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The energy cost of flight: do small bats fly more cheaply than birds?

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Abstract Flapping flight is one of the most expensive activities in terms of metabolic cost and this cost has previously been considered equal for the two extant vertebrate groups which evolved flapping flight. Owing to the difficulty of obtaining accurate measurements without disturbing flight performance, current estimates of flight cost within the group of small birds and bats differ by more than a factor of five for given body masses. To minimize the potential problem that flight behaviour may be affected by the measurements, we developed an indirect method of measuring flight energy expenditure based on time budget analysis in which small nectar-feeding bats (Glossophaginae) could continue their natural rhythm of flying and resting entirely undisturbed. Estimates of metabolic flight power based on 172 24-h time and energy budget measurements were obtained for nine individual bats from six species (mass 7–28 g). Metabolic flight power (P_F) of small bats was found to increase with body mass following the relation $P_F = 50.2\ M^{0.771}$ ($r^2 = 0.96$, $n = 13$, P_F in W, M in kg). This is about 20–25% below the majority of current predictions of metabolic flight cost for small birds. Thus, either the flight cost of small birds is significantly lower than has previously been thought or, contrary to current opinion, small bats require less energy to fly than birds.

Key words Flight power · Daily energy budget · Energy metabolism · Allometry · Glossophaginae

Abbreviations *A* daily assimilated food energy · *DEE* daily energy expenditure · *E* caloric value of body stores · *LD* light/dark ratio · *M* body mass · m_b 24-h body mass change · P_F metabolic flight power · P_R mean resting metabolic rate · t_F time spent in flight during 24 h · t_R time spent resting during 24 h

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Introduction

By gaining access to the skies, flying animals have not only mastered an elite form of locomotion but have also evolved the most economical means of any land-based animal of transporting a unit of body mass over a given distance (Tucker 1970). Nevertheless, in terms of its metabolic requirement, flapping flight is one of the most expensive activities (c.f. Norberg 1990; Chai and Dudley 1995). Detailed analyses of flight energetics have concentrated mostly on large animals, even though the majority of birds and bats are small species which weigh less than 35 g (van Valen 1973). Those estimates of flight cost that are published for the size class below 35 g differ by more than a factor of five for given body masses (Masman and Klaassen 1987; Rayner 1990). Although some of this variation may have a biological basis, most of it is more likely to be due to problems in the interpretation of data collected by techniques that are not very appropriate for small animals.

To minimize the potential problem that either flight behaviour may be affected by the measurements themselves or that the measurement resolution may be compromised by the technique utilized, we have developed an indirect measurement method that allows an individual animal to rest and fly undisturbed in a flight room, following its natural activity rhythm throughout the duration of an experiment over several weeks.

With this method we have determined the metabolic cost of flight and its dependence on body mass for six nectarivorous bat species of body mass in the range 7–28 g. We studied nectar-feeding glossophagine bats because this group meets three important requirements of our indirect method: (1) the natural level of flight activity is very high, 3–8 h per night (von Helversen and Reyer 1984; von Helversen 1986; Winter et al. 1993) and accounts for about 50% of the daily energy budget, (2) the bats remain very active in captivity, and (3) the nectar-sugar diet is almost completely absorbed so that daily energy assimilation can easily be quantified.

Daily energy budget model

Our approach is based on analysis of the 24-h time and energy budgets of individual animals. Time-budget analysis is often used to estimate the daily energy expenditure (DEE) of animals when the costs of the various activities are known. We have reversed this approach in that we start with a known DEE and time budget and proceed to find the costs of the individual types of activity. The energy released by an animal during 24 h is the sum of the energy derived from the assimilated food (= A) and that mobilized from (or deposited as) body stores [= 24-h body mass change (m_b) × caloric value of body stores (E)]. A bat spends its time either flying or hanging at rest, and hence its energy expenditure has two basic components: flight activity [= flying time (t_F) × metabolic cost of flight (P_F)] and the energy-consuming processes during rest, including thermoregulation [= resting time (t_R) × cost of resting (P_R)]. This relation is described by the daily energy balance equation

