

PHYSIOLOGICAL MODELLING OF OXYGEN CONSUMPTION IN BIRDS DURING FLIGHT

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Summary

This study combines data on changes in cardiovascular variables with body mass (M_b) and with exercise intensity to model the oxygen supply available to birds during flight. Its main purpose is to provide a framework for identifying the factors involved in limiting aerobic power input to birds during flight and to suggest which cardiovascular variables are the most likely to have been influenced by natural selection when considering both allometric and adaptive variation.

It is argued that natural selection has acted on heart rate (f_H) and cardiac stroke volume (V_S), so that the difference in the arteriovenous oxygen content ($Ca_{O_2} - C\bar{v}_{O_2}$) in birds, both at rest and during flight, is independent of M_b . Therefore, the M_b exponent for oxygen consumption (\dot{V}_{O_2}) during flight can be estimated from measurements of heart rate and stroke volume. Stroke volume is likely to be directly proportional to heart mass (M_h) and, using empirical data, values for the M_b coefficients and exponents of various cardiovascular variables are estimated. It is concluded that, as found for mammals, f_H is the main adaptive variable when considering allometric variation, although M_h also shows a slight scaling effect. Relative M_h is likely to be the most important when considering adaptive specialisations.

The Fick equation may be represented as:

$$(\dot{V}_{O_2})M_b^z = (f_H)M_b^w \times (V_S)M_b^x \times (Ca_{O_2} - C\bar{v}_{O_2})M_b^y,$$

where w , x , y , z are the body mass exponents for each variable and the terms in parentheses represent the M_b coefficients. Utilising this formula and data from the literature, the scaling of minimum \dot{V}_{O_2} during flight for

bird species with a 'high aerobic capacity' (excluding hummingbirds) is calculated to be:

$$166M_b^{0.77 \pm 0.09} = 574M_b^{-0.19 \pm 0.02} \times 3.48M_b^{0.96 \pm 0.02} \times 0.083M_b^{0.00 \pm 0.05},$$

and for hummingbirds (considered separately owing to their unique wing kinematics) it is:

$$314M_b^{0.90 \pm 0.22} = 617M_b^{-0.10 \pm 0.06} \times 6.13M_b^{1.00 \pm 0.11} \times 0.083M_b^{0.00 \pm 0.05}.$$

These results are largely dependent on the cardiovascular values obtained from pigeons flying near to the minimum power speed of 10 ms^{-1} , but would appear to provide realistic values. Both the measured and the estimated \dot{V}_{O_2} for hummingbirds appear to scale with a larger M_b exponent than that for all other birds, and it is suggested that this is as a result of the larger M_b exponent for flight muscle mass as the larger species of hummingbirds try to maintain hovering performance. It is proposed that estimated \dot{V}_{O_2} for birds during flight, which is based on M_h in combination with estimates of f_H and $Ca_{O_2} - C\bar{v}_{O_2}$, gives an indirect measure of relative aerobic power input and, when corrected for the estimated scaling influences of the mechano-chemical conversion efficiency and lift generation with respect to M_b , may be a useful indicator of the relative capacity of the muscle to sustain power output and lift production during flight.

Key words: oxygen consumption, birds, flight, scaling, heart rate, stroke volume.

Introduction

The energy cost of birds during flight is usually discussed either in terms of the mechanical power output or of the biochemical power input required for gliding or flapping flight. An indirect estimate of the aerobic power input can be calculated from measurements of the amount of oxygen consumed (\dot{V}_{O_2}) while the bird flies in a wind tunnel (Tucker, 1968*b*; Bernstein *et al.* 1973; Butler *et al.* 1977; Hudson and

Bernstein, 1983), although the largest bird which has been flown in a wind tunnel in order to measure \dot{V}_{O_2} is a 0.48 kg white-necked raven (Hudson and Bernstein, 1983).

Allometric scaling of power output with body mass (M_b) is based largely on various modifications of aerodynamic theory (Pennycuik, 1968; Tucker, 1973; Rayner, 1979), and less attention has been focused on the theoretical physiological

limitations of the cardiovascular system to provide oxygen to the locomotor muscles (Tucker, 1968a; Berger *et al.* 1970; Berger and Hart, 1974; Bernstein, 1987). Weibel *et al.* (1991) recently showed that the concept of symmorphosis (i.e. that structural design should be optimised to match functional demand) is valid in mammals for internal compartments of the respiratory system, i.e. variables of the blood, heart, capillaries and mitochondria. Given the functional similarities of these variables in mammals with those in birds, it is likely that natural selection will likewise act to optimise the supply of oxygen so that it matches the species-specific demand of the working tissues of birds. Therefore, at the species level, it is necessary only to quantify the variables involved in the supply of oxygen to the muscles to analyse the allometric scaling of oxygen consumption in birds.

This study analysed data on the scaling of cardiovascular variables with M_b , in combination with data on changes in physiological variables during exercise, to estimate the minimum \dot{V}_{O_2} of birds during flapping flight. Hummingbirds are considered separately because of their unique wing kinematics (Norberg, 1990).

Methodology

The general allometric relationship between \dot{V}_{O_2} and M_b is represented as:

$$\dot{V}_{O_2} = aM_b^b, \quad (1)$$

where M_b is body mass, a is the body mass coefficient and b is the body mass exponent.

The role of the various components of the circulatory system in providing oxygen to the muscles can be described by Fick's formula:

$$\dot{V}_{O_2} = fH \times Vs \times (Ca_{O_2} - C\bar{v}_{O_2}), \quad (2)$$

where \dot{V}_{O_2} is oxygen consumption in ml min^{-1} , fH is heart rate in beats min^{-1} , Vs is the stroke volume of the heart in ml and $Ca_{O_2} - C\bar{v}_{O_2}$ is the difference between the fractional volume of the oxygen contents of arterial and mixed venous blood in ml of oxygen per ml of blood (ml ml^{-1}).

Each variable in the Fick equation may scale independently with body mass, and the sum of the body mass exponents, for each variable on the right-hand side of the equation, will be equal to the body mass exponent for \dot{V}_{O_2} . This relationship can be represented as:

$$(\dot{V}_{O_2})M_b^z = (fH)M_b^w \times (Vs)M_b^x \times (Ca_{O_2} - C\bar{v}_{O_2})M_b^y, \quad (3)$$

where w , x , y and z are the body mass exponents for each variable and the terms in parentheses represent the body mass coefficients.

The body mass exponents can be estimated from data available in the literature, although results concerning heart rate (fH) have been obtained from disparate sources. All calculations of allometric exponents for M_b and flight muscle mass (M_{fm}) were estimated by performing reduced major axis regressions (Sokal and Rohlf, 1981; Rayner, 1985), except for the relationship between Vs and heart muscle mass (M_h), and

the allometric equations for \dot{V}_{O_2} of birds flown in wind tunnels or \dot{V}_{O_2} of hummingbirds while hovering, which were obtained from Grubb (1983a) and Butler (1991), respectively, and which were calculated using least-squares regression.

