

The mechanical power output and flight efficiency of steady flight in the budgerigar (*Melopsittacus undulates*) at various flight speeds

Gemma Pridmore

BSc Zoology

School of Biological Sciences

University of Leeds

Abstract

Seven budgerigars (*Melopsittacus undulates*) were trained to fly in steady flight in a wind tunnel, at varying speeds, and the mechanical power required for flight was determined using high-speed cinematography and calculated using an aerodynamic model based upon wing kinematics. Mechanical power conformed to the predicted U-shaped power curve as a function of speed, and ranged from a maximum of 83.5W/kg to a minimum of 51.5W/kg over air speeds varying between 4ms⁻¹ to 16ms⁻¹. Minimum power speed was found to be approximately 10ms⁻¹, and maximum range speed was found to be approximately 12ms⁻¹ in the budgerigar. Flight muscle efficiency was then calculated, and was found to range between 0.035 and 0.084 (mean = 0.059 +/- 0.017) over varying flight speeds in the budgerigar. This differs significantly to the value of 0.23, which has previously been suggested as a typical value for flight muscle efficiency in birds (Pennycuick, 1975). A flight muscle efficiency of 0.059 rather than 0.23 should therefore be used to in order to calculate the flight costs of budgerigars with greater accuracy.

**The mechanical power output and flight efficiency of steady flight in the
budgerigar (*Melopsittacus undulates*) at various flight speeds**

Contents

Introduction	3
Aims and Objectives	12
Methods and Materials	13
Results	19
Discussion	28
Acknowledgements and References Cited	43
Appendices	46

Introduction

Flight is a phenomenon which has always captured the human mind. Its study has enabled us to understand both the structural and energetic components necessary for flight, and in turn enabled us to become airborne ourselves. Powered flight has evolved at least four times independently throughout life history: in the pterosaurs, birds, bats and insects. It is a form of locomotion that places huge energetic demands on the animal, but also offers many advantages. It opens up a whole new habitat that can be reached by few other animals, offering reduced predation and competition and access to new food sources and living spaces. It is also a much faster and more efficient form of locomotion which enables the animal to travel greater distances to locations which may not be open to other animals. It is no surprise then that all extant flying families are highly successful and diverse. There are over 11,000 species of bat, around 10,000 species of bird and approximately 1,000,000 species of insects. However, despite the fact that flight does offer many advantages to animals, it also implies many conditions and constraints that don't act on terrestrial animals. Flight requires huge power and major physiological adaptations. All flying animals are highly adapted specifically for flight. It is by studying the power required to fly that we can begin to understand flight and in particular the morphological adaptations, the physical limitations and the evolution of flight. The power required for flight is therefore a subject of keen interest and a highly researched topic.

Power Components of Flight:

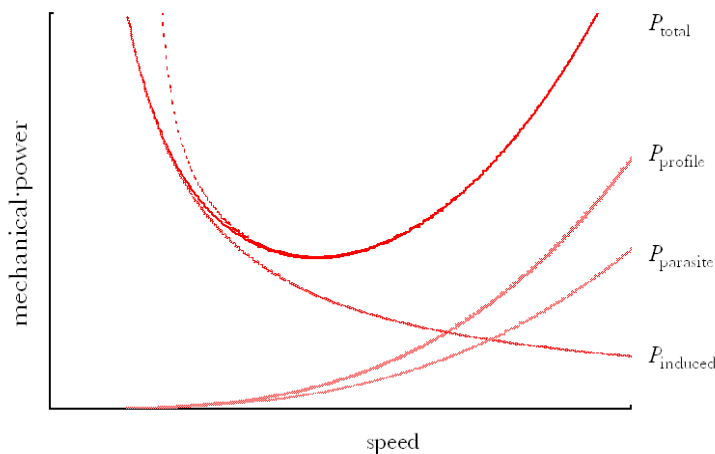
When determining the energetic costs of flight both the metabolic and mechanical power costs are studied. Metabolic power (P_{met}) is defined as the power input to the flight muscles and can be calculated by adding the mechanical power output to the heat loss of the flight muscles (Rayner, 1999a). Mechanical power (P_{mech}) is the power output of the flight muscles, the aerodynamic and inertial power required for flight. Mechanical power can be calculated from the following components (Rayner and Ward, 1999):

$$P_{\text{mech}} = P_{\text{ine}} + P_{\text{pro}} + P_{\text{par}} + P_{\text{ind}}$$

Inertial power (P_{ine}) is the power needed to flap the wings. It is negligible at all but the lowest speeds. Profile power (P_{pro}) is the power needed to overcome drag on the wings and is proportional to wing area and forward velocity cubed. Parasite power (P_{par}) is the power needed to overcome drag on the body and is proportional to frontal body area and forward velocity cubed. Finally, induced power (P_{ind}) is the power required for lift generation, and is proportional to the weight of the bird squared, and inversely proportional to forward velocity. The typical relationship for each of these components with speed can be seen in the *figure 1*.

Flight power is therefore a function of speed and it is typically thought that the relationship between power and speed gives rise to a U-shaped curve (Pennycuick, 1975). However, this is a controversial topic and some believe that it should in fact give rise to an L- or J- shaped curve. Some even believe that the power requirements for flight vary little with speed. The controversy surrounding these curves is largely due to the experimental limitations of the methods used (Rayner and Ward, 1999).

Figure 1: Mechanical Power Consumption in Flapping Flight (Rayner and Ward, 1999); Changes in the profile, parasite, induced, inertial (represented by the dashed line) and total mechanical power, as a function of speed.



Wind Tunnel Flight:

A variety of methods have been used in order to determine both the metabolic and mechanical power requirements of flight. However, it is difficult to measure these

factors directly and each method has its limitations. This inevitably leads to controversy over the accuracy and reliability of methods used and consequently there continues to be major experimental developments in this particular area. Since it is difficult to observe animals flying in particular conditions, over a particular time and distance and in steady flight in the wild, studies often rely upon flying trained animals in a wind tunnel or an enclosed area. The wind tunnel allows the experimenter to set the air speed against which the animal must fly. This forces the animal to fly at a set speed in steady flight for the duration of the time it is kept in the wind tunnel. The animal can be observed flying over a range of enforced speeds and the effect of speed on flight power can be determined. Animals flying in an enclosed area rather than a wind tunnel, however, must be timed over a known distance in order to calculate speed. If air speed within the enclosed area is not still (i.e. due to wind) then it is also necessary to take this into account. Air speed in such situations may be impossible to control and difficult to measure. It has been suggested that the artificial conditions under which the animal is flying in captivity, may in fact affect flight performance (Rayner, 1994). Doppler radar has been used in natural conditions to record timed flight over a known distance. One study found that hawks flew significantly faster under natural conditions than in captive conditions (Brigham *et al.* 1997). Since speed is a direct function of power, this study therefore brings into question the accuracy of power studies based upon flight in an enclosed area. Mechanical power requirements are in fact expected to be lower for flight in an enclosed section of a wind tunnel compared with natural flight, most probably as a direct function of lower flight speeds. There is also concern that stress induced under such artificial conditions may increase metabolic rate and therefore affect the metabolic power of flight (Rayner, 1994). Despite such effects, many physiological studies of flight can only take place under artificial conditions, and are therefore limited in their accuracy. However, it is believed that with acclimatization to experimental conditions such effects can be minimized. The observation of stable and relaxed flight is often a good indicator that an animal has become acclimatized to the surroundings. The performance of flight can also be improved by using a larger test section and by decreasing any turbulence felt in the wind tunnel. However, it is only in free flight conditions that we can guarantee aerodynamic power output will truly reflect that observed under natural conditions.

Determining Metabolic Power:

Mechanical and metabolic powers have been determined using a variety of both theoretical and experimental *in vivo* and *in vitro* approaches. One of the first measurements of metabolic power was estimated using mask respirometry during wind tunnel flight in the budgerigar (Tucker, 1967). This allowed the consumption of oxygen and the production of carbon dioxide to be determined, and from this data the metabolic power of flight at a particular air speed can be calculated. Metabolic power has also been determined using the doubly labelled water technique during free flight (Masman and Klassen, 1987) and from cardiac output (Bishop and Butler, 1995). The doubly labelled water technique uses the turnover of two isotopes of body water to monitor carbon dioxide production in the flying animal. Carbon dioxide can then be used as an indicator of the energy being used in flight. In a similar way, cardiac output can also be used as an indicator of energy requirements during flight.

An alternative approach to determining metabolic flight costs has been through compositional analysis of body stores. An unrestrained bird was allowed to fly in a wind tunnel for a lengthy period which resulted in significant weight loss. It was then allowed a recovery period in order to re-fuel. Energy intake during this time was determined through a feeding balance and indirect calorimetry. It was assumed that what the bird had lost during flight was regained through intake during recovery and this therefore provides some insight into the substrate catabolized and therefore the energy used and power required during flight. Compositional analysis of carcasses may also be used to analyze fuel stores and dropping collection and analysis during long-term flight may provide some insight into the fuel required to power flight (Klaassen *et al.* 2000). However, these methods are all technically difficult to carry out and a much more efficient way of determining metabolic power is to use a theoretical aerodynamic model to calculate mechanical power and to then obtain an estimate of metabolic power from the following (Ward *et al.* 2001):

$$P_{\text{met}} = 1.1 [(P_{\text{mech}}/E_{\text{FM}})+P_{\text{BMR}}] \quad (1.)$$

E_{FM} is the flight muscle efficiency and P_{BMR} is the basal metabolism of the animal under study. Both of these factors can be determined experimentally and may be size

and species dependant. Flight muscle efficiency also varies with speed (Ward *et al.* 2001). Various values for flight muscle efficiency and basal metabolism are available from previous studies. However, since they are dependant on the species, size and speed much more of this data still needs to be amassed in order for this equation to be accurate when using a variety of different animals at different speeds. The value of 1.1 used in this equation, increases the overall value of metabolic power by 10%. This is to allow for the extra costs of respiration and circulation during flight. These costs have been estimated to be 5% each, hence the increase by 10%. However, since it is not possible to partition such metabolic costs experimentally or theoretically; these values have been decided upon arbitrarily and are unproven. Despite claims that overall metabolic power should be relatively insensitive to these values, this arbitrary value stills brings this formula into question over its accuracy. The equation may also be rearranged in order to determine the flight muscle efficiency of a particular species, at a particular speed, if values of both mechanical and metabolic power are available.

Determining Mechanical Power:

As mentioned previously, mechanical power can be calculated using theoretical aerodynamic models. This is a commonly used method and three different models are available. These models are based on the momentum jet theory (Pennycuick, 1989), the vortex ring model (Rayner, 1979a) and the lifting line theory, developed by Lanchester and Prandtl. The momentum jet theory is based upon calculating the air velocities in the momentum jet of air behind the aerofoil, which have been induced by the equal and opposite force of that aerofoil. It is a steady state model that assumes that all the instantaneous forces on the wing are the same as that experienced in steady state motion. It is a simple model but generally believed to be inaccurate in its assumptions, underestimating the forces involved in flight. The lifting line theory is based upon quasi-steady state motion and the hypothesis that a lifting wing can be replaced by a lifting line and that the vortices shed by the wings trail behind in straight lines. The strength of these vortices is proportional to the rate of change of lift along the span and they induce a velocity to the line (or wing). This model is probably the most common and widely used. It is more accurate than the momentum jet theory but it has been suggested that it too underestimates the complex and unsteady forces involved in flight. The vortex ring model is more complex and reflects the

aerodynamics of lift production on the wings in non-steady flight. It is based upon the hypothesis that a circulation bound vortex and either a trailing or transverse vortex are produced as a result of each wing beat. The circulation bound vortex is the upward and forward loop of air that circles the wing giving it lift and thrust. The vortex leaving the wing is an air loop of the opposite rotation (downward and backward) shed by the wing to the air behind and below due to the position of the aerofoil. The development of this theory enabled a greater understanding of flight. Although these aerodynamic models are widely used to calculate mechanical power, they are based on certain critical assumptions and averaged measures of flight performance. They incorporate a number of both kinematic and aerodynamic parameters which are difficult to estimate accurately. The reliability and validity of these models is therefore under continuous discussion.

