

Review

Circulatory variables and the flight performance of birds

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Summary

When considering the ‘burst’ flight performance of birds, such as during take-off, one of the most important structural variables is the ratio of the mass of the flight muscle myofibrils with respect to body mass. However, when considering ‘prolonged’ flight performance the variable of interest should be the body mass ratio of the mass of the flight muscle myofibrils that can be perfused sustainably with metabolites *via* the blood supply. The latter variable should be related to blood flow (ml min^{-1}), which in turn has been shown to be a function of heart muscle mass, the value of which is more easily obtainable for different species than that for the mass of perfused muscle.

The limited empirical evidence available suggests that for birds and mammals the rate of maximum oxygen consumption scales with heart mass (M_h) as $M_h^{0.88}$ and that for birds M_h scales with body mass (M_b) as $M_b^{0.92}$, leading to the conclusion that the rate of maximum oxygen consumption in birds scales with an exponent of around $M_b^{0.82}$. A similar exponent would be expected for the rate of maximum oxygen consumption with respect to the flight muscle mass of birds. This suggests that the sustainable power output from the flight muscles may

ultimately be limiting the flight performance of very large flying animals, but as a result of circulatory constraints rather than biomechanical considerations of the flight muscles *per se*.

Under the particular circumstances of sustainable flight performance, calculations of rates of metabolic energy consumed by the flight muscles can be compared directly with the estimates of biomechanical power output required, as calculated using various aerodynamic models. The difference between these calculated values for rates of energy input and output from the muscles is equivalent to the ‘apparent’ mechanochemical conversion efficiency. The results of one such analysis, of the maximum sustainable flight performance of migratory birds, leads to the conclusion that the efficiency of the flight muscles appears to scale as $M_b^{0.14}$. However, much of this apparent scaling may be an artefact of the application and assumptions of the models. The resolution of this issue is only likely to come from studying bird species at either extreme of the size range.

Key words: aerobic flight, muscle efficiency, scaling, heart mass, avian energetics.

Introduction

Aerodynamic considerations of bird flight suggest that, for geometrically similar animals, the biomechanical power required to fly at the minimum power speed (P_{\min}) is relatively greater for large species than for smaller species, as the biomechanical power required should scale with respect to body mass (M_b) as approximately $M_b^{1.17}$ (Pennycuik, 1975; Rayner, 1979a). When converting the aerodynamic model predictions for biomechanical power output (P_{mech}) in watts (W) into estimates for the rate of metabolic energy input (P_{met}) required to support it (often taken for convenience as equivalent to the rate of oxygen consumed in ml min^{-1}), Pennycuik (1975) assumes that the mechanochemical conversion efficiency of the flight muscles (E_{fm}) is independent of body mass and recommends the use of a constant value of around 0.23. If E_{fm} is a constant and the

‘central’ cardiovascular adaptations closely reflect the ‘peripheral’ aerobic adaptations of the flight muscles, as predicted by the hypothesis of symmorphosis (Weibel et al., 1991), it would be expected that the cardiovascular systems of large birds that are capable of ‘prolonged’ flight should be adapted to meet the relatively high power required. However, it is clear that the relative rate of blood flow available to the flight muscles of large birds is actually reduced compared to small birds, due to the steady decline in maximal heart rate with increasing body mass (Bishop and Butler, 1995; Bishop, 1997), as in mammals (Weibel et al., 1991).

The finding that the maximum heart rate of mammals is primarily an allometric function of body size, regardless of morphological adaptations to sedentary *vs* athletic locomotor performance such as relative heart mass (Weibel et al., 1991),

is nicely supported by work on dogs (Stray-Gundersen et al., 1986) and pigs (Hammond et al., 1992). In both these studies, the pericardial membrane that surrounds the heart was surgically removed and the maximum cardiac output and the rate of maximum oxygen consumption were substantially increased, but maximum heart rate was unaffected. Perhaps surprisingly, in addition to an allometric decline in heart rate measured during the flight of birds, there is also a tendency for the heart mass ratio to decline with increasing body mass (Lasiewski and Calder, 1971; Bishop and Butler, 1995; Bishop, 1997). Indeed, Bishop (1997) calculated that the maximum rate of oxygen consumption $\dot{V}_{O_{2max}}$, in ml min^{-1} of extant species of birds generally scales as approximately $M_b^{0.82 \pm 0.08}$ (body mass exponent \pm standard error), although the intrinsic cardiovascular capacity for the $\dot{V}_{O_{2max}}$ of birds and mammals appears to scale as $M_b^{0.88 \pm 0.02}$ (Bishop, 1999). As suggested by Pennycuick (1989) the exponents for the scaling of basal metabolic rate and maximal metabolic rate appear to be selected for independently in endotherms, with the consequence that the potential for aerobic scope should be greater in both larger birds and mammals (Koteja, 1987; Bishop, 1999; Ellerby et al., 2003).

The minimum rate of oxygen consumption ($\dot{V}_{O_{2min}}$, in ml min^{-1}) measured from birds during flights in wind tunnels scales as approximately $M_b^{0.77}$ (Butler, 1991; Bishop et al., 2002), which is consistent with the calculated scaling factor of $M_b^{0.756}$ for the non-wind tunnel flights of birds (Masman and Klaasen, 1987). Part of the discrepancy between the scaling exponents for P_{met} and P_{mech} could be accounted for by the fact that the aspect ratios of the wings of extant species of birds tend to increase with increasing body mass (Pennycuick, 1982). In addition, smaller species may be flying faster during the non-wind tunnel flights than their minimum power speeds, as it has been suggested that smaller species have a very much greater excess capacity for aerobic flight (Pennycuick, 1996). However, the aerodynamic predictions of minimum power speeds are highly dependent on the values used for body drag coefficients ($C_{D,par}$) and it is not clear what values for drag should be used in these models (Pennycuick et al., 1996; Hedenström and Liechti, 2001). Assuming that both the aerodynamic models and the physiological models and measurements outlined above are broadly correct would lead to the view that the E_{fm} resulting from the conversion of P_{met} into P_{mech} may scale positively with increasing body mass (Rayner, 1988, 1990; Bishop and Butler, 1995; Kvist et al., 2001). It has also been suggested that E_{fm} may change positively with respect to flight speed (Rayner, 1999; Ward et al., 2001).

As the aerodynamic lifting line model of Pennycuick (1975, 1989) in particular has frequently been applied to behavioural, ecological and evolutionary studies (e.g. Hedenström and Alerstam, 1992; Pennycuick et al., 1994; Gudmundsson et al., 1995), it is necessary to be confident that the estimates for P_{mech} and the value of E_{fm} and, thus, the subsequent calculation of P_{met} required to fly at a particular speed, are realistic. This is particularly relevant with regard to

issues such as aerobic scope, the optimisation of bird flight behaviour, the maximum mass-specific power output and $\dot{V}_{O_{2max}}$ of avian muscle and the upper limit to the size of flying animals. Ward et al. (2004) have demonstrated how sensitive estimates for P_{met} are to changes in E_{fm} when based on calculations of P_{mech} , as the latter is such a small part of the overall energy budget.

Bishop (1997) showed that it is possible to provide reasonable predictions for the $\dot{V}_{O_{2max}}$ of birds during flight by assuming that avian cardiac muscle has a similar physiological and biomechanical performance to that of terrestrial mammals. Thus it is now possible, theoretically, to derive and compare two independent estimates for the rate of energy utilisation of birds during maximum sustainable flight activity, and to look at the implications of using the default values for these models for predicting the maximum flight performance of birds and the scaling of E_{fm} .

In the following analysis I have applied my approach (Bishop, 1997) to a study of the maximum sustainable climbing flight of 15 species of birds migrating over southern Sweden (Hedenström and Alerstam, 1992). These authors used the default values from the model of Pennycuick (1975) to estimate the maximum aerobic biomechanical power output continuously available (P_{ac}) from the flight muscles of birds (see Pennycuick, 1972). I have used their data but have recalculated the estimates for P_{ac} using the default values of Pennycuick's computer program 1A (Pennycuick, 1989, version 1.1) as this is easy to use, has the same range of values for the body drag coefficient ($C_{D,par}$ from 0.25 to 0.4) and the results can then be applied with consistency to large numbers of additional species. The two data sets are listed in Appendix A for comparison. On average, the new calculations only lead to a reduction of P_{ac} by 3.4% (range -14.7% to +7.1%) so overall conclusions are not seriously affected. By comparing the estimated values of P_{ac} with those for P_{met} , using calculations of $\dot{V}_{O_{2max}}$ available based on heart mass (Bishop, 1997) and converted to watts, it is possible to estimate the 'apparent' scaling of the E_{fm} . Subsequently, I apply these results to the data collected for 228 species of birds by Magnan (1922), and look at the predictions for the aerobic flight performance of different taxa. I will also discuss the implications for the scaling of power output in birds with respect to the myofibrillar content of the flight muscles.

