FLIGHT COST AND ECONOMY OF NECTAR-FEEDING IN THE BAT *GLOSSOPHAGA SORICINA* (PHYLLOSTOMIDAE: GLOSSOPHAGINAE)

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Abstract. The cost of forward flight for a 11.7 g nectar-feeding bat *Glossophaga soricina* (Phyllostomidae: Glossophaginae) was estimated to be 5.88 kJ h^{-1} (1.63 W). To obtain this estimate, we quantified the amount of time allocated to specific activites and the animal's daily energy intake in captivity for 17 separate 24-hour periods. These data were arranged in a set of daily energy-balance equations with the energy coefficients for each activity as unknown parameters. These equations were solved for the unknown coefficients by multiple linear regression analysis. Using our estimate of flight cost and values for daily energy expenditure from the literature, we estimated how a free-ranging nectar-feeding bat allocates time and energy among different activities.

Key words: Flight cost, daily energy expenditure, time budget, Glossophaga soricina, *Phyllostomidae, nectar-feeding.*

INTRODUCTION

Neotropical nectar-feeding bats (Glossophaginae, Phyllostomidae) have received little attention in comparison to other groups of highly specialized flower visitors (cf. Feinsinger 1987). These bats share several adaptations for nectar-feeding which include an elongated rostrum, a protrusible brush-tip tongue and a highly specialized mode of hovering flight used while feeding from flowers (Dobat 1985; von Helversen 1986 & *this volume*). Despite these adaptations, however, the diversity of anatomical specializations within this group appears to be low. An economic analysis of flower exploitation by nectar-feeding bats is one approach to better understand how nectar sources are utilized and the costs associated with this mode of feeding.

In order to quantify foraging effort the energetic costs of different activities must be known. McNab (1969, 1988) determined basal metabolic rates and thermoregulatory requirements for several species of nectar-feeding bats. von Helversen & Reyer (1984) determined both daily energy expenditure (DEE) and daily nectar intake for *Anoura caudifer* by using the doubly-labeled-water method (DLW). What remains to be determined is an estimate of flight cost.

Because direct measurement of flight cost is difficult for methodological reasons we took an alternative approach based on the analysis of an animal's 24-hour time budget and food intake. Time budget analysis is commonly used to estimate DEE (e.g., Weathers *et al.* 1984). Herein, we reverse that approach by using a known DEE and time budget to estimate the costs of various activities.

For captive animals it is relatively easy to quantify the amount of time allocated to specific activities during a 24-hour period. Such data can then be arranged in a daily energy balance equation with food energy intake, durations of different activities and body mass change as known variables, and energy coefficients for each activity as unknowns. If such data are collected for several 24-hour periods the resulting set of energy balance equations can be used to estimate the unknown energy coefficients. Using such a procedure we estimated the cost of flight for a nectar-feeding *Glossophaga soricina* and arrived at predictions about the economy of flower exploitation by this Neotropical bat.

MATERIAL AND METHODS

The following data were collected for three non-pregnant female *Glossophaga soricina antillarum* (Phyllostomidae) (origin Jamaica) maintained in laboratories at the Institute of Zoology, Erlangen University, during seventeen 24-hour experi-

ments: volume of nectar consumed, duration of time spent resting or in flight, duration of hovering at a feeder, body mass, and ambient temperature. Data for individual bats (nos. 1, 2, and 3) were collected for 1, 2, and 14 days respectively. During each experiment the animal was confined to a U-shaped flight tunnel (total length 14 m, height 2 m and width 1 m) to which it had been acclimated prior to the experiments. Due 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 at mid-day and mid-night was derived from the computer stored data. 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.

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 personal computer equipped with a digital I/O-interface (Meilhaus ME 14-B) with quartz clock and counter functions to provide the timed pulses for the analog 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 tube (diameter 15 mm, depth 40 mm) oriented horizontally, into which nectar was 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 (10—20 μl). 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 1 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. Average flight speed for the 14 m between the two feeders

was estimated from the times of arrival of subsequent visits at the feeders minus hovering duration.

Artificial nectar was made from a solution of sucrose, glucose and fructose (26 : 37 : 37 parts) in tap water with a sucrose/hexose ratio of 0.34 as being typical for nectar from bat flowers (Baker & 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) which also is typical for nectar from bat flowers (von Helversen, *this volume*). 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.