Analysis

Calculation of body mass exponents

$(Ca_{O_2} - C\bar{v}_{O_2})M_b^y$

Birds at rest. Grubb (1983a) investigated the allometric relationships of a number of cardiovascular functions of nine species of non-passerine birds at rest: $\dot{V}_{O_2} \propto M_b^{0.67}$, $fH \propto M_b^{-0.28}$ and $Vs \propto M_b^{0.97}$. These empirical exponents can be substituted into the Fick equation to obtain an estimate of the body mass exponent for $Ca_{O_2} - C\bar{v}_{O_2}$:

$$(\dot{V}_{O_2})M_b^{0.67} = (fH)M_b^{-0.28} \times (Vs)M_b^{0.97} \times (Ca_{O_2} - C\bar{v}_{O_2})M_b^y. \quad (4)$$

Therefore, $y = 0.67 + 0.28 - 0.97 = -0.02$.

Grubb (1983a) also measured the heart masses (M_h) of the nine species of birds and showed that Vs was almost directly proportional to heart mass, $Vs \propto M_h^{1.05}$.

Lasiewski and Calder (1971) also calculated allometric relationships for a number of cardiovascular variables in birds at rest. These authors found that $\dot{V}_{O_2} \propto M_b^{0.72}$, $fH \propto M_b^{-0.23}$ and that $M_h \propto M_b^{0.91}$. Assuming $Vs \propto M_h^{1.05}$ (Grubb, 1983a), then $Vs \propto M_b^{0.96}$. Again substituting these exponents into the Fick equation:

$$(\dot{V}_{O_2})M_b^{0.72} = (fH)M_b^{-0.23} \times (Vs)M_b^{0.96} \times (Ca_{O_2} - C\bar{v}_{O_2})M_b^y. \quad (5)$$

Therefore, $y = 0.72 + 0.23 - 0.96 = -0.01$.

As it is assumed that it is oxygen supply to the muscles that is the critical parameter in determining \dot{V}_{O_2} , then it seems likely that the exponent y should be related to Ca_{O_2} as well as to $Ca_{O_2} - C\bar{v}_{O_2}$. The effect of raising the value of Ca_{O_2} will be to increase the potential $Ca_{O_2} - C\bar{v}_{O_2}$, assuming that $C\bar{v}_{O_2}$ remains constant. Burke (1966) found that, for 25 species of birds, $Ca_{O_2} \propto M_b^{0.05}$, i.e. that $y = 0.05$, although he did not list the species involved in this analysis. The main structural determinant of Ca_{O_2} is likely to be haemoglobin concentration, but there are very few measurements for birds from which to calculate an allometric regression. An indirect estimate for the scaling of Ca_{O_2} may be obtained by measuring haematocrit (Hct). Data shown in Fig. 1 for haemoglobin concentration and Hct in birds (Carey and Morton, 1976; Pages and Planas, 1983; Viscor and Fuster, 1987; Johansen *et al.* 1987) show that there is a tendency for Hct to decrease with increasing body mass ($\text{Hct} = 61M_b^{-0.07 \pm 0.01}$, $r^2 = 0.31$, $P < 0.001$, mean $46.3 \pm 0.6\%$, range 30–59%). Data for hummingbirds give a mean of $56.6 \pm 1.2\%$, range 45–62%. However, although hummingbirds exhibit a very high Hct, they also have very small erythrocytes and, thus, a low red blood cell haemoglobin concentration (Carey and Morton, 1976; Johansen *et al.* 1987).

Birds during flight. Although $Ca_{O_2} - C\bar{v}_{O_2}$ will increase during exercise, the studies by Grubb (1982, 1983b) give little

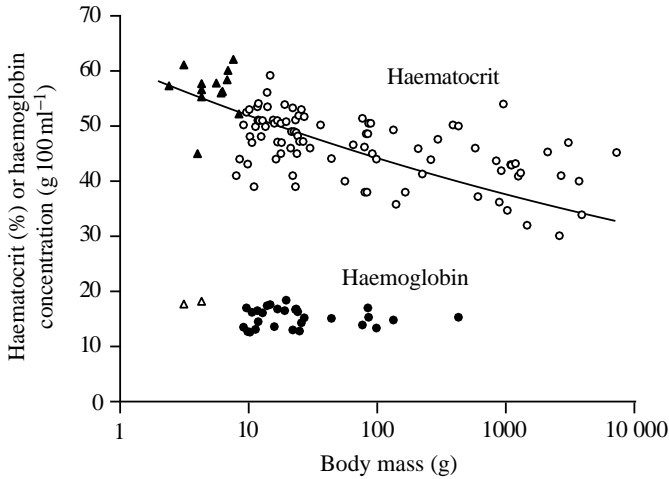


Fig. 1. Haematocrit (%) and haemoglobin concentration ($\text{g } 100 \text{ ml}^{-1}$) plotted against body mass (g). Hummingbirds: haematocrit, filled triangles; haemoglobin concentration, open triangles. All other species: haematocrit, open circles, solid line; haemoglobin concentration, filled circles. Haemoglobin and haematocrit data are taken from Carey and Morton (1976), Pages and Planas (1983), Viscor and Fuster (1987) and Johansen *et al.* (1987).

evidence for a significant effect of body mass on $\text{CaO}_2 - \text{C}\bar{\text{v}}\text{O}_2$ for three species of birds (pigeon, duck and emu) running near maximum speeds. Despite a large difference in body mass, from 0.42 to 37 kg, $\text{CaO}_2 - \text{C}\bar{\text{v}}\text{O}_2$ was between 0.08 and 0.09 ml ml^{-1} in all species. The study of Burke (1966) indicates that maximum CaO_2 may be slightly higher in larger birds, but is contradicted by the physiological measurements of $\text{CaO}_2 - \text{C}\bar{\text{v}}\text{O}_2$ and the values for Hct (Fig. 1). Dimensional or proportionality considerations suggest that there is no reason to expect that body mass should have an important influence on CaO_2 (Schmidt-Nielsen, 1984). The above studies indicate that the M_b exponent y (equation 3) should lie between -0.07 and $+0.05$ and, given the statistical uncertainty involved in all these estimates, for the purposes of this analysis there may be little error in assuming that $\text{CaO}_2 - \text{C}\bar{\text{v}}\text{O}_2$ is independent of M_b , i.e. $M_b^{0.00 \pm 0.05}$. Therefore, it is suggested that natural selection will act on f_H and V_s in allometric variation to maintain $\text{CaO}_2 - \text{C}\bar{\text{v}}\text{O}_2$ at a relatively constant interspecies value during cruising flight. Thus, the body mass exponent for $\dot{V}\text{O}_2$ during flight should be very similar to the body mass exponent for cardiac output ($\dot{V}b$), i.e. the sum of the body mass exponents for f_H and V_s :

$$(\dot{V}\text{O}_2)M_b^z = (\dot{V}b)M_b^{w+x} \times (\text{CaO}_2 - \text{C}\bar{\text{v}}\text{O}_2)M_b^{0.00 \pm 0.05}. \quad (6)$$

$(V_s)M_b^x$

V_s for animals at rest scales in almost direct proportion to heart mass (M_h) both for birds (Grubb, 1983a) and mammals (Holt *et al.* 1968). In addition, it has been reported that, in mammals running at $\dot{V}\text{O}_{2\text{max}}$, V_s is directly proportional to heart mass (Weibel *et al.* 1991). Theoretical dimensional arguments support the assumption that $V_s \propto M_h^{1.00}$ (Schmidt-Nielsen, 1984; Åstrand and Rodahl, 1986). Therefore, it is suggested

