingtip path coherence in flapping organisms. The only prior biological evidence
114 of this phenomenon comes from tethered locusts, where distance manipulations between a
115 leading locust and a follower altered the phase patterns of their wing-beats^{22,23}. Physical models
116 additionally support the potential for aerodynamic advantage due to phasing: appropriate
117 timing between tandem flapping model dragonfly wings improves aerodynamic efficiency²⁴.
118 Theoretical engineering models have taken into consideration flapping flight, and the
119 additional benefits a flapping wing may accrue in formation flight^{12,14}. Such models have
120 suggested that upwards of 20% variation exists in the induced power savings to be gained, if
121 flapping is done optimally in spatial phase, versus out of phase¹² (Supplementary Figure 4).

122 Here, we show that ibis flight in V formation does, on average, match fixed-wing aerodynamic
123 predictions (Fig. 1c, d), but that flock structure is highly dynamic (Fig. 2). Further, temporal
124 phasing of flapping relates to both streamwise and spanwise position. This indicates remarkable
125 awareness of, and ability to respond to, the wingpath – and thereby the spatial wake structure
126 – of nearby flock-mates. Birds flying in V formation flap with wingtip path coherence – the
127 wingtips take the same path – placing wings close to the oscillating positions of maximal
128 upwash. In contrast, birds flying in line flap in spatial antiphase – the wingtip paths are
129 maximally separated – consistent with avoidance of adverse downwash. This raises the

130 possibility that, in contrast with conventional aircraft, following birds may be able to benefit
131 from ‘drafting’ while, to a certain extent, avoiding an increased cost of weight support by
132 evading localised regions of downwash. Optimal flight speeds would differ between solo flight,
133 V formation flight and (whether net-beneficial or not) in-line flight, potentially providing some
134 account for the unstable, dynamic nature of V formation flocks.

135 **METHODS SUMMARY**

136 **Measurements:** We equipped 14 juvenile Northern bald ibises with back-mounted
137 synchronised GPS (5 Hz) and inertial measurement units (IMUs, 300 Hz), mass 23 g
138 (Supplementary Photo 1), which are custom made within our laboratory, and have been tested
139 and validated for accuracy and precision^{15,16}. At the start of migration, the birds mass was 1.30
140 ± 0.73 kg, the 23 g loggers comprising approximately 3% of the body mass of the smallest bird.
141 This is below the recommended 5% for flying animals²⁵. The ibises form part of a large-scale
142 conservation programme and had been hand-reared at Salzburg Zoo (Austria), imprinted onto
143 human foster parents, and taught to follow a powered parachute (paraplane) to learn the
144 migration routes (Full Online Methods). Experiment protocols were approved by the RVC local
145 Ethics and Welfare Committee. A GPS trace of the ibis flight imposed over Google EarthTM
146 (Landsat) can be found in Supplementary Photo 2 as a KML file. GPS data was post-processed
147 using GravNav WaypointTM software^{15,26}, and IMU data via custom-written MATLAB
148 (R2012b, Mathworks, Natick, Mass., USA) programmes^{16,26}. Mean flap frequency, speed and
149 peak detection protocols are detailed in Supplementary Figures 5 and 6. For further details on
150 post-processing, see Full Online Methods.

151 **Statistical Analysis:** Circular statistics¹⁷ were carried out in LabVIEW (NI, Austin, Texas,
152 USA). First order (Rayleigh test) and second order (Hodges-Ajne) statistics were employed to
153 test the phasing of wing-beats for significant deviations from random distribution. For further
154 details on statistical analysis, see Full Online Methods.

155 **Full Methods** and any associated references are available in the online version of the paper at
156 www.nature.com/nature.

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220 the field data. S.J.P., T.Y.H. and J.R.U. undertook the data processing and analyses; J.R.U.
221 performed the circular statistics. S.J.P., T.Y.H, A.M.W. and J.R.U wrote the manuscript, with
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223 Author Information: Reprints and permissions information is available at
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225 (SPortugal@rvc.ac.uk). The authors declare no competing financial interests.

