Flying in a flock comes at a cost in pigeons

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Abstract

Flying birds often form flocks, with social[1], navigational[2] and anti-predator[3] implications. Further, flying in a flock can result in aerodynamic benefits, thus reducing power requirements[4], as demonstrated by a reduction in heart rate and wingbeat frequency in pelicans flying in a V-formation[5]. But how general is an aerodynamic power reduction due to group-flight? V-formation flocks are limited to moderately steady flight in relatively large birds, and may represent a special case. What are the aerodynamic consequences of flying in the more usual 'cluster' [6,7] flock? Here, we use data from innovative back-mounted GPS and 6 degree of freedom inertial sensors to show that pigeons 1) maintain powered, banked turns like aircraft, imposing dorsal accelerations of up to $2g$, effectively doubling body weight and quadrupling induced power requirements; 2) increase flap frequency with increases in all conventional aerodynamic power requirements; and 3) increase flap frequency when flying near, particularly behind, other birds. Therefore, unlike V-formation pelicans, pigeons do not gain an aerodynamic advantage from flying in a flock; indeed, the increased flap frequency – whether due to direct aerodynamic interactions or requirements for increased stability or control – suggests a considerable energetic cost to flight in a tight cluster flock.

We recorded 18 pigeons during seven bouts of voluntary straight and circling flight around their home loft over a period of more than 9 pigeon-hours of flight, 400 pigeon-km, and over 243,000 flaps. Speed and position relative to the ground were determined using back-mounted 10 Hz raw Doppler and pseudorange Global Positioning System (GPS) data. GPS data were post processed relative to local base station data using Waypoint GrafNav 8.10 (Novatel, Canada). Relative airspeeds were calculated by taking account of air velocity measured using a 3D ultrasonic anemometer sited on an adjacent rooftop. Within-wingbeat motions were recorded with 300 Hz inertial measurement units (IMUs) consisting of 3 axes of accelerometer and 3 axes of gyroscope. Flap frequencies and body amplitudes were determined from the dorsal acceleration signal. The quantity and quality of these measurements allow, for the first time, the relationship of flap frequency and body motions with airspeed, induced, climbing and accelerating power, and proximity to other pigeons, to be separated and quantified using multiple polynomial regression.

The pigeons flew in a flock of a range of densities and positions, at a range of speeds, ascended and descended while circling at a range of radii (Supplementary Information shows a movie of one of 7 sequences). By treating GPS velocity measurements and accelerometer and gyroscope recordings independently, we determined that pigeons bank optimally according to aerodynamic theory. Turns require centripetal acceleration $a_{centrip}$

(Figure 1a). If the pigeons bank appropriately, this combines with gravity g to require an increase in dorsal acceleration a_{dorsal}; this is indeed what is observed. Further, to maintain the level of banking for a given turn rate (derived only from GPS measurements) requires a net yaw and pitch every flap (Supplementary Information), and these are close to those calculated by integrating gyroscope-derived pitch and yaw rates (Figure 1b,c). Therefore, during fast, sweeping turns (radius 15-20m), pigeons bank appropriately to load both wings evenly, and increase the average loading on their wings by up to double (>1500 flaps), presenting a relatively unconfounded self-manipulation of induced power via changes in apparent weight. Such flapping turns do not appear to be near a power limit: ascending flight is achieved at over 4 m/s (>8000flaps) – if this climbing power was available to pay the additional induced power costs of turning during constant-speed, level flight, a turn radius of 6.6m would be achievable at 15m/s, concomitantly imposing a 3.6-fold increase in effective body weight. It is likely that powered circling is, at least in part, force-limited, similar to bend-running humans[8,9] because, unlike wheeled vehicles, propeller-driven aircraft and greyhounds[10], the main motors powering bird flight cannot be dissociated from weight-support.

