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Heart mass and the maximum cardiac output of birds and mammals: implications for estimating the maximum aerobic power input of flying animals

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SUMMARY

Empirical studies of cardiovascular variables suggest that relative heart muscle mass (relative M_{h}) is a good indicator of the degree of adaptive specialization for prolonged locomotor activities, for both birds and mammals. Reasonable predictions for the maximum oxygen consumption of birds during flight can be obtained by assuming that avian heart muscle has the same maximum physiological and biomechanical performance as that of terrestrial mammals. Thus, data on M_{h} can be used to provide quantitative estimates for the maximum aerobic power input (aerobic $P_{\mathrm{i,max}}$) available to animals during intense levels of locomotor activity. The maximum cardiac output of birds and mammals is calculated to scale with respect to M_{h} (g) as 213 $M_{\mathrm{h}}^{0.88\pm0.04}$ (ml min^{-1}), while aerobic $P_{\mathrm{i,max}}$ is estimated to scale approximately as 11 $M_{\mathrm{h}}^{0.88\pm0.09}$ (W). In general, estimated inter-species aerobic $P_{\mathrm{i,max}}$, based on M_{h} for all bird species (excluding hummingbirds), is calculated to scale with respect to body mass (M_{b} in kg) as 81 $M_{\mathrm{b}}^{0.82\pm0.11}$ (W). Comparison of family means for M_{h} indicates that there is considerable diversity in aerobic capacity among birds and mammals; for example, among the medium to large species of birds, the Tinamidae have the smallest relative M_{h} (0.25%) while the Otidae have unusually large relative M_{h} (1.6%). Hummingbirds have extremely large relative M_{h} (2.28%), but exhibit significant sexual dimorphism in their scaling of M_{h} and flight muscle mass, so that when considering hummingbird flight performance it may be useful to control for sexual differences in morphology. The estimated scaling of aerobic $P_{\mathrm{i,max}}$ (based on M_{h} and M_{b} in g) for male and female hummingbirds is 0.51 $M_{\mathrm{b}}^{0.83\pm0.07}$ and 0.44 $M_{\mathrm{b}}^{0.85\pm0.11}$ (W), respectively. Locomotory muscles are dynamic structures and it might be anticipated that where additional energetic 'costs' occur seasonally (e.g. due to migratory fattening or the development of large secondary sexual characteristics) then the relevant cardiac and locomotor musculature might also be regulated seasonally. This is an important consideration, both due to the intrinsic interest of studying muscular adaptation to changes in energy demand, but also as a confounding variable in the practical use of heart rate to estimate the energetics of animals. Haemoglobin concentration (or haematocrit) may also be a confounding variable. Thus, it is concluded that data on the cardiovascular and flight muscle morphology of animals provide essential information regarding the behavioural, ecological and physiological significance of the flight performance of animals.

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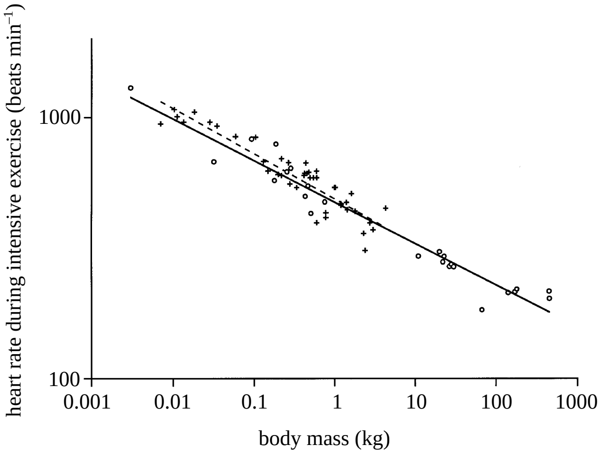

Figure 1. Maximum heart rate recorded during intensive levels of exercise (beats min^{-1}) for birds and mammals plotted against body mass (kg). Data for birds (+ and dashed regression line), see Bishop & Butler (1995). Data for mammals (○ and solid regression line) from Kallen (1977), Baudinette (1978), Gleeson *et al.* (1983), Carpenter (1985, 1986), Karas *et al.* (1987) and Jones *et al.* (1989).

1. INTRODUCTION

Pennycuick (1989, p. 1) made the observation that 'the oxygen consumed by a pigeon flying in a wind tunnel, applies to that particular bird under the conditions of the experiment, but cannot be transferred to predict the energy consumption of other species flying under other conditions'. In other words there is an 'inherent lack of generality' in 'physiological measurements'. However, I believe that this generalization itself overlooks the useful insights to be gained from the study of the cardiovascular adaptations of different species with respect to the energetics of animal flight. In particular, there is a requirement to be able to estimate the power input of exercising animals as this is an important consideration in many ecological and physiological studies, and optimality models, of animal behaviour and evolution.

Bishop & Butler (1995) combined data on the changes in both structural and functional cardiovascular variables of birds with respect to body mass (M_b), heart mass (M_h) and data on cardiovascular variables of pigeons flying in a wind tunnel near the minimum power speed (Butler *et al.* 1977). They concluded that the minimum rate of oxygen consumption of birds during flapping flight ($\dot{V}O_{2\,min}$) should scale in proportion to $M_b^{0.77 \pm 0.09}$, which is in reasonable agreement with the measured $\dot{V}O_{2\,min}$ of seven species of birds flown in wind tunnels as reviewed by Butler (1991). However, a few of these wind tunnel studies may also be useful for assessing the maximum oxygen consumption ($\dot{V}O_{2\,max}$) of birds (Tucker 1968; Torre-Bueno & Larochelle 1978; Gessaman 1980), in addition to the more recent studies of maximum hovering performances of hummingbirds (Wells 1993; Chai & Dudley 1995), and the wind tunnel studies of Thomas & Suthers (1972) and Carpenter (1985) on flying bats.

I will assume that the maximum cardiac output ($\dot{V}_{b,\,max}$) of the heart should be some function of the maximum power output, or biomechanical performance, of the cardiac muscles (cf. Schmidt-Nielsen 1984). Using values for cardiovascular variables from the literature (Gleeson *et al.* 1983; Karas *et al.* 1987; Taylor *et al.* 1987; Jones *et al.* 1989), from mammals during maximum running performance on a treadmill, I will estimate the function relating $\dot{V}_{b,\,max}$ of terrestrial mammals to M_h, and consider the relevance of this function to birds and mammals during flight.

