Comparison between mechanical power requirements of flight estimated using an aerodynamic model and *in vitro* muscle performance in the cockatiel (*Nymphicus hollandicus*)

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SUMMARY

There have been few comparisons between the relationship between the mechanical power requirements of flight and flight speed obtained using different approaches. It is unclear whether differences in the power–speed relationships reported in the literature are due to the use of different techniques for determining flight power or due to inter-specific differences. Here we compare the power–speed relationships in cockatiels (*Nymphicus hollandicus*) determined using both an aerodynamic model and measurements of *in vitro* performance of bundles of pectoralis muscle fibres under simulated *in vivo* strain and activity patterns. Aerodynamic power was calculated using different ranges of values for the coefficients in the equations: induced power factor (k 1.0–1.4), the profile ($C_{D,pro}$ 0.01–0.03) and parasite drag ($C_{D,par}$ 0.05–0.195) coefficients. We found that the aerodynamic power-speed relationship was highly sensitive to the values assumed for these coefficients and best fit the power calculated from *in vitro* muscle performance when k=1.2, $C_{D,pro}$=0.02 and $C_{D,par}$=0.13.

Key words: aerodynamic, flight, pectoralis, power.

INTRODUCTION

All current approaches for determining the mechanical power requirements of flight are indirect and, as a result, require a number of assumptions to be made (e.g. Askew and Ellerby, 2007). This introduces uncertainty into the calculated values of mechanical power. It is therefore useful to compare the mechanical power obtained using different approaches in order to assess the extent to which the methodological approach affects the mechanical power–speed relationship. In spite of this, very few studies have compared the mechanical power–speed relationships derived from more than one approach, either in the same individual birds or even within the same species. Therefore, it is unclear whether the qualitative and quantitative differences between the mechanical power–speed relationships (Tobalske et al., 2003) are due to inter-specific differences or due to the methodology. In the few studies where different approaches have been compared, the sensitivity of the estimates of power to the assumptions made in the approach has been highlighted. For example, a comparison between aerodynamic estimates of flight power and power obtained using an *in vitro* muscle physiology approach (Askew and Ellerby, 2007) illustrated the importance of the values assigned for the induced power factor and the parasite and profile drag coefficients used in the aerodynamic model. In European starlings (*Sturnus vulgaris*), the similarity between estimates of mechanical power calculated from respirometry measurements and values calculated using an aerodynamic model were found to be extremely sensitive to the values assumed for the flight muscle efficiency (Ward et al., 2001). Comparisons between different approaches may be useful in identifying the assumptions that are critical in the estimation of flight mechanical power.

In this study, we compared the mechanical power requirements of flight in the cockatiel (*Nymphicus hollandicus*) determined using, for the same individuals, both an aerodynamic model and

measurements of the physiological properties of the pectoralis muscles (Morris and Askew, 2010). We also compared our data with mechanical power requirements for the same species (but different individuals) determined using measurements of *in vivo* muscle strain and estimates of muscle force (Hedrick et al., 2003).

MATERIALS AND METHODS
Animals and flight training

Seven cockatiels (*Nymphicus hollandicus* Kerr 1792) were purchased from local bird suppliers and housed in an indoor aviary in a temperature (18–24°C) and humidity (45–65%) controlled room with a 12h:12h light:dark cycle. Food and water were available *ad libitum*.

The birds were trained to fly in a variable speed Eifel design low turbulence wind tunnel as described in a companion study (Morris and Askew, 2010).

Flight recordings

Birds were flown at a range of speeds in a random order from 0 to 16 m s^{-1} at 2 m s^{-1} intervals. Flights were recorded at 250 or 125 frames s^{-1} (using either a Troubleshooter, model TS500MS, Fastec Imaging, USA or a Kodak Motion Corder, model SR500, San Diego, CA, USA, respectively) with a shutter speed of 0.2 ms. The camera was positioned laterally to the working section of the wind tunnel to record flights perpendicular to the direction of flight. A mirror was placed on top of the working section at a 45 deg angle to the vertical plane in order to simultaneously record a dorsal view of the bird. Flight recordings were made in both non-instrumented and instrumented birds. The flights in non-instrumented birds (body mass 100.4±7.9 g, mean ± s.d.) were made less than 1 week before the instrumented experiments (body mass 92.1±7.5 g, mean ± s.d.). The instrumented flights were recorded during sonomicrometry and EMG data collection (Morris and Askew, 2010).