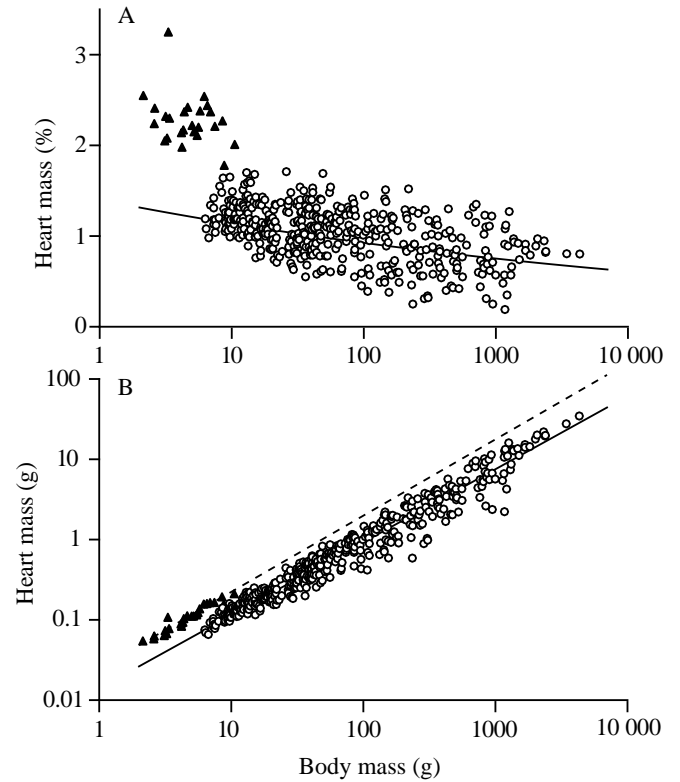


Fig. 2. (A) Heart mass (as a percentage of body mass) and (B) heart mass (g) plotted against body mass (g) for 488 species of birds, including 25 species of hummingbirds. Hummingbirds: filled triangles, dashed line; all other species: open circles, solid line. Data are taken from Hartman (1961) and Bethke and Thomas (1988).

that the heart mass exponent of stroke volume in birds during flight should be similar to that for birds at rest, i.e. $V_s \propto M_h^{1.05}$. However, the absolute value for V_s during flight may be greater than that at rest (see below). Using available heart mass data from Hartman (1961) and Bethke and Thomas (1988) for 463 species of birds (Fig. 2), heart mass (g) was calculated to scale with respect to body mass (g) as:

$$M_h = 0.014M_b^{0.91 \pm 0.02} \quad (r^2 = 0.96, P < 0.001), \quad (7)$$

Therefore, $V_s \propto M_b^{0.96 \pm 0.02}$.

Data for 25 species of hummingbirds (Hartman, 1961) gave:

$$M_h = 0.025M_b^{0.95 \pm 0.11} \quad (r^2 = 0.93, P < 0.001). \quad (8)$$

Thus, $V_s \propto M_b^{1.00 \pm 0.11}$.

$(f_H)M_b^w$

Data for heart rate in flying birds (Berger *et al.* 1970, 1979; Aulie, 1971; Butler and Woakes, 1980; Keskpaik and Leht, 1983; P. J. Butler, A. J. Woakes and R. M. Bevan, unpublished results for Canada goose and blue-eyed shag) for 42 different species (Fig. 3) gives an allometric relationship of:

$$f_H = 480M_b^{-0.19 \pm 0.02} \quad (r^2 = 0.85, P < 0.001), \quad (9)$$

showing that f_H during flight declines as body mass increases.

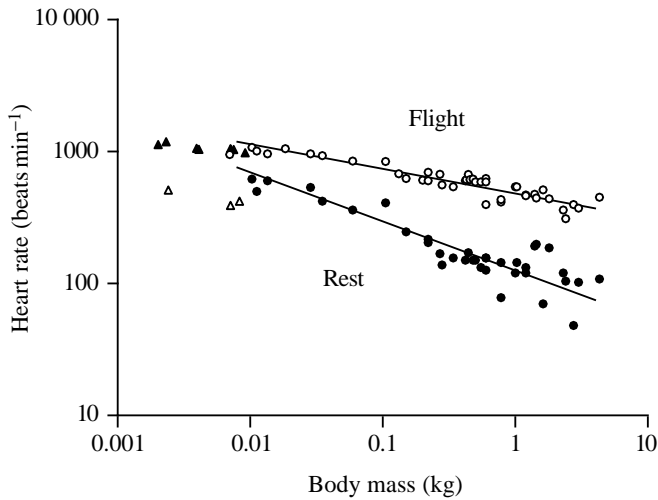


Fig. 3. Heart rate (beats min^{-1}) plotted against body mass (kg) for 49 species of birds, including seven species of hummingbirds at rest (open triangles) and during flight (filled triangles). All other species at rest (filled circles; lower solid line) and during flight (open circles; upper solid line). Data are taken from Berger *et al.* (1970, 1979), Aulie (1971), Butler and Woakes (1980), Keskpaik and Leht (1983) and P. J. Butler, A. J. Woakes, R. M. Bevan and J. E. P. W. Bicudo, unpublished results.

Of the species included in this analysis, there are also data available for f_H from 36 species while at rest (Fig. 3):

$$f_H = 125M_b^{-0.37 \pm 0.06} \quad (r^2 = 0.79, P < 0.001). \quad (10)$$

One of the most important aspects of this result is not so much the exact value of the body mass exponents for f_H but the fact that the two slopes are highly significantly different (Students' *t*-test of slopes, $P < 0.001$), with a shallower slope than that for birds at rest.

Therefore, by addition of the body mass exponents for f_H , V_S and $Ca_{O_2} - C\bar{v}_{O_2}$, it is estimated that the body mass exponent for \dot{V}_{O_2} in birds during flight is:

$$(\dot{V}_{O_2})M_b^{0.77 \pm 0.09} = (f_H)M_b^{-0.19 \pm 0.02} \times (V_S)M_b^{0.96 \pm 0.02} \times (Ca_{O_2} - C\bar{v}_{O_2})M_b^{0.00 \pm 0.05}. \quad (11)$$

Data on f_H for seven species of hummingbirds during flight (Berger *et al.* 1979; J. E. P. W. Bicudo, unpublished data) give:

$$f_H = 617M_b^{-0.10 \pm 0.06} \quad (r^2 = 0.77, P < 0.01). \quad (12)$$

The value of f_H from an eighth species was omitted as it was divergent from the trend shown by the other seven species and there was only a single measurement available. For hummingbirds during flight, therefore:

$$(\dot{V}_{O_2})M_b^{0.90 \pm 0.22} = (f_H)M_b^{-0.10 \pm 0.06} \times (V_S)M_b^{1.00 \pm 0.11} \times (Ca_{O_2} - C\bar{v}_{O_2})M_b^{0.00 \pm 0.05}. \quad (13)$$

Thus, values for the body mass exponents w , x , y and z have now been estimated for birds during flight. Using physiological measurements from studies on pigeons at rest and during

exercise, the body mass coefficients can be estimated for the cardiovascular variables in equation 11.