Modelling the maximal aerobic flight performance of birds

It is usual, when considering the amount of aerobic metabolic energy (P_{met} in W or \dot{V}_{O_2} in ml min^{-1}) that would actually be continuously available to supply the flight muscles ($P_{met,fm}$), to take account of the additional costs of maintaining some kind of basal metabolic rate along with the necessary circulatory and respiratory costs (Pennycuick, 1989). Thus, it is assumed that a proportion of the total \dot{V}_{O_2} equal to basal metabolic rate (BMR) must be spent on general maintenance

of tissue function during flight, while an additional 10% of the remaining \dot{V}_{O_2} is subtracted to cover the respiratory and circulatory costs (Tucker, 1973; Pennycuick, 1975, 1989). Pennycuick (1975, 1989) uses the two basal metabolic rate equations of Lasiewski and Dawson (1967), which give a lower basal metabolic rate for species of non-passerine than species of passerine birds. However, I prefer to take values for BMR from the literature where possible (e.g. Bennett and Harvey, 1987). In addition, where a suitable measure of BMR is not available, I used the more recent work of Prinzing and Hanssler (1980), which suggests that, in general, passerines and non-passerines of a similar body mass have the same basal metabolic rate, and this is also supported by Reynolds and Lee (1996):

$$\text{BMR} = 5.4M_b^{0.72 \pm 0.03} \quad (r^2=0.96) . \quad (1)$$

In order to estimate values for the $\dot{V}_{O_{2\max}}$ available for birds for comparison with the data of Hedenström and Alerstam (1992), I have essentially used my model II approach (Bishop, 1997), which assumes that birds have a similar cardiovascular performance to that of mammals, and is based on the Fick equation:

$$\dot{V}_{O_{2\max}} = \dot{Q} (Ca_{O_2} - C\bar{v}_{O_2}) , \quad (2)$$

where \dot{Q} is maximum cardiac output (ml min^{-1}) and is found to scale as $\dot{Q}=213M_h^{0.88 \pm 0.04}$ (where M_h is in g); Ca_{O_2} is the oxygen content of the arterial blood ($\text{ml O}_2 \text{ 100 ml}^{-1}$ blood) and is calculated as haemoglobin concentration (in g) per 100 ml blood $\times 1.36$ (to calculate saturated oxygen carrying capacity) and then by 0.94 (assuming 94% saturation during maximal activity); and $C\bar{v}_{O_2}$ is the oxygen content of the mixed venous blood returning to the heart and is taken to be 0.038 ($\text{ml O}_2 \text{ 100 ml}^{-1}$ blood) under conditions of $\dot{V}_{O_{2\max}}$ (for details, see Bishop, 1997).

However, to simplify the calculations and the need to estimate haemoglobin concentrations for many different species, particularly when applying the results to the data set of Magnan (1922), I have used the simplified general equation for $\dot{V}_{O_{2\max}}$, which assumes an average value for haemoglobin concentration based on 15 g ml^{-1} blood, where the general equation for mammals was:

$$\dot{V}_{O_{2\max}} = 33M_h^{0.88 \pm 0.09} . \quad (3)$$

Using Eq. 3 and the above assumptions, I have estimated the $\dot{V}_{O_{2\max}}$ available to the flight muscles and hence $P_{\text{met, fm}}$ for various bird species, using relative M_h data from Magnan (1922) and Hartman (1961), available for each individual species in the study of Hedenström and Alerstam (1992), except for a couple of cases where I used a value for the same genus or family.

The energetics of forward flapping flight during maximum sustained climbs

Fig. 1 shows the calculated maximum aerobic $P_{\text{met, fm}}$ available based on heart mass and two estimates for maximum P_{ac} (i) based on the data of Hedenström and Alerstam (1992) and the default values of Pennycuick's computer program 1A (Pennycuick, 1989, version 1.1) with $C_{D, \text{par}}$ ranging from 0.25 to 0.4, and (ii) based on the same approach but using a constant and low $C_{D, \text{par}}$ of 0.1 for all species (see Pennycuick et al., 1996). Data are plotted against body mass for the 15 species of birds during maximum 'sustained' climbing flight (Hedenström and Alerstam, 1992).

Maximum aerobic $P_{\text{met, fm}}$ scales as:

$$P_{\text{met, fm}} = 79M_b^{0.812 \pm 0.02} \quad (r^2=0.994, N=15) , \quad (4)$$

and maximum P_{ac} scales as:

$$(i) P_{\text{ac}} = 24.9M_b^{0.956 \pm 0.028} \quad (r^2=0.988, N=15) \quad (5)$$

or

$$(ii) P_{\text{ac}} = 18.8M_b^{0.999 \pm 0.023} \quad (r^2=0.994, N=15) . \quad (6)$$

These estimates for $P_{\text{met, fm}}$ and P_{ac} clearly have significantly different M_b exponents ($F_{2,39}=16.58, P<0.0001$). In addition, both the M_b exponents and the coefficients are affected by the changes in default $C_{D, \text{par}}$ between the two estimates for P_{ac} ,

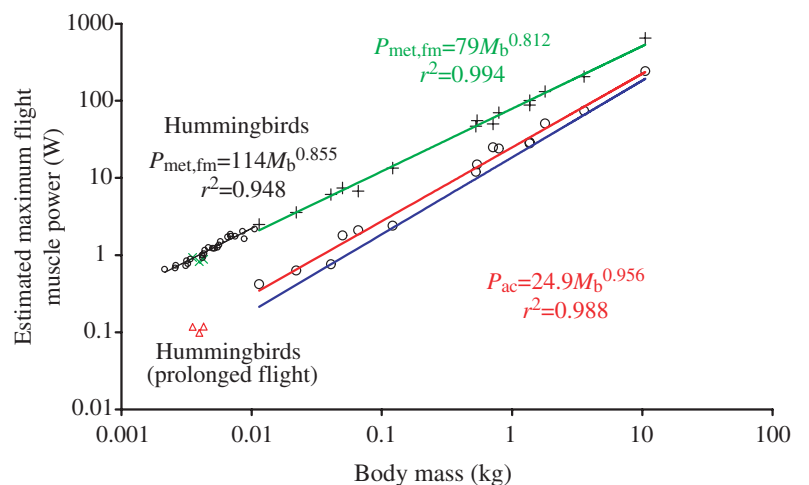


Fig. 1. Estimated maximum aerobic flight muscle power (W) plotted against body mass (kg). Calculated maximum aerobic metabolic power input available to the flight muscles ($P_{\text{met, fm}}$) for 15 bird species studied by Hedenström and Alerstam (1992) during migratory climbing flights (+, green regression line) and for hummingbirds (small circles). Calculations of $P_{\text{met, fm}}$ are based on measurements of heart mass and assume $\dot{V}_{O_{2\max}}=33M_h^{0.88}$ (Bishop, 1997). Estimated maximum biomechanical power output available continuously from the flight muscles (P_{ac}) for the 15 migratory bird species (large circles, red regression line) calculated using Pennycuick's computer program 1A (Pennycuick, 1989, version 1.1) with default values for $C_{D, \text{par}}$ ranging from 0.25 to 0.4. The blue regression line is based on P_{ac} calculated using a value for $C_{D, \text{par}}$ of 0.1 for all species. $P_{\text{met, fm}}$ (green crosses) and P_{ac} (red triangles) are also plotted for three species of hummingbird hovering at a respirometry feeder (Wells, 1993; Chai and Dudley, 1995). Values for M_h are taken from Magnan (1922) and Hartman (1961).

although only the coefficients are significantly different ($F_{1,27}=19.68, P<0.0001$).

Bishop (1997) showed that the estimates for total $\dot{V}_{O_{2max}}$, based on measurements of M_h , are reasonably accurate compared to currently available empirical values from wind tunnel studies, with typical errors ranging up to a maximum of 17%. Recently, Ward et al. (2004) have shown that measurement of P_{met} for starlings *Sturnus vulgaris* flying in a wind tunnel were similar when using three different techniques (doubly-labelled water, mask respirometry and heat transfer modelling) and that they were also similar to measurements made on free-living starlings (Westerberp and Drent, 1985) and those predicted from the cardiac model of Bishop (1997). The slightly more derived estimates for $P_{met,fm}$ depend on the validity of the assumptions for taking into account the costs for maintaining BMR, and covering the circulatory and respiratory functions. However, these assumptions should only introduce a minimal amount of additional error as they represent a relatively small amount of the total energetic costs of flight.

There is currently no similar basis on which to test the aerodynamic predictions for P_{ac} . Eq. 5 and 6 represent two different extreme predictions and vary simply due to alterations in the default values for $C_{D,par}$. The different values are the result of differing assumptions with regard to the scaling effect on body drag of changes in Reynold's number as body mass increases. Eq. 5 is based on Pennycuick (1975, 1989, version 1.1) and uses a default value for $C_{D,par}$ for small birds of 0.4, which is then reduced in magnitude for larger birds down to 0.25. More recent work (Pennycuick et al., 1996) suggested that $C_{D,par}$ could be as low as 0.05–0.1 for even relatively small species of

birds (based on wing beat frequency and estimates of minimum power speeds), and so Eq. 6 is based on an extreme hypothesis of $C_{D,par}$ as 0.1 for all species. However, it should be noted that Hedenström and Liechti (2001) investigated the maximum diving velocities of a range of small passerines and concluded that the original default value of 0.4 for $C_{D,par}$ for this group was probably appropriate. They also found evidence to support the idea that $C_{D,par}$ should be reduced as Reynold's number increases.

The 'apparent' scaling of flight muscle efficiency during flapping flight

The difference between the calculation for the $P_{met,fm}$ available and the two estimates for the P_{ac} required can be used to calculate values for the 'apparent' scaling of E_{fm} (Fig. 2). The results indicate that the E_{fm} of birds performing maximum climbing flights appears to scale positively with respect to body mass as:

$$(i) \text{ apparent } E_{fm} = 0.3M_b^{0.137 \pm 0.028} \quad (r^2=0.659, N=14) \quad (7)$$

or

$$(ii) \text{ apparent } E_{fm} = 0.23M_b^{0.182 \pm 0.026} \quad (r^2=0.806, N=14) \quad (8)$$

The value for the wigeon *Anas penelope* was not included in the analysis as the calculated efficiency (0.49) was very much higher than any other species, despite the wigeon being only 0.7 kg in mass. A relative heart mass value of 0.93% was taken from Magnan (1922) for the wigeon and it seems likely that this may be an underestimate. Two other species of the genus *Anas* had figures of 1.15% and 1.23%, as reported in Hartman (1961), and a relative M_h of 1.2% would have brought the estimate for efficiency down to 0.4, which is similar to those calculated for the other species of migratory wildfowl.