226 **Figure Legends**

227 **Figure 1 V formation flight in migrating ibises. a**, Northern bald ibises (*Geronticus eremita*)
228 flying in V formation during a human-led migratory flight (photo credit, M. Unsöld). **b**, 3D
229 location histogram of the 7 minute flight section, showing position of individual ibis within the
230 V formation, with respect to flock centroid, measured via a 5 Hz GPS data logger. The colour

231 scale refers to the duration (s) a bird was present in each 0.25 m x 0.25 m grid. A plot detailing
232 the formation shape for the duration of the entire flight can be found in Supplementary Figure
233 7. **c**, histogram of number of flaps (colour coded) recorded within each 0.25 m x 0.25 m region
234 between all birds and all other birds. The majority of flaps occurred at an angle of
235 approximately 45 degrees to the bird ahead (or behind). Transects denoted by dashed lines,
236 directly behind or along the most populated V favoured position (just inboard of wingtip to
237 wingtip), are the same as those detailed in Fig. 3. **d**, a histogram detailing the total number of
238 flaps recorded between each bird-bird pair, with respect to position of the following bird. The
239 shaded area (*i-ii*) denotes the limits of optimal relative positioning, based on fixed-wing
240 aerodynamics.

241 **Figure 2 Histograms demonstrating the positional infidelity for each Northern bald ibis**
242 **within the V formation during the migratory flight.** The grey shaded V shape behind each
243 individual histogram ($n = 14$) denotes the structure for all individuals within the flock (see Fig.
244 **1b**). The colour code refers to the duration (s) a bird was present in each 0.25 m x 0.25 m grid.
245 While individual birds showed some bias towards the front, back, left or right regions of the V
246 formation, these positions were not maintained rigidly.

247 **Figure 3 Geometric and aerodynamic implications of observed spatial phase relationships**
248 **for ibises flying in a V formation.** Temporal phase increases as a function of position behind
249 more advanced birds (median +/- 95% CI of phase for each mean bird-bird interaction within
250 a region). When positioned at close to a wavelength in line with the V favoured position (**a-**
251 **c**), wingtip paths approximately match: observed temporal phases agree with those predicted
252 from the significant spatial phase relationship (thick black lines, +/- 95% CI) at the most
253 populated 1 m x 1 m region, using the mean wavelength measured for each position. When
254 positioned directly in line (**d-f**), following birds flap in spatial antiphase, maximally separating
255 wingtip paths. In this case the model line is derived from the median spatial phase for all bird-
256 bird interactions up to 4 m directly behind. Induced flow velocities (blue arrows, **c**, **f**), due to

257 the trailing wingtip vortices of the bird ahead (vortex cores denoted by grey circles), are
258 modelled as infinitely long, parallel vortex filaments. Birds flying in typical V formation keep
259 their wings close to the region of maximal induced upwash (**c**) throughout the flap cycle. Birds
260 flying directly behind flap in spatial antiphase, potentially reducing the adverse effects of
261 downwash (**f**), both in terms of magnitude and direction. For scale, the downwash directly
262 between the vortices would be (-) 0.3 m/s, between trailing vortices for a behind a bird of mass
263 1.3 kg, span 1.2 kg at a speed of 15 m/s (no account is taken of flapping, viscosity or wake
264 contraction). Alternative representations of (**a**) and (**d**) as Cartesian plots can be found in
265 Supplementary Figure 3, and Supplementary Figure 4 details the extended data array displayed
266 beyond the presented model line.