Illumination was kept at an artificial LD cycle of 12 : 12. Temperature and relative humidity within the experimental chamber ranged between 22.5—29.0 °C and 55—60 % respectively during the experiments but were stable for each day.

For a parallel determination of energy expenditure using the DLW method, blood samples of 50—100 μl were taken each day two hours before the onset of the dark phase. This required capturing and handling of the bat for 10—30 min. On DLW-injection days the handling procedure began 3 hours before the onset of the dark phase and lasted for about 90 min with the bat resting in a separate cage during equilibration time. The results from these experiments will be reported elsewhere.

RESULTS

Foraging behaviour

Bats commenced feeding activity at the onset of the dark phase followed by a rapid increase in body mass due to rehydration and the nectar load in the digestive tract. Thereafter, feeding continued in small bursts of activity at regular intervals throughout the night. The average body mass of 10.9 g (range 9.5—12.3) at mid-day increased to 11.7 g (range 10.0—13.0) by midnight. Thus, body mass during flight activity was about 0.8 g higher than during the daytime

resting period. Due to variable fat deposits average body mass of bat no. 3 differed by as much as 3 g on different experimental nights. Body masses of the other two bats were within this range. During an average of 886 feeder visits per night a bat consumed 14.0 ml of the 17 % nectar (range 2.5—23.8). This is equivalent to a daily sugar intake of 2.6 g (range 0.5—4.3) with an energy value of 41 kJ (range 7—68). Flight activity was not restricted to feeding but included periods with no or only occasional visits to the feeder. On average a bat spent 4.2 hours (range 1.0—7.7) in flight which corresponds to a distance of approximately 45 km/night (range 10—80). Body mass decreased linearly during the day when no activity was recorded. For details of the 24-hour activity patterns see von Helversen *et al.* (in prep.).

Mode of flight

A bat needed 4.5 s to fly the 14 m from one feeder to the other which is equal to an average flight speed of 3.1 m/s. Midway during this trip the bat had to make a 180° turn with a radius between 0.1 to 0.9 m. Although no information is available on the flight speed used by this species in nature while commuting, it is likely that this was restricted here due to the limited length of the flight tunnel.

The regression model

The energy value of the daily assimilated food (A) equals the daily energy expenditure ($\dot{H}_{TD}$) plus the energy value of excess food stored as body reserves (E) multiplied by the body mass change ($\dot{m}$).

This is expressed by the equation:

$$A = \dot{H}_{TD} + \dot{m}E \qquad \text{(Eq. 1)}$$

where $\dot{H}_{TD}$ is set equal to specific terms for the energy costs of each major activity: forward (FF) and hovering (FH) flight, rest (R) and thermoregulation (mt). Thus

$$\dot{H}_{TD} = t_{FF}\,\dot{H}_{FF} + t_{FH}\,\dot{H}_{FH} + t_R\,\dot{H}_R + t_R\,[T_{lc} - T_a]\dot{H}_{mt} \qquad \text{(Eq. 2)}$$

where the $\dot{H}$'s on the right hand side of the equation are energy equivalents for different activities ($J\ h^{-1}$) and t's are activity durations ($h\ d^{-1}$) (see List of Symbols). Thermoregulatory costs are expressed by $\dot{H}_{mt}$ as the metabolic heat production for thermoregulation ($J\ °C^{-1}\ h^{-1}$), which is multiplied by both tR and the *difference* between the

lower critical temperature (T_{lc}) for this species of 29 °C (McNab 1969) and ambient air temperature (T_a).

Average body mass during flight activity varied between 10.0—13.0 g on different experimental nights. A preliminary analysis of the data showed that the model could be improved by taking into account this variability by using mass specific energy rates for the costs of flight. This was incorporated into our model by multiplying flight terms by midnight body masses, expressed as

$$\dot{H}_{TD} = t_{FF}\,\dot{H}_{FF}{}^*\,M_{MN} + t_{FH}\,\dot{H}_{FH}{}^*\,M_{MN} + t_R\,\dot{H}_R + t_R\,[T_{lc} - T_a]\dot{H}_{mt} \qquad \text{(Eq. 3)}$$

where the $\dot{H}^*$s are mass specific energy equivalents and M_{MN} is midnight body mass. Resting metabolic rate and metabolic heat production for thermoregulation were not treated as mass specific rates, as it is unknown how differences in body fat content might change these parameters. Substituting $\dot{H}_{TD}$ in Eq. 1 by Eq. 3 yields

$$A = t_{FF}\,\dot{H}_{FF}{}^*\,M_{MN} + t_{FH}\,\dot{H}_{FH}{}^*\,M_{MN} + t_R\,\dot{H}_R + t_R[T_{lc} - T_a]\dot{H}_{mt} + \dot{m}E \qquad \text{(Eq. 4)}$$