$$A + m_b E = t_F P_F + t_R P_R. \qquad (1)$$

The cost of growth can be neglected for adult animals outside the reproductive season. As explained in Fig. 1, four parameters of Eq. 1 can be determined in our flight room with automatic devices for a free-flying bat: the assimilated food energy A, the 24-h body mass change m_b, time spent in flight t_F, and resting time t_R. For each individual 24-h observation period we thus obtain a daily energy balance equation of the form of Eq. 1 with these four known parameters and with three unknowns: flight cost P_F, resting cost P_R and caloric value of body stores E. A series of such experiments for each individual animal produces a set of daily energy balance equations, which can be solved for the three unknowns (P_F, P_R and E) by multiple linear regression analysis through the origin. This analysis with the dependent variable A and the three independent variables t_F, t_R and m_b thus gives three partial slopes for the unknown energy equivalents P_F, P_R and E respectively.

Materials and methods

Animals

The study was based on nine individuals from six species of nectar-feeding bats, half of which were offspring from our breeding colonies maintained in two free-flight tropical greenhouses at Erlangen University. The bats fly about freely and feed by natural hovering in the greenhouses, so that they were well trained for flight even before the experiments. The species and individuals used are listed in the legend to Fig. 2.

Flight cage

Bats were trained to feed in a flight cage by alternately visiting two simulated flowers positioned 14 m apart and hovering in front of them to withdraw the sugar solution (Fig. 1). The flight tunnel had the shape of a flat 'U' with the following dimensions: total length 14 m, height 2 m and width 1 m (inset Fig. 3). Owing to the smooth plastic sides and ceiling of the flight tunnel, bats could only roost on a piece of cork that was suspended from the base of an electronic balance (Mettler PM-100). Thus, from the times of departure and arrival at this balance we could automatically record each flight interval with 1-s resolution. Average body mass was derived from the computer-stored data as the mean of ten measurements. Change of body mass on subsequent days was assumed to represent change in body reserves. Thus, possible differences in the degree of hydration were ignored. 24-h body mass change m_b was derived from measurements at a fixed hour of the daily cycle (1 h before the dark period). Bats were made to void their urine during a short flight (5–20 s) previous to this measurement by tapping on the cage wall. Experiments with the large *Leptonycteris curasoae* were conducted in a similarly equipped but larger flight tunnel which was straight and 35 m in length.

Nectar feeder

One nectar pump and feeder were located at each end of the U-tunnel. A nectar pump consisted of a stepping-motor driving a glass syringe filled with nectar. The motor was controlled by a computer (MS-DOS/286) equipped with a digital I/O-interface (Meilhaus ME 14-B) with quartz clock and counter functions to provide the timed pulses for the stepping-motor driving circuit. The self-written control program also handled the data input from the balance (via the serial port) and from the infrared electronic eyes (via digital inputs).

A feeder consisted of a small glass or plastic tube (diameter 15 mm, depth 40 mm) oriented horizontally, into which nectar was