This self-imposed variability in effective weight support, along with the range of airspeeds (flight speed with respect to the air) V_{air}, ascent speeds V_z and rostral accelerations $a_{rostral}$, imposes largely independent demands of four aerodynamic power components: 1) parasite/ profile power (due to the drag on the body and wings, dependent on airspeed); 2) induced power (due to supporting weight with finite wings); 3) climbing power (due to changes in gravitational potential energy); and 4) accelerating power (due to changes in kinetic energy). Two kinematic parameters are related to variation in speed and power requirements. Flap frequency is expected to have a strong bearing on power[11,12], as it relates to both the aerodynamic forces on the wings – and hence the work per cycle – and the cycle rate. Amplitude of the dorsal body displacement, derived from double integration of the dorsal accelerometer measurements over each flap period, gives an indirect measure of the amplitude of the wing motions. However, the exact relationship between body motions and wing motions is unclear [13,14], depending on both inertial and aerodynamic reactions, and so will be additionally related to speed.

In order both to test whether increases in either kinematic parameter consistently indicate an increase in power and provide insight into the mechanisms of power modulation, while making few *a priori* assumptions about *how* they might vary with speed and power requirement, we fit 3rd order polynomials to each factor, and find partial coefficients that give the best fit for the whole model. In addition, we include two 'Flock Factors' as a metric for the proximity of other birds. This is the proportion of forward or rearward hemisphere view that would be covered by all other pigeons at the instant of each flap (assuming each other pigeon to occlude a circle with diameter of 0.5 m) (Figure 3c).

Each component of the regression model has a strong relationship with flap frequency and dorsal amplitude (Figures 2,3), with increases in each associated with an increase in flap frequency. The influence of airspeed, if the effects of induced power (proportional to the inverse of airspeed) are treated independently, reflect the demands of parasite and profile power. Combining the airspeed polynomial results with those of induced power allows the frequency-speed relationship to be calculated for steady, level flight at a large distance from other pigeons. This (blue line, Figure 2a) shows the familiar U-shaped curve of frequency with airspeed, with higher frequencies at lower speeds, demanded by high induced power requirements, and higher frequencies at higher speeds, related to higher parasite and profile drag requirements. It must be emphasised, however, that while wingbeat frequency is likely to be closely correlated with power at around the minimum power speed[12], it cannot be taken as a direct proxy for aerodynamic power over a range of speeds; the best

measurements to date show minimum power speeds do not occur at the flight speeds of minimum flap frequency[15,16]. But it is reasonable to conclude from our measurements that, once the effects of speed are removed – i.e. *for a given speed* – an increased power requirement is strongly associated with increases in flap frequency.

The relationship of speed and power with body motion is less straightforward: while increases in mechanical power requirements due to ascending or accelerating flight are, perhaps unsurprisingly, related to increases in dorsal amplitude, the opposite is true for speed and induced power (Figure 2 e-h). Pigeons take higher frequency but shallower wingbeats as they fly around tighter circles. In physiological terms, this is counterintuitive: one would expect extra power to be produced with, in addition to increases in frequency and muscle stress (directly related to the increased wing forces due to increased effective weight), an increase in muscle strain from an increased flap amplitude (as is observed for climbing and accelerating powers). So is there an aerodynamic account for this method of modulation in response to induced power demands? Indeed: such flight would ameliorate the increasingly significant induced power costs by reducing the spatial and temporal fluctuations in the wake, pushing the correction factor traditionally applied to induced power calculations[11,17-19] towards unity. In effect, the momentum jet in the wake would be directed ventrally more evenly, and the mass flux increased. If this is the case, some counter-cost must be invoked to account for why this flight style is not always adopted. Given all other aerodynamic powers are either equivalent or also improved with lower amplitude flapping, the inertial power cost of flapping non-massless wings must be considered. Inertial power is proportional to the square of flap amplitude, but the cube of frequency; while a high wingbeat frequency would result in a high aerodynamic efficiency, particularly important under high loads, it would also require a higher inertial power. This observation therefore provides some support for the notion[20,21] that flapping flight involves a trade-off between aerodynamic efficiency (requiring low wingbeat amplitudes at high frequencies) and inertial power costs (requiring low wingbeat frequencies), even during relatively fast flight.