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277 **ONLINE METHODS**

278 **Birds.** Northern bald ibises (*Geronticus eremita*) ($n = 14$) were hatched at Salzburg Zoo in
279 March 2011, and imprinted immediately onto human foster parents (S.H. and D.T.). At four
280 months of age, the birds began training flights behind a powered parachute (paraplane).
281 Training flights lasted between 1-4 hours, and were up to 5 km in length. At the end of July,
282 birds were fitted with dummy loggers to prepare them for being equipped with data loggers for
283 the long-distance migratory flights. The ibis flock comprised 5 females and 9 males. The mass
284 of birds at the start of migration was 1.30 ± 0.73 kg. As such, the 23 g loggers comprised
285 approximately 3% of the body mass of the smallest bird. This is comfortably below the
286 recommended 5% for flying animals^{25,27}. The loggers were externally attached, using Velcro™
287 and a harness (Supplementary Photo 1). The dummy loggers remained on when birds were at
288 rest in the aviary, which was at all times bar the migratory flights. The first migratory flight
289 began in August. The total migratory flight plan was from the training site near Salzburg
290 (47.75377N, 13.052959E), to Orbetello, Italy (42.425484N, 11.232662E). Once en-route, birds
291 were flown, on average, every 3rd day. During flights, the birds followed the paraplane, but
292 were typically to the side of the vehicle, on average 147 m laterally, consistently to the left,
293 except for one turn (see Supplementary Fig. 5 and 6). All loggers functioned fully. The birds
294 were flown early in the morning (6 am departure), due to later flight times increasing the
295 occurrence of thermalling and gliding, resulting in the birds not following the paraplane
296 sufficiently. A GPS trace of the full flight, imposed over Google Earth™ (Landsat), can be
297 seen in Supplementary Photo 2 (as a KML file). The recorded flight was the 2nd stage of the
298 migration.

299 **Data loggers.** Further information pertaining to the loggers can be found in detail in
300 Usherwood *et al.*¹⁵ and Wilson *et al.*¹⁶. Briefly, GPS was recorded at 5 Hz and data were post-
301 processed differentially over the short baseline between base station and ibises, using Waypoint
302 GrafNav™ 8.10. L1 C/A code pseudo-range measurements were used to calculate the position
303 of each GPS loggers, with velocity determined from L1 Doppler measurements. Using this

304 approach can provide positional accuracy to 0.3 m and speed accuracy better than 0.1 m/s.
305 Accelerometer data were recorded at 300 Hz.

306 **Initial data processing.** The flight was checked for any periods when the birds had maintained
307 periods of circling flight (note we do include one circle in our sequence) through examination
308 of the GPS and accelerometer traces, and these sections were removed (less than 4 minutes of
309 the total flight duration). The remaining flight, therefore, consisted of straight-line flight. The
310 take-off and landing periods were removed, as, when taking off, it took approximately 4
311 minutes for the birds to form a coherent flock, and to follow the paraplane. Similarly, when the
312 paraplane began to descend at the end of the flight, the birds separated and begin to glide during
313 descent. The position of the paraplane was recorded and tracked via a data logger (see
314 Supplementary Fig. 5 and 6). The GPS, recorded at 5 Hz, was interpolated (MATLAB,
315 R2012b, Mathworks, Natick, Mass., USA) to the same sampling rate as the accelerometer data,
316 at 300 Hz. The interpolation replaced missing values in the GPS. GPS and accelerometer data
317 were passed through a 4th order Butterworth filter (MATLAB). For the production of the
318 histograms (Fig. 1 *b, c*), the original GPS values were used after being interpolated to a constant
319 5 Hz sampling frequency. In Fig. 1*b* and Fig. 2, the colour scale refers to the duration a bird
320 was present in each 0.25 m x 0.25 m grid. For Fig. 1*c*, the colour scale refers to the number of
321 flaps recorded in each grid. For Fig. 1*c*, the regional transect labelled 'directly behind' is offset
322 because, for display and analysis purposes, all data from the left side is mirrored to the right so
323 all data points are on one side, and so the centre of the first sampled region lies 0.125 m behind
324 the lead bird. Dorsal acceleration was used to determine each wing flap, and the upper reversal
325 point²⁸ of the flap cycle (see Supplementary Fig. 5 and 6). Note that this reversal point in
326 acceleration of the back need not relate to peak wing elevation – or indeed any particular wing
327 kinematic – for the phasing analysis to function.