Kinematics and aerodynamic analysis

Flights were only analysed if there was corresponding *in vitro* mechanical power data for each bird (Morris and Askew, 2010). Recordings were digitised (VideoPoint, Version 2.5.0, Lenox Softworks, MA, USA) in order to obtain wing and body kinematics. The analysed flights varied in duration. In selecting the images to digitise, we selected a sequence in which the bird was in approximately in the same position in the working section of the wind tunnel at the start and end of the flight period analysed, and therefore had a constant average speed. Positional data of the wing tip and base at the start and end of the down stroke were measured in order to calculate wing beat frequency, relative shortening duration, relative flapping duration, stroke amplitude and stroke plane angle relative to the horizontal. The position of the centre of mass of the bird (estimated as the centre of body) was measured in order to calculate the mechanical power required for flight using an aerodynamic model.

Wing beat frequency was calculated for each wing beat as the inverse of the time taken for each wing beat, beginning from either the start or end of the down stroke. Relative shortening duration was calculated from the duration of the down stroke in relation to wing beat duration. Wing beats before and after non-flapping periods were not included in analysis. In cockatiels, intermittent flight in the form of glides with the wings extended away from the bird's body is used to modulate flight power at some flight speeds (Morris and Askew, 2010). These periods are difficult to identify as they often appear as a slight pause in a wing beat cycle. In order to avoid any errors introduced by manually measuring these sometimes subtle periods of non-flapping flight, the relative flapping duration was calculated using the methods of Bundle et al. (Bundle et al., 2007). The expected number of wing beats in a period of flight, including any intermittent flight, was calculated from the average wing beat frequency for each speed and the flight duration (from the start or end of the down stroke to the last in the period of flight analysed). Relative flapping duration was calculated from the number of wing beats observed in a period of flight in relation to the expected number of wing beats.

Aerodynamic model

The aerodynamic analysis was similar to that used by Askew et al. [(Askew and Ellerby, 2007; Askew et al., 2001) based on Wakeling and Ellington (Wakeling and Ellington, 1997)]. The total aerodynamic power was calculated as the sum of parasite, induced and profile power, which were corrected for intermittent flight strategies.

Velocity and acceleration

Positional centre of mass data (x, horizontal and z, vertical) were measured relative to a fixed origin. These data were smoothed using fourth-difference smoothing (Lanczos, 1957; Rayner and Aldridge, 1985) in order to reduce the effects of random digitisation errors and to improve the estimations of velocity and acceleration. Velocities of movement in the x and z directions ($\dot{x}$ and $\dot{z}$) were calculated by differentiating the smoothed positional data. Accelerations in the x and z directions ($\ddot{x}$ and $\ddot{z}$) were calculated by differentiating velocity [using equations 11 and 12 a-d in Rayner and Aldridge (Rayner and Aldridge, 1985)]. The resultant velocity of the centre of mass (v) was calculated from the horizontal and vertical velocities:

$$v = \sqrt{\dot{x}^2 + \dot{z}^2}. \tag{1}$$

Induced power

Induced power (P_{ind}) was calculated as the product of the velocity through the actuator disc (w) and net thrust (T). The induced power factor (k) was included in this equation to correct for tip losses and non-uniformity in the wake (Wakeling and Ellington, 1997):

$$P_{ind} = T(kw - v\sin\alpha'), \tag{2}$$

where $-\alpha'$ is the angle at which the velocity vector is inclined to the actuator disc (Wakeling et al., 1997). The net thrust (T) was calculated as the resultant of the mean horizontal ($F_{x,mean}$; Eqn 5) and mean vertical ($F_{z,mean}$; Eqn 6) forces acting on the bird through out the whole flight period:

$$T = \sqrt{F_{x,mean}^2 + F_{z,mean}^2}, \tag{3}$$

where

$$F_x = (M_b + M_c)\ddot{x} \tag{4}$$

$$F_z = (M_b + M_c)(\ddot{z} - g), \tag{5}$$

and M_b is body mass (kg) and g is the acceleration due to gravity (taken as $9.81\,\mathrm{m\,s^{-2}}$). Note that the mass of the data cable ($M_c=3\,\mathrm{g}$) that linked the bird to the data acquisition system was included in the calculation of thrust.