Such time-averaged models were very useful prior to the recent advances in high-speed imaging and data processing. However, it is now much easier to gain direct measurements of mechanical flight power. In more recent studies the use of high-speed cinematography has, in particular, played an important role. It enables the close observation of flight and allows flight to be digitized in order to analyse the kinematics of each phase of every wing beat if necessary. This can also enable the aforementioned aerodynamic models to be calculated with more accuracy too. One such example of this newly developed technology is computational biological fluid dynamics, which has been used to digitize and visualize flight. Simulation-based computational modelling of biological fluid dynamics through reconstruction of morphology and realistic representation of kinematics of individual objects, allow their flight powers to be determined with great accuracy. Any estimation of flight power requires an understanding of and ability to accurately quantify large-scale vortex flows produced by highly unsteady motions and the complex variable geometry of the flying object. This simulation based approach to flight power allows detailed information about the physical variables of flight (e.g. velocity) to be obtained and helps to bring new understanding to the forces involved in flight. It is therefore a much more accurate method of determining flight power than those previously mentioned (Liu, 2002). Further developments in technology have enabled wing kinematics to be 'replayed' on a dynamically scaled robotic model in order to measure forces produced by the wings. The body centred coordinates of the animal

under study (obtained from high speed film of the animal flying) are replayed on a flapping robot and this enables measurements of the instantaneous wing kinematics and aerodynamic forces, over the course of the wing stroke. The instantaneous power can then be calculated directly from these measurements. This allows a time-resolved estimate of aerodynamics and an analysis of the energetics involved, offering a greater accuracy than time-averaged findings based on aerodynamic models (Fry *et al.* 2005). Finally, both sonomicrometry and electromyography have been used to study flight muscle, both *in vitro* and *in vivo*, in order to determine the power output of these muscles. Electromyography determines the activity patterns of the flight muscles (through detection of nervous electrical impulses) and sonomicrometry determines the strain and strain rate of the muscle fibres as they work to enable flight. *In vivo* conditions can be replicated *in vitro* on isolated flight muscle fibres using the work loop technique (Josephson, 1985), and the strain and activity patterns of the muscles may be measured in this way too. By determining the performance and physiological properties of muscle we can begin to understand muscle limits in terms of flight power. Flight power is a subject which continually demands the developments of new innovations in order to further our understanding of flight. As new methods emerge, both our grasp of the subject and our accuracy in its study, will continue to improve.

Due to the range of methods now available for assessing flight powers, it is useful to compare the mechanical power requirements of a particular species, over a range of flight speeds, with that of the same or other closely-related species in order to gauge how accurate one method or set of results may be, compared to another. By amassing such similar data we can gain an insight into what the power requirements of flight for a particular species may really be, and also as to which methods may prove to be the most reliable and accurate for obtaining such data.

Flight Strategies:

Powered flight is energetically expensive and so quantifying its metabolic and mechanical costs is important. It enables us to understand the ways in which flying animals utilise this advantageous form of locomotion in an energetically efficient manner. This can prove to be valuable information for humans as we develop our own

artificial flight vehicles, helping to minimise our own flight fuel costs. The vortex ring model has enabled us to better understand flight and the gaits which animals may adopt in order to minimise the power requirements. The vortex ring model infers that circulation in the vortices surrounding the wing and leaving it should increase on the down stroke in order to maximise lift and thrust. They should then also be minimised on the upstroke to reduce drag. Many animals therefore adopt an inactive upstroke in order to minimise drag and the power required to fly. This is done either by flexing the wings (bending the elbows) or sweeping back the wingtips. This behaviour has also developed into the power-saving strategy of intermittent flight. Intermittent flight can either be bounding (flap-bounding) or undulating (flap-gliding). Bounding happens when the wings are flexed, and gliding happens when the wings are extended. Recently much work in this area has provided insight into the power required for these flight styles, in order to understand why certain species adopt them. Both of these forms of flight have been proven to decrease the mechanical power requirements of flight. The mechanical power output of flight during bounds and glides is in fact zero, however, this saving maybe offset somewhat by a disproportionate increase in the mechanical power required during intermediate flapping phases in order to maintain support and thrust (Tobalske, 2001). Methods as described above may be used to determine the mechanical power of flap-bounding and flap-gliding at various speeds and to deduce whether it offers the animal any energy-savings. Typically the flight strategy used by an animal depends upon its body size and the speed at which it is travelling. It may also depend upon the species in question, specifically the physiological and skeletal properties of the wings of that species. Alternative strategies may also be used in flight, depending upon the situation. Examples include hovering, thermal soaring and flight take-off strategies. The power requirements of these flight strategies may also be determined using any of the aforementioned methods. The potential aerodynamic advantages of such strategies may then be determined by comparing with those mechanical power requirements for similar, or the same species, in steady flight.

Conclusion:

The powers involved in flight are complex. They are affected by speed, flight style and many other parameters. I have only summarized the basis of methods, on which

many other studies have been built up. There are numerous published papers outlining how flight power may be determined, how it is affected by speed and how findings may be used to build up a greater understanding of flight. Power studies can help us to understand the evolution of flight, the limitations flight imposes, the energetic and structural components necessary for flight, and the ecological behaviours seen in all flying animals. By furthering our understanding of flight we may also gain insight into how muscles function generally, and how other forms of locomotion are powered (i.e. swimming and terrestrial locomotion). It is a subject which still requires further studies and understanding, despite its history. It will continue to evolve as technology develops, and our insight into this rewarding subject will grow with it.

Aims and Objectives

The primary aim of this project is to determine how the power requirements of flight vary with flight speed, in the budgerigar (*Melopsittacus undulates*). I hypothesise that the total mechanical power requirement for flight will produce a U-shaped curve as a function of speed. I hypothesise that both parasite power and profile power requirements will increase as flight speed increases, and that the induced power requirements will decrease as flight speed increases. In order to determine the relationship of each of these power components with speed, I will also be determining how potential and kinetic energies vary throughout steady flight and with varying speeds, and how induced and resultant velocity relate to changing flight speed. In addition I will be determining if wing beat frequency, stroke plane angle and stroke amplitude vary with changing flight speed in the budgerigar, and if flight power requirements between individual budgerigars differ significantly.

I hope to assess how the results (and therefore the method used), compare to other values of mechanical power, determined for both the budgerigar, and similar birds. And, as a secondary aim, I will also compare the results to values for the metabolic power of flight in the budgerigar, in order to determine flight efficiency in this species.

I will be following a method used to previously study the mechanical power output of the flight muscles during take-off in the blue-breasted quail (Askew *et al.* 2001). My method will be based on the movement of the centre of mass of birds filmed in steady flight in a wind tunnel and the aerodynamic analysis of this movement. My study will use seven individual budgerigars, observed a flight speeds ranging from 4ms^{-1} to 16ms^{-1} , with 2ms^{-1} intervals, in order to ensure enough evidence is gathered to support accurate and significant results.

Methods and Materials

Training:

Juvenile budgerigars were purchased from a commercial supplier, and kept housed in wire cages. They were fed commercial seed mix and water *ad libitum*. They were also offered a vitamin-enriched, high protein supplement once a day. Their body masses, wing muscles masses, wing lengths and wing strip areas were measured and recorded. The birds were exercised once a day in the wind tunnel, and the amount of time spent inside the wind tunnel was increased gradually until each bird could sustain fifteen minutes continuous, steady flight at 12ms^{-1} . This took between two to three weeks of gradual wind tunnel exposure. The birds were then exposed to speeds ranging from 4ms^{-1} to 16ms^{-1} . This speed range was determined by observing the speeds at which steady flight could not be sustained for more than 1 minute at a time. These speeds indicated the maximum endurance levels of the budgerigars. The birds were also trained to land on a small perch at the front of the working section.

The wind tunnel and filming:

The working section of the wind tunnel measured 52 x 52 x 95 cm (width x height x length). It was transparent Perspex, with the back wall painted matt black to avoid reflecting images during filming. A nylon line restricted birds to within the working section of the tunnel.

The budgerigars were filmed using a Kodak Motion Corder high-speed camera at a frame rate of 125Hz. The camera was positioned laterally and perpendicular to the working section of the wind tunnel.

Seven individual budgerigars were filmed flying in the wind tunnel in a range of air speeds from 4m/s to 16m/s at 2m/s intervals between each air speed.

Film Analysis:

The films were assessed and periods of approximately 2 seconds of steady flight for each bird, in each air speed, were analysed. The films were analysed by digitizing the flight into frames at every 0.016 seconds. In every frame the estimated centre of mass

of the bird was recorded in both the horizontal (x) and vertical (y) plane. The coordinates of the position of the centre of mass were taken in relation to the coordinates of origins (a pair of fixed points on the screen, one for each plane). The horizontal and vertical calibrations of the film were also calculated from the coordinates of these fixed points. The measurements of stroke plane angle (ϕ) and wing beat frequency (F_w) were also taken directly from the films.

Data smoothing:

A numerical method was used to correct for distortion and smooth the obtained coordinates for the centre of mass. Due to inaccuracies in digitizing and estimating the position of the centre of mass from video images, a sequence of observations such as these can scatter. The influence of such error maybe minimised by ‘smoothing’ the data, using a method known as fourth differences. The argument goes that if each measurement is combined with its two neighbours on either side (giving five consecutive observations), these measurements should lie very close to one another, were it not for experimental error. By combining these observations and determining the differences between them, we can alter our measurements and produce a smoothed set of data (Lanczos, 1957). Every data point is corrected by $-\frac{3}{35} \delta^4 y$, where δ is the difference between the data point and its neighbour (hence, δ^4 is the fourth difference; the difference between a data point and its four neighbours combined) and where y is the data point (i.e. a vertical position coordinate). This method would also be carried out for every horizontal position coordinate, where x would be the data point in question (See *appendix 1*. for a working example of this method).

After smoothing the data, the distance moved by the bird in both the horizontal and vertical planes, between each frame was calculated. These measurements were then corrected for real-life distances using the horizontal and vertical calibration values. At this point both the horizontal and vertical velocities of the bird over each frame were calculated. This would typically be done by dividing the distance moved by the time over which the frame took place. However, in order to minimise the effects of error (as the data becomes smaller and more sensitive) it is possible to calculate velocity (and subsequently acceleration) by once again combining each measurement with its two neighbours on either side. The argument states that velocity or acceleration

should not change much over five consecutive points. Therefore a similar fourth differences method to that previously described may be used. However, in this case it needs to be corrected for the time interval between each observation. The following equation was used to both calculate the velocity of the bird between each data point, and to smooth these velocities (Lanczos, 1957):

$$V_y = [(-2y_{-2}) - (y_{-1}) + (y_1) + (2y_2)]/10t \quad (2.)$$

Where V_y is the velocity of the bird between two consecutive vertical position (y) coordinates, $y_{-2/-1/1/2}$ are the two vertical position coordinates to either side of that coordinate in question, and t is the time difference between each positional coordinate (i.e. the time lapsed between each frame of film). Again this method is used to calculate the smoothed velocities between each horizontal (x) positional coordinate too. The same method can be used to calculate the accelerations between each calculated velocity in both horizontal (x) and vertical (y) plane. To each horizontal velocity the particular air speed at which the bird was being flown must also be added. The overall velocity may then be calculated from the horizontal and vertical velocities using Pythagoras' theorem.