328 **Height.** Height was recorded. The precision of height measurements, however, is lower than
329 for horizontal positions²⁹. This is because there are no satellites below the birds, and this

330 geometry of the satellites causes a reduction in precision²⁹. We do not consider vertical position
331 due to the small 'signal' of interest (very slight vertical deflections) to the relatively high 'noise'
332 (inevitable due to GPS satellite geometry). We chose a section where, according to the
333 available error measurement calculated by WaypointTM (see 'Data loggers'), the height values
334 were relatively consistent and that during this flight portion, the birds were flying close to the
335 same horizontal plane.

336 **Calculating flock formation and individual positioning (Figure 1b, 2, Main Article).** In
337 order to establish positioning of individuals and structure within the flock, a flock centroid was
338 determined. To calculate the centroid of the flock, the MATLAB function "*centroid*" was used.
339 This function calculates the centroid of a polygon. The MATLAB centroid function treated
340 each bird as a point of a polygon, and determined the centroid for each time point. An average
341 speed was calculated and any birds with a speed discrepancy higher than 3 m/s away from the
342 mean flock speed were removed for that time point. From this, the resultant centroid was
343 calculated now containing only birds close in position and speed. A rotation matrix was applied
344 to the data to reorientate the heading so all birds were heading 'up', and the direction of the
345 centroid is always on the positive 'Y' direction. The resultant matrix comprised a position for
346 each bird for each sampling point. Theta (Θ), the angle between each bird and the lead bird,
347 was calculated, transforming Cartesian to polar coordinates (*Cart 2 Pole*, MATLAB). For data
348 presentation in the histograms (Fig. 1b), the field of view being set to 15 m by 15 m, and the
349 area was divided in a 60-by-60 grid of bins (0.25 m x 0.25 m). Position 0/0 is the centroid. The
350 heat histograms are displayed as contour plots with 5 contour levels.

351 During the 7 minute section of V formation flight, individual birds show a certain degree of
352 positional infidelity within the V flock (Fig. 2, see also Supplementary Figure 1 and
353 Supplementary Video 1). While individuals contribute to the statistical V formation, their
354 positioning is inconsistent. Certain individuals showed general preferences for a particular area
355 within the V formation, whether left, right, front or rear, but the variability in positioning

356 resulted in no clear leader within the flock (Fig. 2). Navigational ability and kin selection have
357 been proposed as major drivers of leadership in V formation flight³⁰, with more experienced
358 birds or parents of a family group taking the lead³⁰. The ibis flock in the present study
359 comprised birds of the same age (< 1 year old), with no prior navigational experience of the
360 route and no parent-offspring relationships. The absence of immediate kin selection and learnt
361 navigational ability as possible factors determining a V formation structure in the recorded
362 flight strengthens the evidence for an aerodynamic function behind the V formation observed
363 in the ibis. The young age of the birds, however, may be the main factor as to why there is a
364 lack of a clear leader in the ibis flock, contrasting with previous observations of adult ibises, in
365 which consistent leaders in flocks were identified³¹. Spontaneous and inconsistent leadership
366 has been identified in bird flocks either where no consistent social hierarchy exists³², or when
367 no prior knowledge of a route is known³³. For other 'classic' V formation fliers, the first
368 migration is a significant cause of mortality for young birds, even when migrating with parents.
369 As such, aerodynamic mechanisms that reduce the energetic cost of (albeit only very
370 infrequent) migratory flight, may present considerable selection advantage.

371 **Movement within flock (Supplementary Figure 1).** Movement within the V formation was
372 investigated by taking a 45 degree line, the preferred angle for positioning with the V (Fig. 1c)
373 as a transect from the apex of the V. The apex was determined by the intersection of two 45⁰
374 lines, down each side of the V formation. For every bird for each time point, the distance was
375 taken for how far it is positioned from the 45 degree perpendicular transect line. For simplicity
376 of analysis, all data were flipped (mirrored) to all be plotted against one 45 degree line. For
377 Supplementary Fig. 1 (a), the red circles represent the original positions of the birds, for all
378 birds and all times. From this, the shortest distance to the 45 degree line was calculated (blue
379 line) and the position was projected on the 45 degree line, and then the distance between
380 projected position and green circle (the centroid) was calculated. The standard deviations (SD)
381 are from the blue perpendicular line rather than the absolute distance, and represent how much

382 the position varies with respect to the line. A mean SD was then calculated for each
383 perpendicular/parallel relationship (Supplementary Fig. 1, *b,c*). The positioning of all
384 individuals varies more along the line than out from the line (Supplementary Fig. 1*c*). If the
385 changes in position were due only to logger measurement error, the variation in perpendicular
386 and parallel distance and position would be expected to be equal. Because most of the variation
387 is present along the line, the variation can be confidently attributed predominantly to bird
388 movement, not logger noise.