Obviously, the above calculations only represent the apparent E_{fm} calculated when specifically applying these particular models for estimating $P_{met,fm}$ and P_{ac} to the climbing flight data of Hedenström and Alerstam (1992). The general applicability of this result to bird flight studies will depend on the validity of a number of potential assumptions, and errors in either model will lead to errors in the calculations of E_{fm} . The most striking observation, however, is that the data underlying Eq. 7 exhibit a 2.5-fold range in calculated E_{fm} that scales positively with respect to body mass, with an exponent of 0.14 ± 0.03 . In addition, despite the overall simplicity of the approach, the average calculated E_{fm} for the 14 species was 0.27, which is close to the commonly used value of 0.23 recommended by Pennycuick (1989). The average calculated E_{fm} using a fixed $C_{D,par}$ of 0.1 was 0.2.

Ward et al. (2001) presented data on the possible E_{fm} of starlings *Sturnus vulgaris* flying in a wind

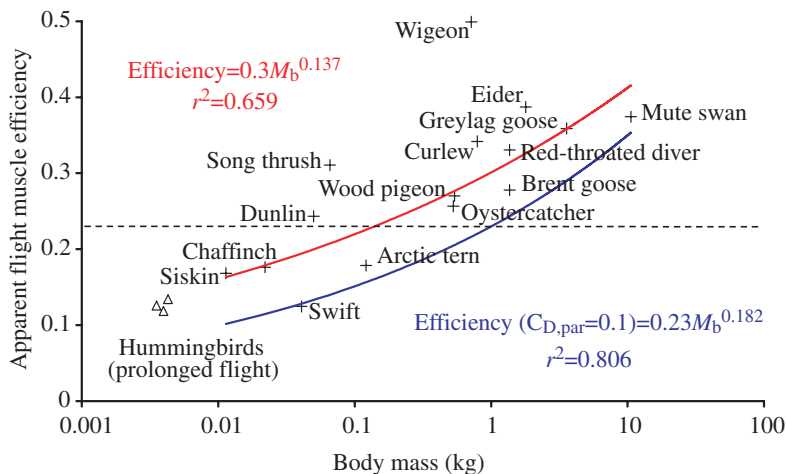


Fig. 2. Estimated 'apparent' flight muscle mechanochemical efficiency plotted against body mass (kg) for 15 bird species during migratory climbing flights (+). The wigeon is left out of the analysis as an outlier. The red regression line is based on the biomechanical power output continuously available (P_{ac}) calculated using default values for $C_{D,par}$ ranging from 0.25 to 0.4 (Pennycuick, 1989). The blue regression line is based on P_{ac} calculated using a value for $C_{D,par}$ of 0.1. Estimates of efficiency for three species of hummingbirds (Δ) are also plotted. Calculations and data sources as in Fig. 1.

tunnel and give a detailed discussion on previous values calculated for the E_{fm} of various species of birds. In general, E_{fm} varies from 0.19 to 0.28 for the budgerigar *Melopsittacus undulatus* (Tucker, 1968) up to 0.32–0.4 for the white-necked raven *Corvus cryptoleucos* (Hudson and Bernstein, 1983). Calculated E_{fm} for the starlings appeared to vary with flight speed, with a range 0.15–0.23 and an average of 0.18, using the lifting line model of Pennycuick (1975). Mean efficiency was found to be similar for the starlings when the vortex ring aerodynamic model of Rayner (1979b) was used to estimate biomechanical power, although apparent E_{fm} appears to increase more steeply with changes in flight speed (Ward et al., 2001). The overall picture from these experimental data sets is that E_{fm} appears to show a tendency to increase with increasing body mass and/or decreasing wing-beat frequency, which is consistent with the modelling approach presented in this review. Clearly, if it really is true that E_{fm} is a constant value of around 0.23 (e.g. Pennycuick, 1989) and does not scale with body mass or wing-beat frequency, then we require an explanation that takes into account the systematic change in ‘apparent’ E_{fm} shown in Fig. 2.

Theoretically, the maximum efficiency of the contractile machinery alone should not exceed 0.39 (Pennycuick, 1992). As this does not take into account the efficiency of oxidising fuel substrates to produce ATP, it should not be possible for muscle fibres to operate with an overall efficiency greater than around 0.28 (Rall, 1985). Thus, in most cases muscle fibres are usually assumed to operate with maximal efficiencies of around 0.2–0.25 (Taylor, 1994). Logically, even if E_{fm} did initially scale with body mass, there should come a point for relatively large species of birds where the E_{fm} must reach a plateau (theoretically at around 0.28), so that very large birds have greatly reduced sustained flight performance as a result (Bishop and Butler, 1995). It has been suggested that bird E_{fm} would be expected to scale independently with respect to body mass (Taylor, 1994), as bird wings have to work against their environment. Thus, the flight muscles should be selected to operate with maximal efficiency and power production (Rome, 1994), rather than for economic force production as appears to be the case in mammals (Taylor, 1994). This would tend to suggest that we should be cautious about the possibility of a 2.5-fold variation of efficiency in birds. There would appear to be a number of possible errors in the above analysis of maximum aerobic flight performance.

The most obvious issue is that the estimated values for $\dot{V}_{O_{2max}}$ are inappropriate. I have already argued above that the limited data available on the circulatory performance of birds during sustainable flight performance are reasonably consistent with those from mammals during maximal activity (Bishop, 1997) and that the errors involved may only account for around $\pm 20\%$. Obtaining values of $\dot{V}_{O_{2max}}$ from birds during flight is extremely difficult and there is very little data. It is possible that, as birds tend to maintain slightly higher body temperatures than mammals, the relationship between $\dot{V}_{O_{2max}}$ and heart mass would be slightly greater for birds. Currently, there is insufficient data on $\dot{V}_{O_{2max}}$ and heart mass

to show such a difference. However, if this turns out to be the case, the potential error in the calculation of E_{fm} is likely to be small, but would reduce it downwards. Of course, errors may also be introduced due to miscalculations of bird morphologies such as relative heart mass, haemoglobin concentration, total body mass and relative fat loading etc. The data for the wigeon suggest that the value for relative M_h used was probably an underestimate. Likewise, the value of 1.06% for the relative M_h of the song thrush *Turdus philomelos* may also be slightly low, as the values of M_h for three other species of *Turdus* taken from Hartman (1961) are 1.04%, 1.22% and 1.31%, and this could account for the rather high value of E_{fm} calculated for this species.

Perhaps the other obvious factor is whether these birds were really performing at a similar level of ‘effort’ and relatively close to their maximal aerobic abilities. If not, then this could account for much of the apparent systematic change in E_{fm} with body mass for the smaller species. The larger species tended to gain altitude at slower rates and did not maintain their climbing flights for as long as the smaller species. As the minimum time recorded for the climbs was 4 min it seems reasonable to assume that the larger species were probably performing aerobically and close to their sustainable limits (Hedenström and Alerstam, 1992). One flock of eider ducks was recorded maintaining near maximal climbing rates for 25 min. Intermediate sized birds, down to the mass of the dunlin, tended to show high climb rates well in excess of 4 min, and data from Piersma et al. (1990) indicated that the dunlin are probably showing climb rates that are proportional to their relative fuel loads. The very smallest species, the chaffinch, siskin and swift, exhibited relatively poor maximal climb rates, which were somewhat at odds with the other species, so it is more difficult to conclude that they are likely to be near their maximal aerobic capabilities, although they were flying quite fast horizontally (Hedenström and Alerstam, 1992). If these last three species were not as close to their maximum sustainable climb rates relative to the other species then the predictions for their rate of \dot{V}_{O_2} would have been overestimates and this would have underestimated their flight muscle efficiencies.

Calculations of P_{ac} are dependent on accurate measurements of drag coefficients, which are difficult to make (Pennycuick, 1989; Spedding, 1994; Hedenström and Liechti, 2001), and there is much uncertainty about the relevant values to incorporate into aerodynamic models of bird flight. The downwards modification of the body drag coefficient along the lines suggested by Pennycuick et al. (1996) clearly has a significant influence on the estimation of P_{ac} and, therefore, the apparent E_{fm} of the flight muscles. The use of a constant and very low value of 0.1 for $C_{D,par}$ would reduce all the species estimates of E_{fm} (mean value of 0.2) but it would also increase the scaling exponent from $M_b^{0.14}$ to $M_b^{0.18}$. The lowering of $C_{D,par}$ for very small species of birds has not been justified on aerodynamic grounds (Hedenström and Liechti, 2001) and the assumption used by Pennycuick et al. (1996) that the minimum wing-beat frequency can be used to

determine the minimum power speed, may not be valid for all species (Tobalske et al., 2003). However, if only the relatively large species of birds, operating at higher Reynold's numbers, actually have $C_{D,par}$ around 0.1 or less then this would account for much of the increase in 'apparent' E_{fm} for the larger species. For example, to bring the E_{fm} estimate for the mute swan down to around 0.28 would require a P_{ac} value of around 180 W and a $C_{D,par}$ of approximately 0.05, but it would increase the estimate of the minimum power speed. It is also possible that some other constant or variable should be adjusted in the model, perhaps concerning the profile power component (Rayner, 1999).