LIST OF SYMBOLS	
A	caloric equivalent of assimilated food ($J\ d^{-1}$)
E	caloric equivalent of body reserves ($J\ g^{-1}$)
$\dot{H}_{FF}$	cost of forward flight ($J\ h^{-1}$)
$\dot{H}_{FF}{}^*$	mass specific cost of forward flight ($J\ g^{-1}\ h^{-1}$)
$\dot{H}_{FH}$	cost of hovering flight ($J\ h^{-1}$)
$\dot{H}_{FH}{}^*$	mass specific cost of hovering flight ($J\ g^{-1}\ h^{-1}$)
$\dot{H}_R$	cost of resting ($J\ h^{-1}$)
$\dot{H}_{mt}$	metabolic heat production for thermoregulation ($J\ °C^{-1}\ h^{-1}$)
$\dot{H}_{TD}$	total daily energy expenditure ($J\ d^{-1}$)
$\dot{m}$	body mass change ($g\ d^{-1}$)
M_{MN}	mean midnight body mass (g)
t_{FF}	time spent for forward flight ($h\ d^{-1}$)
t_{FH}	time spent for hovering flight ($h\ d^{-1}$)
t_R	time spent resting ($h\ d^{-1}$)
T_{lc}	lower critical temperature ($°C$)
T_a	ambient air temperature ($°C$)

TABLE 1. Estimated energy exenditure for forward and hovering flight, rest, thermoregulatory requirements and the energetic equivalent of body mass change in Glossophaga soricina. Coefficients (= energy expenditure) were derived by multiple regression through the origin based on 17 data sets of Eq. 4. For definitions of variables see List of Symbols.

Variable		Energy Expenditure	S.E. of Coefficient	Energy Units	t-Value	p
$\dot{H}_{FF}$[1]	forward flight	5.88	0.44	kJ h^{-1}	13.3	<0.001
$\dot{H}_{FH}$[1]	hovering flight	10.5	11.5	kJ h^{-1}	1.0	<0.36
$\dot{H}_R$	resting	0.477	0.09	kJ h^{-1}	5.2	<0.001
$\dot{H}_{mt}$	thermoregulation	0.108	0.040	kJ °C^{-1} h^{-1}	2.7	<0.015
E	body reserves	38.4	5.4	kJ g^{-1}	7.2	<0.001

$r^2 = 0.968$.

[1] For ease of comparison, the coefficients of the mass specific rates of flight cost used for calculating the regression were converted to 'whole animal' units for this table by multiplying with the mean midnight body mass of 11.7 g.

The last term in the equation is the only one that can be negative. If $\dot{H}_{TD}$ exceeds food intake the excess energy is covered by the consumption of body reserves with a resultant loss in body mass, i.e. a negative $\dot{m}$. An extra term for energy lost via urine and feces was omitted. However, we have assumed that nectar-feeding bats are equal to hummingbirds in their ability to assimilate sugar solution with approximately 98 % efficiency (Hainsworth 1974). To account for this we substracted 2 % from the daily sugar uptake prior to performing the regression analysis. If assimilation is different from 98 % then the energy equivalents reported below will change linearly by the same percentage, i.e. at 97—95 % assimilation efficiency our estimates will decrease by 1—3 %.

The 17 days of observations yielded 17 separate equations (of Eq. 4) with the five energy equivalents on the right hand side as unknowns. Owing to the linearity of the model it was possible to solve this set of equations and derive estimates for the unknowns using multiple linear regression analysis. The results of this analysis are presented in Table 1 and Fig. 1. The regression model explains 97 % of the variation in measured daily energy intake.

Energy expenditure of the 11.7 g bat during forward flight was estimated as 5.88 kJ h^{-1} (1.63 W) and accounted for on average 52 % of $\dot{H}_{TD}$. Although hovering flight appears to be more costly than forward flight we could not determine the cost of the former with any accuracy. The present range of standard errors of our estimate of hovering flight is equal to 1—4 times the cost of forward flight.

