Position and flap phasing between ibises in formation flight: evidence for upwash exploitation and downwash avoidance?

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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[4-12]. 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[4,7,9-13], though a definitive account of the aerodynamic implications of these formations has remained elusive. This has been, in part, due to the lack of suitable technology limiting the study of such behaviour in free-flying birds, and the shortcomings of applying fixed-wing aerodynamic theories to flapping flight. 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 Supplementary 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 Supplementary 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 ("favoured V position") of the bird ahead. This centre of the most populated (0.25 m) spanwise region was at 0.904 m, resulting in a wingtip overlap[9-13] of 0.115 m (Fig. 1*d*, wingspan $b = 1.2$ m). This falls within the bounds of fixed-wing theory predictions[9-13] for maximising the benefits from upwash, which range from zero wingtip overlap (assuming no wake contraction[4]) to, maximally, 0.13 m (assuming elliptical loading over the pair of wings, and full wake contraction from wingspan b to $\pi\, b\,/4$) [9].

During this 7 minute section of V formation flight, individual birds show a certain degree of positional infidelity within the V flock (Fig. 2, see also Supplementary Figure 1 and Supplementary Movie 1). While individuals contribute to the statistical V formation, their positioning is inconsistent. Certain individuals showed general preferences for a particular area within the V formation, whether left, right, front or rear, but the variability in positioning resulted in no clear leader within the flock (Fig. 2). Navigational ability and kin selection have been proposed as major drivers of leadership in V formation flight[17], with more experienced birds or parents of a family group taking the lead[17]. The ibis flock in the present study comprised birds of the same age (< 1 year old), with no prior navigational experience of the route and no parent-offspring relationships. The absence of immediate kin selection and learnt navigational ability as possible factors determining a V formation structure in the recorded flight strengthens the evidence for an aerodynamic function behind the V formation observed in the ibis. The young age of the birds, however, may be the main factor as to why there is a lack of a clear leader in the ibis flock, contrasting with previous observations of adult ibises, in which consistent leaders in flocks were identified[18]. Spontaneous and inconsistent leadership has been identified in bird flocks either where no consistent social hierarchy exists[19], or when no prior knowledge of a route is known[20]. For other 'classic' V formation fliers, the first migration is a significant cause of mortality for young birds, even when migrating with parents. As such, aerodynamic mechanisms that reduce the energetic cost of (albeit only very infrequent) migratory flight, may present considerable selection advantage.

We demonstrate that when flying in a V, ibises position themselves in fixed-wing mathematically predicted positions[4,9-11]. However, the wake path of flapping birds (in this study, ibises spent 97% of their time flapping; Supplementary Methods) is complex[9-14]. Wingtip path coherence, where a flying object flaps its wings in spatial phase with that of the individual it is following, has been proposed as a method that would both utilise and maximise upwash capture in V formation flight of birds and flying robotic devices[12]. Whether birds are able to take advantage of this additional level of complexity present in flapping flight (in comparison to that of fixed-wing flight) had previously remained unanswered.

Within the ibis flock, individual flaps for each bird were described from the dorsal acceleration signal from the IMU[15]. The temporal phase $\phi_{temporal}$ is defined here as the proportion of a flap cycle of a leading bird at which a following bird initiates a flap. A value of π/2 indicates that the following bird started a given flap a quarter of the way through the flap of the bird ahead of it; a value of 3π/2 indicates the following bird initiates a flap ¾ of the way through – equivalent to ¼ or -π/2 behind – the bird it is following. Spatial phase $\phi_{spatial}$ makes use of the temporal phases calculated above, and takes account of the number of wavelengths, λ, between the bird ahead and the bird behind:

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

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

In the most populated 1 m by 1 m favoured V position (Fig. 1*c*), Rayleigh's test[21] for circular statistics indicates a significant unimodal bias in both temporal (Rayleigh, $P = 0.018$, mean phase = 0.857; Hodges-Ajne, $P = 0.012$) and, more strongly, spatial (Rayleigh, $P = 0.003$, mean phase = -1.155; Hodges-Ajne, $P = 0.004$) phases (Fig. 3*a*, *b*) (see Supplementary Table 1 for further statistics; Supplementary Figure 2*a*, 3*a,* 4*a*). Flapping in spatial phase indicates that the wing of a following bird goes up and down following the path through the air previously described by the bird ahead. The following bird then benefits from consistently flapping into the upwash region from the preceding bird (Fig. 3*b*, *c*), presumably reducing the power requirements for weight support. Ibises, when flying in the 45 degree V favoured position (Fig. 1*c*), keep their wings close to the region of maximal induced upwash throughout the entire flap cycle (Fig. 3*c*), by significant spatial wingtip coherence. This wingtip path coherence allows the tracking of the beneficial air throughout the full flap cycle, maximising the potential to capture upwash[12,14].

In contrast, birds flying directly behind, tracking the bird ahead in a streamwise position (sampled region 0.5 m across, 4 m streamwise, Fig. 1*c*) flap in close to spatial antiphase (median = 2.897, where precise antiphase would be +/-3.142), significantly ($P < 0.05$) deviating from flapping 'in' spatial phase (see Supplementary Table 1 for further statistics; Supplementary Figure 2*b*, 3*b*, 4*b*). As such, the wingtip paths of the following bird do not match those of the bird they are following, and the wingtip paths are close to maximally separated. Birds flying directly behind another bird in a streamwise fashion flap in spatial antiphase (Fig. 3*d, e*, see also Supplementary Figure 2*b*, 3*b*), potentially reducing the adverse effects of downwash (Fig. 3*f*), both in terms of magnitude and direction. If this position was aerodynamically adaptive, it would be predicted to be favoured at higher speeds, where parasite power is relatively high[22], compared with the induced power costs of weight support; forms of slipstreaming can reduce the drag experienced by followers[5,6,8,23], even in cases where there is zero net horizontal momentum flux in the wake (i.e. drag=thrust) – as in steady swimming – due to temporal or local spatial[5,25,26] fluctuations from mean wake conditions. Whether the position immediately behind is accidental or intentional, or whether it offers any aerodynamic advantage or cost, is currently unclear. However, the wing-beat phasing observed when in this position would serve to displace the following bird's wings from regions of greatest downwash (presumably immediately inboard of the trailing wing tip vortices, close to wing tip paths described by the previous bird), through most of the flap cycle.

In both the streamwise and V position transects (Fig. 1*c*), temporal phase increases in proportion with distance behind the focal bird (Fig. 3*a*, *d*), with a full 2π cycle change in phase over a complete wavelength; spatial phase is approximately maintained up to 4 m behind the leading bird. Previously, there was much uncertainty about spatial wing-beat phasing and wingtip path coherence in flapping organisms. The only prior biological evidence of this phenomenon comes from tethered locusts in wind tunnels, where distance manipulations between a leading locust and a follower altered the phase patterns of their wing-beats[,26,27]. Similarly, phasing of model dragonfly wings was shown to improve aerodynamic efficiency by recovering energy from the wake wasted as swirl, in a manner analogous to coaxial contra-rotating helicopter rotors[28] Theoretical engineering models have taken into consideration flapping flight, and the additional benefits a flapping wing may accrue in formation flight[12,14]. Such models have suggested that upwards of 20% variation exists in the induced power savings to be gained, if flapping is done optimally in spatial phase, versus out of phase[12] (Supplementary Figure 4).