Rate of change of potential and kinetic energies:

The rate of change in potential energy (dE_p/dt) is the power required to elevate the bird and the rate of change in kinetic energy ($dE_{K,ext}/dt$) is the power required to accelerate the bird. They can be calculated from the following equations:

$$dE_p/dt = M_b g \dot{z} \quad (3.)$$

$$dE_{K,ext}/dt = (M_b/2)(V/\Delta t) \quad (4.)$$

Where M_b is the body mass, g is gravitational acceleration (a fixed value of 9.81m^{-2}), \dot{z} is vertical velocity, V is the overall velocity and Δt is the duration of flight.

The horizontal and vertical velocities and accelerations, the overall velocity and the rates of change in potential and kinetic energies were calculated over the entire flight. Mean averages of each of these were then obtained.

Induced velocity and power:

Induced velocity (V_i) is the downward momentum of air imparted by the wings in order to provide a vertical force during flight. It can be determined using the classical actuator disc theory. The actuator disc represents the area over which the wings interact with the air. Induced velocity is assumed to be constant and steady over disc area and therefore is defined as the minimum momentum flux of air required to support the weight of the bird and any vertical acceleration force. The induced velocity can be calculated from the following equation (Wakeling & Ellington, 1997):

$$V_i^4 - 2VV_i^3 \sin a' + V^2 V_i^2 - (M_b(g + g_a)/(2\rho D))^2 = 0 \quad (5.)$$

where a' is the angle at which forward velocity of the bird is inclined to the actuator disc, g_a is the average vertical acceleration, ρ is air density (a fixed value taken to be 1.2kg/m^3) and D is the actuator disc area. For a more accurate estimate of induced velocity, it is usually multiplied by a correction factor k , which is taken to be 1.2 (Ellington, 1984).

The actuator disc generates a vertical force by imparting a velocity kV_i to the air entering the disc. The rate at which this is done by the disc is known as induced power and is calculated from the following equation:

$$P_{\text{ind}} = ((M_b k V_i)(g + g_a)) + (M_b g \dot{z}) + (M_b g_a \dot{z}) \quad (6.)$$

Parasite power:

Parasite power is required to overcome drag on the body and can be calculated using the following equation (Pennycuik *et al.* 1988):

$$P_{\text{par}} = \frac{1}{2} \rho S_b C_{D,\text{par}} V^3 \quad (7.)$$

where S_b is the frontal area of the body and $C_{D,\text{par}}$ is the drag coefficient of the body. The drag coefficient of the body is a constant. However, values for this coefficient vary greatly in the literature. In these calculations a value of 0.13 will be used, as suggested by more recent studies (Rayner, 1999b). However, since parasite power is

low compared with other power components, any uncertainty concerning the validity of this drag coefficient will have little significant effect on the total power requirements of flight.

Resultant Velocity and Profile Power:

Profile power is required to overcome drag on the wings and is averaged over the entire wing stroke. It is given by (modified from Norberg, 1990):

$$P_{\text{pro}} = 2(\frac{1}{2}\rho V_r^3 S_i C_{D,\text{pro}}) \quad (8.)$$

Where V_r is resultant velocity of the wing strip, S_i is the area of the wing strip and $C_{D,\text{pro}}$ is the profile drag coefficient (a constant taken to be 0.02, as suggested by Rayner, 1979b). V_r can be calculated from the induced velocity, upward velocity and the flapping velocity of each wing as follows:

$$V_r = \sqrt{(V_i + z - \omega r \sin\phi)^2 + (V_h + \omega r \cos\phi)^2} \quad (9.)$$

Where ω is the angular velocity of the wing strip, r is the distance from the shoulder joint to the centre of lift (estimated to be $\frac{2}{3}$ wing length), ϕ is the stroke plane angle with respect to the horizontal and V_h is the average horizontal velocity.

Total Power Requirements:

Finally, the total mechanical power requirement, P_{aero} , could be determined from the equation:

$$P_{\text{aero}} = P_{\text{ind}} + P_{\text{par}} + P_{\text{pro}} \quad (10.)$$

Inertial power requirement is negligible at all but the very lowest speeds and so was not taken into account in this study. The values for P_{aero} , P_{ind} , P_{par} , P_{pro} , V_i , V_r , E_P , $E_{K,\text{ext}}$, ϕ , Φ (stroke amplitude) and F_w were collated for each bird, at each speed they flew at in the wind tunnel and mean values were calculated (See *appendix 2*. for a summary of these components). The calculated power components were corrected for

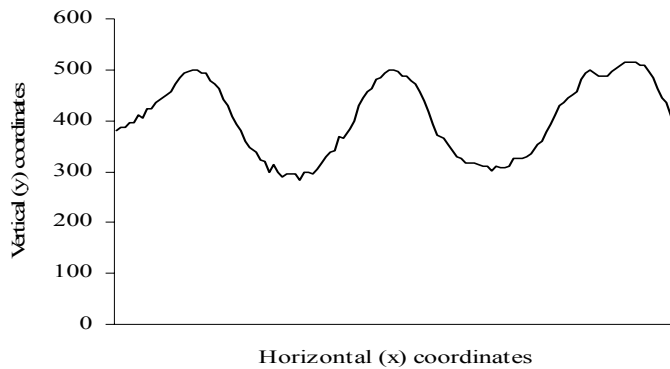
the varying muscle masses between the birds. Analysis of variance statistics (ANOVA) were then used to determine if there was any significant difference between the aforementioned values at different air speeds. The factors which were found to be significantly different at varying air speeds, were then analysed using a Tukey-Kramer pair-wise comparison test, in order to determine between which air speeds, significant differences could be seen.

Results

The fourth differences smoothing method, applied to both the raw positional coordinates of the centre of mass of the bird, and to the calculation of velocities and accelerations throughout flight, produced visibly smoothed data. The differences between the original raw positional coordinates and the smoothed positional data can be seen in *figure 2*. below. Similarly, the difference between smoothed calculated velocities, and those calculated using the simpler method can be observed in *figure 3*.

Figure 2: Typical differences between raw and smoothed positional data, (a) Position of the centre of mass of the yellow/white budgerigar, flown at 12ms^{-1} , in the horizontal (x) and vertical (y) planes throughout flight, as determined from raw positional data, (b) Position of the centre of mass of the yellow/white budgerigar, flown at 12ms^{-1} in the horizontal (x) and vertical (y) planes throughout flight, as determined from fourth differences smoothed positional data.

(a)



(b)

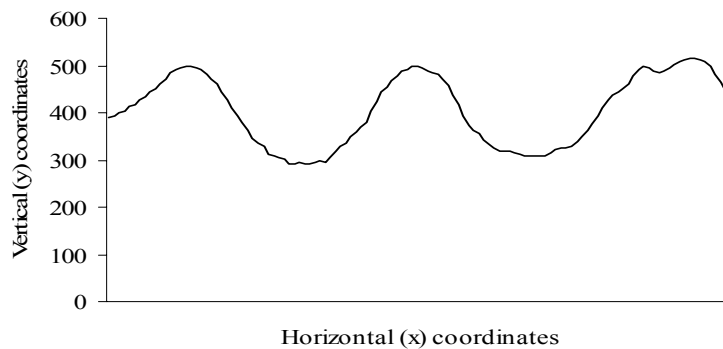
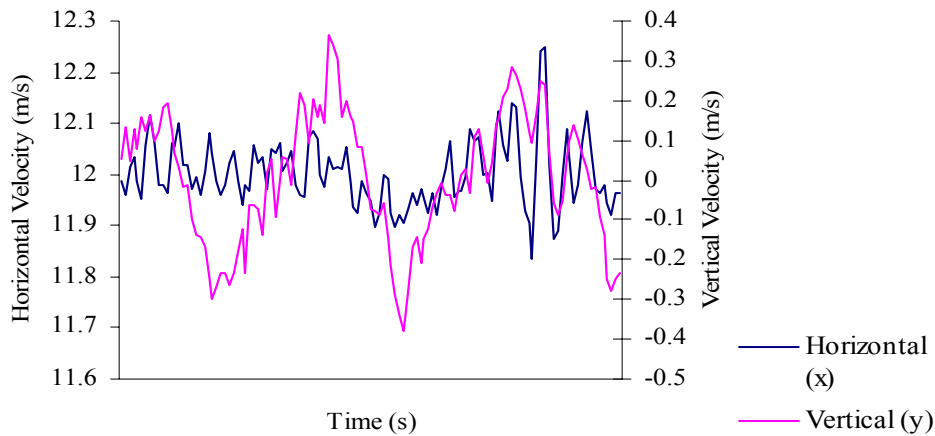
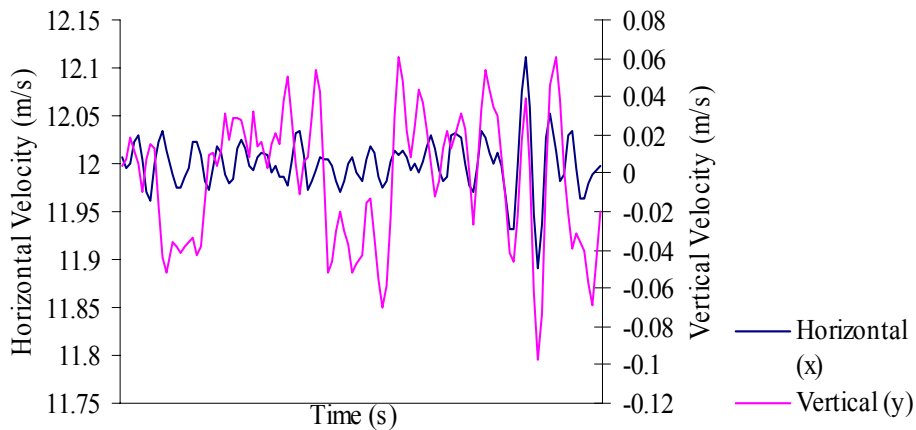


Figure 3: Typical differences between raw and smoothed calculated velocities, (a) Horizontal and vertical velocities calculated using the traditional method, for the yellow/white budgerigar, flown at 12ms^{-1} , (b) Horizontal and vertical velocities calculated using the fourth differences smoothing method, for the yellow/white budgerigar, flown at 12ms^{-1} .

(a)



(b)



The rate of change of potential energy during steady flight, was not significantly affected by air speed ($P>0.5$). In figure 4. below, relatively small, random changes in the rate of change in potential energy at varying air speeds can be seen. The rate of change of potential energy remained close to, and fluctuated around 0W/kg , and the mean rate of change of potential energy was -0.018W/kg .

The rate of change of kinetic energy was not significantly affected by air speed ($P < 0.5$). Relatively small and random changes in the rates of change of kinetic energy, over varying air speeds can be seen in *figure 5*. below. The rate of change of kinetic energy remained close to, and fluctuated around 0 W/kg , and the mean rate of change of potential energy was 0.002 W/kg .