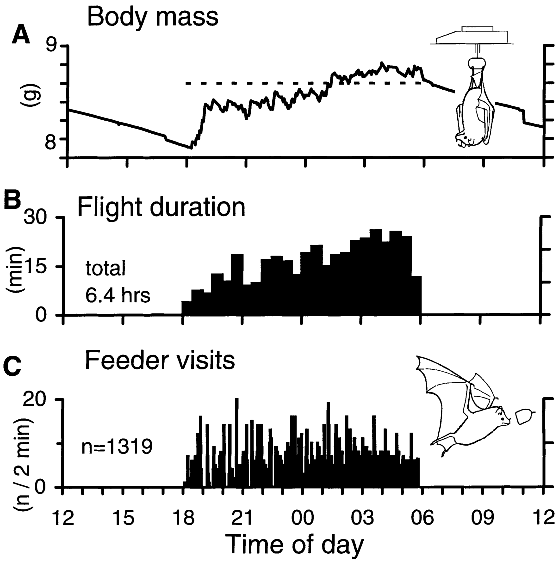

Fig. 1A–C Twenty-four hour activity pattern and food energy intake of a single bat (*G. commissarisi*) in a flight cage under LD 12:12. **A** Body mass and flight activity were monitored automatically as the only roost available to the bat was suspended from an electronic balance. Body mass increased rapidly after the onset of feeding activity owing to rehydration and the ingested food. Sudden mass decreases during daytime were caused by the voiding of urine. The dashed line indicates mean body mass during flight activity. **B** Time spent in flight during consecutive 30-min intervals. Duration of individual flights were calculated from the times of departure and arrival at the balance. **C** Number of feeder visits during consecutive 2-min intervals. During each hovering visit the bat received a fixed amount of "nectar" from a computer controlled pump pumped through a small hose (1 mm diameter). An acrylic tube was placed around the feeder and the hose to prevent the bat from hanging from it. During each feeder visit the bat received a fixed volume of nectar. The feeders were programmed so that the bat had to visit them alternately in order to receive food. During feeding, the rostrum of the hovering bat was partly inserted into the feeder and at times the bat's chin may have supported some of its body mass. Hovering duration was recorded to 5-ms resolution by interruption of an infrared light beam at the feeder opening that responded as soon as the bat inserted the tip of its rostrum into the feeder. Time of arrival at a feeder was recorded with 1-s resolution.

Artificial nectar consisted of a solution of sucrose, glucose and fructose (26:37:37 parts) in tap water with a sucrose/hexose ratio of 0.34 taken as typical for nectar from bat flowers (Baker and Baker 1990). Sugar concentration of the artificial nectar was determined with an Atego refractometer to a precision of ±0.2% and was kept around 17% mass/mass (=183.3 mg ml^{-1}) which is also typical for nectar from bat flowers (von Helversen and Reyer 1984; von Helversen 1993). For the conversion of the refractometer readings to mass/volume the differences in refractive index (Wolf et al. 1983) of the three components of the sugar solution were taken into account. Sugar intake was converted to kJ by multiplying by 15.91 kJ g^{-1}. This value combines the published caloric equivalents of glucose/fructose and sucrose according to their respective concentrations in the nectar solution (Wieser 1986).

The daily assimilated food energy was calculated as the product between total number of feeder visits, caloric value of the food reward and assimilation efficiency for the pure sugar diet of 0.99. This high assimilation efficiency for a pure sugar diet was determined in a separate study by quantitative analysis of sugar residues in fecal/urine samples collected under the bat's roost by using a spectrophotometric UV-method (Bergmeyer and Bernt 1974; Winter 1998). Similar efficiencies are known for hummingbirds (Hainsworth 1974).

It was critical for a correct estimate of daily energy intake that the bats consumed without spillage all nectar delivered. To avoid the problem of spillage, nectar was available to the bats only in quantities (20–50 µl) small enough to be easily absorbed by their brush-tip tongues. In addition, a bat always inserted its forehead into the feeder opening while licking nectar so that the tongue remained entirely within the feeder tube during feeding. Small droplets of liquid that might have fallen from the tongue should thus have remained within the feeder tube.

Flight speed

In both theory and practice flight cost varies nonlinearly with flight speed and reaches a minimum at minimum power flight speed (c.f. Norberg 1990). As flight speed during the experiments was variable, flight cost here probably exceeded the minimum power flight cost which is the standard measure for interspecific comparison. Therefore, we measured flight speed during the experiments with the help of 15 infrared photocells connected to a computer and placed at regular intervals along the flight path between feeders A and B (Fig. 3). Instantaneous flight speed was computed from the time interval between the interruptions of two adjacent photocells. From these measurements we computed the difference between actual flight speed and the theoretically predicted minimum power speed (Norberg and Rayner 1987; see Fig. 3). The extra flight power owing to this deviation from minimum power speed was then estimated from the flight power curve directly measured for a 93 g bat (Thomas 1975). This gave us a percentage estimate of the extra flight power spent by a bat not flying at minimum power flight speed. Periods of hovering flight were not included in this calculation, as hovering flight accounted for only 2–4% of total flight time and the cost of hovering is unknown.