Pennycuick's model approach (Pennycuick, 1975, 1989) ignores the inertial costs of accelerating and decelerating the wing. Pennycuick argues that the wing inertia can be used to do useful aerodynamic work during the deceleration phase and so it should not be added to the overall costs. This would appear to be justified, at least for moderate-to-large species of birds, based on the results of Hedrick et al. (2004) and their analysis of accelerometer measurements of 87 g cockatiels. It is not known, however, if this result can be applied to very small species of birds, such as

hummingbirds, operating at very high wing-beat frequencies where the inertial costs may be relatively large (Van den Berg and Rayner, 1995). The argument used for hummingbirds is usually based on the idea that they may have sufficient elastic storage capabilities that they can store the inertial costs during wing deceleration and use the energy to reaccelerate the wing on the next beat (Wells, 1993; Chai and Dudley, 1995). Any increment of the inertial costs in accelerating the wings of very small species of birds that must be powered by the flight muscles will increase the estimate of the 'apparent' E_{fm} .

Aerobic flight performance of birds based on heart mass

Despite the uncertainties that underlie some of the assumptions involved in calculating flight muscle efficiency, it should still be possible to use Eq. 7 to specifically relate these two models for the maximum aerobic $P_{met, fm}$ available (Bishop, 1997) and the biomechanical power required (Pennycuick, 1989, version 1.1) for flight, and to draw some broad conclusions regarding the aerobic flight performance of particular species of birds. The first step is to calculate the

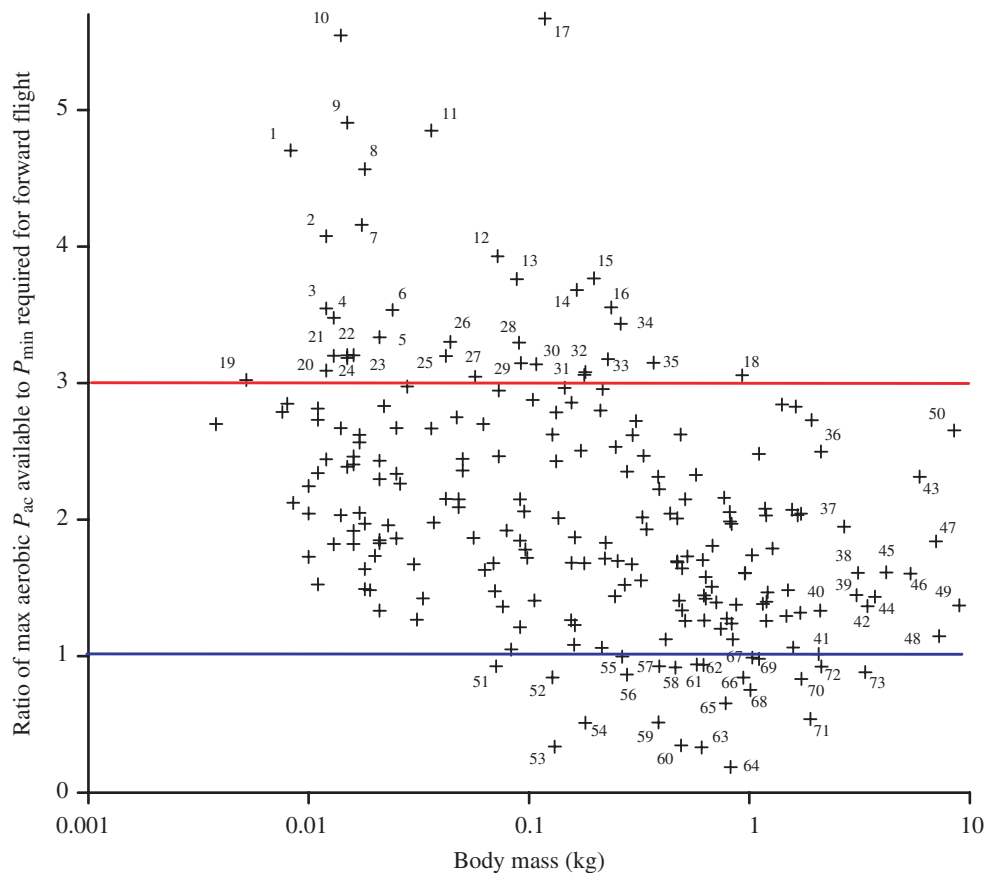


Fig. 3. Ratio of calculated biomechanical P_{ac} and estimated biomechanical P_{min} required for forward flapping flight plotted against body mass (kg). Calculations of P_{ac} assume $\dot{V}_{O_{2max}}=33M_h^{0.88}$ and $E_{fm}=0.3M_b^{0.137}$ (see Fig. 2 and text). Estimates of P_{min} use Pennycuick's computer program 1A (Pennycuick, 1989, version 1.1); default values for $C_{D,par}$ range from 0.25 to 0.4. Bird morphological data based on the study of Magnan (1922); see text. Coloured lines refer to Appendix B.

$\dot{V}_{O_{2max}}$ for various species of birds based on measurements of heart mass and convert this to an estimate for the maximum $P_{met,fm}$ available, and then convert this to an estimate of maximum P_{ac} using Eq. 7. I shall then compare these values for maximum P_{ac} to those for the P_{min} required to fly from the model of Pennycuick (1989, version 1.1). The predictions for $\dot{V}_{O_{2max}}$ based on $33M_h^{0.88}$ and the predictions for P_{min} based on the aerodynamic model are linked by body mass, regardless of whether the change is seen between species or within species. Thus, whenever body mass changes in the calculation a new figure for E_{fm} must be calculated from Eq. 7.

I shall first apply the above models to the excellent data collected by Magnan (1922) on the morphometrics of 228 species of mostly European birds. I shall also consider the importance of some selected measurements of relative heart masses of birds reported by Hartman (1961) and Crile and Quiring (1940). All calculations assume an altitude at sea level (unless otherwise stated). Magnan (1922) collected all the necessary data required to calculate reasonable estimates for the P_{min} required to fly, and to compare them to the potential maximum P_{ac} of each species, except that his measurements for wing area did not include the body area between the wings (Pennycuick, 1989). Fortunately, Hartman (1961) measured the glide, tail and wing area of 340 species of birds. By subtracting the wing and tail areas from the glide area for each species we can estimate the value for body area, which gives a value for the scaling of body area with respect to body mass as:

$$\text{Body area} = 0.018M_b^{0.72} \quad (r^2=0.89) \quad (9)$$

Using Eq. 9 I have arrived at a slightly modified value for the wing areas for Magnan (1922).

Fig. 3 shows the ratio of the calculated maximum P_{ac} available divided by the estimated P_{min} required plotted against M_b (numbered species are listed in Appendix B). Fig. 4 uses the same data to plot the mean family ratio of the P_{ac} available / P_{min} required. It is clear from Figs 3 and 4 that the majority of birds, particularly those less than 0.1 kg in mass, appear to have more than enough power available to 'sustain' at least P_{min} (i.e. a P_{ac}/P_{min} ratio >1) and some of the smaller species appear to be able to sustain up to 3 times the P_{min} required. If we assume that the intra-species scaling of the power required to fly scales at around $M_b^{1.59}$ (Rayner, 1990), then a species with a ratio of $P_{ac}/P_{min} >3$ should be able to sustain P_{min} (in level flight at sea level) when carrying approximately an additional 100% of body mass. Of course, the predicted minimum flight speed will also increase and the bird will probably not be able to take off or land, so this prediction is likely to be a bit optimistic in reality. Errors in the data set will also make individual assessments even more imprecise along with the difficult of motivating a bird to give it a try in the first place! Interestingly, Dial and Biewener (1993) reported on some load-carrying flights for two captive pigeons *Columba livia* trained to fly for 20 m to a perch in an enclosed hall. These two birds could carry and take off from the ground with a weighted backpack representing an additional 50% of body mass and could even manage level flapping flight with 100% additional mass if assisted into the air. Although *C. livia* was not included in the data of Magnan (1922), there is data for *C. palumbus*, *C. oenas* and *Turtur turtur*. All three species are morphologically similar, with average relative M_h of 1.32%, flight muscle masses of 27.3% and a calculated aerobic P_{ac}/P_{min} ratio of 2.05 (1.8, 2.7 and 1.65, respectively). The P_{ac}/P_{min} ratio of ~2 certainly appears broadly consistent with the data of Dial and Biewener (1993) for *C. livia*.

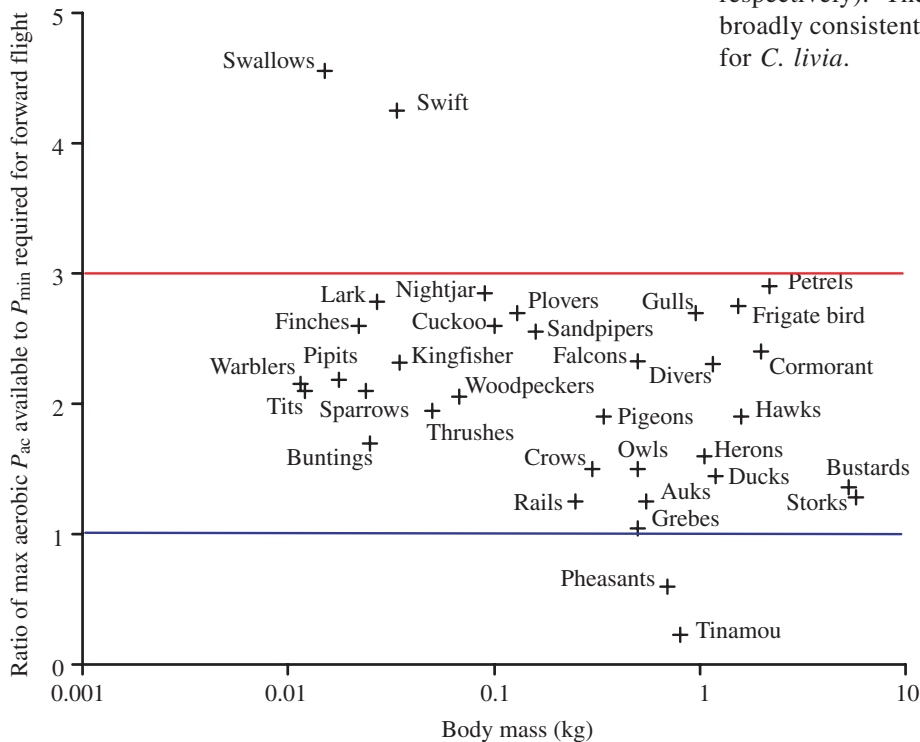


Fig. 4. Mean values for various bird families for the ratio of biomechanical P_{ac} and estimated biomechanical P_{min} required for forward flapping flight plotted against body mass (kg). Calculations and data source as for Fig. 3. Coloured lines refer to Appendix B.