Here, we show that ibis flight in V formation does, on average, match fixed-wing aerodynamic predictions (Fig. 1*d*), but flock structure is highly dynamic (Fig. 2). Further, temporal phasing of flapping relates to both streamwise and spanwise position. This indicates remarkable awareness of, and ability to respond to, the wingpath – and thereby the spatial wake structure – of nearby flock-mates. Birds flying in V formation flap with wingtip path coherence – the wingtips take the same path – placing wings close to the oscillating positions of maximal upwash. In contrast, birds flying in line flap in spatial antiphase – the wingtip paths are maximally separated – consistent with avoidance of adverse downwash. This raises the 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 (Fig. 1*a*) 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]. The mass of birds at the start of migration was 1.30 ± 0.73 kg. As such, the 23 g loggers comprised approximately 3% of the body mass of the smallest bird. This is comfortably below the recommended 5% for flying animals[29]. The ibises form part of a large-scale conservation programme (Waldrappteam, http://www.waldrappteam.at), 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 (Supplementary Methods). Experiment protocols were approved by the RVC local Ethics and Welfare Committee. A GPS trace of the ibis flight imposed over Google Earth^{TM} (Landsat) can be found in Supplementary Photo 2 as a KLM file. GPS data was post-processed using GravNav Waypoint^{TM} software[15,30], and IMU data via custom-written MATLAB (R2012b, Mathworks, Natick, Mass., USA) programmes[16,30]. Mean flap frequency, speed and peak detection protocols are detailed in Supplementary Figures 5 and 6. For further details on post-processing, see Supplementary Methods.

Statistical Analysis: Circular statistics[21] 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 Supplementary Methods.

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

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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trained the birds. S.J.P., T.Y.H. and J.R.U. undertook the data processing and analyses; J.R.U performed the circular statistics. S.J.P. wrote the manuscript with T.Y.H, A.M.W. and J.R.U, with input from all authors.

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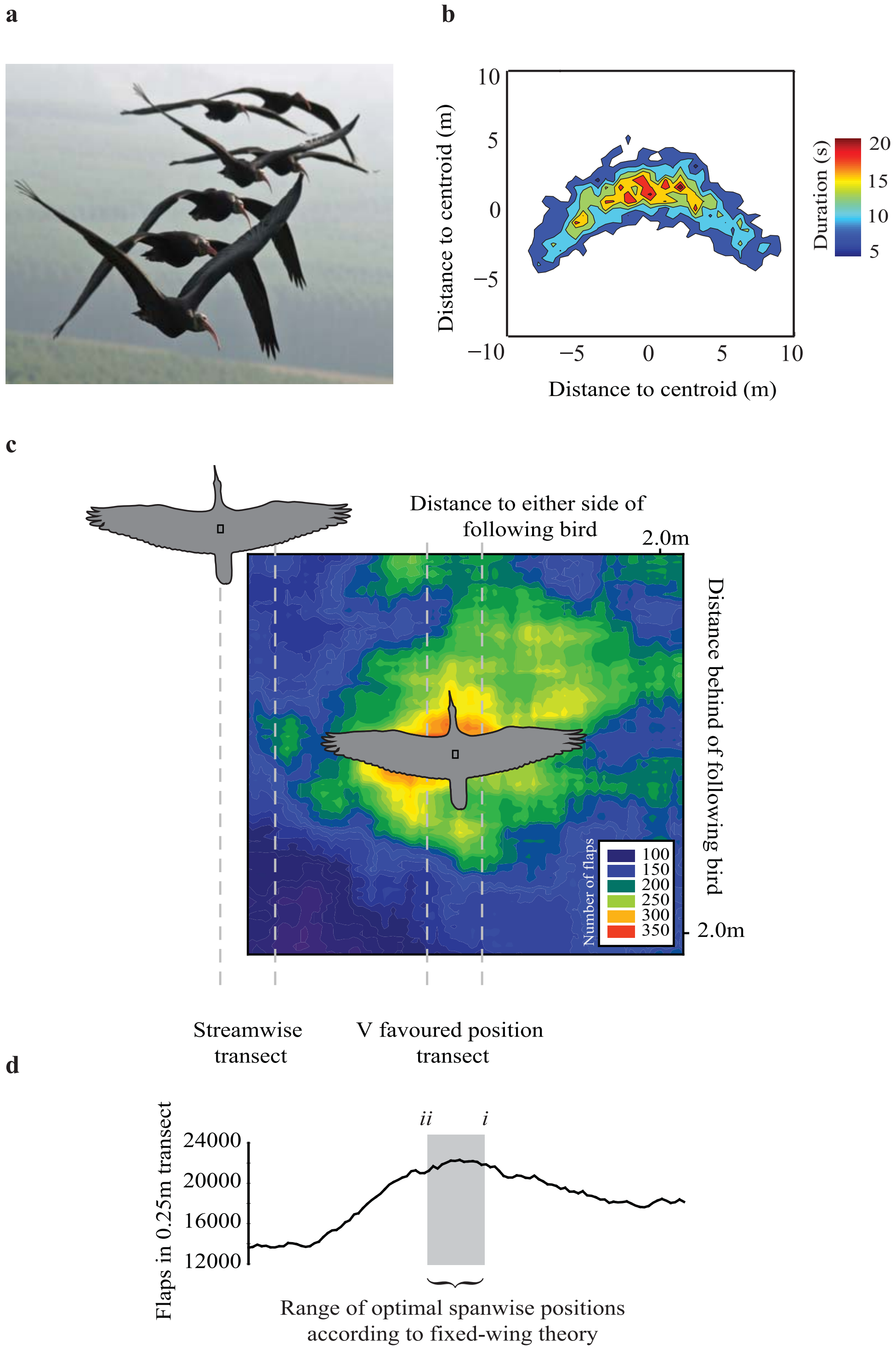
Figure Legends