Experimental procedure

To increase the variability of total flight duration per night on different nights during the experiment, the amount of a single food reward was varied between 10 µl and 50 µl and the light:dark ratio between LD 12:12 and LD 20:4. Two to three days of such experiments on a pure sugar diet were followed by 1–3 "pause" days, during which the animal received a balanced diet. For each individual, the measurement series was preceded by a training phase lasting several weeks.

During experiments with an individual bat, the temperature within the flight cage was stable to ±1 °C but ranged between 16 °C to 28 °C for the experiments with the different individuals (see Table 1). In general, we tried to perform the experiments within the upper range of natural temperatures for these bats, in order to minimize energy expenditure on thermoregulation. The temperatures could not be too high, however, to avoid problems with the heat balance during flight activity. Experiments with the larger *Leptonycteris* could not be conducted at higher temperatures, as our only location for setting up the 35-m flight tunnel necessary for this larger species had a constant temperature of 16 °C. Relative humidity during the experiments was between 55% and 60% and air pressure was around 980 mbar.

Results

As a rule the flight activity was distributed over the whole night, with a total duration of 1–9 h; the total distance covered in a night could be as great as 100 km. The average amount of nectar consumed, during 300 to 2000 feeder visits, corresponded to roughly 150% of an individual's body mass. The trained animals flew in regular alternation between the opposite ends of the flight cage. Only at the beginning of the training phase was the flight activity more general, as the bats closely investigated all corners by hovering and slow manoeuvring flight.

The bats' nocturnal activity was not entirely restricted to feeding flights; on the contrary, the total flying time during a night was longest when large amounts of food were obtainable at each feeder visit. In these circumstances a bat flew back and forth over the length of the cage at its usual speed, but visited a feeder on average only on every tenth approach. Hence prolonged flight activity was not necessitated by small food portions, but rather was a voluntary concomitant of high food availability.

A total of 172 24-h time and energy budgets were recorded from nine individuals of six species of glossophagine bats (Fig. 2, Table 1). The daily energy expenditure increased significantly as a bat spent more time in flight during its activity period. Indeed, the variation in daily energy expenditure was almost completely accounted for by differences in total flight duration. Therefore, the food energy intake A could be satisfactorily explained with the linear energy-balance model formulated by Eq. 1 (r^2 = 0.90–0.98, Table 1). With multiple regression analysis the metabolic cost of flight P_F could be determined with a relative standard error between 2% and 8% (Table 1 and Fig. 2). Flight cost was higher for the larger species. The allometric relationship between P_F and body mass is given in Fig. 4.

The power required for flight at the minimum power flight speed may still be 5–15% lower than the values