Species with ratios >3 have relatively large M_h and, usually, large wing areas and/or high aspect ratio wings, and include some examples of finches, swifts, swallows and martins, common tern, hobby, knot, red kite among others. In general, the reverse is true for those species that fall below the line for a ratio of 1, and these include species such as grouse, pheasants, partridge, an eagle owl and the red-winged tinamou. Also of interest are those relatively large species of birds (>2 kg), which have a ratio between 1 and 3, and these include species such as the common cormorant, gannet, eagles, vultures, storks, geese, whooper swan, wandering albatross and the European great bustard. These latter species are tending to show morphological adaptations either to reduce the costs of flight or to supply increased metabolic input to the muscles. Clearly, despite the uncertainties, some species of birds have a significant amount of extra aerobic capacity above the minimum requirement. Presumably, these abilities have evolved to provide added load lifting and/or enhanced climbing performance as well as the ability to fly much faster than the minimum or even maximum range speed if necessary. However, the results of Ward et al. (2001) appear to indicate that estimates of E_{fm} increase with flight speed, at least for the starling, so that birds flying close to their minimum power speeds may operate with a lower E_{fm} than when near their maximum aerobic speeds. Maximum reported E_{fm} for the two starlings was 0.2 and 0.3, which is similar to that of 0.21 calculated from Eq. 7 for a species of similar body mass. This supports the general approach in estimating maximum P_{ac} using Eq. 7, but also suggests that the excess metabolic capacity above that required to support P_{min} would not be as great as the biomechanical capacity, which is plotted in Figs 3 and 4.

The relative heart mass of the bustard family (Otidae) appears to be unusually large compared to other birds of their mass (Bishop, 1997). The estimated P_{ac} for a 9 kg European great bustard *Otis tarda* is 242 W based on a value for M_h of 1.4% (Magnan, 1922), which is 20% greater than the estimated P_{min} (208 W). The P_{ac} for a large male Kori bustard *Ardeotis kori* studied by Pennycuick (1969), and using a value of 1.0% for M_h (Crile and Quiring, 1940), is 246 W, which is just below P_{min} at both 1500 m (300 W) where the bird was studied, and for sea level (278 W).

The large aerobic capability of some species relative to others requires considerable differences in the biochemistry of their flight muscles (Pennycuick and Rezende, 1984; Rosser and George, 1986). In particular, the relatively aerobic nature of the flight muscles of some relatively large species of birds, such as the bustards and swans, has important implications for the interpretation of the size limitations to the flight performance of birds. The flight muscles of medium to large species of birds are of a mixed composition, with some fast glycolytic (FG) fibres specialised primarily for anaerobic metabolism and some fast oxidative glycolytic (FOG) fibres specialised primarily for aerobic metabolism (Rosser and George, 1986). Thus, it is necessary to

distinguish between 'burst' flight performance, and 'prolonged' or aerobic flight performance (Marden, 1994), and to compare flight muscles that are adapted for similar types of flight. The data of Marden (1987) and Pennycuick et al. (1989) on the maximum load lifting ability of flying animals refer only to 'burst' flight performance, and bird species that have predominantly FG flight muscle fibres will be at an advantage compared to species with predominantly FOG fibres.

Limitations to muscle mass-specific power output

A number of studies contain observations about the limits to bird flight performance that include implicit assumptions concerning the flight muscles, but which do not take explicit account of possible differences in the 'physiological' or functional characteristics of those flight muscles. Two examples are discussed below, during which I shall assume that all the flight muscle myofibrils are recruited during burst flight activity, while only those fibres that reside in the highly oxygenated regions of the flight muscles are recruited during aerobically 'prolonged' activity.

Example 1

Ellington (1991) concludes that perhaps the available P_{mech} may not be limiting burst flight performance in large birds, as the analysis of Marden (1987, 1990) suggests that the 12 kg Kori bustard should just be capable of a standing take-off, although this is apparently not the case (Pennycuick, 1969). In contrast, Marden (1994) observed that the 10 kg North American wild turkey *Meleagris gallopavo* was capable of a near-vertical take-off from a standing start. Like other Galliformes, the turkey probably has a relatively small M_h and the flight muscles are relatively large and predominately made up of FG fibres (Rosser and George, 1986). This contrasts with the Kori bustard, which has a relatively large M_h of 1% (Crile and Quiring, 1940) but moderately sized pectoralis musculature of around 16.4% (Pennycuick, 1969). Therefore, the average body mass-specific mass of myosin and actin myofibrils in the Kori bustard is probably considerably lower than those of large Galliformes such as the wild turkey. If we assume that the FOG fibres of large birds can only deliver $2/3$ of the P_{mech} of FG fibres and that the Kori bustard's flight muscles are composed of 50% FOG and 50% FG, then the P_{mech} would be $5/6$ of the predicted value if the muscles were made up of 100% FG, i.e. equivalent to a flight muscle ratio of only 13.7%. In addition, some account must be taken of the altitude at which the Kori bustard was studied. Therefore, in the case of the Kori bustard at 1500 m, it may still be that the available P_{mech} was limiting take-off performance. The lowland living European great bustard has both a relatively larger M_h of 1.4% and relatively larger flight muscles of 22.5% (Magnan, 1922) and appears to be capable of local migratory flights. I would predict that this species should be more capable

during take-off than that of the Kori bustard. This argument would also apply to birds such as swans, which have a relatively large M_h (around 1.1%). Thus, when considering 'burst' flight performance such as required for take-off, the important variable is not the flight muscle mass ratio but the myofibrillar protein mass ratio.

Example 2

Gudmundsson et al. (1995) studied the migration of brent geese *Branta bernicla* from Iceland to Greenland, and tracked them by satellite as they flew up to and across the Greenland ice-cap. These authors concluded that the failure of brent geese (fitted with 57 g satellite transmitters) to fly continuously over the Greenland ice-cap supports the predictions of Pennycuick (1969, 1989), that the myofibrillar mass-specific P_{mech} available from the flight muscles *per se* scales directly in proportion to wing beat frequency, so that large birds should show a severely restricted capacity to fly with heavy fuel burdens during climbing flight. Gudmundsson et al. (1995) contrast this prediction with the conclusions of Marden (1987) and Ellington (1991) that the size-dependent P_{mech} constraints may not be so acute. However, the results of Marden's studies are only relevant to the first few seconds of flight and so large species of birds would not be capable of sustaining these power outputs. As we have seen, this is primarily due to the negative scaling of the mass-specific oxygen supply to the muscles, due to the reduction in the maximum heart beat frequency with increasing body mass and the failure of relative M_h to scale positively in order to compensate for this shortfall. Thus, while anaerobic flight performance may be almost independent of body mass, the aerobic flight performance of relatively large birds such as geese must decline. Marden's results should, therefore, be fully compatible with the study by Gudmundsson et al. (1995) and explain why these geese would have been able to perform the presumably short anaerobic flights required for them to travel over the Greenland ice-cap.

The biomechanical P_{ac} calculated for the brent geese (estimated M_b of 1.364 kg) tracked climbing at 0.53 m s^{-1} over southern Sweden, at a horizontal speed of 16.4 m s^{-1} , was 32 W, of which 7.1 W was required for the climb (Hedenström and Alerstam, 1992). The first 21 km of the Greenland ice-cap would have required brent geese to climb at a rate of around 0.7 m s^{-1} , using an additional 2.3 W, or 7% extra P_{mech} . Thus, it would appear that the birds migrating across Sweden with a relatively low fat loading (estimated ratio of 1.1 with a lean mass of 1.24 kg) and at low altitude would not have been capable of flying aerobically up the first face of the Greenland ice-cap, but it would have been a close call. The next 95 km required a climb rate of only 0.21 m s^{-1} and the Swedish brent geese should have been able to cope with the second part of the climb. Indeed, one flock of 26 Swedish greylag geese *Anser anser* (estimated M_b of 3.58 kg) achieved an overall climb rate of 0.32 m s^{-1} for 20 min (Hedenström and Alerstam, 1992).

Post-moult adult barnacle geese *Branta leucopsis* with a body mass of 1.8 kg have a relative heart ventricular mass of 0.86%, while pre-migratory barnacle geese with a body mass of 2.372 kg have a relative ventricular mass of 0.83% (Bishop et al., 1998). Thus, it seems reasonable to assume that the pre-migratory brent geese preparing to head towards Greenland might have showed a similar heart hypertrophy and could retain a relative heart mass of around 1.07% of body mass (Magnan, 1922) during the migration. Gudmundsson et al. (1995) calculated a provisional estimate of 1.8 kg for the body mass of the brent geese as they arrived at Greenland, which would require a P_{min} of 37 W. A relative M_h of 1.07% would yield an estimated P_{ac} of 44.6 W (at an apparent efficiency of 34%), giving a climb power of only 7.6 W, instead of the 12.4 W required for the first phase of the climb. The second phase of the climb would have required only 3.7 W of climbing power and, therefore, it should have been possible to maintain flight. These calculations suggest, at the very least, that even a shallow climb could bring these migratory geese close to the threshold of their aerobic abilities. Any further burden, such as that caused by carrying a 57 g satellite transmitter, may have forced them to utilise supplementary anaerobic metabolism. This could have forced them to take much longer over the traverse of Greenland, as lactate takes much longer to remove from the tissues than to produce it.