Flight within a flock, if the effects of airspeed and conventional aerodynamic power relationships are accounted for, results in an increase in flap frequency and decrease in flap amplitude (Figure 3). Given that 1) V-flying birds benefiting from aerodynamic interaction fly with reduced wingbeat frequency, and 2) an increase in each form of aerodynamic power is associated with an increase in frequency in pigeons, the increase in flap frequency with proximity to other birds indicates an increased power requirement due to flying within a cluster flock. The ultimate cause for this relationship is currently unclear. While aerodynamic interactions are certainly feasible – modal nearest neighbour distance was 1.49m (close to the mean of 1.54m reported from photogrammetric studies of a turning pigeon flock[22]), well under a flapping wavelength – the magnitude of the change is not well predicted by simple downwash calculations. The downward velocity of the wake close behind another pigeon would, from momentum-flux considerations, be approximately 0.4m/s; if this was evenly distributed, even following tightly in a flock with a Flock Factor of 10%, this would require a relative climbing speed of only 0.04m/s. This ascent velocity would result in an increase in flap frequency of only 0.001Hz instead of the observed 0.1Hz. So either the assumption of uniform downwash is incorrect, the pigeons are disturbed by some other aerodynamic interaction, or they increase their flap frequency for reasons that are not directly aerodynamic. This last option appears most parsimonious. The benefits of high frequency, low amplitude flight may well be increased opportunity for control and collision avoidance: higher flap frequencies can allow both a greater manoeuvrability and passive stability[22]; lower amplitudes (Figure 3c) would allow a higher flock density without risk of collision or requirement of accurate wingpath coherence between birds (of which we find no evidence). But whatever the ultimate cause driving the higher flap frequency in

denser pigeon flocks, this observation indicates that, unlike the V-formation, flight in a cluster flock comes at an energetic cost.

Methods summary

Measurements

We recorded a flock of 18 trained racing pigeons (*Columba livia*, mean mass 0.461kg, standard deviation (SD) 0.045kg; mean span 0.691m, SD 0.039m) during voluntary flights with synchronised back-mounted 10 Hz raw Doppler and pseudorange GPS and 300Hz 12 bit precision tri-axial accelerometers (+/− 12 *g*) and tri-axial gyroscopes (+/− 2000dps). Sensor, logger and mounting mass (35g) constituted <8% body mass – while this is larger than usually accepted on wild-bird studies, and would also have imposed a slight increase in body drag, the fact that extended, voluntary flights were performed, including circling at 2 *g*, demonstrates that this load was not prohibitive. Experiment protocols were approved by the RVC local Ethics and Welfare committee. A GPS base station (Novatel FlexPak G2L and GPS-702-GG antenna) and ultrasonic anemometer (1Hz, WindMaster (Gill Instruments Ltd., UK)) on a nearby rooftop provided synchronised measurements. For further details on post processing and turning calculations, see Supplementary Information.

Power models

We found best fit (least squares) partial regression coefficients K for third order polynomials of airspeed, induced power factor, climbing power factor, acceleration power factor (Figure 2) and Flock Factors FF_{ahead} and FF_{behind} using the following expressions:

	Frequency (Hz) or dorsal amplitude (m) =
Airspeed component	$K_1 V_{air} + K_2 V_{air}^2 + K_3 V_{air}^3$
Induced power component	$+ K_4 \dfrac{\overline{a_{dorsal}}^2}{V_{air}} + K_5 \left(\dfrac{\overline{a_{dorsal}}^2}{V_{air}}\right)^2 + K_6 \left(\dfrac{\overline{a_{dorsal}}^2}{V_{air}}\right)^3$
Climbing power component	$+ K_7 V_z + K_8 V_z^2 + K_9 V_z^3$
Acceleration power component	$+ K_{10} \overline{a_{rostral}} V_{GPS} + K_{11} \left(\overline{a_{rostral}} V_{GPS}\right)^2 + K_{12}\left(\overline{a_{rostral}} V_{GPS}\right)^3$
Forward Flock Factor component	$+ K_{13} FF_{ahead} + K_{14} FF_{ahead}^2 + K_{15} FF_{ahead}^3$
Rear Flock Factor component	$+ K_{16} FF_{behind} + K_{17} FF_{behind}^2 + K_{18} FF_{behind}^3$
Constant	$+$Constant

