

Mechanical Power Output of Cockatiel Flight in Relation to Flight Speed

Caroline H. Brighton

Institute of Integrative and Comparative Biology,
University of Leeds, Leeds LS2 9JT

Summary

The shape and magnitude of the mechanical power-speed relationship for bird flight remains controversial. This relationship is central to our understanding of the ecology and evolution of bird flight behaviour. We estimated the mechanical power requirements of active flight over a range of speeds, in cockatiels (*Nymphicus hollandicus*) using a quasi-steady aerodynamic model. The power curve for cockatiel flight was found to be J-shaped, and the minimum power speed was 8 m s⁻¹. This is consistent with metabolic measurements on the same species, but disagree with previous measurements of mechanical power. This suggests that methods that rely on bone strain as an index of muscle force as a component of the approach to measure mechanical power output are unreliable.

Introduction

The most significant advance in the evolution of flight was the transition from gliding flight to active forward flight achieved by flapping of the wings and the generation of mechanical power by the flight muscles. The power required for flapping flight varies with speed; however, the power-speed relationship ("power curve") still represents an area of controversy¹¹. Aerodynamic theory predicts that qualitatively the mechanical power curve should be U-shaped: drag forces on the body and wings increase concomitantly with speed while drag associated with generating the aerodynamic force decreases with increasing speed. Therefore minimum power will be at an intermediate flight speed. Contrary to aerodynamic predictions, experimental studies on birds flying in wind tunnels have obtained J-shaped and L-shaped power curves, and there is lack of quantitative agreement between studies of the same and similar species. For example, in the cockatiel (*Nymphicus hollandicus*) metabolic measurements report a minimum power speed of 10 m s⁻¹, whereas mechanical power estimates suggest that the minimum power speed is 5 m s⁻¹ and mechanical power curve is J-shaped^{11, 12}.

For the first time, we applied a quasi-steady aerodynamic model, to calculate the mechanical power requirements of cockatiels flying over a range of speeds (4 – 16 m s⁻¹), in order to resolve the controversy over the shape and magnitude of the flight power curve.

Methods

Cockatiels were trained to fly in a variable-speed wind tunnel until they could sustain approximately 10 minutes of continuous flight at a range of speeds. Trained birds were flown at a range of speeds and lateral and dorsal views of the bird were simultaneously recorded using high-speed video at 125 fps. Wing and body kinematics were obtained by digitising the video recordings. These

kinematic data and morphological measurements were used to calculate the total aerodynamic power output (P_{aero}) from the induced (P_{ind}), parasite (P_{par}) and profile (P_{pro}) power components:

$$P_{aero} = [P_{ind}] + [P_{par}] + [P_{pro}]$$

$$= M_b k w (g + v_y) + (1/2 M_b V_x^2 + M_b g y) + 1/2 \rho S_b C_{D,par} V^3 + 2 \Sigma ((1/2) \rho V_R^3 S_r C_{D,pro})$$

where M_b is body mass, k is the correction factor taken to be 1.2, w is induced velocity - calculated using actuator disk theory and stroke amplitude measurement^{13,10}, g is gravitational acceleration, v is velocity, V_x is overall velocity in the horizontal direction, y is vertical movement; ρ is air density, S_b is frontal body area¹, $C_{D,par}$ is the parasite power coefficient supposed to be 0.13; V_R is the resultant velocity¹, S_r is the wing area and $C_{D,pro}$ is the profile power coefficient taken to be 0.02. Power output was expressed relative to pectoralis muscle mass (W/kg).

Results

Mechanical power-speed relationship

The total mechanical power output varied as an asymmetric J-shaped relationship with speed, with the power at the slowest speeds being lower than the power at the highest speeds (Fig. 1).

The minimum power was 50 W kg⁻¹ at 8 m s⁻¹. There was a statistically significant increase in power with speed above and below the minimum power speed (146 W kg⁻¹ at 16 m s⁻¹ and 70 W kg⁻¹ at 4 m s⁻¹; ANOVA $p < 0.05$). The shape of the power curve was determined by the relationship between the induced, profile and parasite

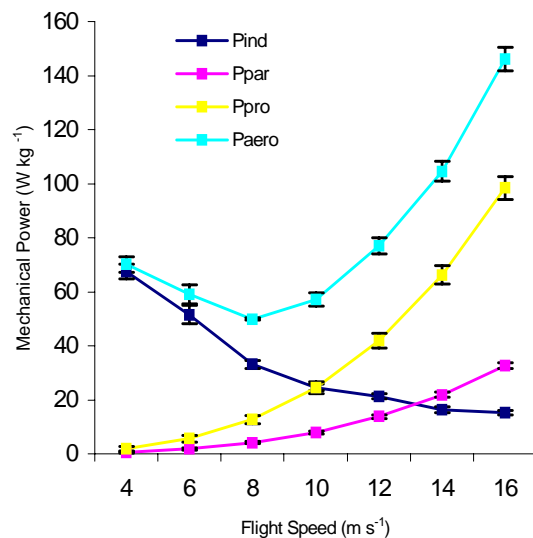


Fig. 1. Total mechanical power output during flapping flight in relation to flight speed in cockatiels. The induced, parasite and profile power components are also shown. Data represents means \pm standard error.