In conclusion, I suggest that the empirical data of Gudmundsson et al. (1995) are compatible with the predictions of Marden (1987, 1990) and Bishop (1997) and show that it is not the P_{mech} available from the flight muscle myofibrils *per se* that is primarily limiting the performance of larger migratory birds. When considering aerobic flight performance, the important variable is the body mass ratio of the mass of myofibrils that can be continuously supported by the surrounding tissue.

Myofibrillar mass-specific power output

Data from Marden (1987, 1990) showed that flight muscle mass-specific lifting force during take-off appeared to scale almost directly with body mass, and was not closely correlated with wing beat frequency (assuming no additional inertial energy is required). Ellington (1991) also interpreted these data to indicate that muscle mass-specific 'burst' P_{mech} might even scale with a very slightly positive exponent with respect to body mass. Pennycuick (1969, 1989) predicted that regardless of the muscle type, the mass-specific P_{mech} should scale directly with wing beat frequency, i.e. negatively relative to increasing body mass, as work per unit myofibrillar mass should be a constant. The data of Marden (1987, 1990) appear to contradict these predictions. Detailed work on the take-off performance of different species of Phasianidae have also shown that myofibrillar power output appears to show very little scaling with body mass (Askew et al., 2001).

Little is known, however, about prolonged or aerobic flight performance. The original calculations of Hedenström and Ålerstam (1992) also appeared to contradict the predictions for muscle mass-specific power output of Pennycuick (1969, 1989) and, similar to that of take-off power, the maximal P_{ac} appears to scale almost directly with respect to body mass and flight muscle mass (M_{fm}) as $P_{ac}=128M_{fm}^{0.978}$. These authors assumed that flight muscle mass was around 20% of lean body mass. I have recalculated their data using flight muscle masses from the literature, as flight muscle mass can be more accurately estimated from Magnan (1922) and Hartman (1961) for all 15 species (except for the eider duck, for which I used data from Parker and Holm, 1990), and these values can vary greatly from that of 20% (data in Appendix A). In addition, I have used actual body mass as the reference (rather than lean body mass), because it is clear from numerous studies that flight muscles are dynamic structures that usually undergo hypertrophy in association with total body mass changes (Fry and Ferguson-Lees, 1972; Marsh, 1984; Driedzic et al., 1993; Bishop et al., 1996; Lindström et al., 2000; Swaddle and Biewener, 2000). Unfortunately, even this is a simplification as small species may tend to exhibit a relatively smaller hypertrophy than larger species (cf. Driedzic et al., 1993). Nevertheless, the results again support the apparent scaling of P_{ac} almost independently of body mass and flight muscle mass ($P_{ac}=109M_{fm}^{1.01}$). If we plot estimated $\dot{V}_{O_{2max}}$ against body mass we find that it scales as $\dot{V}_{O_{2max}}=274M_b^{0.807}$, which is not quite directly proportional to that for wing-beat frequency, where $f_H=5.33M_b^{-0.139}$.

If we plot $\dot{V}_{O_{2max}}$ against flight muscle mass we find that it scales as $\dot{V}_{O_{2max}}=880M_{fm}^{0.837}$, which demonstrates that the relative volume of blood being delivered to the flight muscles declines as bird species scale up in mass. This explains why larger species of birds must develop flight muscles with mixed fibre type compositions. We might hypothesise that blood flow to the muscles should be in proportion to their aerobic or FOG fibre content, with the consequence that the effective proportion of flight muscle actually being recruited during maximum sustainable climbing flights would decline as the bird species increased in mass. If the $\dot{V}_{O_{2max}}$ estimates based on M_h from Bishop (1997) are reasonable and E_{fm} were really a constant then we would predict that P_{ac} per unit FOG muscle mass, or perhaps more accurately per FOG myofibrillar protein mass, would be a constant ($M^{1.0}$) as appears to be the case for 'burst' power output (Marden, 1987; Ellington, 1991; Askew et al., 2001). If the scaling of P_{ac} follows the predictions calculated from Pennycuick's model (Pennycuick, 1989, version 1.1) and the volume of FOG fibres in the flight muscles is proportional to the estimated $\dot{V}_{O_{2max}}$ based on Bishop (1997), then it would be predicted that P_{ac} should scale with respect to FOG myofibrillar protein mass with an exponent of around $M^{1.17}$ or more, which might seem unlikely.

Discussion

In conclusion, there would appear to be insufficient data to completely differentiate between the hypotheses that the 'true' E_{fm} is either a constant, or that it scales with a positive exponent with respect to body mass for smaller species followed by a plateau for the larger species. However, given the extremely simple models used in the current analysis and the uncertainties regarding the maximal climbing rates of the smaller species studied by Hedenström and Ålerstam (1992), there is a close agreement between the expected E_{fm} of around 0.2–0.25 and the overall average calculated value of 0.2–0.27. The E_{fm} values for the larger species are unacceptably high but it could be argued that it is these very species that are most likely to be flying close to their maximal capabilities. Either the heart mass approach underestimates maximal $\dot{V}_{O_{2max}}$ for these species, or the aerodynamic model is overestimating the P_{ac} , or both. It is possible that the values used for M_h are too low or that there is an additional influence of an increase in haemoglobin (Landys-Ciannelli et al., 2002), which would lead to an underestimate of $\dot{V}_{O_{2max}}$. If avian cardiac hypertrophy has the potential to be very rapid, as in the Burmese python *Python molurus* (Andersen et al., 2005), then it may be necessary to sample birds actually migrating in order to accurately assess their relative heart size. It is tempting to assume that the smaller species of passerines were not flying near their maximum capabilities but Hedenström and Ålerstam (1992) point out that both the chaffinch and the siskin were flying forward at quite a fast speed for their body mass. The swift would appear to be the weakest performer overall. While it would seem to be impossible that the larger species could really have such high E_{fm} , it remains possible that the smaller species that are operating with relatively high wing-beat frequencies are suffering a real reduction in E_{fm} , as appears to be the case for hummingbirds (assuming perfect elastic storage of inertial energy). The resolution of these issues is only likely to come from studying species at either extreme of the size range.

Current aerodynamic theories suggest that for birds of similar proportions the cost of flight should scale as $M_b^{1.17}$, and this exponent will be slightly reduced due to the tendency for larger birds to have higher aspect ratio wings (Pennycuick, 1989, 1996). During primarily anaerobic 'burst' activity this scaling exponent for the power required could be partially compensated for by having a larger mass of total myofibrils per unit M_b . This might be done by increasing the proportion of anaerobic fibre types within the flight muscle without increasing the relative M_{fm} per unit M_b . Alternatively, a similar result could be achieved by increasing the total relative M_{fm} . However, as we have seen M_{fm} generally scales independently of M_b so it would appear that the latter strategy is not adopted by larger species of flying animals. Why not?

Ultimately, sustained flight performance is constrained by the performance of the respiratory and cardiovascular system. For birds specialising in prolonged flight it would be wasteful

to have an ability to take-off with a body mass that greatly exceeded its ability to sustain that mass during forward flight (although it might improve take-off speed and, therefore, predator avoidance). The empirical evidence is that $\dot{V}_{O_{2max}}$ scales approximately with $M_h^{0.88 \pm 0.02}$, and that M_h scales approximately as $M_b^{0.92 \pm 0.01}$, with the result that $\dot{V}_{O_{2max}}$ scales with respect to both M_b and M_{fm} with an exponent of approximately $M_b^{0.82 \pm 0.08}$ (Bishop, 1997). Why not increase relative M_h ? If the analysis of Bishop (1997) is broadly accurate, then for a large bird to maintain a similar body mass-specific $\dot{V}_{O_{2max}}$ as that of a smaller bird, M_h must increase with respect to around $M_b^{1.13}$. Eventually, whatever the exact nature of the limiting factors, the upward divergence from direct proportionality might prove to be too costly.

It is interesting that one of the most extreme examples from the M_h data sets of Magnan (1922) and Hartman (1961) is that of the Otidae. If these medium-to-large, savannah-living birds, had flight muscles consisting completely of anaerobic FG fibres (perhaps similar to the Phasianidae), rather than a mosaic of FG and FOG fibres, then they might be capable of a standing take-off but at the cost of only being able to fly for an extremely limited distance and becoming highly vulnerable to cursorial predation. As they are not forest dwelling species like the Phasianidae, the bustard's best strategy is a compromise in which it is able to sustain flight for long enough to cover a sufficient distance as to exceed the give-up time of any potential predators. The only alternative strategy would be to give up flight altogether and to become a fast runner like the ostrich *Struthio camelus*.

Studies of exercising mammals and migratory species of birds have indicated that both the pectoralis and cardiac musculature are dynamic structures that can vary in mass seasonally and in direct response to changing circumstances (Marsh, 1984; Bishop et al., 1996; Lindström et al., 2000; Swaddle and Biewener, 2000). This raises the interesting question as to whether the appropriate response in any given situation, or for a particular species, should be primarily anaerobic or aerobic. Maximal animal flight performance reflects a continuum between species specialised for burst activity, through to species adapted primarily for prolonged activity. Wing morphology can modify, to a certain extent, the power required for flight, but the power available is provided by the wing and cardiac muscles. If a species is adapted for prolonged flight activity then there may be a cost to carrying large amounts of anaerobic muscle fibres, or even excess aerobic fibres that cannot be adequately perfused by the blood supply. Thus, even large species of birds, such as swans, which undertake long distance aerobic flights, appear to have fairly average sized flight muscle masses of between 18–22% (Magnan, 1922; Hartman, 1961). However, even these species have anaerobic FG fibres, which are presumably important in providing extra power during take-off and brief manoeuvres. It would be expected that birds undergoing

migratory fattening before long distance flights should require an hypertrophy of both FG and FOG fibres. It would seem to be logical that these species only acquired sufficient FG fibres to enable them to take-off with a load that is not much greater than that which can then be supported aerobically by the FOG fibres, during subsequent prolonged flights.