Figure 4: Summary of the mean (+/-s.d.) pectoralis mass-specific rate of change of potential energy (dE_P/dt), calculated for seven budgerigars, as a function of air speed.

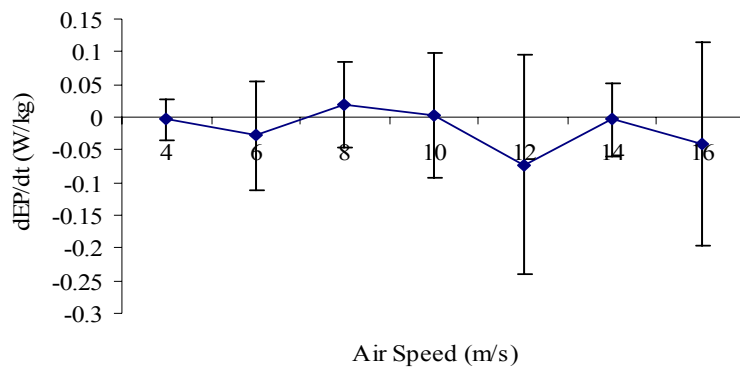
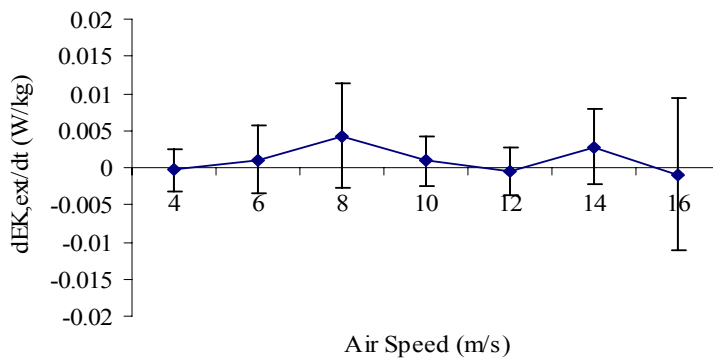
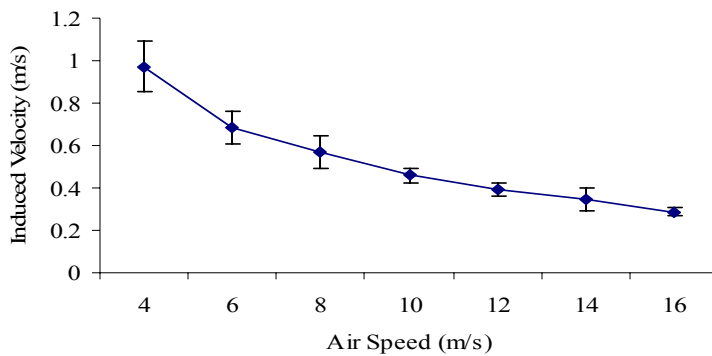


Figure 5: Summary of the mean (+/-s.d.) pectoralis mass-specific rate of change of kinetic energy ($dE_{K,ext}/dt$), calculated for seven budgerigars, as a function of air speed.



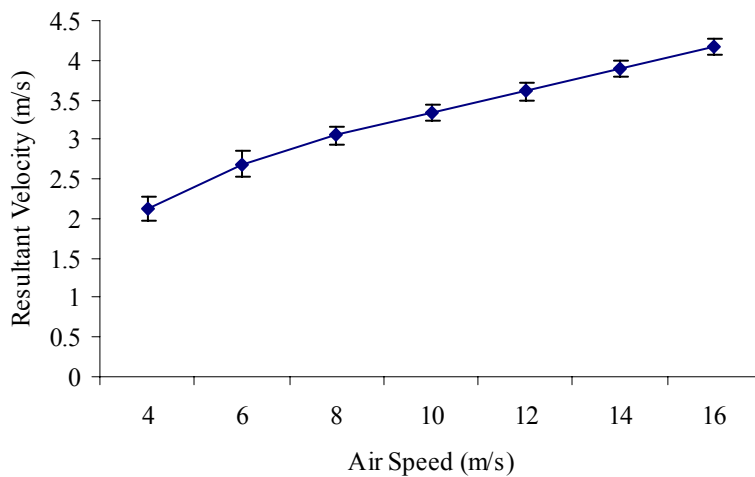
Induced velocity decreased significantly with increasing air speed ($P < 0.01$). As air speed increased, the rate of change in induced velocity decreased. Induced velocity fell from a maximum of 0.97 ms^{-1} at 4 ms^{-1} to a minimum of 0.28 ms^{-1} at 16 ms^{-1} . Pair-wise statistical comparisons revealed that values for induced velocity are significantly different ($P < 0.05$) between all speeds, with a few exceptions between only the highest adjacent air speeds, where values were relatively indistinguishable (e.g. induced velocity was not significantly different between 14 ms^{-1} and 16 ms^{-1}).

Figure 6: A summary of the mean (\pm s.d.) induced velocities, calculated for seven budgerigars, as a function of air speed.



Resultant velocity increased significantly with increasing air speed ($P < 0.01$). The rate of increase in resultant velocity can be seen to be relatively equal between most air speeds, appearing to be greatest between only the very lowest speeds. Mean resultant velocity rose from a minimum of 2.12ms^{-1} at 4ms^{-1} to a maximum of 4.17ms^{-1} at 16ms^{-1} . Pair-wise statistical comparisons revealed that values for resultant velocity are significantly different ($P < 0.05$) between all air speeds.

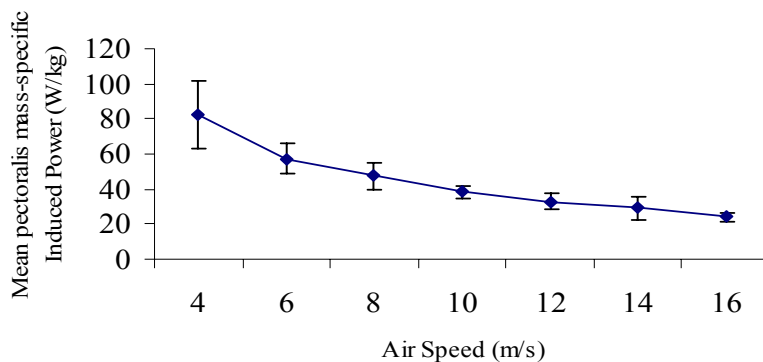
Figure 7: A summary of the mean (\pm s.d.) resultant velocities, calculated for seven budgerigars, as a function of air speed.



Induced power decreased significantly with increasing air speed ($P < 0.01$). The rate of increase in induced power between air speeds became smaller as air speed increased. Induced power fell from a maximum of 82.43W/kg at 4ms^{-1} to a minimum of 23.98W/kg at 16ms^{-1} . Pair-wise statistical comparisons revealed that values for induced power are significantly different ($P < 0.05$) between most air speeds, with a

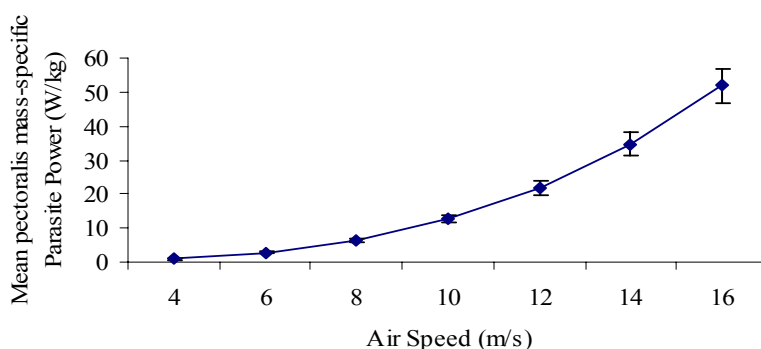
few exceptions between adjacent and other close air speeds. These exceptions were typically found to be at the fastest speeds where values were relatively indistinguishable (e.g. induced power was not significantly different between 12ms^{-1} and 16ms^{-1}).

Figure 8: A summary of the mean (\pm s.d.) pectoralis mass-specific induced power, calculated for seven budgerigars, as a function of air speed.



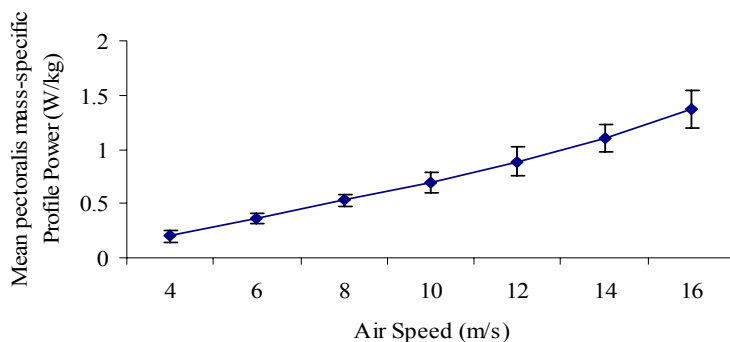
Parasite power increased significantly with increasing air speed ($P < 0.01$). The rate of increase in parasite power between air speeds became greater as air speed increased. Parasite power rose from a minimum of 0.84W/kg at 4ms^{-1} to a maximum of 51.79W/kg at 16ms^{-1} . Pair-wise statistical comparisons revealed that values for parasite power are significantly different ($P < 0.05$) between all speeds, with a few exceptions between only the lowest adjacent air speeds, where values were relatively indistinguishable (i.e. for example, parasite power was not significantly different between 4ms^{-1} and 6ms^{-1}).

Figure 9: A summary of the mean (\pm s.d.) pectoralis mass-specific parasite power, calculated for seven budgerigars, as a function of air speed.



Profile power increased significantly with increasing air speed ($P < 0.01$). The largest increases in profile power can be observed at the fastest air speeds, with increases becoming gradually smaller as air speed decreases. Profile power rose from a minimum of 0.20 W/kg at 4 ms^{-1} to a maximum of 1.36 W/kg at 16 ms^{-1} . Pair-wise statistical comparisons revealed that values for profile power are significantly different ($P < 0.05$) between all speeds, with a few exceptions between only the lowest adjacent air speeds, where values were relatively indistinguishable (i.e. for example, profile power was not significantly different between 4 ms^{-1} and 6 ms^{-1}).

Figure 10: A summary of the mean (\pm s.d.) pectoralis mass-specific profile power, calculated for seven budgerigars, as a function of air speed.



Total mechanical power for flight produced a significant U-shaped relationship with air speed ($P < 0.01$). In *figure 11*, below mechanical power can be seen to initially decrease with increasing air speed, and to subsequently increase as air speed is increased further. Mechanical power fell from a maximum of 83.47 W/kg at 4 ms^{-1} to a minimum of 51.61 W/kg at 10 ms^{-1} , and then further increased to 77.13 W/kg at 16 ms^{-1} . Pair-wise statistical comparisons revealed that values for mechanical power are significantly different ($P < 0.05$) between only the fastest or lowest speeds (i.e. 4 ms^{-1} or 16 ms^{-1}) and the mid-range speeds (i.e. 8 ms^{-1} , 10 ms^{-1} and 12 ms^{-1}). The values for mechanical power between mid-range speeds were not found to be significantly different to one another as they were too small. Similarly, values at the highest or lowest speeds were not found to be significantly different from one another for the same reason.