Resting metabolic rate was estimated as 477 J h^{-1} (0.132 W) or 43.7 J g^{-1} h^{-1}, when divided by the average mid-day body mass of 10.9 g. The combined cost of resting metabolism and thermoregulation accounted for an average 42 % of $\dot{H}_{TD}$. The estimated energy equivalent of body reserves of 38.4 kJ g^{-1} was 2.4 times the 15.9 kJ g^{-1} of the dietary sugar.

Further results

In addition to the parameters contained in the model (Eq. 4) we also tested for the influence of number of feeder visits per night. In Eq. 4 the cost of a feeder visit is determined solely by the cost of hovering in front of the feeder. However, it might be possible that an additional cost occurs when a bat brakes and positions itself in front of the feeder before inserting its rostrum. This would not have been accounted for in Eq. 4. However, incorporation of 'number of feeder visits' into this model did not reveal any such effect.

DISCUSSION

The approach of using multiple regression analysis to solve a set of time budget/food intake equations for the unknown cost coefficients allowed us to estimate the cost of forward flight in Glossophaga soricina antillarum. The high degree of correspondence between the predictions of the regression model and the measured energy intake rate (Fig. 2, $r^2 = 97$ %) were made possible by using a fully automated timing, weighing, and food dispensing system which minimized disturbance and handling of the
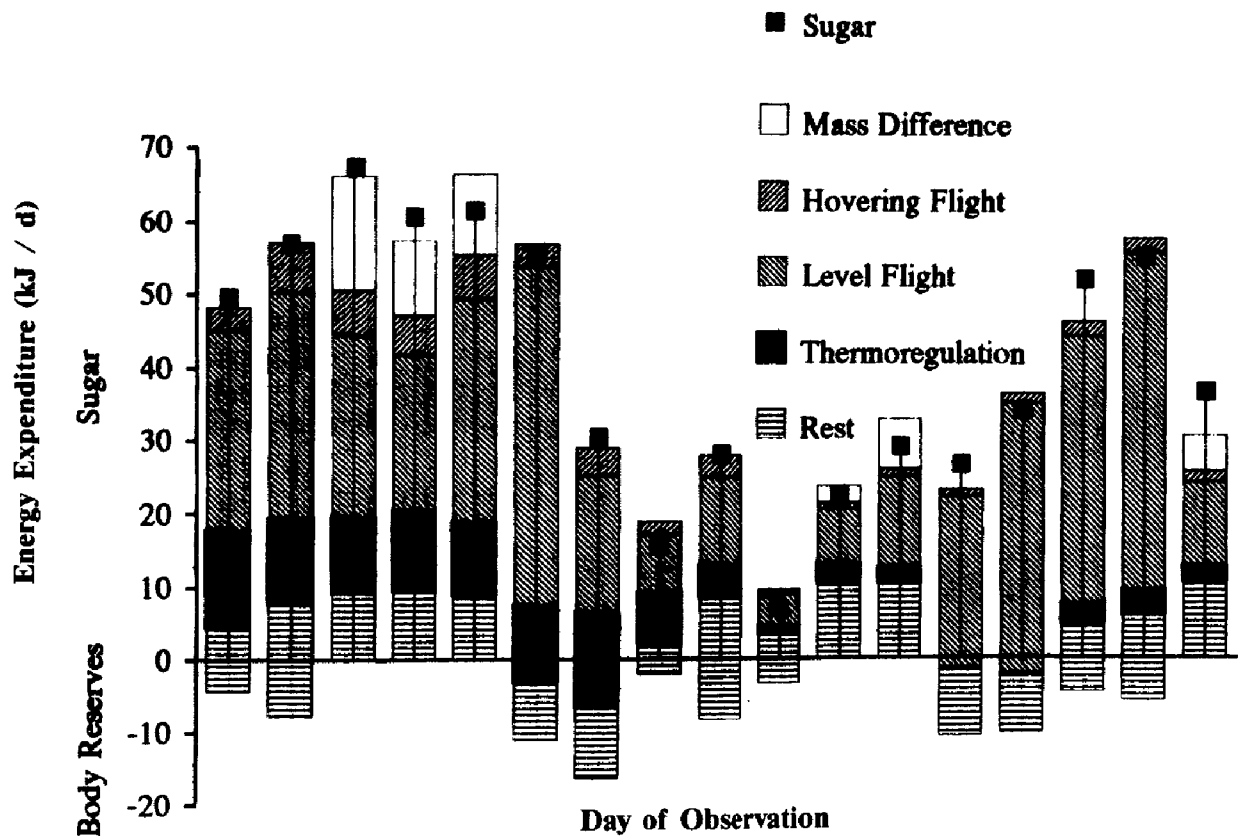
FIG. 1. Comparison between *measured* energy intake (solid squares) and *predicted* energy intake (composite columns) for each 24-hour observation period in *Glossophaga soricina*. Predicted values were calculated using Eq. 4 and Table 1. Data are arranged in chronological order. The shaded segments within each composite column represent daily energy expenditure. The white (open) segment represents the energy value of ingested food converted to body reserves. Columns shown below zero are shown for days when energy expenditure was partially covered by the consumption of body reserves.