The pigeon Columba livia

The only study to calculate all four variables of the Fick equation in a bird during flight is that of Butler *et al.* (1977) on the pigeon *Columba livia*. This study showed that there was only a slight increase in V_S between pigeons at rest and during flight, in contrast to results from pigeons while running, which did show an increase in V_S compared with values at rest (Grubb, 1982). The data for pigeons at rest in these two studies are compared in Table 1, which also gives values obtained from pigeons during flight. The only significant difference between the two studies is in their values for \dot{V}_{O_2} at rest (in both studies, V_S was calculated from the measurement of the other three variables). Butler *et al.* (1977) argued that they were unable to use their measured value of \dot{V}_{O_2} for pigeons at rest (8.97 ml min^{-1} , taken from uncannulated pigeons with an f_H of 115 beats min^{-1}) because, when cannulated, the f_H of the birds at rest had been 171 beats min^{-1} . Therefore, in order to calculate the V_S of pigeons at rest, they substituted a value of 11.3 ml min^{-1} for \dot{V}_{O_2} , taken from a previous study (Butler, 1970) where the birds had a similarly high f_H . However, there is now evidence to indicate that, while cannulation of an artery in birds can cause a large increase in f_H , it may have almost no effect on \dot{V}_{O_2} (Woakes and Butler, 1986). Therefore, Butler *et al.* (1977) may have been over cautious in substituting a different value for \dot{V}_{O_2} in the pigeons at rest. Using the resting \dot{V}_{O_2} of 9 ml min^{-1} , the recalculated value for V_S is 1.14 ml at rest, compared with 1.59 ml in the birds while flying, a 1.4-fold increase. This also agrees with data from emus running near their maximum sustainable speed (Grubb, 1983b), which showed a similar increase in V_S .

Using the values for f_H , V_S and $Ca_{O_2} - C\bar{v}_{O_2}$ for pigeons (Butler *et al.* 1977; Table 1) and substituting into equation 11, it is estimated that \dot{V}_{O_2} during flight for birds such as the pigeon, which have a 'high aerobic capacity', should scale as:

$$166M_b^{0.77 \pm 0.09} = 574M_b^{-0.19 \pm 0.02} \times 3.48M_b^{0.96 \pm 0.02} \times 0.083M_b^{0.00 \pm 0.05}. \quad (14)$$

As the results of Butler *et al.* (1977) were from pigeons flying at 10 m s^{-1} , which is thought to be close to their minimum power speed, equation 14 could be viewed as the scaling of minimum \dot{V}_{O_2} during flight (although no account has been taken of the additional costs of flying with a mask and trailing leads). This result compares with the allometric equation for the minimum \dot{V}_{O_2} of seven species of birds during flight in a wind tunnel (Butler, 1991) of:

$$\dot{V}_{O_2} = 150M_b^{0.73}. \quad (15)$$

The M_h of the pigeons ($M_b = 0.442 \text{ kg}$) studied by Butler *et al.* (1977) is not known but, assuming that M_h in the pigeon is approximately 1.1% of body mass (Grubb, 1982), it is calculated that V_S for birds during flight will scale as $0.3M_h^{1.05}$.

Table 1. Cardiovascular variables in the pigeon *Columba livia* at rest and during flight

	\dot{V}_{O_2} (ml min ⁻¹)	f_H (beats min ⁻¹)	V_s (ml)	$Ca_{O_2}-C\bar{v}_{O_2}$ (ml ml ⁻¹)	Reference
Rest	7.2	178	0.83	0.049	Grubb (1982)
Rest	11.3	171	1.44	0.046	Butler <i>et al.</i> (1977), Butler (1970)
Rest	9.0	171	1.14*	0.046	Butler <i>et al.</i> (1977)
Flight	88	670	1.59	0.083	Butler <i>et al.</i> (1977)

*Value recalculated from data in Butler *et al.* (1977).

See text for details.

\dot{V}_{O_2} , rate of oxygen uptake; f_H , heart rate; V_s , cardiac stroke volume; $Ca_{O_2}-C\bar{v}_{O_2}$, arteriovenous oxygen content difference.

Calculation of body mass coefficients

However, many of the 463 species (excluding hummingbirds) for which we have heart mass data, e.g. pheasants, may not be capable of sustaining flapping flight for more than a few minutes, i.e. they have a 'low aerobic capacity', whereas pigeons are capable of flying for many hours. A more generally applicable equation may have to take these differences into account. The average heart mass for species used in this analysis, with body masses between 350 and 550 g ($N=27$), was only $0.79\pm 0.05\%$ (mean for all 463 species was $1.03\pm 0.01\%$). Therefore, a more appropriate value for V_s may be $2.50M_b^{0.96}$. Combining this value with the general term of $f_H=480M_b^{-0.19}$ (equation 9) gives a final version of equation 11 for all bird species (excluding hummingbirds) of:

$$100M_b^{0.77\pm 0.09} = 480M_b^{-0.19\pm 0.02} \times 2.50M_b^{0.96\pm 0.02} \times 0.083M_b^{0.00\pm 0.05}, \quad (16)$$

while for hummingbirds:

$$314M_b^{0.90\pm 0.22} = 617M_b^{-0.10\pm 0.06} \times 6.13M_b^{1.00\pm 0.11} \times 0.083M_b^{0.00\pm 0.05}. \quad (17)$$

Equation 16 yields considerably lower values than does equation 15 for the seven species of birds flown in wind tunnels (Butler, 1991), while equation 17 yields values similar to \dot{V}_{O_2} for seven species of hummingbirds while hovering (Butler, 1991):

$$\dot{V}_{O_2} = 371M_b^{0.87}. \quad (18)$$

To summarise, it would appear that equations 14 and 17 give estimates for \dot{V}_{O_2} which are in reasonable agreement with the measured values for forward flapping flight (equation 15) and for hovering flight in hummingbirds (equation 18), respectively. However, the more general equation (equation 16), for \dot{V}_{O_2} during flight for all birds, gives a much lower estimate than that measured for forward flapping flight (equation 15).

Columba livia are capable of many hours of sustained

flapping flight; thus, measured \dot{V}_{O_2} should be representative of the true aerobic cost of flight. Therefore, equation 14 for birds with a 'high aerobic capability' should also be representative of the aerobic costs of flight and directly comparable to the estimates for the mechanical power output required for flight (Pennycuik, 1975; Rayner, 1979). As all the seven species for which oxygen consumption has been directly measured during sustained flapping flight have, by definition, a 'high aerobic capacity', then it is expected that equation 14 should be in good agreement with equation 15. However, many species of birds may utilize behavioural strategies, such as gliding, to reduce the costs below that of continuous flapping flight. In addition, some species may include varying degrees of anaerobic metabolism to provide the 'instantaneous' biochemical power required.

An example of the latter strategy may be provided by the European pheasant (*Phasianus colchicus*), which is capable of powerful flight over a short duration. As expected, it has large flight muscles but a small heart (0.43% of body mass; C. M. Bishop, unpublished data) and the pectoralis muscles consist predominantly of fast glycolytic or type IIB fibres (Newsholme and Leech, 1983), with relatively low levels of aerobic enzymes such as citrate synthase and carnitine palmitoyltransferase (Crabtree and Newsholme, 1972; Alp *et al.* 1976). The 'instantaneous' biochemical power required for flight in the pheasant is, therefore, provided by anaerobic glycolysis, and it is assumed that a large proportion of the true cost of these explosive flights must be 'paid' while the bird is resting on the ground following the flight. An estimate of the true total flight cost based on \dot{V}_{O_2} would have to include the post-flight period of recovery.