The induced velocity (w) for forward flapping flight was calculated as in Wakeling and Ellington (Wakeling and Ellington, 1997) using classic actuator disc theory. Induced velocity was determined by solving Eqn 7 for w:

$$w^4 - 2vw^3\sin\alpha' + v^2w^2 - \left(\frac{T}{2\rho D}\right)^2 = 0, \tag{6}$$

where D is the area of the actuator disc:

$$D = \phi l_w^2, \tag{7}$$

where ϕ is the stroke amplitude and l_w is the wing length during the down stroke. Aerodynamic power was calculated using a range of values for the induced power factor (see below).

Parasite power

Parasite power (P_{par}) is the power required to overcome the drag acting on the body (Pennycuick, 1968; Pennycuick, 1975). As the flights were instrumented, the drag from the data collection cable was included in the calculation of parasite power. Parasite power was calculated as:

$$P_{par} = \frac{1}{2}\rho S_b C_{D,par}v^3 + F_c v, \tag{8}$$

where ρ is air density ($1.2\,\mathrm{kg\,m^{-3}}$), S_b is the frontal body area of the bird [calculated following Pennycuick et al. (Pennycuick et al., 1988)], $C_{D,par}$ is the parasite drag coefficient and F_c is the force that the data cable imparts onto the bird. This force was measured in the wind tunnel at speeds ranging from 0 to $16\,\mathrm{m\,s^{-1}}$ at $2\,\mathrm{m\,s^{-1}}$ intervals by attaching the data cable to a force transducer (FORT100, WPI, FL, USA) in a position that reproduced its attachment to the bird during flight.

The parasite drag coefficient represents how streamlined the bird's body is (Ellington, 1984; Pennycuick et al., 1988). In this study the aerodynamic power was calculated using a range of values for the parasite drag coefficient (see below).

Profile power

The profile power (P_{pro}) required to overcome the drag on the wings during the down stroke (Eqn 10) was calculated during the flapping periods:

$$P_{pro} = \rho v_R^3 \, S_w \, C_{D,pro} \,, \qquad (9)$$

where S_w is wing area, $C_{D,pro}$ is the profile drag coefficient and v_R is the resultant velocity (Eqn 11) at the wing's centre of lift [see the electronic supplement of Askew and Ellerby (Askew and Ellerby, 2007)]. The position of the centre of lift was estimated as $2/3 \, l_w$ [estimated from hovering flight in the pigeon (Pennycuick, 1967)] as in the electronic supplement of Askew and Ellerby (Askew and Ellerby, 2007):

$$v_R = \sqrt{\left(\dot{x} + \frac{4}{3} \, \phi l_w n \cos\beta \right)^2 + \left(w + \dot{z} - \frac{4}{3} \, \phi l_w n \sin\beta \right)^2} \,, \quad (10)$$

where n is wing beat frequency and β is the angle of the stroke plane relative to the horizontal. Aerodynamic power was calculated using a range of values for the profile drag coefficient (see below).

Accounting for ground effect

Ground effect results in the distortion of the air flow due to interference from the solid walls of the working section of the wind tunnel (Rayner, 1993). This reduces the amount of induced power the bird has to produce during a period of flight because of the recirculation of air (Rayner, 1993; Rayner, 1994). As a result of ground effect the mechanical power generated by the flight muscles may differ between different sized wind tunnels. To allow comparison between our data and that collected by Hedrick et al. (Hedrick et al., 2003), we corrected our measurements of *in vitro* mechanical flight power in the wind tunnel for ground effect to give an estimate of free-flight power, following Rayner's approach for closed work sections (Rayner, 1994).

Coefficients

We used a minimum, typical (i.e. commonly used) and high range of values for the coefficients previously reported in the literature. Minimum values: k=1.0 (Pennycuick, 1969), $C_{D,par}$=0.05 (Pennycuick et al., 1996; Tucker, 2000), $C_{D,pro}$=0.01 (Tobalske et al., 2003). Typical values [following Askew and Ellerby (Askew and Ellerby, 2007)] k=1.2 (Pennycuick, 1975), $C_{D,par}$=0.13 (Rayner, 1999), $C_{D,pro}$=0.02 (Rayner, 1979). High values [following Tobalske et al. (Tobalske et al., 2003)]: k=1.4, $C_{D,par}$=0.195, $C_{D,pro}$=0.03. Note that higher values have been reported for each of these coefficients than used in our high range [$C_{D,par}$=0.4 (Pennycuick et al., 1988); $C_{D,pro}$=2.0 (Usherwood and Ellington, 2002)] however, these are not realistic when applied across a range of flight speeds.