animals. Only the energy expenditure of hovering flight, which contributed less than 10 % to the daily energy expenditure, could not be estimated with accuracy.

Resting energy expenditure

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 metabolic rate (RMR) is higher than basal metabolic rate (BMR). All the same the RMR of 44 J g^{-1} h^{-1} estimated here nearly equals the measured BMR of 46 J g^{-1} h^{-1} for the smaller, nominal subspecies of *G. soricina* weighing only 9.6 g (McNab 1988). This may indicate, as has been suggested before (v. Helversen & Reyer 1984), that McNab measured RMR at thermoneutrality rather than BMR.

The daily handling of the animals during DLW-injection and blood sampling most likely had an additional influence on resting metabolic

rate during our study. Although this treatment was given in each of the 17 experiments, it was not uniform as the duration of the procedure varied from between 10 minutes to 90 minutes on DLW-injection and bleeding days. This introduced a source of variability into the data that, unfortunately, cannot be accounted for separately.

During our experiments bats were exposed to ambient temperatures between 22.5 and 29 °C. Thus the difference between ambient temperature and 29 °C (the lower critical temperature for this species, McNab 1969) was between 0 and 6.5 °C. Our estimate of the metabolic cost of thermoregulation for a 10.9 g bat is 108 J °C^{-1} h^{-1}, which is 1.23 times the value of 88 J °C^{-1} h^{-1} reported by McNab (1969) for 9.6 g individuals of this species.

Conversion of assimilated sugar to body fat

One gram of body fat has an energy value of 39.2 kJ (Wieser 1986). During our experiments a bat consumed 38.4 kJ above its daily metabolic re-
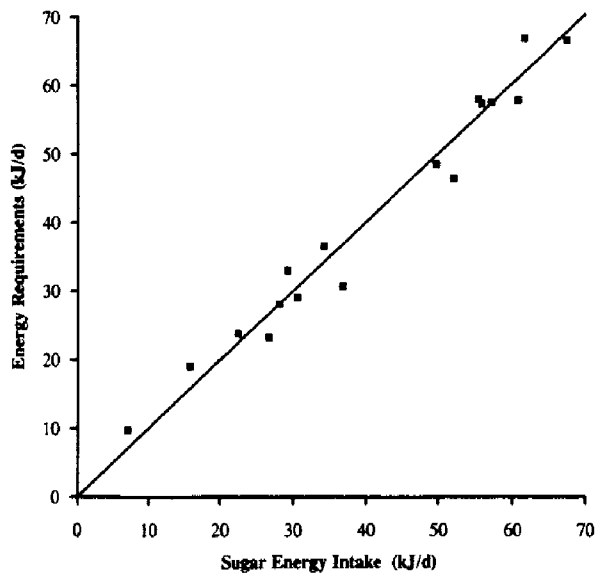
FIG. 2. Relationship between measured sugar intake and energy requirements expected from time budget and body mass changes for each of the 17 days of observation. Expected energy requirements were calculated based on Eq. 4 and the results from regression analysis (Table 1).

quirements to gain 1 g in body mass. This is a clear indication that these bats convert sugar into fat as their major energy reserve. The remaining difference here between 38.4 and 39.2 kJ may be accounted for by water of which body fat contains up to 10 % (Schmidt-Nielsen 1983 p. 341). 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 p. 181). Such a mechanism of fat storage is also known for nectar-feeding hummingbirds (Suarez *et al.* 1990).

The cost of flight

The energy cost of forward flight as determined in the present study is based on a combination of linear and manoeuvering flight. This mode of flight is more costly than 'minimum power' flight (i.e. the minimum power required to stay aloft) which is a standard physiological measure used to compare the energy requirements of flight between different species. In nature we would expect *Glossophaga soricina* to fly at least at 'maximum range' speed (minimum cost per unit distance) during commuting trips which is faster and more costly (per time) than minimum power speed. Thus the estimate of flight cost derived in the present study and the expected cost of flight in the natural environment should exceed the cost of 'minimum power' flight.