Figure 1 **V formation flight in migrating ibises.** **a**, Northern bald ibises (*Geronticus eremita*) flying in V formation during a human-led migratory flight (photo credit, M. Unsöld). **b**, location histogram of the 7 minute flight section, showing position of individual ibis within the V formation, with respect to flock centroid, measured via a 5 Hz GPS data logger. The colour scale refers to the duration (s) a bird was present in each 0.25 m x 0.25 m grid. A plot detailing the formation shape for the duration of the entire flight can be found in Supplementary Figure 7. **c**, histogram of number of flaps (colour coded) recorded within each 0.25 m x 0.25 m region between all birds and all other birds. The majority of flaps occurred at an angle of approximately 45 degrees to the bird ahead (or behind). Transects denoted by dashed lines, directly behind or along the most populated region (just inboard of wingtip to wingtip), are the same as those detailed in Fig. 3. **d**, histogram detailing the total number of flaps recorded between a bird-bird pair, with respect to position of the following bird. The shaded area denotes the limits of optimal relative positioning, based on fixed-wing aerodynamics (see references 9-11).

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

Figure 3 **Geometric and aerodynamic implications of observed spatial phase relationships for ibises flying in a V formation**. Temporal phase increases as a function of position behind more advanced birds (median +/- 95% CI of phase for each mean bird-bird interaction within a region). When positioned at close to a wavelength inline with the V favoured position (**a-c**), wingtip paths approximately match: observed temporal phases agree with those predicted from the significant spatial phase relationship (thick black lines, +/- 95% CI) at the most populated 1 m x 1 m region, using the mean wavelength measured for each position. When positioned directly in line (**d-f**), following birds flap in spatial antiphase, maximally separating wingtip paths. In this case the model line is derived from the median spatial phase for all bird-bird interactions up to 4 m directly behind. Induced flow velocities (blue arrows, **c**, **f**), due to the trailing wingtip vortices of the bird ahead (vortex cores denoted by grey circles), are modelled as infinitely long, parallel vortex filaments. Birds flying in typical V formation keep their wings close to the region of maximal induced upwash (**c**) throughout the flap cycle. Birds flying directly behind flap in spatial antiphase, potentially reducing the adverse effects of downwash (**f**), both in terms of magnitude and direction. 