Using the approach of Bishop & Butler (1995), and making some simple assumptions with regard to the oxygen carrying capacity of avian and mammalian blood and the potential for oxygen extraction by the tissues, I use data on relative M_h to calculate estimates for the $\dot{V}O_{2\,max}$ of various different species of birds and bats and compare the results with measurements available in the literature. I will show that 'physiological' data measured from birds and bats flying near their maximum aerobic power inputs should fulfil the requirements for 'generality'.

2. GENERAL METHODOLOGY

I shall use the same symbols and general methodology as used by Bishop & Butler (1995). Thus, the Fick equation for the convection of blood can be represented as

$$(\dot{V}O_2)\,M_b^z = (f_H)\,M_b^w \times (V_s)\,M_b^x \times (C_{aO_2} - C_{\bar{v}O_2})\,M_b^y, \quad (1)$$

where w, x, y and z are the body mass exponents for each variable and the terms in parentheses represent the body mass coefficients, respectively. $\dot{V}O_2$ is oxygen consumption in ml min^{-1} (STPD), M_b is body mass in kg, f_H is heart rate in beats min^{-1}, V_s is the stroke volume of the heart in ml and $C_{aO_2} - C_{\bar{v}O_2}$ 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 $\dot{V}O_2$.

The body mass exponents (±95% confidence limits) and body mass coefficients can be estimated from data available in the literature (references will be given in the relevant sections). All calculations of allometric exponents for M_b and M_h were estimated by performing reduced major axis regressions (Sokal & Rohlf 1981; Rayner 1985), except for the relationship between V_s and M_h during rest, which were obtained from Grubb (1983) and calculated using least-squares regression.

As the watt (W) is the SI unit for power and is equivalent to joules per second (J s^{-1}), it will be necessary to provide an estimate for power input (P_i) by converting $\dot{V}O_2$ (ml min^{-1}) to W. Schmidt-Nielsen (1990) gives the following values for fuel energy equivalents; 1 ml of O_2 is equivalent to 20.9 J during carbohydrate oxidation and 19.7 J during fat oxidation. During short duration exercise it is likely that carbohydrate oxidation will dominate, e.g. short hovering flights during foraging in hummingbirds

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(Suarez *et al.* 1990), but during longer bouts of exercise it is likely that fat oxidation will become dominant. Therefore, apart from hovering flight in hummingbirds, I shall use the compromise figure of 20.1 J (Schmidt-Nielsen 1990) for calculations of power input during aerobic activity.

3. COMPARISON OF CARDIOVASCULAR VARIABLES OF BIRDS AND MAMMALS

The relatively complete studies, conducted by Gleeson *et al.* (1983), Karas *et al.* (1987), Taylor *et al.* (1987) and Jones *et al.* (1989), on the cardiovascular variables of mammals during maximal running, cover only seven species ranging in mass from the rat (0.333 kg) to the horse (446 kg). However, these studies are particularly useful as they also provide information on M_h for each species. Values for cardiovascular variables during rest are also given and these were taken while the animals were quiet but standing. The most comprehensive studies on birds are those of Butler *et al.* (1977), Grubb (1982), Grubb (1983) and Grubb *et al.* (1983), and cover nine species ranging from the budgerigar (0.035 kg) to the emu (37 kg).

(*a*) *Arteriovenous difference* $(C_{aO_2} - C_{\bar{v}O_2})\, M_b^y$

For the purpose of modelling the potential for arterial oxygen-carrying capacity, an estimate can be made for the saturated oxygen content of the blood C_{aO_2} by multiplying the haemoglobin concentration by 1.36 (Larimer 1959). Schmidt-Nielsen (1990) concluded that the haemoglobin concentration in mammals shows no significant trend with body mass while, in a large survey of birds, Prinzinger & Misovic (1994) found that the haemoglobin content scales as

$$\text{Haem} = 16.6\, M_b^{-0.02}. \tag{2}$$

The mean value of haemoglobin concentration for birds, reported by Prinzinger & Misovic (1994), was 0.1513 g ml^{-1} while the mean value for mammals is also around 0.15 g ml^{-1} of blood (Schmidt-Nielsen 1990). Thus, $\dot{V}O_{2\,max}$ of both birds and mammals should scale in proportion to $\dot{V}_{b,\,max}$ (cf. Bishop & Butler 1995).

(*b*) *Heart beat frequency* $(f_H)\, M_b^w$

The maximum f_H of eutherian mammals while running has been reported by a number of authors (Baudinette 1978; Gleeson *et al.* 1983; Taylor *et al.* 1987; Jones *et al.* 1989). Values for f_H during flight for birds and bats are also available from the literature (Carpenter 1985; Carpenter 1986; cf. Bishop & Butler 1995), and while they may not represent 'true' maximal values, for this analysis I have assumed that they are likely to be close to maximal values. Figure 1 shows the data for heart rate during intense activity plotted against body mass (kg). The allometric relationship for 42 species of birds (cf. Bishop & Butler 1995), is

$$f_H = 488\, M_b^{-0.187 \pm 0.022} \ (r^2 = 0.855). \tag{3}$$

While that for 24 species of mammals (this study), is

$$f_H = 477\, M_b^{-0.163 \pm 0.017} \ (r^2 = 0.948). \tag{4}$$

The maximal heart rates of birds and mammals appear to have a very similar body mass scaling function, which is approximately equivalent to $M_b^{-1/6}$.

(*c*) *Stroke volume* $(V_s)\, M_b^x$

Bishop & Butler (1995) assumed that the stroke volume of birds during flight should scale with respect to M_h with a similar exponent to that measured for birds at rest. Grubb (1983) showed that V_s at rest scaled as

$$V_{s,\,rest} = 0.18\, M_h^{1.05}. \tag{5}$$

Bishop & Butler (1995) substituted the value for the stroke volume of pigeons flying in a wind tunnel at the minimum power speed (Butler *et al.* 1977) to estimate the heart mass-specific scaling of V_s during flight as

$$V_{s,\,flight} = 0.3\, M_h^{1.05}. \tag{6}$$

Figure 2*a* shows that for the seven species of mammal studied at rest and while running at $\dot{V}O_{2\,max}$ (Gleeson *et al.* 1983; Karas *et al.* 1987; Taylor *et al.* 1987; Jones *et al.* 1989), it would seem that the heart mass exponent for $V_{s,\,max}$ does indeed scale with a similar exponent to that for V_s at rest:

$$V_{s,\,rest} = 0.252\, M_h^{1.068 \pm 0.085} \ (r^2 = 0.995), \tag{7}$$

while for mammals during $\dot{V}O_{2\,max}$

$$V_{s,\,max} = 0.377\, M_h^{1.016 \pm 0.046} \ (r^2 = 0.998). \tag{8}$$

Figure 2*b* shows cardiac output $(\dot{V}_b)$ plotted against M_h for the same seven mammal species as those shown in figure 2*a*. Grubb (1983) did not report $\dot{V}_b$, rest as a function of M_h but, from the data on M_h and the relationship between $\dot{V}_{b,\,rest}$ and M_b, it is possible to estimate the regression for $\dot{V}_{b,\,rest}$ with respect to M_h, which is plotted in figure 2*b*. Values for $\dot{V}_b$ during maximal running are available for three species of birds, pigeon, duck and emu, from Grubb (1982) and Grubb *et al.* (1983), and these values are also plotted in figure 2*b*. For mammals at rest

$$\dot{V}_{b,\,rest} = 85.2\, M_h^{0.807 \pm 0.09} \ (r^2 = 0.990) \tag{9}$$

while for mammals at $\dot{V}O_{2\,max}$

$$\dot{V}_{b,\,max} = 212.7\, M_h^{0.879 \pm 0.036} \ (r^2 = 0.999). \tag{10}$$

Thus, $\dot{V}_{b,\,max}$ appears to be very closely correlated with cardiac muscle mass in these seven mammalian species. However, while the heart mass exponents of $V_{s,\,rest}$ for birds (equation (5)) and mammals (equation (7)) are similar, the coefficient for birds has a value that is lower than that for mammals. This would imply that there must be a difference in the blood pressure or peripheral resistance to blood flow of birds and mammals at rest, as blood pressure is equal to $\dot{V}_b$ multiplied by peripheral resistance (cf. Schmidt-Nielsen 1990).

(*d*) *Blood pressure* (P_b)

In general, it is reported that blood pressure scales independently with body mass (Schmidt-Nielsen 1984), but that birds have a higher blood pressure than mammals (Spector 1956; Grubb 1983). Spector (1956)

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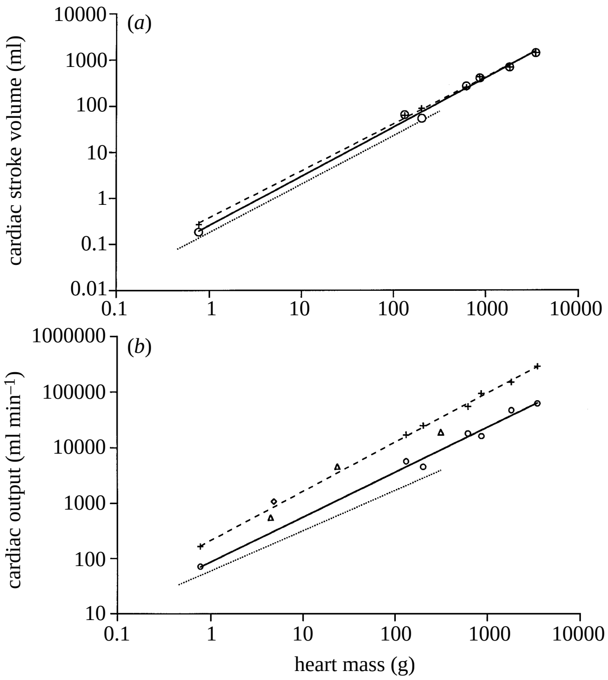

Figure 2. (*a*) Stroke volume of the heart (ml) and (*b*) cardiac output (ml min^{-1}) of birds and mammals plotted against heart mass (g). Data for mammals while running at maximum speed (+ and dashed regression line) and while at rest (○ and solid regression line). Data for birds at rest (dotted regression line) estimated from Grubb (1983). Data for birds during maximum running (△) from Grubb (1982) and Grubb *et al.* (1983), and pigeon during flight (◇) from Butler *et al.* (1977).

gives values for the mean arterial blood pressure of 17 species of mammals (excluding juveniles) and 20 species of birds at rest, and the means are 14.26 (kPa) and 20.13 (kPa), respectively. However, the principal interest in this analysis is in values obtained during intense levels of exercise, for which there are fewer values available.

In mammals it is clear that blood pressure (P_b) is higher during maximal exercise than at rest. For the species of mammal studied by Taylor *et al.* (1987) and Jones *et al.* (1989), P_b at rest was 14.66 kPa ($n = 6$) while during maximal running it was 20.26 kPa ($n = 6$). By contrast, the P_b of birds during intense activity does not increase to such a marked degree. The resting P_b of the pigeon was 18.66 kPa, and this only increased to 19.6 kPa during flight (Butler *et al.* 1977). As mentioned above, different studies often yield different values, for example Grubb (1982) reports the resting P_b of the pigeon as 14.13 kPa which increases to 15.73 kPa while running. A selection of authors give the following values for the P_b of various species of birds: emu 17.73 (rest)/18.4 (run); duck 17.86 (rest)/20.26 (run); tufted duck 19.33 (rest)/24.13 (swim); barnacle goose 17.73 (rest)/20.26 (swim) and lesser scaup 23.46 (rest)/24.53 (swim) (Grubb 1982; Grubb *et al.* 1983; Woakes & Butler 1986; Bevan 1990). These values for birds give a mean of 18.4 (rest) and 20.4 (active). While the data are rather scarce, it would appear that the difference in P_b seen in birds and mammals during rest is not so obvious during maximal exercise. However, inter-species differences in P_b may occasionally arise as a result of adaptive selection (rather than as a result of allometric variation), as in the case of giraffes, which have an enlarged heart to cope with very high P_b of around 35 kPa (Pedley *et al.* 1996).

In general, I conclude that P_b in both mammals and birds during intense activity is approximately 20 kPa. Therefore, I would also expect that $\dot{V}_{\mathrm{b,\,max}}$ during exercise should also be quite similar for hearts of the same mass. Figure 2*b* shows that the values for $\dot{V}_\mathrm{b}$ for the three species of birds during maximum running are quite close to the values for mammals. It would not necessarily be expected that these values from the birds would be maximal during running, but it is interesting that if we plot the estimated value of $\dot{V}_\mathrm{b}$ for the pigeons flown by Butler *et al.* (1977) in a wind tunnel (Bishop & Butler 1995) then this value also lies close to the line for running mammals (figure 2*b*).