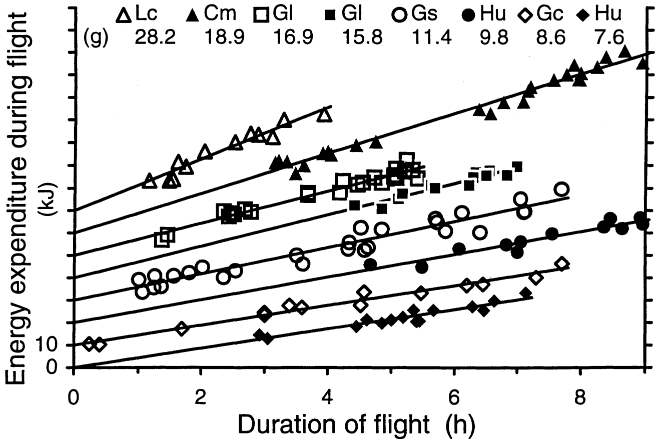

Fig. 2 Flight energy expenditure of glossophagine bats as a function of daily flight duration. Data are from 24-h recordings of time budget and energy intake as explained in Fig. 1 (numbers are mean body masses during flight; for clarity in the graph the zero offset was incremented by 10 kJ for successive data sets; see Table 1 for slopes of regressions). Slopes for individual bats were derived by multiple regression through the origin based on the linear model of Eq. 1 with the dependent variable *daily assimilated food energy* (A) and the three independent variables *flying time* (t_F), *resting time* (t_R) and *24-h body mass change* (m_b). This gave three partial slopes for the unknown energy equivalents P_F, P_R und E respectively. The partial slopes for metabolic flight energy expenditure (P_F) are shown here (all highly significant with $P < 0.001$). Energy expenditure during flight (plotted here) was calculated from daily energy expenditure ($=A + m_b E$) minus energy expenditure for resting ($= t_R P_R$). An additional data set for *Cm* is included only in Table 1. The abbreviations identify the species as follows (origin in brackets): *Cm Choeronycteris mexicana* (Mexico), *Gc Glossophaga commissarisi* (Costa Rica), *Gl G. longirostris* (Grenada), *Gs G. soricina antillarum* (Jamaica), *Hu Hylonycteris underwoodi* (Costa Rica), *Lc Leptonycteris curasoae* (Mexico) (Chiroptera: Phyllostomidae)

determined here. This is due to the deviation of flight speed during the experiments from the (predicted) minimum power flight speed (Fig. 3). This estimate of the difference between flight power measured here and minimum flight power must be regarded with caution, however, as the underlying assumption, namely that contemporary aerodynamic models accurately predict the relationship between flight power and flight speed in small vertebrates, still needs to be verified.

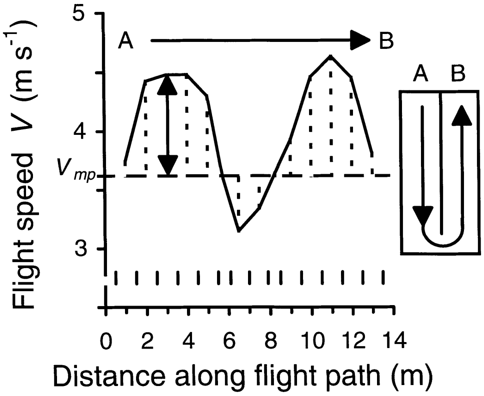

Fig. 3 Flight speed profile (solid curved line) of a bat (*G. soricina*) flying from feeder A to B along a U-turn flight path (inset right = top view). Flight speed reached a minimum during the U-turn at 7 m. The horizontal dashed line indicates the predicted minimum power speed ($V_{mp} = 3.69$ m s^{-1}, for mass 11.7 g, wing span 0.269 m and wing area 0.0108 m^2, Norberg and Rayner 1987). The vertical dotted lines and double headed arrow mark the *difference* between measured flight speed and minimum power speed. Data points are means from more than 1000 passes of the bat between A and B, timed by a computer connected to 15 infrared photocells (positions of photocells indicated by dashes along abscissa)

Discussion

The approach of using multiple regression analysis to solve a set of time budget/energy intake equations for the unknown cost coefficients allowed us to estimate the cost of forward flight. The high degree of correspondence between the predictions of the regression model and the measured energy intake rates ($r^2 \geq 90\%$, Fig. 2,

Table 1 Energy expenditure for flight (P_F) and rest (P_R) and the caloric equivalent of body stores (E) in nectar-feeding glossophagine bats as determined by regression analysis from 24-h time and energy budget measurements. See Fig. 2 for species abbreviations and method of analysis. s = standard error of the regression coefficient, n = number of 24-h time and energy budget measurements of type Eq. 1. *Mass* is mean body mass during flight activity (see Fig. 1); daytime mass of the resting bat was approximately 10% lower (see Fig. 1). T_a is ambient temperature in °C during the experiments. *%DEE* shows the relative contributions of the expenditures for flight and resting to daily energy expenditures