Figure 12, below shows how mechanical power requirements varied between individual birds. All of the birds produced a U-shaped relationship for mechanical

power as a function of air speed; however, they varied significantly in the levels of mechanical power required at varying air speeds ($P < 0.05$). Statistical pair-wise comparisons revealed that the only significant difference was between the pale blue/orange budgerigar and the blue/dark green budgerigar ($P < 0.05$). *Figure 12* clearly shows the pale blue/orange budgerigar to display the lowest set of mechanical power requirements over varying air speeds, and the blue/dark green budgerigar to have the highest set of mechanical power requirements. The pale blue/orange budgerigar also tended to have lower profile, parasite and induced power requirements, and the blue/dark green budgerigar tended to have higher profile, parasite and induced power requirements.

Figure 11: A summary of the mean (+/-s.d.) pectoralis mass-specific total mechanical power, calculated for seven budgerigars, as a function of air speed.

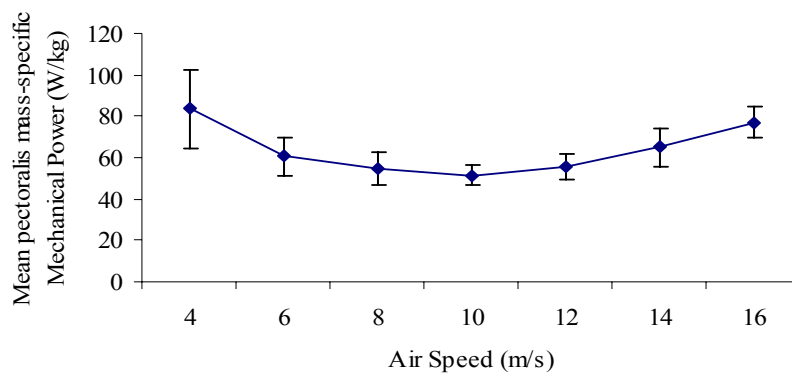
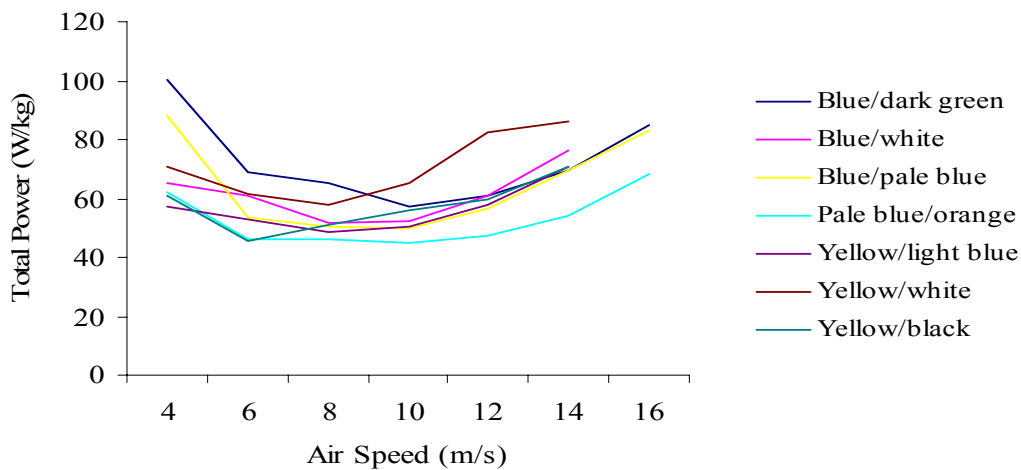
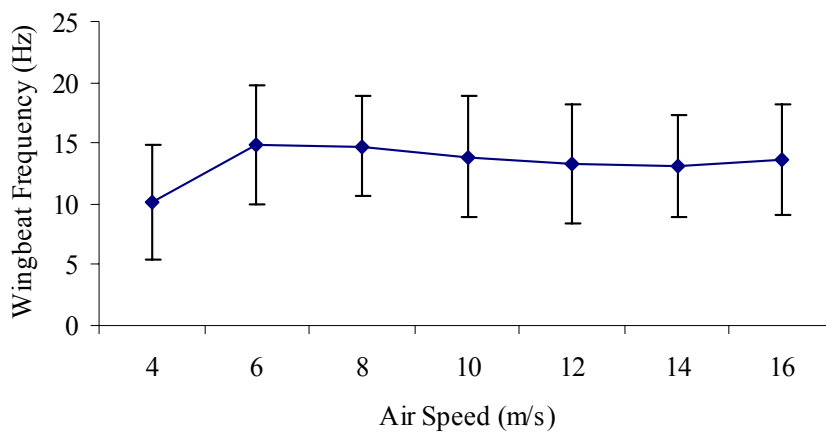


Figure 12: Individual variation in pectoralis mass-specific total mechanical power, calculated in seven budgerigars, as a function of air speed.



There was no significant relationship between wingbeat frequency and air speed ($P>0.5$). Changes in wingbeat frequency, between varying air speeds were small, and seemingly random (as seen below in *figure 13*). Mean wingbeat frequency over all air speeds was 13.37Hz. The wingbeat frequency of pale blue/orange budgerigar, and that of the blue/pale blue budgerigar were found to be significantly lower than those other the other budgerigars ($P<0.05$). Such differences may have implications in the total mechanical power requirements for flight or in the flight strategy used.

Figure 13: A summary of the mean (+/-s.d.) wingbeat frequencies, calculated for seven budgerigars, as a function of speed.



There was no significant relationship between stroke amplitude and air speed ($P>0.5$). Changes in stroke amplitude, between varying air speeds were small, and seemingly random (as seen below in *figure 14*). Mean stroke amplitude, over all air speeds was 2.08 radians (119°).

There was no significant relationship between stroke plane angle and air speed ($P>0.5$). Changes in stroke plane angle, between varying air speeds were small, and seemingly random (as seen below in *figure 15*). Mean stroke plane angle, over all air speeds was 1.0 radians (57.3°).

Figure 14: A summary of the mean (\pm s.d.) stroke amplitudes, calculated for seven budgerigars, as a function of speed.

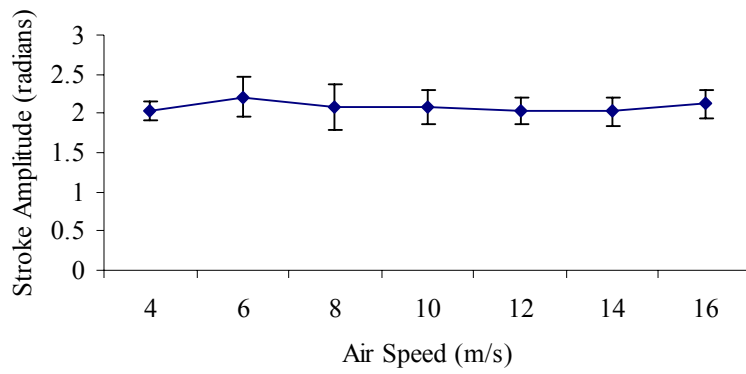
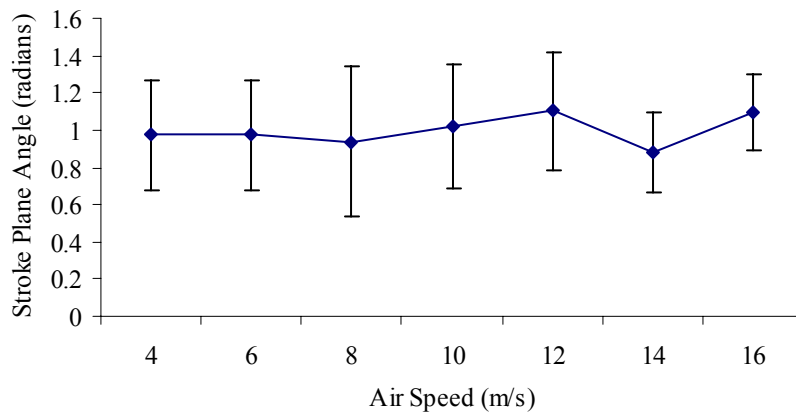


Figure 15: A summary of the mean (\pm s.d.) stroke plane angles, calculated for seven budgerigars, as a function of speed.



Discussion

Power Components of Flight:

The rate of change of potential energy during steady flight was found to be minimal throughout the range of flight speeds, due to the limited space available for vertical acceleration or deceleration within the wind tunnel. Therefore there was minimal opportunity for any significant change in potential energy during flight in this investigation, despite the consequences of changing flight speed. The rate of change of kinetic energy during steady flight was also found to be minimal throughout the range of flight speeds, due to the limited space available for acceleration or deceleration within the wind tunnel. Therefore there was minimal opportunity for any significant change in kinetic energy during flight in this investigation, despite the consequences of changing flight speed.

Induced power is the rate at which a vertical force or downwash (induced velocity) must be imparted to the air, in order to generate lift during flight (and to overcome induced drag). In order to generate lift in flight, air must be accelerated downwards by the wings. However, this change in the direction of the air, not only produces lift, but also a resistance known as induced drag. As forward motion of the bird increases with increasing air speed, more of the downwash required to produce lift comes from the increased air flow over the wings. Therefore proportionally less of the downwash is produced by the flapping wings as speed increases. This means that the downwash produced by the wings at increased air speeds is of a lower induced velocity and requires a lower rate of working (induced power) in order to support the weight of the bird and any lift production. As would be predicted induced velocity therefore significantly decreases with increasing air speed and consequently induced power also significantly decreases with increasing air speed.

Resultant velocity is the combined velocity of all forces acting upon the wings in flight. During flight, air flow over the wings occurs as a result of the flapping of the wings and as a result of the forward movement of the bird. Therefore, at increased air speeds, air flow over the wings occurs due to continued flapping, but is also increased

as a result of the increased forward movement of the bird in air. As would therefore be predicted, resultant velocity significantly increases with increasing air speed.

In order to fly at a particular uniform air speed, an animal must produce a thrust force equal to the drag experienced on the body and wings in a horizontal direction. The drag experienced across the body is known as parasite drag, and a parasite power component is required to overcome this. The drag experienced across the wings is known as profile drag, and a profile power component is required to overcome this. These drag forces increase with increased air flow over the body and wings of the bird and are therefore proportional to velocity squared. Since the power components required to balance these drag forces are equal to drag times velocity, then these power components are proportional to velocity cubed. As would be predicted, both parasite power and profile power were therefore found to increase significantly with increasing air speed.

Total mechanical power can be defined as the power output of the muscles during flight, and is the sum of induced power, parasite power and profile power. It is predicted that mechanical power will produce a U-shaped relationship with air speed, as a combined result of the separate relationships that each power component of flight experiences, as a function of speed. Mechanical power will be minimal when induced, profile and parasite power are at their collective minimum (see *figure 1.* for an illustration of this reasoning). Mechanical power was found to produce a U-shaped relationship with air speed, and this relationship has been proven significant. The minimum power speed, as determined in this investigation is approximately 10ms^{-1} and the maximum range speed (that at which the most distance is covered per unit work) is approximately 12ms^{-1} .