Statistical analysis

To test for differences in aerodynamic power and flight kinematics between non-instrumented and instrumented flights a paired *t*-test was used. The aerodynamic power was calculated using a range of coefficients and the combination that best fits the *in vitro* mechanical power. A paired *t*-test was also used to test for differences in aerodynamic power and *in vitro* muscle power. Kinematic parameters included wing beat frequency, relative shortening duration, relative flapping duration, stroke amplitude and stroke plane angle relative to the horizontal. Statistical analysis was performed in SPSS (version 14.0.2, SPSS Inc., USA).

RESULTS
Mechanical power–speed relationship

The aerodynamic power–speed relationship calculated using a range of different values for k, $C_{D,pro}$ and $C_{D,par}$ is shown relative to the mechanical power determined from *in vitro* muscle performance following correction for ground effect (Fig. 1A–C).

No one set of coefficients fits the *in vitro* physiological estimate of mechanical power across all flight speeds. Calculating power with k=1.0 produced the best estimate of flight power at low speeds
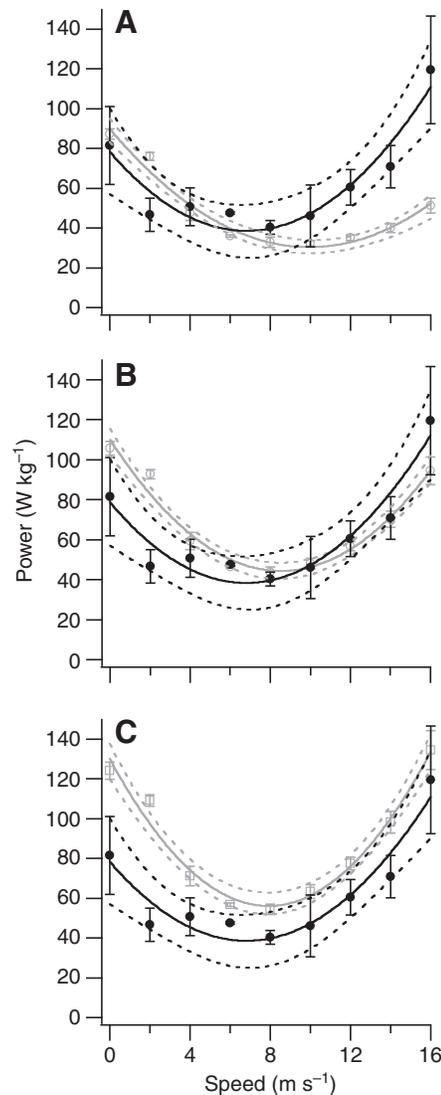

Fig. 1. The relationship between power–speed curves calculated using an aerodynamic model and determined from physiological measurements on the pectoralis muscle. Flight muscle power output calculated from measurements of *in vitro* muscle performance (closed circle, solid black line) (Morris and Askew, 2010) is shown in relation to aerodynamic power (open circles, solid grey line) calculated using a range of (A) minimum (k=1.0, $C_{D,par}$=0.05, $C_{D,pro}$=0.01), (B) typical (k=1.2, $C_{D,par}$=0.13, $C_{D,pro}$=0.02), and (C) maximum (k=1.4, $C_{D,par}$=0.195, $C_{D,pro}$=0.03), coefficients. Data are shown as mean ± s.e.m. Third-order polynomials have been fit to the data (solid lines) and the 95% confidence bands of the fit to the data are indicated (dashed lines). Aerodynamic power: N=4, 3, 5, 3, 4, 3, 7, 2, 4 for speeds 0, 2, 4, 6, 8, 10, 12, 14, 16 m s^{-1}, respectively; *in vitro* muscle power: N=4, 4, 5, 3, 4, 3, 7, 3, 4 for speeds 0, 2, 4, 6, 8, 10, 12, 14, 16 m s^{-1}, respectively.