Scaling of flight muscle mass

Marden (1987, 1990) showed that the 'flight muscle ratio', defined as the total flight muscle mass (M_{fm}) divided by body mass, is one of the best indicators of relative lifting ability during take-off. As shown by Marden (1987), total M_{fm} expressed as a percentage of M_b scales independently of M_b (Fig. 4) and gives an approximate indication of the relative maximum power output available from the muscles (Ellington, 1991). However, sustainable power output during flight is dependent primarily on the supply of oxygen to the flight muscles. Hartman (1961) and Bethke and Thomas (1988) measured the total M_{fm} of 407 species of birds, including 21 species of hummingbirds. Using the f_H terms from equations 9 and 12, for all other birds and hummingbirds, respectively, and M_h data for these species, an estimate can be made for \dot{V}_{O_2} during flapping flight and this can be plotted against M_{fm} (Fig. 5). Interestingly, the extrapolation of the hummingbird line ($\dot{V}_{O_2}=1.9M_{fm}^{0.79\pm 0.08}$, $r^2=0.90$) lies along the top edge of the data set for all other birds ($\dot{V}_{O_2}=1.5M_{fm}^{0.76\pm 0.22}$, $r^2=0.92$). Thus, as hummingbirds increase in mass, the M_b exponent for the scaling of \dot{V}_{O_2} should be approximately 0.13 greater than that found for all other birds, while the M_{fm} exponent for \dot{V}_{O_2} should be very similar to that of all birds with a 'high aerobic capacity'. This

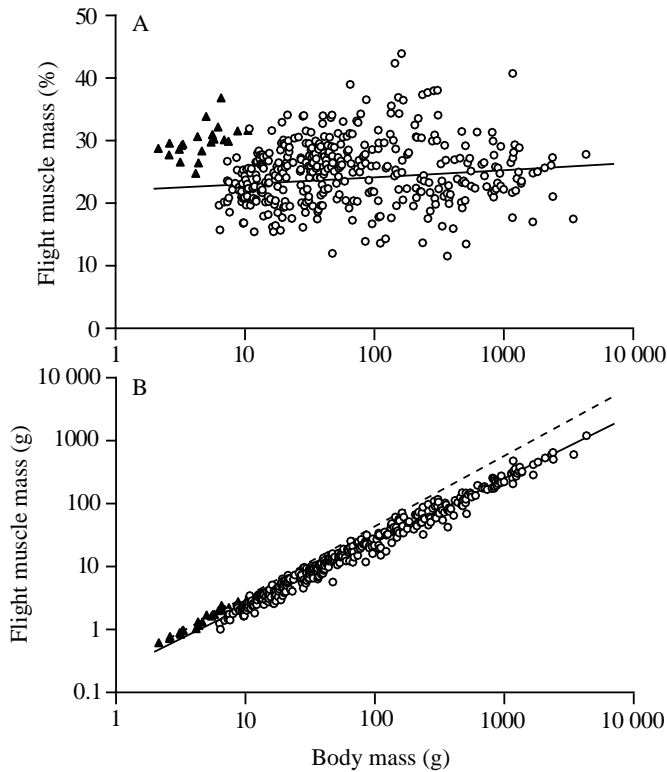


Fig. 4. (A) Flight muscle mass (as a percentage of body mass) and (B) flight muscle mass (g) plotted against body mass (g) for 407 species of birds, including 21 species of hummingbirds. Hummingbirds (filled triangles; dashed line); all other species (open circles; solid line). Data are taken from Hartman (1961) and Bethke and Thomas (1988).

analysis indicates that the flight muscles of larger birds have a lower mass-specific oxygen supply and, thus, provides a prediction for the scaling of mitochondrial volume density in the flight muscles of birds with a 'high aerobic capacity'. As $\dot{V}_{O_{2max}}$ is expected to be proportional to the volume fraction of mitochondria (Weibel *et al.* 1991), muscle mass-specific volume density of mitochondria should scale proportional to $M_{fm}^{-0.21 \pm 0.08}$. This negative scaling relationship for mass-specific mitochondrial volume should also be found within the hummingbird family and would suggest that there should be a negative mass-specific scaling of mitochondrial enzyme activity, and a positive scaling of anaerobic enzyme activity, with increasing M_{fm} and M_b .

Estimating the oxygen uptake of an individual species

It should be possible, on the basis of the above analysis, to calculate a rough estimate for the minimum oxygen uptake of a particular species during flapping flight, depending on the information available concerning the values of the individual cardiovascular variables, fH , V_s and $Ca_{O_2} - C\bar{V}_{O_2}$. (a) As fH is relatively easy to measure, either the actual measurements for a particular species can be utilised or, if the body mass and heart rate are known for a closely related species, then fH can be adjusted for body mass differences using the M_b exponent

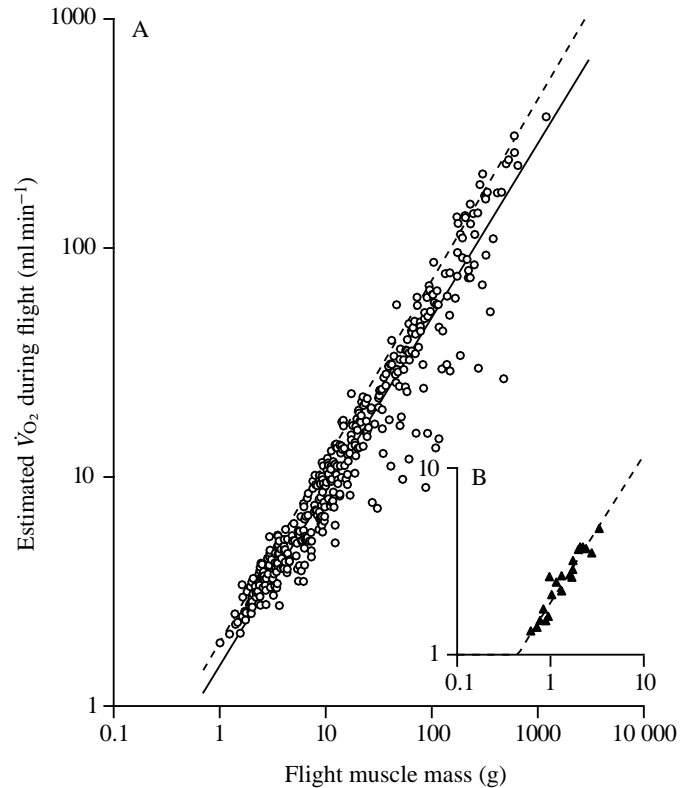


Fig. 5. Estimated \dot{V}_{O_2} (ml min^{-1}) during flight (calculated from measured values for M_h and estimated values of fH based on equation 9), plotted against flight muscle mass (g) for (A) 386 species of birds (open circles; solid line) and (B) 21 species of hummingbirds (filled triangles; dashed line). The regression line for hummingbirds is also shown on A as a dashed line. Data are taken from Hartman (1961) and Bethke and Thomas (1988).

of the fH term (equation 9 or 14, as appropriate). (b) If M_h is known for a particular species, then it is possible to estimate V_s using $V_s = 0.3M_h^{1.05}$. (c) When considering adaptive variation, i.e. when comparing different species with approximately the same body mass, it is expected that Ca_{O_2} would be directly related to haemoglobin concentration or haematocrit (Weibel *et al.* 1991). Therefore, estimated oxygen uptake could be adjusted for the relative haemoglobin concentration. This factor is not included in the model because of a lack of relevant data.