Wing Kinematics

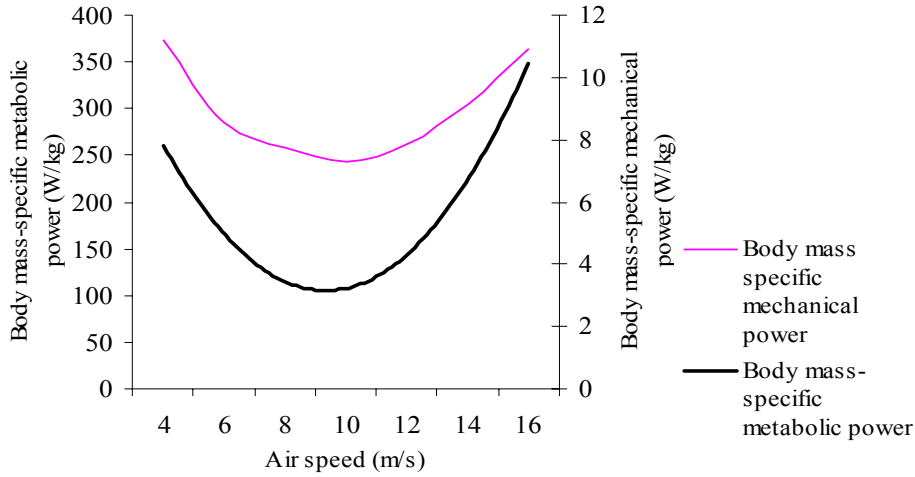
Stroke amplitude, stroke plane angle and wingbeat frequency are all parameters of pectoralis muscle shortening velocity, and all are expected to be affected by changes in flight speed. However, in this investigation on budgerigars no significant relationship was found for any of these parameters as a function of air speed. Other parameters of muscle shortening velocity, including the proportion of time spent in

the upstroke and downstroke of a wingbeat, are required in order to understand the apparent lack of any relationship between air speed and these factors. Knowledge of other parameters involved in muscle shortening velocity and the proportion of time spent flapping in flight would allow determination of the flight strategy being adopted at that particular air speed in budgerigars, and may help to explain the minimal changes in stroke amplitude, stroke plane angle and wingbeat frequency over varying flight speeds. The budgerigars may for example, alter their flight strategy with changing air speed, in order to minimise mechanical power requirements, and in doing so also minimise any change in muscle shortening velocity and its parameters too. Tobalske and Dial (1994) have in fact produced evidence of budgerigars using facultative intermittent glides at slow flight speeds and adapting their behaviour to use facultative intermittent bounds at faster flight speeds. However, the results for these parameters as determined in this investigation produced no significant findings, and may therefore be due to chance or error, rather than any observed change in flight strategy.

Flight efficiency

Flight efficiency and flight muscle efficiency were calculated from the mean mechanical power values, and from values of metabolic power previously estimated from oxygen consumption and carbon dioxide production during flight in a wind tunnel, over a range of air speeds (Tucker, 1967) as seen in *figure 16*. The metabolic power of flight shows a similar relationship with air speed, to mechanical power. It produces a U-shaped curve, with metabolic power initially decreasing with increasing air speed, and subsequently increasing, as air speed increases further. However, the magnitude of the metabolic requirements for flight are much greater than the mechanical power requirements of flight.

Figure 16: Body-mass specific metabolic power of flight, as a function of speed, as obtained by Tucker, (1967) and body-mass specific mechanical power of flight, as a function of speed, as obtained in this study.



Flight efficiency and muscle efficiency are the percentage ratios of mechanical power output to metabolic power input of the whole body and pectoralis muscles respectively. Metabolic power which is not used to produce mechanical power output may be used in muscles other than the pectoralis (e.g. the supracoracoideus muscle) or in the increased energetic costs of respiration and circulation during flight, or even in basic bodily processes. Metabolic power may also be lost as heat. Flight efficiency was calculated by simply dividing mechanical power output with metabolic power input. Muscle efficiency was calculated by re-arranging *equation 1.*, used typically to calculate metabolic power, as outlined in Ward *et al.* (2001). The equation was rearranged to give:

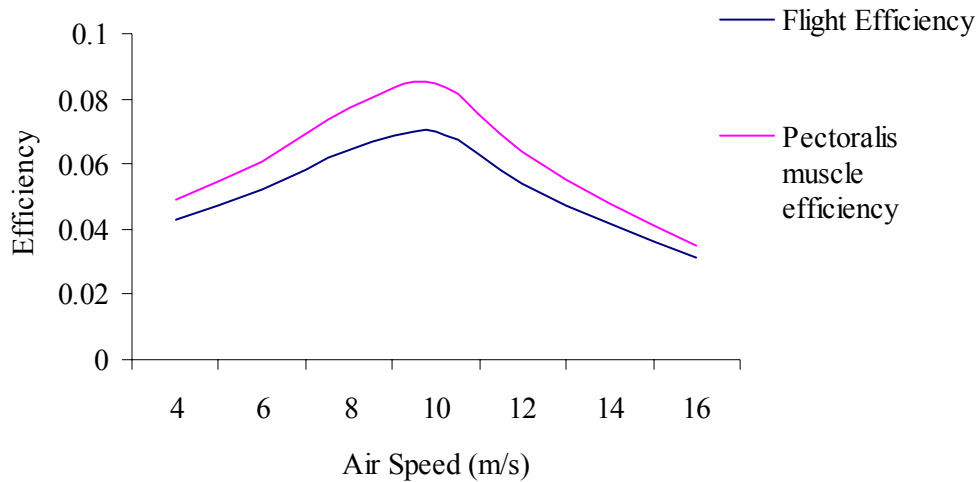
$$E_{FM} = P_{mech} / [(P_{met}/1.1) - P_{BMR}] \quad (11.)$$

Basal metabolic rate for the budgerigar (P_{BMR}) was calculated as an average for the birds used in this study from the following equation (Lasiewski and Dawson, 1967):

$$P_{BMR} = 3.73M_b^{0.723} \quad (12.)$$

This gave a value of 8.779W/kg. Flight efficiency and muscle efficiency produced similar shaped curves, with differing magnitudes, as a function of air speed (see *figure 17*). Typically both flight efficiency and muscle efficiency have been found to increase with increasing speed (Ward *et al.* 2001). However in this case both flight and muscle efficiency produced an opposite relationship to that produced by both mechanical and metabolic power as a function of air speed. They initially increasing as air speed increases, subsequently decreasing as air speed increases further. This is due to the differing magnitudes of the power curves for mechanical and metabolic power and hence the differing magnitudes in increases and decreases in values between different flight speeds. At the lowest and highest speeds, the ratio of mechanical to metabolic power is lowest (mechanical power accounts for less of the produced metabolic power) and flight efficiency is at its poorest, whereas at the more intermediate air speeds, the ratio of mechanical to metabolic power is greater (mechanical power accounts for more of the produced metabolic power), and flight efficiency is at its greatest. It therefore appears that when flight costs are highest in the budgerigar, efficiency is lowest, and when flight costs are at a minimum, efficiency is at its highest. Flight efficiency rises from approximately 0.04 at 4ms^{-1} to a maximum of approximately 0.07 at 10ms^{-1} , then falling again to a minimum of approximately 0.03 at 16ms^{-1} . Muscle efficiency is greater in magnitude than flight efficiency, with the greatest difference being observed at the most intermediate flight speeds. It initially rises from approximately 0.05 at 4ms^{-1} to a maximum of approximately 0.085 at 10ms^{-1} , falling to a minimum of approximately 0.035 at 16ms^{-1} . Muscle efficiency differs from flight efficiency in that it takes into account the basal metabolic rate of the animal, and a proposed 10% increase in the energetic costs of circulation and respiration that is experienced during flight, as an allocated proportion of produced metabolic power. Therefore this allocation of metabolic power does not reach the flight muscles for use in mechanical power, and is not included in the ratio of mechanical to metabolic power of the flight muscles. Muscle efficiency is therefore higher than flight efficiency, and produces a curve greater in magnitude, as a function of air speed. Muscle efficiency is also more sensitive to differences in the ratio of mechanical power output to metabolic power input, because its original allocation of metabolic power is smaller.

Figure 17: A summary of mean flight efficiency and flight muscle efficiency as a function of speed for available air speeds. (Calculated using metabolic power estimates for the budgerigar, from Tucker, 1967).



A value of 0.23 (mechanical power output represents 23% of metabolic power input) has previously been suggested for flight muscle efficiency (Pennycuik, 1975), as an averaged value, typical for vertebrate flight. However, since muscle efficiency has been found to increase with body size in running mammals and birds, and flying insects, it is assumed that the same will be true for flying birds (Ward *et al.*, 2001). If this is the case then this uniform value is unreliable. Flight muscle efficiency of the European starling (*Sturnus vulgaris*) has been determined using a similar method to that used in this investigation, as outlined by Ward *et al.* (2001). A value of 0.18 (18%) was determined as a fixed flight muscle efficiency typical of starlings and similar sized birds (0.075 – 0.1 kg), and an estimated range of 0.13 - 0.23 was proposed for muscle efficiency generally, depending upon the species and flight speed. In this investigation however, the still smaller budgerigar species (0.045 kg) produced a mean flight muscle efficiency of 0.06 (6%). I can therefore confirm that in smaller species of birds, a uniform value of 0.23 is too high, and that as bird size decreases, so does flight muscle efficiency. I also suggest that a much wider range than that proposed by Ward *et al.* (2001) should be considered for values of muscle efficiency. Further investigations into muscle efficiency would enable reliable species and flight speed specific data to be compiled so that metabolic power requirements may be calculated with greater accuracy from known values of mechanical power. Estimated metabolic power from aerodynamic models is highly sensitive to muscle

efficiency, mainly because mechanical power is only a small component of the total metabolic power requirements. A change in muscle efficiency of only 0.01 represents a 5 % change in metabolic power (Ward *et al.*, 2001). Further study may also reveal patterns in efficiency variation across individuals and species with different flight morphology, and above all with different mass, and may help to determine the mechanisms that cause efficiency to vary.

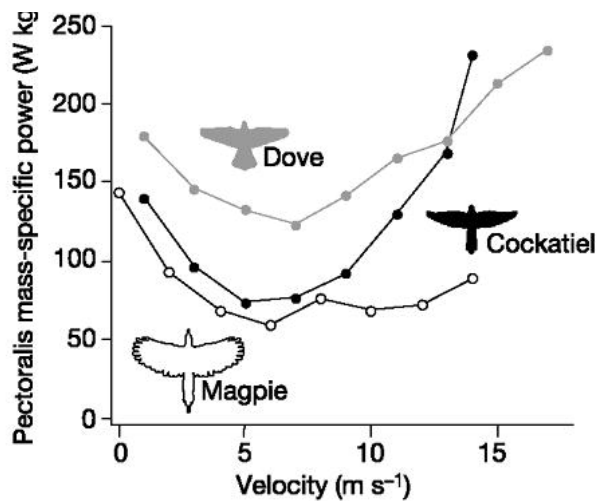
Comparative Power Curves

Figure 18. may be observed with *figure 19.* in order to make comparisons between the mechanical power curves for the species detailed, and that produced as a result of this investigation on the mechanical power requirements of flight in budgerigars. The mechanical power curves for the cockatiels (*Nymphicus hollandicus*) and ringed turtle doves (*Streptopelia risoria*) were obtained using an integrated approach involving *in vivo* measurements of pectoralis force and length change, and an aerodynamic model requiring data on wing and body movement (Tobalske *et al.*, 2003). The mechanical power curve for the magpie (*Pica pica*) was obtained from *in vivo* bone strain measurements of pectoralis muscle force, coupled with wing kinematics (Dial *et al.*, 1997). The magpie produced a relatively flat power curve as a function of speed, and values for mechanical power were statistically indistinguishable over most intermediate speeds. It was only during hovering (flight speed = 0ms^{-1}) and at the very lowest flight speeds that mechanical power requirements were found to be significantly higher (Dial *et al.*, 1997), suggesting an L-shaped, rather than a U-shaped power curve for this species. In comparison, the power curve produced for cockatiels is acutely U-shaped, whereas that for doves is much more intermediate in shape, with much higher mass-specific power output over the range of speeds. The power curve for the budgerigar appears to be relatively flat in comparison to the more acutely concave cockatiel and dove power curves. The magnitude of the budgerigar power curve also appears to be much lower than those produced for the cockatiel and dove. However, over the range of speeds for which mechanical power was calculated in the budgerigar, both the magnitude and shape of the power curve appears to closely resemble that of the magpie power curve. At the very lowest speeds, the power requirements of the magpie rise sharply. This may also be proven true of the budgerigar, if the mechanical power of flight at these speeds was calculated. If this is