(Fig. 1A). Flight power at low speeds was over-estimated using k=1.4 (Fig. 1C). The power requirements of flight at higher speeds are dominated by the profile and parasite power components. The aerodynamic power best fit the *in vitro* physiological estimate of mechanical power at high speeds when the typical coefficients were used: k=1.2, $C_{D,par}$=0.13, $C_{D,pro}$=0.02 (Fig. 1B). Both the aerodynamic and *in vitro* muscle power had a minimum power speed of approximately 8 m s^{-1} when the typical and maximum coefficients were used (Fig. 1B,C). At high flight speeds, when the minimum drag coefficients are used to calculate power, the aerodynamic power is lower than the physiological estimate of power (Fig. 1A). The high values for these coefficients resulted in aerodynamic flight powers that exceeded the *in vitro* muscle power (Fig. 1C).

Pre- and post-surgery flight kinematics

There was a significant difference in wing beat frequency (paired *t*-test, t=2.430, N=35, P=0.021; Fig. 2A) and proportion of time spent flapping (paired *t*-test, t=3.327, N=35, P=0.002; Fig. 2E) between instrumented and non-instrumented flights. However, qualitatively the relationship between both wing beat frequency and the proportion

of time spent flapping and flight speed was similar (Fig. 2A,E). No significant differences were detected in shortening duration (paired *t*-test, t=−1.730, N=35, P=0.093), relative shortening duration (paired *t*-test, t=1.723, N=35, P=0.094; Fig. 2B), stroke amplitude (paired *t*-test, t=1.629, N=35, P=0.113; Fig. 2C) and stroke plane angle relative to the horizontal (paired *t*-test, t=0.493, N=35, P=0.625; Fig. 2D) between instrumented and non-instrumented birds.

Correction for ground effect

The height (H) and width (B) of the working section were equal (B/H=1). Birds flew at a height (h) above the midline of the wind tunnel (h/H=0.25) and approximately equidistant from the walls. The wingspan ($2b$) was 80% of the width of the wind tunnel [$B/2b$=1.25; following Rayner (Rayner, 1994)]. Correction of wind tunnel flight power for ground effect (i.e. to estimate free flight power requirements) increased the power requirements at all flight speeds (Figs 1 and 3). The corrections for ground effect had less of an effect on flight power as flight speed increased where the induced power became a smaller component of total flight power.
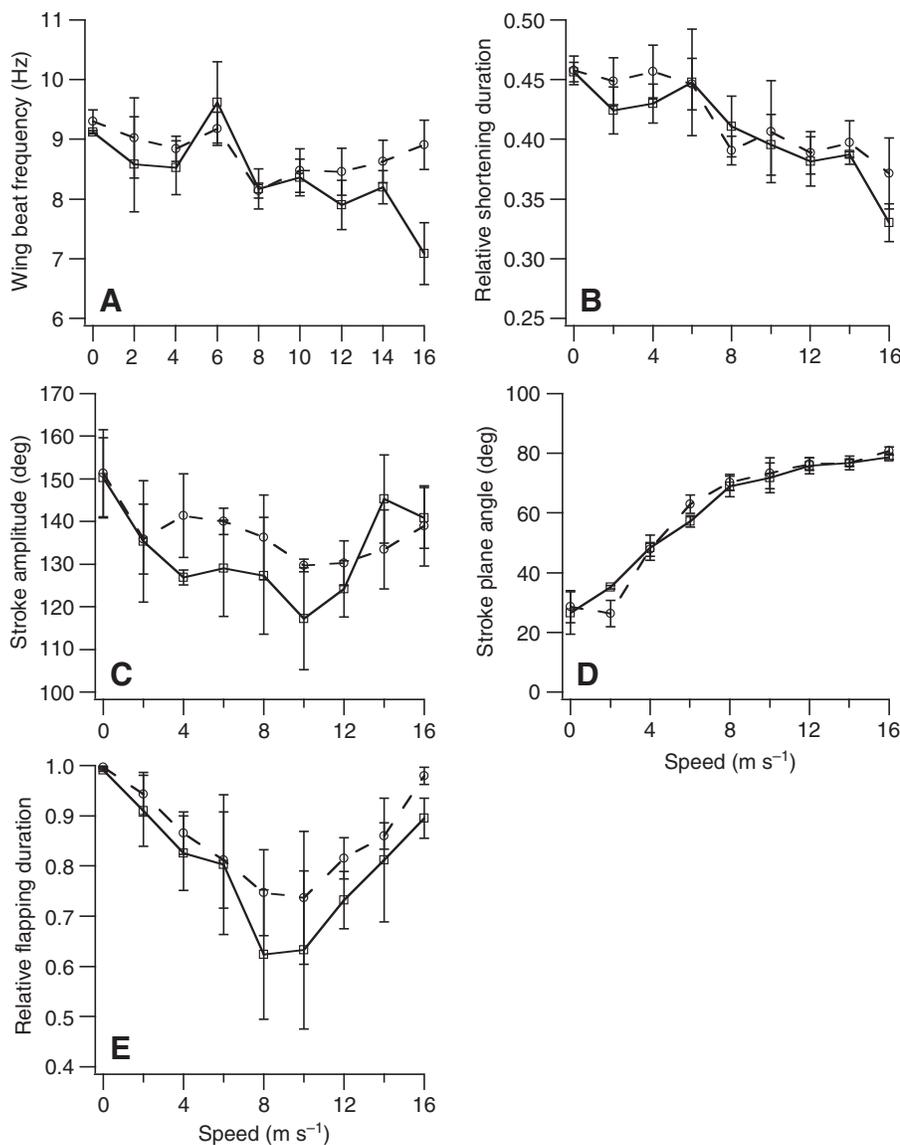