4. ESTIMATING THE MAXIMUM OXYGEN UPTAKE ($\dot{V}O_{2\,\max}$) OF FLYING ANIMALS USING CARDIAC MASS

I propose two similar methods for estimating the maximum oxygen consumption of mammals and birds utilizing data for cardiac mass. Both methods rely on either published values for $C_{\mathrm{aO_2}}$, or estimates of $C_{\mathrm{aO_2}}$ based on haemoglobin concentration (as above). Where I have not found a suitable reference for a particular species I have used the haemoglobin values from Prinzinger & Misovic (1994), citing the average values for different families of birds. Where no suitable value could be found even at the familial level then I have used the average value for all birds of 0.1513 (g ml^{-1}). I have also assumed that *in vivo* the arterial blood is 94% saturated, as this is the mean value found for the seven species of mammals running at $\dot{V}O_{2\,\max}$. Finally, to estimate the maximum $C_{\mathrm{aO_2}}-C_{\bar{\mathrm{v}}\mathrm{O_2}}$ of animals flying at maximum aerobic power I have assumed that $C_{\bar{\mathrm{v}}\mathrm{O_2}}$ does not fall below 0.038. Again, this is the mean value of the seven species of mammals running at $\dot{V}O_{2\,\max}$.

(i) *Method 1*

Each of the variables f_H and $C_{\mathrm{aO_2}}-C_{\bar{\mathrm{v}}\mathrm{O_2}}$ can be measured directly, or f_H can be estimated from the f_H terms for mammals (equation (4)) and birds (equation (3)), and $C_{\mathrm{aO_2}}-C_{\bar{\mathrm{v}}\mathrm{O_2}}$ can be estimated from haemoglobin concentration (as above). V_s can be estimated from M_h for mammals (equation (8)) and for birds (equation (6)) using M_h, and all these values are then substituted into the Fick equation to give $\dot{V}O_{2\,\max}$ (cf. Bishop & Butler 1995).

(ii) *Method 2*

The second method simply assumes that $\dot{V}_{\mathrm{b,\,max}}$ is a function of M_h and that there is no difference between birds and mammals during maximum cardiovascular performance. Thus, for both mammals and birds $\dot{V}_{\mathrm{b,\,max}} = 213\,M_\mathrm{h}^{0.88\pm0.04}$ (equation (10)), and $C_{\mathrm{aO_2}}-C_{\bar{\mathrm{v}}\mathrm{O_2}}$ is estimated from haemoglobin concentration as in method 1.

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(*a*) *Examples for birds*

(i) *American kestrel* (Falco sparverius)

Gessaman (1980) reported a $\dot{V}O_{2\max}$ for the American kestrel (M_b is 0.120 kg) flying at high speed in a wind tunnel of 41.3 ml min^{-1} with an average f_H of 715 beats min^{-1}. M_h is 1.01 % of body mass (Hartman 1961) which gives an M_h of 1.212 g, equivalent to a V_s of 0.367 ml. Haemoglobin concentration in Falconiformes is 0.154 g ml^{-1} (Prinzinger & Misovic 1994) which is equivalent to a maximum $C_{aO_2}-C_{\bar{v}O_2}$ of 0.159. Thus, the estimated $\dot{V}O_{2\max}$ is

Method 1: $\dot{V}O_{2\max} = 715 \times 0.367 \times 0.159$
$= 41.7$ ml min^{-1} (error of $+1.0$ %).

Method 2: $\dot{V}O_{2\max} = 252 \times 0.159$
$= 40.1$ ml min^{-1} (error of -2.9 %).

(ii) *European starling* (Sturnus vulgaris)

Torre-Bueno & Larochelle (1978) plotted a value of 22 ml min^{-1} (figure 2, p. 226) for the rate of CO_2 production of *S. vulgaris* (M_b is 0.0728 kg) flying at 18 m s^{-1}. With an RQ of 0.7 (Torre-Bueno & Larochelle 1978) this equates to an oxygen consumption of 31.4 ml min^{-1}. f_H is estimated to be 790 beats min^{-1} while M_h is 1.28 % (Magnan 1922), and this gives an M_h of 0.932 g and an estimated V_s of 0.279 ml. Using the average haemoglobin concentration for Passeriformes of 0.1595 (Prinzinger & Misovic 1994) gives an estimate for maximum $C_{aO_2}-C_{\bar{v}O_2}$ of 0.166. Thus, the estimated $\dot{V}O_{2\max}$ is

Method 1: $\dot{V}O_{2\max} = 790 \times 0.279 \times 0.166$
$= 36.6$ ml min^{-1} (error of $+16.6$ %).

Method 2: $\dot{V}O_{2\max} = 200 \times 0.166$
$= 33.2$ ml min^{-1} (error of $+5.7$ %).

(iii) *Budgerigar* (Melopsittacus undulatus)

The highest value of $\dot{V}O_2$ measured for *M. undulatus* (M_b is 0.035 kg) by Tucker (1968) was 20.8 ml min^{-1} while flying at 11.7 m s^{-1} in a wind tunnel with a +5° angle of tilt. f_H for budgerigars was measured as 930 beats min^{-1} (Aulie 1971), M_h as 1.4 % (Hartman 1961) giving M_h as 0.49 g and estimated V_s as 0.142 ml, and haemoglobin concentration of Psittaciformes as 0.1489 (Prinzinger & Misovic 1994). Thus, estimated $\dot{V}O_{2\max}$ is

Method 1: $\dot{V}O_{2\max} = 930 \times 0.142\ 0.152$
$= 20.1$ ml min^{-1} (error of 3.4 %).

Method 2: $\dot{V}O_{2\max} = 114 \times 0.152$
$= 17.3$ ml min^{-1} (error of -16.8 %).

(iv) *Ruby-throated hummingbird* (Archilochus colubris)

Chai & Dudley (1995) in their figure 4*a* (p. 725) plot a figure of 62 ml of oxygen g^{-1} h^{-1} for *A. colubris* flying in Heliox at an air density of 0.6 (kg m^{-3}), just prior to aerodynamic failure at air densities of 0.55–0.5. This value is equal to 3.65 ml min^{-1} for the average body mass in this study of 3.525 g ($n = 4$). An estimated f_H of 1085 beats min^{-1} is calculated from Bishop & Butler (1995; equation (12)). M_h is 2.3 % (Hartman 1961) which gives an M_h of 0.0812 g and an estimated V_s of 0.0215 ml. Average oxygen capacity in hummingbirds for six different species is 0.221 ml ml^{-1} (Johansen *et al.* 1987) which gives an estimate of 0.170 for maximum $C_{aO_2}-C_{\bar{v}O_2}$. Thus, the estimated $\dot{V}O_{2\max}$ is

Method 1: $\dot{V}O_{2\max} = 1085 \times 0.0215 \times 0.17$
$= 3.97$ ml min^{-1} (error of $+8.8$ %).