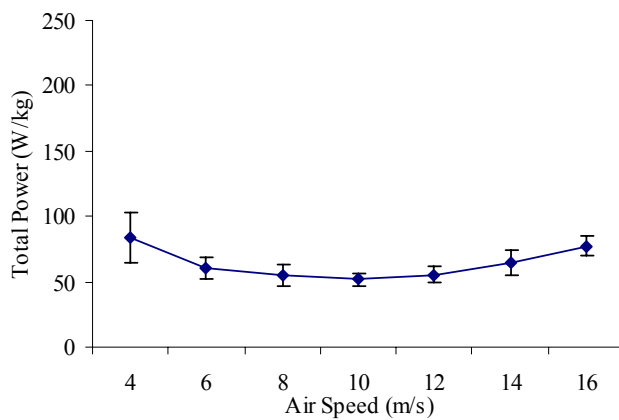
the case then we may describe the budgerigar power curve as L-shaped, rather than U-shaped as initially suggested. However, this is currently unknown, although we can confirm that the power curve of the budgerigar, over a range of intermediate and higher speeds, does indeed resemble that of the magpie.

Figure 18: (a) Comparative pectoralis mass-specific mechanical power requirements, as a function of speed in the dove, cockatiel and magpie (Tobalske et al., 2003), (b) Comparative mean pectoralis mass-specific mechanical power requirements, as a function of speed in the budgerigar.

(a)



(b)



Mass-specific pectoralis power output has also been estimated in the blue-breasted quail (*Coturnix coturnix*) during take-off (Askew *et al.*, 2001). The method used in this investigation on budgerigars was based upon the method outlined in this paper. The mean muscle-mass specific power output during take off in the quail was approximately six times the mean muscle-mass specific power output, over a range of speeds in the budgerigar. Most of this power was required to increase the potential energy of the bird ($81\%P_{\text{mech}} = De_p/dt$). The rate of change in potential energy during quail take-off flight was over 1000 times higher than that demonstrated over a range of flight speeds in the budgerigar. This is due to the vertical acceleration involved in quail take-off flight, as it gains significant height in a very short space of time. The budgerigar in comparison could not gain any significant height in this investigation, due to the restrictions of the wind tunnel. Quail take-off flight also required a much greater increase in kinetic energy, than was observed over a range of flight speeds in the budgerigar (over 200x increase mean rate of change in kinetic energy). Again, this may be accounted for as a result of the physical limitations imposed upon the budgerigars in the wind tunnel. Pheasant-like birds (galliforms), such as the quail are specifically designed for short-term maximum power burst flight performance. Their muscles are designed to produce power rapidly, and to an extreme extent, in order to enable them to reach a significant height from standing. They use flight almost only as an escape mechanism, tiring soon after take-off, and returning to the ground to run or hide. In comparison the budgerigar is designed to support flight on a much more long-term basis before tiring. This is made possible by limiting its maximum power output at any one time.

Aspects of morphology, muscle physiology, wing kinematics and flight style can greatly affect the shape and magnitude of a species' power curve and differences of magnitude in power curves within a species. Differences in the magnitude of a power curve may be due to variations in wing disc loading (body weight: area swept by wings). Those species or individual birds with higher wing disc loading will have proportionally greater induced power requirements, and therefore higher mechanical power requirements, especially at slower flight speeds. Although differences in disc loading between the budgerigars used in this study were relatively small (mean disc loading in the budgerigars was $11.35 \text{ N/m}^2 \pm 0.77 \text{ N/m}^2$), typically those budgerigars with lower disc loading displayed lower mechanical power requirements over varying

air speeds, and those budgerigars with higher disc loading displayed higher mechanical power requirements over varying air speeds. Differences in disc loading may also explain the much larger differences in the magnitude and shape of power curves between species. If disc loading is relatively low within a species, this will imply decreased induced power requirements and therefore decreased mechanical power requirements, particularly at slower speeds (flattening the left side of the power curve).

Wing and tail morphology may also explain differences between species' power curves. Differences in aspect ratio (wingspan^2 : area) can offer explanations as to the differences in both the magnitude and shape of a species power curve, and to the differing flight capabilities of various species. High aspect ratio wings are typically long and pointed, and offer reduced profile power requirements (due to reduced profile drag) as a result of the proportionally small wing area. High aspect ratio wings are also efficient in producing lift, and therefore minimise induced power requirements. Low aspect ratio wings are typically broad and rounded and result in increased profile power requirements (due to increased profile drag) as a result of the proportionally larger wing area. Magpies typically have low aspect ratio wings and a long tail, which will result in increased profile power requirements. Cockatiels and doves have relatively higher aspect ratio wings and proportionally smaller tails, offering lower induced and profile power requirements (Tobalske *et al.*, 2003). Budgerigars also typically have high aspect ratio wings, offering lower induced and profile power requirements (Tobalske and Dial, 1994). Lower induced power requirements within a species may imply proportionally lower mechanical power requirements, particularly at the lowest speeds (flattening the left side of the power curve), whereas lower profile power requirements within a species may imply lower mechanical power requirements at the fastest speeds (flattening the right side of the power curve).

The type of muscle fibre which produces the mechanical power required for flight may also help to explain the capabilities of a species, in terms of maximum burst power output and stamina. Budgerigars have only one muscle fibre present in their pectoralis, a fast-twitch oxidative glycolytic (FOG) fibre (Tobalske and Dial, 1994). The fixed-gear hypothesis (Rayner, 1985) suggests that such homogeneity in

pectoralis muscle fibre constrains a bird to a restricted range of force production. However, Tobalske and Dial (1994) found that budgerigars violated the fixed-gear hypothesis, and that force production during flapping flight in this species is highly variable. Fast twitch muscle fibres are capable of producing the rapid, high power bursts that are required for energy-expensive flight. They typically have few mitochondria and work anaerobically, using glycolysis to produce energy. Glycolysis enables rapid high power bursts of energy to be produced when required (e.g. for escape and take-off) but is however unsustainable and inefficient over periods of prolonged exercise, which is why the budgerigar muscle fibres also have an oxidative element to them. For a more lengthy period of flight the pectoralis will use mitochondria to produce energy aerobically. The maximum burst power of the pectoralis may be constrained while functioning aerobically, but energy production will be more sustainable and efficient. FOG fibres therefore enable budgerigars to alter their mode of energy production, depending upon the situation. In comparison, a galliform such as the blue-breasted quail has high-glycolytic and low-oxidative pectoralis fibres (Askew *et al.*, 2001), which are restricted to producing short, high power bursts of energy. The maximum burst power of these fibres is no doubt much greater than that of the budgerigar FOG fibres. However, such effort is unsustainable in galliform species, whereas budgerigars are capable of sustaining much more lengthy periods of flight.

Finally flight style, or the strategy adopted when flying at a particular speed can affect the shape and magnitude of a species' power curve. A species may typically alter its flight strategy or wing kinematics as flight speed changes, in order to minimise mechanical power requirements over a range of speeds. It may also use such changes to control altitude, stability and speed. Magpies typically fluctuate their wing-beat gait and use intermittent flight styles. This may enable them to alter their power requirements at intermediate and fast speeds, so that the right side of the power curve remains relatively flat for this species (Tobalske *et al.*, 2003). Budgerigars have been observed using continuous flapping flight at slow speeds, as well as using intermittent glides and bounds at more intermediate and faster speeds. Typically as flight speed increases, budgerigars decrease the proportion of glides and increase the proportion of bounds in all non-flapping phases of flight. The pectoralis has been found to be inactive during bounds and glides in the budgerigar, and intermittent flight strategies

are consistent with minimising mechanical power output in line with aerodynamic theory (Tobalske and Dial, 1994).

Limitations and Inaccuracies of this Study

It has previously been suggested that flight performance and mechanical power output maybe affected in captive conditions (Rayner, 1994). It is therefore necessary to consider that due to the artificial conditions under which the budgerigars were studied in this investigation, values for mechanical power may be underestimated. However, the budgerigars studied in this investigation underwent an extensive schedule of gradual exposure and training, which ensured that by the time that their flight was studied, they had become fully acclimatized to the conditions in which they were flying. This should minimise any undesirable effects on flight performance and therefore the mechanical power values obtained. The observation of steady and calm flight is a strong indication of acclimatization to the wind tunnel conditions. Generally, the films showed steady and relaxed flight among all the budgerigars. However, at the highest and lowest speeds flight could sometimes be erratic, with increased movement about the wind tunnel. Particularly at the fastest air speeds, flight appeared to be unsustainable for long periods, as the budgerigars were frequently forced to the back end of the wind tunnel, unable to sustain flight against that particular air speed. In these circumstances, the budgerigars may have been stressed, and their flight performance would not have reliably reflected that observed under natural conditions. Values obtained for mechanical power at the highest and lowest speeds may therefore be unreliable.

The method used in this investigation was based upon the tracing the centre of the mass of each budgerigar, at each flight speed, in order to determine its flight path within the wind tunnel. The position of the centre of mass was estimated throughout and is therefore not completely reliable as an indicator of the movements of the budgerigars in flight. However, the fourth differences smoothing method was applied to each estimated positional coordinate obtained from flight and therefore any error associated with estimating the centre of mass of the bird has been minimised. We should also consider that movement during flight occurs in three dimensions, but that in this investigation only two dimensions of movement (horizontal and vertical) have

been considered. Further study, allowing for considerations of three dimensional movement during flight would perhaps produce more accurate and reliable estimations of the mechanical power requirements of flight.

The power components determined in this investigation have been calculated using equations based upon aerodynamic theory and its assumptions, and therefore may be subject to dispute over their reliability and accuracy. The estimation of drag coefficients poses the major problem of the aerodynamic theory and the method used here. It is little understood how these coefficients vary with flight speed and wing morphology. Until more reliable estimates of these coefficients are obtained for a range of bird wings and flight speeds, the optimum strategy is to assume they are constant and to use values, based upon measurements of real birds (Rayner, 1999b). These drag coefficients have been revised and re-assessed frequently, however, much uncertainty still surrounds them. Despite this, any variability in the drag coefficients used should have little significant effect on the accuracy of the results obtained and the values calculated in this study should be considered as reliable as those calculated by any other method based upon aerodynamic theory.