Examples will be presented for the calculation of the estimated \dot{V}_{O_2} for birds in flight by using actual measurements of fH and M_h . The results will be compared with the values predicted from the allometric equations 15 and 18.

Geese

A 1.6 kg pre-migratory barnacle goose *Branta leucopsis* has an estimated heart mass of 18 g (Bishop *et al.* 1995). Thus, using the fH measured from two barnacle geese, with an average body mass of 1.6 kg, trained to fly behind a truck (Butler and Woakes, 1980), and substituting the V_s calculated from the estimated heart mass (using $V_s = 0.3M_h^{1.05}$), estimated \dot{V}_{O_2} is 264 ml min^{-1} (i.e. $512 \text{ beats min}^{-1} \times 6.20 \text{ ml} \times 0.083$). The

allometric equation (equation 15) predicts that \dot{V}_{O_2} will be approximately 211 ml min^{-1} for a 1.6 kg barnacle goose during flight.

In this case, the allometric equation predicts a lower value for \dot{V}_{O_2} than the value based on the cardiovascular variables. Information from a preliminary study of a 1.6 kg barnacle goose flown in a wind tunnel (P. J. Butler, A. J. Woakes and R. Stephenson, unpublished data) indicates that \dot{V}_{O_2} during flight may be closer to 300 than to 200 ml min^{-1} . In addition, the predicted V_s of 6.2 ml is close to that predicted by multiplying the measured value of 4.0 ml for a 1.7 kg barnacle goose at rest (Bevan, 1990) by 1.4 (see calculation for Table 1) to obtain an estimate of V_s during flight of 5.6 ml.

Pheasants

The European pheasant *Phasianus colchicus* has a heart mass is 0.43 % of body mass, while f_H of a 1.44 kg bird is $444 \text{ beats min}^{-1}$ (Keskpaik and Leht, 1983). Therefore, the estimated \dot{V}_{O_2} during flight is 75 ml min^{-1} (i.e. $444 \text{ beats min}^{-1} \times 2.04 \text{ ml} \times 0.083$). The allometric equation (equation 15) predicts that \dot{V}_{O_2} will be approximately 196 ml min^{-1} for a 1.44 kg pheasant during flight.

In this case, the allometric equation predicts a much higher value for \dot{V}_{O_2} than the value based on the cardiovascular variables. It is predicted, therefore, that the pheasant would quickly build up an 'oxygen debt' and have to spend additional time on the ground to recuperate.

Hummingbirds

J. E. P. W. Bicudo has kindly supplied us with unpublished data for the Brazilian hummingbird *Amazilia lactea* ($M_b=3.94 \text{ g}$, $M_h=0.09 \text{ g}$). During hovering, *A. lactea* had an f_H of $1056 \text{ beats min}^{-1}$ and a \dot{V}_{O_2} of 2.3 ml min^{-1} . This analysis suggests that \dot{V}_{O_2} for *A. lactea* is 2.1 ml min^{-1} (i.e. $1056 \text{ beats min}^{-1} \times 0.024 \text{ ml} \times 0.083$), while the allometric equation (equation 18) predicts that \dot{V}_{O_2} will be approximately 3.0 ml min^{-1} .

Thus, the calculation based on the cardiovascular variables results in an underestimate for *A. lactea* of 9%, while the allometric equation gives an overestimate of 30%.

Inter-species comparison of aerobic flight performance

The inter-species comparison of aerobic flight performance is complicated by a number of factors. (1) The relative wing morphology, which has been discussed in detail (Rayner, 1988; Pennycuik, 1989) and which will not be incorporated into this analysis. (2) The possible scaling of the mechano-chemical conversion efficiency, which may increase significantly with M_b (Rayner, 1990). (3) In addition, the analyses by Ellington (1991) and Marden (1994) of the data from Marden (1987, 1990) indicated that the maximum lift production (N) during take-off, or slow flight, may scale with a smaller M_b exponent than that for the total mechanical power output (W).

Re-analysis of the data from Marden (1987, 1990) for eleven

species of birds shows that maximum lift production (L) during take-off divided by the calculated maximum mechanical power output (P_{\max}) scales as:

$$L/P_{\max} = 0.265M_b^{-0.1 \pm 0.05} \quad (r^2=0.6). \quad (19)$$

Thus, small birds generate a greater lift for a given power output than large birds during slow flight (Marden, 1994), and it is assumed that this relationship is independent of whether the power output is for burst or sustainable activity.

For practical purposes, some authors have considered that the mechano-chemical conversion efficiency is a constant with respect to body mass (Pennycuik, 1989). If this is correct, then it would be expected that aerobic lift production would decline rapidly with respect to M_b (see Marden, 1994) even within the hummingbird family, which has an M_b range of approximately fivefold. Alternatively, Rayner (1990) suggested that efficiency can be estimated as the ratio of the calculated mechanical output and metabolic input powers. However, it is not possible to use the mechanical power output values calculated from the data of Marden (1987, 1990), as this work was concerned with burst activity during take-off and it is unlikely that these values would reflect aerobic power output. However, Hedenstrom and Alerstam (1992) used radar tracking data from 15 species of migrating birds (M_b ranging between 0.01 and 10 kg) to measure sustained climbing and airspeeds. They argued that these migrants would expend maximum aerobic power during climbing flight and calculated total aerobic power outputs for these species. Re-analysis of their data (Hedenstrom and Alerstam, 1992; Table 3) shows that maximum aerobic power output (W) scales as:

$$\text{Maximum aerobic power output} = 27M_b^{0.98 \pm 0.05} \quad (r^2=0.99). \quad (20)$$

Butler *et al.* (1977) found that Ca_{O_2} in pigeons during flight was 0.137 ml ml^{-1} . If it is assumed that during maximum aerobic flight performance birds can extract almost all the oxygen from their mixed venous blood (see Weinstein *et al.* 1985), then the maximum available value of $Ca_{O_2} - C\bar{v}_{O_2}$ during flight would be approximately 0.13 ml ml^{-1} . Taking equation 14 for the scaling of \dot{V}_{O_2} for species with a 'high aerobic capacity' and substituting a value of 0.13 ml ml^{-1} for $Ca_{O_2} - C\bar{v}_{O_2}$ gives an estimate for the scaling of maximum aerobic power input (W) during flight as:

$$\text{Maximum aerobic power input} = 87M_b^{0.77 \pm 0.09}, \quad (21)$$

assuming that 1 ml of oxygen is equivalent to 20.1 J (Schmidt-Nielsen, 1990).