389 **Circular statistics and phasing analysis.** Circular statistics were applied using LabVIEW (NI,
390 Austin, Texas, USA), following that of Fisher³⁴⁻³⁷. All height data were included for circular
391 statistical analysis, but the data were not filtered. The filtered *X* and *Y* data were used, as
392 detailed above. The *X* and *Y* positions were calculated with respect to the direction of travel.

393 The relative positions (in the direction of flight) and phase relationships (as a proportion of the
394 flap cycle of each 'ahead' bird) was determined for every bird following every other bird.
395 Determining appropriate independent sample criteria when considering phases is vital³⁷, and
396 presents a challenge when analyzing phase relationships. Consider the case of two birds flying
397 at the same relative position and at the same frequency; they would maintain the same phase
398 relationship indefinitely. Each flap would certainly not be considered an independent sample.
399 As a conservative alternative, we take a mean phase for any bird-bird pairing for a given area
400 to be an independent sample; no account is taken of the length of time or number of flaps spent
401 within the area. Perversely, this technique actually makes use of the variability in relative
402 position, and would be poor for absolutely rigid V formations.

403 Statistical tests³⁴⁻³⁷ were performed for two regions, combining left and right sides: one
404 representing V formation flight, (from 0.49 m to 1.49 m both spanwise and streamwise),
405 containing the highest density of flaps; the other for nose-to-tail, streamwise flight, covering a

406 volume 0.25 m spanwise from midline (so 0.5 m behind) and 4 m behind. This provided $n=165$
407 and $n=160$ bird-bird pairs for V formation and nose-to-tail regions respectively.

408 The Rayleigh test was applied to determine the presence of a single unimodal direction in phase
409 without preconceptions of any mean direction. This found a significant departure from
410 randomness – a significant unimodal bias – in phase (whether temporal or spatial) for the V
411 formation region. Both Rayleigh's test (parametric) and Hodges-Ajne³⁴⁻³⁷ (a non-parametric
412 test) on this region indicate that both the temporal phase and the spatial phase (taking into
413 account the wavelength of whichever bird is ahead) are significantly different from those that
414 would be found from a random distribution^{38,39}.

415 The median phase for a given region – and its 95% confidence intervals – allows a specified
416 alternative to be tested against. Fig. 3*a,d* and Supplementary Fig. 3*a,b* shows the median
417 statistics in graphical form for the two regions. Zero or 'in' spatial phase falls outside the 95%
418 confidence intervals for the nose-to-tail region.

419 The median spatial phases for the two regions described above were used to predict the
420 temporal phases for 0.25 m x 0.25 m along two streamwise transects using the wavelength
421 measured for each volume along the transect. If the median spatial phase was π – out of phase,
422 as it is close to in the nose-to-tail transect – we would predict it to be π every integer number
423 of wavelengths, and 0 or 'in' temporal phase at $\frac{1}{2}$, $\frac{3}{2}$, $\frac{5}{2}$ etc. wavelengths. The model – with
424 bounding confidence intervals due the spatial median – is shown as lines in Fig. 3*a,d*. Measured
425 median temporal phases (+/- 95% confidence intervals of the median) broadly match the
426 predicted values (see also Supplementary Fig. 3*a,b*, which gives the same data in Cartesian
427 form). While the fit between model and observed temporal phases is visually convincing,
428 formal statistical treatment is avoided because of uncertainty over independence between
429 neighbouring spatial regions along the transects.