One way of reducing the requirement to have large amounts of excess FG fibres is to gain speed by running before taking off, and a number of species of birds that are capable of prolonged types of flapping flight run across the surface of the ground (or water) before becoming airborne. Thus, the flight muscles of most extant species of birds that are capable of prolonged flight are likely to reflect the compromise between the 'burst' power required for take-off and the aerobic power required to sustain flight. The 'running take-off' of some large bird species, such as swans, could be viewed as a behavioural adaptation to minimise the mass of the additional FG fibres required for take-off, thus optimising the requirement for \dot{V}_{O_2} and the number of FOG fibres in order to prolong flight activity and/or improve aerobic load-lifting capacity. Likewise, the relatively small flight muscle mass of diving species, such as the red-throated diver *Gavia stellata*, could be viewed as being the result of selection for enhanced underwater swimming performance. Running during take-off for this species could then be viewed as a behavioural adaptation for improved diving efficiency.

List of symbols and abbreviations

BMR	basal metabolic rate
Ca_{O_2}	arterial oxygen content
$C_{D,par}$	body drag coefficient
$C\bar{V}_{O_2}$	mixed venous oxygen content
E_{fm}	flight muscle efficiency
f_H	wing beat frequency
FG	fast glycolytic muscle fibres
FOG	fast oxidative glycolytic muscle fibres
M_b	body mass
M_{fm}	flight muscle mass
M_h	heart mass
P_{ac}	mechanical power continuously available
P_{mech}	mechanical power
P_{met}	metabolic power
$P_{met,fm}$	metabolic power of flight muscles
P_{min}	mechanical power at minimum flight speed
\dot{Q}	cardiac output
\dot{V}_{O_2}	rate of oxygen consumption
$\dot{V}_{O_{2max}}$	maximum rate of oxygen consumption

I would like to thank the two anonymous referees for their helpful comments.

Appendix A. Data for the 15 species of birds studied by Hedenström and Alerstam (1992) as the birds performed steep climbing flights when migrating over Sweden

Species	M_h (% M_b)	M_{fm} (% M_b)	Sustainable	P_{ac} (W) ^a	P_{ac} (W) ^b
			$P_{met,fm}$ (W)		
Mute swan <i>Cygnus olor</i>	1.13	21.8	649	274	243
Greylag goose <i>Anser anser</i>	0.92	27.1	206	80	74
Eider <i>Somateria mollissima</i>	1.1	25.5	132	55	51
Red-throated diver <i>Gavia stellata</i>	0.92	16.0	87.7	34	29
Brent goose <i>Branta bernicla</i>	1.07	24.7	101	32	28
Curlew <i>Numenius arquata</i>	1.22	25.8	70.2	23	24
Wigeon <i>Anas penelope</i>	0.93	26.2	50.1	26	25
Wood pigeon <i>Columba palumbus</i>	1.37	35.8	55.5	14	15
Oystercatcher <i>Haematopus ostralegus</i>	1.16	22.3	46.8	13	12
Arctic tern <i>Sterna paradisaea</i>	1.24	22.8	13.5	2.5	2.4
Song thrush <i>Turdus philomelos</i>	1.06	31.1	6.76	2.0	2.1
Dunlin <i>Calidris alpina</i>	1.52	26.3	7.4	1.8	1.8
Swift <i>Apus apus</i>	1.5	26.6	6.09	0.83	0.76
Chaffinch <i>Fringilla coelebs</i>	1.52	32.0	3.57	0.6	0.63
Siskin <i>Carduelis spinus</i>	1.94	28.6	2.5	0.4	0.42

^aHedenstrom and Alerstam (1992).

^bThis study, based on Pennycuick (1989, v1.1).

Appendix B. Ratio of estimated maximum aerobic P_{ac} available / P_{min} required for forward flapping flight

>3		1–3 ($M_b > 2$ kg)	<1
1. Canary	23. Linnet	36. Common cormorant	51. Green jay
2. Citril finch	24. Lesser spotted woodpecker	37. Gannet	52. Water rail
3. Siskin	25. Calidris spp.	38. Bean goose	53. Common pheasant
4. Winchat	26. Dunlin	39. Greylag goose	54. Little grebe
5. Chaffinch	27. Jack snipe	40. Bateleur eagle	55. Moorhen
6. Greenfinch	28. Dotterel	41. Bonelli's eagle	56. Hazel grouse
7. Storm petrel	29. European nightjar	42. White stork	57. Chough
8. Swallow	30. Turnstone	43. Whooper swan	58. Rock ptarmigan
9. Crag martin	31. Golden plover	44. Golden eagle	59. Grey partridge
10. House martin	32. Ruff	45. Common crane	60. Red-legged partridge
11. Swift	33. Black-tailed godwit	46. Lammergeier	61. Common coot
12. Golden oriole	34. Black-headed gull	47. Marabou stork	62. Willow grouse
13. Knot	35. Common gull	48. Griffon vulture	63. Partridge spp.
14. Hobby		49. European great bustard	64. Red-winged tinamou
15. Bar-tailed godwit		50. Wandering albatross	65. Razorbill
16. Montagu's harrier			66. Black grouse (f)
17. Common tern			67. Black grouse (m)
18. Red kite			68. Guillemot
19. Phylloscopus warbler spp.			69. Mallard
20. Pied flycatcher			70. Eagle owl
21. Common redstart			71. Capercaillie (f)
22. Wallcreeper			72. Grey eagle-buzzard
			73. Capercaillie (m)

Numbers of species relate to data in Fig. 3.

f, female; m, male.

Based on data taken from Magnan (1922).

