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

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Many species travel in highly organised groups[1-3]. The most quoted function of these configurations is to reduce energy expenditure and enhance locomotor performance of individuals within the assemblage[4-11]. The distinctive V formation of bird flocks has long intrigued researchers and continues to attract both scientific and popular attention[4,7,9-14]. The well held belief is that such aggregations give an energetic benefit for those birds which are flying behind and to one side of another bird through using the regions of upwash generated by the wings of the preceding bird[4,7,9-11], though a definitive account of the aerodynamic implications of these formations has remained elusive. Here we show that individuals flying within a V flock position themselves in aerodynamically optimum positions, in so far as they agree with aerodynamic theoretical predictions. Furthermore, we demonstrate that birds exhibit wingtip-path coherence when flying in V positions, flapping spatially in phase enabling upwash capture to be maximised throughout the entire flap cycle. In contrast, when birds fly immediately behind another bird – in a streamwise position – there is no wingtip path coherence; the wing-beats are in spatial anti-phase. This could potentially reduce the adverse effects of downwash for the following bird. These aerodynamic accomplishments were previously not thought possible for birds because of the complex flight dynamics and sensory feedback that

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

Fixed-wing aerodynamic theories have predicted the exact spanwise positioning that birds should adopt within a V formation flock to maximise upwash capture[4,9-14]. The primary empirical evidence to confirm that this mechanism is used is a reduction in heart rate and wing-beat frequency in pelicans flying in a V formation[7]. There is a general lack of experimental data from free-flying birds, mainly due to the complications of measuring the intricate and three-dimensional complexity of formation flight, and the lack of appropriate devices to monitor and record such information. Therefore, the precise aerodynamic interactions which birds employ to exploit upwash capture have not been identified. To investigate the purported aerodynamic interactions of V formation flight, we studied a free-flying flock of critically endangered Northern bald ibises (*Geronticus eremita*) (Fig. 1*a*). We used novel technology[15,16] to measure the position, speed and heading of all birds within a V formation. We recorded position and every wing flap of 14 birds during 43 minutes of migratory flight using back-mounted integrated Global Positioning System (5 Hz) (GPS) and inertial measurement units (300 Hz) (IMUs) (see Full Online Methods)[15,16]. The precision of these measurements allows the relative positioning of individuals within a V to be tracked, and the potential aerodynamic interactions to be investigated at a level and complexity not previously feasible.

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

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54   populated (0.25 m) spanwise region was at 0.904 m, resulting in a wingtip overlap[9-13] of 0.115

55   m (Fig. 1*c, d*, wingspan b = 1.2 m). This falls within the bounds of fixed-wing theory

56   predictions[9-13] for maximising the benefits from upwash, which range from zero wingtip

57   overlap (assuming no wake contraction[4]) to, maximally, 0.13 m (assuming elliptical loading

58   over the pair of wings, and full wake contraction from wingspan b to π 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 complex[9-14]. 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 devices[12]. 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 IMU[15]. 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    $$\phi_{spatial} = \phi_{temporal} - 2\pi\lambda$$

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. 1*c*), Rayleigh's test[17] 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. 3*a*, *b*) (see Supplementary Table 1 for

85   further statistics; Supplementary Figure 2*a*, 3*a*, 4*a*). 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. 3*b*, *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. 1*c*) 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 2*b*, 3*b*, 4*b*). 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. 3*d, e*, see also Supplementary Figure 2*b*, 3*b*), potentially reducing the adverse

98   effects of downwash (Fig. 3*f*), 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 high[18], 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. 1*c*), temporal phase

110   increases in proportion with distance behind the focal bird (Fig. 3*a, 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 efficiency[24].

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 phase[12] (Supplementary Figure 4).

122   Here, we show that ibis flight in V formation does, on average, match fixed-wing aerodynamic

123   predictions (Fig. 1*c, 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

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

METHODS SUMMARY

Measurements: We equipped 14 juvenile Northern bald ibises with back-mounted synchronised GPS (5 Hz) and inertial measurement units (IMUs, 300 Hz), mass 23 g (Supplementary Photo 1), which are custom made within our laboratory, and have been tested and validated for accuracy and precision[15,16]. At the start of migration, the birds mass was 1.30 $\pm$ 0.73 kg, the 23 g loggers comprising approximately 3% of the body mass of the smallest bird. This is below the recommended 5% for flying animals[25]. The ibises form part of a large-scale conservation programme and had been hand-reared at Salzburg Zoo (Austria), imprinted onto human foster parents, and taught to follow a powered parachute (paraplane) to learn the migration routes (Full Online Methods). Experiment protocols were approved by the RVC local Ethics and Welfare Committee. A GPS trace of the ibis flight imposed over Google Earth™ (Landsat) can be found in Supplementary Photo 2 as a KML file. GPS data was post-processed using GravNav Waypoint™ software[15,26], and IMU data via custom-written MATLAB (R2012b, Mathworks, Natick, Mass., USA) programmes[16,26]. Mean flap frequency, speed and peak detection protocols are detailed in Supplementary Figures 5 and 6. For further details on post-processing, see Full Online Methods.

Statistical Analysis: Circular statistics[17] were carried out in LabVIEW (NI, Austin, Texas, USA). First order (Rayleigh test) and second order (Hodges-Ajne) statistics were employed to test the phasing of wing-beats for significant deviations from random distribution. For further 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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218   **Author contributions** S.J.P., S. Hailes., A.M.W. and J.R.U. developed the concept of the

219   paper. J.F., S.H. and D.T. reared and trained the birds. S.J.P., S.H., D.T., B.V. and J.F. collected

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

222   input from all authors.

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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   1**b**). 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[TM]

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[TM] (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[TM] 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 point[28] 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 positions[29]. This is because there are no satellites below the birds, and this

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330   geometry of the satellites causes a reduction in precision[29]. 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 Waypoint^{TM} (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. 1*b*), 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

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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 flight[30], with more experienced

358 birds or parents of a family group taking the lead[30]. 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 identified[31]. Spontaneous and inconsistent leadership

366 has been identified in bird flocks either where no consistent social hierarchy exists[32], or when

367 no prior knowledge of a route is known[33]. 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. 1*c*)

373 as a transect from the apex of the V. The apex was determined by the intersection of two 45^0

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

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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 Fisher[34-37]. 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 vital[37], 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 tests[34-37] 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-Ajne[34-37] (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 ½, 3/2, 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.

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

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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 45^0 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.

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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

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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   Earth^{TM} (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 (± SD) and, (**c**) average flap frequency (±

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 Earth^{TM} (Landsat),

542   can be seen in Supplementary Photo 2 as a KML file. The blue line represents the path of the

543   paraplane containing the foster parent. (**b**) average speed (± SD) and (**c**) average flap frequency

544   (± 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. 1*b*). 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[TM] fastening

557   to a plate, which in turn is attached to a harness.

558   **SUPPLEMENTARY PHOTO 2**

559   Google Earth[TM] (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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