Method 2: $\dot{V}O_{2\max} = 23.38 \times 0.17$
$= 3.97$ ml min^{-1} (error of $+8.8$ %).

(v) *Broad-tailed hummingbird* (Selasphorus platycercus)

Wells (1993) studied the aerodynamic performance of *S. platycercus* while hovering with artificially added weights. Mean values for power input (W) are not reported but an adult female of 3.66 g (unloaded) had the highest body mass-specific power input figure of 400 W kg^{-1} (Wells 1993, figure 6). This value is equal to around 4.2 ml min^{-1}. f_H is estimated to be 1081 beats min^{-1} (Bishop & Butler 1995). M_h is 2.36 % (Hartman 1961) which gives an M_h of 0.0864 g and an estimated V_s of 0.0229 ml. Thus, the estimated $\dot{V}O_{2\max}$ is

Method 1: $\dot{V}O_{2\max} = 1081 \times 0.0229 \times 0.17$
$= 4.2$ ml min^{-1} (error of 0 %).

Method 2: $\dot{V}O_{2\max} = 24.69 \times 0.17$
$= 4.2$ ml min^{-1} (error of 0 %).

(*b*) *Examples for bats*

(i) *Megachiropteran* (Pteropus poliocephalus)

The highest value for $\dot{V}O_2$ reported by Carpenter (1985) was 154.9 ml min^{-1} for a 0.669 kg bat flying at 4 m s^{-1} airspeed. Mean f_H was 476 beats min^{-1} although this was measured at 6 m s^{-1}. M_h is 0.8 % of body mass (Carpenter 1985), which gives an M_h of 5.35 g and an estimated V_s of 2.1 ml. Haemoglobin concentration was around 0.169, which gives an estimated $C_{aO_2}-C_{\bar{v}O_2}$ of 0.178. Estimated $\dot{V}O_{2\max}$ is

Method 1: $\dot{V}O_{2\max} = 476 \times 2.1 \times 0.178$
$= 177.9$ ml min^{-1} (error of $+14.8$ %).

Method 2: $\dot{V}O_{2\max} = 932 \times 0.178$
$= 165.9$ ml min^{-1} (error of $+7.1$ %).

(ii) *Microchiropteran* (Phyllostomus hastatus)

$\dot{V}O_2$ measured by Thomas & Suthers (1972) from an individual *P. hastatus* ($M_b = 101$ g) flying at 5.8 m s^{-1} was 46.3 ml min^{-1}, and the mean f_H observed was 780 beats min^{-1}. Mean oxygen capacity was measured as 0.275, giving an estimated maximum $C_{aO_2}-C_{\bar{v}O_2}$ of 0.22. M_h was 0.94 % giving an estimated V_s of 0.36 ml. Estimated $\dot{V}O_{2\max}$ is

Method 1: $\dot{V}O_{2\max} = 780 \times 0.36 \times 0.22$
$= 61.8$ ml min^{-1} (error of $+33.5$ %).

Method 2: $\dot{V}O_{2\max} = 204 \times 0.22$
$= 44.9$ ml min^{-1} (error of 3.0 %).

The average error for predicting $\dot{V}O_{2\max}$ of birds is $+6.0$ % for method 1 and 1.0 % for method 2. The average error for predicting $\dot{V}O_{2\max}$ of bats is $+24.1$ % for method 1 and $+2.0$ % for method 2.

Both methods appear to give reasonable predictions for $\dot{V}O_{2\max}$, particularly given that none of the species

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examples consisted of variables measured from the same individuals. However, method 2 has a smaller overall error in the case of bats and birds and has the advantage of simplicity, and would appear to be the 'method of choice'.

5. SCALING OF MAXIMUM POWER INPUT ($P_{\mathrm{i,max}}$) OF BIRDS AND MAMMALS USING CARDIAC MASS

Figure 3*a* shows the heart masses of birds and mammals plotted against body mass; data for birds from Magnan (1922) and for adult mammals from primarily Crile & Quiring (1940). For birds M_{h} scales as

$$M_{\mathrm{h}} = 9.63\,M_{\mathrm{b}}^{0.93\pm0.02}\ (r^2 = 0.976,\ n = 228), \qquad (11)$$

where M_{b} is in kg and M_{h} is in g. For mammals M_{h} scales as

$$M_{\mathrm{h}} = 6.83\,M_{\mathrm{b}}^{0.959\pm0.024}\ (r^2 = 0.983,\ n = 105). \qquad (12)$$

However, the majority of mammals in the sample are larger than 1 kg in M_{b} while the majority of birds are less than 1 kg. This is clearly seen in figure 3*b*, which plots the relative heart mass of birds and mammals (as % of M_{b}) against M_{b}. The heart masses of the larger mammals (> 2 kg M_{b}) appear to lie within the extrapolated range for the birds, while the heart masses of the smaller mammals (< 2 kg M_{b}) appear to lie at the bottom of the range for birds (cf. Poupa & Ostadal 1969; Poupa & Lindstrom 1983). Very few small mammals have heart masses greater than 1% of M_{b}. One notable exception is that of the male and female weasel with heart masses of around 1.5% of M_{b}, which is the highest of any of the sampled mammals including the bats. For five species of bat, the mean relative M_{h} was only $1.0 \pm 0.07\%$ of M_{b}, ranging from the 5 g *Pipistrellus pipistrellus* ($M_{\mathrm{h}} = 1.26\%$) to the 146 g *Rousettus aegyptiacus* ($M_{\mathrm{h}} = 0.84\%$).