430 **Modelled induced flow behind flapping birds.** The implications of flap phasing in terms of
431 potential interaction with induced flows are shown in Fig. 3 (*c,f*). For this model, it is assumed
432 that the wingtip vortex left behind a bird ahead of a follower (the grey bird) follows the wingtip
433 path through space – the convection of the vortex core (which, on average, will be inwards and
434 downwards) is neglected^{40,41}. Induced flow-fields are modelled following the Biot-Savart
435 law^{42,43}, treating the wingtip vortices as infinitely long, parallel filaments; no account is taken
436 of variation in lift throughout the wingstroke cycle. Induced flows near the vortex cores are not
437 modelled; these regions are represented by grey circles. That, while being correct given the
438 reductions and assumptions described, should not be taken as accurate quantitative calculations
439 of the local flowfield. However, the principles they demonstrate – the strongest region of
440 upwash and downwash close outboard and inboard respectively of the wingtip path – meets
441 basic aerodynamic expectations and recent modelling results^{42,43}. For scale, the downwash
442 directly between the vortices would be (-) 0.3 m/s, between trailing vortices for a behind a bird
443 of mass 1.3 kg, span 1.2 kg at a speed of 15 m/s, (without modelling flapping or wake
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477

478 **SUPPLEMENTARY TABLE 1**

479 Statistical parameters and summary for circular statistical analysis of wing-beat phasing (see
480 Supplementary Information Text). $P < 0.05$ indicates a significant directional preference. When
481 flying in a favoured V position, birds exhibit significant temporal and spatial phasing of their
482 wing-beats, which is absent when in a streamwise position. For the favoured V position, 165
483 bird-bird pairs were analysed, which incorporated 3816 flap-flap interactions. For the
484 streamwise position, 160 bird-bird pairs were analysed, incorporating 3153 flap-flap
485 interactions.

486 **SUPPLEMENTARY TABLE 2**

487 Raw data used for phasing analysis.

488 **SUPPLEMENTARY FIGURE 1**

489 Confirmation that movement within the flock is not a result of potential logger measurement
490 error. The red circles (a) represent the positions of the birds, for all birds and all times, with
491 respect to the flock centroid. From this, the shortest distance (red lines) to the 45 degree line
492 (blue line) was calculated and the position was projected on the 45 degree line, and then the
493 distance between projected position and green dot (the centroid) was calculated (a). The
494 standard deviations (SD) are from the blue perpendicular line rather than the absolute distance,
495 and represent how much the position varies with respect to the line. A mean SD was then

496 calculated for each perpendicular/parallel relationship (**b,c**). The positioning of all individuals
497 varies more along the line than out from the line (**c**). If the changes in position were logger
498 measurement error alone, the variation in perpendicular and parallel distance and position
499 would be expected to be equal. Instead, there is greater variability along the 45⁰ line, indicating
500 apparent motions within the V formation where not merely logger error artefact.

501 **SUPPLEMENTARY FIGURE 2**

502 Median spatial phase bounded by 95% confidence intervals (grey shading) for flying in the
503 most populated 1 m square (V formation, **a**, $n=165$ bird-bird pairs) or in a 0.5 m region directly
504 behind for 4 m streamwise (**b**, $n=160$ bird-bird pairs).

505 **SUPPLEMENTARY FIGURE 3**

506 Alternative representation of Fig. 3 plots in Cartesian coordinates. The black line indicates the
507 predicted temporal phase (directly upward being in phase - flapping at the same time) as a
508 function of distance from relative 'ahead' bird (indicated by radial distance). The temporal
509 phase is predicted from 1) the median spatial phase at the most populated 1 m x 1 m region (V
510 formation, **a**) or the region directly behind each 'ahead' bird (0.5 m across, 4 m behind, **b**), and
511 2) the mean measured wavelength between birds for a 0.25 m x 0.25 m area along a transect in
512 line with the most populated region (**a**) or directly streamwise, nose-to-tail (**b**). Median
513 measured values for each area within each transect (grey dots; grey curves denote 95%
514 confidence intervals of the median) broadly match prediction up to 4 m between birds.