power components with speed. Parasite power increased gradually from 0.60 – 36.1 W kg⁻¹ with flight speed (ANOVA $p < 0.001$). Profile power increased more rapidly from 1.98 – 98.4 W kg⁻¹ (ANOVA $p < 0.001$). Induced power decreased steadily with speed, from 67.5 – 15.1 W kg⁻¹ (ANOVA $p < 0.001$). This was consistent with the aerodynamic theory. The difference between the J-shaped

power curve obtained here and the U-shaped power curve predicted from aerodynamic theory results from the difficulty of getting the birds to fly at speeds below 4 m s⁻¹. Speeds below 4 m s⁻¹ are probably not encountered during natural flight in cockatiels.

Flight kinematics

Variation in power output as a function of speed is associated with changes in wing kinematics. Wingbeat frequency, stroke plane angle and wingspan were adjusted according to speed. Wingbeat frequency decreased with speed, measuring 7.38Hz at 4m s⁻¹ and reaching a minimum of 4.8Hz at 14ms⁻¹, followed by a final increase at 16ms⁻¹ (ANOVA: p<0.1). Stroke plane angle was found to increase slightly with speed estimated as 46.5° at 4m s⁻¹, increasing to 83.3° at 16m s⁻¹. (ANOVA: P<0.1). The wingspan at the start of the downstroke in the cockatiels was found to decrease as speed was increased averaging 0.15m at slow speeds (4m s⁻¹) and 0.098m at fast speeds (14m s⁻¹) (ANOVA: P<0.05).

Wing morphology

Cockatiels have intermediate aspect ratio wings with low wing loading (G.N. Askew, pers. com.), representing a trade-off between flight efficiency and ability for rapid acceleration on demand. Average values of 6.4±0.89 and 29.1±2.36 N m² were calculated for aspect ratio and wing loading, respectively.

Discussion

Mechanical Power

The mechanical power-speed relationship in cockatiels followed an asymmetric J-shaped power curve. All current aerodynamic models agree that during slow flight the induced power is high⁸. It is likely that if the cockatiels were able to fly at slow speeds, a U-shaped curve would be obtained, consistent with aerodynamic theory and measurements in magpies³.

Qualitatively, the results here are similar to previous mechanical power estimates for the cockatiel¹¹. However, quantitatively there is considerable disagreement with previous research, specifically relating to the low minimum power speed and high mechanical power estimates (1.5-1.6x higher than reported here). In support of our results, power requirements for flight (minimum of 50±0.4 W kg⁻¹ at 8 m s⁻¹ and maximum of 146±4.3 W kg⁻¹ at 16 m s⁻¹) fall within the established range for cockatiel flight muscle (<185 W kg⁻¹)¹⁵ and metabolic power-speed estimates also indicate a similar minimum power speed of 10 m s⁻¹.¹⁶

Muscle efficiency can be calculated from mechanical power output and metabolic power input by rearranging equation 5 from Rayner 1999⁸ as follows:

$$\text{efficiency} = k_{\text{pos}} \times P_{\text{mech}} / (P_{\text{met}} - P_{\text{b}})$$

where k_{pos} represents the 'postural' cost of flight (taken to be 1.1)⁸, P_{mech} is the mechanical power, P_{met} is the metabolic power and P_{b} is basal metabolic rate (calculated to be 50.7 W kg⁻¹)¹⁹. Using Bundle and Dial's measurements of metabolic power¹⁶, our mechanical powers show pectoralis muscle efficiency to be 7 to 17%; and for Tobalske's mechanical powers, efficiency is 11 to 27% (across the speed range). The maximum efficiency value reported for mammalian muscle is 19%¹⁸ (no data exists for birds); therefore Tobalske's mechanical powers are likely to be erroneous. Our mechanical powers give efficiencies that fall in the expected range for mammalian

muscle, giving support to our values and indicating that Tobalske's are significantly over-estimated. Their approach used strain gauges attached to the deltopectoral crest (DPC) of the humerus to measure tensile bone strain during contraction of the pectoralis muscle. These strain gauges are sensitive to the direction of application of force, so there are difficulties in obtaining a reliable calibration between bone strain and the force applied, *post mortem*^{5,11}. Since the orientation of the humerus changes throughout the wing stroke, bone strain is thus an unreliable indicator of muscle force.

