**Supplementary Information**

**Birds invest wingbeats to keep a steady head and reap the ultimate benefits of flying together**

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**S1 Text.** Analysis of accelerometer output

The purpose of this section is to provide a rigorous（嚴格的） analysis of the oscillatory（振動） accelerations experienced by an accelerometer worn on a bird’s back during flapping flight. Here, the axis（軸） of the accelerometer is assumed to be aligned dorsoventrally（背腹側） on the bird, and possible angular（角度） changes in the inclination（傾角） of this axis with respect to the Earth are assumed to be sufficiently small or slow that the dorsoventral component of gravitational acceleration that the accelerometer experiences can be considered constant and hence neglected（忽視） in an analysis of the oscillatory accelerations.

（認為拍打翅膀的時候，背部的加速度與gravity方向是平行的（沒有夾角）；）

Under Newton’s Second Law, an accelerometer placed at the centre of mass of an object experiences an acceleration equal to the net external force on the object divided by its mass. If the accelerometer is placed away from the centre of mass, then the angular motion（角度運動 vs line motion） of the bird will also contribute to the sensed acceleration（如果把加速規放在重心的位置，那摩鴿子的角度運動，也會被加速規檢測到）, but this effect may be neglected（忽視） in non-manoeuvring（非機動） flight. Under sinusoidal aerodynamic forcing（

空氣力：

https://en.wikipedia.org/wiki/Aerodynamic\_force

正弦的空氣力（這個是怎麼知道的？）

）, the accelerometer therefore experiences an aerodynamic acceleration:

（

(Eq. S1)

（空氣動力學的加速度 ft = 次數，也就是說頻率 = f）

**波浪號**（tilde、**~**）是一個有許多用途的[標點符號](https://zh.m.wikipedia.org/wiki/標點符號)。原本它作為[縮寫](https://zh.m.wikipedia.org/wiki/縮寫)符號的一個字母，但亦有作為[變音符號](https://zh.m.wikipedia.org/wiki/變音符號)或單一文字的用途。在[數學](https://zh.m.wikipedia.org/wiki/數學)上，它是代表[等價關係](https://zh.m.wikipedia.org/wiki/等價關係)的[數學符號](https://zh.m.wikipedia.org/wiki/數學符號)。在最後一個用途裡（尤其是在[辭書學](https://zh.m.wikipedia.org/wiki/辭書學)裡），它有時會被當做**代字號**。）

(

正弦函數（sinusoidal function）

[https://zh-yue.wikipedia.org/wiki/%E6%AD%A3%E5%BC%A6%E6%B3%A2](https://zh-yue.wikipedia.org/wiki/正弦波)

f 是一個實數：

[https://www.quora.com/How-does-the-term-sin-2\*pi\*f\*t-come-from-I-know-that-sin-and-cosine-take-radians-as-arguments-which-will-be-pi-2-\*-no-of-degrees-but-why-do-we-mulitply-f\*t-Isnt-f\*t-1](https://www.quora.com/How-does-the-term-sin-2*pi*f*t-come-from-I-know-that-sin-and-cosine-take-radians-as-arguments-which-will-be-pi-2-*-no-of-degrees-but-why-do-we-mulitply-f*t-Isnt-f*t-1)

也就是說，可以通過log看到f的大小；f = total次數/時間；

f = 所以加速規的震盪次數/總時間 ；

比如f是4的時候，比如t從（0～1）是一個周期的話，對a來說，t從（0～1）是經歷了4個周期，也就是說（0～1/4）是a的一個周期；

sin的取值範圍是（-1～1）,

a的取之範圍是(-F/m~F/m)，

第一個例子中：也就是說a的peak是3.5 g = 3.5\*9.8 m/s2 =34.3 ，m是452克 = 0.452kg，那摩F是34.3 \*0.452 = 15.5036 kg·m/s

)

where is the aerodynamic（空氣動力學） forcing（強迫） amplitude（振幅）, is the wingbeat frequency, is time, and is the mass. Integrating（整合） twice with respect to time（d距離=1/2 **\*a \***square t ）, this aerodynamic acceleration is associated with an oscillatory（振動的） displacement of the centre of mass(

這個空氣動力學的加速度，相關聯的重心的振動位移是：

):

(Eq. S2)

（

-ma/（4square(pi)square(f)\*m） = - a/(4square(pi)square(f)) = -(3.5g)/(4square(pi)square(f))

= 34.4 （m/s2）/1236.78 = 0.02773 m = 27.73mm，與下文的計算結果一致；

）

Other things being equal, the aerodynamic displacement of the centre of mass therefore scales as , such that the 18% increase in wingbeat frequency that we measured between solo and paired flights (Table S1) could be expected to cause a 28% reduction in the amplitude of the aerodynamic body displacement. （

1/square(1+0.18),d- = 0.718d

）This conclusion holds provided that the increase in wingbeat frequency is not accompanied by any increase in the amplitude of the dorsoventral aerodynamic forcing, which is a reasonable assumption in sustained level flight(這個結論說明，振翅頻率增加，不會導致後背的振幅的增加), for which the time-averaged vertical force must always balance the weight of the bird. This being so, it follows that a bird can reduce the bobbing（擺動） motion that its head or body experiences in flight simply by increasing its wingbeat frequency.