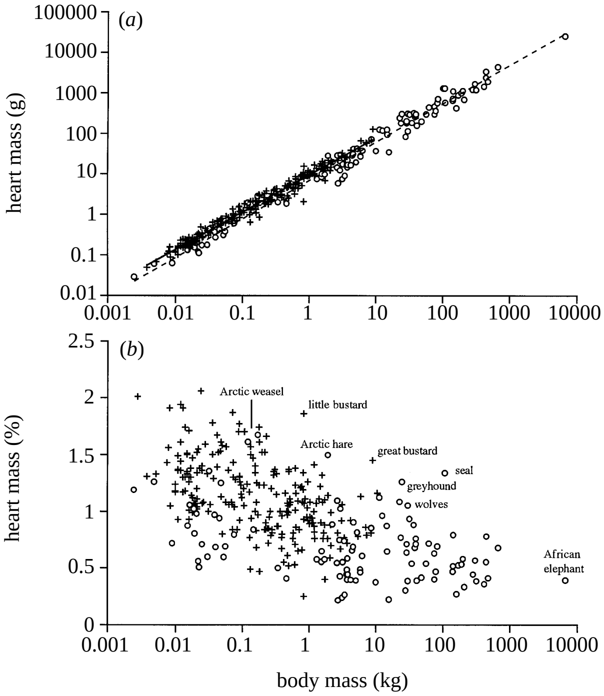

Figure 3. (*a*) Heart mass (g) and (*b*) relative heart mass as percentage (%) of body mass, of birds (+) and mammals (○) plotted against body mass (kg). Data for birds from Magnan (1922) and for mammals from Crile & Quiring (1940) and Kallen (1977).

An estimate for the scaling of maximum aerobic power input (aerobic $P_{\mathrm{i,max}}$) with respect to body mass can be calculated from the data for M_{h}, using the average figure for haemoglobin concentration for mammals and birds of 0.15, assuming that maximum $C_{\mathrm{aO_2}} - C_{\bar{\mathrm{v}}\mathrm{O_2}}$ scales with body mass as $M_{\mathrm{b}}^{0.00\pm0.05}$ (cf. Bishop & Butler 1995).

The estimated aerobic $P_{\mathrm{i,max}}$ for all birds (excluding hummingbirds due to their unique wing kinematics) is

$$\text{aerobic } P_{\mathrm{i,max}} = 80.6\,M_{\mathrm{b}}^{0.818\pm0.106}, \qquad (13)$$

and the estimated aerobic $P_{\mathrm{i,max}}$ for all mammals is

$$\text{aerobic } P_{\mathrm{i,max}} = 59.6\,M_{\mathrm{b}}^{0.844\pm0.11}. \qquad (14)$$

Thus, the aerobic $P_{\mathrm{i,max}}$ of birds and mammals appears to scale with a similar body mass exponent. The example of the weasel (figure 3*b*) suggests that the differential distribution of relative heart masses between birds and small mammals (< 2 kg M_{b}) is most likely to reflect a fundamental difference in their respective ecologies and limb musculature, rather than a fundamental biomechanical constraint that applies to the design of the cardiovascular system of mammals < 2 kg of M_{b}. For example, small mammals are mostly nocturnal and may be less reliant on escaping predation by the use of sustained levels of exercise, while the larger mammals are primarily diurnal and may be required to use relatively more sustained levels of activity when travelling around their territories or avoiding predation.

6. DISCUSSION

The conclusion from the above analysis is that reasonable predictions for the maximum oxygen consumption of birds during flight can be obtained by assuming that avian heart muscle has the same maximum physiological and biomechanical performance as that of terrestrial mammals, in contrast to the views of Pennycuick (1995, 1996). Relative M_{h} should be a good indicator of adaptive specialization for prolonged or sustained activities of both birds and mammals, and can be used to estimate a value for the maximum aerobic $P_{\mathrm{i,max}}$ using equation (10) and an estimate for maximum $C_{\mathrm{aO_2}} - C_{\bar{\mathrm{v}}\mathrm{O_2}}$. If no estimate for maximum $C_{\mathrm{aO_2}} - C_{\bar{\mathrm{v}}\mathrm{O_2}}$ is available, then it is reasonable to substitute the mean value for all birds and mammals of 0.154. In which case, $\dot{V}\mathrm{O}_{2\,\mathrm{max}}$ can be estimated from the cardiac muscle mass of both birds and mammals as approximately

$$\dot{V}\mathrm{O}_{2\,\mathrm{max}} = 33\,M_{\mathrm{h}}^{0.88\pm0.086}, \qquad (15)$$

while estimated aerobic $P_{\mathrm{i,max}}$ is approximately

$$\text{aerobic } P_{\mathrm{i,max}} = 11\,M_{\mathrm{h}}^{0.88\pm0.086}. \qquad (16)$$

Thus, relative aerobic adaptation can be assessed by plotting relative M_{h} against body mass, or by converting M_{h} into an estimate of $P_{\mathrm{i,max}}$.

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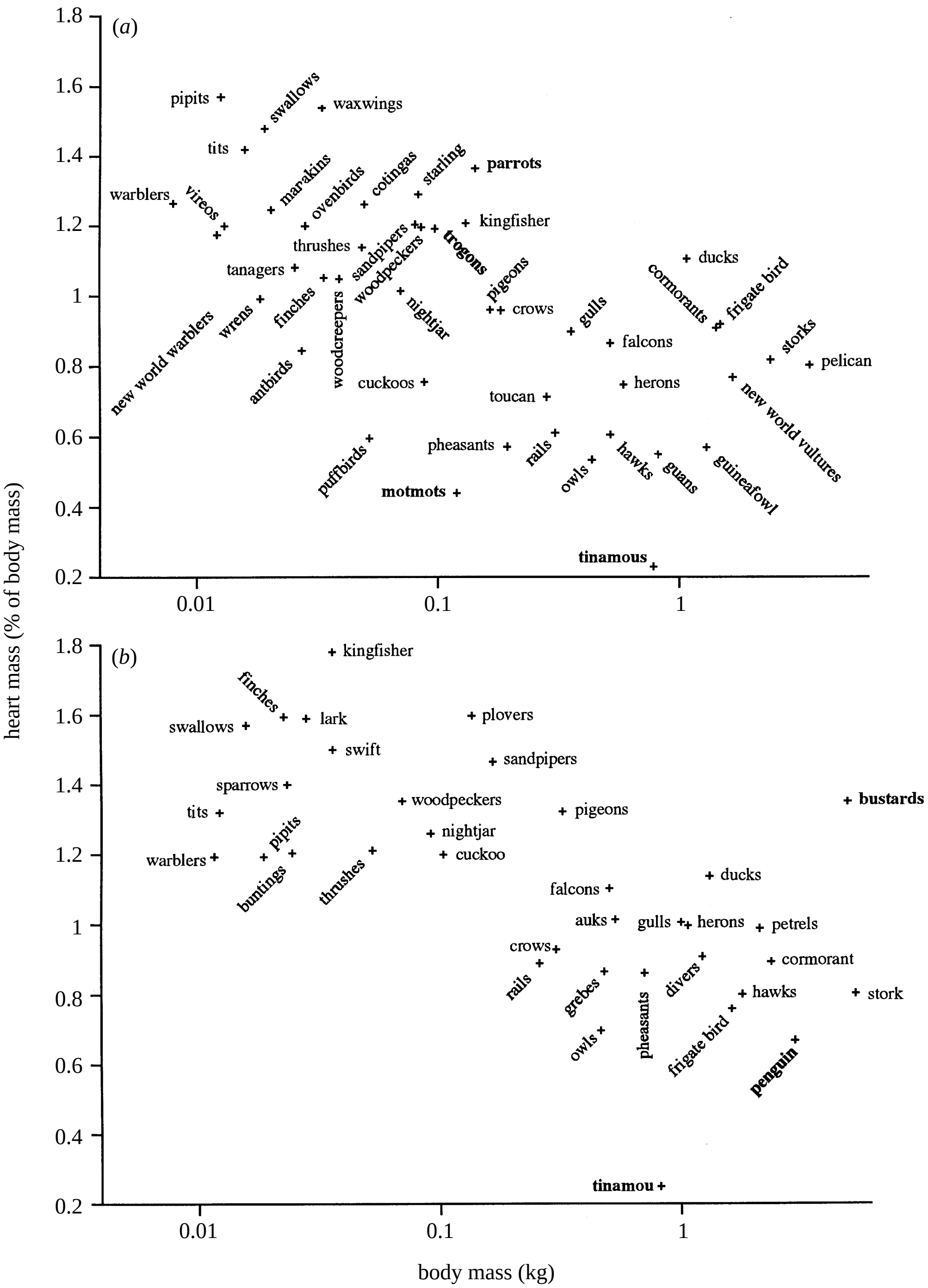