Flight kinematics and aerodynamics

Aerodynamic models predict the existence of critical flight speeds, above or below which a bird must change its wingbeat kinematics in order to alter the aerodynamic force and maintain sufficient thrust and vertical force for steady flight. When a bird is unable to change its wingbeat kinematics sufficiently over a range of speeds, it must increase aerodynamic force by changing gait. The increase in wingbeat frequency at 16ms⁻¹ may represent a gait transition in which wing kinematics change fundamentally from those at slower speeds. This may be evidence of a third flapping gait performed at the fastest flight speeds. However, flow visualisation experiments have not currently been accomplished at sufficiently high speeds to confirm the existence of a third gait.

Concluding remarks

In estimating flight power requirements it is important to critically evaluate the results in the light of available independent, physiological data. Our mechanical power estimates obtained using an aerodynamic model in comparison with previously recorded metabolic data, yield pectoralis muscle efficiencies that concur with measurements made from mammalian muscles. The minimum power speed estimated from the power curve agrees with that estimated from metabolic measurements. Critical evaluation of previous estimates that have relied on bone tensile strain as an index of muscle force indicate that this approach is unreliable. In order to gain insight into the ecology and evolution of bird flight behaviour, it is vital that reliable estimates of flight power in relation to flight speed are used.

1. Askew, G.N., Marsh, R.L., Ellington, C.P. (2001). The mechanical power output of the flight muscles of blue-breasted quail (*Coturnix chinensis*) during take-off. *J. Exp. Biol.* **204**, 3601-3619.
2. Coen Van De Berg, Rayner, J.M.V. (1995). The moment of inertia of bird wings and the inertial power requirement for flapping flight. *J. Exp. Biol.* **198**, 1655-1664.
3. Dial, K.P., Biewener, A.A., Tobalske, B.W., Warrick, D.R. (1997). Mechanical power output of bird flight. *Nature*. **120**, 941-952.
4. Ellerby and Askew, in prep.
5. Hedrick, T.L., Tobalske, B.W., Biewener, A. A. (2003). How Cockatiels (*Nymphicus hollandicus*) modulate pectoralis power output. *J. Exp. Biol.* **206**, 1363-1378.
6. Pennycuik, C.J. (1996). Wing beat frequency of birds in steady cruising flight: new data and improved predictions. *J. Exp. Biol.* **199**, 1613-1618.
7. Pennycuik, C.J., Hedenström, A., Rosen, M. (2000). Horizontal flight of a swallow (*Hirundo rustica*) observed in a wing tunnel, with a new method for directly measuring mechanical power. *J. Exp. Biol.* **203**, 1755-1765.
8. Rayner, J.M.V. (1999). Estimating power curves of flying vertebrates. *J. Exp. Biol.* **202**, 3449-3461.
9. Stiles, F.G., Altshuler, D.L., Dudley, R. (2005). Wing morphology and flight behavior of some north american hummingbird species. *Auk*. **122**, 872-886.
10. Tobalske, B.W., Peacock, W.L., Dial, K.P. (1999). Kinematics of flap-bounding flight in the zebra finch over a wide range of speeds. *J. Exp. Biol.* **202**, 1725-1739.

11. Tobalske, B.W., Hedrick, T.L., Dial, K.P., Biewener, A.A. (2003). Comparative power curves in bird flight. *Nature*. **421**, 363-366.
12. Tobalske, B.W., Hedrick, T.L., Biewener, A.A. (2003). Wing kinematics of avian flight across speeds. *J. Exp. Biol.* **34**, 177-184.
13. Wakeling, J. M., Ellington, C. P. (1997). Dragonfly flight III lift and power requirements. *J. Exp. Biol.* **200**, 583-600.
14. Ward, S., Moller, U., Rayner, J.M.V., Jackson, D.M., Bilo, D., Nachtigall, W., Speakman, J.R. (2001). Metabolic power, mechanical power and efficiency during wind tunnel flight by the European starling *Sturnus vulgaris*. *J. Exp. Biol.* **204**, 3311-3322.
15. Hedrick, T. L., Usherwood, J. R., Biewener, A. A. (2004). Wing inertia and whole-body acceleration: an analysis of instantaneous aerodynamic force production in cockatiels (*Nymphicus hollandicus*) flying across a range of speeds. *J. Exp. Biol.* **207**, 1689-1702.
16. Bundle, M. W., Dial, K. P. (2002). Changes in flight morphology influence the shape of the avian power curve. In *World Congress of Biomechanics*. Calgary.
17. McNeill, A. R. (2004). Models and the scaling of energy costs for locomotion. *J. Exp. Biol.* **208**, 1645-1652.
18. Smith, N. P., Barclay, C. J., Loiselle, D. S. (2005). The efficiency of muscle contraction. *Progress Biophys. Mol. Biol.* **88**, 1 – 58.
19. Lasiewski, R. C., Dawson, W. R. (1967). A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor*. **69**, 13-23.

Acknowledgements I would like to thank my dissertation supervisor, Dr G.N. Askew, for his efforts and contribution to my study.