Fig. 2. Flight kinematics in relation to flight speed in instrumented and non-instrumented birds. Instrumented birds (open circles, dashed line) and non-instrumented birds (open squares, solid line). (A) Wing beat frequency. (B) Relative shortening duration. (C) Stroke amplitude. (D) Stroke plane angle. (E) Relative flapping duration. Data are shown as mean ± s.e.m. (N=4, 3, 5, 3, 4, 3, 7, 2, 4 for speeds 0, 2, 4, 6, 8, 10, 12, 14, 16 m s^{-1}, respectively).

DISCUSSION
Comparison of power-speed relationships obtained using different approaches

Two independent approaches were used to determine the mechanical power–speed relationship in cockatiels. One approach used *in vitro* muscle performance as a basis for estimating flight power (Morris and Askew, 2010). There are two reasons for having a certain amount of confidence in these estimates. First, several indicators of muscle performance (e.g. isometric stress, mean stress difference) suggest that the pectoralis muscle preparation functions at a level expected from a muscle tissue of this type (Morris and Askew, 2010). Second, comparison between the mechanical power data and whole animal metabolic rate yields whole animal efficiencies that fall within the range previously reported (Morris et al., 2010; Videler, 2005). The other approach used an aerodynamic model to estimate flight power. The major uncertainty in deriving power using this approach is the choice of coefficients in the calculations. In order to establish the sensitivity of the power–speed relationship to the choice of these coefficients, power was estimated using a range of different values taken from the literature. There was quite good qualitative and quantitative agreement between the power–speed relationships obtained using aerodynamic theory and *in vitro* measurements of muscle performance (Fig. 1). However, power calculated using aerodynamic analysis was highly sensitive to the values assumed for the induced power factor, and the parasite and profile drag coefficients (Fig. 1). Power varied 1.4- to 3.0-fold when calculated using the minimum and maximum range of coefficients (Fig. 1A,C). Across all flight speeds, the closest match between the results from aerodynamic theory and the *in vitro* measurements of muscle performance was obtained with an induced power factor of 1.2 and parasite and profile drag coefficients of 0.13 and 0.02, respectively (Fig. 2B). These coefficients are within the range of values previously used in aerodynamic models (e.g. Pennycuick, 1975; Tobalske et al., 2003). However, calculating power with the minimum set of coefficients produced the best estimate of flight power at low speeds (Fig. 1A). An induced power factor of 1.0 represents an ideal case in which acceleration of air across the actuator disc is equal and only in the axial direction (Tucker, 1973): such conditions are physically unlikely. However, there is some evidence to suggest that animal wings are rather efficient [k=1.04 (Spedding, 1987); k=1.12 (Bomphrey et al., 2006)].

Mechanical power calculated using aerodynamic analyses has been used to estimate the metabolic power requirements of flight (Pennycuick, 1968; Pennycuick, 1969; Tucker, 1973), flight muscle efficiency (Tucker, 1972; Ward et al., 2001) and to calibrate *in vivo* measurements of bone strain to pectoralis muscle force (Hedrick et al., 2003; Tobalske et al., 2003). This study together with earlier work indicates that care must be taken in selecting appropriate coefficients for the aerodynamic models, and that arbitrarily assigning values to the coefficients in the equations across all flight speeds is not be appropriate (Usherwood et al., 2005) and will affect the accuracy of such analyses (Fig. 1) (Askew and Ellerby, 2007).