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 (no account is taken of flapping, viscosity or wake contraction). Alternative representations of (**a**) and (**d**) as Cartesian plots can be found in Supplementary Figure 3, and Supplementary Figure 4 details the extended data array displayed beyond the presented model line.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Distance to centroid (m)
Distance to centroid (m)
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Distance to either side of following bird
2.0m
Distance behind of following bird
2.0m
Number of flaps
100
150
200
250
300
350
Streamwise transect
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Flaps in 0.25m transect
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ii
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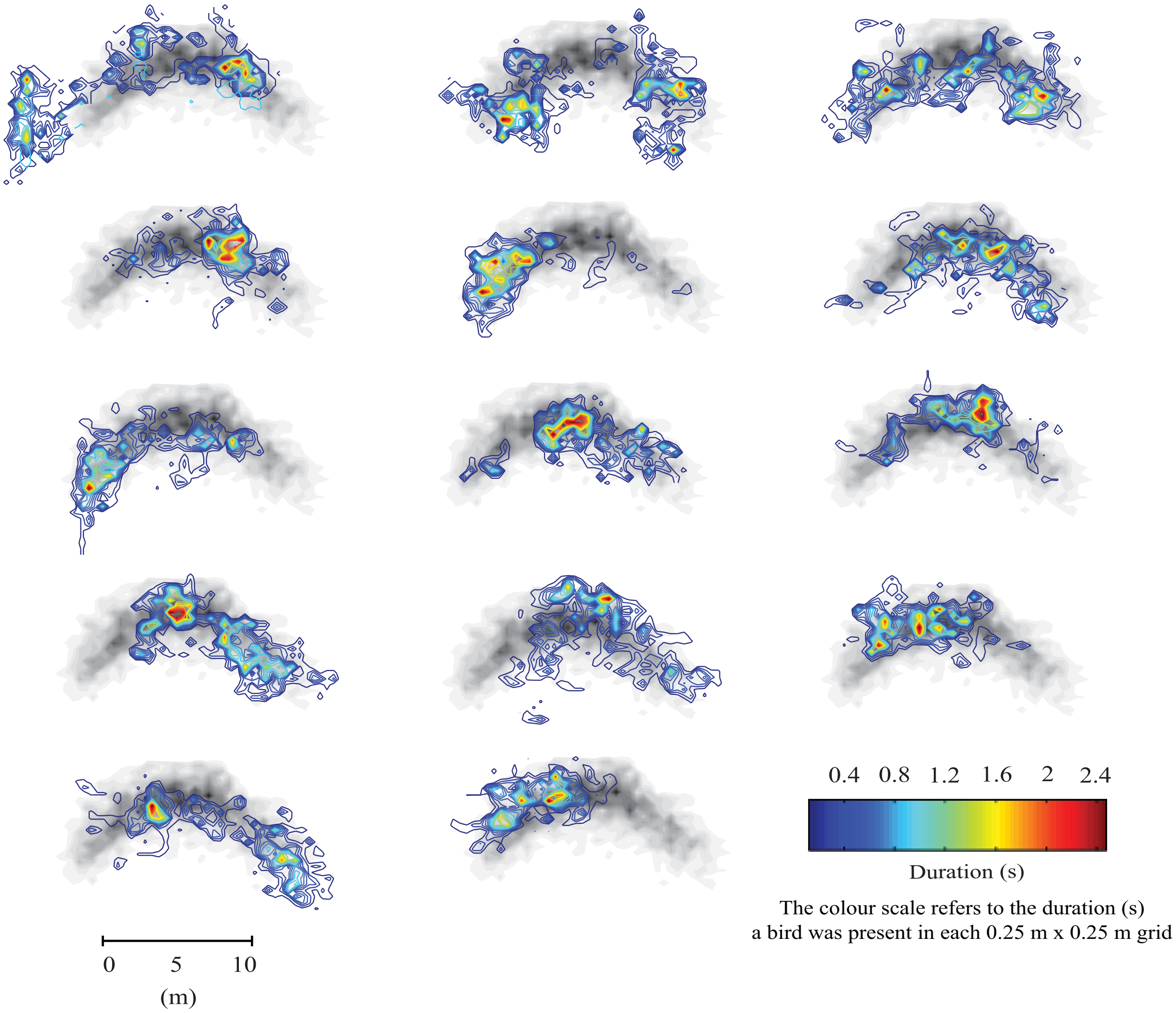
Range of optimal spanwise positions according to fixed-wing theory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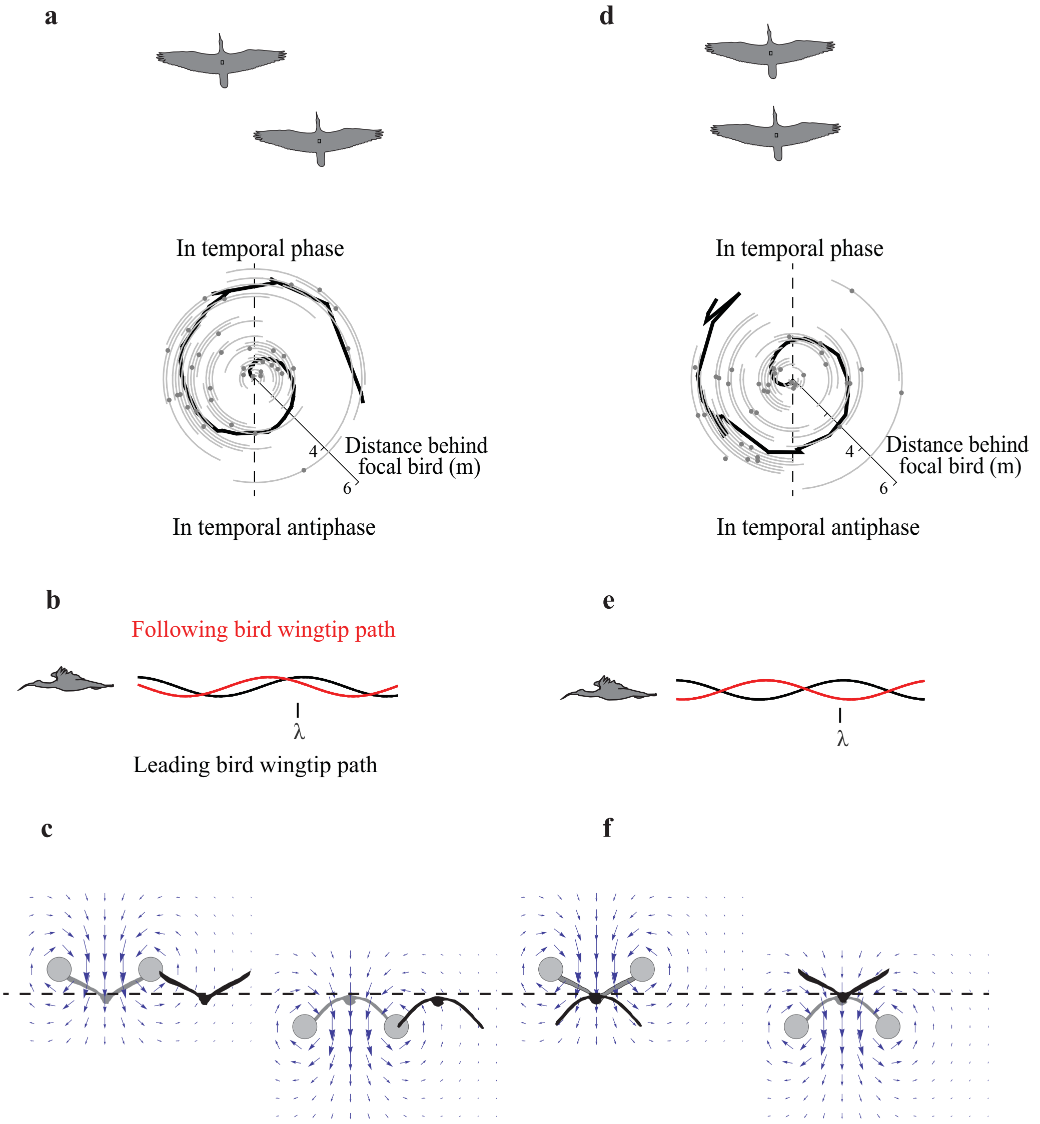
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