Each power component takes account of the kinematic contribution towards power – for instance, induced power is proportional to the square of body weight (hence dorsal acceleration to take account of turns) and inversely proportional to airspeed[11]. Individual pigeon was included as a categorical variable, thus taking some account of the morphological variability between pigeons. The dataset was first bounded to remove extreme values (frequencies 5 to 10Hz; air speed 11-18m/s; dorsal acceleration 8.81 to 20.81 ms^{-2}; V_z=−4 to 4m/s; Flock Factors<0.1; acceleration power within +/− 39.2 W/kg, equivalent to the V_z bounding), leaving 171,209 flaps. The overall model fitted the data with R^2=0.48 (frequency) or R^2=0.37 (dorsal amplitude) (statistical tables in Supplementary Information).

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

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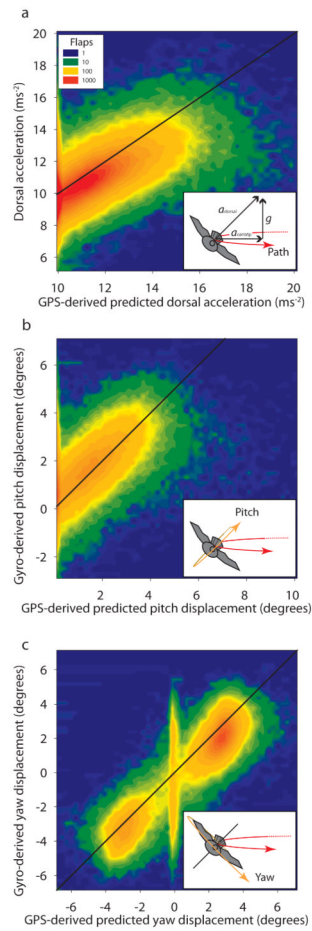
Figure 1.
Flap-number histogram contour plots for flap-averaged dorsal acceleration (a), and net pitch (b) and yaw (c) angular displacements (averaged over 5 flaps). Turning with optimal banking requires an increase in dorsal acceleration, and pitch and yaw displacement every flap (insets). Black lines show the predicted (from GPS alone) against observed (IMU alone) relationships for birds, assuming they bank optimally during turns.