Comparison with other mechanical power data for cockatiels

Another study has quantified the mechanical power requirements of flight in the cockatiels (Hedrick et al., 2003). These estimated powers are much higher than those presented in this and a companion study (Morris and Askew, 2010) (Fig. 3). The differences in the flight power requirements could be real or could result from inaccuracies in either of the two approaches used. The possible reasons for the large differences will be considered below.
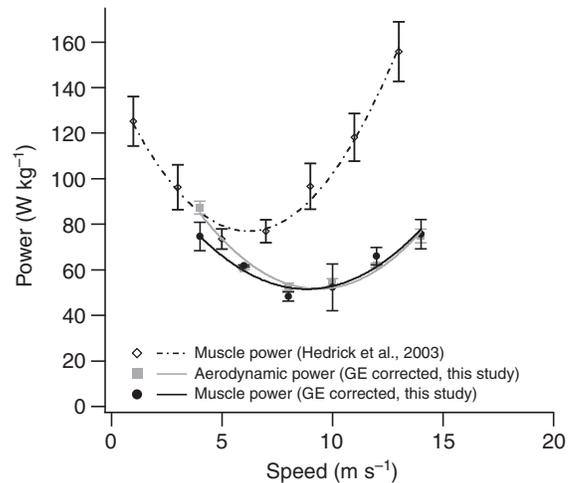

Fig. 3. Mechanical power–flight speed relationship in cockatiels (*Nymphicus hollandicus*) estimated using different techniques. *In vitro* muscle power and speed corrected for ground effect; aerodynamic power calculated using k=1.2, $C_{D,par}$=0.13, $C_{D,pro}$=0.02 corrected for ground effect; and pectoralis muscle power estimated using measurements of bone and muscle strain (Hedrick et al., 2003) – note that these data are not corrected for ground effect. Data are presented as mean ± s.e.m. (*N* as reported in the legend of Fig. 1).

The first reason why the mechanical powers presented here (this study) (Morris and Askew, 2010) are lower than those previously reported (Hedrick et al., 2003) may be that the mechanical power requirements differed between the two wind tunnels as a result of distortion of air flow by the walls of the wind tunnel. The smaller size of the wind tunnel used in this study (0.52 m×0.52 m×0.95 m) compared with that used in the Hedrick et al. study (1.2 m×1.2 m×1.4 m) (Hedrick et al., 2003) are likely to have greater effect in reducing the mechanical power requirements of flight as a result of greater interference of flow by the walls of the wind tunnel. Hedrick et al. (Hedrick et al., 2003) estimated that the effects were relatively small, potentially reducing mechanical power by up to 10%. In our study the free flight mechanical power requirements were estimated from wind tunnel estimates of mechanical power (Morris and Askew, 2010) by taking into account ground effects. The potential reduction in mechanical power was much larger than in the Hedrick et al. study (e.g. 42% lower than free flight at 2 m s^{-1} and 5% lower at 14 m s^{-1}). However, the estimated *free flight* power output was still much lower than the *wind tunnel* power outputs previously reported (Fig. 3), so it is unlikely that the differences between these two studies is solely due to interference of flow by the walls of the wind tunnel.

Secondly, estimating mechanical power from *in vitro* muscle performance (Morris and Askew, 2010) requires some assumptions that may introduce some uncertainty. For example, it was assumed that muscle performance *in vitro* reflects muscle performance *in vivo*. We have assumed that the similarity of a number of parameters indicative of muscle performance with other *in vitro* measurements on isolated muscles [table 1 (ESM) in Morris and Askew (Morris and Askew, 2010)] is a good indicator of the reliability of the power measurements from our muscle preparations. A further assumption is that *in vivo* muscle performance could be reliably derived from supramaximal *in vitro* muscle performance and relative EMG intensity *in vivo* (Morris and Askew, 2010). The justification for this assumption is that there is a linear relationship between EMG

intensity and work (see Biggland and Lippold, 1954; Adams et al., 1992; Del Valle and Thomas, 2005) and between motoneuron firing rate and force (Tansey et al., 1996).