Figure 4. Mean family values for cardiac muscle mass as a percentage of body mass (%) plotted against body mass (kg). (*a*) Data from Hartman (1961) and (*b*) data from Magnan (1922).

Selected avian family means for relative M_h are plotted in figure 4*a* and figure 4*b* and indicate the inter-family adaptive diversity in aerobic capacity. The very small relative M_h of all three species of tinamou indicate that this family has the lowest aerobic ability of all bird species, although they have exceptionally large flight muscles. These birds live in tropical forests, have relatively small wings, and only perform burst flight when disturbed or when flying into trees to roost. 'Sit-and-wait' foragers such as the motmots also appear to have very small M_h. This contrasts with the large M_h of some other bird families that also live in forests, such as the parrots and trogons. The single species of penguin (figure 4*b*) is also of interest as it would indicate that these marine flightless birds are towards the lower end of the range of avian mass-specific aerobic capabilities. In contrast, figures 3*b* and 4*b* show that the representatives of the bustard family (Otidae) appear to range above the general allometric trend. The relative M_h of the 0.83 kg little bustard (*Tetrax tetrax*) and the 8.95 kg great bustard (*Otis tarda*) are 1.8% and 1.4%, respectively. These relative M_h values are even larger than those of the Anatidae which typically range from 0.8% to 1.1%. It may be tempting to dismiss these values as 'mistakes', but two other observations appear to substantiate the unusual nature of bustard flight muscles. Crile & Quiring (1940)

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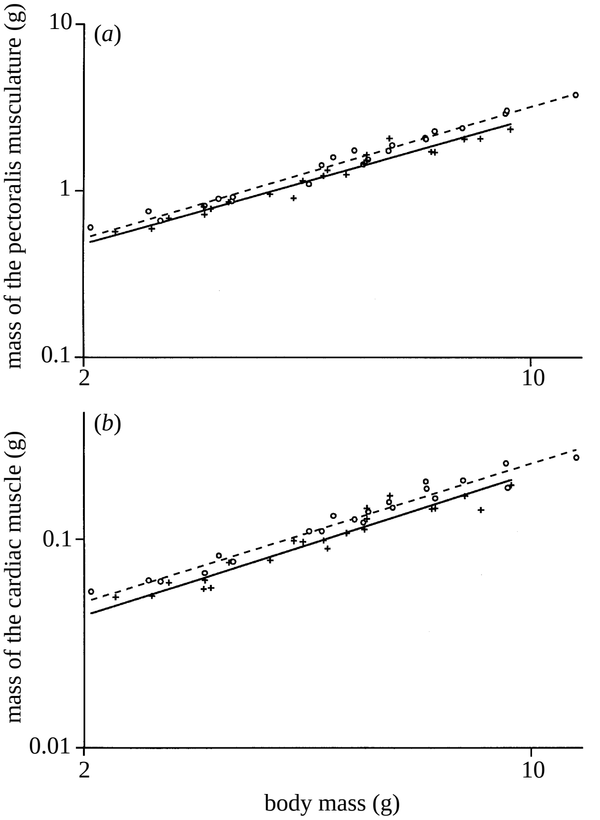

Figure 5. (*a*) Mass of pectoralis musculature (g) and (*b*) cardiac muscle mass (g), of male (○) and female (+) hummingbirds plotted against body mass (g). Data from Hartman (1961).

gave the following values for the relative heart masses of the African Kori bustard (*Choriotis kori*); a 5.54 kg female Kori bustard (1.1 %), a 10 kg male Kori bustard (1.0 %). In addition, Stickland (1977) showed that while 100 % of the area of the pectoralis muscle of the African helmeted guinea-fowl is made up of 'white' muscle fibres, 82 % of the area of the pectoralis muscle of the similarly sized white-bellied bustard is made up of 'red' fibres. European species of bustards may undergo local migrations, and great bustards have been recorded on a number of occasions in the UK. Thus, *O. tarda* may be the largest extant species of bird which is capable of a 'prolonged' mode of flight.

There are also some interesting intra-family differences in aerobic capacity indicated in the M_h data of Hartman (1961) and Magnan (1922). The 19 species of Columbidae (pigeons and doves) have the following relative heart mass means of 1.294 %, 1.023 %, 1.155 % and 1.23 % for the genera *Columba*, *Columbigallina*, *Claravis* and *Turtur*, respectively, and 0.663 % and 0.57 % for *Leptotila* and *Geotrygon*, respectively. The 11 species of Falconidae (falcons) have means of 1.142 % and 1.11 % for the genus *Falco* and *Caracara*, respectively, and 0.64 % and 0.6 % for *Micrastur* and *Herpetotheres*, respectively. In both the above examples, differences in M_b and mass of the pectoralis musculature do not reflect these differences in relative M_h, but the genus with the relatively small hearts occurs predominantly in tropical forests and is likely to be relatively sedentary. As intra-family pectoralis muscle mass is fairly constant in these examples, it is reasonable to assume that the relatively sedentary species are more dependent on anaerobic metabolism to support their flight activity.