Species	Mass	Regression analysis										
		Flight cost P_F			Resting cost P_R				Storage E		r^2	n
	g	W	± s	% DEE	W	± s	T_a	% DEE	kJ g^{-1}	± s		
H.u.	7.6	1.20	0.09	69	0.19	0.027	27°	31	33.0	5.6	0.91	15
G.c.	8.6	1.23	0.06	51	0.25	0.016	28°	49	23.4	2.0	0.98	14
H.u.	9.8	1.41	0.11	63	0.27	0.054	27°	37	22.8	8.5	0.90	12
G.s.	11.4	1.63	0.07	56	0.27	0.015	26°	44	39.0	3.3	0.94	28
G.l.	15.8	1.96	0.16	62	0.38	0.053	23°	38	30.9	3.4	0.91	13
G.l.	16.9	1.99	0.08	47	0.43	0.017	22°	53	41.9	2.6	0.96	24
C.m.	18.9	2.45	0.06	60	0.51	0.021	23°	40	10.7	2.7	0.97	28
C.m.	20.2	2.69	0.12	47	0.53	0.030	24°	53	36.3	3.1	0.96	25
L.c.	28.2	3.16	0.28	24	1.03	0.029	16°	76	42.5	4.8	0.90	13

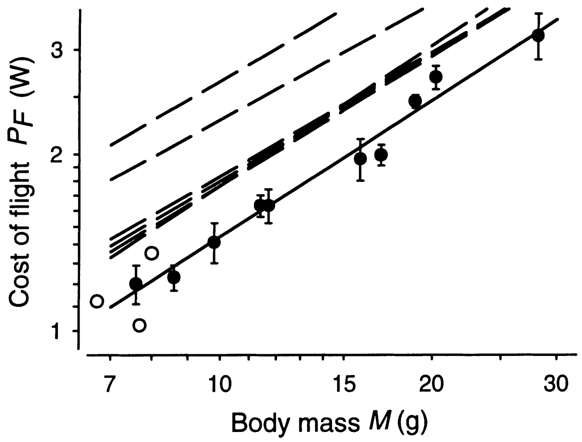

Fig. 4 Energy expended in flight by small bats and birds as a function of body mass. Closed symbols are estimates of metabolic flight cost (P_F) from this study (see Table 1) as given by the analysis of the data in Fig. 2 and include a value for *Gs* 11.7 g published previously (Winter et al. 1993). Open symbols are the only other data available for small bats (Speakman and Racey 1991). The best fit equation (solid line) relating flight energy expenditure to body mass for this data set of small bats was $P_F = 50.2\ M^{0.771}$ (P_F in W, M in kg, $r^2 = 0.96$, $n = 13$). Dashed lines are allometric functions relating flight cost with body mass in birds [references from top left down are: Kendeigh et al. 1977 (passerines); Wieser 1986; Kendeigh et al. 1977 (non-passerines); Berger and Hart 1974; Butler and Woakes 1985; Rayner 1990; Masman and Klaassen 1987 non-windtunnel]

Table 1) was made possible by using a fully automated timing, weighing, and food dispensing system which minimized disturbance and handling of the animals.

The reliability of the flight cost estimate with this indirect method depends on the accuracy with which the energy equivalents of the two other parameters in the model are determined. These other parameters are the cost of resting P_R and the energetic equivalent of body stores E. The behavioural category "resting" as used in the present study combines an alert resting (between flight activity) during the night in absorptive condition and a daytime resting of the animal in post-absorptive condition. Such an average resting metabolism is higher than the standard resting metabolic rate. Rates determined here (Table 1) were therefore approximately 25% higher than previous measurements of oxygen consumption during rest that are available for the two species *G.s.* (McNab 1969, 1988) and *L.c.* (Carpenter and Graham 1967) taken at corresponding ambient temperatures.

The tropical glossophagine bats are incapable of entering deep torpor (McNab 1969; McManus 1977) and this inability was an important prerequisite for our methodological approach based on time and energy budget analysis. Our observations confirmed that bats were always immediately active when disturbed at their roost and thus never showed any obvious sign of a hypothermic state. Therefore, drastic changes in resting energy expenditure during a single measurement series are unlikely to have been a significant source of error or bias for this present study.