A third explanation for the discrepancy between the two studies might result from Hedrick et al.'s approach to estimating the mechanical power requirements of flight in the cockatiels (Hedrick et al., 2003). In this earlier study pectoralis muscle force was estimated using strain gauges attached to the deltopectoral crest of the humerus to give an index of muscle force and sonomicrometry was used to determine pectoralis muscle length change. The authors of this study reported difficulties in obtaining a reliable relationship between bone strain and pectoralis muscle force. Hedrick et al. (Hedrick et al., 2003) concluded that previous methods used (i.e. the "direct pull calibration" method) to calibrate the strain gauges were unreliable and alternatively calculated a calibration factor, converting bone strain into pectoralis force by assuming the total uncalibrated power produced by both pectoralis muscles at 7 and $9\,\mathrm{m\,s^{-1}}$ was equal to the total aerodynamic power required for flight, calculated from aerodynamic models (Hedrick et al., 2003; Tobalske et al., 2003). This may have introduced error into the calculated mechanical power output because of uncertainty over drag coefficients and other constants used in aerodynamic models and the sensitivity of the calculation of power to these values (Hedrick et al., 2003; Askew and Ellerby, 2007). However, the aerodynamic coefficients used in the Hedrick et al. analysis were the same as those found to give the best fit to our *in vitro* muscle performance derived powers across the range of flight speeds (Fig. 1B) and therefore are unlikely to be the source of the large discrepancy between the two studies. Additionally, changes in the loading pattern on the deltopectoral crest that might result from speed-related adjustments in wing kinematics, may prevent pectoralis muscle force being derived from bone strain using a single conversion factor. Other potential sources of difference are a number of errors in the aerodynamic model used by Hedrick et al. First, the total aerodynamic power was calculated as the sum of the induced, profile and parasite power components, as well as the rate of change of potential energy of the centre of mass [equation 2 in Hedrick et al. (Hedrick et al., 2003)]. However, this is incorrect, because the induced power term (as calculated in their equation 6) includes the rate of change of potential energy (Hedrick et al., 2003). This error is likely to have been negligible as the potential for climbing flight in a wind tunnel is minimal. Second, parasite power has been included twice [in both equations 2 and 6 in Hedrick et al. (Hedrick et al., 2003)]. It is probable that these errors will have overestimated aerodynamic power. However, at the speeds (7 and $9\,\mathrm{m\,s^{-1}}$) at which the aerodynamic power and power derived from the bone strain were assumed to be equal, doubling of the parasite power component results in only a 7–14% [based on our aerodynamic calculations using the same values for k, $C_{\mathrm{D,pro}}$ and $C_{\mathrm{D,par}}$ as Hedrick et al. (Hedrick et al., 2003)] overestimation of mechanical power (this error would be constant across all flight speeds – i.e. a constant error in their calibration factor, F). The magnitude of this potential error is insufficient to explain the observed discrepancy between the two estimates of power. Additionally, the cable used in the Hedrick et al. (Hedrick et al., 2003) study was four times heavier than the cable used here. This will increase the power required to support the weight and to overcome the drag of the cable, and will increase flight power across all speeds; but the effects are unknown.

Finally, the differences between the two studies could be largely real and may result from differences in strain of bird or training and experimental protocols. Indicative that this might be the case is the fact that both the strain and strain rate in the earlier study (Hedrick et al., 2003) is higher than it is in our study (Morris and Askew, 2010). However, these differences in strain and strain rate occur generally across the full range of flight speeds, not just at the highest speeds where the differences between the two studies are greatest (Fig. 3).

Effects of instrumentation on flight kinematics

In order to obtain direct measurements of muscle activity and length change it was necessary to instrument the birds with sonomicrometry transducers and EMG electrodes and to attach these transducers to a recording apparatus *via* a light-weight data acquisition cable. Instrumentation affected flight kinematics as has been found in similar studies, although the effects reported here were not as great as have been reported in some smaller species (Fig. 3) (Ellerby and Askew, 2007; Tobalske et al., 2005; Bundle et al., 2007). Although wing beat frequency and the proportion of time spent flapping increased in instrumented birds (compared with pre-surgery flight), qualitatively the relationships between these variables and flight speed were similar to pre-surgery birds (Fig. 3A,C). It is necessary to instrument the birds and to fly them in a wind tunnel in order to obtain the data presented in this and a companion study (Morris and Askew, 2010). This affects the birds' flight performance, and our data must be interpreted with this in mind.

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