Finally, some controversy may surround the reliability of values obtained for flight muscle efficiency as they are calculated from an equation based upon several assumptions. These include the assumption that both the values of mechanical power and metabolic power we have used are reliable and accurate. If the aerodynamic theory used to obtain values of mechanical power is unreliable, or the method used to determine metabolic power is subject to limitations, then the calculated values of flight muscle efficiency are inaccurate. The assumption that basal metabolic rate should be taken into account, and that the energetic costs of respiration and circulation rise by 10% during flight must also be considered. These extra energetic costs have not been directly measured during flight and are therefore an arbitrary value, which may have been grossly under- or over-estimated. However, this method of determining flight muscle efficiency is for now, the most reliable method available, without requiring any direct measurements. It is certainly more reliable than that used previously, taking into account both the species and speed of the bird in question rather than merely determining an averaged assumption of efficiency typical for general vertebrate flight (Pennycuick, 1975). The final limitation that must be

considered in the calculations of efficiency is that different birds were used to obtain the mechanical power and metabolic power requirements of flight. Individual differences between these birds could result in, for example, values of metabolic power significantly smaller than those that may be required in the birds used to determine mechanical power, and this may result in unreliable estimates of efficiency. However, variation between budgerigars should be minimal and we can assume that the values for flight efficiency obtained in this investigation are representative estimates for the species as a whole.

Conclusion

The mechanical power requirements of steady flight in the budgerigar appear to conform to a predicted U-shaped curve as a function of air speed, and give rise to a minimum power speed of approximately 10ms^{-1} , and maximum range speed of approximately 12ms^{-1} . However, compared to those power curves produced for other species which are more acutely U-shaped, the power curve for budgerigars is relatively flat. With further investigation into the mechanical power requirements of flight at slower speeds and for hovering in the budgerigar, it would be possible to determine whether this species power curve would in fact be L-shaped rather than U-shaped as originally predicted.

Parameters of muscle shortening velocity observed in this study were not affected by changing air speed. However, further study into these parameters specifically would help to determine the flight strategies used over varying air speeds and how changes in flight strategy affect the mechanical power requirements of flight and muscle shortening velocity parameters. An investigation into the most preferential flight strategy could also provide some insight into budgerigar flight energetics and behaviour.

Finally, both whole body flight efficiency and flight muscle efficiency were found to change with flight speed, in a relationship opposite to that produced by both the mechanical and metabolic power requirements of flight. Flight efficiency was found to average at approximately 5%, and muscle efficiency was found to average at approximately 6% over a range of flight speeds in the budgerigar. The range of

efficiencies determined in this investigation is much lower than has been previously predicted for any bird. However, the method used to determine efficiencies in this investigation has many limitations and in order to confirm the findings it would be advisable to develop and follow a much more reliable procedure. Further detailed study may therefore broaden our understanding of the range of potential flight efficiencies of birds as well as providing some insight into the factors that affect efficiency.

Acknowledgements

I would like to thank Dr Graham Askew for his supervision of and assistance with this investigation, and for providing the film footage of budgerigars in flight.

References Cited

Askew G.N., Marsh R.L. and Ellington C.P. (2001), The mechanical power output of blue-breasted quail (*Coturnix chinensis*) during take-off. *J. Exp. Biol.* **204**, 3601-3619.

Bishop C.M. and Butler P.J. (1995), Physiological modelling of oxygen consumption in birds during flight. *J. Exp. Biol.* **198**, 2153-2163.

Brigham R.M., Fenton M.B. and Aldridge H.D.J.N. (1997), Flight speed of foraging common night hawks (*Chordeiles minor*): Does the measurement technique matter? *American Midland Naturalist.* **139**, 325-330.

Dial K.P., Biewener A.A., Tobalske B.W. and Warrick D.R. (1997), Mechanical power output of bird flight. *Nature.* **390**, 67-70.

Ellington C.P. (1984), The aerodynamics of hovering insect flight. VI. Lift and power requirements. *Phil. Trans. R. Soc. Lond. B.* **305**, 145-181.

Fry S. N., Sayaman R. and Dickinson M.H. (2005), The aerodynamics of hovering flight in *Drosophila*. *J. Exp. Biol.* **208**, 2303-2318.

Josephson R.K. (1985), Mechanical power output from striated muscle during cyclical contractions. *J. Exp. Biol.* **114**, 493-512.

Klaassen M., Kvist A. and Lindstrom A. (2000), Flight costs and fuel composition of a bird migrating in a wind tunnel. *The Condor.* **102**, 444-451.

Lanczos C. (1957), *Applied Analysis*. Sir Issac Pitman and Sons Ltd, London.

Lasiewski R.C. and Dawson W.R. (1967), A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor*. **69**, 13-23.

Liu H. (2002), Computational biological fluid dynamics: Digitizing and visualizing animal swimming and flying. *Int. and Comp. Biol.* **42**, 1050-1059.

Masman D. and Klassen M. (1987), Energy expenditure during free flight in trained and free-living Eurasian kestrels (*Falco tinnunclus*). *Auk*. **104**, 603-616.

Norberg U.M. (1990), *Vertebrate flight: Mechanics, physiology, morphology, ecology and evolution*. Springer-Verlag, Berlin.

Pennycuik C.J. (1975), Mechanics of flight. In *Avian Biology*. **5**, 1-75. Academic Press, New York.

Pennycuik C.J., Obrecht H.H. and Fuller M.R. (1988), Empirical estimates of body drag of large waterfowl and raptors. *J. Exp. Biol.* **135**, 253-264.

Pennycuik C.J. (1989), *Bird flight performance: A practical calculation manual*. Oxford University Press, New York.

Rayner J.M.V. (1979a), A vortex theory of animal flight. Part 2. The forward flight of birds. *J. Fluid Mech.* **91**, 731-763.

Rayner J.M.V. (1979b), A new approach to animal flight mechanics. *J. Exp. Biol.* **80**, 17-54.

Rayner J.M.V. (1985), Bounding and undulating flight in birds. *J. Theo. Biol.* **117**, 47-77.

Rayner J.M.V. (1994), Aerodynamic corrections for the flight of birds and bats in wind tunnels. *J. Zool.* **234**, 537-563.

Rayner J.M.V. and Ward S. (1999a), On the power curves of flying birds. In N. J. Adams and R. H. Slotow (eds.), *Proc 22nd Int. Ornithol. Congr*, 1786-1809. Bird Life South Africa, Johannesburg.

Rayner J.M.V. (1999b), Estimating power curves of flying vertebrates. *J. Exp. Biol.* **202**, 3449-3461.

Tobaske B.W. and Dial K.P. (1994), Neuromuscular control and kinematics of intermittent flight in budgerigars (*Melopsittacus undulates*). *J. Exp. Biol.* **187**, 1-18.

Tobalske B.W. (2001), Morphology, velocity and intermittent flight in birds. *American Zoologist.* **41**, 177-187.

Tobalske B.W., Hendrick T.L., Dial K.P. and Biewener A.A. (2003), Comparative power curves in bird flight. *Nature.* **421**, 363-366.

Tucker V.A. (1967), Respiratory exchange and evaporative water loss in the flying budgerigar. *J. Exp. Biol.* **48**, 67-87.

Wakeling J.M. and Ellington C.P. (1997), Dragonfly flight. III. Lift and power requirements. *J. Exp. Biol.* **200**, 583-600.

Ward S., Moller U., Rayner J.M.V., Jackson D.M., Biol D., Nachtigall W. and 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.

Appendices

Appendix 1: A working example of the fourth differences smoothing method (Lanczos, 1957) as applied to the horizontal (x) positional coordinates of the centre of mass during flight at 12ms^{-1} in the yellow/white budgerigar.

<u>Raw x</u>					—	<u>Smoothed X</u>
<u>coordinates</u>	δx	$\delta^2 x$	$\delta^3 x$	$\delta^4 x$	$(3/35)\delta^4 x$	<u>coordinates</u>
938						
940	2					
942	2	0			0.0	942.0
942	0	-2	-2		-0.9	941.1
938	-4	-4	-2	0	0.5	938.5
938	0	4	8	10	1.5	939.5
944	6	6	2	-6	-2.4	941.6
940	-4	-10	-16	-18	0.9	940.9
938	-2	2	12	28	-0.2	937.8
940	2	4	2	-10	1.5	941.5
950	10	8	4	2	-1.0	949.0
954	4	-6	-14	-18	-1.2	952.8
950	-4	-8	-2	12	1.4	951.4
950	0	4	12	14	0.0	950.0
950	0	0	-4	-16	-2.4	947.6
946	-4	-4	-4	0	5.7	951.7
962	16	20	24	28	-6.9	955.1
956	-6	-22	-42		5.7	961.7
966	10	16			-3.3	962.7
964	-2					
960						

Appendix 2: A summary of the components used in the flight power equations.

Wing beat frequency	F_w (Hz) ^a
Stroke plane angle with respect to the horizontal	ϕ (degrees) ^b
Rate of change of potential energy	dE_p/dt (W) ^c
Rate of change of kinetic energy	$dE_{K,ext}/dt$ (W) ^d
Body mass	M_b (Kg)
Gravitational acceleration	g (ms ⁻²) ^e
Average Vertical Velocity	\dot{z} (ms ⁻¹)
Average Overall Velocity	V (ms ⁻¹) ^f
Duration of flight	Δt (s)
Induced Velocity	V_i (ms ⁻¹) ^g
Angle at which forward velocity of bird is inclined to the actuator disc	a' (degrees) ^h
Average Vertical Acceleration	g_a (ms ⁻²)
Air density	ρ (kg/m ³) ⁱ
Disk area	D (m ²) ^j
Induced Power	P_{ind} (W) ^k
Parasite Power	P_{par} (W) ^l
Frontal Area of Body	S_b (m ²) ^m
Drag coefficient of the body	$C_{D,par}$ ⁿ
Profile Power P_{pro}	(W) ^o
Resultant Velocity	V_r (ms ⁻¹) ^p
Area of the wing strip	S_i (m ²)
Profile drag coefficient	$C_{D,pro}$ ^q
Angular velocity of the wing strip	ω (degrees/s) ^r
Distance from wing strip to shoulder joint	r (m) ^s
Average horizontal velocity	V_h (m/s)
Stroke Amplitude	Φ (degrees) ^t
Total mechanical power	P_{aero} (W) ^u
Flight muscle efficiency	E_{FM} ^v
Basal metabolic rate	P_{BMR} (W) ^w

- ^a $F_w = 1/T$ (Where T is the time taken for one full wing beat)
- ^b Calculated using trigonometry, from direct measurements of the wing tip to the centre of mass.
- ^c Calculated from equation 3.
- ^d Calculated from equation 4.
- ^e Constant value of 9.81 ms^{-2}
- ^f $V = \sqrt{V_x^2 + V_y^2}$ (Where V_x is horizontal velocity and V_y is vertical velocity)
- ^g Calculated from equation 5.
- ^h $\mathbf{a}' = -\phi + \mathbf{elevation}$ (Elevation is assumed to be zero in steady flight)
- ⁱ Constant value of 1.2 kg/m^3
- ^j $\mathbf{D} = \Phi \mathbf{R}^2$ (Where R is wing length)
- ^k Calculated from equation 6.
- ^l Calculated from equation 7.
- ^m $\mathbf{Sb} = 0.00813 M_b^{0.666}$ (Pennycuick *et al.* 1988)
- ⁿ Constant value of 0.3
- ^o Calculated from equation 8.
- ^p Calculated from equation 9.
- ^q Constant value of 0.02
- ^r $\omega = \Phi / (2/F_w)$ (Assuming that the upstroke and down stroke make up equal components of the entire wing beat)
- ^s $r = \frac{2}{3} \mathbf{R}$ (Where R is wing length)
- ^t Data previously obtained, but may be calculated from direct measurements of the wing.
- ^u Calculated from equation 10.
- ^v Calculated from equation 11.
- ^w Calculated from equation 12.