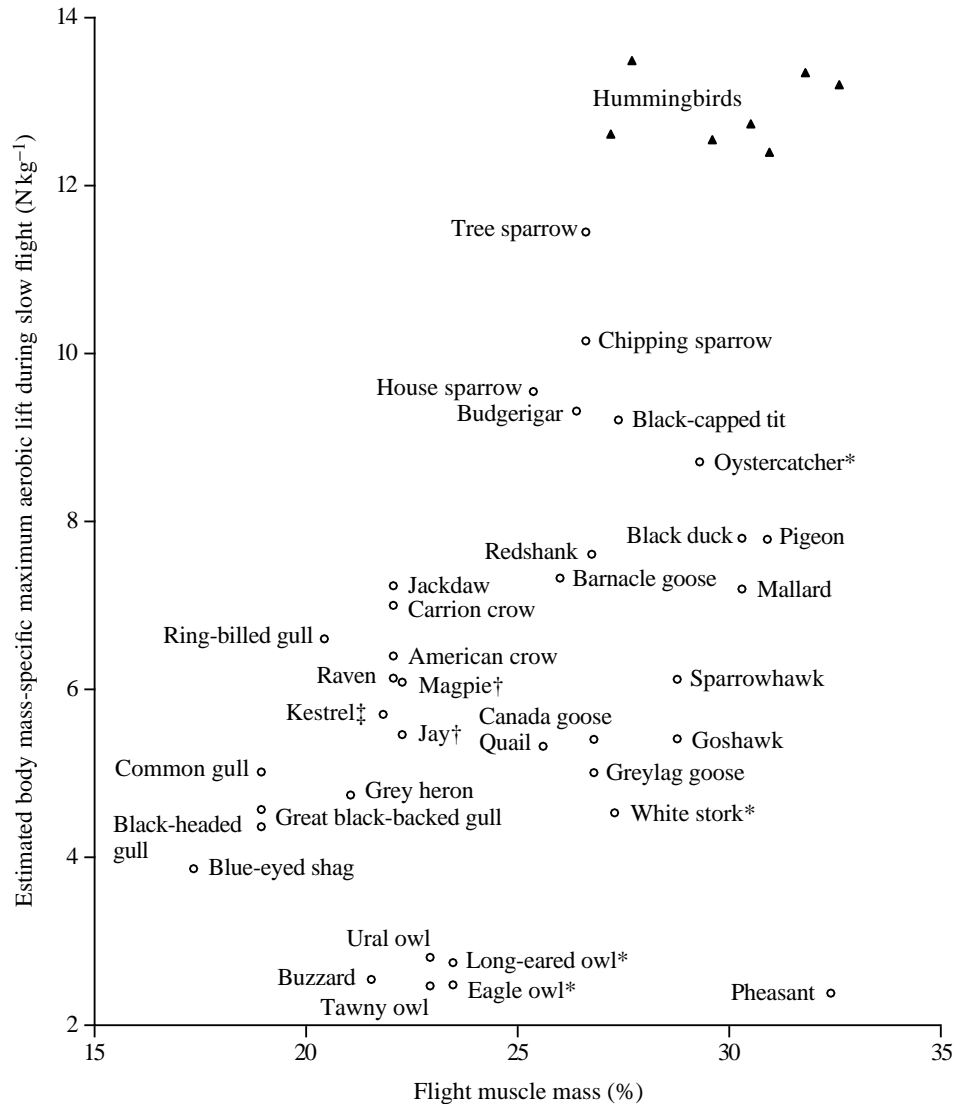
Taking the ratio of equations 20 and 21 gives an estimate for the scaling of efficiency as:

$$\text{Efficiency} = 0.31M_b^{0.21 \pm 0.14}. \quad (22)$$

Thus, equations 22 and 19 can be used to modify the estimates of \dot{V}_{O_2} to give relative estimates for aerobic power output and aerobic lift production, respectively.

To compare the relative aerobic capacity of birds in more detail, M_h and M_{fm} for 43 species (including seven species of

Fig. 6. Estimated body mass-specific maximum aerobic lift during slow flight (N kg^{-1}) plotted against flight muscle mass (M_{fm}) expressed as a percentage of body mass for 43 species of birds. Calculations of lift are based on estimated maximum \dot{V}_{O_2} (ml min^{-1}) during flight (calculated from measured values for f_{H} and M_{h} , see text) and converted to power output and lift production, utilising equation 22 and 19, respectively. All species of birds (open circles) excluding seven species of hummingbirds (filled triangles). f_{H} was obtained from Berger *et al.* (1970, 1979), Aulie (1971), Butler and Woakes (1980), Keskaik and Leht (1983) and unpublished data for two species of hummingbirds from J. E. P. W. Bicudo; Canada goose and blue-eyed shag data from P. J. Butler, A. J. Woakes and R. M. Bevan. M_{h} and M_{fm} were obtained from Hartman (1961), either for the same species or genus, although for a few species (*) it was necessary to use a family average; for species marked † a closely related genus was used. f_{H} data for the kestrel (‡) were measured from the European kestrel *Falco tinnunculus*, while values of M_{h} were obtained from the American kestrel *Falco sparverius*.



hummingbirds), for which there were data available on M_{b} and f_{H} during flight, were estimated from values in the literature. In many cases these were from the same species or genera, but in a few cases it was necessary to take an average for the family (see legend Fig. 6). As in the previous section, maximum \dot{V}_{O_2} during flight for each species was estimated from the measured values for f_{H} and M_{h} and using a value of 0.13 ml ml^{-1} for $\text{CaO}_2 - \text{C}\bar{\text{v}}\text{O}_2$. These values for \dot{V}_{O_2} were converted into aerobic power output using equation 22 (assuming that 1 ml of oxygen is equivalent to 20.1 J). Equation 19 was then used to provide an estimate for maximum aerobic lift during slow flight, and these values were plotted against M_{fm} as a percentage of M_{b} (Fig. 6). Species that are placed higher up the ordinate should have a relatively high capacity to sustain lift production during slow flight, while species further along the abscissa should have a relatively high maximum lifting ability during burst activity. Given that many errors may have arisen from the disparate sources from which the data have been acquired, the relative positions of most of these species appear logical. Interestingly, the results

plotted in Fig. 6 indicate that, if overall efficiency does scale proportional to $M_{\text{b}}^{0.21 \pm 0.08}$, then aerobic lift production during slow flight should be nearly constant within the hummingbird family.

Discussion

The purpose of this attempt to calculate the scaling factors for the cardiovascular variables of the Fick equation was to bring some focus to the problem of supplying oxygen to the flight muscle of birds and to indicate where natural selection is likely to have its most fundamental effects. Given the lack of information currently available regarding the cardiovascular variables of birds during flight, it is not surprising that estimations for the allometric variation of \dot{V}_{O_2} are difficult to substantiate. It is anticipated that more accurate predictions of the values for the various cardiovascular variables would result if the data were collected in a more standardised manner and if the relevant wing morphology was also taken into account (Rayner, 1988; Pennycuik, 1989). In addition, it is necessary

to be able to predict how these cardiovascular variables will respond to changes in flight speed. This should prove to be an interesting area for future research.

Equation 14 for predicting the minimum \dot{V}_{O_2} of birds with a 'high aerobic capacity' is very close to the measured allometric equation 15, calculated by Butler (1991). However, in general, both equations may be of little use when applied to birds with an 'intermediate' or 'low' capacity to sustain high power output. Therefore, it is suggested that the use of M_h as an indicator of V_s , in combination with estimates of f_H and $Ca_{O_2} - C\bar{v}_{O_2}$, gives a more accurate estimate of \dot{V}_{O_2} during flight than is possible using the general allometric term based on M_b alone. Estimates of \dot{V}_{O_2} for hummingbirds (0.004 kg) and barnacle geese (1.6 kg) show that, given the measured values of f_H and M_h , the error in estimating \dot{V}_{O_2} during cruising flight for species with a 'high aerobic capacity' may be relatively small, despite the simple assumptions of the model. This lends some credibility to the suggestion that bird species with a 'high aerobic capacity' appear to fly utilising similar values for $Ca_{O_2} - C\bar{v}_{O_2}$.