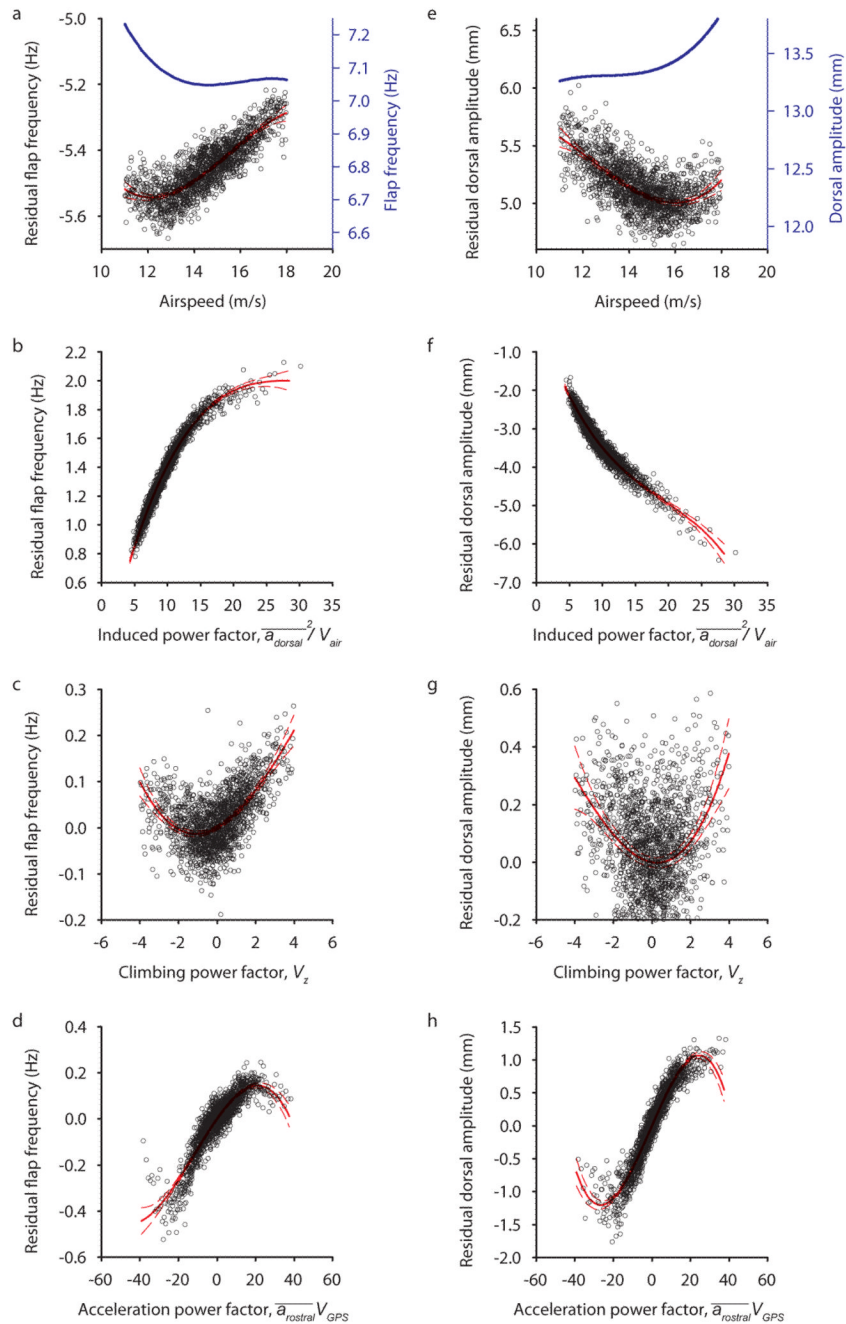
Figure 2.
The influence attributable to airspeed (a,e), induced power (b,f), climbing power (c,g) and accelerating power (d,h) on flap frequency (a-d) and dorsal amplitude (e-h) over each flap (18 pigeons, 171,209 flaps). Red curves show 3rd order polynomial fits; points show the values once the influence of all other factors have been removed. Each point represents the average of 100 flaps, binned along the x-axis. Dashed red lines show +/− 99.99% confidence intervals. Blue curves (a,e) show the relationship predicted if the effect of both airspeed and induced power (which includes airspeed as a term) are combined; in effect, the relationship that would be observed for steady, straight, level flight.
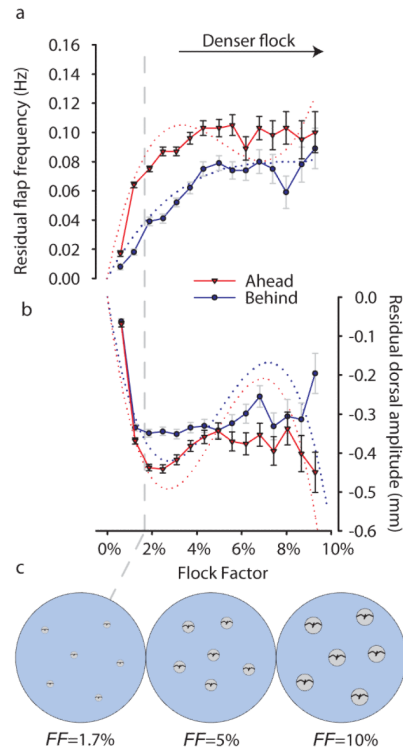
Figure 3.
The relationship between Flock Factor – the proportion of hemisphere-view covered by other pigeons for every flap, illustrated graphically with six neighbouring birds (c) – and flap frequency (a) or dorsal displacement amplitude (b). The vertical grey dashed line indicates the mean Flock Factor (1.7%), the underlying dotted lines the 3rd order polynomial fits used in the statistical separation of factors, and error bars show s.e.m. Flight in a cluster flock, particularly when flying behind other birds, is associated with an increase in flap frequency and decrease in dorsal amplitude.