Other interesting examples might be found by looking at sexually dimorphic examples of M_h, or by investigating closely related species that may have very different flight demands. Hartman (1961) found 19 species where the male had significantly larger heart mass ratios than the female, and nine of these were hummingbirds. Hummingbirds are numerically one of the most successful families of birds, and are thought to be the most specialized for dependence on aerobic metabolism. Thus, it would be expected that there should be a close relationship between flight muscle mass and heart muscle mass. It is interesting to note, therefore, that there is a consistent sexual dimorphism in data on both total flight muscle mass (M_{fm}) and relative M_h for 22 species of hummingbird (Hartman 1961). Figure 5 shows that, while there is no significant sexual dimorphism in the body mass scaling exponents for either M_{fm} or M_h, female hummingbirds tend to have significantly smaller flight muscles than those of males (male $M_{fm} = 0.237\ M_b^{1.131 \pm 0.077}$, $r^2 = 0.979$; female $M_{fm} = 0.227\ M_b^{1.08 \pm 0.106}$, $r^2 = 0.955$), and significantly ($P < 0.001$) smaller M_h than those of males (male $M_h = 0.026\ M_b^{0.945 \pm 0.081}$, $r^2 = 0.966$; female $M_h = 0.022\ M_b^{0.97 \pm 0.123}$, $r^2 = 0.926$), but that this difference is not evident when heart mass is plotted against flight muscle mass. This is consistent with the hypothesis that there should be a close relationship between flight muscle mass and the flow of blood that is required to support the extra aerobic tissue (Bishop & Butler 1995; Bishop *et al.* 1996). The estimated scaling of the aerobic $P_{i,\max}$ of male hummingbirds, with respect to M_b (g), and based on M_h (g), is

$$\text{male aerobic } P_{i,\max} = 0.51\ M_b^{0.832 \pm 0.071}, \tag{17}$$

while the estimated aerobic $P_{i,\max}$ of female hummingbirds is

$$\text{female aerobic } P_{i,\max} = 0.44\ M_b^{0.853 \pm 0.108}. \tag{18}$$

This slight sexual dimorphism in the morphology of the locomotor musculature suggests that when considering hummingbird flight performance it may be useful to control for sexual differences. The other ten species of birds where males had significantly larger heart mass ratios (Hartman 1961) were widely distributed taxonomically, and included finches, tanagers, wrens, tyrant flycatchers, ovenbirds, woodcreepers and the domestic chicken. In almost all cases, the male also had relatively larger flight muscle masses than the female, which would indicate that the male might require an additional aerobic locomotor capacity perhaps associated with courtship or the carrying of sexual adornments.

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 demand (Hickson *et al.* 1983; Marsh 1984; Dreidzic *et al.* 1993; Bishop *et al.* 1996). Thus, it might be anticipated that where additional energetic 'costs'

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occur seasonally (e.g. due to migratory fattening or the development of secondary sexual characteristics) then the relevant cardiac and locomotor musculature might also be regulated seasonally. However, it is obviously important that samples are taken at the relevant time of year. For example, the eight species of trogon do not display any sexual difference in heart mass in the sample collected by Hartman (1961) although the male of one of the species, the resplendent quetzal (*Pharomachrus mocinno*), has up to 1 m long tail feathers during the breeding season. The male resplendent quetzal does have slightly larger pectoralis musculature and may rely on additional anaerobic metabolism, but it is not clear if the samples were collected during the breeding season. In contrast, Bishop *et al.* (1996) showed that both cardiac and pectoralis muscles hypertrophy during the pre-migratory fattening period of the barnacle goose (*Branta leucopsis*). Thus, the fact that the cardiac muscle may be capable of a limited amount of seasonal hypertrophy is an important observation, both due to the intrinsic interest of studying cardiovascular adaptation to changes in energy demand, and also as a confounding variable in the practical use of f_H to estimate the energetics of animals in the field (Nolet *et al*. 1992; Bevan *et al*. 1995; Butler *et al*. 1995; Woakes *et al*. 1995). For example, when large changes in structural M_b are expected to occur during the period of monitoring f_H it may be important to incorporate data on any possible changes in M_h, or alternatively it may be necessary to carry out $\dot{V}O_2$ and f_H calibrations during more than one time in the year. It should also be assumed that haemoglobin concentration (or haematocrit) may also be a confounding structural variable. Thus, it is concluded that data on cardiovascular and flight muscle morphology provide essential information regarding the behavioural, ecological and physiological significance of the flight performance of animals. Routine collection of data on f_H, relative M_h, haematocrit and haemoglobin concentration, could provide a reasonably simple method for the monitoring of possible seasonal variation in energetic costs (or perhaps inter-individual variation in heart-rate calibration and exercise performance) and with an enhanced accuracy to that of monitoring f_H alone.

The limited information on the relative M_h of bats (Kallen 1977; Carpenter 1985, 1986), suggests that they generally have lower maximum body mass-specific aerobic capacities than those of birds of a similar body mass. This is also consistent with the results of Carpenter (1985, 1986) who reported that a number of species of Megachiropteran bats appeared to have a very limited range of speeds over which they were capable of 'prolonged' continuous flights in a wind tunnel. In addition, bats appear to have relatively smaller flight muscle masses than birds (Thomas 1989) and should, therefore, require relatively less cardiovascular support. A 5 g *Pipistrellus pipistrellus* bat has a relative M_h (1.26 %) that is slightly larger than that of a 3 g *Suncus etruscus* shrew (1.19 %), but nothing like as large as that of a typical small species of hummingbird at around 2 % of M_b. Conversely, given the tremendous range in relative M_h that evidently occurs in both birds and mammals, it is unwise to assume that all birds have a larger M_h and, therefore, a greater 'aerobic scope' than that of similarly sized mammals (Magnan 1922; Crile & Quiring 1940; Hartman 1961; Grubb 1983). Wild dogs and wolves have a relative M_h of around 0.7 to 1.0 % of M_b (cats are usually around 0.4 to 0.6 %) and this is fairly similar to that of various species of swans and geese (0.9 to 1.1 %) and that of the cursorial emu (0.85 %), while male and female Arctic hares appear to have a relative M_h of between 1.1 and 1.5 %, respectively. The three-toed sloth has a relative M_h of only 0.24 %, but so do some species of tinamou.

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