A bird is not a rigid（僵） body, however, and flapping its wings will cause its overall mass distribution to vary periodically（定期）（煽動翅膀的時候，會導致它的重量分布發生變化）. An accelerometer placed at any anatomically fixed point on the bird’s body will therefore experience an additional inertial（慣性） acceleration due to the displacement of the bird’s body in relation to its overall centre of mass. The wings of a pigeon together comprise（構成） 13% of its overall mass, and their respective centres of mass move on radii（半徑） of 0.07m from the shoulder joint [1]. Lowering the wings from the extreme dorsal to the extreme ventral（腹側） position will therefore raise the bird’s body by 0.018m relative to its overall centre of mass, calculated as 13% of the peak-to-peak displacement of the wing’s centre of mass. Based on the wingtip（翼尖） kinematics（運動學）（根據已知的理論，翅膀從最上面，煽到最下面，會導致身體相對於重心，向上移動0.018m） presented by Tobalske & Dial [2], an inertial displacement nearer 80% of this extreme seems realistic at the 20ms-1 airspeed that we observed (Table S1), bringing the expected peak-to-peak amplitude of the oscillatory inertial displacement to approximately(大約) 0.015m. Since the amplitude of this displacement is independent of the wingbeat frequency（這個位移的振幅是與振翅頻率無關的）, the presence of this inertial forcing is expected to attenuate（衰減） the overall reduction of body displacement that would otherwise result from increasing the frequency of the aerodynamic（空氣動力學的） forcing, which qualitatively（定性的） speaking is what we observed (see below).

Neither the aerodynamic（由於[馬赫數](https://zh.wikipedia.org/wiki/马赫数)（即流體速度與音速之比）小於 0.3，所以屬於亞音速空氣動力學） nor the inertial component of the total displacement is expected to be perfectly sinusoidal, but it is nevertheless informative to consider how their waveforms（波形） would be expected to combine if as a good first approximation（近似） they were. Approximating the dorsoventral motion of the wing’s centre of mass as a simple sinusoid yields the following expression for the inertial displacement（

把作為翅膀的中心的背部的運動，看作是一個簡單的正弦函數的話；可以得到下面這個慣性位移；（對應的上面的位移公式是“空氣動力的位移公式”）

）:

(Eq. S3)

where is the phase of the motion with respect to the aerodynamic displacement in Eq. S2, and where the numerical constant is half the peak-to-peak amplitude. Because the upward aerodynamic acceleration of the accelerometer is expected to peak at mid-downstroke（加速規的峰值應該是翅膀往下煽動的最擴展的時候（材料中有圖片））, its upward aerodynamic displacement is expected to peak at mid-upstroke (see Eq. S2). Hence, since the upward inertial displacement of the accelerometer peaks at the bottom of the downstroke, it follows that the inertial displacement leads the aerodynamic displacement by approximately 90˚ such that .

The amplitude of a waveform combining two sinusoids with a 90˚ phase lag is just the square root of the sum of the squared amplitudes of the two sinusoids. Subtracting the squared peak-to-peak amplitude of the predicted displacement due to inertial forcing (0.015 m) from the squared peak-to-peak amplitude of the measured displacement (0.027 m in solo flight *versus* 0.022 m in paired flight; Table S1) （

radicand（square(da)-square(di)）=0.0224499443206；

）and taking the square root, we therefore arrive at a robust empirical estimate of the peak-to-peak amplitude of the displacement due to aerodynamic forcing, which is 0.022m in solo flight and 0.016m in paired flight. The resulting empirical（經驗） estimate of a 27% reduction in the peak-to-peak amplitude of the aerodynamic displacement between solo and paired flight coincides almost exactly with the 28% reduction that we predicted theoretically from the accompanying 18% increase in wingbeat frequency using Eq. S2 above. These two estimates are mathematically independent, and therefore provide a useful internal validation（驗證） of our analysis. Moreover, these figures are modified only slightly if we assume that flying in pairs is associated with a 10% decrease in the wingbeat amplitude, as is argued in the main text. Multiplying our empirical estimates of the peak-to-peak amplitude of the aerodynamic displacement by the factor in the denominator of Eq. S2, we arrive at an estimate of 2.7*g* for the peak-to-peak amplitude of the acceleration due to aerodynamic forcing in solo flight, and 2.8*g* in paired flight. This is consistent with our earlier argument that the amplitude of the dorsoventral aerodynamic forcing should have been similar in paired and solo flight, on the basis that the time-averaged vertical aerodynamic force must have balanced the weight of the bird under both flight conditions (see also the main text).

1. van den Berg C, Rayner J. The moment of inertia of bird wings and the inertial power requirement for flapping flight. J Exp Biol. 1995;198: 1655–64. Available: http://www.ncbi.nlm.nih.gov/pubmed/9319563

2. Tobalske BW, Dial KP. Flight kinematics of black-billed magpies and pigeons over a wide range of speeds. J Exp Biol. 1996;199: 263–280. Available: http://www.ncbi.nlm.nih.gov/pubmed/9317775