References

- Andersen, J. B., Rourke, B. C., Caiozzo, V. J., Bennett, A. F. and Hicks, J. W. (2005). Postprandial cardiac hypertrophy in pythons. *Nature* **434**, 37-38.
- Askew, G. N., Marsh, R. L. and 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.
- Bennett, P. M. and Harvey, P. H. (1987). Active and resting metabolism in birds: allometry, phylogeny and ecology. *J. Zool. Lond.* **213**, 327-363.
- Bishop, C. M. (1997). Heart mass and the maximum cardiac output of birds and mammals: Implications for estimating the maximum aerobic power input of flying animals. *Phil. Trans. R. Soc. Lond. B* **352**, 447-456.
- Bishop, C. M. (1999). The maximum oxygen consumption and aerobic scope of birds and mammals: getting to the heart of the matter. *Proc. R. Soc. Lond. B* **266**, 2275-2281.
- Bishop, C. M. and Butler, P. J. (1995). Physiological modelling of oxygen consumption in birds during flight. *J. Exp. Biol.* **198**, 2153-2163.
- Bishop, C. M., Butler, P. J., El Haj, A. J., Egginton, S. and Loonen, M. J. J. E. (1996). The morphological development of the locomotor and cardiac muscles of the migratory barnacle goose (*Branta leucopsis*). *J. Zool.* **239**, 1-15.
- Bishop, C. M., Butler, P. J., El Haj, A. J. and Egginton, S. (1998). Comparative development of captive and migratory populations of the barnacle goose. *Physiol. Zool.* **71**, 198-207.
- Bishop, C. M., Ward, S., Woakes, A. J. and Butler, P. J. (2002). The energetics of barnacle geese (*Branta leucopsis*) flying in captive and wild conditions. *Comp. Biochem. Physiol.* **133**, 225-237.
- Butler, P. J. (1991). Exercise in birds. *J. Exp. Biol.* **160**, 233-262.
- Chai, P. and Dudley, R. (1995). Limits to vertebrate locomotor energetics suggested by hummingbirds hovering in heliox. *Nature* **377**, 722-725.
- Crile, G. and Quiring, D. P. (1940). A record of the body weight and certain organ and gland-weights of 3690 animals. *Ohio J. Sci.* **XL**, 219-259.
- Dial, K. P. and Biewener, A. A. (1993). Pectoralis-muscle force and power output during different modes of flight in pigeons (*Columba livia*). *J. Exp. Biol.* **176**, 31-54.
- Driedzic, W. R., Crowe, H. L., Hicklin, P. W. and Sephton, D. H. (1993). Adaptations in pectoralis muscle, heart mass, and energy metabolism during premigratory fattening in semipalmated sandpipers (*Calidris pusilla*). *Can. J. Zool.* **71**, 1602-1608.
- Ellerby, D. J., Cleary, M., Marsh, R. L. and Buchanan, C. I. (2003). Measurement of maximum oxygen consumption in guinea fowl *Numida meleagris* indicates that birds and mammals display a similar diversity of aerobic scopes during running. *Physiol. Biochem. Zool.* **76**, 695-703.
- Ellington, C. P. (1991). Limitations on animal flight performance. *J. Exp. Biol.* **160**, 71-91.
- Fry, C. H. and Ferguson-Lees, I. F. (1972). Flight muscle hypertrophy and ecophysiological variation of yellow wagtail (*Motacilla flava*) races at Lake Chad. *J. Zool. Lond.* **167**, 293-306.
- Gudmundsson, G. A., Benvenuti, S., Alerstam, T., Papi, F., Lillendahl, K. and Åkesson, S. (1995). Examining the limits of flight and orientation performance: satellite tracking of brent geese migrating across the Greenland ice-cap. *Proc. R. Soc. Lond. B* **261**, 73-79.
- Hammond, H. K., White, F. C., Bhargava, V. and Shabetai, R. (1992). Heart size and maximal cardiac output are limited by the pericardium. *Am. J. Physiol.* **263**, H1675-H1681.
- Hartman, F. A. (1961). Locomotor mechanisms of birds. *Smithson. Misc. Collns* **143**, 1-91.
- Hedenström, A. and Alerstam, T. (1992). Climbing performance of migrating birds as a basis for estimating limits for fuel-carrying capacity and muscle work. *J. Exp. Biol.* **164**, 19-38.
- Hedenström, A. and Liechti, L. (2001). Field estimates of body drag coefficient on the basis of dives in passerine birds. *J. Exp. Biol.* **204**, 1167-1175.
- Hedrick, T. L., Usherwood, J. R. and 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**, 1689-1720.
- Hickson, R. C., Galassi, T. M. and Dougherty, K. A. (1983). Repeated development and regression of exercise-induced cardiac hypertrophy in rats. *J. Appl. Physiol.* **54**, 794-797.
- Hudson, D. M. and Bernstein, M. H. (1983). Gas exchange and energy cost of flight in the white-necked raven, *Corvus cryptoleucus*. *J. Exp. Biol.* **103**, 121-130.
- Koteja, P. (1987). On the relation between basal and maximum metabolic rate in mammals. *Comp. Biochem. Physiol.* **87**, 205-208.
- Kvist, A., Lindström, Å., Green, M., Piersma, T. and Visser, G. H. (2001). Carrying large fuel loads during sustained bird flight is cheaper than expected. *Nature* **413**, 730-732.
- Landys-Ciannelli, M. M., Jukema, J. and Piersma, T. (2002). Blood parameter changes during stopover in a long-distance migratory shorebird, the bar-tailed godwit *Limosa lapponica taymyrensis*. *J. Avian Biol.* **33**, 451-455.
- Lasiewski, R. C. and Calder, W. A. (1971). A preliminary allometric analysis of respiratory variables in resting birds. *Respir. Physiol.* **11**, 152-166.
- 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.
- Lindström, Å., Kvist, A., Piersma, T., Dekinga, A. and Dietz, M. W. (2000). Avian pectoral muscle size rapidly tracks body mass changes during flight, fasting and fuelling. *J. Exp. Biol.* **203**, 913-919.
- Magnan, A. (1922). Les caractéristiques des oiseaux suivant le mode de vol. *Ann. Sci. Nat.*, ser. **10**, 5, 125-334.
- Marden, J. H. (1987). Maximum lift production during takeoff in flying animals. *J. Exp. Biol.* **130**, 235-258.
- Marden, J. H. (1990). Maximum load-lifting and induced power output of Harris' hawks are general functions of flight muscle mass. *J. Exp. Biol.* **149**, 511-514.
- Marden, J. H. (1994). From damselflies to pterosaurs: how burst and sustainable flight performance scale with size. *Am. J. Physiol.* **266**, R1077-R1084.
- Marsh, R. L. (1984). Adaptations of the gray catbird *Dumetella carolinensis* to long-distance migration: flight muscle hypertrophy associated with elevated body mass. *Physiol. Zool.* **57**, 105-117.
- Masman, D. and Klaassen, M. (1987). Energy-expenditure during free flight in trained and free-living Eurasian kestrels (*Falco tinnunculus*). *Auk* **104**, 603-616.
- Parker, H. and Holm, H. (1990). Patterns of nutrient and energy expenditure in female common eiders nesting in the high arctic. *Auk* **107**, 660-668.
- Pennycuik, C. J. (1969). The mechanics of bird migration. *Ibis* **111**, 525-556.
- Pennycuik, C. J. (1972). *Animal flight. The Institute of Biology's Studies in Biology no. 33*. London: Edward Arnold (Publishers) Limited.
- Pennycuik, C. J. (1975). Mechanics of flight. In *Avian Biology*, vol. 5 (ed. D. S. Farner and J. R. King), pp. 1-75. New York: Academic Press.
- Pennycuik, C. J. (1982). The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. *Phil. Trans. R. Soc. B* **300**, 75-106.
- Pennycuik, C. J. (1989). *Bird Flight Performance*. Oxford: Oxford University Press.
- Pennycuik, C. J. (1992). *Newton Rules Biology: A Physical Approach to Biological Problems*. Oxford: Oxford University Press.
- Pennycuik, C. J. (1996). Stress and strain in the flight muscles as constraints on the evolution of flying animals. *J. Biomech.* **29**, 577-581.
- Pennycuik, C. J., Fuller, M. R. and McAllister, L. (1989). Climbing performance of Harris' hawks (*Parabuteo unicinctus*) with added load: implications for muscle mechanics and for radiotracking. *J. Exp. Biol.* **142**, 17-29.
- Pennycuik, C. J., Fuller, M. R., Oar, J. J. and Kirkpatrick, S. J. (1994). Falcon versus grouse - flight adaptations of a predator and its prey. *J. Avian Biol.* **25**, 39-49.
- Pennycuik, C. J., Klaassen, M., Kvist, A. and Lindström, Å. (1996). Wingbeat frequency and the body drag anomaly: wind-tunnel observations on a thrush nightingale (*Luscinia luscinia*) and a teal (*Anas crecca*). *J. Exp. Biol.* **199**, 2757-2765.
- Pennycuik, C. J. and Rezende, M. A. (1984). The specific power output of aerobic muscle, related to the power density of mitochondria. *J. Exp. Biol.* **108**, 377-392.
- Piersma, T., Zwarts, L. and Bruggemann, J. H. (1990). Behavioural aspects of the departure of waders before long-distance flights: flocking, vocalizations, flight paths and diurnal timing. *Ardea* **78**, 157-184.
- Prinzinger, R. and Hansler, I. (1980). Metabolism-weight relationship in some small non-passerine birds. *Experientia* **37**, 1299-1300.
- Rall, J. A. (1985). Energetic aspects of skeletal muscle contraction: Implications of fiber types. *Exer. Sport Sci. Rev.* **13**, 33-74.
- Rayner, J. M. V. (1979a). A new approach to animal flight mechanics. *J. Exp. Biol.* **80**, 17-54.

- Rayner, J. M. V.** (1979b). A vortex theory of animal flight. Part 2. The forward flight of birds. *J. Fluid Mech.* **91**, 731-763.
- Rayner, J. M. V.** (1988). Form and function in avian flight. *Curr. Orn.* **5**, 1-77.
- Rayner, J. M. V.** (1990). The mechanics of flight and bird migration performance. In *Bird Migration: Physiology and Ecophysiology* (ed. E. Gwinner), pp. 283-299. Berlin: Springer-Verlag.
- Rayner, J. M. V.** (1999). Estimating power curves of flying vertebrates. *J. Exp. Biol.* **202**, 3449-3461.
- Reynolds, P. S. and Lee, R. M.** (1996). Phylogenetic analysis of avian energetics: Passerines and nonpasserines do not differ. *Am. Nat.* **147**, 735-759.
- Rome, L. C.** (1994). The mechanical design of the muscular system. *Adv. Vet. Sci. Comp. Med.* **38A**, 125-179.
- Rosser, B. W. C. and George, J. C.** (1986). The avian pectoralis: histochemical characterization and distribution of muscle fiber types. *Can. J. Zool.* **64**, 1174-1185.
- Spedding, G. R.** (1994). On the significance of unsteady effects in the aerodynamic performance of flying animals. *Cont. Math.* **141**, 401-419.
- Stray-Gundersen, J., Musch, T. I., Haidet, G. C., Swain, D. P., Ordway, G. A. and Mitchell, J. H.** (1986). The effect of pericardiectomy on maximal oxygen consumption and maximal cardiac output in untrained dogs. *Circ. Res.* **58**, 523-530.
- Swaddle, J. P. and Biewener, A. A.** (2000). Exercise and reduced muscle mass in starlings. *Nature* **406**, 585-586.
- Taylor, C. R.** (1994). Relating mechanics and energetics during exercise. *Adv. Vet. Sci. Comp. Med.* **38A**, 181-215.
- Tobalske, B. W., Hedrick, D. L., Dial, K. P. and Biewener, A. A.** (2003). Comparative power curves in bird flight. *Nature* **421**, 363-366.
- Tucker, V. A.** (1968). Respiratory exchange and evaporative water loss in the flying budgerigar. *J. Exp. Biol.* **48**, 67-87.
- Tucker, V. A.** (1973). Bird metabolism during flight: evaluation of a theory. *J. Exp. Biol.* **58**, 689-709.
- Van den Berg, C. and 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.
- Ward, S., Moller, U., Rayner, J. M. V., Jackson, D. M., Bilo, 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.
- Ward, S., Moller, U., Rayner, J. M. V., Jackson, D. M., Nachtigall, W. and Speakman, J. R.** (2004). Metabolic power of European starlings *Sturnus vulgaris* during flight in a wind tunnel, estimated from heat transfer modelling, doubly labelled water and mask respirometry. *J. Exp. Biol.* **207**, 4291-4298.
- Weibel, E. R., Taylor, C. and Hoppeler, H.** (1991). The concept of symmorphosis: A testable hypothesis of structure-function relationship. *Proc. Natl. Acad. Sci. USA* **88**, 10357-10361.
- Wells, D. J.** (1993). Muscle performance in hovering hummingbirds. *J. Exp. Biol.* **178**, 39-57.
- Westerterp, K. and Drent, R.** (1985). Energetic costs and energy-saving mechanisms in parental care of free-living passerine birds as determined by the D₂O method. *Acta XVIII int. Ornithol. Congr.* **1**, 392-398.