The second energy parameter estimated here was the caloric value of body stores E with a mean value of 31 kJ g^{-1} (Table 1). It should be noted that the mass difference m_b measured here was not the instantaneous mass loss during prolonged flight activity without food intake (Nachtigall 1995) but instead the mass difference of the animal between successive 24-h intervals. Thus, m_b could be negative (fuel mobilization) or positive (fuel storage). The estimated 31 kJ g^{-1} for E is a clear indication that the bats converted sugar into fat (39.2 kJ g^{-1}, Wieser 1986) as their major energy reserve. This conversion mechanism, which results in a 9-fold reduction in mass over glycogen storage, reduces the cost of transport and appears to be common in a wide range of animals (Schmidt-Nielsen 1983). Such a mechanism of fat storage is also known for nectar-feeding hummingbirds (Suarez et al. 1990). The remaining difference between the energy coefficients estimated here and the caloric value of fat of 39.2 kJ g^{-1} may be accounted for by three different factors: (1) the loss of water associated with the depletion of fat reserves (body fat contains up to 10% water, Schmidt-Nielsen 1983), (2) a variable degree of glycogen mobilization or deposition and (3) error of estimate. An error in the determination of the energy equivalent of body stores E, however, had only a small effect on the overall estimate of daily energy expenditure. The average contribution of body reserves to the total daily energy input during the experiments was ±7%. Thus even a 50% error in the estimate of the energy equivalent E would lead to an error of only 3.5% of the DEE.

Our flight power estimates are corroborated by the only other data set for flight costs of small bats, which was obtained outside a windtunnel using the doubly labelled water technique (Speakman and Racey 1991; see Fig. 4). In the latter experiments the bats flew in "slow flight with frequent turning and occasional hovering" (Racey and Speakman 1987), which these authors also interpreted as involving flight costs higher than minimum power flight cost. Combining the data for small bats (mass 7–28 g) yields the allometric relationship $P_F = 50.2\ M^{0.771}$ ($r^2 = 0.96$, $n = 13$, P_F in W, M in kg). Metabolic flight power as given by this equation is 15 times the basal metabolic rate as predicted by an allometric equation for bats (McNab 1988). Maximum values of flight power in bats may still be 70% higher than the values found here. This is predicted from an analysis of windtunnel measurements of large bats at maximum speeds (Thomas 1987).

It has been generally assumed that the cost of flapping flight is the same for small birds and bats (Rayner 1990; Norberg 1990; Speakman and Racey 1991). Empirical predictions for flight cost of small birds may be obtained from allometric equations derived by bivariate correlation analysis from the over 100 metabolic flight power measurements published for birds by various authors. Such analyses have provided some explanations for the large variance in the data available for birds (Masmann and Klaassen 1987; Rayner 1990). Measurements obtained from flight in windtunnels tend to be higher than those measured outside windtunnels. Small birds with specialized adaptations to flight such as found in the *extremely aerial species* (e.g. swifts and swallows) are associated with a lower metabolic flight cost while the flight style of hummingbirds can lead to extremely high values of metabolic flight power (Berger 1985; Chai and Dudley 1995). In comparision to small bats, the flight power of small birds as predicted by the majority of allometric equations, is 20–100% higher (Fig. 4). The predictions of the two most comprehensive analyses of the available data for birds exceed the values found for small bats by 20–25% (Masmann and Klaassen 1987; Rayner 1990). Only one recent analysis, based on a subset of the data analysed by these authors, predicts a metabolic flight power for small birds that is within the range of values found in the present study for bats (Norberg 1996). The different values obtained in this latter analysis may come from the larger number of *extremely aerial species* in the data set, underlining the fact that the accuracy of such allometric equations as a predictor of flight metabolism in small birds is still uncertain.

The difference between the flight power of small bats and birds is likely to be a conservative estimate, as the cost of minimum power flight in small bats is probably even lower than the values found here. In view of the methodological difficulty of measuring the flight costs of small birds (Masman and Klaassen 1987; Rayner 1990), it cannot be ruled out that previous estimates were on average too high – that is, that the metabolic cost of flapping flight in small vertebrates is lower than has previously been thought. If this is not the case, it follows that cost of flapping flight is distinctly less for small bats than for small birds. While separating these two options is the most interesting aspect, more reliable data for small birds is needed for its resolution. A potential energetic advantage for small bats may, however, result from the lower wingloading, wingbeat frequency and minimum power speed of bats as compared to birds (Norberg and Rayner 1987; Norberg 1990; Rayner 1990).

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