515

516

517 **SUPPLEMENTARY FIGURE 4**

518 Phase data as for Fig. 3 and Supplementary Fig. 3, but for an extended streamwise range, also
519 indicating the number of bird-bird pairs of flap-flap interactions has histograms, either in line

520 with the V favoured position **(a)**, or directly streamwise, nose-to-tail **(b)**. Note that the
521 underlying (grey) line is *not* the same as shown (black line) in Fig. 3 and Supplementary Fig.
522 3. In this case, it shows the phase predicted to be optimal through theoretical, supported by
523 numerical modelling. Maximum benefit would be achieved in line with the V favoured position
524 if the following bird wings exactly followed the trailing wingtip vortices – and so,
525 approximately, the wingtip path – of the bird ahead; the wings should be ‘in’ spatial phase, or
526 ‘in’ temporal phase every whole-integer wavelength behind the bird ahead. Minimum
527 detriment due to downwash for a bird flying directly behind another if the wingpaths were out
528 of phase; the wings should flap in temporal antiphase every whole-integer wavelength behind
529 the bird ahead.

530 **SUPPLEMENTARY FIGURE 5**

531 Three panelled figure focusing on 43 minutes of one migratory flight for the 14 Northern bald
532 ibises, detailing: **(a)** GPS trace of the 14 birds, the close proximity of the individuals precluding
533 the identification of single traces. An example of a single flight trace, imposed over Google
534 EarthTM (Landsat), can be seen in Supplementary Photo 2 as a KML file. Further details can be
535 found in Supplementary Fig. 6. **(b)** average speed (\pm SD) and, **(c)** average flap frequency (\pm
536 SD). The shaded grey area refers to the 7 minute section of clear V formation flight used for
537 subsequent analysis (see Fig. 2, and Supplementary Fig. 6).

538 **SUPPLEMENTARY FIGURE 6**

539 Highlight of the grey shaded area in Supplementary Fig. 5, highlighting the 7 minute V
540 formation section of migratory flight for the 14 Northern bald ibises, detailing: **(a)** GPS trace
541 of the 14 birds. An example of a single flight trace, imposed over Google EarthTM (Landsat),
542 can be seen in Supplementary Photo 2 as a KML file. The blue line represents the path of the
543 paraglider containing the foster parent. **(b)** average speed (\pm SD) and **(c)** average flap frequency
544 (\pm SD). **(d)** example dorsal acceleration trace taken from the 300 Hz Inertial Measurement

545 Unit. The black box positioned at 150 s refers to the zoomed in section displayed in (e), which
546 demonstrates how each flap was detected via our peak detect analysis (see Full Online
547 Methods). The red line denotes the raw trace, and the blue line the filtered data. The circles
548 highlight position of identified peaks.

549 **SUPPLEMENTARY FIGURE 7**

550 Location histogram of the 7 minute flight section, showing position of individual ibis within
551 the V formation, measured via a 5 Hz GPS data logger. The grey scale refers to the duration
552 (s) a bird was present in each 0.25 m x 0.25 m grid. The outer red line denotes the flock shape
553 for the entire 43 minutes duration of the flight, superimposed around the 7 minute section (See
554 Fig. 1b). The red line encloses 95% of available data points.

555 **SUPPLEMENTARY PHOTO 1**

556 Photograph of a Northern bald ibis, showing data logger attachment via a Velcro™ fastening
557 to a plate, which in turn is attached to a harness.

558 **SUPPLEMENTARY PHOTO 2**

559 Google Earth™ (Landsat, KML file) image displaying the full flight of the ibis flock, recorded
560 via the 5 Hz GPS data logger.

561 **SUPPLEMENTARY VIDEO 1**

562 An animated GIF showing a section of the ibis flight, taken from the 5 Hz GPS logger data.
563 Each individual bird is identified by a number displayed on the tip of the left wing. To play the
564 Video, download the file and open in a web browser. The Video will then play automatically.

565 **SUPPLEMENTARY VIDEO 2**

566 A short video clip of the ibis flying behind the paraplane during a training flight.

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