A comparison with previously published results of flight costs can provide a rough estimate of the difference between the cost of flight determined here and that at minimum power speed. The model by Norberg & Rayner (1987), based on aerodynamic theory, predicts 3.77 m/s as the minimum power speed for a bat with a mass of 11.7 g, a wing span of 0.258 m, and a wing area of 0.0107 m². The average flight speed of 3.1 m/s used during our experiments is 18 % below Norberg and Rayner's estimate. In previous measurements in four medium to large bat species (Thomas 1975; Carpenter 1985, 1986; summarized in Norberg 1990) flight power increased by 6—16 % following a decrease in flight speed to 18 % below minimum power speed. Thus, at the flight speed observed during our experiments, flight power may have been approximately 10 % higher than at minimum power speed. This comparison, however, remains speculative for two reasons. First, the predictive value of aerodynamic theory as it is currently applied to bird and bat flight (and which was used here to estimate minimum power flight speed) remains to be verified for animals of small size. Secondly, flight cost at different flight speeds as summarized by Norberg (1990) has until now only been measured for medium and larger sized bats and birds.

A mass specific flight cost of 502 J g^{-1} h^{-1} is about eleven times the BMR of 46 J g^{-1} h^{-1} (McNab 1988). As discussed above, both the BMR for *G. s. antillarum* should be lower than McNab's estimate, and the cost of flight at minimum power speed should be below the cost of flight determined here. At present it remains unknown whether these effects will compensate for each other.

Based on a recently derived allometric equation for the cost of flight in bats (Speakman & Racey 1991), the cost of flight should be 1.69 W for an 11.7 g bat. This is 4 % above the 1.63 W estimated in the present study and possibly 15 % above the flight cost at minimum power speed. This deviation from the allometric curve may be due to the fact that Speakman & Racey used a mix of results at various speeds for its calculation. It is rather likely that the small insectivorous bats that were included in their calculation, and flying 'in a large room' during the measurements (Speakman & Racey 1991), spent a significant portion of their flight in a more costly manoeuvering activity. As a consequence, their equation may be biased at lower body

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masses towards bats that did not use minimum power speed during the measurement period but instead an energetically more expensive mode of flight.

As should be expected, and contrary to the findings of Speakman & Racey (1991), we found a dependency of flight cost on body mass even within the same individual. Our regression model (Eq. 4), which uses mass-specific energy rates for the costs of flight, provided a better fit than a preliminary regression model at an early stage of our analysis which did not consider variability in body mass.

The power requirement for hovering flight appears to be higher than for forward flight but could not be determined with any accuracy from our data. With a contribution of about 7 % to the daily energy expenditure, this parameter was significantly affected by the remaining 3 % of unexplained variance in the data. All the same, the value estimated here is within the range of our parallel estimate of the cost of hovering based on aerodynamic theory (Norberg et al. submitted).

The economy of flower-visiting

Based on our estimate of flight cost it is now possible to predict how free-ranging nectar-feeding bats allocate time and energy among different activities. In von Helversen & Reyer's (1984) study of the 11.5 g nectar-feeding bat *Anoura caudifer* they used the DLW-method to estimate both DEE (51.9 kJ) and daily nectar intake (15.5 ml of 20 % nectar). They also determined nectar intake per flower visit in the similar sized *Glossophaga longirostris* to be about 18 μl per visit. To ingest 15.5 ml under these conditions, a similar-sized bat would therefore need to visit 860 flowers each night.

The cost of a flower visit consists of the cost of commuting to the flower and the hovering cost during feeding. Assuming an allocation of 60 % of DEE to foraging activity, as found in our study at an average temperature of 26 °C, the combined cost of commuting and hovering would be 31.3 kJ. Hovering duration of a feeder visit during our experiments was on average 0.75 s. At 2.9 J/s such a visit would cost 2.2 J and 860 visits 1.9 kJ. This leaves 29.4 kJ for commuting flight which is equal to a flight time of 5 hours at 5.9 kJ/h. On average one flower would therefore be visited every 21 seconds. At 4 m/s as a conservative estimate of flight speed an *A. caudifer* bat would cover 72 km per night.

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