The value of 0.083 ml ml^{-1} for $Ca_{O_2} - C\bar{v}_{O_2}$ is rather low, given the values recorded from humans and other animals during intense exercise (Åstrand and Rodahl, 1986; Weibel *et al.* 1991; Butler *et al.* 1993), and the following points should be considered. (1) The model is highly dependent on a single study of *Columba livia* in which the birds were flying near their minimum power speed of 10 m s^{-1} . Therefore, the estimates for \dot{V}_{O_2} are likely to represent close to minimum values. However, it is predicted that if less effort is required to fly, e.g. during gliding flight, then $Ca_{O_2} - C\bar{v}_{O_2}$ may fall to near-resting values of $0.05\text{--}0.06 \text{ ml ml}^{-1}$, along with near resting values for f_H . (2) In the studies of Butler *et al.* (1977) and Grubb (1982, 1983*a,b*), V_s was not measured directly but was calculated from measured values of the other three variables of the Fick equation (equation 2). It is likely that the values for f_H and \dot{V}_{O_2} would be reasonably accurate, so the biggest errors may occur in the measurements of Ca_{O_2} and $C\bar{v}_{O_2}$. Any error in these measurements would result in an equal but opposite error in the value for V_s . Therefore, the relationship between these two variables was not altered in the current analysis. (3) It may be that some species can operate with a relatively small heart and a large $Ca_{O_2} - C\bar{v}_{O_2}$. However, there may be a number of adaptive advantages to having a large cardiac output relative to the normal demands of cruising flight.

During flight, the normal level of \dot{V}_{O_2} is below $\dot{V}_{O_{2\max}}$. This might be advantageous for species which are largely dependent on fatty acid metabolism to fuel their flights. It is well established in humans that fatty acids are not as easily mobilised as carbohydrates and that peak performance in aerobic sports is lowered when carbohydrates are exhausted (Shephard and Åstrand, 1992). In addition, in individual birds, \dot{V}_{O_2} is thought to scale in proportion to $M_b^{1.59}$ (Rayner, 1990); thus, it may be necessary for relatively lean birds that have to fatten for migration to retain some scope for increasing $Ca_{O_2} - C\bar{v}_{O_2}$.

Adaptation to a relatively small $Ca_{O_2} - C\bar{v}_{O_2}$ may pre-adapt some species for high-altitude flight. Tucker (1968*a*), in his

study of sparrows (*Passer domesticus*) flying in a simulated atmosphere of 6100 m, calculated that the value for Ca_{O_2} may have been around 0.12 ml ml^{-1} . In addition, bar-headed geese (*Anser indicus*) running in a simulated atmosphere of approximately 9500 m (Fedde *et al.* 1989) had a measured Ca_{O_2} of 0.12 ml ml^{-1} and $C\bar{v}_{O_2}$ of 0.04 ml ml^{-1} . Even if it is assumed that during flight birds are capable of removing nearly all the oxygen from the mixed venous blood (see Weinstein *et al.* 1985), then the maximum available $Ca_{O_2} - C\bar{v}_{O_2}$ for both sparrows and bar-headed geese would have been less than 0.12 ml ml^{-1} . It may be possible to increase the potential $Ca_{O_2} - C\bar{v}_{O_2}$ by increasing the concentration of haemoglobin prior to high-altitude flights, but it is clear that selection for a relatively high cardiac output would be of major advantage for high-flying migrants such as certain species of swans and geese.

Relatively large birds, such as ducks, geese and swans, which are capable of very long flights, appear to have relative heart masses of up to approximately 1.1% of M_b . However, as shown in Fig. 2, some small species of birds appear to be capable of developing very much larger relative heart masses. Therefore, it would appear that there may still be some potential for large flying birds to achieve higher cardiac outputs through natural selection. In this context, it is interesting that both the heart and pectoralis muscles of barnacle geese are capable of hypertrophy prior to migration, although the skeletal size of these birds remains unaltered (Bishop *et al.* 1995).

All the evidence suggests that \dot{V}_{O_2} scales with a M_b exponent less than 1. If the power output required for flight scales between approximately $M_b^{1.00}$ and $M_b^{1.17}$ (Ellington, 1991; Hedenstrom and Alerstam, 1992), then the mechano-chemical conversion efficiency must increase with increasing body mass, as suggested by Rayner (1988, 1990). If for some reason the mechano-chemical conversion efficiency reaches a maximum in very large birds, or a minimum in very small ones, then the \dot{V}_{O_2} required for sustained flight will start to scale directly with power output, i.e. between $M_b^{1.00}$ and $M_b^{1.17}$, rather than at the calculated value of $M_b^{0.77}$. Thus, the required level of oxygen supply might rapidly become unsupportable.

The oxygen requirement of a flying bird of a given M_b will, to a certain degree, reflect the morphological characteristics of the species and the conditions in which the bird is flying, i.e. the speed and the degree of 'effort' the animal is having to expend relative to its maximum capability. However, it would appear that all three cardiovascular variables of the Fick equation are co-adapted such that, in birds of similar M_b , those with the smallest \dot{V}_{O_2} during exercise have relatively small hearts, a lower mean f_H and a lower haematocrit. In birds of different body masses, f_H is the most influential variable, along with a slight trend for a decrease in relative M_h with increasing M_b .

The M_b exponents of measured and estimated \dot{V}_{O_2} , M_h and M_{fm} are consistently greater for hummingbirds than for all other birds. It would appear that these M_b exponents may be the result of selection on the larger species of hummingbirds in order to maintain aerobic hovering performance because the

M_{fm} exponent for estimated \dot{V}_{O_2} appears to be similar to that of all birds that have a 'high aerobic capacity'. Thus, it is suggested that the M_{fm} exponent for the scaling of \dot{V}_{O_2} in hummingbirds may reflect a fundamental trade-off between selection for aerobic and anaerobic power output of flight muscle (Fig. 5). An increase in the M_{fm} exponent would result in an excess supply of oxygen that would greatly exceed demand, while a decrease in the M_{fm} exponent would require the use of additional anaerobic metabolism. It may not be possible to increase the potential for flight muscle mass-specific oxygen consumption, for example by increasing the volume density of mitochondria, without adversely reducing the volume density of the force-producing myofibrillar proteins.

It is proposed that the estimated \dot{V}_{O_2} based on M_h , in combination with estimates of fH and $CaO_2 - C\bar{v}O_2$, gives an indirect measure of relative aerobic power input and, when corrected for the estimated scaling influences of the mechanochemical conversion efficiency and lift generation with respect to M_b , is a useful indicator of the relative capacity of the muscle to sustain power output and lift production during flight. Marden (1987, 1990) showed that total M_{fm} , expressed as a percentage of M_b , is a relative indicator of lifting ability during take-off and should be a good predictor of maximum power output (Ellington, 1991). Thus, it may be possible to characterize the physiological nature of bird flight performance by using M_{fm} (expressed as a percentage of M_b) as an indicator of maximum lift production during slow flight, in conjunction with a corrected estimate of \dot{V}_{O_2} as an indicator of the relative capacity to sustain lift production (Fig. 6).

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